

ECOLOGY AND MANAGEMENT OF WETLAND FORESTS DOMINATED BY  
*Prioria copaifera* IN DARIEN, PANAMA

By

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by

William Thomas Grauel

Dedicated to the memory of Jack Westoby, who knew that forestry is more about people  
than about trees.

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Abstract of Dissertation Presented to the Graduate School  
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ECOLOGY AND MANAGEMENT OF WETLAND FORESTS DOMINATED BY  
*Prioria copaifera* IN DARIEN, PANAMA

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Chair: Francis E. Putz

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The state of knowledge of Neotropical swamp forests dominated by *Prioria copaifera* (cativo) is reviewed based on the available literature. Results of two silvicultural experiments (liana-cutting and reforestation) are reported, forest-stand dynamics are described, and growth and yield projections are presented.

Permanent sample plots at four sites in three watersheds in Darien, Panama were installed in 1997 and 1998. Woody plants  $\geq 1$  cm diameter at breast height (dbh, 1.3 m above the ground) were tagged, mapped and measured, and censused annually to gather demographic information on growth, recruitment, and mortality. Cativo regeneration (trees  $< 1$  cm dbh) was also censused at short intervals to monitor seedling dynamics. Cativo growth was studied at an additional six sites along an inundation gradient that varied in water salinity and hydroperiod.

Cativo growth was slow to moderate at sites flooded by tidal waters, moderate at inland swamps flooded for long periods, and moderate to fast at riverine sites flooded by

fresh water; mean annual diameter growth ranged from 0.05 – > 0.8 cm/year. Mortality and recruitment rates of cativo varied widely among sites and years as well, with mortality exceeding recruitment at two sites for two of the five years of monitoring. At one slow growing site, trees that died during the study grew significantly slower prior to death than trees that lived, demonstrating the occurrence of species-level growth-dependent mortality for the first time in tropical forest.

Unlogged inland swamps contained very large standing volumes in trees  $\geq 60$  cm dbh (up to 180 m<sup>3</sup>/hectare). Riverine forests that were repeatedly logged during 1950–2000 contained few large trees, but showed potential for future timber harvests in the form of abundant regeneration and large standing volumes in trees 40–60 cm dbh. Sixty year volume projections suggest that higher dbh cutting limits and longer cutting cycles reduce residual damage, and can produce high timber yields for inland swamps and riverine forests, respectively.

Volatile world timber markets and log shortages may be reducing incentives for cativo logging (and thus swamp forest conservation) in the face of large development projects and increased colonization in Darien, Panama. Cativo swamp forests have important hydrological and carbon-sequestering values that should be incorporated in land-use decisions.

CHAPTER 1  
LITERATURE REVIEW OF *Prioria copaifera*

**Introduction**

Unlike the vast majority of tropical tree species, much is known about the ecology of the swamp species *Prioria copaifera* Griseb. (hereafter cativo). Its potential commercial value was recognized in the 1920s, but thousands of hectares of cativo-dominated forests had already been cleared to make way for the banana boom of the early twentieth century. By the end of the century much had been converted to agriculture and of the remainder, most had been cutover and degraded.

**Distribution**

Cativo is found from Nicaragua to Colombia, and is also present in Jamaica (Figure 1–1, Holdridge 1970). Although cativo was included in lists of the tree species of the coastal region of Ecuador by Rimbach (1932) and Acosta Solís (1947) its presence in that country is not confirmed. Barbour (1952) reported that the commercial range includes the Atlantic coast of Central America from Nicaragua to Panama, the watershed of the Bayano River, the rivers flowing into the Gulf of Darien (Golfo de San Miguel), and the area around the mouth of the Atrato River in northwest Colombia. Cooper (1928) referred to enormous stands of cativo in the Valle Estrella of Costa Rica and the Laguna de Chiriqui in Panama. In 1987, it was estimated that cativo forests covered 49,000 ha in Panama, with the major concentration in the easternmost Province of Darien but including eastern Panama Province ( INRENARE, Instituto Nacional de Recursos Naturales Renovables 1987). The same report noted 4000 ha of cativo on Coiba Island

and 17,000 ha in the Chucunaque River watershed; 9000 ha in the combined watersheds of the Tuira, Balsas, and Marea Rivers; and an additional 4000 ha in adjacent swampy areas. By 1999, the National Ministry of the Environment in Panama estimated an area of only 15,000 ha of cativo in the country (ANAM 1999a).

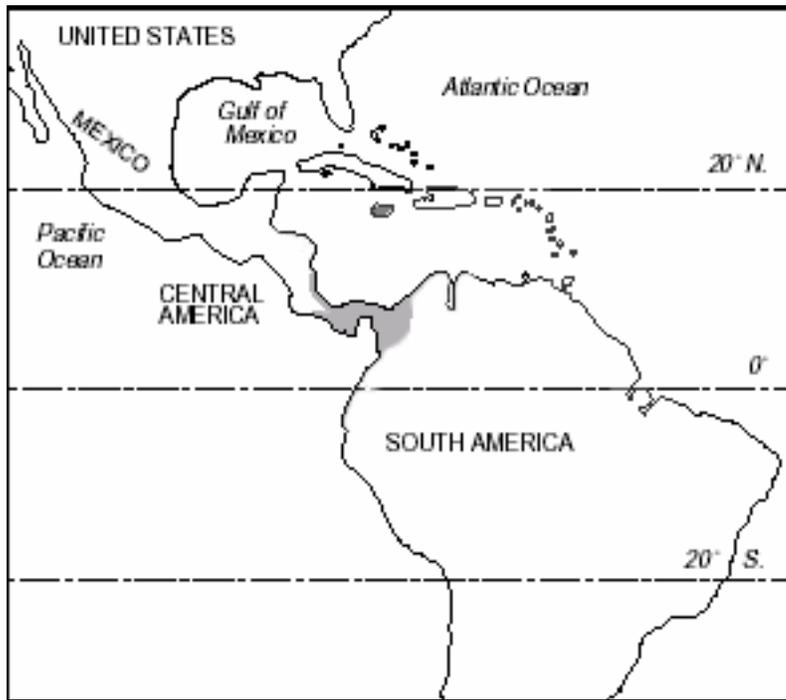


Figure 1–1. Distribution of *Prioria copaifera*.

In Colombia, Linares Prieto (1988) described cativo's range as including the watersheds of the Atrato and Leon Rivers in the Uruba region in the northwest of the country. According to Escobar and Vasquez (1987), cativo is also found in the Departments of Antioquia and Choco. Tosi (1976) stated that cativo was not found on the Pacific side of Colombia or south of Buchado in the Department of Choco, but Escobar and Vasquez (1987) reported cativo in the low-lying areas around the village of Santa Marta along the Nechi River and referred to a sample of cativo in the Gabriel Gutierrez "Medel" Herbarium of the Agronomy Department at the National University in Medellin collected in the Department of Magdalena in 1949, all of which are on the

Pacific. Colombia contained 363,000 ha of cativo forest (Linares Prieto 1987b, c, González Pérez. et al. 1991). Subsequently, the area was estimated at 173,000 ha in 1978 (Linares Prieto 1987b); and in the late 1980s estimates ranged from 60,000 ha (Linares Prieto 1987c), to 90,000 ha (Linares Prieto 1987b), to 163,000 ha (Linares Prieto 1988). In Costa Rica, the areas of cativo-dominated forests on the Pacific (Allen 1956) as well as on the Atlantic side of the country (Bethel 1976) have been severely reduced (Veiman 1982) and today the species is listed as threatened in the country (Jiménez Madrigal 1995).

### **Species Description**

*Prioria copaiifera* is the only species in the genus, and is in the subfamily Caesalpinioideae of the Fabaceae. Average adult height is 25–30 m, with a dbh (diameter at breast height, 1.3 m) from 45 to 100 cm (INRENARE 1987a), although the trees reach 180 dbh (Grauel, unpublished data) and 40 m in height (Del Valle 1972). The branches of mature trees are somewhat arched and the foliage is distributed uniformly in a round, thick crown (Escobar and Vasquez 1987). The bark is smooth, brownish-gray to gray in color, and with abundant lenticels found in continuous horizontal bands (Echavarría A. and Varón P. 1988). Cativo has no buttresses, and its compound leaves generally have four opposite leaflets, elliptic-lanceolate in shape, with a swollen petiole. The leaflets are 16 cm long and 8 cm wide, asymmetric, rounded at the base and with an acuminate apex. The tiny, white flowers develop in panicles (Muñoz Valencia 1966). The flowers have 10 stamens and no petals, but the sepals resemble petals (Gentry 1996). The fruit is a flat indehiscent pod, with one side slightly convex and the opposite side concave, 10 cm long, 7 cm wide, 3 cm thick, woody, with a single seed (Mahecha Vega et al. 1984). Seeds are large (mean fresh weight = 48 g, Lopez 2001, to 96 g, Dalling et

al. 1997) and dispersed by water. In addition to the common name “cativo”, *P. copaiifera* has been known as cautivo, kartiva, trementino, floresa, tabasara, amanza mujer, camibar, murano, and Spanish walnut (Schmieg 1927, Anonymous 1933, Harrar 1941, Hess et al. 1950, Escobar and Vasquez 1987).

### **Phenology**

Del Valle [cited in Escobar and Vasquez (1987)] noted that cativo leaf-drop is uniform throughout the year and the species is evergreen. Cooper (1928) found that the species flowers generally in March and April and fruits in October and November, but also found a tree with flowers and immature fruits in February. Linares Prieto (1988) reported that flowering typically begins in June and peaks in August and September. Fruiting then begins in September and October and peaks in April and May. In Colombia, seedling recruitment peaks at the beginning of the rainy season from April to June (Linares and Martinez Higuera 1991). Although cativo produces seeds twice a year, large seed crops seem to be produced once every 2 years (Pizano SA 1995, Grauel in review 2004a).

### **Ecology**

Holdridge (1964) reported that throughout its range from eastern Nicaragua into northwestern South America, cativo is found in the Tropical Moist, Wet, and Rain Forest lifezones. According to Tosi (1976), the cativo forests of Colombia are found in the Tropical Moist Forest and Tropical Wet Forest lifezones of the Holdridge classification system; annual precipitation ranges from 2000 to 8000 mm with average annual temperature of 24° to 28° C (González Pérez et al. 1991), while in Darien, Panama, cativo is found in the Tropical Moist Forest lifezone (Holdridge and Budowski 1956).

Cativo is found in four distinct habitats:

- On the Atlantic coast of Costa Rica, Panama, and Colombia, it is found just inland from mangrove forests where salt water does not intrude.
- Along the many rivers of southern Central America and northwest Colombia, *cativo* is found in alluvial valleys that are flooded periodically, generally in the rainy season.
- Away from major rivers *cativo* is found in low-lying areas that are inundated for extended periods, up to the entire 9-month rainy season in Darien, Panama.
- *Cativo* is also found in upland forests, but never as abundant and dominant as in flooded habitats. Although Consultores Ambientales LTDA (1995) declared that *cativo* cannot germinate or develop in well-drained soil, it is a common component of the upland, mixed-species forest on Barro Colorado Island in Panama (Condit et al. 1993b, 1995a, Sheil and Burslem 2003).

Colombian researchers have classified several types of “*cativales*” based on landscape position and duration of inundation. Linares Prieto (1988) used landscape position to classify *cativo* forests as low, medium, and high alluvial plains. The National Corporation for Forest Research and Promotion (CONIF, Corporación Nacional de Investigación y Fomento Forestal, cited in Echavarría A. and Varón P. 1988) classified different types of *cativo* forest according to length of inundation as greater than 6 months, 3 to 6 months, and less than 3 months. González Pérez et al. (1991), referring to the Instituto Geográfico Agustín Codazzi cited in Gómez (1990), defined the inundation periods as permanent, 6 to 8 months, 3 to 6 months, and less than three months. In a study of early natural *cativo* regeneration, Martínez Higuera (1989) defined their two study sites as low alluvial plain frequently flooded and low alluvial plain infrequently flooded.

Linares Prieto (1987b) offered various criteria for the classification of *cativo*-dominated forests:

- three types of forest distinguished by landscape position (plain, terrace, and alluvial fans).

- six types of cativales defined by the combination of life zone and landscape position.
- number of cativo stems per hectare; median cativo basal area, average distance between trees, number of trees of other species, the number of other species apart from cativo, median basal area of other species than cativo, and median total basal area per hectare.
- phytosociology of *Prioria* in terms of abundance, frequency, dominance, importance, and productivity.
- common associates being *Cynometra* spp, *Pterocarpus officinalis*, *Gustavia* spp, *Carapa guianensis*, *Anacardium excelsum*, *Eschweilera* spp, nuánamo (Myristicaceae), *Castilla elastica*, and *Lecythis* spp., the number of species increasing with elevation and with better drained soils.

In a study that used life zone and landscape position as classification criteria, Escobar and Vasquez (1987) proposed nine types of cativo forest but concluded that their mathematical analysis failed to support the categories.

A defining ecological characteristic of cativo-dominated forests is their monodominance or low species diversity within stands. Maximum homogeneity is found in the riverine forests inundated by high Pacific Ocean tides in Darien, Panama. In these sites, cativo can comprise more than 95% of the stems  $\geq 1$  cm dbh and the forest contains less than ten woody species per hectare (Grauel and Kursar 1999, Grauel and Putz 2004). Along the Marea River in Darien, cativo had a relative abundance of 91% in a 10 x 1000 m transect that included five other tree species and one palm ( $\geq 10$  cm dbh, Mayo Melendez 1965). Away from the influence of tides, floristic diversity increases. Linares Prieto (1988), citing the thesis of Escobar and Vasquez (1987), reported the relative basal area dominance of cativo as 50 to 92%. In Colombia, González Pérez et al. (1991) found that cativo-dominated forests contain approximately 60 tree species, 15 of which comprise 95% of the individuals and are in the families *Fabaceae*, *Bombacaceae*, and

*Sterculiaceae*, although the minimum diameter of the study was not stated. In cativo-dominated forests in the area of Domingodo-Truando in the Colombian Department of Choco, Consultores Ambientales LTDA (1995) found 86 tree species per hectare ( $\geq 10$  cm dbh). In Darien, Panama, Golley et al. (1975) found 44 species of trees per hectare in a cativo-dominated forest along the Chucunaque River. Elsewhere in Darien, Holdridge (1964) found *Carapa guianensis* to be the only other large tree associated with cativo, although he noted that *Pterocarpus officinalis* was restricted to the edges of small streams in the same forest.

The dominance of cativo in seasonally flooded habitats was suggested as being attributed to the better competitive ability conferred by ectomycorrhizae (EM) compared to vesicular-arbuscular mycorrhizae (VAM, Connell and Lowman 1989); but Torti et al. (1997) showed the existence of VAM in cativo. Lopez and Kursar (1999) demonstrated that 3 tierra firme species survived inundation as well as “flood-tolerant” cativo, and suggested that a cycle of inundation and drought-induced water stress may better explain patterns of tree diversity than inundation alone.

An inventory of animal diversity in a cativo forest in Colombia reported 24 species of mammals, 16 species of birds (principally in the families Sittacidae, Cracidae, and Ramphastidae), 6 species of fish, and 7 species of reptiles (Martínez Higuera 1989). Several of these mammal, bird, and reptile species are becoming increasingly rare due to hunting pressure, including *Tapirus bairdii*, *Mazama americana reperticia*, *Penelope purpurascens wagler*, *Crax rubra*, *Lutra longicandis*, and *Caiman sclerops* (Linares Prieto 1988). Some other studies on wildlife in cativo forests include those of

Mondragón et al. (1994), Ospina Torres (1994, 1995a, 1995b, 1996, 1997), and Orozco Rey (1995).

Holdridge (1964) described how cativo forests alternate with monospecific forests dominated by *Mora oleifera* along the Tuirá and Tucuti (Balsas) Rivers. *Mora*-dominated forests are typically found at slightly lower elevations where the effects of brackish water from high tides are greater, but cativo trees can be found in *Mora*-dominated forests (Porter 1973). Cativo forests are characterized by a distinct microtopography where adult trees are surrounded by mounds 20 to 30 cm in height and 5 m in diameter (Duke 1964). Duke (1964) also mentioned that fallen cativo trees were very common. Although adult cativo trees are shallow-rooted, in a comparison of cativo-dominated “gallery” forests with tropical moist, premontane, and mangrove forests. Golley et al. (1969) found belowground biomass to be greatest in mangrove forests, and similar among the other forest types. Overstory biomass, however, was notably higher in gallery (cativo) forests, with over 100 Mg/ha dry weight in stems alone. Holdridge (1964) estimated a leaf area index of 6.1 in a cativo forest along the Tuirá River in Darien, Panama.

In Colombia, soil fertility of cativo forests varies from very low to moderate (Martínez Higuera 1989) with fine to medium texture, pH from 5.1 to 6.0, and poor drainage in general (Linares Prieto 1987c). Soils of riverine cativo forests in Panama are composed of clay to loamy clay with pH 5.2 to 6.8 (Mariscal et al. 1999, Tapia 1999) while soils of inland swamps are more clayey and acidic (pH 4.4–6.0, Tapia 1999). The Colombian Institute of Hydrology and Soil Use, cited in Linares Prieto (1988) and

Martínez Higuera (1989), classified soils of cativo forests as Inceptisols (63%) and Entisols (37%).

### **Wood Uses and Properties**

The value of cativo wood lies in its historic abundance and accessibility, not necessarily in its inherent properties. Early descriptions noted cativo for its cylindrical form and general abundance (Kluge 1926, Cooper 1928) as well as its potential for supplying raw material for architects and interior decorators (Schmiege 1927), although Pittier and Mell (1931) considered the wood to be of little or no use.

Later, cativo was included in a series of studies before (Kynoch and Norton 1938) and during WWII (Harrar 1941, 1942a, b) that sought to provide technical information on the physical and mechanical properties of foreign and domestic woods. Further research beginning in 1947, funded by the U.S. Office of Naval Research, resulted in recommendations of cativo for plywood, cabinetry, and furniture (Hess et al. 1950). Similar studies of potential applications of cativo occurred later in Colombia (Hoheisel and López G. 1972, Universidad Nacional de Colombia 1984).

Several authors have mentioned the abundant resin that bleeds from freshly cut logs and can make sawing difficult (Cooper 1928, Hess et al. 1950, Barbour 1952, Del Valle 1972). The copious resin of cativo was used by indigenous groups for such diverse uses as repairing boats and for medicine (Cooper 1928, Duke 1986). By using high temperatures during kiln-drying, appreciable amounts of resin can be removed from the lumber with the additional benefit of relieving some of the internal stresses that are caused by the presence of tension wood (Kukachka 1965).

Table 1–1. Cativo wood properties

| Author             | Specific gravity<br>(g cm <sup>-1</sup> ) | Shrinkage %    |
|--------------------|-------------------------------------------|----------------|
| Harrar (1941)      | 0.48                                      | 9.87           |
| Hess et al. (1950) | 0.40                                      | 8.9            |
| Barbour (1952)     | 0.41 sapwood                              | 9.2 sapwood    |
|                    | 0.50 heartwood                            | 22.9 heartwood |
| Kukachka (1965)    | 0.40                                      | 8.8            |

Cativo wood properties have been investigated extensively (Kynoch and Norton 1938, Hernandez Hurtado 1984, Jaramillo Gallego and Velasquez Salazar 1992, Escobar C. and Rodriguez 1993). It is moderately light in weight (Table 1–1) and although it is relatively nondurable with respect to both fungal decay and insect attack, cativo has good dimensional stability and was used as a base for piano keyboards for that reason (Kukachka 1965).

Cativo veneer from Panama was marketed in Canada and the United States in 1933 (Anonymous 1933). Large-scale imports of cativo to the United States occurred in the mid to late 1940s from Costa Rica (Hess and Record 1950). By 1952, almost 9500 m<sup>3</sup>/yr were exported from Colombia and Costa Rica to the US, the figure increasing to over 47,000 m<sup>3</sup>/yr by 1958 (Kukachka 1965).

While some cativo from the Caribbean side of western Panama was exported, it eventually supplied 90% of the raw material for the domestic plywood industry and 50% of sawn-wood production in the country (FAO, Food and Agriculture Organization 1982). The Panamanian Institute of Renewable Natural Resources recommended using cativo for furniture, packing crates, and cabinetry (INRENARE 1987a).

### Diseases and Insects

Cativo was classified as moderately to non-durable in its resistance to the white-rot fungus *Polyporus versicolor* (*Trametes versicolor*) and durable to non-durable for the

brown rot fungus *Poria monticola* (Hess et al. 1950). Ferrer (1999 ) collected 615 fungi associated with living and dead cativo trees in five different forests, and found 58% Ascomycetes and 42% Basidiomycetes. Apparently, it is not known how many of these are pathogens, saprophytes, or mutualists. In a cativo forest along the Sambu River in Darien, Panama, Ferrer (1999) found that 27% of the Basidiomycetes belong to the genus *Phellinus*, one of which is among the most important tree pathogens of temperate forests (*Phellinus weirri*).

Hess et al. (1950), Barbour (1952), and Kukachka (1965) mention the susceptibility of the boles of recently felled trees to attack by ambrosia beetles. Insects that perforate recently cut logs belong principally to the families Scolytidae and Platypodidae, and occasionally Brentidae and Tenebrionidae (Romero 1982). The species most commonly found on recently cut logs, but not specific to *Prioria*, are *Platypus parallelus* Fabricius and *Xyleborus affinis* Eichhoff (Estrada López and Gómez Quiceno 1988). Some protection from attack is rendered by direct sunlight, immersion of the logs in water, and the presence of bark; one application of insecticides may prevent attack for 6 to 15 days (Romero 1982, Estrada López and Gómez Quiceno 1988).

### **Yield**

Early research on cativo as a timber source stressed the large sizes and clear boles of the trees. Cooper (1928) noted an average size of 60 to 90 cm dbh. Barbour (1952) found the commercial size range of the species to be 60 to 120 cm dbh, with maximum sizes of 150 to 180 cm. Barbour (1952) emphasized the straight form of the trunks, without branches for 12 m (and many times branchless up to 30 m in height).

From 1951 to 1953 Bruce Lamb studied the forests of Darien for the Panama Forest Products Company to develop log-supply sources and determine available timber

volumes for both upland and lowland forests. Lamb estimated cativo wood volume along the Chucunaque, Tuira, Balsas, Sambu, Congo, and Cucunatí Rivers and around the Laguna de la Pita (today called Matusagaratí). Along the Balsas River, Lamb found pure stands of cativo for a distance of 20 km and up to a km in width on each side of the river. He estimated an average volume of  $71 \text{ m}^3/\text{ha}$  and a total of  $141,600 \text{ m}^3$  for the watershed (Lamb 1953). On the Tuira River, Lamb encountered cativo forests 25 km upriver from the Tuira's confluence with the Balsas River up to the mouth of the Chucunaque River. In this area of approximately 4000 ha, volumes averaged  $24 \text{ m}^3/\text{ha}$ . Although Lamb did not examine the forests upriver from the mouth of the Chucunaque, there were reports of cativo forests up to Boca Cupe, and he estimated a total of  $23,600 \text{ m}^3$  for the Tuira watershed. According to Lamb, the highest-quality cativo wood came from the Chucunaque River watershed, and he estimated a total volume of  $47,200 \text{ m}^3$  along the 80-km course of the river. Along the Sambu River, Lamb found cativo 10 km from the river's mouth at the confluence of the Jesús River up to the Sambu's confluence with a small stream called Morobichi (8 km further upriver). This cativo forest extended up to 1500 m inland from the river, and Lamb estimated an average volume of  $35 \text{ m}^3/\text{ha}$  and a total of  $23,600 \text{ m}^3$  for the Sambu watershed. Lamb estimated a total of  $1,180,000 \text{ m}^3$  for the entire province (Lamb 1953).

Cativo forests are known to contain large wood volumes per hectare, but comparison of different estimates is difficult where the minimum diameter is not specified; in addition, some estimates are for commercial volume and others for total volume. In a previously unlogged inland swamp in the Balsas River watershed (near a small stream called Naranzati),  $96 \text{ m}^3/\text{ha}$  of commercial ( $\geq 60 \text{ cm dbh}$ ) cativo wood was

measured in 1999 (Grauel, unpublished data). Also in 1999, a 100% inventory was carried out of a 50-ha plot along the Sambu River in Darien where cativo comprises 95% of the species diversity. Using a form factor specifically developed for *Prioria*, a mean volume of 65 m<sup>3</sup>/ha was calculated for trees  $\geq$  60 cm dbh; while across the river in a series of smaller permanent plots, mean volume totaled only 40 m<sup>3</sup>/ha for the same forest type. The difference can probably be attributed to different management histories under different ownership regimes: the latter being found on open-access public land that is subject to frequent, low-intensity timber harvesting by local loggers; while the 50-ha plot is located on land belonging to Embera-Wounaan indigenous communities who harvest cativo much less frequently. When considering a minimum diameter of 40 cm dbh and the commercial height to the lowest branch, this 50-ha plot contains 190 m<sup>3</sup>/ha (Grauel, unpublished data). Recent volume measurements in cativo forests along the Balsas River ranged from 20 m<sup>3</sup>/ha ( $\geq$  60 cm dbh, Grauel, unpublished data) to 25 m<sup>3</sup>/ha (total volume, Mariscal et al. 1999).

In Colombia, Linares Prieto (1987b) stated that a cativo forest contained more than 150 m<sup>3</sup>/ha in commercial wood and a mean of 80 to 100 m<sup>3</sup>/ha for trees  $\geq$  52 cm dbh. In a cativo forest with 60 tree species where cativo comprises 60% of the basal area, Linares Prieto (1988) measured a total volume of 123 m<sup>3</sup>/ha and 46 m<sup>3</sup>/ha in trees  $\geq$  40 cm dbh. In a cativo forest with 5 other commercial tree species in Podega, Colombia Escobar Munera (1981) calculated a mean of 36 m<sup>3</sup>/ha for all species. In another forest inventory of trees  $\geq$  49 cm dbh of 15 tree species, a mean of 7.3 individuals and 27 m<sup>3</sup>/ha, cativo comprised 36% of the total volume (Consultores Ambientales LTDA 1995).

### **Growth and Mortality**

As with volume estimates, growth estimates vary and depend on the methodology, age and size of the trees, management history of the forest, and site-specific biotic, abiotic, and climatic factors. Comparisons of growth estimates are difficult where different field methodologies and modeling approaches are used.

Like many tropical trees, *cativo* produces growth rings, but no dendrochronology based on crossdating has been performed to show that the rings are produced annually. Using the pinning technique (Kuroda and Shimaji 1984) where wood is wounded and subsequent growth is measured with destructive harvesting, however, McKenzie (1972) concluded that *cativo* produces annual rings. I strongly suspect that *cativo* may produce one or more rings per year.

*Cativo* diameter growth is probably influenced by many variables. Londoño Londoño and Gonzalez Pérez (1993) reported that crown area, crown position, and Hegyi's diameter-distance competition index had significant effects on growth of *cativo* in less diverse forests but not in the more diverse sites. In an unlogged *cativo* forest with 50 to 60 tree species, Del Valle (1979) found that maximum diameter increment was attained by trees approximately 70 cm dbh. Two studies in Panama found maximum diameter increment in medium-sized trees, from 20 to 50 cm dbh depending on the site. In an upland forest in Panama, Condit et al. (1993a) measured maximum annual diameter increments of 2 to 4 cm, while *cativo* from flooded forests showed maximum annual growth rates of 1.5 to 2.0 cm, with means of 0.6 to 1.0 cm (Grauel 1999).

Several modeling approaches have been used to estimate lifetime growth trajectories based on short-term growth rates. Del Valle (1979) used a matrix modeling approach to produce an estimate of 98 years for a 10 cm dbh tree to reach 60 cm.

González Pérez (1995) developed a von Bertalanffy growth model for cativo, and produced an estimate of 90 years for a 14.5 cm dbh tree to reach 60 cm. In a comparative study of two sites where diameter structure, floristic diversity, spatial distribution, and growth were contrasted, González Pérez et al. (1991) found growth to be three times greater in the more diverse forests. Although the authors admit to small sample sizes, they estimated 168 years in less diverse forests and 77 years in more diverse forests for a 10 cm dbh tree to reach 60 cm (González Pérez et al. 1991). There was no difference in growth between diverse and cativo-dominated forests in another study in Colombia, where Linares Prieto (1987b) estimated that a tree would reach optimum harvest size (60 cm dbh) in 55 years in less diverse forests and in 60 years in the more diverse forests. In a different study, the same author estimated that a tree could reach 60 cm dbh in only 38 years, and suggested that this time period could be reduced with “adequate silvicultural techniques” (Linares Prieto 1988). In a study of growth and yield potential of cativo on an upland site in Panama, Condit et al. (1995b) estimated a period of 130 years for a stem to grow from 1 cm dbh to 60 cm, based on mean growth using data from 1982-1985, and 180 years based on data from 1985-1990. Using the same modeling approach and based on data from 1997-2001, I found two sites with similar inundation regimes to vary considerably; one requiring 315 years, and the other 179 years for a 1 cm dbh stem to grow to 60 cm. At another forest farther upriver, only 80 years would be required for a 4 cm dbh tree to reach 60 cm. For an inland swamp, based on growth data from 1997-2000, 157 years would be required for a 1 cm dbh tree to reach 60 cm, and 186 years to reach 80 cm.

### **Natural Regeneration**

In a demographic study of *cativo* in Colombia, Montero (1996) estimated 30,490 seeds/ha were produced during the 6-month period from December to May. Montero (1996) noted that trees with relatively low seed production tended to produce greater numbers of established seedlings than trees that had greater seed production and hypothesized that there was some optimal period for seedfall that resulted in higher probability of survival and maximum recruitment rates.

Linares and Martinez Higuera (1991) found lower densities of *cativo* natural regeneration in frequently inundated forests than in less frequently flooded forests, although the tendency toward monodominance was greater where flooding was more frequent. Linares and Martinez Higuera (1991) also found a strong correlation between mean monthly precipitation and seedling density, and determined that 2% of the large initial seedfall became established. Lopez (2002) followed a 1997 cohort of *cativo* seedlings and found 2.5% survivorship after 3 years.

Dalling et al. (1997) found that less than 10% of *cativo* seeds were viable 2 months after seedfall, and that 30% of the viable seeds had suffered damage by insects or pathogens. Even with up to 60% of the seedmass damaged, however, there was no reduction in the probability of germination; and seeds with up to eight insect larvae germinated as often as seeds with no infestation (Dalling et al. 1997). Furthermore, *cativo* seeds have the ability to produce an average of 2.1 additional, sequential resprouts after the initial sprout is damaged or lost (Dalling et al. 1997).

Tamayo Velez (1991) determined that a germinating seed required 48 days to develop into a 29-cm tall seedling, and declared that height growth of *cativo* plants between 30 and 150 cm in height was 50-60 cm/month. Martínez Higuera (1989)

suggested an annual growth rate of 2.4 m for trees in the same height range. In two strongly monodominant cativo forests in Darien, Panama, density of cativo natural regeneration (trees < 1 cm dbh) varied widely, from less than 5,000/ha at one site to over 17,000/ha at the other. Mean annual height growth for trees between 30 and 150 cm tall varied little, from 2-5 cm, with maximum annual growth rates of 15-25 cm (Grauel, in review 2004a).

### **Artificial Regeneration**

In a study of artificial regeneration of cativo carried out in Urubá, Colombia, Linares Prieto (1987a) tested five planting methods and two planting seasons, and determined that average survival and height were greatest for bare root seedlings planted during the dry season. After 4 years, these seedlings had reached 2.7 m in height (Linares Prieto 1987a). Caycedo (1988), cited by Martínez Higuera (1989), measured annual height growth in seedlings of 70 cm. Cativo seedlings of two ages were planted in three habitats in Darien, Panama. Seedling mortality after 4 years was highest in the natural habitat of the forest understory (89%) and lowest in partial sun on the edge of the forest bordering a treeless marsh (54%, Grauel in review 2004b). Maximum height growth was observed in the full sun, where seedlings of both ages grew approximately 50 cm/yr.

### **Conclusion**

Relatively few tropical tree species have been studied as extensively as cativo. Because of its accessibility, abundance, form, and wood properties, cativo logging has provided livelihoods for thousands of rural Latin Americans as well as for forest industries in North, Central, and South America. Little research has been carried out on the importance of the ecosystem services that cativo forests provide, however.

Unfortunately, the existence of technical, silvicultural, and ecological knowledge of cativo and the forests where it is abundant has not resulted in sustainable management. As is frequently the case in natural resource management, technical knowledge is insufficient when social and economic forces can influence the strength of forest policies that determine the quality of management carried out on the ground. Nevertheless, technical knowledge can form the foundation for research that links ecological dynamics with the social and economic policies that affect forest management, with the aim of promoting socioeconomic development that conserves natural ecosystems.

CHAPTER 2  
EFFECTS OF LIANAS ON GROWTH AND REGENERATION OF *Prioria copaifera*  
IN DARIEN, PANAMA

**Introduction**

The abundance and ecological roles of lianas in tropical forests have long attracted the attention of tropical silviculturists (Fox 1968, Appanah and Putz 1984, Chaplin 1985, Putz 1991, Vidal et al. 1997, Carse et al. 2000). Because lianas are a major component of woody plant diversity and provide important food sources for wildlife, they play critical roles in maintaining biological diversity (Nabe-Nielsen 2001, Burnham 2002, Schnitzer and Bongers 2002). Unfortunately, where sustainable forest management is the primary tool for forest conservation and the primary objective is timber production, lianas can be a major impediment. Given that the likelihood of forest conversion to more profitable land uses than forestry is enhanced if prospects for subsequent timber harvests are not economically competitive, liana proliferation can contribute indirectly to forest loss.

The large trees that provide the timber value of a forest are more likely than smaller trees to be infested with lianas (Putz 1984, Putz and Chai 1987, Nabe-Nielsen 2001, Perez-Salicrup et al. 2001), and lianas can have various silvicultural implications for forest management. During harvesting operations for example, felling of liana-laden trees can induce excessive stand damage, because their crowns are likely to be connected to their neighbors (Putz 1984). Avoidance of this accessory damage has frequently, but not always (Parren and Bongers 2001), been accomplished through pre-felling liana cutting (Fox 1968, Appanah and Putz 1984, Johns et al. 1996). An additional benefit of pre-

felling liana cutting is the post-harvest reduction in liana proliferation in logging gaps (Alvira et al. 2004, Gerwing and Vidal 2002). Reducing post-logging liana infestations is desirable, because lianas can seriously impede succession in gaps (Schnitzer et al. 2000) and diminish opportunities for rapid recruitment and growth of desirable timber species. In addition to physically impeding establishment of seedlings and saplings of tree species in logging gaps, lianas can reduce host tree fecundity (Stevens 1987), lowering the reproductive output of valuable timber species in forests where natural regeneration is the only cost-effective silvicultural option for stand perpetuation. Heavy liana infestations can also substantially reduce diameter growth of adult trees (Whigham 1984, Gerwing 2001, Clark and Clark 1990), which lowers the net present value of future timber yields by prolonging cutting cycles.

*Prioria copaifera* (hereafter “cativo,” Fabaceae), a canopy tree found in freshwater wetland forests from Nicaragua to Colombia, has been exploited for timber for decades (Barbour 1952), with little apparent concern for long-term management. Today, commercial stands are found principally in eastern Panama and northwest Colombia. Repeated logging of monodominant cativo stands during 40 years of exploitation testifies to the regenerative capacity of the species. Nevertheless, large areas of cativo forest have been converted to agricultural production or to mixed-species secondary forest and liana tangles as a result of overharvesting. Of the original 363,000 ha of cativo in Colombia for example, less than 90,000 ha remain (Linares Prieto 1987b). Similarly, extensive stands of cativo were once found in western as well as eastern Panama, but today commercial stands are found only in Darien Province. Of 30,000 ha of cativo-dominated forest in Darien in 1987 (INRENARE 1987a), an estimated 15,000 ha remained in 1999

(ANAM 1999a). Increasingly, Panamanian foresters as well as local Darien community members desire to promote sustainable logging of the remaining cativo forests.

The stands of almost pure cativo that are found as bands along the principal rivers of Darien vary between 100 m and 1 km in width. Behind the forest, treeless wetlands composed of the palms *Elaeis oleifera* and *Oenocarpus mapora* and various lianas including *Dalbergia brownei*, *Combretum sambuensis*, *Elachyptera floribunda*, *Tetrapteris macrocarpa*, *Allamanda cathartica*, *Phryganocydia corymbosa*, *Cydistia diversifolia*, *Smilax spinosa*, *Banisteriopsis* spp., and *Heteropteris* spp. often dominate the landscape. In the absence of silvicultural interventions other than logging, high-statured riverine forests are likely to be converted into palm- and liana-dominated vegetation.

Present day stand structure of many riverine cativo forests in Darien is a result of traditional logging methods that do not employ heavy machinery (Grauel and Pineda M. 2001). Instead, logs are levered or rolled by hand towards the river on roads constructed from 15 to 30 cm dbh (diameter at breast height, 1.3 m) cativo trunks cut and laid end to end to form two parallel rails. In many riverine cativo forests, the combination of removing all harvestable-size trees as well as many subcanopy individuals for rail building has left a very discontinuous canopy and large multiple-tree gaps, which are habitats favorable for liana proliferation.

The leguminous liana *Dalbergia brownei* proliferates abundantly in disturbed cativo forests. A principal component of the treeless wetlands found behind the natural river levees where cativo dominates, this liana uses cativo forest edges to climb into the forest canopy. Although this species does not establish in the deep shade of the cativo

forest understory, large stems (up to 20 cm diameter) are commonly found hanging from the 30-40 m high canopy in many of the cativo forests of the lower Balsas, Sambu, and Tuirá Rivers (Grauel and Pineda M. 2001). Areas with high liana densities seem to have developed in large logging gaps created 20-30 years ago. Many mature cativo trees in heavily infested areas are visibly deformed, apparently from having developed while carrying large liana loads or from having been damaged during logging. In other areas that have been continually and recently subjected to small scale harvesting, *D. brownei* is proliferating on the ground in large canopy gaps and appears to delay cativo regeneration. In the present study I measured, by observation and experimental liana removal, the effect of lianas on cativo adult stem growth as well as on seedling height growth, recruitment, and mortality.

### Study Site

The study was conducted in a riverine cativo forest along the Balsas River in eastern Panama (8° 07' N, 77° 52' W). Mean annual precipitation at Camogantí, the nearest town (approximately 8 km from the study site), is 2457 mm (based on Government of Panama published reports for 1978-1982, 1984, 1986, and 1988-1994) while rainfall measured at the study site in 1998 and 1999 totaled 2970 mm and 2758 mm, respectively. The forest is inundated periodically with rainwater during the 9-month wet season from April to December. In addition, it is flooded twice per day for about five days during the monthly spring tides known locally as the 'aguaje.' The freshwater backup caused by the Pacific spring tides affects the riverine forests as far as Camogantí, 73 km from the mouth of the Tuirá River at the Gulf of San Miguel. Although at the study site the tidal flooding is mostly the freshwater backup, soil samples show a slight brackishness (electrical conductivity 5.0 mmhos/cm) and mangrove forests are found

only 7 km downriver from the study site. Soils at the study site are heavy clays classified in the suborders fluvent and aquept, are acidic to slightly acidic, and poorly drained (Tapia 1999).

The study site is on private land owned by a logger and is next to an operating sawmill. The owner, who has been logging cativo in Darien since 1960, is currently logging further upriver and has protected the forest where the study took place because he values it for hunting and aesthetics, although he told us that he had harvested a few scattered trees about ten years prior to the study. This cativo forest is composed of about 95% *Prioria copaifera* of all size classes (Grauel and Kursar 1999). Other tree species include *Pterocarpus officinalis*, *Mora oleifera*, and *Carapa guianensis*. Results from a 1 ha permanent plot show 10 cativo trees per hectare  $\geq 60$  cm dbh, the legal cutting limit, but the majority of these were left due to bad form or hollowness. Regeneration of cativo of all sizes is abundant.

### Methods

In September 1997 six 25 x 25 m plots were installed in a line at 50-75 m intervals in areas with intact canopies but with relatively high densities of lianas compared to the forest overall. Each plot was subdivided into twenty-five 25-m<sup>2</sup> subplots to facilitate stem mapping. Inside the plots I measured all trees  $\geq 4$  cm dbh as well as the diameters of all ascending liana stems  $\geq 1$  cm at breast height. I did not attempt to differentiate genetically distinct lianas; every stem encountered at 1.3 m above the ground was measured. To increase the sample size for the growth analyses of cativo, additional trees were measured up to 5 m outside of each plot, but no lianas were measured outside the plots. Every plant was tagged and mapped and subsequent censuses were carried out in

1998, 1999, and 2001. For the growth analysis, diameter classes for trees were selected based on relative canopy position; 15 cm dbh was used as the cutoff between canopy and understory individuals. Due to the low canopy of the forest where lianas are abundant, even trees 15-30 cm dbh may receive substantial direct illumination, while trees < 15 cm dbh are generally in the understory.

During the initial measurements, each tree was classified as severely or lightly infested by lianas. Severely infested trees had at least five individual liana stems hanging from the crown and some stems or branches apparently deformed by lianas. Lightly infested trees had fewer than five liana stems hanging from the crown and no visible deformations. For the growth analyses, growth rates of liana-free trees were included in the lightly infested category. All lianas were cut with a machete inside and up to 10 m outside of three randomly chosen plots.

In 10 randomly chosen 25m<sup>2</sup> subplots in each plot, all natural regeneration of cativo from seedlings to small trees 1 cm in diameter were counted, tagged, and measured (height) before the vine cutting treatment and two years later. Where necessary to reduce heteroskedasticity, seedling frequency data were natural log-transformed. Mean relative height growth for seedlings in treated and control plots was compared with a two-sample t-test and the difference of mean absolute height growth was tested by ANOVA using initial height as a covariate. Mortality of these seedlings and small trees in treatment and control plots was also compared. Two years after the initial census, the same subplots were surveyed for new cativo regeneration. Treatment differences in mean density of seedlings recruited per plot was compared with t tests.

For several reasons, including the observation that increases in cross sectional area of lianas are associated with much larger increases in leaf area than in trees (Putz 1983), it is desirable to estimate diameter growth rates of lianas. In 2001, four years after the initial measurements, 56 *Dalbergia brownnei* lianas in the control plots were again measured to estimate stem diameter growth. Individuals  $< 6$  cm dbh were measured with dial calipers; a mean diameter was calculated from measurements of the long and short axes. Lianas  $\geq 6$  cm dbh were measured with a diameter tape. Wood density was estimated using ten bark-free stem samples, to allow comparisons with other studies. While growth rates of trees are often negatively correlated with wood density, this pattern may not hold for lianas that do not produce structural wood for support.

Canopy openness above 2 m was measured immediately before and two months after liana cutting in all plots with a vertical densitometer (Stumpf 1993). Both measurements were made during the rainy season. This instrument projects a point vertically upward that encounters either canopy or open sky at each evenly spaced sample point along a linear transect. Canopy openness is estimated as the proportion of points of open sky along three transects in each plot.

To compare rates of cativo growth and regeneration in heavily vine-infested areas with forest with low liana infestation, data from the six plots of the present study were compared with data from plots selected at random for a demographic study of cativo in the same forest. The demographic study was based on five 20 x 20 m and five 40 x 40 m plots established in March 1997. All trees  $\geq 10$  cm dbh were tagged, mapped, and measured (dbh), while trees  $\geq 1$  cm dbh were measured in all five 20 x 20 m plots and in five randomly chosen 20 x 20 m subplots in each of the 40 x 40 m plots. All trees were

measured annually from 1997 to 2001. In addition, all trees < 1 cm dbh in eight randomly chosen 5 x 5 m subplots of each plot were tagged and mapped and were measured (height only) in November 1997. This population of seedlings and saplings was censused approximately every two months for two years whereas height was measured annually.

### Results

Two months after cutting lianas, significant but modest increases in canopy openness were observed in the treated plots. There was no difference in the before and after canopy coverage in the three control plots, while the three treated plots showed a mean increase of 7% ( $p < 0.01$ ) in canopy openness.

Mean annual diameter growth of *Dalbergia brownii* was  $1.3 \text{ mm yr}^{-1}$  ( $n = 56$ ,  $sd = 1.4$ , range = -0.8 to 5.5 mm). Mean wood density of *D. brownii* (dry weight/fresh volume) based on ten samples was  $0.38 \text{ g cm}^{-3}$  ( $sd = 0.047$ ).

Based on the mean number of stems  $\geq 4 \text{ cm}$  from the six 25 x 25 m plots, cativo dominated the forest with  $1320 \text{ stems ha}^{-1}$  ( $sd = 212$ ), virtually identical to nearby areas of riverine forest with lower liana densities ( $1338 \text{ stems ha}^{-1}$ , Grauel and Kursar 1999). *Pterocarpus officinalis*, the only other abundant tree species, was represented by  $51 \text{ stems ha}^{-1} \geq 4 \text{ cm dbh}$ . The  $35.1 \text{ m}^2 \text{ ha}^{-1}$  of cativo basal area represents 96.6% of the total basal area of trees  $\geq 4 \text{ cm dbh}$ .

For all cativo trees  $\geq 4 \text{ cm dbh}$ , 71% had lianas hanging from the crowns, while 93% of mid- and upperstory trees ( $\geq 15 \text{ cm dbh}$ ) had lianas. There were  $1757 \text{ ascending liana stems ha}^{-1} \geq 1 \text{ cm dbh}$  ( $sd = 270$ ), with a mean liana basal area of  $3.40 \text{ m}^2 \text{ ha}^{-1}$  ( $sd = 0.8$ ). Of the two liana species found, *Dalbergia brownii* comprised 96.9% of the basal

area. The only other liana encountered, *Elachyptera floribunda* (Hippocrateaceae), was mainly represented by small stems, with 75% of the ascending stems < 3 cm in diameter, while over 80% of the *D. brownei* stems were  $\geq 3$  cm in diameter (Figure 2–1).

Prior to liana cutting, in the six heavily liana-infested plots the mean density of cativo seedlings and saplings (< 1 cm dbh) was  $707 \text{ ha}^{-1}$  (sd = 1154). In contrast, in the ten randomly located plots for the demographic study of cativo at the same site, the mean density of cativo seedlings and saplings was  $6350 \text{ ha}^{-1}$  (sd = 12882, Figure 2–2).

Although this was almost an order of magnitude difference and is plainly discernible in the forest, variability was large due to the clumped distributions of seedlings, but the difference was significant ( $t = 3.12$ ,  $df = 14$ ,  $p = 0.008$ ).

For cativo regeneration present at the beginning of the study, relative and absolute height growth over two years did not differ between liana-cut and control plots.

Although mean initial height for seedlings and saplings happened to be significantly greater in the three control than in the three treatment plots, there was no difference in initial height of only those trees that survived to produce growth records. Cativo seedling and sapling mortality was nearly double in treated than in control plots (63% vs. 36%, Pearson  $\chi^2 = 6.2$ ,  $p = 0.01$ ).

Cativo seedling recruitment during two years after liana cutting was more than three times greater in the treated than in the control subplots but, due to large variability, was not statistically significant ( $t = 1.30$ ,  $df = 4$ ,  $p = 0.26$ , Figure 2–3). On a per ha basis, over 7700 cativo seedlings recruited during two years after lianas were cut compared to just over 2200 seedlings for the control plots.

Mean annual diameter growth of cativo trees during 1997-2001 was about twice as rapid in the liana-cut compared to the control plots (Figure 2–4). For trees  $\geq 15$  cm dbh the difference was significant ( $t = 3.41$ ,  $df = 4$ ,  $p = 0.03$ ), while for trees between 4 and 15 cm the difference was not statistically significant ( $t = 2.61$ ,  $df = 4$ ,  $p = 0.06$ ). Surprisingly, severity of liana infestation had little apparent effect (no significant differences found) on cativo diameter growth for either control or treated plots (Figure 2–5). The largest difference was for canopy trees in the control plots, where severely infested trees grew slightly slower than lightly infested trees.

### Discussion

Despite their abundance, liana cutting had only a slight (7%) but statistically significant ( $p < 0.01$ ) effect on canopy openness of the cativo forest, because most of the liana foliage is displayed on the tops of tree crowns. Liana-infested cativo forests look “feathery” at the top of the canopy, due to the abundant emergent branches of small-leaved *D. brownii* searching for higher trellises. Two years after liana cutting, canopy openness was similar for all plots, perhaps because the cativo canopies increased leaf production after liana cutting. In contrast, Gerwing (2001) found that increases in canopy light transmittance persisted for two years following vine cutting, and Perez-Salicrup (2001) measured no change in canopy openness four months after vine cutting in a Bolivian lowland forest but an increase in openness two years later. Both the Bolivian and Brazilian studies took place in much drier forests and probably on less fertile soils than the present study; perhaps the cativo trees were better able to take advantage of the removal of lianas and produce foliage rapidly.

The low diameter growth rate of *Dalbergia brownii* is similar to the growth rate found by Putz (1990,  $1.4 \text{ mm yr}^{-1}$ ) for fifteen liana species from a tropical moist forest in

Panama. In a lowland wet forest in Ecuador the most abundant liana, *Machaerium cuspidatum*, had an average annual growth rate of  $1.4 \text{ mm yr}^{-1}$  for stems between 30 and 50 mm (Nabe-Nielsen 2002). In contrast to these low diameter growth rates, a single shoot of *D. brownei* was observed to grow 1.24 m in length in 71 days.

Increased mortality of cativo seedlings in liana-cut plots compared to control plots appeared to be due to numerous large liana stems falling from the canopy, most within the first year following cutting. In addition, floodwaters commonly move coarse woody material around on the forest floor, which frequently results in the bending and breakage of seedlings. This additional impact may explain why tree seedling mortality increased significantly following liana-cutting here but not in a tropical tierra firme forest in Bolivia with higher liana densities (Perez-Salicrup 2001).

Enhanced seedling recruitment in liana-cut plots (Figure 2–3) more than compensated for increased mortality of the initially scarce regeneration in these heavily liana-infested areas. Large cativo seed crops were produced in 1997 and 1999, and the germinated seedlings from the May-June 1999 seedfall were captured in the plot census in November 1999 before dry season (January-April) mortality occurred. Three possible mechanisms for this increased seedling recruitment following liana removal include: 1) reduced seed movement out of the liana-cut plots; 2) enhanced seedling survival; and, 3) increased seed production.

Reduced seed movement could result because cativo seeds are large (mean fresh wt = 48 g, Lopez 2001) and mainly dispersed by water. Seeds that fall and that are not partially buried in the heavy wet soil may be transported by the monthly spring tides or

the periodic flooding caused by wet season rains. Fallen liana stems could have acted as small dams inhibiting cativo seed movement during inundation.

If seed production and retention as well as capture of water dispersed seeds were equal in all plots, high early mortality rates in the control plots would explain the difference in seedling densities between control and treatment plots. But most cativo seedling mortality occurs during the short dry season from January to April (Lopez 2002), and the plots were censused after seedfall but before the onset of the dry season of the second year after liana cutting.

Catavo trees newly liberated from lianas may have produced more seeds. A possible mechanism that could help explain an increased production of seeds by cativo is that lianas interfere with cativo flower or seed production, either physically or through competition for light. *D. brownii* produces long recurved spines that wrap around small diameter objects that they encounter, such as flower-bearing branches. A drain on host resources caused by the constriction of vascular elements in branches or twigs was proposed by Stevens (1987) to explain the negative effect of lianas on the fecundity of *Bursera simaruba* trees in Costa Rica, and a similar mechanism may be at work in the cativo/*Dalbergia* canopy.

Another possible mechanism for the proposed increased seed production in the treated plots is the removal of belowground competition after the death of the lianas, resulting in increased nutrient availability. Increased water availability may also have been a factor, since seasonally flooded cativo forests can experience severe short-term annual droughts. Putz (1991) suggests that because lianas do not need to produce large diameter structural roots, root systems of lianas may be more efficient in water and

nutrient uptake. Lianas were also experimentally shown to be effective belowground competitors in a study with north temperate vine species (Dillenburg et al. 1993).

Although liana cutting resulted in a notable positive increase in *Prioria copaifera* stem diameter growth, lianas may not be solely responsible for low forest-wide growth rates, as proposed by Gerwing (2001) for a seasonal Amazonian forest in Brasil. In the riverine cativo swamps in Panama discussed in this study, mean annual growth of trees in the control plots was not significantly different than similar sized trees in the nearby permanent plots where lianas were generally less abundant (data not shown).

Mean annual growth of cativo trees of all sizes in both treatment and control plots was greatest during the second year following liana cutting and then declined (Table 2–1). Although the liana leaves fell during the first two months after cutting and the hanging stems fell within the first year following treatment, this pattern of increased growth followed by decline is probably not due to a “fertilizer effect” from the fallen liana material; forest-wide growth rates for cativo, based on permanent plots at this site and three others in different watersheds in Darien Province, showed the same pattern, suggesting a correlation with climate.

The observation that the growth rates of liana-infested control plot trees  $\geq 15$  cm dbh did not differ from growth rates of trees of the same dbh in adjacent permanent plots with few lianas (data not shown) could be attributed to the lower overall canopy height in the area of the liana-cutting plots. With fewer large trees in the liana-abundant areas of the forest, trees that otherwise would be subcanopy individuals may receive more light than a similar sized tree in adjacent non-liana forest. This interpretation suggests that these liana-abundant areas are old canopy gaps in the process of recovery, similar to the

“vine-dominated disclimax” of Whigham (1984) or the “stalled gap” of Schnitzer et al. (2000).

The profound negative effect of lianas on cativo growth and reproduction probably results from a combination of aboveground and belowground influences. Lianas were estimated to occupy 31% of the forest canopy surface area during the wet season in a seasonally dry tierra firme forest in central Panama (Avalos and Mulkey 1999) and liana leaves might significantly reduce light availability for cativo leaves. Belowground competition for nutrients and water in the dry season could also be a factor. Given that rooting depth in cativo forests is limited by the high water table (Lopez 2002), belowground competition for water may be severe during the dry season because root systems die back during wet season flooding (Lopez 2002). In a semi-deciduous lowland forest in Bolivia, Perez-Salicrup and Barker (2000) found significantly less negative water potentials in *Senna multijuga* trees where lianas were cut as well as increased tree diameter growth. In contrast, in the same forest after liana cutting, Barker and Perez-Salicrup (2000) found no difference in water status of mahogany trees with and without lianas and concluded that lianas and trees had access to different sources of water due to different rooting depths.

Two issues pertinent to considerations of liana cutting as a silvicultural tool are cost of implementation and biodiversity impacts. Based on the experimental plots, it would require 16 person-hours to treat one hectare of forest. Although the experiment took place on private land, the majority of these degraded forests are on state land managed by the Panamanian Environmental Ministry (ANAM). Currently, ANAM is working with several communities in Darien to develop a partnership whereby forest areas are

identified for potential timber production and legal tenure is transferred to local community groups. The government intends to train community members in mapping, inventory, and other management activities; liana cutting could be one of the recommended silvicultural treatments.

Conservation of biodiversity is a critical issue in our study area, especially because of the presence of Darien National Park and the current improvement of the Pan-American highway that will doubtlessly increase colonization rates and forest clearing. Liana-cutting in seasonally flooded cativo forests is not expected to have severe effects on species diversity for several reasons. Tree species diversity is extremely low in tidally-flooded cativo forests (Grauel and Kursar 1999) and only one species of liana seems to have proliferated excessively as a result of several decades of uncontrolled timber exploitation. Because this species, *Dalbergia brownii*, is also a common component of nearby treeless wetlands, attempts at controlling its proliferation in cativo forests suited for timber production probably will never eliminate it. Promoting sustainable management of cativo forests for timber production could actually serve as a biodiversity conservation tool. By providing local communities with viable economic activities in the areas surrounding Darien National Park, pressure to exploit the natural resources of the park could be reduced.

Table 2–1. Mean ( $\pm 1$  SE) annual diameter growth (mm) of *Prioria copaifera* one, two, and two to four years after liana cutting.

| Treatment  | Liana Infestation | 1997-1998 |                            | 1998-1999 |                            | 1999-2001 |                            |
|------------|-------------------|-----------|----------------------------|-----------|----------------------------|-----------|----------------------------|
|            |                   | N         | Mean Annual Increment (mm) | N         | Mean Annual Increment (mm) | N         | Mean Annual Increment (mm) |
| Control    | light             | 171       | 1.5 (0.2)                  | 168       | 2.2 (0.3)                  | 152       | 1.6 (0.2)                  |
|            | severe            | 204       | 1.6 (0.2)                  | 196       | 3.1 (0.3)                  | 181       | 1.8 (0.2)                  |
| Lianas Cut | light             | 166       | 2.2 (0.2)                  | 164       | 4.1 (0.4)                  | 144       | 2.7 (0.3)                  |
|            | severe            | 180       | 3.3 (0.3)                  | 172       | 6.6 (0.4)                  | 154       | 4.5 (0.3)                  |

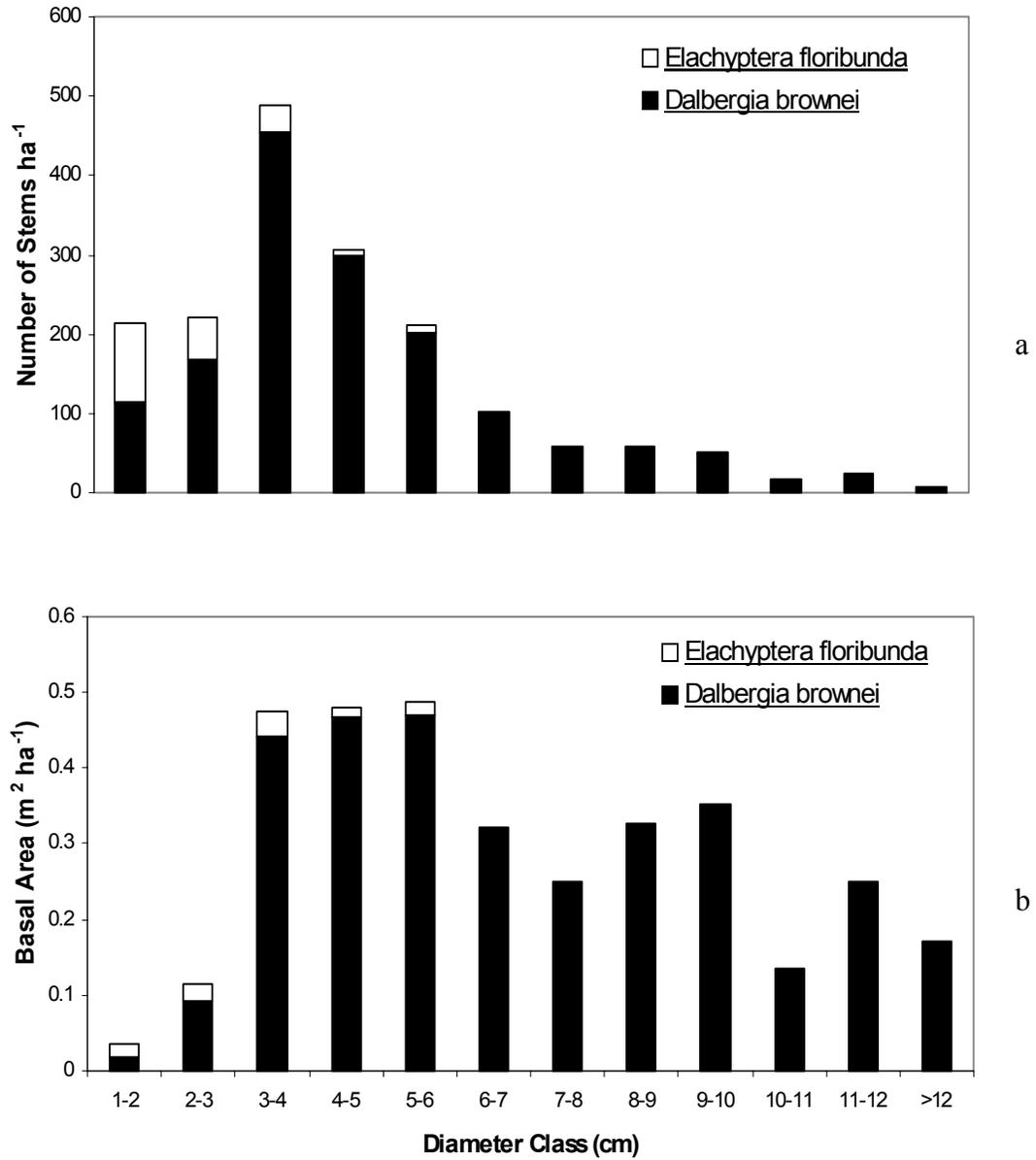


Figure 2-1. Diameter distributions of ascending lianas in six 25 x 25 m plots in heavily infested riverine *Pitaria copaifera* forest degraded by repeated entry logging. a) Number of stems per hectare. b) Basal area in square meters per hectare.

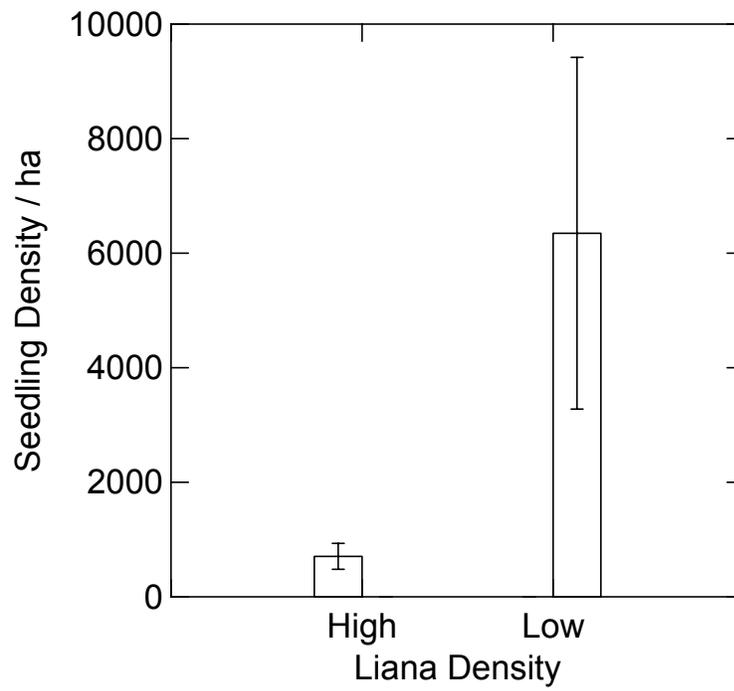


Figure 2–2. Mean ( $\pm 1$  SE) density of *Prioria copaifera* regeneration (< 1 cm dbh) in areas of high (N = 10) and low (N = 6) liana densities.

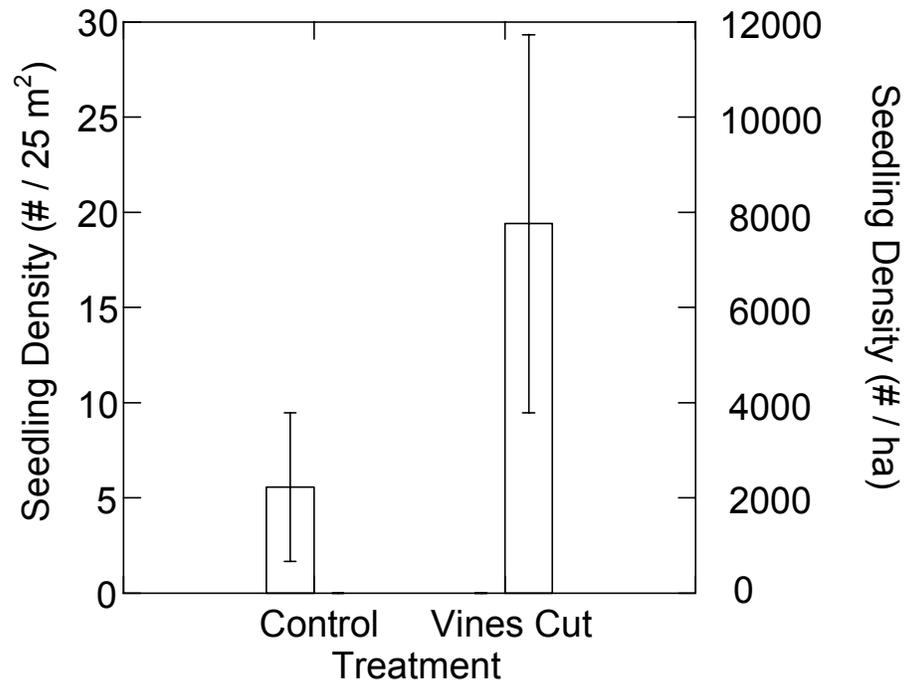


Figure 2-3. Mean ( $\pm 1$  SE) *Prioria copaifera* seedling recruitment censused two years after liana cutting in three control and three treatment plots.

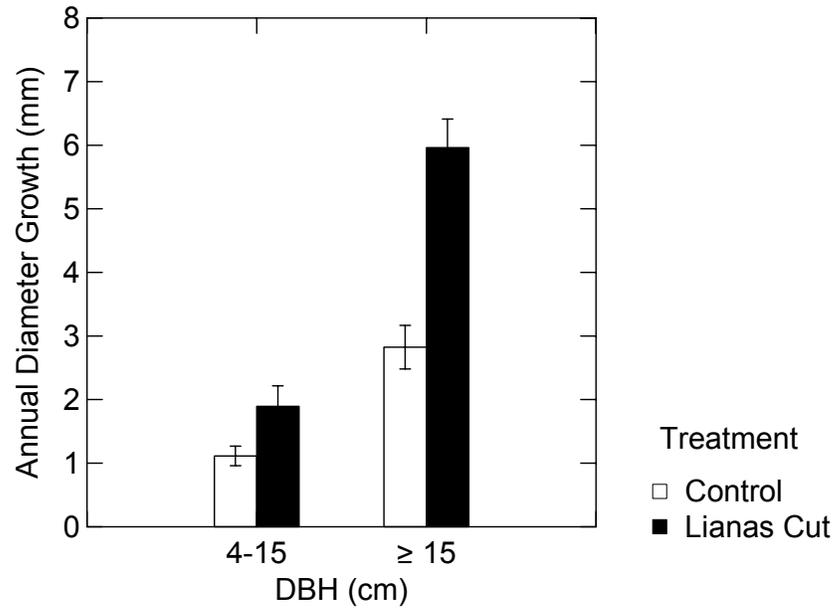


Figure 2–4. Mean ( $\pm 1$  SE) annual *Prioria copaifera* diameter growth based on five annual censuses of all trees  $\geq 4$  cm dbh in three control plots and three plots in which all lianas were cut at the beginning of the study.

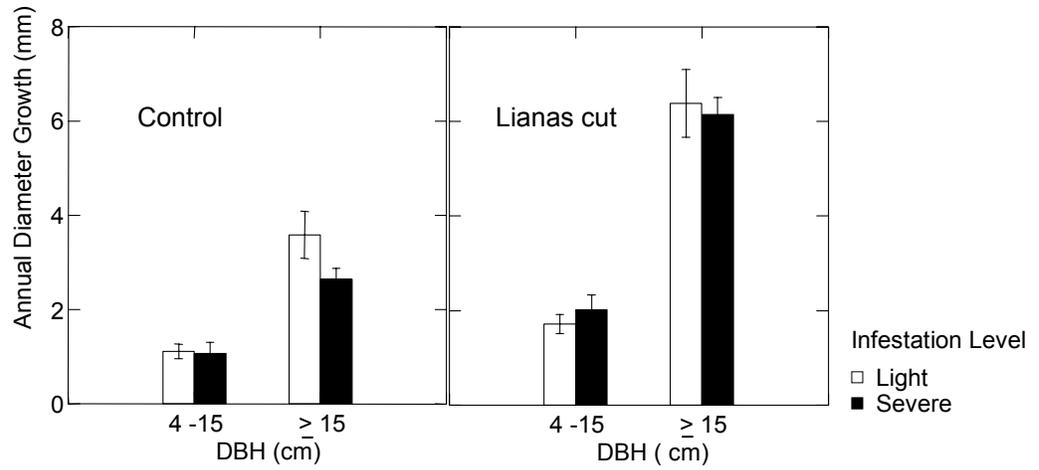


Figure 2–5. Mean ( $\pm 1$  SE) annual *Prioria copaifera* diameter growth of cativo based on five annual censuses according to liana infestation level in control and treatment plots.

CHAPTER 3  
GROWTH AND SURVIVAL OF *Prioria copaifera* SEEDLINGS PLANTED ALONG  
A HABITAT GRADIENT IN A PANAMANIAN SWAMP

**Introduction**

Until relatively recently, native tropical species have been little utilized for reforestation programs (Evans 1992). For plantation forestry in the past, a general lack of information led to a reliance on few familiar exotic species with high growth rates. Concern over the loss of biodiversity as well as recognition of other production systems besides monospecific plantations has increased attention on native species for reforestation (e.g., Butterfield 1995, Haggard et al. 1998). Furthermore, much effort has now been expended in acquiring knowledge about growth and mortality rates, as well as propagation techniques, of native tree species in the tropics, often with the specific aim of identifying promising candidates for reforestation (Condit 1995, Foroughbakhch et al. 2001, Wightman et al. 2001, Moulart et al. 2002).

Reforestation with native tropical species may be carried out for timber production (Keenan et al. 1999), site restoration (Parrotta and Knowles 1999, Engel and Parrotta 2001, Montagnini 2001), fuelwood production (Katakis and Konwer 2002), carbon sequestration (Silver et al. 2000), biodiversity conservation (Blakesley et al. 2002a, Blakesley et al. 2002b), or other reasons. For a given end use, species choice should not be based solely on site characteristics or growth rates because the purposes for which trees are planted may vary not only with the type of tree but also with the type of ‘user’ (Raintree 1991). Certain landowners may be more amenable to reforestation with native

species where opportunity costs for labor are low or motivation consists of a wider range of benefits than only financial profitability (Putz 2000).

In this study, a valuable native timber tree, *Prioria copaifera* (hereafter ‘cativo’), was planted to evaluate growth and mortality rates in different habitats in swamp forests in eastern Panama. I hypothesized that both mortality and growth would be greatest in the high-light environment and lowest in the forest understory where cativo natural regeneration was abundant.

Cativo is a large Caesalpinoid timber tree that has been harvested commercially for decades (Anonymous 1933, Hess and Record 1950, Kukachka 1965). Originally distributed from Nicaragua to Colombia, logging and conversion to banana plantations have severely reduced the area of cativo forests in Costa Rica and western Panama (Veiman 1982, Jiménez Madrigal 1995). Today, commercial stands are restricted to eastern Panama and northwest Colombia. Cativo is known principally from single species or monodominant stands in swamp and riparian habitats, but is also found, less frequently, in upland soils where it sometimes dominates (Condit et al. 1993b).

In Darien, Panama, the area of cativo-dominated forests has been reduced to less than 15,000 ha from an original coverage of 60,000 ha (Grauel and Pineda M. 2001). Many riverine cativo forests are adjacent to extensive marshes composed of palms, dense liana tangles, and occasional “vine towers” where trees still stand from the remnant forest. In the early 1950s Lamb (1953) described a belt of commercial cativo forests along the Balsas River that averaged 1km in depth on each bank of the river, but in 2000 the belt was only 100m deep in some areas. Decades of logging has left many of these cativo forests badly liana-infested and otherwise severely degraded (Grauel and Putz

2004). Hence, an important objective of the study was to determine the feasibility of restoring treeless marshes to cativo forests.

### Study Site

The study was conducted in a forest on private land along the banks of a tributary of the Tuira River, the Balsas River, in Darien Province in eastern Panama (8° 07' N, 77° 52' W), 48 km from the mouth of the Tuira River at the Gulf of San Miguel. The landowner has been logging cativo in Darien for forty years, and although he has cut only a few scattered trees at the study site within the last ten years, it is likely that this forest was subjected to an initial selective cutting around thirty years ago. In an early survey of cativo-dominated forests Barbour (1952) noted that commercial-sized trees ranged from 60 to 120 cm in dbh (diameter at breast height, 1.3 m), with occasional specimens of 150 to 180 cm dbh. Today, few large trees are found in these easily accessible riverine forests (Grauel and Kursar 1999).

The arboreal component of the study site is composed of 95% cativo (basal area and stems ha<sup>-1</sup>) of all sizes (Grauel and Kursar 1999). Other tree species that occur in the stands include *Pterocarpus officinalis*, *Mora oleifera*, and *Carapa guianensis*. Marshes are found adjacent to the cativo forest and are composed of scattered palms (*Elaeis oleifera*), liana tangles, and occasional “vine towers”, suggesting that the tall forest has been displaced. The lianas of the marsh, principally *Dalbergia brownnei*, climb the tree canopy at the well-defined edge of the forest where there is abundant light, but seldom colonize the understory of the high-statured forest where little light penetrates.

Mean annual precipitation at Camogantí, the nearest town (approximately 8 km from the study site), is 2457 mm (based on Government of Panama published reports for 1978–1982, 1984, 1986, and 1988–1994) while rainfall measured at the study site in 1998

and 1999 totaled 2970 mm and 2758 mm, respectively. The study site is subjected to periodic flooding from rain events during the 9-month wet season (April-December) and is also flooded when river water is backed up by high monthly tides. The slightly brackish soils at the study site (electrical conductivity 5.0 mmhos/cm) are heavy clays classified in the suborders Fluvents and Aquepts, are acidic to slightly acidic, and are poorly drained (Tapia 1999).

### **Methods**

In August and September 1997, cativo wildings of two ages were dug up in the forest and planted in three different habitats with distinct light environments. First year seedlings, seeds that matured in May-June of 1997, were identified by having an attached seed and little woody tissue. Individuals referred to as “older seedlings” had no attached seed and had woody stems. These latter seedlings may have been 3 years or older given that cativo seedlings can survive for a number of years with little or no growth (Lopez 2002). These latter seedlings were likely 2–4 years old.

I tested the effects of 3 levels of canopy cover on two ages of seedlings in four sites (= blocks) separated by 50-200 m along forest-marsh interfaces. In each of four blocks, side-by-side pairs of 7 x 7 m plots were installed in the shade of the forest, on the edge between the forest and treeless marsh, and in the marsh in full sunlight. Site preparation in the marsh involved extensive liana cutting to establish plots and facilitate access but only moderate liana cutting in the edge habitat where liana density was not as abundant due to the partial shade of the adjacent forest canopy. Seedlings were carefully dug up and bare root planted at 1 x 1 m spacing. For each plot pair in a given light environment, seedling age was randomly assigned and 49 seedlings of a given age were planted in each plot. Therefore, for each habitat – seedling age combination, 196 seedlings were planted

for a total of 1176 seedlings. In the first plot that was planted, the seedlings (older, shade) were transplanted with entire blocks of soil to protect the roots. This practice proved to be excessively laborious and was abandoned. All subsequent results exclude these 49 seedlings that had high survivorship but little height growth at the end of the study.

Canopy openness is defined as the proportion of the sky hemisphere that is not obscured by vegetation when viewed from a single point (Jennings et al. 1999). At the center of each plot, canopy openness at 1.3 m above the ground was measured with a spherical densiometer (Lemmon 1957) by averaging four readings taken in the cardinal directions.

After planting in August and September 1997, seedlings were tagged, each stem was marked at 20 cm above the ground, and two perpendicular diameter measurements were taken with Vernier calipers and averaged. Total height of each seedling was also measured. Both height and diameter were recorded at approximately six month intervals for two years; final measurements were made after an additional 20 months had elapsed (July 2001). Repeated measures analysis of covariance was used with either initial height or diameter as the covariate to test the significance of seedling age (between-subjects), habitat (within-subjects), and their interaction. In addition, final mean and maximum height and diameter were each compared between seedling ages within habitats. Height and diameter data were natural log-transformed to comply with the ANOVA assumption of normality. For tests on seedling sizes after the initial measurements, Geisser-Greenhouse adjusted p-values were used because the assumption of homogeneity of variances of treatment-differences was not met (Maxwell and Delaney 1999).

Seedling survival was censused five times in the first two years (1997-1999) with a final tally in July 2001. Survival among the three habitats was compared for each seedling age with one-way ANOVA, then Bonferroni post-hoc tests were used to determine differences among means. All data were arcsine square root-transformed to reduce the unequal variances found in a few plots.

Annual rates of absolute and relative growth in height and diameter were calculated for one year, two years, and four years after planting. Growth was first examined for each seedling age by comparing performance among the three habitats with ANOVA and Bonferroni comparisons. Younger and older seedling growth was then compared with t-tests for each habitat. For growth over the entire four years of the study, as well as final seedling size, comparisons could only be made between the edge and sun habitats because of high seedling mortality in the shade.

## **Results**

Canopy openness among the three habitats ranged from 10–85% (Table 3–1). The high variability for the readings in the edge environment resulted from one reading capturing the forest canopy, one capturing the open sky of the marsh, and the other two including both canopy and sky.

Younger and older seedlings differed significantly in both height and diameter at the time of planting (Table 3–2). Older seedlings were twice as large in diameter and about 25% taller than first year seedlings.

The repeated measures ANCOVA revealed that only habitat, not seedling age, had significant effects on height and diameter (both G-G adjusted  $p < 0.001$ ) during the six measurements, and there was no age-habitat interaction (Figure 3–1). Maximum heights for both seedling ages were found in the full sun, where mean maximum height among

the four blocks for younger seedlings was 382 cm and for older seedlings 350 cm. Within the edge and sun habitats, however, there was no significant difference in maximum or mean height attained between seedling ages at the end of the four year study. Because of high mortality of first-year seedlings in the shade, no comparisons could be made regarding final size attained in that habitat.

The planted seedlings were also largest in diameter in the full sun habitat. The only significant difference in all comparisons of diameter and DBH, however, was found in mean stem diameter, where older seedlings were slightly larger than younger seedlings in the sun (38.6 mm vs 32.2 mm,  $t = 2.5$ ,  $df = 6$ ,  $p = 0.047$ ).

For the edge and sun habitats, 88% - 99% of total four year mortality occurred in the first seven months after planting (Figure 3–2). Seedlings initially survived better in the shade but at the end of the study mortality was highest for both seedling ages in the shaded understory. Results from the ANOVAs showed that survival was consistently highest for both seedling ages in the edge habitat, but the Bonferroni tests revealed no significant differences in survival at the end of the study between the edge and full sun habitats for either seedling age. Furthermore, for the older seedlings there was no significant difference between survival in the shade and full sun habitats. Variation among plots was fairly modest (Figure 3–2).

Maximum mean annual height and diameter growth for both seedling ages occurred in the sun habitat during 1999–2001, when seedlings grew about 1 cm in diameter (at 20 cm stem height) and from 80–90 cm in height (Table 3–3). For each seedling age, absolute and relative height and diameter growth were significantly different in most habitat comparisons. The few exceptions occurred when growth in the edge habitat was

similar to growth in either the full sun or the shade habitat for a few growth intervals. In comparisons of seedling ages within each habitat, annual relative height growth was never significantly different for any growth period. During the 12 months after planting, younger seedlings grew relatively faster in diameter than older seedlings in the shade and edge habitats. In the second year after planting, younger seedlings' relative diameter growth was faster only in the shade. Annual relative diameter growth rates for the period 1997–2001 were significantly greater for younger seedlings than older seedlings in both the edge and sun habitats.

### **Discussion**

This experiment was motivated by the continuing decrease in the area of cativo-dominated swamp forests due to degradation from repeated entry logging. Planting cativo wildings in the understory of the forest provided a baseline for comparison of growth and survival with wildings planted in two habitats that might be considered when the restoration of degraded swamps is a land management objective. There is a tradeoff in terms of growth and survival and the labor requirements of site preparation and maintenance. Initial clearing of dense, extensive liana tangles by hand proved to be much more difficult than clearing areas in the edge habitat, and periodic cleaning was also much easier in the edge habitat because lianas did not resprout as vigorously there.

Cativo has often been described as shade tolerant (Linares Prieto 1987a, 1988, Tamayo Velez 1991) or as shade tolerant early in life but requiring high light levels for further development (Linares Prieto et al. 1997). Younger seedlings had much higher mortality in the shade of the forest understory than in the high light habitat, while older seedlings had similar mortality rates in these two habitats, suggesting that seedling establishment requires more than a single year.

Mortality rates observed in this study were generally higher than in a *cativo* reforestation experiment in Colombia that examined the effects of different types of planting techniques and timing of planting (Linares Prieto 1987a). That study occurred on abandoned agricultural soils while the study site in Darien is less suited for agriculture due to a slight brackishness in the soil and long hydroperiods (Tapia 1999).

Although mortality was highest in the shaded understory of the forest, seedling deaths were not solely attributable to shade or root competition. During periodic inundations, fallen branches float around and damage small *cativo* seedlings. Several planted seedlings in the understory were found bent over completely by coarse woody debris. Liana tangles in open habitats, in contrast, prevent this woody debris from moving. Another agent of mortality present in the forest but not likely in liana-infested areas was trampling by people, particularly hunters.

These findings add to the already highly variable published growth rates of *cativo* seedlings and saplings. Maximum mean annual height growth after four years in the present study was observed in the high light environment, where younger and older seedlings grew 48 and 54 cm yr<sup>-1</sup>, respectively. These growth rates are similar but predictably lower than those from a reforestation experiment in Colombia on less acidic soils and in high light, where Linares Prieto (1987) reported annual rates of height growth ranging from 67–76 cm yr<sup>-1</sup>. In that study, slow plantation height growth was attributed to a lack of suitable mycorrhizae, infertile soils, or poor plantation management. Still, plantation growth greatly exceeds seedling growth in natural forest. In natural *cativo*-dominated forest in Darien, Panama, a large population (~ 1300 trees) of natural regeneration, from newly germinated seedlings to small saplings 150 cm tall, revealed

essentially zero mean height growth for trees between 60 cm and 150 cm tall. Mean annual height growth of seedlings less than 30 cm tall was 15 cm yr<sup>-1</sup> and for seedlings between 30 and 60 cm tall mean annual height growth was 5 cm yr<sup>-1</sup> (Grauel 1999). Cativo's fastest height growth seems to occur after germination until seed reserves are exhausted (Tamayo Velez 1991).

In certain cases cativo may have the desirable socioeconomic and biophysical attributes that would make it the opportune choice for reforestation. Small landholders or cooperatives may have more reasons than just timber production for reforestation. During the course of this study the author was asked by a member of a small-scale loggers' cooperative about the feasibility of restoring degraded swamps by planting cativo. A comment was also made regarding the lack of wildlife in the increasingly extensive teak plantations in Panama, implying that native species attract wildlife. Cativo seeds are consumed by agoutis (*Dasyprocta aguti*) and its leaves by land crabs (possibly *Gecarcinus* spp), a species that also is harvested by local people.

Cativo is the principal raw material for the domestic plywood industry in Panama but is also used locally for furniture and construction; its value lies in its relative abundance and accessibility. Native timber species such as *Tabebuia rosea*, *Dalbergia retusa*, *Astronium graveolens*, and *Pachira quinata* are currently being planted on a commercial scale in Panama (Mariscal et al. 2002, Wishnie et al. 2002a, Wishnie et al. 2002b), but it remains to be seen if cativo can compete with other, more valuable hardwoods, both native and exotic, for planting on upland soils. This study demonstrates that cativo is particularly suited to reforesting severely degraded sites that are unsuited for agriculture due to flooding and that previously were in cativo.

Table 3–1. Mean canopy openness at 1.3 m above the ground as estimated with a spherical densiometer, arranged by seedling age and habitat.

| Seedling Age | Habitat | % Openness | Standard Deviation |
|--------------|---------|------------|--------------------|
| Younger      | shade   | 10.7       | 0.7                |
|              | edge    | 38.7       | 12.3               |
|              | sun     | 83.9       | 4.1                |
| Older        | shade   | 11.1       | 1.6                |
|              | edge    | 27.8       | 13.4               |
|              | sun     | 85.2       | 9.2                |

Table 3–2. Initial mean seedling height and diameter (at 20 cm above the ground; standard errors noted parenthetically). All differences between seedling ages are significant ( $p < 0.01$ ) based on t-tests.  $N = 4$  plots in blocks 2-4 and  $N = 3$  plots in block 1.

| Age   | Younger     | Older       | Younger       | Older      |
|-------|-------------|-------------|---------------|------------|
| Block | Height (cm) |             | Diameter (mm) |            |
| 1     | 41.4 (0.75) | 56.9 (1.56) | 2.7 (0.05)    | 5.6 (0.25) |
| 2     | 40.0 (0.82) | 55.1 (1.94) | 2.6 (0.08)    | 5.8 (0.41) |
| 3     | 43.3 (0.39) | 60.5 (2.60) | 2.7 (0.02)    | 5.9 (0.21) |
| 4     | 50.4 (2.73) | 65.8 (1.33) | 3.0 (0.19)    | 6.5 (0.45) |

Table 3–3. Mean annual growth rates. Units of absolute growth are millimeters for diameter and centimeters for height. Comparisons are among habitats within each seedling age for different time periods throughout the study. All comparisons are significantly different ( $P < 0.05$ ) except where noted, “a” indicates no difference between edge and sun, and “b” indicates no difference between edge and shade.

| Diameter Growth |         | Y e a r           |                    |           |                  |                   |          |           |                  |
|-----------------|---------|-------------------|--------------------|-----------|------------------|-------------------|----------|-----------|------------------|
|                 |         | 1997-1998         |                    | 1998-1999 |                  | 1999-2001         |          | 1997-2001 |                  |
| Seedling Age    | Habitat | Relative          | Absolute           | Relative  | Absolute         | Relative          | Absolute | Relative  | Absolute         |
|                 | Sun     | 1.27              | 4.0                | 1.11      | 8.0              | 0.62              | 9.6      | 2.44      | 7.5              |
| Younger         | Edge    | 0.83 <sup>a</sup> | 2.6 <sup>a,b</sup> | 0.54      | 3.0 <sup>b</sup> | 0.28 <sup>b</sup> | 3.1      | 1.03      | 3.3 <sup>b</sup> |
|                 | Shade   | 0.27              | 0.7                | 0.14      | 0.6              | 0.04              | 0.1      | 0.05      | 0.2              |
|                 | Sun     | 0.54              | 3.5                | 0.98      | 9.7              | 0.51              | 10.4     | 1.30      | 8.3              |
| Older           | Edge    | 0.33              | 1.9                | 0.46      | 3.7 <sup>b</sup> | 0.24              | 3.2      | 0.53      | 3.1              |
|                 | Shade   | 0.02              | 0.1                | 0.04      | 0.2              | 0.05              | 0.3      | 0.05      | 0.3              |

| Height Growth |         | Y e a r           |                    |           |          |                   |                   |                   |                   |
|---------------|---------|-------------------|--------------------|-----------|----------|-------------------|-------------------|-------------------|-------------------|
|               |         | 1997-1998         |                    | 1998-1999 |          | 1999-2001         |                   | 1997-2001         |                   |
| Seedling Age  | Habitat | Relative          | Absolute           | Relative  | Absolute | Relative          | Absolute          | Relative          | Absolute          |
|               | Sun     | 0.36              | 18.2               | 0.45      | 31.4     | 0.80              | 79.7              | 0.99              | 48.4              |
| Younger       | Edge    | 0.15 <sup>b</sup> | 7.3 <sup>a,b</sup> | 0.18      | 11.6     | 0.27 <sup>b</sup> | 22.0 <sup>b</sup> | 0.32 <sup>b</sup> | 16.0 <sup>b</sup> |
|               | Shade   | -0.01             | -0.6               | -0.10     | -5.5     | 0.04              | 1.8               | 0.02              | 0.8               |
|               | Sun     | 0.25              | 15.8               | 0.48      | 39.4     | 0.74              | 87.2              | 0.87              | 54.0              |
| Older         | Edge    | 0.09 <sup>b</sup> | 4.9                | 0.25      | 17.4     | 0.23              | 22.5 <sup>b</sup> | 0.26              | 16.1              |
|               | Shade   | -0.03             | -2.2               | 0.01      | 0.4      | -0.02             | -1.4              | -0.01             | -0.07             |

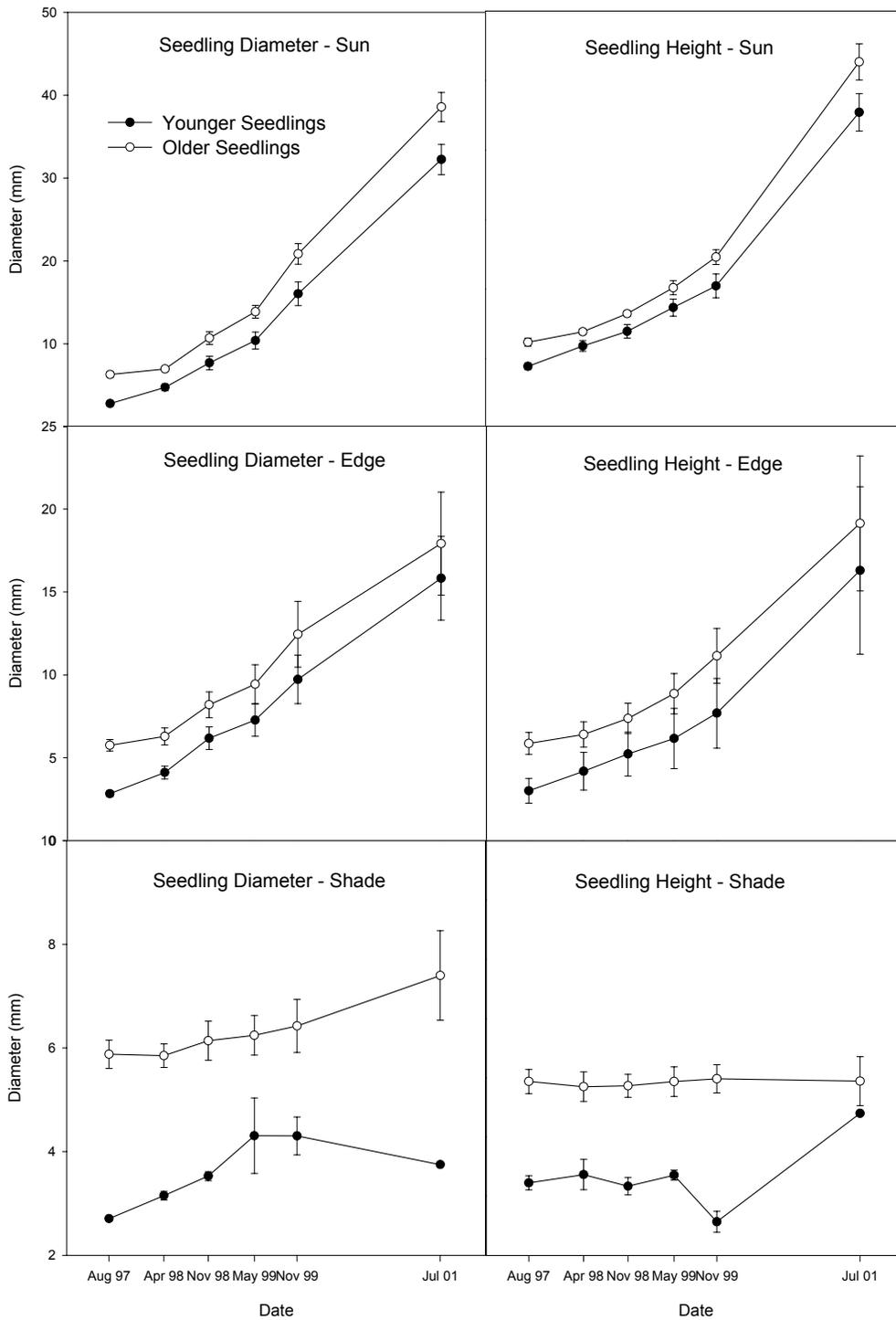


Figure 3–1. Mean diameters and heights ( $\pm 1$  SE) of planted *Prioria copaifera* (cativo) seedlings. Repeated measures analysis showed significant differences in size among habitats but not between seedling ages when initial size (at time of planting) was included as a covariate.

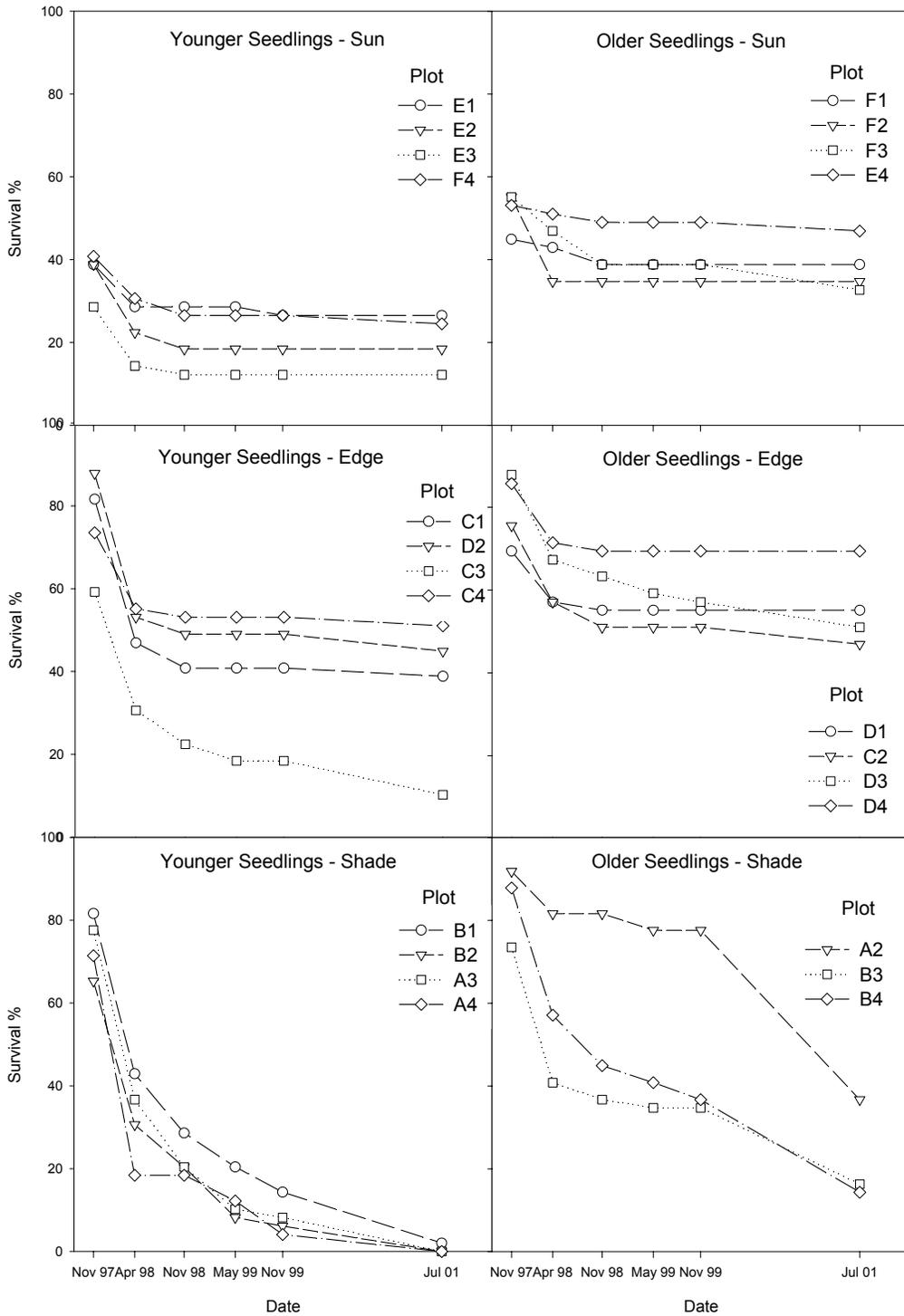


Figure 3-2. Percent seedling survival, beginning with the first census (November 1997) after planting (September 1997). Each point pertains to percent survival of the original 49 seedlings planted. Plot letters refer to pairs within habitats (A and B shade, C and D edge, E and F sun), plot numbers refer to blocks.

CHAPTER 4  
STRUCTURE, COMPOSITION, AND DYNAMICS OF *Prioria copaifera*-  
DOMINATED SWAMP FORESTS IN DARIEN, PANAMA

**Introduction**

Unplanned selective timber harvesting over time results in a pattern of chronic disturbance that strongly shapes forest structure and composition (Kittredge et al. 2003). Timber harvesting is a discrete event that, alone, does not necessarily lead to forest degradation. But where logging is poorly done or is too frequent, forests may become susceptible to fires and liana infestations (Nepstad et al. 1999, Pinard et al. 1999, Gerwing 2002). Given the unfortunate commonness of this disturbance regime, an understanding of forest stand development in response to chronic degradation is critical to the pursuit of sustainable forest management because the diverse values of forests depend largely on forest structure and species composition (Oliver and Larson 1996).

The disturbance history of a site substantially influences present day forest stand structure and productivity. Unfortunately, detailed site histories are usually unavailable and evidence of past disturbances may not be obvious. Given that stand structure alone is insufficient to indicate population trends in natural forests (Condit et al. 1998), understanding patterns of recovery in degraded forests requires demographic information as well. Without knowledge of how species, cohorts, and even individual trees respond to disturbances such as logging, predictions cannot be made regarding the likely responses of forest stands to further management interventions.

Neotropical swamp forests dominated by *Prioria copaifera*, a Caesalpinoid legume, were long ago noted for their theoretical ease of management due to their low diversity and the ability of this species to regenerate naturally (Barbour 1952, Holdridge 1964). These traits have apparently allowed *Prioria*-dominated forests to be especially resilient to repeated-entry logging. While potentially easy to manage, managers of *Prioria*-dominated forests suffer from a lack of demographic information. In more diverse forests where trees of most species are scarce, predictions are often based on small sample sizes, although recent innovations such as large plots (Condit et al. 1999) and landscape-scale sampling (Clark and Clark 1994, 1999) are addressing this limitation. But with few exceptions (but see Favrichon 1998, Finegan and Camacho 1999, Fredericksen and Mostacedo 2000), most information has been derived from unlogged forest preserves that bear little resemblance to the actual working forests where harvesting occurs. And rarely have studies of a particular forest type been replicated at different sites.

Although forest stand structure can reveal clues about disturbance regimes and past uses, simple size distributions of stems often obscure underlying dynamic processes. In particular, resprouting from snapped or partially uprooted trees can greatly influence demographic parameters such as growth, recruitment, and mortality. Although resprouting is increasingly recognized as an important component of forest dynamics, many forest dynamic models omit this mechanism of regeneration and consequently overestimate forest recovery rates (Paciorek et al. 2000).

Foresters typically focus on growth rates and on the adequacy of regeneration, overlooking the importance of mortality rates of target species in the development of management plans, often because they lack data. Although correlations have been made

between mortality and stand density (Lugo and Scatena 1996), light environment (Davies 2001), forest fragmentation (Mesquita et al. 1999), and climate (Condit et al. 1995b, Aiba and Kitayama 2002), the estimation of a given species' mortality rate is usually difficult due to small sample sizes and limited study periods. Although my study is based on only five annual censuses, I had the advantage of fairly large sample sizes that permitted examination of mortality by stem type (fallen, inclined, resprout from erect stem, stem sprout from prostrate or inclined stem) as well as evidence of growth-dependent mortality. Although growth-dependent mortality has been reported for temperate forests using growth estimates derived from tree rings (Kobe et al. 1995, Pacala et al. 1996, Kobe and Coates 1997, Wyckoff and Clark 2000, Caspersen and Kobe 2001, Lin et al. 2001, Bigler and Bugmann 2003, van Mantgem et al. 2003), a frequent lack of tree rings, inadequate sample sizes, and insufficient numbers of censuses have precluded investigations of growth-dependent mortality in tropical forests (but see Finegan and Camacho 1999 for a stand-level analysis).

Studying forests dominated by *Prioria copaifera* allowed collection of a large dataset for a single, commercially important species and its main associates. In this paper I describe the stand structure of five *P. copaifera* dominated forests in eastern Panama and report on stand dynamics of four of those five sites based on five years of monitoring data; I also supply tree growth data from an additional six sites. All trees were described on the basis of evident lean, breakage, and resprouting. Because *P. copaifera* sprouts from erect broken stems as well as from inclined and partially uprooted trees, I differentiate between these sprout types in presentations of data on growth, recruitment, and mortality rates.

Distributed from Nicaragua to Colombia and also found in Jamaica, *Prioria copaiifera* (hereafter “cativo”) was recognized as a potential source of commercial timber in the first half of the twentieth century (Kluge 1926, Schmieg 1927, Anonymous 1933). During and after WWII, interest in cativo wood increased (Harrar 1941, 1942a, b, Hess and Record 1950, Hess et al. 1950, Barbour 1952). Much of the cativo forest in Costa Rica was exploited to the point of current scarcity (Veiman 1982, Jiménez Madrigal 1995), while in the more remote parts of Panama and Colombia cativo forests were and continue to be subjected to silvicultural experimentation and intensive timber harvesting (Lamb 1953, Mayo Melendez 1965, Christiansen 1980, FAO 1982, INRENARE 1987, Linares Prieto 1988, FAO 1990, Alvarado Q. et al. 1996, CONIF 1997, Mariscal et al. 1999, Grauel and Pineda M. 2001). Although limited in extent, wetland forests dominated by cativo are valued as sources of timber because of their large commercial volumes (Golley et al. 1969, Grauel and Pineda M. 2001) and their ready accessibility by river.

### **Study Sites**

Permanent plots were installed in 1997 at four sites in three watersheds in Darien, Panama (Figure 4–1). Small populations of cativo trees at an additional six sites provided additional information about growth of this species under a range of inundation regimes. Eight of the ten sites were previously logged at various intensities and frequencies, most recently three years before this study began. Plots were also installed at a remote site near the Colombian border in Darien National Park where there was no evidence of cativo logging.

### Principal Sites

Casarete is located along the banks of the Balsas River ( $8^{\circ} 07' 11\text{--}14''$  N,  $77^{\circ} 52' 19\text{--}47''$  W), 19 km upriver from its confluence with the Tuira River and 48 km from the Tuira's mouth at the Gulf of San Miguel (Figure 4–1). Soils are heavy clays classified in the suborders Fluvent and Aquept, are acidic to slightly acidic (pH 5.2–6.5), poorly drained, and slightly brackish (electrical conductivity 5.0 mmhos/cm, Tapia 1999); mangrove forests are found only 7 km downriver. Rainfall measured at the study site in 1998 and 1999 was 2970 mm and 2758 mm, respectively. Mean annual rainfall at Camogantí, the nearest town, (8.5 km from the study site), is 2457 mm (República de Panama 1995). Because the forest owner values the area for hunting and aesthetics he protected it from logging for approximately 25 years (but did harvest a few large trees approximately ten years before the study).

The Sambu River site ( $8^{\circ} 03' 49''\text{--}04' 06''$  N,  $78^{\circ} 13' 16\text{--}33''$  W) at the mouth of the small Chunga River, is 17 km upstream from the Sambu's mouth at the Gulf of San Miguel. This site is approximately 4.5 km from Boca de Sabalo, also on the Sambu River, and 9.5 km from the Wounaan village of Taimati, on the coast of the Gulf of San Miguel, where mean annual precipitation is 1342 mm and 1592 mm, respectively (República de Panama 1995). Soils are similar in texture but slightly less acidic than Casarete (pH 5.7–6.8), and although it is nearer to the ocean, there was no evidence of salinity (Tapia 1999). The forest is located on open-access, public land and was repeatedly logged, the most recent entry three years before the study began.

Juanacati is 65 km from the mouth of the Tuira River near the town of El Real ( $8^{\circ} 04' 38\text{--}49''$  N,  $77^{\circ} 46' 37\text{--}48''$  W). Mean annual rainfall at El Real (5 km from the site) is 2096 mm (República de Panama 1995). Although Juanacati, like the previous riverine

sites, is flooded by monthly spring tides, no soil salinity is evident and soil pH is higher than the other sites (pH 6.2–6.3). There is no evidence of recent logging, but anecdotal evidence and the forest's proximity to El Real suggest that the site was repeatedly logged in the past. Indeed, L.R. Holdridge noted the presence of stumps only a few kilometers downriver from this site in 1962 (Holdridge 1964).

The fourth site is an inland location near a small intermittent stream called Naranzati ( $8^{\circ} - 02' 58'' - 4' 26''$  N,  $77^{\circ} - 55' 40'' - 58' 02''$  W), approximately 7 km west of the town of Camogantí. Unlike the three riverine study sites, this forest is flooded for the entire nine month wet season (April to December). Due to its inaccessibility, this site and other inland swamps were subject to logging only recently as riverine cativo forests became increasingly depleted of large trees.

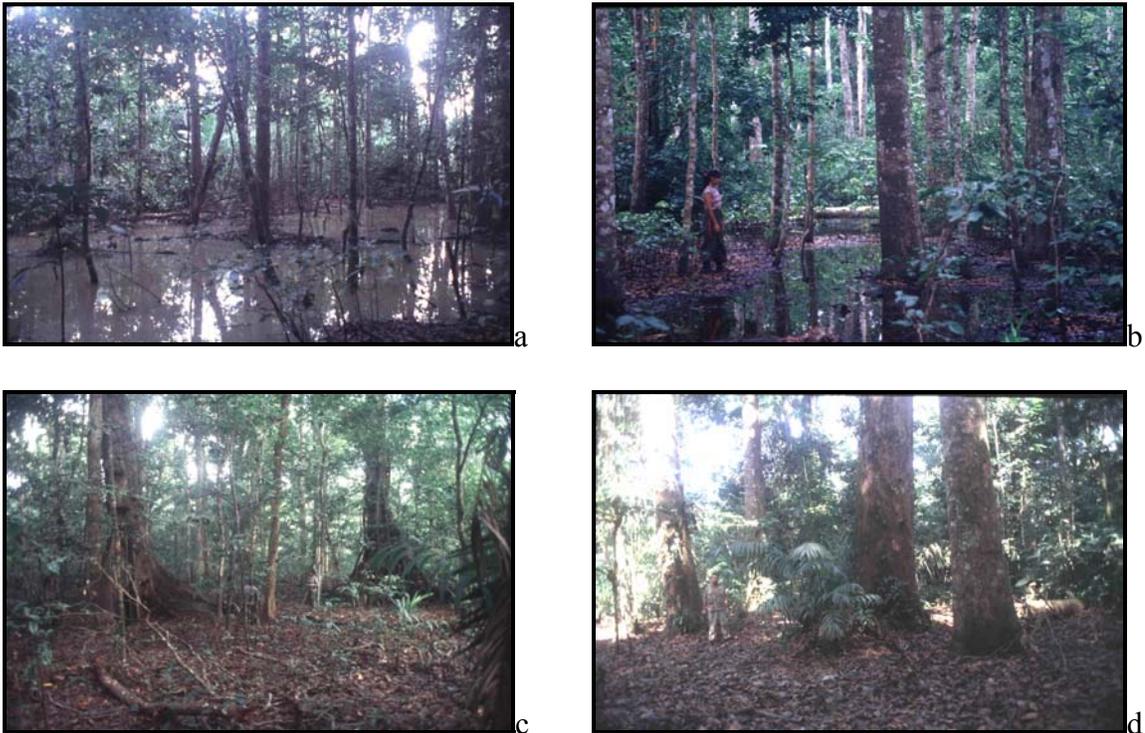


Figure 4–1. Principal study sites. a) Casarete, b) Sambu, c) Juanacati, and d) Naranzati.

## Secondary Sites

To compare cativo growth in different landscape positions and flooding regimes, I chose three sites adjacent to mangrove forests and subject to brackish water inundation. Bajo Grande (8° 22' 23" N, 78° 09' 24–31" W) is an area near La Palma on the coast of the Gulf of San Miguel; the study site is a few hundred meters inland from the coast, behind the coastal *Rhizophora mangle* forests. The other two tidal sites are slightly upriver from the transition zone of red mangrove to cativo forest, one along the Tuirá River (8° 10' 13–33" N, 77° 50' 18–23" W) and the other along the Balsas River (8° 09' 03–17" N, 77° 53' 04–10" W). All three tidal sites are monodominant, uneven-aged cativo stands.

Additionally, I chose three sites that are unaffected by brackish water for monitoring cativo growth. Two of these freshwater sites are along the Balsas River, between the principal Balsas River site (Casarete) and the community of Camogantí (Bongales: 8° 05' 30" N, 77° 51' 35" W and Limón: 8° 04' 13" N, 77° 53' 16" W). Although these sites are occasionally inundated by high tides, the floodwaters are comprised of freshwater tidal backup and are not brackish. The final freshwater site is an inland swamp far up the Amarradero River, a small tributary of the Balsas River (8° 00' 48–55" N, 77° 49' 38–41" W). All six secondary sites, except possibly the latter inland swamp, were subjected to intermittent logging during the last decades of the 20<sup>th</sup> Century. A seventh site is found near the headwaters of the Balsas River inside Darien National Park near the Colombian border (7° 34' 23"–35' 32" N, 77° 47' 02–11" W), 130 km upriver from the mouth of the Tuirá River. This site was probably never logged for cativo due to its remoteness, a condition that limited my access to a single visit.

## Methods

### Plot Descriptions

Because of the low tree species diversity of cativo-dominated forests, I was able to use small plots and still gather sufficient demographic information for cativo and several common associates. To capture landscape heterogeneity, and because some cativo forests are limited to narrow bands along rivers, many small plots were installed at each site instead of single large plots. Casarete has five 40 x 40 m and five 20 x 20 m plots, Sambu has five 40 x 40 m plots, and at Naranzati there are five 40 x 40 m and three 40 x 20 m plots. At Juanacati, all trees  $\geq 4$  cm dbh were measured in six 50 x 50 m plots. At the other three sites, all trees  $\geq 10$  cm dbh were measured in all plots and trees  $\geq 1$  cm dbh were measured in a randomly chosen 20 x 20 m quadrant of each plot, or in the entire plot if it was 20 x 20 m (Table 4-1).

Most plots were installed in early to mid-1997, but the work was interrupted at Naranzati and Juanacati and was completed in early 1998. All trees were tagged and mapped at the time of plot installation and all plots were subdivided into 5 x 5 m subplots to facilitate mapping. Trees  $\geq 7$  cm dbh were measured with a diameter tape to the nearest millimeter while smaller trees were measured with calipers, with two perpendicular measurements being averaged.

### Sampling and Analyses

To increase the sample size for large cativo trees, additional trees outside the permanent plots were tagged and measured at Casarete and Naranzati. This approach was not feasible at Juanacati and Sambu due to the overall scarcity of large cativo trees.

Three of the eight plots at Naranzati were mistakenly logged two months before the 1999 census. Analyses after that time were done using data from only the unlogged plots.

In late 1997 and early 1998 all cativo stems  $< 1$  cm dbh in 80 randomly chosen 5 x 5 m subplots within the larger plots at Casarete and 28 subplots at Sambu were tagged, mapped, and measured (height); dbh was also measured for those saplings  $> 1.5$  m tall. These two populations of seedlings as well as new cativo recruits at these sites were tagged, measured, and mapped approximately every two months for two years and marked seedlings were measured annually.

The permanent plots were censused annually until 2001, except the Naranzati site which was last censused in 2000. At the secondary sites trees  $\geq 20$  cm dbh were measured in 1997, 1998, and 1999, except the Amarradero site, which was logged after the 1998 census. Inter-census intervals were always nearly annual to minimize seasonal effects on growth.

Methods of censusing and measuring trees as well as the approach to data checking generally followed Condit (1998). During each census, in addition to recording each tree's status (alive, dead, recruit), diameter (trees  $\geq 1$  cm dbh), and height (trees  $< 1$  cm dbh), codes were assigned to denote if a stem was prostrate, inclined  $> 45^\circ$  from vertical but not lying on the ground, broken above or below the point of measurement (POM), resprouting from a broken stem, or sprouting from a prostrate or inclined stem. I report the incidences of these stem types, but for growth analyses I exclude fallen stems and combine erect and inclined stems. I refer to stems that show evidence of previous breakage and subsequent resprouting as broken stems. Although I separately coded trees

that had broken depending on if the break was above or below the POM, in this paper I combine the two because there were only a few cases where a substantial recorded loss in diameter was the result of stem breakage and subsequent resprouting. Living fallen stems were measured if possible but were always tagged and mapped because they served as hosts for vertical sprouts. References to prostrate stems refer to uprooted, not snapped, stems. I measured all vertical sprouts from prostrate stems and from inclined stems if they emerged from  $< 1.3$  m from the ground.

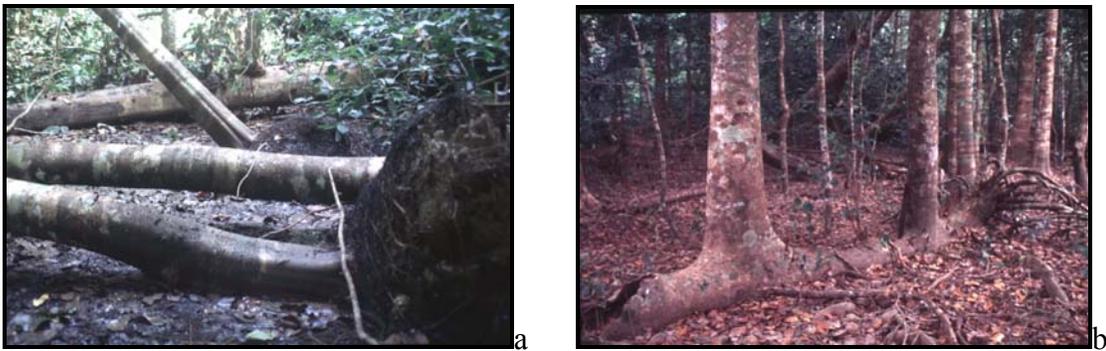


Figure 4–2. Stem types: a) prostrate and inclined and b) vertical sprouts from a fallen stem.

Two professional foresters performed all the  $\sim 22,000$  dbh measurements in the permanent plots. One forester measured trees only in 1997 and 1998, while the other (the author) measured half the trees in 1997 and 1998 and all trees from 1999-2001, overall measuring 80% of the trees in the study. I was also responsible for all error checking and database management.

All data were independently entered into a computerized database by two different people immediately upon return from the field. Any discrepancies between the dbh measurements that could not be corrected in the office were noted, and follow-up field trips a few weeks after the principal census were carried out to remeasure trees or confirm codes.

Within sites, I first examined variability among plots of each year's annual cativo growth of erect, broken, and vertical sprouts with ANOVA and Tukey post-hoc tests. Data were natural log-transformed if variances were substantially unequal. For these comparisons, the longest annual growth record available was used. Of 3065 cativo trees in the four principal sites, 80% of the annual growth records were for the period 1997–2001, 14% were for 1998–2001, and 6% were for 1997–2000. For cativo, growth was then compared among normal stems, broken stems, and sprouts from inclined/prostrate stems within five diameter classes using ANOVA and Bonferroni post-hoc tests. To explore inter-annual growth of cativo I used five diameter classes and I combined all stem types but excluded those that were prostrate on the ground. I also report annual diameter growth of cativo's three principal arboreal associates.

I report annual recruitment and mortality rates for cativo at the four principal sites using four diameter classes for trees  $\geq 1$  cm dbh and five height classes for smaller trees at the two sites where cativo regeneration was studied. In each census I used the totals of stems from the previous census, that is, I do not calculate demographic parameters using only the originally-tagged 1997 population (see Sheil and May 1996). The monitored large trees outside the plots at Casarete and Naranzati were included in calculations of mortality rates. Furthermore, in the few cases where trees were not found in a particular year's census, those trees were subtracted from the previous year's total number of trees to exclude them from calculations of recruitment rates, instead of assuming the trees had died.

I evaluated the extent to which cativo mortality varied with recent growth rates. With five censuses at most sites, I was able to compare annual growth for a maximum of

three years between trees that were alive at the end of the study and those that died during the study. I used two size classes ( $< 10$  and  $\geq 10$  cm dbh) and performed one-tailed  $t$ -tests on populations with at least five dead stems to test the hypothesis that slower growing trees suffered a higher probability of mortality.

I report species diversity using Fisher's alpha and the Shannon-Weiner (S-W) index in two ways, first with only all stems  $\geq 4$  cm dbh so that all four sites can be compared. Then I also calculated the S-W index for the three sites with minimum dbh of 1 cm. Voucher specimens were collected from the four principal sites in 2000; unidentified species were not separated into morphospecies; I noted the number of unidentified species at each site and considered all unknown trees as a single species in the diversity calculations.

## Results

### Tree Species Diversity and Stand Structure

Although cativo dominated all four principal sites, species diversity varied substantially. The riverine sites on the Sambu and Balsas (Casarete site) Rivers showed the greatest cativo dominance, with cativo comprising 95 and 96% of the stems of all size classes, respectively (Table 4-2). Diversity indices grouped the four sites into pairs, with Casarete and Sambu being strongly monodominant and Juanacati and Naranzati being relatively more diverse. Only seven tree species were tallied at each of the former two sites, while 48 and 54 species were identified at Juanacati and Naranzati, respectively. For trees  $\geq 10$  cm dbh at the five sites with plots, cativo comprised from 46-96% of the stems and from 33-96% of the basal area (Table 4-3). *Pterocarpus officinalis* was cativo's principal associate common to all four sites, making up 2-10% of the stems. Other common overstory trees at Juanacati were *Pentaclethra macroloba* (10.2%),

*Carapa guianensis* (7.2%), *Licania platypus* (3.3%), and *Mora oleifera* (1.3%). At the Naranzati inland swamp, cativo tended to dominate the overstory with *P. officinalis* and *P. macroloba*, but understory associates included *Andira inermis* (1.3%), *Eschweilera integrifolia* (4.7%), *Gustavia nana* (2.0%), and *Brownea rosa-de-monte* (2.5%). The palms *Oenocarpus mapora* and *Astrocaryum standlyanum* were common understory species at the two more diverse sites as well, comprising 2–8% of the stems.

Stand density and basal area varied considerably among sites (Table 4–3). Stand density of trees  $\geq 10$  cm dbh ranged from 328 trees/ha (Darién NP) to 757 trees/ha (Casarete). Stand basal area varied less markedly, but most cativo basal area was represented by trees  $\geq 60$  cm dbh at the inland swamp (Naranzati) and in Darién NP, and by stems 10–60 cm dbh in the riverine forests.

Cativo made up  $\sim 95\%$  of stand basal area at the riverine Sambu and Casarete sites and  $\sim 83\%$  at the inland Naranzati swamp (Table 4–3). The Juanacati site was visually dominated by 14 huge, emergent *Mora oleifera* trees per hectare that made up 21% of stand basal area, the same percentage as *Pterocarpus officinalis*, while cativo comprised 33% of basal area and *Pentaclethra macroloba* 14%.

For all species, substantially more large prostrate and severely inclined trees were found at the three riverine sites than at the inland swamp or the remote Darién NP site. No prostrate, living trees were noted at either Naranzati or Darién NP. In contrast, large prostrate stems were fairly common at the three riverine sites, where 1–5% of live stems  $\geq 10$  cm dbh were on the ground (Table 4–4). Large inclined stems were also more prevalent in the riverine forests, where 4–8% of all stems were partially uprooted and leaning  $> 45^\circ$ .

The rates at which trees partially uprooted and fell to the ground or leaned  $> 45^\circ$  were generally higher at all sites for trees  $\geq 10$  cm dbh than for smaller trees (Table 4–5). Consistent with the proportion of live fallen and inclined stems recorded at the beginning of the study, rates of falling and inclination were higher at the riverine sites than the inland swamp, but rates varied greatly among years within sites.

At the time of plot installation a modest proportion of stems showed signs of previous stem breakage at most sites. Where trees  $< 10$  cm dbh were measured, between 6–11% were broken, and approximately 3–6% of large stems had suffered but recovered from stem breakage. No broken and resprouted stems were noted in the plots at Darien NP.

Sprouts from prostrate and inclined stems were much more prevalent in the riverine forests than inland swamps. Less than 2% of small stems ( $< 10$  cm dbh) at the inland Naranzati swamp consisted of these sprouts, and no larger sprouts were found. In contrast, 6–17% of smaller stems were sprouts at the riverine sites. Among the riverine sites, Casarete stood out by having more large than small stems classified as sprouts, where 12% of all stems  $\geq 10$  cm dbh were sprouts from prostrate or inclined parent trees. The 23.5 m long stem of a 33 cm dbh cativo that partially uprooted and fell to the ground at Casarete between the 1999 and 2000 censuses produced 175 vertical sprouts  $\geq 1.5$  m tall by the 2001 census. Fifteen of these shoots were inside the plot (within 5.7 m from the root system of the parent tree) and were tallied as recruits in 2001, with mean and maximum diameters of 1.7 and 3.2 cm dbh, respectively.

### **Cativo Growth, Mortality, and Recruitment**

Relative rates of cativo growth of three stem types (undamaged, broken/resprouting, or sprouting from inclined and prostrate trunks) are unique to each

site. Sprouts grew faster than either undamaged or broken stems at Casarete for stems <40 cm dbh, while at Sambu the smallest sprouts grew slower than undamaged stems and only sprouts 4–10 cm dbh from inclined or prostrate stems grew faster than undamaged stems of the same size. Undamaged stems grew faster than broken stems at Juanacati but growth rates of normal stems and sprouts from prostrate/inclined trunks were similar (Table 4–6).

Cativo annual diameter growth varied considerably among both sites and years, but a few patterns were apparent. Growth was slowest, with some exceptions, during the El Niño year of 1997–1998 and fastest for the following census period (1998–1999). For trees < 10 cm dbh, the Casarete and Naranzati sites were both characterized by very slow growth rates, while stems of this size class grew significantly faster in almost all years at Sambu and Juanacati (Table 4–7). Mean diameter growth rates within the larger size classes ( $\geq 10$  cm dbh) varied notably among the 9 sites (10 sites for 1997), ranging from only 0.5 mm to > 8 mm per year.

Sprouts from prostrate or inclined stems made up a significant portion of forest-wide recruitment in many cases (Table 4–8). About 50% of saplings entering the 1 cm dbh size class at Casarete were sprouts of this type. Also at Casarete, these sprouts consistently comprised substantial portions of the recruitment into the 10 cm dbh size class.

Recruitment and mortality rates for cativo show similar inter-site patterns to those observed for growth. Mortality equaled or exceeded recruitment at Casarete and Naranzati for trees <10 cm dbh in the first two years of the study (Table 4–9). In general,

recruitment of *cativo* at Sambu and Juanacati greatly surpassed mortality for all size classes and years.

Mortality rates of different *cativo* stem types varied among sites, but in general, sprouts from prostrate/inclined trunks and undamaged stems showed the highest mortality rates at Casarete and Sambu (Table 4–10). No sprouts from prostrate/inclined trunks died at either Juanacati or Naranzati; at these two sites either broken or prostrate stems had mortality rates that approached or occasionally exceeded those observed for undamaged stems.

### **Growth of other Tree Species**

*Pterocarpus officinalis* was the fastest growing tree species at all four sites, with mean annual diameter growth of 9–11 mm for trees  $\geq 10$  cm dbh in three of the four forests (Figure 4–2b). The other two most common associates of *cativo*, *Carapa guianensis* and *Pentaclethra macroloba*, had mean annual growth of large trees  $\geq 10$  cm dbh that approached 5 mm at the two more diverse sites where they were found.

### **Growth–dependent Mortality of *Cativo* Trees**

Surviving trees grew significantly faster ( $p \leq 0.05$ ) than trees that died for nine of ten t–test comparisons (Table 4–11). The non–significant case revealed significance when the size class was further divided. For 1997–1998 growth, survivors at Casarete  $<10$  cm dbh grew equally slowly as those trees that subsequently died, but when these smaller trees were analyzed as two size classes, surviving trees between 1–4 cm dbh grew significantly faster than those trees that died (mean 0.1 vs.  $-0.1$  mm,  $df = 90$ ,  $t = 3.1$ ,  $p = 0.002$ ), while trees 4–10 cm dbh in both groups had essentially zero growth.

### **Cativo Regeneration**

Regeneration was much more abundant at the more recently logged Sambu River site than at Casarete (Table 4–12). Small seedlings (< 30 cm tall) were not abundant at either site, suggesting that they grow rapidly after germination. Seedlings 30–60 cm tall were most abundant at Casarete, while at Sambu seedlings 60–90 cm tall were the most common. Due to a large seedfall in April and May 1999, annual cativo seedling recruitment rates based on the period November 1998 – November 1999 for Casarete and Sambu were 136.6% and 29.1%, respectively. Annual mortality for the same period was similarly high for seedlings < 30 cm tall but differed substantially for taller trees between the two sites (Table 4–13). Mean annual height growth was generally < 5 cm at each site (Table 4–14). Exceptions were the relatively small number of seedlings < 30 cm tall at both sites and saplings > 90 cm tall at Sambu, both of which grew rapidly.

### **Discussion**

Forests dominated by cativo in Darien, Panama vary substantially in structure, species composition, and stand dynamics. Flooding regimes and management histories appear to be the main determinants of present-day structure and dynamics. Slight soil salinity, in particular, seems to favor cativo dominance (Mayo Melendez 1965). Cativo forests near mangrove forests exhibit almost total dominance by cativo, whereas inland swamps and riverine forests that escape tidal flooding with brackish water contain relatively high tree species diversity.

Cativo dominance can probably be attributed to a variety of mechanisms. Flood tolerance alone is an insufficient explanation because other flood tolerant species are generally rare in cativo forests (Lopez and Kursar 1999). Cativo's root system dies back to a much lesser extent than other flood tolerant species and gives the species competitive

advantage in seasonally flooded forests that are subject to short but severe annual droughts (Lopez 2002). High leaf area index, as shown by Holdridge (1964), may modify the understory environment to be more favorable for cativo seedling survival than for other species. Such a modification was attributed to *Gilbertiodendron dewevrei*, a tropical tree species that forms monodominant stands in West Africa. Although the crab species common to riverine cativo forests have not been studied in Darien, the land crab *Gecarcinus quadratus* was shown to affect species diversity in a coastal Costa Rican forest by selective seedling consumption (Sherman 2002).

The degree of cativo dominance varies widely in Panama. Cativo is a locally common species in the 50 ha forest dynamics plot on Barro Colorado Island, with a mean of 27–29 trees  $\text{ha}^{-1} \geq 1$  cm dbh and a maximum of 223 (Condit et al. 1993b). The three sites in Darien for which I have comparable data have densities of cativo 5–15 times greater than on BCI. Similar to cativo swamps in Darien, the relative basal area dominance of cativo in Colombia is 50–92% (Escobar and Vasquez 1987). Anecdotal evidence suggests that *Carapa guianensis*, a species that produces wood of a similar quality as mahogany, was probably much more common in the past in some cativo forests and L.R. Holdridge (1964) identified *C. guianensis* as cativo's sole associate in a 1962 transect very near the Juanacati site on the Tuira River.

The histories of timber harvesting of these forests undoubtedly influence present day stand structure and dynamics, but details on logging frequencies and intensities are largely unknown. It is likely that all the riverine forests were repeatedly logged since the 1950s (República de Panamá 1978). Although I characterized the inland swamps and the

Darien NP site as intact forests, it is possible that even these remote forests were logged for mahogany several decades ago.

Stand structure analyses of cativo forests reveal high timber volumes or at least the potential for high volume production. The forest at Darien NP stands apart from all other sites with the lowest density of stems but the largest stand basal area. The other sites (except Juanacati) contain higher basal areas than most other tropical forests (Leigh 1999). This is notable because the riverine cativo forests of Darien were identified for their timber potential in the 1950s (Lamb 1953) and L.R. Holdridge noted stumps from harvesting activities in the early 1960s near the Juanacati site (Holdridge 1964). The history of logging is undoubtedly responsible for the paucity of trees  $\geq 60$  cm dbh (the legal cutting limit), but these riverine forests still contain a similar number of stems  $\geq 10$  cm dbh as most other lowland tropical forests (Leigh 1999).

High stem density at Casarete may be a result of the site's management history. Having been protected by its owner from the repeated logging that typically occurs on open access state land, this forest may have passed through a period of enhanced recruitment after the first wave(s) of logging in the 1950s and 1960s. Increased recruitment and growth of undamaged residual trees after logging is a well-documented phenomenon (e.g. Magnusson et al. 1999, Parrotta et al. 2002). The Casarete forest 40 years ago may have been similar to the present-day Sambu forest that was recently logged and exhibits high seedling and sapling densities, fast sapling growth, and low sapling mortality.

Sprouting is a well-recognized regeneration strategy in tropical forest (Putz and Brokaw 1989, Rijks et al. 1998, Gavin and Peart 1999, Kammesheidt 1999, Negreros-

Castillo and Hall 2000, Yamada et al. 2001) but sprout density varies from being common (Paciorek et al. 2000) to absent in mature forests (Kammesheidt 1998). Vegetative sprouts from various sources may be the principal colonizers of gaps (Putz and Brokaw 1989, Negrelle 1995), but mortality rates of resprouted broken stems are generally higher than non-sprouts (Guariguata 1998, Paciorek et al. 2000, Ickes et al. 2003). In cativo dominated forests it is important to distinguish between resprouts originating from erect, broken trees and those that emerge from fallen and inclined trees. Sprouts from fallen or inclined trunks are frequently much more common, often grow more rapidly than trees originating from seed but have the highest mortality rates of any stem type, including trees that have uprooted and are lying on the ground.

The tree recruitment assemblage in newly formed treefall gaps in cativo forests may not be dominated by true seedlings. In some cativo forests the principal gap colonists were not newly germinated seedlings or established shade tolerant saplings; instead, regeneration was dominated by sprouts from inclined or prostrate stems. For example, at least half the recruitment of 1 cm dbh stems every year at Casarete was comprised of sprouts from fallen stems, which also grew faster than their conventionally rooted counterparts. Sprouts from prostrate stems develop their own root systems composed of roots that emerge from the bottom of the parent stem. At Casarete, these sprouts continued their superior growth rates at least into the subcanopy after which it was difficult to determine their mode of regeneration.

The three riverine sites share a somewhat similar history of logging as well as a higher proportion of live prostrate and inclined trees than the inland swamps that have not been logged. Logging and inclined or prostrate trees may not necessarily be related,

however. Riverine cativo forests were characterized by a large number of fallen trees at about the time that widespread commercial logging was beginning in Darien (Duke 1964, Holdridge 1964), but recent logging has been sporadic due to scarcity of commercial-sized trees. Cativo sawnwood and plywood production during the late 1990s was only a quarter of its peak in the late 1960s (Romero M. et al. 1999). I conclude that fallen and inclined cativo trees may be a common feature of riverine forests due to their shallow root systems and saturated soils, with logging being a lesser factor.

Growth rates of the various stem types at different sites may vary with forest structure but may also be limited by different factors depending on stem type. Although sprouts from inclined/prostrate trunks at Sambu and Casarete grew at similar rates, undamaged stems and broken stems at Sambu grew four to five times faster than their counterparts at Casarete, presumably because the recent logging at Sambu left a more open canopy.

Growth of all cativo stem types increased with increasing distance from tidal influences but decreased with increasing hydroperiods. In general, cativo trees in the inland swamps that are flooded continuously during the rainy season grew more slowly than in the riverine forests, and the riverine sites further upriver (Juanacati, Bongales, Limón) showed faster mean cativo growth than downriver sites.

Diameter increment of canopy trees varied by site and year, but the patterns of variability differed among sites. Canopy tree growth at Casarete varied up to 2-fold, with 1997 as the slowest growing year. At the other three principal sites, canopy tree growth varied less, and the census period that spanned the 1997–1998 El Niño was not always the slowest growing year. These findings stand in contrast to the strong reductions in tree

growth in Costa Rica during the 1997–1998 El Niño, which were negatively correlated with daily minimum temperatures (Clark et al. 2003).

The fastest growing tree species in my sample plots was *Pterocarpus officinalis*, which is not considered a timber tree. Cativo's two other most common associates, *Carapa guianensis* and *Pentaclethra macroloba*, are harvested in both Panama and Costa Rica (Webb 1997, Siteo et al. 1999). *C. guianensis* in particular is valued by Darien loggers, while *P. macroloba* produces less valuable wood. *C. guianensis* is more abundant in riverine forests flooded only with freshwater, and has moderate growth rates and relatively high densities in some Darien cativo forests. This species may have been locally extirpated in some riverine forests but could be reintroduced by seed scattering as was recommended by Webb (1997) for logging gaps in swamp forest in Costa Rica.

In the absence of spatially–explicit data that allow for the development of competition indices and the construction of distance–dependent forest dynamic models, higher survival of faster growing trees (growth–dependent mortality) should be taken into account when projecting growth trajectories. When mean growth of a large population of small trees is low, modeling lifetime growth based on mean growth may result in unrealistically long trajectories (Grauel and Kursar 1999), especially if a large proportion of slow growing trees die before reaching commercial size.

I noted heavy seedfall during plot installation in April 1997, but the regeneration study began in September 1997 at one site and May 1998 at the other, so I measured recruitment in 1998–2000 at one site and 1999–2000 at the other. Although cativo produces some seeds twice a year, large seedfalls seem to occur once every two years

(Pizano SA 1995), and I also measured a large pulse of seedling recruitment from July to November 1999, two years after the large observed seedfall in April–May 1997.

When stand structures and dynamics vary so markedly among forests, it seems inadvisable to extrapolate results widely. Witness the difference in cativo dynamics between these Darien cativo forests and the population of cativo on Barro Colorado Island. With much lower mortality rates and generally higher mean and maximum growth rates for cativo on BCI, use of their data for management tasks such as timber harvest scheduling or yield projections would justify over-harvesting of most Darien cativo forests. Mortality, more than growth, was shown to be a pivotal factor in the simulated sustainability of cativo harvest potential based on BCI data (Condit et al. 1995a), but annual mortality rates of Darien cativo forests varied greatly and were sometimes much higher than on BCI.

A critical aspect for understanding present day forest structure and dynamics is the history of use that has resulted in what are now degraded forests. Increasingly, these degraded forests will be a source for wood and non-wood products as the area of intact, mature tropical forest declines. For example, the forest most recently logged in this study (Sambu) is one of the most dynamic and resilient, with relatively high growth and recruitment rates, low mortality, and sufficient densities of advance regeneration to theoretically provide additional timber harvests. Forest history, although it may only be inferred, can yield insights into today's forest and perhaps help to guide management direction.

This study highlights the importance of examining stand development patterns at a variety of sites, even when a single “forest type” is identified based on species

composition and landscape position. Only where variability is recognized can it be considered when making forest management decisions. Anthropogenic disturbance may have been the primary factor in shaping the structure and function of many cativo-dominated forests in Darien, but the persistence of these forests after decades of harvesting attests to their resilience and should serve as inducement for better management.

Table 4–1. Total plot area measured for different minimum tree diameters and number of tree species found.

| Site      | Plot Area (ha) |       |        | Number of Tree Species |       |        | % unidentified |
|-----------|----------------|-------|--------|------------------------|-------|--------|----------------|
|           | ≥1 cm          | ≥4 cm | ≥10 cm | ≥1 cm                  | ≥4 cm | ≥10 cm |                |
| Casarete  | 0.4            | 0.4   | 1.0    | 8                      | 7     | 6      | < 0.1          |
| Sambu     | 0.2            | 0.2   | 0.8    | 7                      | 5     | 5      | 0.0            |
| Juanacati | —              | 1.5   | 1.5    |                        | 48    | 24     | 0.4            |
| Naranzati | 0.32           | 0.32  | 0.96   | 54                     | 42    | 28     | 1.5            |

Table 4–2. Species diversity indices and relative dominance of cativo (*Prioria copaifera*).

| DBH ≥ 1cm |                   |      |          |         |                  |
|-----------|-------------------|------|----------|---------|------------------|
| Site      | Fisher's $\alpha$ | S–W  | Evenness | Simpson | Cativo dominance |
| Casarete  | 1.10              | 0.20 | 0.09     | 0.93    | 0.96             |
| Sambu     | 1.00              | 0.22 | 0.11     | 0.91    | 0.95             |
| Naranzati | 12.37             | 2.10 | 0.53     | 0.32    | 0.55             |
| DBH ≥ 4cm |                   |      |          |         |                  |
| Site      | Fisher's $\alpha$ | S–W  | Evenness | Simpson | Cativo dominance |
| Casarete  | 1.01              | 0.22 | 0.10     | 0.92    | 0.96             |
| Sambu     | 0.76              | 0.28 | 0.16     | 0.87    | 0.93             |
| Juanacati | 9.52              | 2.09 | 0.54     | 0.25    | 0.47             |
| Naranzati | 7.19              | 1.81 | 0.52     | 0.36    | 0.59             |

Table 4–3. Stem density and basal area of all species (above) and cativo only (below).

| Site      | Stems/ha           | Stems/ha           | Stems/ha           | BA/ha (m <sup>2</sup> )           |                    |                                   |
|-----------|--------------------|--------------------|--------------------|-----------------------------------|--------------------|-----------------------------------|
|           | 1–4 cm             | 4–10 cm            | ≥10 cm             | ≥10 cm                            |                    |                                   |
| Casarete  | 1460               | 705                | 757                | 43.3                              |                    |                                   |
| Sambu     | 2095               | 785                | 484                | 48.9                              |                    |                                   |
| Juanacati | —                  | 500                | 426                | 31.4                              |                    |                                   |
| Naranzati | 1675               | 1057               | 339                | 47.1                              |                    |                                   |
| Darien NP | —                  | —                  | 328                | 71.1                              |                    |                                   |
|           | Cativo<br>Stems/ha | Cativo<br>Stems/ha | Cativo<br>Stems/ha | Cativo<br>BA/ha (m <sup>2</sup> ) | Cativo<br>Stems/ha | Cativo<br>BA/ha (m <sup>2</sup> ) |
|           | 1–4 cm             | 4–10 cm            | ≥10 cm             | ≥10 cm                            | ≥60 cm             | ≥60 cm                            |
| Casarete  | 1415               | 668                | 727                | 41.5                              | 8                  | 2.5                               |
| Sambu     | 2030               | 690                | 463                | 39.9                              | 12                 | 4.4                               |
| Juanacati | —                  | 229                | 195                | 10.3                              | 3                  | 0.9                               |
| Naranzati | 732                | 457                | 240                | 39.3                              | 51                 | 29.2                              |
| Darien NP | —                  | —                  | 160                | 48.8                              | 58                 | 45.4                              |

Table 4–4. Incidence (%) of prostrate, inclined, broken stems and sprouts from prostrate trunks. Other stems showed no signs of earlier breakage and presumably regenerated from seed.

| Site      | Prostrate Stems |           | Inclined Stems |           | Broken Stems |           | Sprouts from<br>Inclined or<br>Prostrate Stems |           |
|-----------|-----------------|-----------|----------------|-----------|--------------|-----------|------------------------------------------------|-----------|
|           | <10<br>cm       | ≥10<br>cm | <10 cm         | ≥10<br>cm | <10 cm       | ≥10<br>cm | <10 cm                                         | ≥10<br>cm |
| Casarete  | 0.0             | 5.0       | 3.0            | 7.7       | 8.2          | 4.5       | 8.3                                            | 12.0      |
| Sambu     | 0.0             | 3.1       | 1.9            | 7.2       | 6.1          | 4.0       | 16.7                                           | 1.6       |
| Juanacati | 2.1             | 1.1       | 4.2            | 4.1       | 10.9         | 5.6       | 5.9                                            | 0.7       |
| Naranzati | 0.0             | 0.0       | 3.5            | 0.9       | 9.7          | 3.1       | 1.8                                            | 0.0       |
| Darien NP | —               | 0.0       | —              | 0.0       | —            | 0.0       | —                                              | 0.0       |

Table 4–5. Forest-wide annual treefall and tree incline rates (i.e., partial uprooting) for small (above) and large (below) trees for four sites.

| < 10 cm dbh | 1997–98 |      | 1998–99 |      | 1999–2000 |      | 2000–01 |      |
|-------------|---------|------|---------|------|-----------|------|---------|------|
|             | Incline | Fall | Incline | Fall | Incline   | Fall | Incline | Fall |
| Casarete    | 0.40    | 0    | 0       | 0    | 3.22      | 0.57 | 0.23    | 0.23 |
| Sambu       | 0.17    | 0    | 0       | 0    | 0.13      | 0.13 | 0.15    | 0    |
| Juanacati   | 1.48    | 0.37 | 0.97    | 0    | 1.18      | 0.34 | 0.49    | 0    |
| Naranzati   | 0.87    | 0    | 0.55    | 0    | 1.16      | 0.93 | —       | —    |
| ≥ 10 cm dbh | 1997–98 |      | 1998–99 |      | 1999–2000 |      | 2000–01 |      |
|             | Incline | Fall | Incline | Fall | Incline   | Fall | Incline | Fall |
| Casarete    | 0.56    | 0    | 0.26    | 0    | 2.38      | 1.68 | 0.46    | 0.58 |
| Sambu       | 1.43    | 0    | 1.08    | 0.81 | 1.87      | 0.42 | 0.46    | 0    |
| Juanacati   | 0.88    | 1.32 | 0.73    | 0.36 | 0.53      | 1.24 | 0.26    | 0.38 |
| Naranzati   | 0       | 0    | 0.29    | 0.58 | 0.33      | 0.33 | —       | —    |

Table 4–6. Mean annual diameter growth (mm/year) of cativo trees of three stem types, based on 1997–2001, 1998–2001, or 1997–2000 census periods. Within diameter classes, different letters denote significant differences ( $p \leq 0.01$ ) among stem types, (sample sizes noted parenthetically).

| C a s a r e t e   |                         |                       | S a m b u                              |        |                        |                         |                                        |
|-------------------|-------------------------|-----------------------|----------------------------------------|--------|------------------------|-------------------------|----------------------------------------|
| DBH cm            | Undamaged               | Broken                | Sprouts from prostrate/inclined trunks | DBH cm | Undamaged              | Broken                  | Sprouts from prostrate/inclined trunks |
| 1–4               | 0.35 <sup>a</sup> (427) | 0.3 <sup>a</sup> (33) | 0.9 <sup>b</sup> (25)                  | 1–4    | 1.5 <sup>a</sup> (301) | 1.5 <sup>a,b</sup> (24) | 1.0 <sup>b</sup> (66)                  |
| 4–10              | 0.7 <sup>a</sup> (205)  | 0.9 <sup>a</sup> (20) | 1.2 <sup>a</sup> (14)                  | 4–10   | 2.0 <sup>a</sup> (117) |                         | 4.1 <sup>b</sup> (20)                  |
| 10–20             | 1.8 <sup>a</sup> (288)  | 1.6 <sup>a</sup> (22) | 4.0 <sup>b</sup> (63)                  | 10–20  | 4.6 <sup>a</sup> (140) | 6.5 <sup>a</sup> (6)    | 6.6 <sup>a</sup> (6)                   |
| 20–40             | 3.5 <sup>a</sup> (204)  | 1.2 <sup>a</sup> (4)  | 5.4 <sup>b</sup> (19)                  | 20–40  | 4.2 <sup>a</sup> (101) | 2.2 <sup>a</sup> (4)    | —                                      |
| ≥ 40              | 2.6 (120)               | 0.6 (3)               | —                                      | ≥ 40   | 2.8 (103)              | 0.8 (2)                 | —                                      |
| N a r a n z a t i |                         |                       | J u a n a c a t i                      |        |                        |                         |                                        |
| DBH cm            | Undamaged               | Broken                |                                        | DBH cm | Undamaged              | Broken                  | Sprouts from prostrate/inclined trunks |
| 1–4               | 0.9 <sup>a</sup> (92)   | 2.7 <sup>a</sup> (8)  | —                                      |        |                        |                         |                                        |
| 4–10              | 1.2 <sup>a</sup> (79)   | 2.6 <sup>a</sup> (5)  | —                                      | 4–10   | 3.0 <sup>a</sup> (288) | 2.0 <sup>b</sup> (34)   | 2.7 <sup>a,b</sup> (15)                |
| 10–20             | 2.7 <sup>a</sup> (61)   | 1.7 <sup>a</sup> (5)  | —                                      | 10–20  | 5.3 <sup>a</sup> (164) | 2.8 <sup>a</sup> (9)    | 5.7 <sup>a</sup> (3)                   |
| 20–40             | 4.7 (43)                | —                     | —                                      | 20–40  | 8.5 <sup>a</sup> (70)  | 2.5 <sup>b</sup> (7)    | —                                      |
| ≥ 40              | 4.5 (140)               | —                     | —                                      | ≥ 40   | 7.1 (32)               | —                       | —                                      |

Table 4–7. Mean annual diameter growth (mm/year) of cativo trees. Statistical comparisons are vertical, within diameter classes and among sites; different letters denote significant differences ( $p \leq 0.01$ ; sample sizes noted parenthetically). All stem types except prostrate are grouped.

| <b>1997–98</b> | <b>1–4 cm</b>          | <b>4–10 cm</b>           | <b>10–20 cm</b>           | <b>20–40 cm</b>           | <b>≥ 40 cm</b>           |
|----------------|------------------------|--------------------------|---------------------------|---------------------------|--------------------------|
| Casarete       | 0.1 <sup>b</sup> (485) | 0.0 <sup>b</sup> (242)   | 1.2 <sup>b</sup> (374)    | 2.3 <sup>c</sup> (230)    | 1.7 <sup>b</sup> (123)   |
| Sambu          | 1.8 <sup>a</sup> (396) | 2.2 <sup>a</sup> (138)   | 4.4 <sup>a</sup> (153)    | 4.3 <sup>b</sup> (108)    | 3.3 <sup>a,b</sup> (107) |
| Naranzati      | 0.3 <sup>b</sup> (64)  | 0.2 <sup>b</sup> (52)    | 1.0 <sup>b</sup> (37)     | 3.0 <sup>b,c,d</sup> (20) | 3.5 <sup>a</sup> (23)    |
| Juanacati      | —                      | 3.1 <sup>a</sup> (118)   | 4.7 <sup>a</sup> (53)     | 5.4 <sup>a,b</sup> (26)   | 7.5 <sup>a</sup> (9)     |
| Bajo Grande    | —                      | —                        | 2.0 <sup>a,b</sup> (9)    | 1.7 <sup>c,d</sup> (70)   | 1.9 <sup>b</sup> (48)    |
| Rio Amarradero | —                      | —                        | 0.7 <sup>a,b</sup> (11)   | 0.5 <sup>c,d</sup> (51)   | 2.0 <sup>b</sup> (92)    |
| Rio Balsas I   | —                      | —                        | —                         | 0.5 <sup>d</sup> (96)     | –0.5 <sup>b</sup> (21)   |
| Bongales       | —                      | —                        | 3.1 <sup>a,b</sup> (11)   | 5.8 <sup>a,b</sup> (62)   | 5.9 <sup>a</sup> (34)    |
| Limon          | —                      | —                        | 5.0 <sup>a,b</sup> (4)    | 8.4 <sup>a</sup> (36)     | 8.1 <sup>a</sup> (8)     |
| Rio Tuira      | —                      | —                        | 3.1 <sup>a,b</sup> (11)   | 2.0 <sup>c,d</sup> (151)  | 1.2 <sup>b</sup> (38)    |
| <b>1998–99</b> | <b>1–4 cm</b>          | <b>4–10 cm</b>           | <b>10–20 cm</b>           | <b>20–40 cm</b>           | <b>≥ 40 cm</b>           |
| Casarete       | 0.5 <sup>b</sup> (491) | 0.9 <sup>b</sup> (237)   | 2.5 <sup>c</sup> (376)    | 4.3 <sup>c</sup> (227)    | 3.5 <sup>c</sup> (126)   |
| Sambu          | 1.6 <sup>a</sup> (410) | 3.7 <sup>a</sup> (148)   | 6.4 <sup>b</sup> (156)    | 5.6 <sup>b,c</sup> (105)  | 3.9 <sup>c</sup> (104)   |
| Naranzati      | 0.6 <sup>b</sup> (185) | 1.2 <sup>b</sup> (117)   | 2.4 <sup>c</sup> (97)     | 4.2 <sup>c</sup> (67)     | 3.5 <sup>c</sup> (176)   |
| Juanacati      | —                      | 4.5 <sup>a</sup> (332)   | 8.2 <sup>a</sup> (179)    | 10.5 <sup>a,b</sup> (78)  | 9.4 <sup>a,b</sup> (31)  |
| Bajo Grande    | —                      | —                        | 3.7 <sup>a,b,c</sup> (8)  | 8.0 <sup>b</sup> (68)     | 11.0 <sup>a</sup> (49)   |
| Rio Balsas I   | —                      | —                        | —                         | 3.2 <sup>c</sup> (98)     | 4.1 <sup>b</sup> (20)    |
| Bongales       | —                      | —                        | 4.5 <sup>a,b,c</sup> (9)  | 8.7 <sup>a,b</sup> (57)   | 7.2 <sup>b</sup> (36)    |
| Limon          | —                      | —                        | 6.8 <sup>a,b,c</sup> (3)  | 12.0 <sup>a</sup> (34)    | 12.7 <sup>a</sup> (10)   |
| Rio Tuira      | —                      | —                        | 4.6 <sup>a,b,c</sup> (11) | 7.2 <sup>b</sup> (144)    | 5.7 <sup>b,c</sup> (39)  |
| <b>1999–00</b> | <b>1–4 cm</b>          | <b>4–10 cm</b>           | <b>10–20 cm</b>           | <b>20–40 cm</b>           | <b>≥ 40 cm</b>           |
| Casarete       | 0.5 <sup>b</sup> (483) | 1.1 <sup>b</sup> (238)   | 1.7 <sup>b</sup> (372)    | 5.0 <sup>b</sup> (226)    | 3.2 <sup>c</sup> (128)   |
| Sambu          | 1.3 <sup>a</sup> (427) | 2.6 <sup>a,b</sup> (162) | 4.2 <sup>a,b</sup> (157)  | 3.8 <sup>b</sup> (110)    | 2.3 <sup>c</sup> (104)   |
| Naranzati      | 1.6 <sup>a</sup> (100) | 1.7 <sup>b</sup> (83)    | 2.6 <sup>b</sup> (66)     | 5.4 <sup>b</sup> (43)     | 5.1 <sup>b</sup> (139)   |
| Juanacati      | —                      | 3.0 <sup>a</sup> (338)   | 5.1 <sup>a</sup> (190)    | 8.4 <sup>a</sup> (81)     | 7.8 <sup>a</sup> (39)    |
| <b>2000–01</b> | <b>1–4 cm</b>          | <b>4–10 cm</b>           | <b>10–20 cm</b>           | <b>20–40 cm</b>           | <b>≥ 40 cm</b>           |
| Casarete       | 0.8 <sup>a</sup> (479) | 1.0 <sup>b</sup> (243)   | 2.1 <sup>b</sup> (355)    | 3.6 <sup>b</sup> (224)    | 2.0 <sup>b</sup> (126)   |
| Sambu          | 1.1 <sup>a</sup> (459) | 1.9 <sup>a</sup> (170)   | 4.0 <sup>a</sup> (169)    | 3.3 <sup>b</sup> (116)    | 1.6 <sup>b</sup> (107)   |
| Juanacati      | —                      | 1.3 <sup>b</sup> (332)   | 2.6 <sup>b</sup> (197)    | 5.1 <sup>a</sup> (83)     | 5.2 <sup>a</sup> (40)    |

Table 4–8. Ingrowth by stem type. Percentage of recruited individuals from broken stems, undamaged stems, or sprouts from prostrate and inclined trees.

| Site      | DBH<br>cm | 1997–98                                     |        |           | 1998–99                                     |        |           | 1999–00                                     |        |           |
|-----------|-----------|---------------------------------------------|--------|-----------|---------------------------------------------|--------|-----------|---------------------------------------------|--------|-----------|
|           |           | Sprouts from<br>inclined/prostrate<br>stems | Broken | Undamaged | Sprouts from<br>inclined/prostrate<br>stems | Broken | Undamaged | Sprouts from<br>inclined/prostrate<br>stems | Broken | Undamaged |
| Casarete  |           | 50                                          | 0      | 50        | 63                                          | 6      | 31        | 53                                          | 33     | 14        |
| Sambu     | 1–4       | 5.5                                         | 5.5    | 89        | 11                                          | 4      | 85        | 0                                           | 0      | 100       |
| Naranzati |           | 0                                           | 0      | 100       | 50                                          | 0      | 50        | 0                                           | 20     | 80        |
| Casarete  |           | 0                                           | 0      | 100       | 11                                          | 0      | 89        | 0                                           | 0      | 100       |
| Sambu     | 4–10      | 29                                          | 0      | 71        | 7                                           | 0      | 93        | 21                                          | 0      | 79        |
| Juanacati |           | 0                                           | 50     | 50        | 6                                           | 0      | 94        | 25                                          | 6      | 69        |
| Naranzati |           | 0                                           | 0      | 100       | 0                                           | 0      | 100       | 0                                           | 0      | 100       |
| Casarete  |           | 50                                          | 0      | 50        | 38                                          | 0      | 62        | 20                                          | 0      | 80        |
| Sambu     | 10–       | 0                                           | 0      | 100       | 30                                          | 0      | 70        | 0                                           | 0      | 100       |
| Juanacati | 40        | 0                                           | 0      | 100       | 0                                           | 0      | 100       | 0                                           | 0      | 100       |
| Naranzati |           | 0                                           | 0      | 100       | 0                                           | 0      | 0         | 0                                           | 0      | 100       |
| Casarete  |           | 0                                           | 0      | 100       | 0                                           | 0      | 100       | 0                                           | 0      | 100       |
| Sambu     | ≥ 40      | 0                                           | 0      | 100       | 0                                           | 0      | 100       | 0                                           | 0      | 100       |
| Juanacati |           | 0                                           | 0      | 100       | 0                                           | 0      | 100       | 0                                           | 0      | 100       |
| Naranzati |           | 0                                           | 0      |           | 0                                           | 0      | 100       | 0                                           | 0      | 100       |

Table 4–8. Continued

| Site      | DBH<br>cm | 2000–01                                     |        |           |
|-----------|-----------|---------------------------------------------|--------|-----------|
|           |           | Sprouts from<br>inclined/prostrate<br>stems | Broken | Undamaged |
| Casarete  |           | 89                                          | 2      | 9         |
| Sambu     | 1–4       | 61                                          | 6      | 33        |
| Naranzati |           | —                                           | —      | —         |
| Casarete  |           | 25                                          | 0      | 75        |
| Sambu     | 4–10      | 11                                          | 0      | 89        |
| Juanacati |           | 50                                          | 5      | 45        |
| Naranzati |           | —                                           | —      | —         |
| Casarete  |           | 57                                          | 0      | 43        |
| Sambu     | 10–40     | 14                                          | 0      | 86        |
| Juanacati |           | 20                                          | 0      | 80        |
| Naranzati |           | —                                           | —      | —         |
| Casarete  |           | 50                                          | 0      | 50        |
| Sambu     | ≥ 40      | 0                                           | 0      | 100       |
| Juanacati |           | 0                                           | 0      | 100       |
| Naranzati |           | —                                           | —      | —         |

Table 4–9. Cative annual recruitment and mortality rates (%) by stem diameter class for four census periods.

| Site      | DBH<br>cm | Recruitment Rates |             |             |             | Mortality Rates |             |             |             |
|-----------|-----------|-------------------|-------------|-------------|-------------|-----------------|-------------|-------------|-------------|
|           |           | 1997–<br>98       | 1998–<br>99 | 1999–<br>00 | 2000–<br>01 | 1997–<br>98     | 1998–<br>99 | 1999–<br>00 | 2000–<br>01 |
| Casarete  |           | 1.2               | 3.0         | 3.2         | 10.7        | 8.3             | 4.6         | 2.8         | 2.1         |
| Sambu     | 1–4       | 8.4               | 11.6        | 3.0         | 3.7         | 1.9             | 1.6         | 1.7         | 0.6         |
| Naranzati |           | 3.9               | 1.7         | 4.8         | —           | 3.9             | 4.3         | 3.0         | —           |
| Casarete  |           | 1.0               | 3.6         | 3.1         | 2.8         | 7.2             | 2.8         | 0.4         | 0.7         |
| Sambu     | 4–10      | 11.2              | 10.2        | 6.9         | 4.9         | 0               | 0           | 0.5         | 0           |
| Juanacati |           | 1.6               | 5.5         | 5.2         | 4.6         | 1.6             | 0.4         | 0           | 0.7         |
| Naranzati |           | 5.0               | 2.1         | 8.1         | —           | 2.5             | 2.1         | 1.2         | —           |
| Casarete  |           | 0.3               | 1.3         | 0.9         | 1.0         | 1.4             | 1.0         | 1.1         | 1.1         |
| Sambu     | 10–40     | 2.1               | 3.9         | 2.1         | 2.2         | 0.4             | 0.8         | 0           | 0.6         |
| Juanacati |           | 4.8               | 7.7         | 5.9         | 1.4         | 0               | 0           | 1.6         | 0.6         |
| Naranzati |           | 2.4               | 0           | 4.4         | —           | 0               | 0.7         | 0.8         | —           |
| Casarete  |           | 0.8               | 2.7         | 1.0         | 1.6         | 0               | 1.5         | 0.8         | 0           |
| Sambu     | ≥ 40      | 1.7               | 1.0         | 0.8         | 0.9         | 0               | 1.0         | 0           | 0           |
| Juanacati |           | 7.3               | 8.0         | 4.9         | 8.4         | 0               | 0           | 0           | 0           |
| Naranzati |           | 0                 | 1.9         | 8.4         | —           | 0               | 0           | 0.7         | —           |

Table 4–10. Annual mortality rates (%) of cativo trees by stem type and stature for four census periods.

| DBH<br>cm | 1997–98   |                                    |           |          |        | 1998–99                            |           |          |           |       |
|-----------|-----------|------------------------------------|-----------|----------|--------|------------------------------------|-----------|----------|-----------|-------|
|           | Broken    | Sprouts from<br>inclined/prostrate |           |          | Broken | Sprouts from<br>inclined/prostrate | Prostrate | Inclined | Undamaged |       |
|           |           | stems                              | Prostrate | Inclined |        |                                    |           |          |           | stems |
| Casarete  | 0.83      | 2.51                               | 0.21      | 0.83     | 3.56   | 0.13                               | 1.16      | 0        | 0.39      | 2.33  |
| Sambu     | 0.18      | 1.06                               | 0         | 0        | 0.18   | 0.19                               | 0.57      | 0        | 0         | 0.38  |
| Juanacati | 0         | 0                                  | 0.81      | 0        | 1.62   | 0                                  | 0         | 0.35     | 0         | 0.70  |
| Naranzati | 3.32      | 0                                  | 0         | 0        | 0      | 1.42                               | 0         | 0        | 0         | 1.89  |
| Casarete  | 0         | 0.23                               | 0.23      | 0.46     | 0.23   | 0.13                               | 0.13      | 0.26     | 0.13      | 0.40  |
| Sambu     | 0         | 0                                  | 0         | 0.25     | 0      | 0                                  | 0         | 0.56     | 0         | 0.28  |
| Juanacati | 0         | 0                                  | 0         | 0        | 0      | 0                                  | 0         | 0        | 0         | 0     |
| Naranzati | 0         | 0                                  | 0         | 0        | 0      | 0.33                               | 0         | 0        | 0         | 0     |
|           |           |                                    |           |          |        |                                    |           |          |           |       |
| DBH<br>cm | 1999–2000 |                                    |           |          |        | 2000–01                            |           |          |           |       |
|           | Broken    | Sprouts from<br>inclined/prostrate |           |          | Broken | Sprouts from<br>inclined/prostrate | Prostrate | Inclined | Undamaged |       |
|           |           | stems                              | Prostrate | Inclined |        |                                    |           |          |           | stems |
| Casarete  | 0.29      | 0.58                               | 0         | 0        | 1.16   | 0                                  | 0.70      | 0        | 0.35      | 0.59  |
| Sambu     | 0         | 0.98                               | 0         | 0        | 0.42   | 0                                  | 0.45      | 0        | 0         | 0     |
| Juanacati | 0         | 0                                  | 0         | 0        | 0      | 0.48                               | 0         | 0        | 0         | 0.24  |
| Naranzati | 0.54      | 0                                  | 0         | 0        | 1.63   | —                                  | —         | —        | —         | —     |
| Casarete  | 0.15      | 0.15                               | 0         | 0.29     | 0.44   | 0                                  | 0         | 0.12     | 0.35      | 0.47  |
| Sambu     | 0         | 0                                  | 0         | 0        | 0      | 0                                  | 0         | 0        | 0         | 0.47  |
| Juanacati | 0         | 0                                  | 0         | 0        | 1.39   | 0                                  | 0         | 0        | 0.49      | 0     |
| Naranzati | 0         | 0                                  | 0         | 0        | 0.75   | —                                  | —         | —        | —         | —     |

Table 4–11. Mean annual growth (mm/year) of cativo trees that were alive at the end of the study and those that died during the study for which there was one or more years of growth data.

|           |        | 1997–98 growth |            |    |     |         |
|-----------|--------|----------------|------------|----|-----|---------|
| Site      | DBH cm | Alive 2001     | Dead 2001  | df | t   | p       |
| Casarete  | 1–10   | 0.04 (683)     | –0.09 (44) | 65 | 1.6 | 0.05    |
|           | ≥ 10   | 1.7 (712)      | 0.3 (17)   | 25 | 5.1 | < 0.001 |
| Sambu     | 1–10   | 1.9 (519)      | 0.5 (14)   | 16 | 3.4 | 0.002   |
|           | ≥ 10   | —              | —          | —  | —   | —       |
| Naranzati | 1–10   | 0.2 (107)      | 0.6 (9)    | 9  | 0.5 | 0.32    |
|           | ≥ 10   | —              | —          | —  | —   | —       |
| Juanacati | 4–10   | —              | —          | —  | —   | —       |
|           | ≥ 10   | —              | —          | —  | —   | —       |

|           |        | 1998–99 growth |           |    |     |         |
|-----------|--------|----------------|-----------|----|-----|---------|
| Site      | DBH cm | Alive 2001     | Dead 2001 | df | t   | p       |
| Casarete  | 1–10   | 0.6 (707)      | 0.2 (21)  | 33 | 4.4 | < 0.001 |
|           | ≥ 10   | 3.3 (718)      | 1.6 (13)  | 13 | 2.5 | 0.01    |
| Sambu     | 1–10   | 2.2 (545)      | .03 (12)  | 14 | 6.3 | < 0.001 |
|           | ≥ 10   | —              | —         | —  | —   | —       |
| Naranzati | 1–10   | —              | —         | —  | —   | —       |
|           | ≥ 10   | —              | —         | —  | —   | —       |
| Juanacati | 4–10   | —              | —         | —  | —   | —       |
|           | ≥ 10   | 8.7 (294)      | 3.6 (6)   | 5  | 2.5 | 0.025   |

|           |        | 1999–00 growth |           |    |      |         |
|-----------|--------|----------------|-----------|----|------|---------|
| Site      | DBH cm | Alive 2001     | Dead 2001 | df | t    | p       |
| Casarete  | 1–10   | 0.7 (711)      | –0.1 (10) | 11 | 4.9  | < 0.001 |
|           | ≥ 10   | 3.6 (722)      | –0.8 (7)  | 15 | 17.2 | < 0.001 |
| Sambu     | 1–10   | —              | —         | —  | —    | —       |
|           | ≥ 10   | —              | —         | —  | —    | —       |
| Naranzati | 1–10   | —              | —         | —  | —    | —       |
|           | ≥ 10   | —              | —         | —  | —    | —       |
| Juanacati | 4–10   | —              | —         | —  | —    | —       |
|           | ≥ 10   | —              | —         | —  | —    | —       |

Table 4–12. Abundance of cativo trees < 1 cm dbh by height class. Trees were tallied but not measured at Casarete in December 1999.

| Height (cm)      | C a s a r e t e |          |          | S a m b u |           |           |
|------------------|-----------------|----------|----------|-----------|-----------|-----------|
|                  | Nov 1997        | Nov 1998 | Dec 1999 | June 1998 | July 1999 | June 2000 |
| < 30             | 485             | 110      | —        | 222       | 341       | 526       |
| 30–60            | 3995            | 2275     | —        | 5956      | 6281      | 3937      |
| 60–90            | 1210            | 1195     | —        | 6889      | 6548      | 6063      |
| 90–150           | 745             | 860      | —        | 2667      | 3363      | 3558      |
| >150 – <1 cm dbh | 390             | 215      | —        | 1378      | 993       | 1326      |
| total            | 6825            | 4655     | 12045    | 17111     | 17526     | 15411     |

Table 4–13. Annual mortality rates (%) of cativo trees by height class for the period November 1998 – November 1999.

| Height (cm)      | Casarete | Sambu |
|------------------|----------|-------|
| < 30             | 51.4     | 63.3  |
| 30–60            | 30.0     | 9.9   |
| 60–90            | 13.2     | 1.2   |
| 90–150           | 3.2      | 0.0   |
| >150 – <1 cm dbh | 6.6      | 2.0   |

Table 4–14. Mean annual height (cm/year) and diameter (mm/yr) growth rates for cativo trees < 1 cm dbh, (sample sizes noted parenthetically).

| Casarete         | Nov 97–Dec 98      |                 | Dec 98–Dec 99      |                 |
|------------------|--------------------|-----------------|--------------------|-----------------|
|                  | Height Growth (cm) | Dbh Growth (mm) | Height Growth (cm) | Dbh Growth (mm) |
| < 30             | 18.5 (25)          |                 | 8.3 (4)            |                 |
| 30–60            | 4.9 (432)          |                 | 1.9 (117)          |                 |
| 60–90            | 2.1 (155)          |                 | 1.4 (94)           |                 |
| 90–150           | 2.1 (106)          |                 | 1.4 (101)          | 0.3 (24)        |
| >150 – <1 cm dbh |                    | 0.3 (71)        | 3.0 (26)           | 0.4 (24)        |
| Sambu            | June 98–July 99    |                 | July 99–June 00    |                 |
|                  | Height Growth (cm) | Dbh Growth (mm) | Height Growth (cm) | Dbh Growth (mm) |
| < 30             | 1.9 (8)            |                 | 13.3 (8)           |                 |
| 30–60            | 2.5 (338)          |                 | 2.8 (157)          |                 |
| 60–90            | 2.4 (416)          |                 | 2.2 (242)          |                 |
| 90–150           | 4.4 (168)          |                 | 5.3 (140)          | 0.8 (17)        |
| >150 – <1 cm dbh |                    | 0.9 (70)        | 10.1 (43)          | 0.6 (38)        |

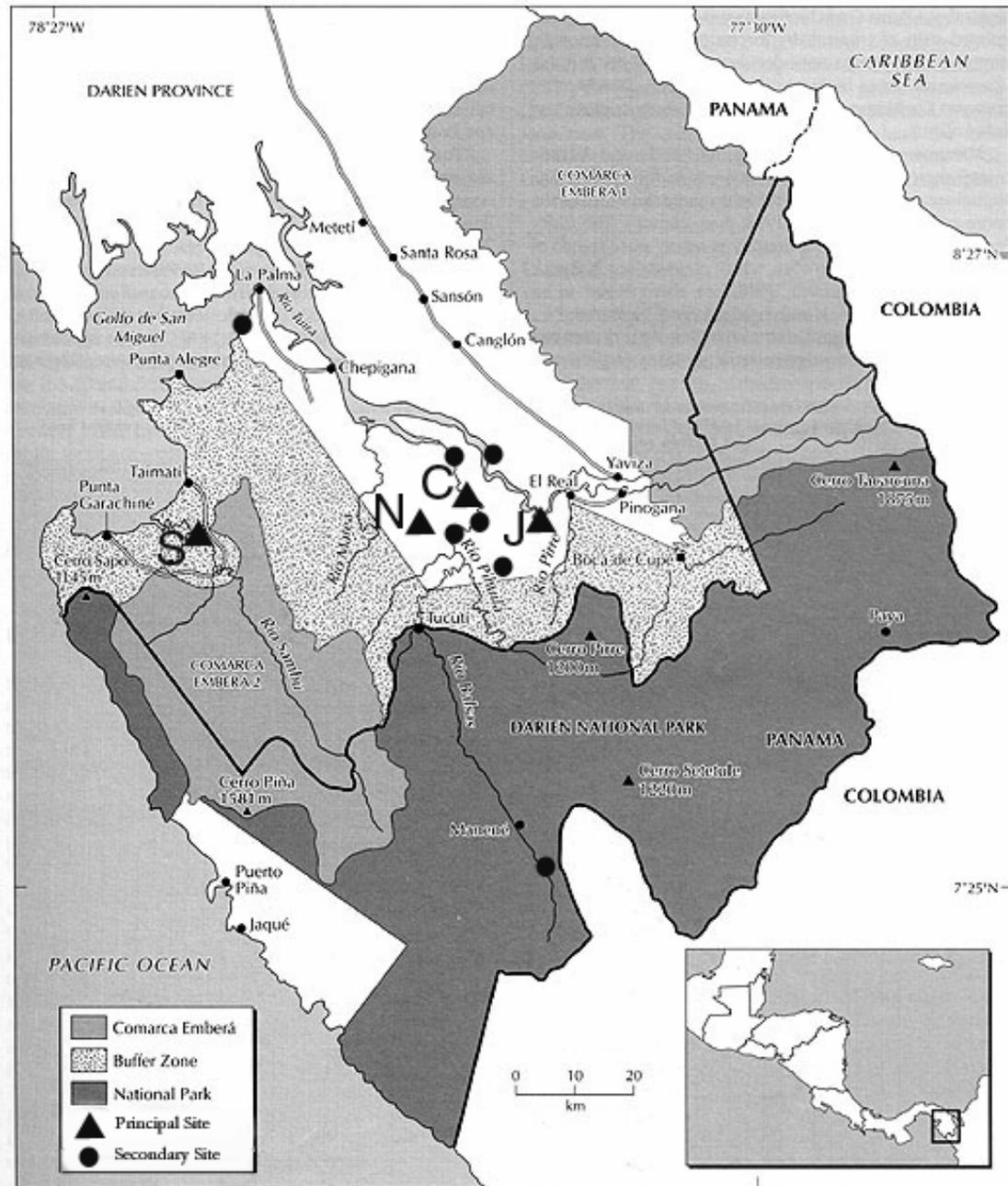


Figure 4-3. Darien Province, Panama showing principal sites (S=Sambu, N=Naranzati, C=Casarete, J=Juanacati) and seven secondary sites.

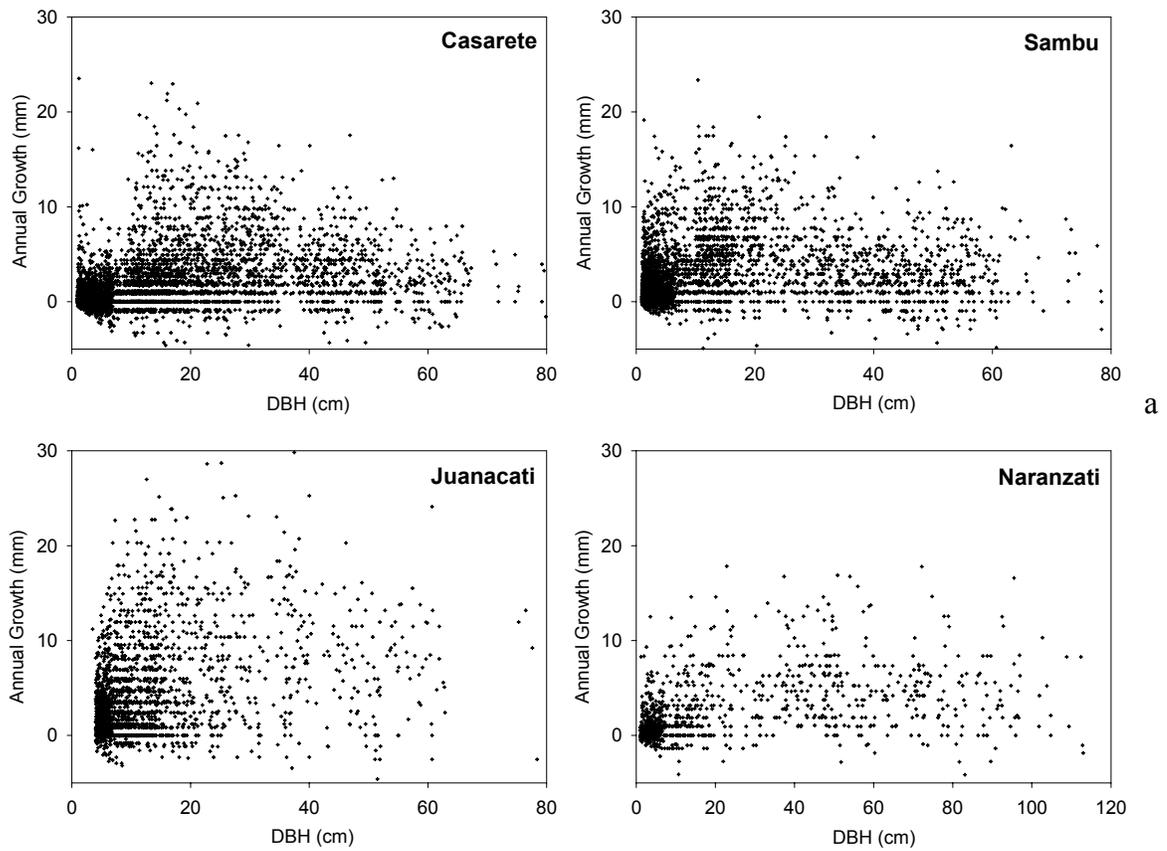
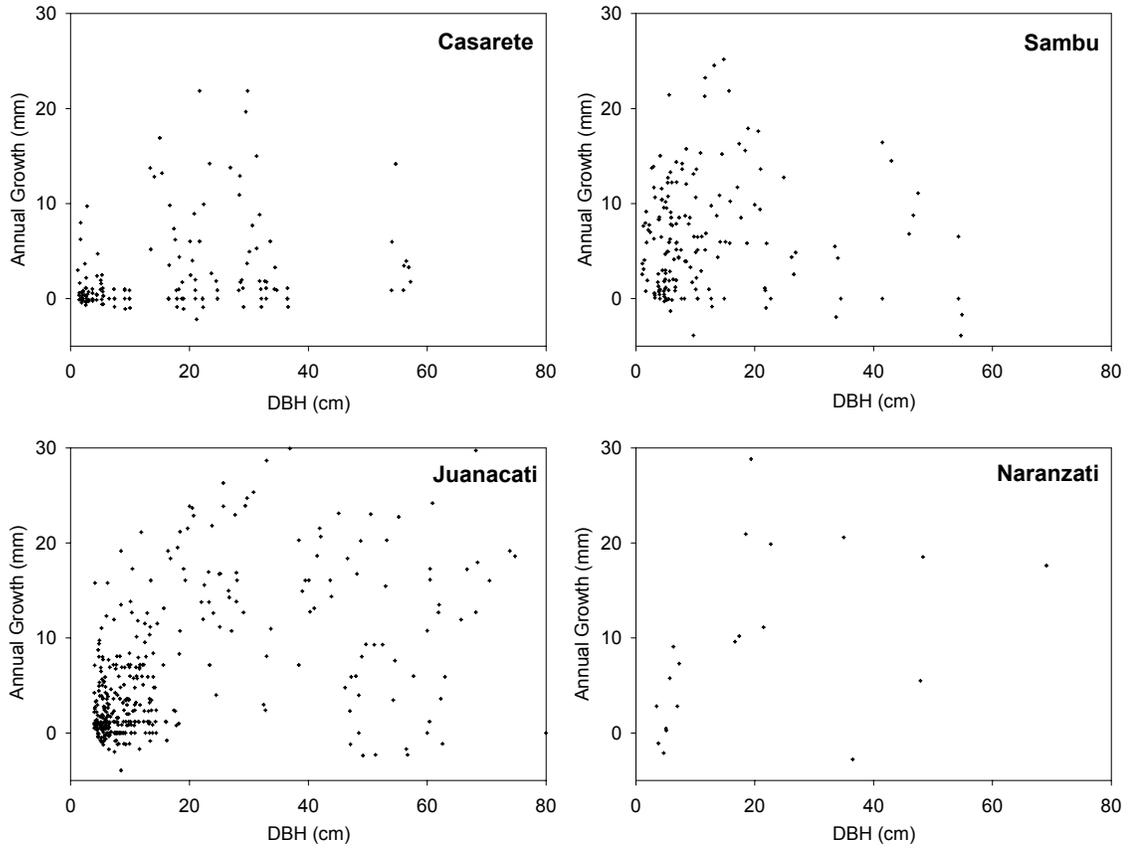


Figure 4-4. Annual diameter growth (mm/year). a) *Prioria copaifera* (cativo),  
 b) *Pterocarpus officinalis*, c) *Carapa guianensis*, d) *Pentaclethra macroloba*.



b

Figure 4-4 Continued.

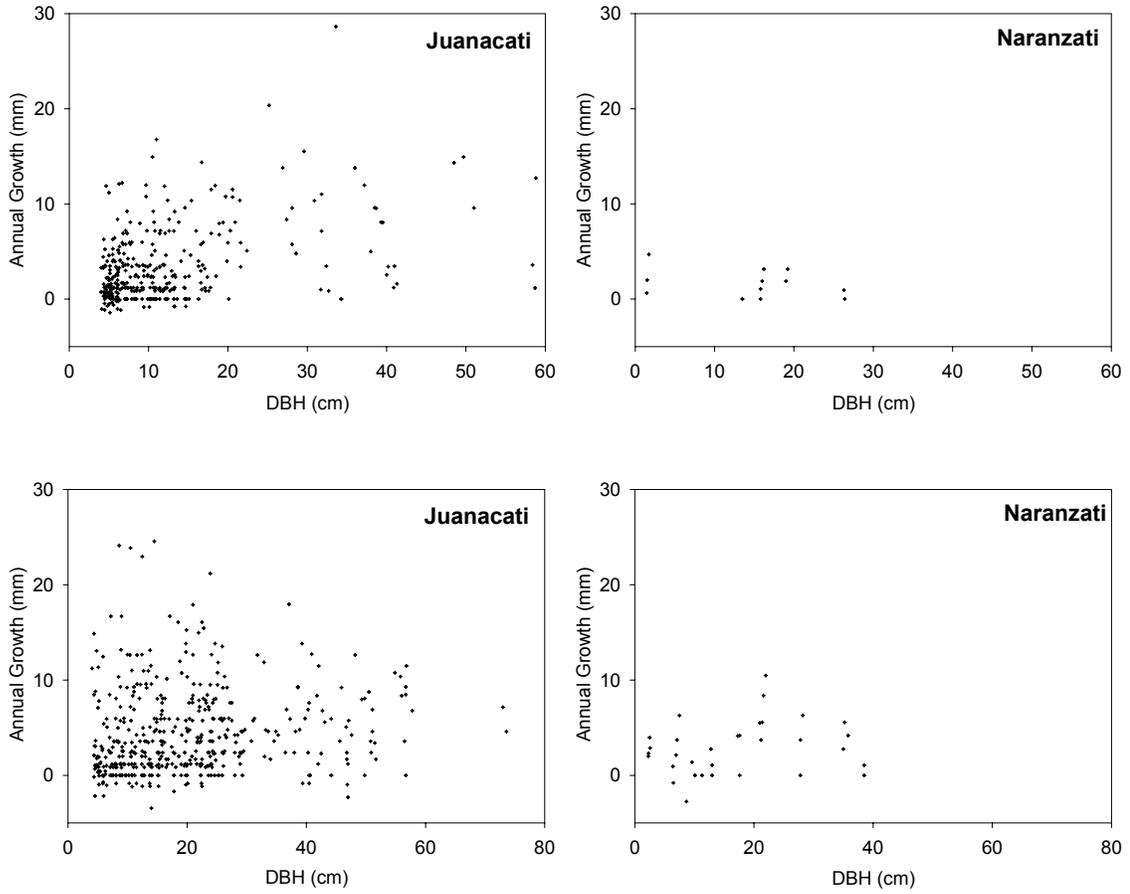


Figure 4-4 Continued.

CHAPTER 5  
GROWTH AND YIELD PROJECTIONS OF *Prioria copaifera* FROM FOUR SWAMP  
FORESTS IN DARIEN, PANAMA

**Introduction**

Tropical forests historically were viewed by foresters in temperate countries primarily as sources of valuable woods (Whitford 1921, Record 1925). Only relatively recently have concerns about biodiversity and other less financially-tangible values become prominent (Putz et al. 2000b). Research has shown that tropical forests have many diverse values that differ among stakeholders (Godoy et al. 2002, Kainer et al. 2003, van Beukering et al. 2003). Despite growing awareness of the values of tropical forests, forest degradation as well as deforestation continue due to a wide variety of factors such as rising agricultural and timber prices, low rural wages, and few employment opportunities other than forestry or agriculture, among others (Kaimowitz and Angelsen 1998, Barbier and Burgess 2001). In many countries, when forests have been depleted of marketable wood, their perceived value is lost and the land is converted for agricultural uses that may be no more sustainable than the timber mining that preceded them. Increasingly recognized is the need for permanent forest estates and for policies that promote not just a forest products industry, but forest management that is more than just one step in the process of deforestation (Verissimo et al. 2002).

Although forests have many values, timber is still the forest output that is in greatest demand worldwide. Unfortunately, continuing demand for timber has not been sufficient to lead to forest conservation for a variety of reasons. Often, the benefits of

intact forests have been undervalued and the benefits of forest conversion overestimated (Repetto 1988). Logging, at least as it is conventionally carried out, not only depletes the forest of the available valuable timber but causes residual damage to soils and vegetation that reduces subsequent harvests. Improved forest management techniques are infrequently employed because they are perceived as being more expensive than conventional logging (Putz et al. 2000a), despite accumulating evidence to the contrary (Holmes et al. 2002, Boltz et al. 2003). Other variables that limit commercial interest in sustaining timber yields from natural forests in the tropics are high discount rates, unknown or slow volume increments, tenurial insecurity, and fluctuating timber prices (Pearce et al. 2003).

Scarcity of trees of valuable species and low rates of increment in commercial volumes are the principal biological constraints on timber production from tropical forest and necessitate long cutting cycles. Plantations often produce more timber more often than natural forests not only because of intensive silvicultural practices that increase growth, but also because every stem on a given hectare is available for harvest. Natural forest management for timber production would be more competitive if commercial species were more abundant or if the timber was more highly valued. Monodominant forests composed of a commercially valuable species meet the former requirement. This study examines the wood producing potential of a unique Neotropical forest type for which species composition and regeneration capacity are such that, despite only moderate stem diameter growth rates, many forests of this type have sustained several decades of timber harvesting and still contain an abundance of potentially valuable trees. Using data on forest structure and stand dynamics from permanent plots at four sites, I estimate

future commercial timber volumes under a variety of cutting rotations (years between harvests) and diameter limits.

Neotropical swamp forests dominated by *Prioria copaifera* (cativo) have long been valued for their timber (Barbour 1952, Lamb 1953). Indeed, the common pattern of a timber species being depleted and its use replaced by other species occurred with cativo in at least part of its range (Veiman 1982). In Darien, Panama, in contrast, sites that started being logged for cativo in the 1950s and 1960s are still cativo-dominated forests, albeit degraded to different degrees (Holdridge 1964, Grauel and Putz 2004).

Timber harvesting in Darien can be characterized as either labor- or capital-intensive. Labor-intensive logging occurs in riverine forests by local community members as part of a diverse livelihood strategy that may also include farming, hunting, non-timber forest product collecting, and fishing. Permits are obtained for harvesting individual trees, and heavy machinery is not used for road building or log extraction. After target trees are felled, the loggers fell additional trees 25–35 cm dbh and position them end-to-end to form two parallel rails. This practice facilitates the manual rolling or levering of the harvested logs to the river. Easily-accessed forests are repeatedly logged, and well-formed trees larger than the legal cutting limit of 60 cm dbh are consequently scarce. Other evidence of repeated logging including the frequency of damaged crowns among the residual trees, liana tangles, and common, large canopy gaps.

Capital-intensive timber harvesting in Darien occurs mostly in a mosaic of inland cativo swamps and “tierra firme” (unflooded) forests. Logging concessionaires float heavy machinery as far upriver as is feasible and then build roads and logging camps; logging is restricted to the short annual dry season ( $\leq 3$  months). Although forest

management plans are required by law, most consist of volume and species estimations based on a few sample plots. Because logging concessions are limited to five years and renewal is uncertain, there is little incentive for the long-term planning of subsequent timber harvests and roads are poorly constructed and maintained. After cativo, *Anacardium excelsum* is the most common commercial species harvested in this landscape.

### Study Sites

Cativo-dominated swamp forests are found both along rivers and in interior lowlands of Darien Province of Eastern Panama. Inland swamps are flooded continuously over the 9 month wet season whereas forests adjacent to major rivers are flooded periodically by wet season rains and by monthly spring tides that can reach 70 km or more upriver. Forests closest to the influence of tides are strongly monodominant (> 95% cativo in all size classes) and may contain < 10 species ha<sup>-1</sup> whereas riverine and inland forests outside of tidal influence are relatively more species rich. These forests may contain 40–60 species ha<sup>-1</sup> although cativo can still comprise over 80% of the overstory (Linares Prieto 1988).

The four sites in this study vary by landscape position, flooding regime, species diversity, and management history (Table 5–1). Soils at all sites are fine textured and poorly drained. Slight brackishness was detected in the soil only at the Casarete site (Tapia 1999). The three riverine sites have all been logged in the past and although cativo regeneration of all sizes is abundant, large trees are relatively scarce. Although there was a logging concession nearby at the time of this study (1997–2001), the inland swamp in this study had not been logged at the time of plot installation (1997–1998).

## Methods

The stand structure, growth, and mortality data for this study were collected between 1997 and 2001. All plots were installed in 1997 or 1998; trees were marked, mapped, and measured annually up to 2001. The minimum diameter measured was 1 cm dbh at three of the sites (Casarete, Sambu, Naranzati) and 4 cm at Juanacati, but in this paper only data for trees  $\geq 10$  cm was used. I excluded trees  $< 10$  cm dbh because in preliminary analyses no trees smaller than 10 cm dbh entered the harvest projections during the 60 year simulation, and because variability in growth rates is much higher for small trees than large ones. Data on large trees was generally scarce at the riverine sites, and few trees attain large sizes due to intense logging pressure. For the riverine sites I used only data for trees  $\leq 60$  cm dbh, the legal cutting limit, because data for larger trees were scarce. At the inland swamp, trees  $\geq 60$  cm are abundant, but because the harvest simulation uses a maximum diameter cutting limit of 100 cm dbh, and because growth data for trees  $> 100$  cm dbh were scarce, I used data for trees between 10 and 100 cm dbh. Data on diameter growth rates were derived from the longest possible measurement interval for each tree. Of 3065 cativo trees in the four sites, 80% of the annual growth records were for the period 1997–2001, 14% were for 1998–2001, and 6% were for 1997–2000.

The wood volume of each tree  $\geq 40$  cm dbh was estimated by multiplying its basal area by a species-specific form factor (Philip 1994) and then by commercial height, defined as the height to the lowest branch. Commercial height was estimated for trees 40–50 cm dbh, 50–60 cm dbh, and  $\geq 60$  cm dbh after measuring about two dozen trees  $\geq 40$  cm dbh to the lowest branch with a telescoping measuring pole at both Casarete and Sambu. Commercial height estimates from the Casarete site were used for the Naranzati

and Juanacati sites. Volume estimates were based on a form factor specifically developed for cativo using 23 trees felled along the Balsas River near the Casarete site by Mariscal et al. (1999, Grauel and Pineda M. 2001). Volume of those trees was determined by the method of height accumulation by which successive diameters are measured at known heights along the stem (Philip 1994). Volume (V) was calculated using Smalian's formula:

$$V = (h/2) * (A_b + A_u)$$

where  $h$  = height

$A_b$  = cross sectional area at base

$A_u$  = cross sectional area at top.

Form factor (F) is defined as

$$F = V / ((A_{bh}) * h)$$

where  $V$  = volume

$A_{bh}$  = cross sectional area at breast height, 1.3m

$h$  = height.

The mean form factor for the 23 trees 49–95 cm dbh was 0.641513 (standard deviation = 0.0916; (Grauel and Pineda M. 2001). During each simulation, as individual trees “grew” into the 40, 50, and 60 cm dbh size classes, different appropriate commercial heights were applied to their volume calculation.

Growth projections were made using the method described in Condit et al. (1993) in which growth is expressed as a function of dbh with a polynomial equation and the resulting parameters are used to develop a diameter trajectory through time (see Appendix A for details). The resulting growth curve expresses dbh as a function of time with the initial condition (time = 0) as the minimum diameter (10 cm dbh).

Volume was projected by calculating the “age” (the time since the minimum diameter, 10 cm dbh) of each individual stem in the plots (year 2000 dbh), projecting its growth, and calculating future diameter and associated volume (Condit et al. 1995a). I estimated volume in this way for all trees as they attained 40 cm dbh in five year increments beginning with the year 2000. This approach allowed me to simulate a timber harvest at 2005 and then at any interval I chose by selecting trees and their associated volumes that surpassed a given diameter limit in any future year.

For all projections I applied the site-appropriate annual mortality rate ( $m$ ) to the volume ( $v$ ) at a given year ( $t$ ) with  $v * e^{-mt}$ , where  $t$  is the number of years beyond the year 2000. Based on five census years at the permanent plots, annual mortality rates of cativo trees  $\geq 10$  cm dbh at Casarete, Sambu, Juanacati, and Naranzati were 1.15%, 0.45%, 0.55%, and 0.50%, respectively.

### Scenarios

For all sites I projected timber volume out to the year 2065, but I modeled timber harvests differently for capital-intensive logging (inland swamp, Naranzati) and labor-intensive logging (riverine forests—Casarete, Sambu, and Juanacati) for several reasons. Stand structures were quite different between the previously logged riverine sites focused on by community loggers and the unlogged inland swamp typical of concession logging. Furthermore, the labor-intensive logging that is carried out in riverine forests occurs at higher frequencies but lower intensities than the capital-intensive logging of inland swamps. At inland swamps with extremely large standing volumes in commercial-sized trees, the logging concessionaires’ fellers seek out the largest stems since they are paid by the amount of volume felled. For purposes of comparison with the riverine sites, I simulated a 60 cm dbh cutting limit at the inland swamp, but higher diameter cutting

limits probably better represent reality and would be silviculturally more appropriate if the aim is to perpetuate the stand. In addition to the legal cutting limit (60 cm dbh), I simulated cutting limits of 80 cm, 90 cm, and 100 cm dbh every 20 years beginning in 2005 because many Panamanian foresters feel that the 5 year concession period will soon be legally extended to 20 years. In addition to the four fixed dbh cutting limits, a fifth scenario adjusted the cutting limit according to stand structure – after an initial 100 cm dbh cutting limit in 2005, the cutting limit was reduced to 90 cm for the final three harvests.

The labor-intensive timber harvesting common in the riverine forests is quite haphazard because individual local community members are free to seek out harvestable trees without the spatial constraints of a logging concession, and harvesting can potentially occur year round. Due to easy accessibility of riverine forests and low capital requirements for this sort of logging, the return time for harvesting to occur on a given hectare is probably less than for inland swamps where roads and skid trails have to be constructed for log extraction. The legal diameter cutting limit (60 cm dbh) is generally adhered to because log rafts are checked at government stations downriver. For the three riverine sites I simulated only the legal cutting limit at 5, 10, and 20 year cutting cycles.

Residual stand damage resulting from logging can vary greatly depending on harvest intensity, stand structure, and the machinery employed, as well as worker training and supervision. Because I had no data on logging damage in Darien, for all scenarios and sites I modeled logging damage as a linear relationship with harvest intensity that was developed by Webb (1997) from a comparison of tropical logging operations. In this

way, future yields were reduced according to the cumulative damage in all previous harvests.

Both natural and logging-induced mortality were applied after the total harvest volume was calculated. This approach eliminated the need to simulate the death of individual stems because mortality was simulated as a reduction in potential harvest volume (Condit et al. 1995a)

For the 2005 harvest simulation in the unlogged inland swamp, I included trees that were greater than or equal to the simulated diameter cutting limit in 2000. In contrast, for all riverine sites I excluded the few trees that were  $\geq 60$  cm in the year 2000 from subsequent harvests because observations indicate that they were not harvested previously due to poor form or hollowness. Hence, for all riverine sites, only trees that were  $< 60$  cm dbh in 2000 but  $\geq 60$  cm in 2005 are included in the first simulated harvest of 2005.

In the harvest projections for the riverine, labor intensive logging, I monitored the year 2000-diameter of all trees when they reached harvestable size (60 cm dbh) in future years. During each harvest, community loggers cut some 25–35 cm dbh trees to position as parallel rails for log extraction, so it was necessary to reduce the number of trees in that size class in any future harvest that included them (i.e. when they had attained 60 cm dbh). For instance, in the 2005 simulated harvest, loggers would cut some trees 25–35 cm dbh to use as rails, so when that size class reached harvestable size (60 cm dbh) in say, 2045, there would be fewer trees available for harvest. Modeling the reduction of future yields due to the felling of trees for rails was problematical because the number of trees felled depends on distance from the nearest river rather than on the number of

commercial-sized trees harvested or total volume available. Based on observations of previously used “roads” (parallel, end-to-end rails) and numbers of smaller stumps at the most recently logged site, I reduced future volumes by 10% for every harvest that includes trees that were 25–35 cm dbh in the year 2000.

### Results

In 2000, standing volume in commercial-sized trees  $\geq 60$  cm was  $10\text{--}40\text{ m}^3\text{ ha}^{-1}$  at the riverine sites and approached  $200\text{ m}^3\text{ ha}^{-1}$  at the inland swamp (Table 5–2). Two riverine forests had substantial volumes in trees 40–60 cm dbh. Mean annual volume increment of large trees ( $\geq 60$  cm dbh) was greatest at the inland swamp and up to two orders of magnitude greater than the slowest volume-accreting site, but increment for trees 40–60 cm dbh was lowest at the inland swamp. Commercial volume increments of large trees at all three riverine sites were rather low and never exceeded  $0.6\text{ m}^3\text{ ha}^{-1}\text{ yr}^{-1}$ . For trees 40–60 cm dbh, however, the three riverine sites had annual volume increments  $1.1\text{--}2.2\text{ m}^3\text{ ha}^{-1}\text{ yr}^{-1}$ . Lifetime growth trajectories also varied considerably among sites, with the time to grow from 10 cm to 60 cm dbh ranging from 72 to 203 years (Figure 5–1).

All three riverine forests yielded the most total volume per hectare after 65 years in the 20-year cutting cycle scenario (Table 5–3), and maximum yield in this scenario was at year 65 at all sites (Figure 5–2). All sites yielded little wood at the first harvest in 2005, but production increased thereafter. Volume yield after year 20 fluctuated at Casarete, was relatively constant at Sambu, and increased at Juanacati. For Casarete and Sambu, there was about a 25% higher total yield per ha in the 20-year compared to the 5-year cutting cycle scenario, while at Juanacati the 20-year cutting cycle yielded  $> 40\%$  more wood volume than the 5-year scenario (Table 5–3).

Future yields were reduced at the Juanacati site because of the practice of cutting trees for road building. For those harvests that included trees that were about 35 cm dbh in the year 2000, yields were reduced 21% in the five year cutting cycle scenario and 12% and 11% in the 10 and 20 year cutting cycles, respectively. Trees of the size used for rails for log extraction began to enter the legal diameter cutting limit of 60 cm around 2045 and 2050 at Juanacati. (Figure 5–3). At the slower growing Casarete and Sambu sites, no trees of suitable size for rails attained legal harvest size during the simulation to the year 2065.

Total volume yields per hectare for the 20 year cutting cycle (4 harvests) from the inland swamp under the 60, 80, 90, and 100 cm dbh cutting limits were 227, 191, 150, and 72 m<sup>3</sup>, respectively, while the variable cutting limit scenario yielded 141 m<sup>3</sup>. Using the legal 60 cm dbh cutting limit, 98.6% of the total 60 year yield was contained in the first harvest. Yields using the variable dbh cutting limit were the most consistent throughout the 65 year simulation compared with the fixed dbh limits, with no single harvest extracting more than 44% of the 60 year total yield. With the exception of the initial harvest in 2005, the variable dbh limit yielded the most volume at each future harvest (Figure 5–4).

Simulated logging damage for a given harvest at the riverine forests increased with cutting cycle length because longer cutting cycles allowed for greater accumulation of volume, and damage was modeled as a linear function of volume. The largest reductions of yield due to residual logging damage over the 65 year simulation were for the 5-year cutting cycle for all three riverine sites. Volume reductions due to logging damage ranged from 40–57% for the riverine sites under the 5-year cutting cycle and 15–38% for

the 20-year cutting cycle (Table 5–4). For the inland swamp, yield reduction due to logging-induced damage was similar for the 60, 80, 90, and variable dbh cutting limit scenarios and ranged from 26% for the 90 cm limit to 31% for the 80 cm limit. Overall yield reduction due to residual damage under the 100 cm dbh cutting limit was only about 7%.

### **Discussion**

All four sites in this study show reasonable potential for wood production, but the sources of that potential vary. The inland swamp contains large standing stocks of commercial sized trees while one riverine forest has very high cativo stem diameter growth rates and the other two have the advantage of very low species diversity. Standing commercial volumes of cativo wood in trees  $\geq 60$  cm dbh in two of the three riverine forests ( $20\text{--}40\text{ m}^3\text{ ha}^{-1}$ ) seem to indicate that little degradation has occurred. Indeed, the forest most recently logged, Sambu, contained more volume in trees  $\geq 60$  cm dbh in the year 2000 than a 1953 estimate for the cativo forests along the Sambu River by F. Bruce Lamb, a professional forester who surveyed the major watersheds of Darien for potential log sources (Lamb 1953). His surveys spanned all three logged sites included here. For the cativo forests that included the Casarete, Sambu, and Juanacati sites, he estimated mean volumes of 71, 35, and  $24\text{ m}^3\text{ ha}^{-1}$ , respectively (Lamb 1953). Although these forests are often described today as degraded, the Sambu and Casarete forests show a tremendous resilience in the form of large volumes contained in trees 40–60 cm dbh (Table 5–2). A major caveat, however, is that tree form is not taken into account in this study, and the abundance of trees with small, broken crowns and deformed stems testify to the repeated entries that are typical to the labor-intensive logging common in the

riverine forests. In addition, many riverine forests are susceptible to infestations by lianas that can negatively affect stem form, regenerative capacity, and diameter growth (Grauel and Putz 2004).

Besides assuming that all trees have merchantable stems, the model assumes constant mean growth throughout the 65 year time period, regardless of harvest frequency or intensity. Conventional wisdom holds that growth of residual trees increases after logging because of increased light availability, but this may not always hold. At the Sambu site for example, growth of trees 40-60 cm dbh seems to be better correlated with crown form than with crown illumination (Grauel, unpublished data). Severe crown damage from repeated logging entries slow the growth of trees, even those with full crown illumination. Interannual climate variability was large during the five years when data were collected for this study, and mean diameter growth rates are reasonable to use in projecting future growth where climate-induced effects on forest productivity are unknown. In addition, variability in relative diameter growth rates were greatest in trees  $< 10$  cm dbh, and by using data  $\geq 10$  cm dbh, this source of uncertainty is reduced somewhat. Estimates of growth, volume, and both natural and logging-induced mortality are all sources of uncertainty, but the model nevertheless serves as a useful tool for comparing future wood yields both among sites and among logging scenarios.

The inland swamps that were the object of most capital-intensive, mechanized logging of the 1990s and early 2000s are quite different in terms of stand structure compared to the riverine forests. Although the inland swamp forests are rarely found in patches  $> 10$  ha, commercial volumes are typically very large due to the dominance of *Prioria* and historical inaccessibility. The  $182 \text{ m}^3 \text{ ha}^{-1}$  of commercial wood volume

found in this study is similar to the standing volume of some southeast Asian tropical forests (Sist et al. 1998) and is probably among the largest commercial volumes per area found in the Neotropics.

Per-area volume increments of large cativo trees ( $\geq 60$  cm dbh) are more a reflection of stem density than of growth rates of individual trees. All three logged sites have annual increments substantially less than the volume increment of the unlogged inland swamp, even though cativo in two of the three logged sites has shorter lifetime growth trajectories than cativo in the unlogged swamp. Volume increments of trees 40–60 cm dbh reflect stand density, species composition, and also growth rates. The annual increments ranging from 1.6–2.2 m<sup>3</sup> ha<sup>-1</sup> at Casarete and Sambu are in large part due to the fact that these forests are composed of 95% cativo of all size classes. With such large standing volumes of the commercial species, even moderate growth rates can result in large volume increments. Juanacati, with much less standing volume in cativo but the fastest diameter growth rates of all sites, still had annual volume increment of 1.1 m<sup>3</sup> ha<sup>-1</sup>.

In the riverine forests, longer cutting cycles yielded more wood over the 65 years than shorter cycles because there was less frequent damage to the residual stand from logging. Even though the average amount of residual damage per entry was higher for the longer cutting cycles, higher yields resulted because total damage, as estimated here with reduction of yield, was lower.

Another timber harvest simulation for Panamanian tierra firme forest also found that longer cutting cycles yielded more cativo timber than shorter cycles. In a comparison of timber yields of seven commercial species, Condit et al. (1995) concluded that low natural mortality rates and abundant advance regeneration of cativo in unlogged

forest imparted an advantage in sustaining timber yields, but in that study residual damage from logging was held at 15%. By modeling damage as a function of available volume for harvest, I conclude that mortality of residual trees due to logging has a greater influence on future yields than natural mortality. My estimates of logging-induced mortality are probably conservative because, although not explicitly included in this study, tree mortality resulting from injury during logging may also increase in the months and years immediately following logging (Pinard and Putz 1996, Sist and Nguyen-The 2002).

There should generally be less damage from timber harvesting in the riverine forests subject to labor-intensive harvesting than where heavy machinery is used during logging. Depending on harvest intensity, road building and the maneuvering of heavy machinery are usually the principal causes of canopy cover reduction and ground area disturbance (Jackson et al. 2002). Log extraction with skidders may even be the principal cause of tree death (Bertault and Sist 1997), although Johns et al. (1996) found that tree felling caused more damage than any other single aspect of logging in the eastern Amazon. A source of uncertainty regarding the amount of damage caused by labor-intensive logging in riverine cativo forests is the question of the number of trees used for rail-laying. In forests that are composed of 95% of a single commercial species, it might seem that repeatedly thinning a subcanopy size class would severely restrict opportunities for future harvests. Although trees of the size used for rail building did not enter the simulated harvests at Casarete and Sambu, the present day stand structures have probably been influenced by this practice. At the site with the fastest mean cativo diameter growth (Juanacati), the potential for yield reductions due to the depletion of smaller trees for rails

would be even greater, but higher species diversity suggests that non-commercial species could be used for rails there.

At the more species-diverse inland swamps (Naranzati) where capital-intensive, mechanized logging is employed, the amount of residual damage may determine whether sustainable timber yield is possible. Many studies have found a positive correlation between logging damage and the volume extracted (e.g., Bertault and Sist 1997, Webb 1997, Panfil and Gullison 1998, Sist et al. 1998, Pereira et al. 2002), but differences in logging techniques may reduce such a correlation (Pinard and Putz 1996). At low harvest intensities, road building with heavy machinery may be the principle cause of residual damage but as extracted volumes increase, secondary damage from tree felling and skidder operation cause a higher proportion of damage (Gullison and Hardner 1993). With locally large volumes, the potential for severe damage and greatly reduced subsequent yields is great at inland cativo swamps (Figure 5–4). Without improved forest management in the form of better harvest planning, worker training, and careful supervision, diameter cutting limits alone can allow massive damage to the residual stand (Sist et al. 2003).

Maintenance of species composition is desirable in cativo forests because their homogeneity imparts a substantial advantage in terms of wood production. Although species composition of cativo-dominated swamp forests is largely determined by environmental factors such as the interaction of flooding and drought (Lopez and Kursar 1999, Lopez 2002), logging might lead to shifts in species composition. Simulation models of other tropical forests have shown shifts in species composition after logging, particularly with shorter cutting cycles (Kurpick et al. 1997, Favrichon 1998, Huth and

Ditzer 2000, Phillips et al. 2003). The potential for changes in species composition after logging inland swamp forests that are relatively more diverse than riverine forests is unknown. But in a descriptive study of relatively species-rich cativo forests in Colombia 21 years after logging, Linares Prieto et al. (1997) suggest that management should increasingly focus on “second growth” cativo forests. The variable dbh cutting limit scenario in this study is probably most likely to perpetuate a cativo-dominated forest because over-harvested or cleared cativo forests have been observed to shift species composition away from cativo (Barbour 1952, Holdridge 1964). Apparently, species composition has not changed substantially in at least two of the riverine forests as a result of their logging history; they remain 95% cativo of all size classes although they are increasingly susceptible to degradation by lianas (Grauel and Putz 2004). The third riverine forest (Juanacati) is composed of 50% cativo stems but is dominated by an overstory of a few, scattered, emergent *Mora oleifera* trees. Cativo growth and recruitment rates at this site were among the fastest of ten sites and *M. oleifera* regeneration was scarce, suggesting a species shift towards cativo.

A key disincentive to improved concession-based forest management in Darien is the current forest law that limits concession periods to 5 years, with uncertain possibilities of renewal. Longer concession periods by themselves may not prevent timber mining, but given the adequate stocking and moderately fast growth rates of most cativo forests, they could help to give concessionaires financial interests for maintaining forest productivity (Gillis 1992).

This study shows the potential for continuous flows of timber from cativo-dominated swamp forests in Darien, Panama, even after 50 years of repeated-entry

logging in easily-accessed riverine forests. Inland swamps only relatively recently subjected to logging contain wood volumes rivaling those once harvested from Asian dipterocarp forests (Manokaran 1998). Despite the inherent advantages for forest management of these low diversity forests, the key to sustainability may lie in keeping society's demands for timber within the range of the forest's capacity to produce it (Johnson and Cabarle 1993).

Table 5–1. Characteristics of 4 cativo-dominated forests in Darien, Panama. “Flooding Regime” refers to the 9 month rainy season. Precipitation data are from the nearest measuring station, < 10 km away in all cases.

| Site      | Coordinates         | Landscape Position | Flooding Regime | Relative Species Diversity | Management History | Annual Precipitation (mm) | Ownership |
|-----------|---------------------|--------------------|-----------------|----------------------------|--------------------|---------------------------|-----------|
| Casarete  | 8° 07' N, 77° 52' W | riverine           | periodic        | low                        | logged             | 2457                      | private   |
| Sambu     | 8° 04' N, 78° 13' W | riverine           | periodic        | low                        | logged             | 1342                      | public    |
| Juanacati | 8° 05' N, 77° 47' W | riverine           | periodic        | higher                     | logged             | 2096                      | private   |
| Naranzati | 8° 03' N, 77° 57' W | inland             | continuous      | higher                     | intact             | 2457                      | public    |

Table 5–2. Cative volume ( $\text{m}^3 \text{ha}^{-1}$ ) and volume increment ( $\text{m}^3 \text{ha}^{-1} \text{yr}^{-1}$ ) of four cative-dominated forests in Darien, Panama.

| Site      | 40–60 cm        |                  | $\geq 60$ cm    |                  |
|-----------|-----------------|------------------|-----------------|------------------|
|           | Standing Volume | Volume Increment | Standing Volume | Volume Increment |
| Casarete  | 131.9           | 1.56             | 19.8            | 0.09             |
| Sambu     | 163.5           | 2.23             | 40.0            | 0.58             |
| Juanacati | 30.5            | 1.12             | 9.8             | 0.36             |
| Naranzati | 33.0            | 1.00             | 182.2           | 1.52             |

Table 5–3. Total volume yield after 65 years of growth and harvest simulations at three different cutting cycles for three riverine swamp forests in Darien, Panama.

| Cutting Cycle (years) | Volume $\text{ha}^{-1}$ ( $\text{m}^3$ ) |       |           |
|-----------------------|------------------------------------------|-------|-----------|
|                       | Casarete                                 | Sambu | Juanacati |
| 5                     | 36.7                                     | 74.8  | 92.4      |
| 10                    | 44.3                                     | 91.3  | 135.5     |
| 20                    | 48.5                                     | 103.2 | 165.0     |

Table 5– 4. Percentage total volume reduction due to logging-induced damage for three riverine forests at three cutting cycles.

| Cutting Cycle (years) | Casarete | Sambu | Juanacati |
|-----------------------|----------|-------|-----------|
| 5                     | 39.9     | 47.4  | 57.1      |
| 10                    | 25.8     | 36.1  | 46.4      |
| 20                    | 14.6     | 27.9  | 38.0      |

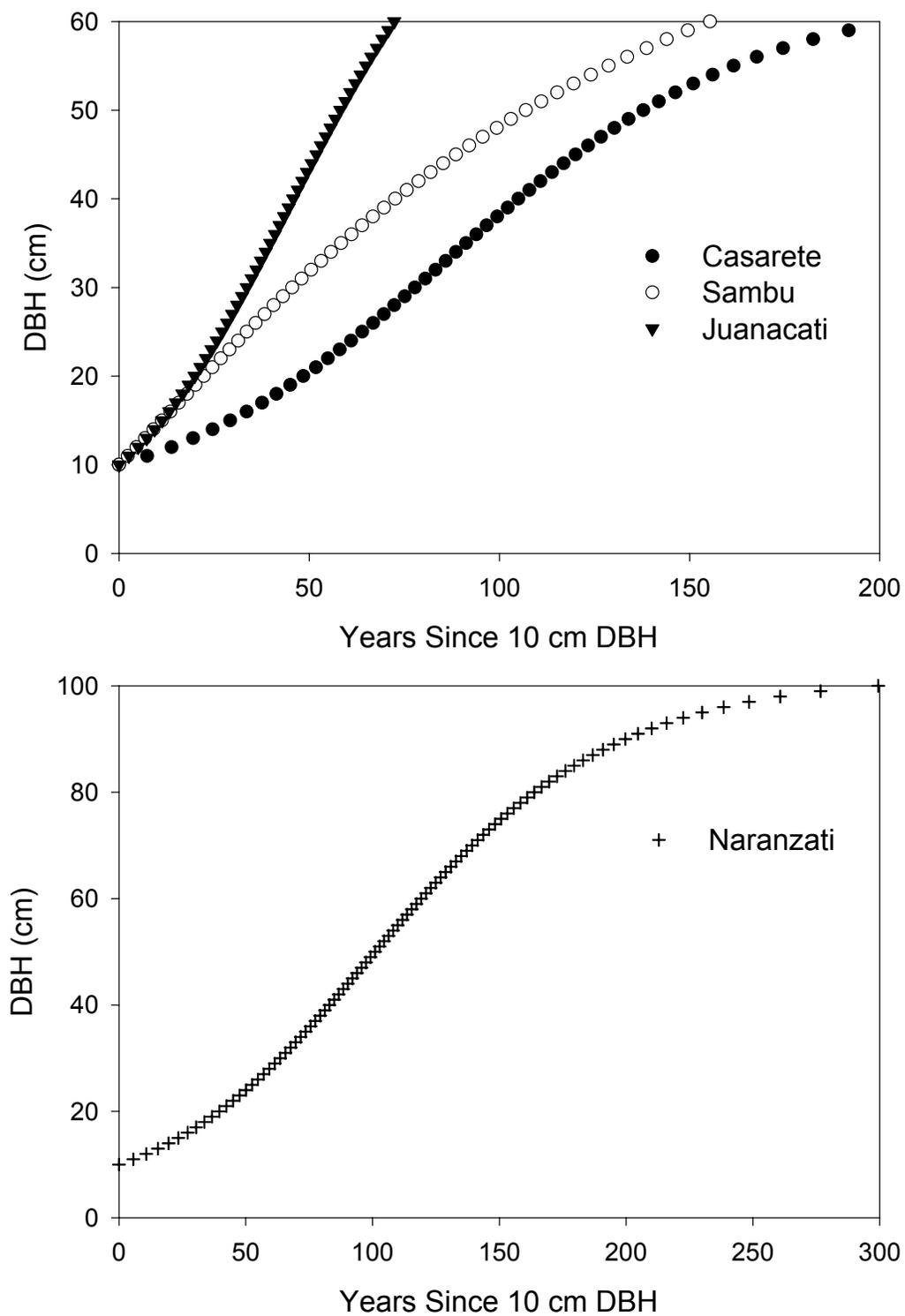


Figure 5–1. Growth trajectories of cativo at four sites in Darien, Panama starting at 10 cm dbh.

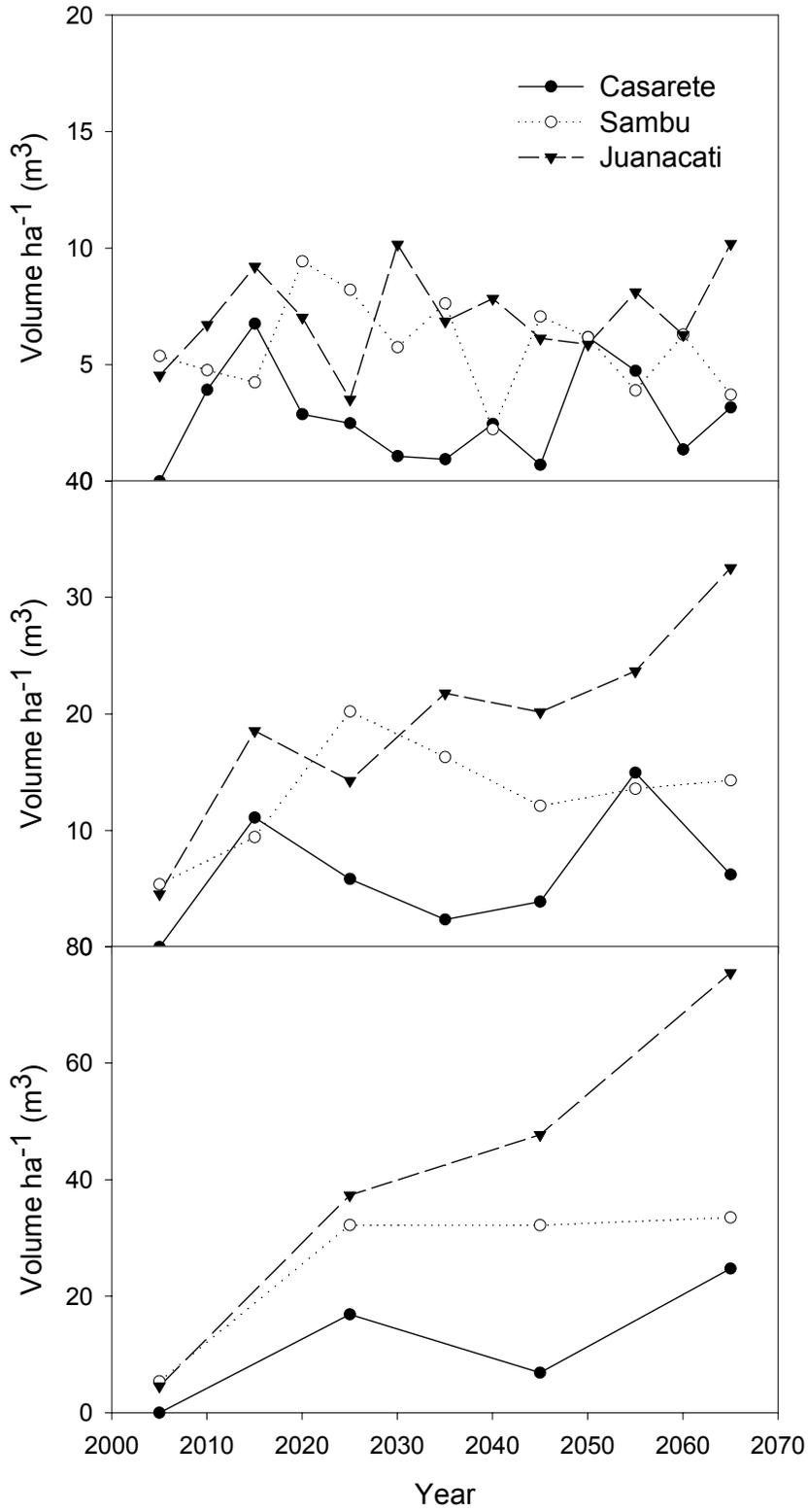


Figure 5–2. Cativo volume projections for three previously logged riverine forests in Darien, Panama. A fixed 60 cm dbh cutting limit simulated for 5-, 10-, and 20-year cutting cycles.

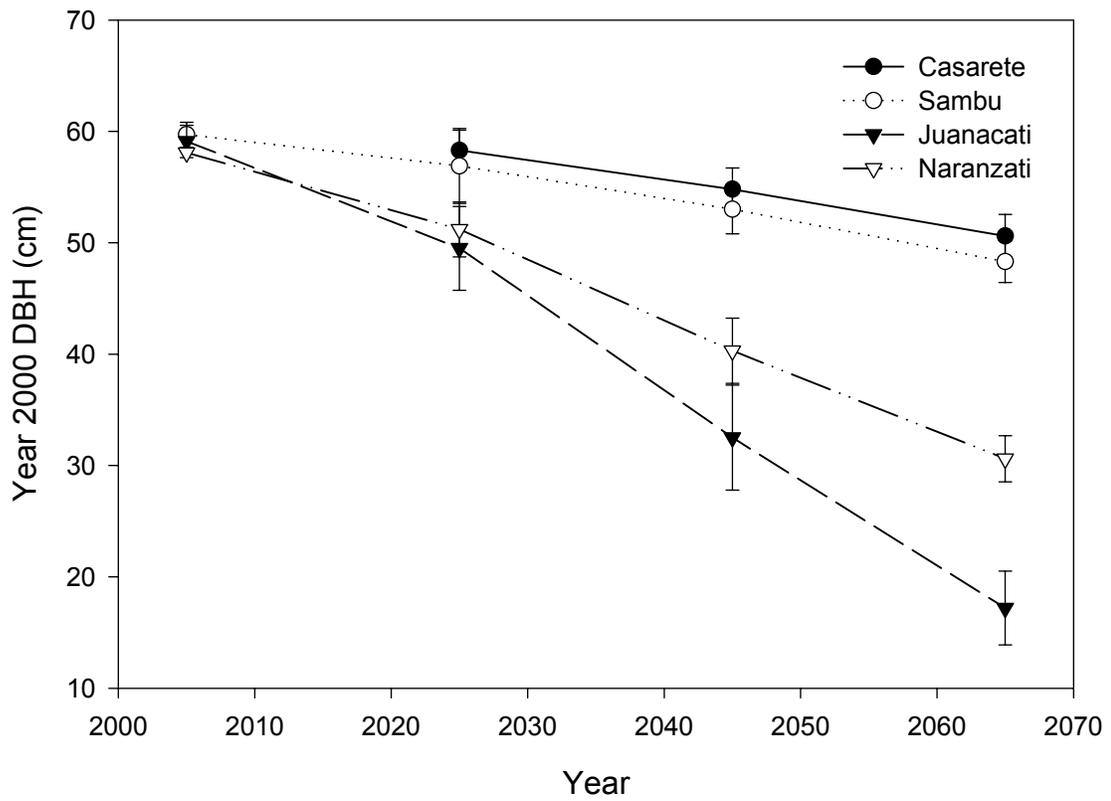


Figure 5-3. Year 2000 dbh for trees as they attain 60 cm dbh during harvest simulation of a 20-year cutting cycle. Error bars are standard deviations.

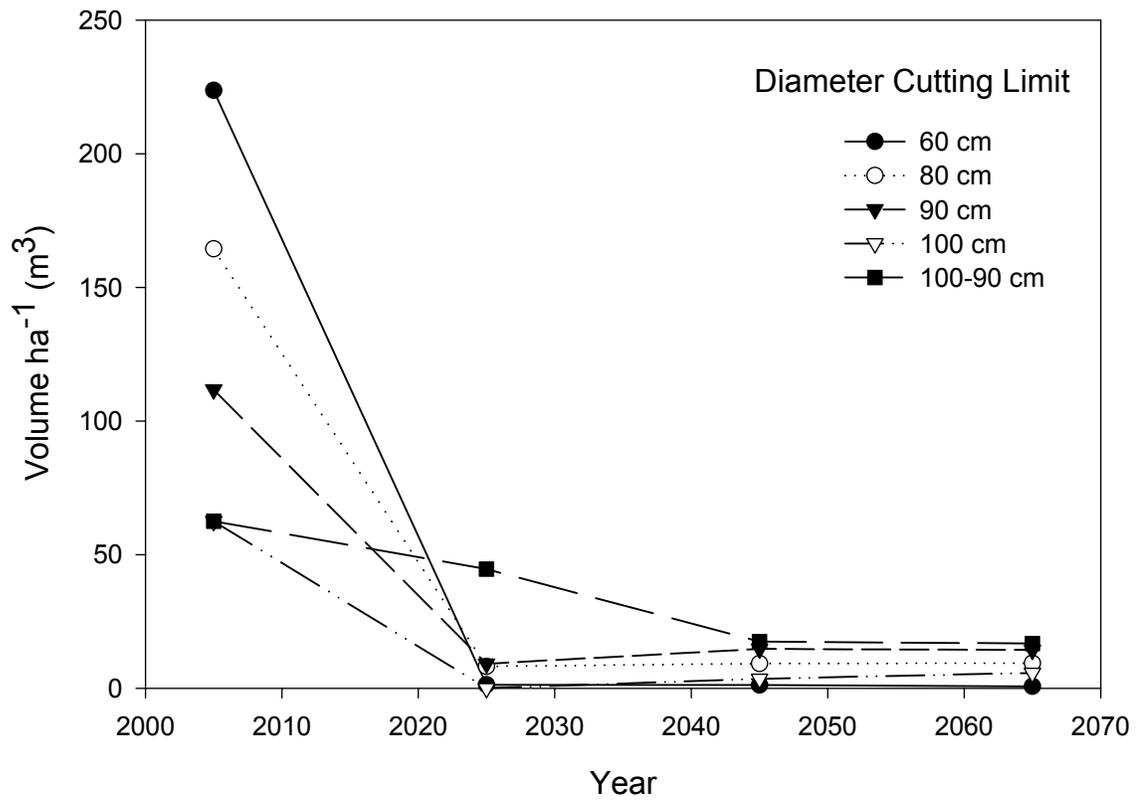


Figure 5–4. Catio volume projections for an unlogged inland swamp forest in Darien, Panama. Four fixed dbh cutting limits simulated for a 20-year cutting cycle beginning in 2005. The fifth projection is based on a 100 cm dbh cutting limit in 2005 followed by a 90 cm dbh cutting limit at subsequent harvests.

CHAPTER 6  
GEOGRAPHICAL, ECOLOGICAL, SOCIAL, AND SILVICULTURAL CONTEXTS  
FOR CATIVO (*Prioria copaifera*) SWAMP CONSERVATION IN THE DARIEN OF  
PANAMA

**Introduction**

The cativo (*Prioria copaifera*)-dominated swamp forests of Darien, Panama that have been repeatedly subjected to uncontrolled logging since the 1950s occur in rich ecological, social, and cultural landscapes. These landscapes offer opportunities but also present constraints for cativo swamp forest conservation through active management. Although many of the ecological characteristics of cativo swamp forests could foster natural forest management for timber, the forests are subject to social, economic, and political forces that have created disincentives for sustainable forest management and led to forest degradation and conversion. This paper explores the settings in which cativo forests are embedded in Darien, and tracks the historical trends of cativo timber production and swamp forest conversion.

The abundance of large, cylindrical-trunked cativo trees in the forests of Darien was noted in the 1920s (Kluge 1926, Cooper 1928), but large-scale commercial exploitation of cativo wood began in the early 1950s (Lamb 1953, OEA, Organización de Estados Americanos 1978). From the 1950s through the 1990s, cativo supplied about 50% of all sawn wood in Panama and represented 50% of the production from concessions in Darien (Castillo M. 1999). The Panamanian government has long recognized that cativo logging generates many livelihoods for people in Panama's largest and poorest province, Darien (Castillo M. 1999).

The original distribution of cativo forests has been greatly reduced by logging, development, and conversion to agriculture. In the 1950s-1970s, much cativo wood was harvested from Caribbean coastal cativo forests located behind mangrove forests in Costa Rica, Panama, and Colombia. Now, in the early 2000s, commercial stands of cativo are found only in eastern Panama and northwestern Colombia. Although cativo is also abundant in some upland forests, it never dominates the forest to the degree found in inundated forests (Condit 1993b).

Flooded forests dominated by cativo, called “cativales”, are found either as narrow bands along rivers or as inland swamps. In Darien, riverine forests are flooded periodically during the wet season (9 month) by rain and by mostly freshwater backed up by the large Pacific tides that can reach 70 km upriver. Where tidal flooding is common, many forests are strongly monodominant, with cativo comprising 95% of the woody species of all size classes. Tree growth under these conditions is slow to moderate, possibly due to the mild brackishness of floodwaters. Riverine forests far enough upriver to escape the salinity of tidal waters are more species diverse, especially in the understory, and tree growth can be quite rapid. The average size of adult trees was estimated to be 90 cm dbh (Lamb 1953), and because of their accessibility, most riverine cativo forests have been repeatedly logged. As a result, very few well-formed trees  $\geq 60$  cm in diameter at breast height (1.3 m, dbh) can be found in riverine cativales. Generally, cativo regeneration is very abundant even in forests that have been repeatedly logged, although overharvesting can result in vine infestations that can impede cativo regeneration (Grauel and Putz 2004).

Inland cativales are flooded for longer durations, up to the entire rainy season. While the forest overstory is composed of around 80% cativo, the understory is more diverse and overall tree growth is moderate. Unlogged inland swamps contain large wood volumes in well-formed, large trees. Because of their isolation and inaccessibility, many of these swamps have only started being logged in the early 1980s.

Cativo forests are found in one of the most biologically diverse regions in Central America (Herrera-MacBryde and ANCON 2001), and any approach to cativo forest conservation and management should consider the potential impacts on this biodiversity. The Gulf of San Miguel, for example, holds 46% of the mangroves of the entire country and the nearly pure stands of *Rhizophora brevistyla* rank among the world's tallest mangroves at 41m. Evergreen riparian forests are found along the major rivers Tuira, Balsas, Chucunaque, as well as many smaller streams. Cativo can be found in nearly pure stands, although the riverine forests may contain up to 66 tree species (Duke 1975).

Cativo forests are also found in and around Darien National Park, one of the largest protected areas in Central America (579,000 ha) that was established in 1980 and designated as a World Heritage Site and Biosphere Reserve shortly thereafter. Its unique flora and fauna have varying affinities due to the location's mixed biogeographical and geological history of isolation and connection. Other protected areas include various indigenous and forest reserves that, together with the national park, comprise the more than half of the province that is under some sort of management category involving environmental protection (Herrera-MacBryde and ANCON 1992).

The three dominant ethnic groups that influence the fate of cativales in Darien can be distinguished on the basis of race, culture, and historical origins (Heckadon M. et al.

1982), and have divergent views of the utility of cativo forests. Mestizo descendents of the Spaniards historically dominated Panamanian history and culture and are the most recent arrivals in Darien. These colonists from Panama's western, and largely deforested provinces, generally view forests as obstacles to agricultural and livestock production. Widening deforestation in the northern part of Darien testifies to their increasing numbers. Clearing forest and producing crops or cattle helps colonists establish land tenure rights, but cativo forests that are cleared are eventually abandoned and become mixed-species secondary growth.

African-American descendents of escaped slaves (Darienitas) dominate the politics and culture of many of the principal towns in Darien, many of which are along rivers where cativo forests are common. Slaves in increasing numbers were brought by the Spaniards to work in gold mines as indigenous populations diminished; substantial populations of Darienitas occupied Darien as early as 1770 (Cansari et al. 1993). Other African-Americans who are more recent immigrants from Colombia are referred to as Chocoanos. Cativo logging has been a principal livelihood for the black (Darienita and Chocoano) inhabitants of riverine communities such as Yaviza, El Real, Camogantí, and Sambu. They also practice subsistence agriculture and have converted many riverine cativo forests for production of plantains, rice, and root crops, especially yams and cassava.

The three indigenous groups who inhabit the province are forest-dependent groups who have generally conserved cativo forests where they have legal land tenure. Many Kuna, Embera, and Wounaan live in established, politically-recognized areas (comarcas) but others are scattered throughout the province where they have less certain land tenure.

Indigenous groups seldom engaged in cativo logging in the past, at least partly due to lack of capital. In the 1990s and early 2000s, however, they increasingly started to sell harvesting rights to cativales on the comarcas to logging companies. Even indigenous communities outside the politically-recognized lands negotiate for payment from loggers for access rights to nearby forests, despite the fact that their land claims are not yet legally recognized.

### **Timber Harvesting in Darien**

The southern portion of Darien Province is not connected to the national road system and rivers serve as the primary transportation routes. The lack of roads and the high cost of river transport have almost certainly slowed rates of colonization and consequently forest conversion (Kursar and Grauel 2002). Population density in this area in 1990 was only around 2 inhabitants per square kilometer (Cansari et al. 1993). On the other hand, the proximity of many cativo forests to rivers has undoubtedly facilitated their logging by forest product companies because transporting logs by water eliminates the need to construct roads. Cativo log rafts are either floated to La Palma for loading on barges or hauled as rafts all the way to sawmills in Panama City.

Although limited in extent, cativo forests have historically been highly valued for their timber. Cativo wood is not particularly hard, durable, or attractive; its value lies in its historical abundance and accessibility. The coastal cativo forests on the Caribbean side of Costa Rica, Panama, and Colombia supplied large quantities of raw material to the United States plywood market in the years after World War II. The cativo forests of Darien, in contrast, supplied raw material primarily for the Panamanian domestic plywood market, and it had other general uses in construction and even furniture-making. Cativo supplied 90% of the raw material for the domestic plywood industry in Panama

and 50% of sawn wood production in the country (FAO 1982). Wood production from cativo declined after reaching a peak in the late 1960s, and by the late 1990s was only a quarter of its peak (Romero M. et al. 1999). The estimated original 60,000 ha of cativo forests has been reduced to 15,000 at the end of the 20<sup>th</sup> century (ANAM 1999) and much of what remains is degraded from repeated-entry logging.

Large scale cativo harvesting in the Darien started in 1950, long before any emphasis was put on sustainable forest management (Bachmura 1972, Christiansen 1980, 1984, Martín Nuñez 1984). At the time, laws and regulations relating to forestry focused on timber extraction and reforestation rather than forest management. The policies that promoted timber harvesting were tailored to different stakeholders, but the end result of non-sustainable extraction was the same.

There are three types of tree harvesting permits that can be obtained through the Panamanian environmental ministry, ANAM (Autoridad Nacional del Ambiente). Subsistence permits are available to individuals that allow them to harvest individual trees. Community permits are limited to maximum areas of 100 ha, while concession permits allow companies to harvest timber within 2000–5000 ha areas for five years with possibilities of extension. Many of Darien's inhabitants can fit the definition of "persons of scarce resources" in Panama's Forestry Law No. 1 of February 3, 1994 and can obtain subsistence permits to harvest timber. Subsistence permits allow the holder to harvest a few individual trees each month. If the wood is destined for the plywood market, the 60 cm dbh minimum legal cutting limit is generally adhered to because the plywood factories in Panama City cannot utilize smaller logs (Castillo M. 1999). Logging with subsistence permits is carried out in the more accessible riverine forests. The local

community members cut harvestable trees as well as many smaller trees to lay end to end as a series of parallel rails. The rails facilitate the rolling of the harvested logs over the wet, soft ground to the river. This labor-intensive type of timber harvesting is potentially less damaging to forests because no heavy machinery is employed for road building or log extraction. Often however, middlemen visit the riverine communities, buy many subsistence permits from their holders, and supply chainsaws and gasoline so that the riverine cativo forests have been logged repeatedly. This practice increases the frequency with which the riverine forests are logged because community members who would not otherwise engage in logging are encouraged and paid to do so by the middlemen.

Private Panamanian companies, usually from outside Darien Province, solicit permits for forest concessions of 2000–5000 ha. Such concessions are generally located away from the major rivers and include upland forests as well as inland cativales. Currently, the maximum duration of these concessions is five years, but they are typically renewed multiple times with two-year extensions. This capital intensive logging is generally beyond the capacity of Darienitas or indigenous communities, but some Darien inhabitants obtain employment with concession operators. Management plans are required of the concessionaires by law, but they generally consist of volume and species estimates based on a few small plots and are essentially short-term harvesting plans. Concession owners operate with little incentive to plan for multiple rotation-forestry. In addition, by using heavy equipment operators who often have more experience in urban construction than in forest operations, as well as employing unsupervised fellers with informal training at best, many concessions have caused unnecessary forest damage and waste.

Community permits are typically obtained by indigenous groups for timber harvesting on the politically recognized comarcas. Although indigenous communities can obtain logging permits, they usually contract out the actual harvesting to commercial-scale concessionaires because the indigenous communities lack the capital for mechanized logging. They are free to harvest timber from riverine *cativo* forests using labor-intensive methods. Indigenous communities that are outside of the comarcas are unable to obtain community logging permits because their land tenure is uncertain. Land claims by indigenous communities outside of the comarcas are not yet politically recognized and obtaining legal land tenure is one of their principal desires (TechnoServe-Panamá 1996). A common practice is for these “*tierras colectivas*” (collective lands) communities to make agreements with commercial-scale logging concessionaires for access to logging concessions where the access routes pass through land claimed by the indigenous community.

In Darien, the amount of all timber harvested, including *cativo*, under the three different types of permits, and consequently by the different stakeholders, has varied considerably in recent years. Between 1982 and 1990, 79% of the volume of all species reportedly extracted from Darien’s forests was through concession-based logging, but in the early 1990s more wood was extracted with subsistence permits than through concessions (Torrealba 1996). Wood harvested under community permits fluctuated in the 1990s but remained a minor contribution in comparison to the other two types of permits, but this may be changing. No logging concessions have started or been renewed in the early 2000s, and Panama’s principal environmental non-government organization, Association for the Conservation of Nature (ANCON) is increasingly concerned about

the impact of community-based logging by indigenous groups (Bethancourt 2004). Because indigenous communities lack the capital necessary for mechanized logging, they typically contract out the work to concessionaires (González Apolayo 2003). Private companies who may be facing log shortages from their own poorly managed logging concessions are often willing to enter somewhat informal agreements with indigenous communities to extract logs. Such agreements usually involve cash payments as well as promises to provide infrastructure improvements such as wells or aqueducts. Problems arise particularly when agreements are made with *tierras colectivas* communities. Loggers reportedly often harvest outside of agreed upon boundaries and damage agricultural fields, actions against which indigenous communities typically find that they have little legal recourse (Vargas 2003). *Cativo* forests and other forest types have been degraded through all three types of permits by different stakeholders, but in general few benefits of timber harvesting have remained with Darien inhabitants (Vargas 2003, Bethancourt 2004).

### **Forest Conservation Perspectives**

*Cativo* forests as well as other forest types in Darien Province have been under substantial pressure from both logging and agriculture since the 1950s. The province, Panama's largest, provides the vast majority of the timber from natural forests in the country but has also experienced rapid deforestation (Torrealba 1996). Annual rates of population increase in Darien between 1980 and 1990 were greater than 5% (ANAM 1999), and from 1992-2000 the Province suffered the highest rates of deforestation in the country as 172 km<sup>2</sup> of forest were converted annually, mainly to pasture (República de Panamá 2003).

The challenges for conservation of cativo forests are similar to those facing many tropical forests. Forest degradation and deforestation increase with rising income (up to a point), rising agricultural prices, and greater accessibility (Kaimowitz and Angelsen 1998, Contreras-Hermosilla 2000). Darien Province has been a focus for colonization and development in Panama since 1950 (Hernández 1970). Now, in the early 2000s, the colonization of Darien continues, with major infrastructure developments and other projects that could result in substantial reductions in the area of cativo forests and in further degradation of the forests that remain.

Surfacing the Pan American Highway to its end in the town of Yaviza, at the confluence of the Chucunaque and Tuira Rivers, is predicted to more than halve the area of cativo forest by lowering transportation costs for timber whose principal transportation route is the Pan American Highway. The primary effect on logging of high-value species probably resulted when the road to Yaviza was opened in the 1980s. It is likely that most of the Province has been selectively cut for high value timber already. Nelson et al. (1999) concluded that the cutting of high value timber such as *Swietenia macrophylla* and *Pachira quinata* would probably not increase because their profitability of extraction would be unchanged. In other words, any reduction of transportation costs from surfacing the road would not induce increased logging of those high value species that are now only found in remote locations. Where high value species are still found, the major cost of transportation is in moving the logs from the forest to the highway. In the case of cativo forests, however, the model shows that the profitability of other land uses, especially agriculture or pasture, would increase and create financial incentives to convert some cativo forests.

Much discussion in the environmental literature has focused on the costs, benefits, and tradeoffs between natural area preservation and sustainable forest management as viable conservation tools in the tropics (e.g., Dickinson et al. 1996, Rice et al. 1997, Bowles et al. 1998, Lugo 1999, Rice et al. 2001, Wilshusen et al. 2002, Romero and Andrade 2004) but strict preservation of the remaining *cativo* forests in the buffer zones of Darien National Park would be an inappropriate conservation strategy. Where the goal is limited to biodiversity conservation, protected areas such as national parks and biosphere reserves can be effective in stopping land clearing and in mitigating the occurrence of other uses (Bruner et al. 2001). Even where biodiversity has been affected by logging, some argue for a cessation of attempts at forest management and the designation of such sites as protected areas (Reid and Rice 1997, Rice et al. 1997). Some *cativo* forests were never logged due to their remoteness and are now protected in Darien National Park, but the majority of wetland forests dominated by *cativo* are found in the buffer zones surrounding the park. Such areas were so designated specifically to provide livelihoods to local communities, and low diversity *cativo* swamps are less valued for biodiversity conservation by most people in any case. The Panamanian Environmental Ministry has designated *cativo* forests of all types in the buffer zone of Darien National Park as production forests, and their conservation should be based on their capacity to provide benefits to the local communities that live near them. Furthermore, sustainable forest management and strict preservation need not be viewed as exclusive strategies; they can be viewed as complementary ones when the perspective is on the scale of landscapes (Cabarle 1998, Lugo 1999, Whitmore 1999). A regional management approach addresses the conservation value of even human-affected areas and embeds

sustainable forest management in a diverse cultural and ecological landscape (Cannon et al. 1998, Chazdon 1998). Cative forest management is promising because it would be applied in conjunction with protected areas. Cative forests are particularly suited to being actively managed within their landscape due to their resilience and potential for wood production, even after repeated-entry logging.

Disincentives for cative forest conservation may result if prices for plywood made from cative remain low in Panama. Reduced wood production from cative forests is probably due in part to decreasing log supplies, but dynamic international tropical hardwood markets probably also played a role. Little plywood made from Panamanian cative is exported, but the prices for plywood imported into Panama have dropped and created disincentives for Panamanian producers to continue to harvest cative since plywood consumers can buy cheaper imported plywood. At the end of May 2003, prices for tropical hardwood plywood were only 50-60% of prices in 1997 (Adams 2003, ITTO Secretariat, International Tropical Timber Organization 2003). For various reasons, tropical plywood prices are among the most volatile of any commodity (ITTO Secretariat 2003), and if international prices rise, incentives for cative harvesting will also increase. But as long as imported plywood is cheaper than domestically produced plywood in Panama, decreased timber harvesting from cative forests may present an obstacle for their conservation. Logging concessions might be neglected or abandoned, for example, and left open to clearing and conversion to agriculture by colonists. Degraded riverine forests might be seen by local community members not as future sources of timber but as more valuable for subsistence crop production and consequently cleared. Alternatively,

higher prices alone may not lead to conservation of cativo forests but instead simply result in continued, unsustainable logging.

Strict financial arguments almost always favor rapid exploitation of marketable forest resources and the conversion from natural forest management to more intensive land uses (Pearce et al. 2003). Because time, more so than most other production processes, is a major input for wood production from natural forests, short-term land uses are usually more financially remunerative (Leslie 1977). Increasingly, economic arguments now include the concepts of economic equity and economic sustainability as well as simple efficiency in terms of minimizing costs and maximizing profits (Ruitenbeek and Cartier 1998). It is now generally agreed that the economic arguments against tropical forest management and conservation are incomplete unless they include non-revenue producing benefits and external effects (Leslie 1987, Barbier 1995, Pearce et al. 2003). Direct financial benefits for Darien communities from timber harvesting have apparently been limited, but cativo forests also provide benefits such as non-timber forest products and watershed services that are seldom explicitly valued by policy makers.

Historically, the economic importance of cativo swamp forests has been tied to their value for wood production, but little is known about the role they play in the hydrological cycle. Most Darien riverside communities depend to various extents on fishing for subsistence or income, but apparently no research has been done on the use of flooded cativo forests by fish. Changes in water quality or timing of flows may strongly affect fish populations and consequently those whose livelihoods or diets depend on fish (Aylward 2000). Logging has the potential to have profound effects on the physical and biological structure of streams (Campbell and Doeg 1989), especially logging of riparian

forests. Floodplain forests in Brasil were shown to be critical feeding habitats as well as refuges for many species of fish in both whitewater and blackwater rivers (e.g., Saint-Paul et al. 2000). Furthermore, increased sedimentation and turbidity resulting from deforestation can dramatically decrease fish biomass productivity (e.g., Johnson and Kolavalli 1984). Valuation of fisheries is problematical, particularly when subsistence is the end use, but undervaluing fisheries could result in an underestimation of the value of intact flooded forests and the overestimation of the value of competing land uses (Ronnback and Primavera 2000).

Despite their limited extent, cativo swamps may have an inordinate value for carbon sequestration because of their large biomass per unit area, but have not been considered separately from other forests in the same ecological lifezone (Corrales 1998). Forest conservation and land use change have major implications when formulating strategies for mitigating future carbon emissions, but patterns of deforestation and forest regrowth can vary dramatically and make estimating carbon fluxes at the regional level difficult (Saleska et al. 2003). Although it is not yet agreed upon that tropical forests are net carbon sources or carbon sinks (Clark 2002), estimates of the amount of biomass in standing forests are necessary in order to estimate the amount of carbon that would be released if forests are converted to other land uses. In tropical moist forest in Panama, Chave et al. (2003) estimated 281 Mg ha<sup>-1</sup> of aboveground biomass. In a comparison of tropical moist forest in Darien with riparian forests dominated by cativo, Golley et al. (1969) estimated over 1000 Mg ha<sup>-1</sup> in stems alone in a 0.25 ha plot in riparian forest along the Chucunaque River..

Using a regression equation published by Chave et al. (2001) from a pantropical dataset, I estimated 486 Mg ha<sup>-1</sup> of aboveground biomass for an unlogged inland swamp and 360 Mg ha<sup>-1</sup> in a riverine logged forest along the Sambu River in Darien. The inland swamp is composed of 80% cativo while the riverine forest is 95% cativo, and both estimates are for only cativo trees  $\geq 10$  cm dbh. Natural forest management on communal lands is certainly a more cost efficient manner of sequestering carbon than forest conversion for short-term agriculture, pasture, or fallows (De Jong et al. 2000).

### **Conclusions**

In addition to explicitly assigning values to environmental services of forests, a key to slowing conversion of forests designated for wood production to other land uses is to maintain their value for timber production. This idea presumes that production forests are found on land suitable for dryland agriculture or pasture, and at least some cativo forests are not so suited. Riverine cativo forests that are near mangrove forests may be inundated by slightly brackish water, while some inland swamps are probably unsuitable for the sorts of agriculture practiced in Darien due to prolonged flooding. Unfortunately, the former are degraded from repeated-entry logging under the subsistence permit system and are increasingly infested by lianas (Grauel and Putz 2004). Inland swamps and most other forest types in Darien that are logged by private companies with either concession or community permits, are subjected to timber harvesting but not forest management. Current practices, under all permit types, degrade production forests by damaging advanced regeneration.

Logging of riverine forests by labor-intensive methods and capital-intensive, mechanized logging of inland swamps may result in similar trajectories of land use change if the species of timber sought are the same. Similar to the landscape in the

Colombian province of Choco where these two types of timber harvesting occur, the southern half of Darien is characterized as a region of small agricultural holdings embedded in a relatively stable landscape of heavily degraded forests (Sierra et al. 2003). Although it appears that the “boom” period of cativo logging has passed, sustainable forest management by smallholders is still possible in such a landscape (Pinedo-Vasquez et al. 2001).

The Panamanian Environmental Ministry (ANAM) has taken measures to improve forest management in Darien, but a few additional steps could substantially increase progress towards the goal of sustainable forest management of cativo forests. With various international funding sources, particularly the International Tropical Timber Organization (ITTO), ANAM has installed permanent plots in different forest types to gather basic demographic and forest dynamic information, a critical prerequisite for realistic setting of harvest cycles and intensities (INRENARE 1982, Mariscal et al. 1999, Grauel and Pineda M. 2001). ITTO funded projects in the late 1990s and early 2000s to promote sustainable management of cativo and mangrove forests as well as the tagua palm (*Phytelephas seemanii*), a key non-timber forest species. Now that important baseline information is available, ITTO could fund efforts at strengthening the capacities of the various stakeholders involved in timber harvesting in Darien to employ reduced-impact harvest techniques such as management planning and improved tree felling and log extraction techniques. Even indigenous communities who don't carry out logging themselves would benefit. Although many such communities have legal land tenure and contract out the actual logging, they often lack the information necessary to be able to

distinguish good logging practices from bad. Such training efforts could steer what is now essentially timber mining towards true forest management.

Foresters called for a change in policy (INRENARE 1987) and the Panamanian government designated forests not suitable for agricultural use as production forests in the Forestry Law of 1994. Many Panamanian foresters recognize the potential benefits of extending the current concession period from five to twenty years. Combining longer concession periods with regulations stipulating improved forest management methods could help assure that production forests are maintained under forest cover and reduce the possibility of forest conversion after timber mining.

The goal of forest conservation is to optimize in a sustainable and equitable manner the contribution of forests to the prosperity and well-being of a wide variety of stakeholders (Poore et al. 1998). Forest degradation is not caused by local populations' disinterest in conservation but in part by historic centralization of control over forest resources, and the resulting problems of enforcing property rights while promoting sustainable livelihoods (Forest Trends 2003). The Panamanian Environmental Ministry is actively pursuing innovative partnerships with riverine communities in Darien to promote *cativo* forest management by transferring certain tenure rights to the communities over what is now public land. Although *cativo* forests seem to be in a transition phase during which their value as sources of timber is declining, this could change suddenly given that their main wood output (plywood) is produced for a highly volatile market. The watershed and carbon storage benefits that result from conserving *cativo* forests accrue to society as a whole, but the costs are borne by local communities

in the form of foregone agricultural production. The challenge is to create incentives for swamp forest conservation that benefit the people who determine their fates.

APPENDIX A  
MODELING METHODOLOGY USED IN CHAPTER 5

Regression analyses are used to fit growth estimates as a continuous function of diameter, and then instantaneous changes in dbh are calculated by treating the growth curve as a differential equation (Condit et al. 1993a). The method begins by fitting a quadratic regression to data on relative diameter growth. For each site, I expressed growth as a function of diameter with:

$$g = aL^2 + bL + c \quad \text{Eq. 1}$$

where  $g$  is instantaneous growth,  $L$  is natural log-transformed dbh, and  $a$ ,  $b$ , and  $c$  are parameters. Instantaneous growth as defined by Condit et al. (1993) is:

$$[\ln(dbh_t) - \ln(dbh_0)]/t \quad \text{Eq. 2}$$

where the subscripts  $t$  and zero denote measurements taken at time  $t$  and time 0. At low growth rates, instantaneous growth differs little from relative growth (Condit et al. 1993a).

Note that all diameters in my database are in mm, although I present results in cm. Variable names are lower case and Systat commands are upper case. The command in Systat 9.01 to express growth as a function of diameter is:

```
NONLIN  
MODEL g = a*(LOG(dbhmm)^2)+b*LOG(dbhmm)+c  
ESTIMATE / GN
```

and results in parameter estimates (Table A-1) and scatter plots with fitted lines (Figure A-1).

Table A-1. Parameter estimates for the four sites

| Site      | Parameter Estimates |           |           |
|-----------|---------------------|-----------|-----------|
|           | a                   | b         | c         |
| Casarete  | -0.009143           | 0.094461  | -0.228965 |
| Sambu     | 0.006201            | -0.090492 | 0.327912  |
| Juanacati | -0.008008           | 0.073781  | -0.133809 |
| Naranzati | -0.005378           | 0.054901  | -0.122269 |

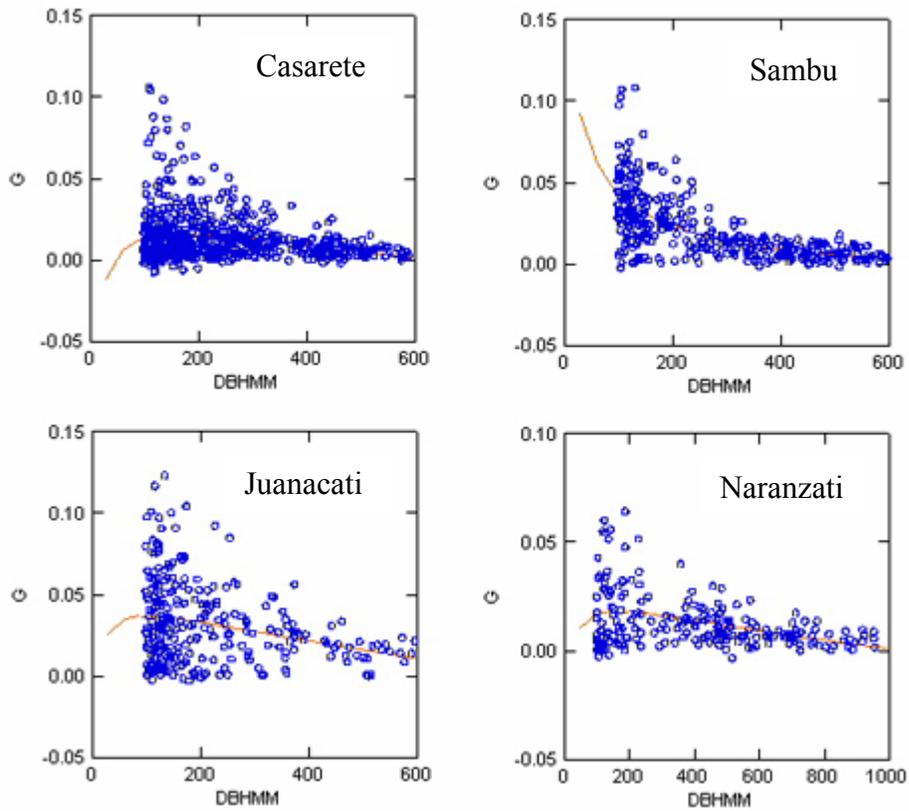


Figure A-1. Quadratic regression curves fit to relative growth data for the four sites.

An explicit solution to Eq. 1, found by direct integration, takes on different forms for different parameter values (Condit et al. 1993a). If  $b^2/4a^2 < c/a$  and  $a \neq 0$ , then, letting  $k^2 = c/a - b^2/4a^2$ , the solution is:

$$t = (1/ak) * \arctan[(L+b/2a)/k] + m \quad \text{Eq. 3}$$

If  $b^2/4a^2 > c/a$  and  $a > 0$ , letting  $k^2 = b^2/4a^2 - c/a$ , the solution becomes:

$$t = (1/2ak) * \ln[(L+b/2a-k) / (L+b/2a+k)] + m \quad \text{Eq. 4}$$

The third solution applies if  $b^2/4a^2 > c/a$  but  $a < 0$ , and, letting  $k^2 = b^2/4a^2 - c/a$ , is:

$$t = (1/2ak) * \ln[(L+b/2a+k) / (-L-b/2a+k)] + m \quad \text{Eq. 5}$$

where  $t$  is time and  $L$  is natural log-transformed dbh. The constant  $m$  is the constant of integration and is found at the initial conditions of  $t = 0$  at  $L = \ln(10 \text{ cm})$ . For Casarete, Juanacati, and Naranzati, the parameter estimates resulted in the solution of Eq. 5, while the parameter values for the Sambu data led to Eq. 4. Solving the respective equations for  $m$  at time  $t = 0$  is the next step, and the resulting constants of integration were: Casarete 38.612; Sambu 60.940; Juanacati 0.042; and Naranzati 28.700. The growth trajectories in Figure 5–1 are the result of solving the site-appropriate equation (in this case either Eq. 4 or Eq. 5) for the entire range of diameters in 1 cm steps.

In order to project future volumes with this method, the “age”, that is, the time-since-minimum-diameter (in this case 10 cm) must be estimated for each stem. Using the parameters for Casarete as an example, the Systat code to calculate this “starting age” (variable *initime*) is

```
LET a = -.009143
LET b = .094461
LET k = 1.302807
LET m = 38.612355
LET L00 = LOG(dbhmm00)
LET eq5 = -(1/(2*a*k))*(LOG((L00+(b/(2*a))+k)/(-L00-(b/(2*a))+k)))
LET initime = eq5+m
```

The variable which I called “*initime*” is necessary in order to project future diameters using either equation 3, 4 or 5 above. Next, the appropriate equation is rearranged to solve for the future diameter. In the case of Casarete, rearranging Eq.5 to estimate the diameter 5 years in the future is accomplished with the following line of Basic code:

```
LET dbh5yr = exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+5)-m)))+(k*exp((-2*a*k)*((initime+5)-m)))/(1+exp((-2*a*k)*((initime+5)-m)))
```

I used this code in a single short program that uses height estimates and basal area to estimate the commercial volume of each tree. The program applies different height estimates depending on the diameter of the tree at any given 5 year point in time. For example, to estimate volume of trees  $\geq 40$  cm in the year 2000:

```
IF dbhmm00>=600 THEN LET ht00=12
IF (dbhmm00=>400) AND (dbhmm00<600) THEN LET ht00=11.02
IF dbhmm00=>400 THEN LET vol00=.64151329*ba00m2*ht00
```

For Casarete, the remainder of the program estimates volume every 5 years up to 65 years in the future:

```
LET dbh5yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+5)-m)))+(k*exp((-2*a*k)*((initime+5)-m)))/(1+exp((-2*a*k)*((initime+5)-m)))
LET ba5=dbh5yr^2*.0000007854
IF dbh5yr>=600 THEN LET ht5=12
IF (dbh5yr=>400) AND (dbh5yr<600) THEN LET ht5=11.02
IF dbh5yr=>400 THEN LET vol5=.64151329*ba5*ht5
```

```
LET dbh10yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+10)-m)))+(k*exp((-2*a*k)*((initime+10)-m)))/(1+exp((-2*a*k)*((initime+10)-m)))
LET ba10=dbh10yr^2*.0000007854
IF dbh10yr>=600 THEN LET ht10=12
IF (dbh10yr=>400) AND (dbh10yr<600) THEN LET ht10=11.02
IF dbh10yr=>400 THEN LET vol10=.64151329*ba10*ht10
```

```
LET dbh15yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+15)-m)))+(k*exp((-2*a*k)*((initime+15)-m)))/(1+exp((-2*a*k)*((initime+15)-m)))
LET ba15=dbh15yr^2*.0000007854
IF dbh15yr>=600 THEN LET ht15=12
IF (dbh15yr=>400) AND (dbh15yr<600) THEN LET ht15=11.02
IF dbh15yr=>400 THEN LET vol15=.64151329*ba15*ht15
```

```
LET dbh20yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+20)-m)))+(k*exp((-2*a*k)*((initime+20)-m)))/(1+exp((-2*a*k)*((initime+20)-m)))
LET ba20=dbh20yr^2*.0000007854
IF dbh20yr>=600 THEN LET ht20=12
IF (dbh20yr=>400) AND (dbh20yr<600) THEN LET ht20=11.02
IF dbh20yr=>400 THEN LET vol20=.64151329*ba20*ht20
```

```
let dbh25yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+25)-m)))+(k*exp((-2*a*k)*((initime+25)-m)))/(1+exp((-2*a*k)*((initime+25)-m)))
```

```
LET ba25=dbh25yr^2*.0000007854
```

```
IF dbh25yr>=600 THEN LET ht25=12
```

```
IF (dbh25yr=>400) AND (dbh25yr<600) THEN LET ht25=11.02
```

```
IF dbh25yr=>400 THEN LET vol25=.64151329*ba25*ht25
```

```
LET dbh30yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+30)-m)))+(k*exp((-2*a*k)*((initime+30)-m)))/(1+exp((-2*a*k)*((initime+30)-m)))
```

```
LET ba30=dbh30yr^2*.0000007854
```

```
IF dbh30yr>=600 THEN LET ht30=12
```

```
IF (dbh30yr=>400) AND (dbh30yr<600) THEN LET ht30=11.02
```

```
IF dbh30yr=>400 THEN LET vol30=.64151329*ba30*ht30
```

```
LET dbh35yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+35)-m)))+(k*exp((-2*a*k)*((initime+35)-m)))/(1+exp((-2*a*k)*((initime+35)-m)))
```

```
LET ba35=dbh35yr^2*.0000007854
```

```
IF dbh35yr>=600 THEN LET ht35=12
```

```
IF (dbh35yr=>400) AND (dbh35yr<600) THEN LET ht35=11.02
```

```
IF dbh35yr=>400 THEN LET vol35=.64151329*ba35*ht35
```

```
LET dbh40yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+40)-m)))+(k*exp((-2*a*k)*((initime+40)-m)))/(1+exp((-2*a*k)*((initime+40)-m)))
```

```
LET ba40=dbh40yr^2*.0000007854
```

```
IF dbh40yr>=600 THEN LET ht40=12
```

```
IF (dbh40yr=>400) AND (dbh40yr<600) THEN LET ht40=11.02
```

```
IF dbh40yr=>400 THEN LET vol40=.64151329*ba40*ht40
```

```
LET dbh45yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+45)-m)))+(k*exp((-2*a*k)*((initime+45)-m)))/(1+exp((-2*a*k)*((initime+45)-m)))
```

```
LET ba45=dbh45yr^2*.0000007854
```

```
IF dbh45yr>=600 THEN LET ht45=12
```

```
IF (dbh45yr=>400) AND (dbh45yr<600) THEN LET ht45=11.02
```

```
IF dbh45yr=>400 THEN LET vol45=.64151329*ba45*ht45
```

```
LET dbh50yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+50)-m)))+(k*exp((-2*a*k)*((initime+50)-m)))/(1+exp((-2*a*k)*((initime+50)-m)))
```

```
LET ba50=dbh50yr^2*.0000007854
```

```
IF dbh50yr>=600 THEN LET ht50=12
```

```
IF (dbh50yr=>400) AND (dbh50yr<600) THEN LET ht50=11.02
```

```
IF dbh50yr=>400 THEN LET vol50=.64151329*ba50*ht50
```

```
LET dbh55yr=exp((-b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+55)-m)))+(k*exp((-2*a*k)*((initime+55)-m)))/(1+exp((-2*a*k)*((initime+55)-m)))
```

```
LET ba55=dbh55yr^2*.0000007854
```

```

IF dbh55yr>=600 THEN LET ht55=12
IF (dbh55yr=>400) AND (dbh55yr<600) THEN LET ht55=11.02
IF dbh55yr=>400 THEN LET vol55=.64151329*ba55*ht55

LET dbh60yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+60)-m)))+(k*exp((-2*a*k)*((initime+60)-m)))/(1+exp((-2*a*k)*((initime+60)-m))))
LET ba60=dbh60yr^2*.0000007854
IF dbh60yr>=600 THEN LET ht60=12
IF (dbh60yr=>400) AND (dbh60yr<600) THEN LET ht60=11.02
IF dbh60yr=>400 THEN LET vol60=.64151329*ba60*ht60

LET dbh65yr=exp(-(b/(2*a))-k-((b/(2*a))*exp((-2*a*k)*((initime+65)-m)))+(k*exp((-2*a*k)*((initime+65)-m)))/(1+exp((-2*a*k)*((initime+65)-m))))
LET ba65=dbh65yr^2*.0000007854
IF dbh65yr>=600 THEN LET ht65=12
IF (dbh65yr=>400) AND (dbh65yr<600) THEN LET ht65=11.02
IF dbh65yr=>400 THEN LET vol65=.64151329*ba65*ht65

```

Once the variables ‘volxx’ were created, for each 5, 10, or 20 year “harvest”, I selected only trees  $\geq 60$  cm dbh, but  $< 60$  cm dbh 5, 10, or 20 years previously (depending on the cutting cycle being simulated), calculated the total volume, and estimated their average diameter as it was in the year 2000. For example, the following two blocks of code simulate a harvest at years 15 and 20, in which only trees that attained 60 cm dbh in a given 5 year period can be included in a harvest:

```

SELECT (dbh15yr=> 600) AND (dbh10yr< 600)
STATS vol15 / SUM N
STATS dbhmm00 / MEAN SD N

SELECT (dbh20yr=> 600) AND (dbh15yr< 600)
STATS vol20 / SUM N
STATS dbhmm00 / MEAN SD N

```

In this way I simulated a timber harvest every 5 years (as well as 10 and 20 years for the riverine sites) with a 60 cm dbh cutting limit (as well as 80, 90, and 100 cm dbh limits for the inland swamp site).

APPENDIX B  
SOURCE DATA FOR CHAPTERS 4 AND 5

The data in identical files *cativodata.xls* and *cativodata.csv* are the source data for Chapters 4 and 5. These files contain all diameter measurements, associated codes and notes, and annual growth and basal area calculations for each individual stem. The species names recorded in the year 2000 are the most reliable, as earlier years contain some common names or misidentifications. Codes for individual stems, initially designated in Spanish, are:

- S = suelo; a prostrate stem.
- I = inclinado; an inclined stem.
- M = múltiple; erect stem sprouts from an inclined or prostrate stem.
- R = rebrote; resprouted erect stem.
- B = bifurcado; a forked stem.
- Q = quebrado; a broken stem.
- E = herido; a wounded trunk;
- H = hinchado, swollen trunk;
- A = arqueado, a stem arched over, by a fallen tree or branch.

Most column titles are self-explanatory. The column titles *agroXX-XX* and *rgroXX-XX* refer to annual absolute growth and annual relative growth, respectively, for given census intervals. The column title *POMm* contains the Point Of Measurement above the ground of individual stems in meters; *M distance from root m (resprouts)* pertains to stems coded as *M* and is the distance in meters that these stems are found from the roots of the parent, inclined or prostrate, stem. The *crown illumination index* in this data is from Clark and Clark (1999). The columns *longagro* and *longrgro* contain annual growth increments (absolute and relative growth, respectively) based on the longest census interval available

for each tree. Because plot installation work was interrupted in 1997 at Juanacati (paramilitary incursion) and Naranzati (I contracted dengue), and some plots were installed in 1998, the last column *origdbhmm* contains the first diameter measurement, whether from 1997 or 1998, in a single column.

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