

SHORT COMMUNICATION

Demography, phenology and sex of *Calophyllum brasiliense* (Clusiaceae) trees in the Atlantic forest

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Further studies on growth and reproduction of many tree species are needed to know the regeneration patterns of tropical forests (Clark & Clark 1987, Heideman 1989). Thus, the need for studies on the *c.* 3% of Atlantic forest that remains in Brazil is acute, particularly in the rarely studied swamp habitats (Scarano *et al.* 1997). We studied the canopy tree species *Calophyllum brasiliense* Camb. (Clusiaceae) in flooded and unflooded habitats of a coastal lowland rain forest, in order to describe demography, sexual expression, phenology and flower and fruit production. We report the differences of such traits among three contiguous habitats found in the lowlands – unflooded forest, freshwater-flooded forest and mangrove.

The genus *Calophyllum* comprises *c.* 175 tree and shrub species, mainly found in lowland rain forests of Southeast Asia (Stevens 1980). *Calophyllum brasiliense* is a common canopy tree (~20 m height) found in South and Central American forests (Holl 1998, Reitz *et al.* 1978). It is often planted in reforestation efforts and its wood is commercially exploited in the Amazon (Alencar *et al.* 1981, Holl 1998). *Calophyllum brasiliense* does not propagate vegetatively (Scarano *et al.* 1997). The small (< 1 cm diameter) ‘pollen flowers’ are mainly pollinated

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by halictid bees. Fruits are spherical drupe-like berries with one large (18–23 mm diameter) spherical seed. At the study site, *C. brasiliense* seeds were dispersed from parents by gravity or by the phyllostomid bats *Artibeus lituratus*, *A. obscurus*, *Carollia perspicillata* and *Pygoderma bilabiatum* (pers. obs.). Bats eat the pulp and discard seeds under their feeding roosts (Sazima *et al.* 1994). Seeds can also be secondarily water-dispersed, being carried and deposited downstream (Fischer 1997, Marques & Joly 2000a).

The study was conducted in old-growth forest near the estuary of Rio Verde at the Juréia Ecological Station, southeastern Brazil (24°30' S, 47°15' W). The climate is tropical and wet, with a modest dry season from April to August. The average annual rainfall is 4200 mm and average temperature is 23 °C. The lowland forest near the Rio Verde estuary comprises *c.* 116 ha surrounded by hills and the ocean (for study site description, see Fischer 1997, Fischer & Araujo 1995). We investigated three habitats at the Rio Verde estuary with different flooding conditions: freshwater-flooded forest along tributaries of the Rio Verde, mangrove at the river salinity gradient, and unflooded forest with dense canopy away from water-courses. For 45 mo, from July 1988 to March 1992, we visited the study site monthly to record flowering and fruiting *C. brasiliense* trees, and also the periods of seed dispersal and germination in the three habitats. Every month we inspected *c.* 1.3 ha in unflooded forest, 0.8 ha in mangrove and 0.4 ha in freshwater-flooded forest.

In August 1989 and again in February 1991, individuals of *C. brasiliense* were censused in eight 10-m × 10-m plots in order to study demography. Two plots were in unflooded forest, and three plots were in each of the other two habitats, freshwater-flooded forest and mangrove. Before locating the plots, we selected sections of existing trails that were representative of such habitats to use as transect lines. To avoid possible edge effects near the trail, we decided to place the plots 50 m to the right of the transect line, 200 m apart. Individuals within the plots were mapped and their heights were registered. Individuals up to 2 m were measured with a metre tape, and heights of taller individuals were estimated to ± 0.5 m. They were classified according to developmental stage (cf. Gatsuk *et al.* 1980): seedlings (up to 0.4 m height, the maximal height of individuals presenting cotyledons), juveniles (0.4 < height ≤ 1.0 m), immatures (1.0 < height ≤ 3.0 m) and adults (taller than 3.0 m, the minimum height of flowering trees at the study site). Between the census dates we recorded no fruiting, so there was no input of seeds during the 18-mo interval. Annual mortality rates were estimated using the model of Swaine & Lieberman (1987), and annual transitions were estimated using the same model but substituting the number of dead individuals with the number of individuals that grew up to the subsequent stage. We recorded no transitions to previous stage.

During the flowering season of November 1991 we found 66 flowering trees – one in unflooded forest, 38 in mangrove and 27 in freshwater-flooded forest. To determine sexual expression, we climbed 22 of these trees and sampled flowers

in different parts of their crowns. The 22 trees were the first ones found in each habitat. Nine trees (8.6 ± 2.4 m in height) were in freshwater-flooded forest, 12 trees (9.2 ± 2.3 m in height) in mangrove, and one tree (7 m in height) in unflooded forest. Of these 22 trees, we haphazardly selected five hermaphrodite trees in freshwater-flooded forest, five hermaphrodite and five male trees in mangrove, plus the only one found in unflooded forest. From November 1991 to March 1992, we climbed these 16 trees biweekly to monitor their flower and fruit production. We counted the flowers produced in at least 10 inflorescences per tree, and counted inflorescences on different branches totalling 35–50% of the crown. By extrapolation we estimated the number of inflorescences in the total crown, and multiplied it by the mean number of flowers per inflorescence to estimate the total number of flowers produced per tree. To estimate number of mature fruits per tree, we counted immature infructescences in the entire crown and bagged 10–15 of them with tulle to monitor abortion in early stages and to avoid dispersal of mature fruits. Based on the mean ripe fruits among bagged infructescences, multiplied by the number of infructescences in the crown, we estimated the number of mature fruits per tree.

At the Rio Verde estuary, *C. brasiliense* presented the general reverse-J frequency of size distribution, indicating that the species recruits young individuals through time. With data from the three habitats pooled, size structures differed between the two censuses dates ($\chi^2 = 64.3$, $df = 3$, $P < 0.001$), mainly due to variation in the seedling size class. At the first census in the eight plots, the number of seedlings was greater than that of individuals in other stages. In mangrove, the number of adults and immatures was greater than the number of juveniles; the opposite was found in freshwater-flooded forest. Individuals taller than seedlings were absent in the two plots in unflooded forest. Particularly in mangrove, immatures and adults were more abundant than seedlings at the second census, indicating a relatively low seedling recruitment in this habitat.

Calophyllum brasiliense presented the general pattern of size-dependent survivorship described for tree species (Clark & Clark 1987, De Steven 1994). The total density declined *c.* 50% throughout the 18-mo interval, from 1539 to 759 individuals in the 800 m² surveyed, with an overall mortality rate of 47.1% y^{-1} (Table 1). The proportion of individuals dying in the time interval differed among stages ($\chi^2 = 17.1$, $df = 2$, $P < 0.001$). Mortality rates varied from 50.7% y^{-1} in seedlings to 6.4 % y^{-1} in immatures, with no mortality of adults. In spite of the overall high mortality, seedlings of *C. brasiliense* occurred through the 45-mo study period, forming a seedling bank at the study site (Fischer 1990). The proportion of individuals dying in the time interval also differed among habitats ($\chi^2 = 14.9$, $df = 2$, $P < 0.001$). Mortality rate of juveniles was three times higher in freshwater-flooded forest than in mangrove, but mortality of seedlings, immatures and adults were similar between these two habitats (Table 1). Although presenting higher juvenile mortality, density of juveniles

Table 1. Annual mortality and transition rates of *Calophyllum brasiliense* in different stages and habitats at the Juréia Ecological Station, Brazil. Estimations were based on an 18-mo interval between two censuses; numbers of individuals in the first census are in brackets.

Stages		Habitats			Total			
		Unflooded forest	Freshwater-flooded forest	Mangrove				
Mortality	Seedling	0.988	(22)	0.503	(1390)	0.462	(30)	0.507
	Juvenile	–	–	0.245	(26)	0.079	(9)	0.198
	Immature	–	–	0.064	(11)	0.064	(22)	0.064
	Adult	–	–	0	(10)	0	(19)	0
	Total	0.988		0.487		0.170		0.471
Transitions	Seedling → Juvenile	0	(22)	0.006	(1390)	0.070	(30)	0.007
	Juvenile → Immature	–	–	0.082	(26)	0.270	(9)	0.125
	Immature → Adult	–	–	0.064	(11)	0.134	(22)	0.110

in freshwater-flooded forest slightly increased in the second census (1991) because transitions from seedlings overcompensated mortality of juveniles. Seedling mortality in unflooded forest was much higher than in the other habitats, and contrasted with the low mortality described for seedlings of shade-tolerant tree species (e.g. De Steven 1994). Transitions of *C. brasiliense* individuals into taller size classes during the 18-mo interval occurred in freshwater-flooded forest and mangrove only (Table 1). Transition rates in mangrove were higher than in freshwater-flooded forest, but in both habitats transition rates were higher from juveniles to immatures and lower from seedlings to juveniles. Fischer (1990) pointed out that the most extreme shade condition occurs in unflooded forest, followed by intermediate shading in freshwater-flooded forest, with mangrove being an open canopy site. Therefore, the transition rates decreased (and mortality increased) as shade intensity increased among the habitats, which agrees with that found for other *C. brasiliense* populations (Holl 1998, Marques & Joly 2000b).

Flowering and fruiting of *C. brasiliense* appear to be supra-annual and irregular events (*sensu* Newstrom & Frankie 1994). The time interval between the two consecutive fruiting episodes at the study site was *c.* 41 mo; the first one (1988) occurred in the dry season and the last (1992) during the wet season (Figure 1). Individuals in different habitats were synchronous, except that three plants in mangrove presented male flowers in December 1989. Other long-term phenological data for *C. brasiliense* were not found, but the period of fruiting season reported for this species in Brazil differs among authors (Inoue *et al.* 1984, Lorenzi 1992, present study). A supra-annual, irregular phenological pattern is less common among neotropical tree species (Newstrom & Frankie 1994), but it is a notable feature of trees in Southeast Asia where most *Calophyllum* species occur (Stevens 1980, Yap & Chan 1990). The unpredictability of *C. brasiliense* reproductive episodes near the Rio Verde estuary might allow temporal escape from herbivory for flowers and seeds. In addition, unpredictable

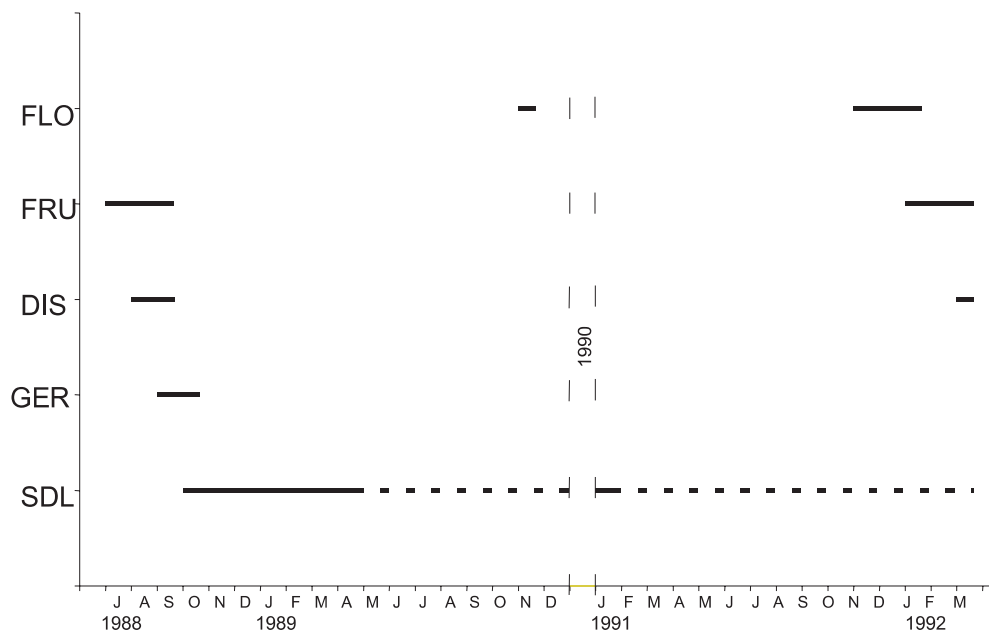


Figure 1. Phenological events of *Calophyllum brasiliense* near the Rio Verde Estuary, Juréia Ecological Station, Brazil. FLO, flowering; FRU, fruiting; DIS, seed dispersal from parents; GER, seed germination; SDL, seedling establishment (continuous line) and seedling occurrence throughout the study (dashed line). Note 1990 is omitted since no events occurred in this year.

breeding seasons disfavour specialization of plant–animal interactions and should imply associations with generalist flower and fruit visitors, such as found for *C. brasiliense* at the study site. Seeds of *C. brasiliense* germinated soon after dispersal (Figure 1). Most seeds that failed to germinate during this period were preyed on by vertebrates, such as *Sciurus aestuans* (Sciuridae), or consumed by fungus and invertebrates. Attacks of seed consumers are reported to be high at the Rio Verde estuary, and seeds apparently need to germinate rapidly to escape predation (Fischer 1997). Since seeds of *C. brasiliense* are potentially dormant and might remain in the soil for an increased time (Marques & Joly 2000a, Scarano *et al.* 1997), attacks of seed consumers may be abbreviating the period in which seeds germinate at the study site.

Calophyllum brasiliense presented male and hermaphrodite flowers. The male flowers were similar to hermaphrodites in size and morphology, except for the absence of a pistil. Most neotropical Clusiaceae are dioecious, but neotropical species in the subfamily Calophylloideae are regarded as having perfect flowers (Gentry 1996). The presence of male flowers for *C. brasiliense* at the study site may be the first record among neotropical *Calophyllum* species; dioecy is already known for this genus in the Old World tropics (Stevens 1980). Each tree of *C. brasiliense* presented only one flower type, so individuals were males or hermaphrodites. The proportion of male trees was significantly ($\chi^2 = 4.42$, $df = 1$, $P < 0.05$) higher in mangrove than in freshwater-flooded forest. All nine inspected trees in freshwater-flooded forest were hermaphrodites, the 12 trees

in mangrove were males (58%) or hermaphrodites (42%), and the only one found in unflooded forest was hermaphrodite. Nonetheless, outside the studied lowland forest (at rocky shores, see Fischer & Araujo 1995), we found an individual that showed both flower types with 1:8 hermaphrodite-male ratio ($n = 900$ flowers inspected). The male flowers of *C. brasiliense*, therefore, occurred only in the saline habitats at the Rio Verde estuary. Segregation of sexes according to habitats with different conditions has been commonly documented for dioecious trees; indeed such a pattern of sex distribution indicates one route to evolution of dioecy (Bawa 1980, Iglesias & Bell 1989). Additionally to the sexual variance among habitats, we recognized one *C. brasiliense* tree in mangrove that had produced seeds (and so hermaphroditic flowers) in 1988 but it was male in 1992, an anecdotal record suggesting that *C. brasiliense* may also change sexual expression among flowering seasons. Switches from male to female and vice versa have rarely been documented for tropical trees because most studies are based on a single flowering season, as is this one (but see Wheelwright & Bruneau 1992).

Among the *C. brasiliense* trees sampled biweekly for flower and fruit production, those hermaphrodites in freshwater-flooded forest produced *c.* 15 times more flowers (mean \pm SD; $42\,000 \pm 8600$, $n = 5$) and 80 times more fruits (1600 ± 700 , $n = 5$) than hermaphrodites in mangrove (2900 ± 2000 flowers and < 20 fruits, $n = 5$). For all hermaphrodite trees pooled, number of ripe fruits was a function of flowers produced (Fruits = 0.04 Flowers; $r^2 = 0.95$; $P < 0.001$; $n = 10$). The low flower and seed production might imply a reduced fitness through female function for the hermaphrodite trees in mangrove. In addition, the male *C. brasiliense* trees produced four times more flowers ($12\,000 \pm 9900$, $n = 5$) than hermaphrodites in mangrove, so males might have more opportunities for siring offspring and they may present higher fitness through the male function than the hermaphrodites in this habitat (Klinkhamer *et al.* 1994). Mean height of flowering trees in mangrove did not significantly differ from those in freshwater-flooded forest ($P = 0.56$; t-test) and tree height was not correlated ($P > 0.05$) with flower or fruit production. Mean height did not differ between males and hermaphrodites in mangrove ($P = 0.36$; t-test). The only flowering tree in unflooded forest produced *c.* 8000 flowers and 980 mature fruits, values that were closer to trees in freshwater-flooded forest. It has been found that male flowers tend to occur in harsh habitats whereas most females occur in more favourable sites (e.g. Freeman *et al.* 1981), thus sexual trends indicate that mangrove may be a harsher habitat for reproduction of *C. brasiliense*.

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