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ESTABLISHMENT AND DEATH OF TWO DRY TROPICAL FOREST WOODY SPECIES IN DRY AND RAINY SEASONS IN NORTHEASTERN BRAZIL¹

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Abstract: The influence of dry and rainy seasons on the establishment and death of individuals of *Croton sonderianus* and *Caesalpinia pyramidalis* was investigated in a caatinga dry tropical forest in Caruaru, Pernambuco, NE Brazil (8°14' S, 35°55' W, 537m altitude) during 1995 (rainy and dry seasons) and 1996 (rainy season). The rates of birth and population growth increased during the rainy seasons and remained stable during the dry season. Both species responded in different ways to rainy or dry season. During the rainy seasons, *C. pyramidalis* had birth rates similar to or larger than *C. sonderianus*. Seeds are dormant in *C. sonderianus* and quiescent in *C. pyramidalis*, and both species form seed bank. *C. pyramidalis* seeds are dispersed from the middle of the rainy season (these germinate immediately) to the beginning of the dry season (these germinate at the beginning of the following rainy season). If there is sporadic rain during a dry season, births occur, but mortality affects most seedlings. The dispersion of *C. sonderianus* seeds is concentrated in the middle of the rainy season, but they germinate only at the beginning of the next rainy season. *C. sonderianus* seedlings have more time to establish, but a sporadic dry episode during a rainy season may cause high mortality. The maintenance of *C. sonderianus* population during dry years is helped by vegetative reproduction. The ration between the number of individuals of the two populations did not alter during the study period.

Key Words: Caatinga, *Caesalpinia pyramidalis*, *Croton sonderianus*, population dynamics, population rates, dry tropical forest

Introduction

In dry forests, the temporal patterns of the biological activities of plants, such as reproduction and growth, and the geographical distribution of some species are influenced by water availability during certain periods of the year (Murphy & Lugo,

1986). Species in dry forests have their reproductive, physiological and morphological characteristics synchronized with local water availability (Bullock, 1995; Holbrook *et al.*, 1995). The diversity, growth forms and phenodynamics of the vegetation, as well as population rates and biotic interactions are strongly influenced by climate.

In Brazil, Dry forests occur mostly in the northeastern region as different xerophilous vegetation formations, which in conjunct are called caatinga (singular) or caatingas (plural). Many different studies were made on the caatingas (Sampaio *et al.*, 1996), but so far no research on aspects of population dynamics has been developed (Araújo, 1998). The caatingas are characterized by lower species diversity than other less dry forest formations, but, as the floristic composition changes between different physiognomies, considerable species richness is found when the entire caatinga domain is considered. The caatinga vegetation is exposed to strong climatic seasonality and it is considered as one abiotical factor stress. The rainy season is characterized by erratic, irregularly distributed rains, while the dry season lasts approximately seven months. The majority of woody species is deciduous during the dry season, replacing the leaves at the onset of rains. Such species present periodic, intermittent growth, but may last years without producing flowers or fruits (Araújo, 1998; Machado *et al.*, 1997).

Considering the importance of water in dry forests (Murphy & Lugo, 1986), we could expect dry or rainy season to exert a powerful influence upon rates of establishment and death, regulating population dynamics of coexistent species in the plant communities of the caatingas. If water availability were a prevailing factor controlling establishment and death rates, we would expect these rates to differ between rainy and dry seasons, with the establishment rate higher during the rainy season and the death during the dry season. The balance between establishment and death rates should result in population increase during the rainy season and decrease during the dry season. This study aims to evaluate the effect of dry and rainy seasons on the rates of establishment and death in two dry forest woody populations by answering the following questions: 1) What would happen to population size through a period of one and half year? 2) Are the establishment and death rates different between rainy and dry seasons? 3) Do populations of coexisting species respond similarly to rainy and dry seasons?

Material and methods

Study area - The study was conducted in the experimental research station of the Empresa Pernambucana de Pesquisa Agropecuária — IPA (8°14' S, 35°55' W, 537 m altitude), in the municipality of Caruaru, state of Pernambuco, northeastern Brazil. The

study area consists of a 30-ha fragment of dry forest on Podzolic soil, and has been protected against fire since 1965 (Alcoforado-Filho *et al.* 2003). The annual average temperature is of 22.7 °C and 710 mm rainfall, most falling between February and August. Variations may occur between years, with dry episodes soon after the beginning of the first rains, causing a short drought. In 1995, rains were erratic with almost no precipitation in March (Araújo 1998), but in the study area, trees had leaves during March to August both in 1995 and 1996, and were completely leafless from September 1995 to February 1996. This kind of caatinga is regionally called agreste, with a forest physiognomy and floristic predominance of Leguminosae and Euphorbiaceae (Alcoforado-Filho *et al.*, 2003).

Species studied - The species considered in this study, *Caesalpinia pyramidalis* Tul. (Caesalpinaceae) and *Croton sonderianus* Muell. Arg. (Euphorbiaceae), have wide distribution and high density in the caatingas in northeastern Brazil (Araújo 1990, Araújo *et al.* 1995b). In the study area, *C. pyramidalis* and *C. sonderianus* have higher relative density than other species with which they coexist (Alcoforado-Filho *et al.*, 2003). Both species are perennial, iteroparous, and locally used for firewood, charcoal, and honey production (Pereira *et al.*, 1989; Sales & Araújo-Lima, 1989).

C. pyramidalis, commonly known as catingueira, is a tree up to 8 m high and trunk diameter up to ca. 27 cm at ground level, with barocoric dispersion, and seeds with varied size). *C. sonderianus*, commonly called marmeleiro, is a shrub up to 4 m high and a trunk diameter up to ca. 15 cm at ground level; primary dispersion is explosive-autochoric, secondary dispersion is myrmecochoric, and its seeds are polymorph in shape, size and color (Araújo, 1998; Araújo *et al.*, 1995ab; Machado *et al.*, 1997). Both species are deciduous in the dry season, and all individuals in the study area completely lost their leaves at the very beginning of the dry season and remained so until the first rains. Many other species in the community showed a similar response to drought, so that young unbranched individuals of woody species looked like skewers fixed in the soil.

Experiments on germination carried out in the field, in the laboratory and in the glasshouse (unpublished data), and the observations we made on the field showed that both species can form seed banks. *C. pyramidalis* has quiescent seeds, that is, the seeds germinate as soon as water is available. *C. sonderianus* has dormant seeds, which germinate only about one year after being produced, that is, they germinate at the beginning of the rainy season in the next year after their dispersion. Controlled pollination experiments were also carried out (unpublished data), and showed that *C. pyramidalis* reproduces only sexually, while *C. sonderianus* can reproduce sexually, by vegetative propagation, and by viable seeds produced by agamospermy. During the

study period, the liberation of seeds from the mother plants concentrated in the middle of the rainy season in *C. sonderianus*, but extended from the middle of the rainy season until the beginning of the drought in *C. pyramidalis*.

Data collection and analysis - A grid of 400 (20 X 20) contiguous 5 X 5 m numbered quadrats was demarcated on level terrain in a stand of vegetation with homogeneous physiognomy. One hundred quadrats (2.500 m²) were sampled at random, and all the individuals of *C. sonderianus* and *C. pyramidalis* within them were identified, counted and labeled.

Every stem that did not connect at the ground (soil surface) level with any other stem was considered an individual. Presence or absence of underground connections was investigated by digging (1 to 15 cm depth) at the base of each stem. Digging was done carefully to avoid damage to the root system, which was subsequently covered. Individuals were classified in two types: 1) plants with a well developed root system, with the main root well defined and penetrating deep layers of the soil, with or without underground connection with another plants; 2) plants without their own root system and connected under the ground through bud-bearing roots to individuals of type one. Type one individuals were considered as having grown from seeds, and were called independent plants (not genets because *C. sonderianus* has agamospermic seeds); while type two individuals, arising from vegetative reproduction, were called dependent plants because they presented partial trophic dependence on the mother plant, as a result of the absence of a developed subterranean system.

The study period lasted from March 1995 to July 1996, during which fifteen observations were made at intervals ranging from 18 to 49 days. At each observation, we recorded the number of born, dead and surviving individuals of each species within the quadrats, as well as the loss and production of leaves, the beginning and end of flowering, and the beginning of seed liberation from the mother plants. All the born individuals (B) that appeared in the quadrats due to seed germination or vegetative propagation were also marked and considered in estimating birth rates (b). We considered the born individuals and the birth rates as part of the process of establishment of new plants, so that, in this paper, we use "birth rate" as an expression of establishment. However, recording the number (D) of dead individuals posed difficulty, because deciding whether a plant was dead and when it died was not so easy. As soon as drought began, all individuals lost their leaves, and we could observe three events, as follow. 1) Some young tagged individuals just could not be seen anymore – we considered them disappeared dead. 2) Some other young individuals dislodged easily and completely from the soil – we considered them confidently dead (m). 3) Still

other individuals remained fixed in the soil; for these we assessed mortality at the beginning of the rainy season, and call them dead standing.

A bigger problem was to determine when a dead standing individual died — surely, we could not consider that almost all deaths occurred at the beginning of the rainy season. Considering that the soil water deficiency increases through the dry months, we then assumed that mortality should also increase as the dry season progressed. Therefore, a greater number of individuals would be standing dead at each observation made in the dry season, so that the largest number of deaths would occur at the end of the dry season and beginning of the rainy season. Taking these premises into account, we hypothesized an exponential model to estimate the number of individuals that died in each month during the dry season. We then calculated the number of deaths (D) in each dry month by adding these estimates to the number (m) of individual that confidently died in the month considered:

$$(1) D_T = m + \text{INT}(e^{dT});$$

where: d = death rate (see equation 3); T = time interval between two consecutive observations; and INT indicates the entire part of the number, despising the decimals.

The influence of the rainy and dry season was evaluated by estimating the rates of monthly, seasonal and annual population increment (r), death (d) and birth (b) using the equations (Condit *et al.* 1996, Swaine & Lieberman 1987):

(2) $r = \ln[(N_0 + B - D)/N_0]/T$; (3) $d = \ln[(N_0 - D)/N_0]/T$; (4) $b = \ln[(N_0 + B)/N_0]/T$; where: N_0 = initial number of individuals; B and D = number of individuals respectively born and dead in the time interval between two consecutive observations.

The total study time included three seasons: 1) from April to August (1995 rainy season, 143 days); 2) from September 1995 to February 1996 (dry season, 180 days); and 3) from March to July (1996 rainy season, 150 days). The first survey began in March 1995 and finished in April 1995 (N_0). To calculate seasonal rates of increment, death, and birth, the seasons were standardized to 180 days. To calculate the annual rates, we used the time interval between middle April 1995 (N_0) and March 1996, corresponding to 0,953 year. The time used to estimate the monthly rates was standardized for 30-day periods. The calculations were based on the number of individuals at the beginning of each period (considered as N_0) and the total of births (B) and/or deaths (D) during each period. The statistical significance of population rates of birth (b), death (d) and increase (r) was tested through χ^2 with Yates correction (Zar, 1984), considering $r = 0$ (population stability) as the null hypothesis. The same procedure was followed regarding vegetative reproduction, considering the proportion between dependent (type 2) and independent (type 1) plants at the beginning of each period.

Results

The population of *C. sonderianus* had a density around three times greater than *C. pyramidalis*. *C. pyramidalis* density varied between months from 436 to 610 ind./2500 m² (average \pm standard deviation of 508.3 ± 57.5), while *C. sonderianus* density varied from 1469 to 1801 ind./2500 m² (1576.7 ± 142.3). Between months, the density of *C. sonderianus* independent (type 1) plants varied from 1317 to 1551 ind./2500 m² (1374.8 ± 74.0), and the density of dependent (type 2) plants varied from 136 to 324 ind./2500 m² (201.8 ± 75.2). During the rainy months (March – August), the populations sometimes increased and sometimes declined, but the increase in density was more evident in the second (1996) rainy season. However, the density of both populations kept stable or declined in the dry months (September – February) (Figure 1).

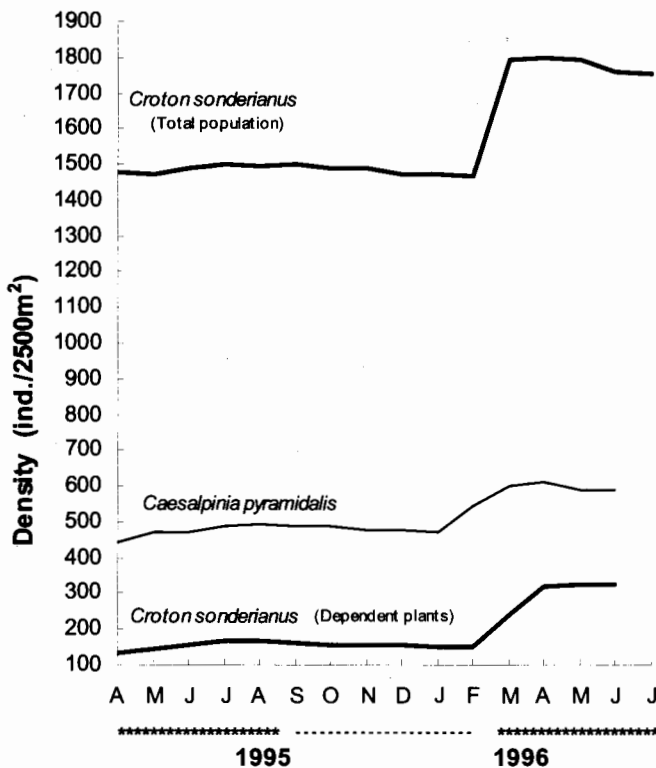


Figure 1. Population density of woody populations in a dry tropical forest in Pernambuco state, northeastern Brazil. *** = rainy season; --- = dry season.

In both populations establishment was predominantly seasonal (Figure 2), being greater in the rainy than in the dry season ($\chi^2 = 91.02$; $df = 14$; $p < 0.01$). In both populations, seedlings emerged before reproductive individuals had produced flowers and liberated seeds, indicating that both populations form seed banks that last at least one year. During the dry season, establishment occurred only in September, the first dry month (Figure 2). In *C. sonderianus*, establishment concentrated in the early months of the rainy season, while in *C. pyramidalis*, though more intense in the early

months, establishment spread through the rainy season. The birth rates were higher in 1996 in both populations, but during the rainy months of 1995, *C. pyramidalis* had a higher birth rate than *C. sonderianus* ($\chi^2 = 7.28$; $df = 1$; $p < 0.01$, Figure 2, Table 1). In *C. sonderianus*, the vegetative reproduction contributed 52% (1995) and 40 % (1996) to establishment in the rainy season (Table 1).

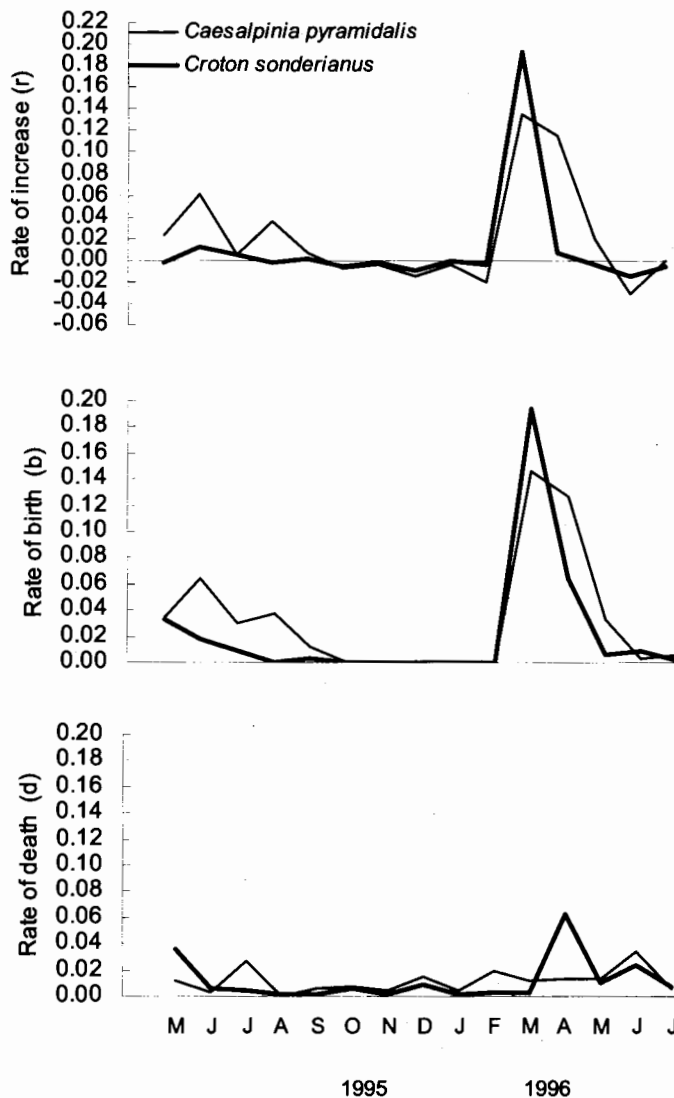


Figure 2. Monthly rates of increment, birth and mortality of woody populations in a dry tropical forest in Pernambuco state, northeastern Brazil. *** = rainy season; --- = dry season.

In *C. sonderianus* and *C. pyramidalis*, a total of 8 and 12 uncertainly standing dead individuals, respectively, was exponentially redistributed along the dry months and added to the number of confidently dead individuals in each month. The respective proportion of the redistributed uncertainly standing dead individuals corresponded, respectively, to 52.2% and 34.4% of the total number of *C. pyramidalis* and *C. sonderianus* individuals that died in the dry season.

Table 1. Seasonal rates of increment (r), birth (b), and mortality (d) in the populations [N_0 = initial number of individuals; N_1 = final number of individuals ($N_0 + B - D$); B = number of born individuals; D = number of dead individuals; $p > 0.05$ indicates $r = 0$, * indicates $r \neq 0$ at $p \leq 0.01$; pi = independent plants (type 1, see text); pd = dependent plants (type 2, see text).

Populations	N_0	N_1	B	D	r	b	d
1995 rainy season							
<i>Caesalpinia pyramidalis</i>	436	488	67	15	0,141*	0,180	0,044
<i>Croton sonderianus</i> (pi+pd)	1476	1496	68	48	0,017	0,057	0,042
pi of <i>C. sonderianus</i>	1340	1331	32	41	-0,008	0,030	0,039
pd of <i>C. sonderianus</i>	136	165	36	7	0,243	0,295	0,066
1995 dry season							
<i>Caesalpinia pyramidalis</i>	488	472	7	23	-0,033	0,014	0,048
<i>Croton sonderianus</i> (pi+pd)	1496	1469	5	32	-0,018	0,003	0,022
pi of <i>C. sonderianus</i>	1331	1317	4	18	-0,011	0,003	0,014
pd of <i>C. sonderianus</i>	165	152	1	14	-0,082	0,006	0,089
1996 rainy season							
<i>Caesalpinia pyramidalis</i>	472	588	163	47	0,264*	0,356	0,126
<i>Croton sonderianus</i> (pi+pd)	1469	1753	460	176	0,212*	0,327	0,153
pi of <i>C. sonderianus</i>	1317	1429	272	160	0,098	0,225	0,155
pd of <i>C. sonderianus</i>	152	324	188	16	0,908	0,970	0,133

The death of individuals due to disappearance or dislodgement from the soil occurred during the dry season until December. In January and February, the whole mortality (Figure 2) was a consequence of the redistribution of the uncertainly dead individuals according to the adopted model for both populations. Hence, it was not possible to determine whether the death rates varied between the months of the dry season.

Death rates in the rainy seasons were higher than in the dry season, and higher in 1996 than in 1995 ($\chi^2 = 10.32$; $df = 2$; $p < 0.01$, Table 1). In the rainy seasons (1995 and 1996), death rates were similar between species, but in the dry season, it was higher in *C. pyramidalis* ($\chi^2 = 9.05$; $df = 1$; $p < 0.01$). In *C. sonderianus*, dependent (type

2) plants accounted for about 15% of the deaths during rainy seasons and 43% of the deaths in the dry season. In the dry season, dependent plants (type 2) had a higher death rate than the independent (type 1) plants ($\chi^2 = 31.65$; $df = 1$; $p < 0.01$; Table 1).

The causes of mortality were not identified. However, during the rainy seasons, at least 50% of the dead individuals had disappeared from the quadrats, while in the dry season, the frequency of uncertainly dead individuals was greater in both populations (Figure 3). The disappearance of individuals during rainy seasons was thought to have resulted from herbivory. The kind of herbivore was not identified, except in some cases, when cutter ants (*Atta* spp) were observed destroying an individual or cutting a high proportion of its leaves. *C. sonderianus* showed greater mortality in the months of maximum seedling emergence, during rainy seasons; while in *C. pyramidalis*, mortality exceeded birth only in two rainy months.

C. pyramidalis population increased during both rainy seasons, while *C. sonderianus* remained stable during the 1995 rainy season, and both populations remained stable during the dry season. The establishment of dependent (type 2) plants kept *C. sonderianus* population size stable during the 1995 rainy season, otherwise it would have decreased (Table 1).

The annual rate of increase (r) was 20.9 % in *C. sonderianus* ($N_0 = 1476$; $B = 500$; $D = 175$; $df = 1$; $\chi^2 = 71.34$; $p < 0.01$) and 33.1 % in *C. pyramidalis* ($N_0 = 436$; $B = 212$; $D = 50$; $df = 1$; $\chi^2 = 59.82$; $p < 0.01$). Dependent (type 2) plants ($N_0 = 136$; $B = 207$; $D = 26$) of *C. sonderianus* had higher increase rate (88.7 %, $\chi^2 = 150.45$; $df = 1$; $p < 0.01$) than independent (type 1) plants (10.7%, $N_0 = 1340$; $B = 293$; $D = 149$). Therefore, vegetative propagation contributed 55.7% to the annual increase rate of *C. sonderianus* population. Even without vegetative propagation, *C. pyramidalis* had a larger population increase ($\chi^2 = 6.03$; $df = 1$; $p < 0.01$) than *C. sonderianus*, due to a higher annual birth rate ($\chi^2 = 19.26$; $df = 1$; $p < 0.01$). The annual birth rate in *C. sonderianus* was 30.2% and in *C. pyramidalis* 41.6%. Both populations showed similar annual death rates (12.8 % in *C. pyramidalis* and 13.2 % in *C. sonderianus*). In spite of the different rates of increase, the ratio of total numbers of individuals between the two populations (about 1:3) changed little during the study period (Figure 1).

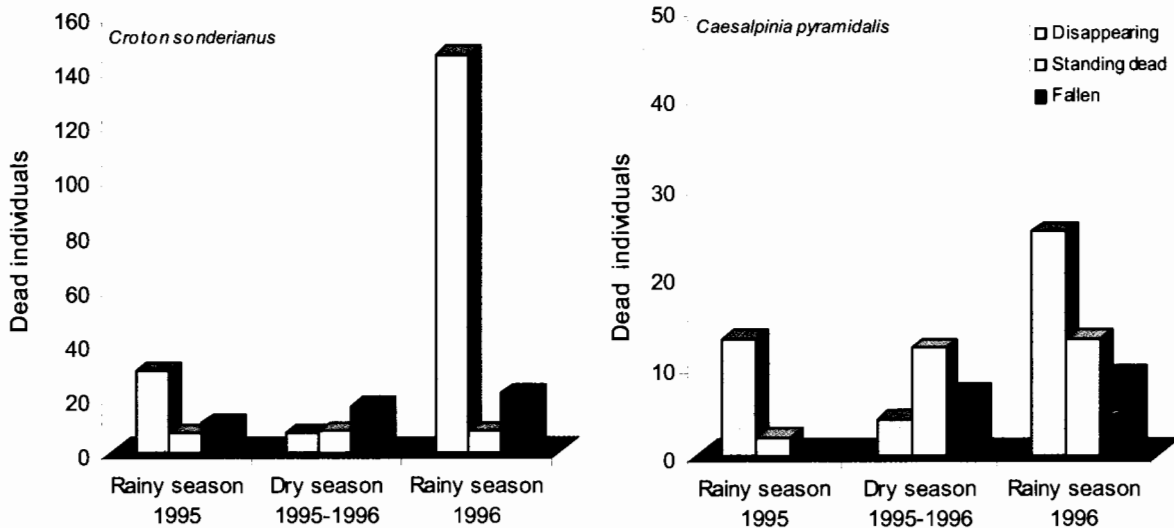


Figure 3. Number of dead individuals according to different death causes in *Caesalpinia pyramidalis* (a) and *Croton sonderianus* (b) in rainy (1 = 1995, 3 = 1996) and dry (2 = 1995) seasons, in a dry tropical forest in Pernambuco state, northeastern Brazil.

Discussion

In wet tropical forests, the dry season has a strong impact on the structure and composition of communities, acting differently upon different populations, through inducing high death rates, opening gaps, generating difference between niches, influencing the abundance of populations and diversity of species (Condit, 1995, Condit *et al.*, 1992; 1995; 1996). The effect of drought in wet tropical forests may still increase the possibility of fire occurrence, which enhances mortality rates and modifies the biomass and diversity of life forms (Nykqvist, 1996; Woods, 1986). We, therefore, expected that the dry season would have a negative influence on the woody plant populations of the caatinga, but we found out that during the dry season, the study species maintained stable populations.

Murphy & Lugo (1986) considered the seasonality of rainfall to be a dominant ecological factor in dry tropical forests. Indeed, rain seasonality influenced the size of the populations we studied. However, in the caatinga, the largest variation of population size occurred during rainy season, in contrast to wet tropical forests (Condit, 1995, Condit *et al.*, 1992; 1995; 1996, Woods, 1986). *C. pyramidalis* and *C. sonderianus* populations increased during the rainy seasons and fell slightly in the dry season. The intensity of the influence exerted by each climatic season on the populations we studied seemed to depend on biological characteristics of each species.

Emergence of seedlings of both *C. sonderianus* and *C. pyramidalis* since the first rainy weeks, before the liberation of new seeds by reproductive individuals, confirmed the results obtained in our previous experiments (unpublished data) and indicated that both species form seed bank. However, as the seeds of *C. pyramidalis* are quiescent and those of *C. sonderianus* are dormant, as showed by our experiments on germination (unpublished data), different dynamics were observed in each population.

Emergence of new *C. pyramidalis* seedlings occurred throughout the rainy season and beginning of the dry season, thus indicating that seeds germinate as soil water is available. Seeds of *C. pyramidalis* liberated at the beginning of the dry season, when soil water is thought to be unavailable, remain in the seed bank to emerge at the beginning of the next rainy season. Therefore, establishment in *C. pyramidalis* was the outcome of germination of seeds produced in past and present reproductive events in the same rainy season. In contrast, as *C. sonderianus* seeds are dormant, the seeds set during a rainy season remain in the seed bank and germinate only at the onset of rains in the following year, thus causing a maximum of seedling emergence at the first rainy weeks, as observed during the rainy season of 1996. Hence, the establishment of *C. sonderianus* in a rainy season relies upon the germination of seeds produced in past reproductive events.

If seedling emergence is concentrated at the onset of rains, as it happens in *C. sonderianus*, high mortality rates are expected when a dry episode (sporadic drought) occurs during the rainy season. The rainy season of 1995 showed a dry episode in March. We think that, in the rainy season of 1995, both *C. sonderianus* and *C. pyramidalis* had high birth rates, which were followed by high mortality rates that were not recorded in this study, because we started the measurements at the end of March. After the dry episode in the rainy season of 1995, we observed the emergence of very few seedlings of *C. sonderianus*, but the population did not decline substantially, instead it held stable through vegetative reproduction. Besides being a relevant strategy to overcome increased seedling mortality in sporadic drought during the rainy season, vegetative reproduction in *C. sonderianus* can also rapidly increase population size during normal rainy seasons, as it happened in 1996.

The absence of dormancy in *C. pyramidalis* seeds enables their recruitment to be resumed soon after the return of the rains at the end of a sporadic dry episode, as happened in 1995. We believe this is the reason why only *C. pyramidalis* had a population increase in the rainy season of 1995. Thus, the differences between the specific rates of birth and death in rainy and dry seasons, and the different biotic characteristics of *C. sonderianus* and *C. pyramidalis* result in two types of population dynamics: *C. sonderianus* seems to be adjusted to rain seasonality, while *C.*

pyramidalis would be able to compensate for the occurrence of sporadic droughts during a rainy season and for long rainy seasons. The strategy of a concentrated period of seed germination at the beginning of the rainy season is considered disadvantageous when compared to germination over the whole rainy season, because the occurrence of a dry episode could result in high rates of seedling mortality (Cook, 1980; Elberse & Breman, 1990). However, it was *C. pyramidalis* that had the higher mortality rate during drought. Therefore, both models of dynamics offer advantages and disadvantages, but make the existence of abundant populations possible in the dry tropical forest we studied.

The emergence of seedlings at the beginning of the rainy season can increase the chances of establishment and survival during the dry season, if resources are allocated to the growth of the root system as soon as the seedling emerges (Aguiar *et al.*, 1992; Condit *et al.*, 1995; Cook, 1979; Osunkoya *et al.*, 1993, Reichenberger & Pyke, 1990). We suggest that the time of germination in relation to the duration of the rainy season may have an important role for plant survival and in the dynamics of perennial species populations in the caatingas. After seedling emergence, the root growth should be greater than the stem growth, thereby increasing the prospects of obtaining water during the dry season and allowing a greater resource allocation to stem growth in the next rainy season. Long-term studies are required to evaluate this hypothesis and to better understand the population dynamics of these species.

Under unfavorable conditions, survival rates are typically greater for clonal than for non-clonal plants (Hara *et al.*, 1993; Wijesinghe & Handel, 1994). However, in *C. sonderianus*, the vegetative reproduction allowed a rapid population increase in the rainy season, but during drought, dependent (type 2) plants showed a higher mortality than independent (type 1) plants. Caraco & Kely (1991) proposed that, during unfavorable seasons, mother plants of small size could abandon the offspring ramets, thereby reallocating resources for their own survival and growth. Such increased mortality of ramets may have occurred in the *C. sonderianus* population during the dry season.

Although the annual rate of increase in *C. sonderianus* (20.9%) was smaller than in *C. pyramidalis* (33.1%), the balance of relative abundance between the two species was not altered during the study period. This could indicate that the climatic seasonality, when considered in a short time, is not likely to drastically alter the ratio between populations with dynamics similar to those of *C. pyramidalis* and *C. sonderianus* in a caatinga community. This implies that, if the rates keep constant, the abundance ratio between the two populations is likely to alter through longer time. However, the proportion between independent (type 1) and dependent (type 2) plants

in the population of *C. sonderianus* did change from about 9:1 at the beginning to about 4:1 at the end of the study period. The rates of increase were mainly determined by birth rates, but caatinga woody species may not reproduce sexually in some years (Pereira *et al.*, 1989, Machado *et al.*, 1997). The irregularity of rains in 1995 and the inter-season difference in the rates of increase between the populations studied show that the effect of dry and rainy seasons in the population dynamics may vary from year to year. Hence, the absence of sexual reproduction in some years and the different effect of dry and rainy seasons on the dynamics of *C. sonderianus* and *C. pyramidalis* populations can result in fluctuations in population size from year to year. However, we believe that, considering long periods of time, the densities of the populations studied may oscillate around an average.

Both species studied seem to have high-risk strategies of producing large offspring. In unfavorable years, with few, erratic rains and longer drought season, both species respond similarly by producing many seedlings. In favorable years, the vegetative reproduction in *C. sonderianus* would represent a way to rapidly increase population size and occupy a larger space in the community. Inter-year variation in seedling emergence is considered an important aspect of natural selection, mainly in the case of populations with a seed bank, and the selective importance of a year depends on the fraction of seeds recruited in that year and the specific age of the seeds recruited (Rees & Long, 1993). *C. sonderianus* produces viable seeds by sexual reproduction and by agamospermy. We do not know whether there is an influence of climatic seasonality on the reproductive system of *C. sonderianus*, but we believe that the selective importance of a year also depends on the proportion of agamospermic and recombinant seeds that are recruited from the seed bank in that year. We suggest that the annual variation in the seedling recruitment has also an important role in the organization of dry forest communities. Also, we suggest further studies during a longer time to evaluate the models of population dynamics we proposed for *C. sonderianus* and *C. pyramidalis*, and to verify the implication of seasonal variation between years in the population dynamics and in the organization of communities in the caatingas.

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