



Original article

Are tree ontogenetic structure and allometric relationship independent of vegetation formation type? A case study with *Cordia oncocalyx* in the Brazilian caatinga

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ABSTRACT

In temperate and tropical rainforests, ontogenetic structure and allometry during tree ontogeny are often associated with light gradients. Light is not considered a limiting resource in deciduous thorny woodland (DTW), but establishment and growth occur during a short rainy period, when the canopy is fully leaved and light in the understory may be modified. Our aim was to investigate whether the light gradient in DTW and the biomechanical limitations of tree growth would be enough to produce an ontogenetic structure and allometric growth similar to rainforest canopy trees. We investigated the ontogenetic stages and diameter–height relationship of *Cordia oncocalyx* (Boraginaceae), a dominant canopy tree of the DTW of semiarid northeastern Brazil. We tagged, measured and classified the ontogenetic stages of 2,895 individuals in a 1 ha area (5°6′58.1″S and 40°52′19.4″W). In the rainy season only 4.7% of the light falling on the canopy reached the ground. Initial ontogenetic stages, mainly infant (50.9%) and seedling (42.1%), were predominant in the population, with the remaining 7% distributed among juvenile, immature, virginile and reproductive. The ontogenetic structure was similar to that of rainforest tree species, but the population formed both permanent seed and infant banks in response to long dry periods and erratic rainy spells. Like many other Boraginaceae tree species in tropical rainforests, *C. oncocalyx* has a Prévost architectural model, but allometric growth was quite different from rainforest trees. *C. oncocalyx* invested slightly more in diameter at first, then in height and finally invested greatly in diameter and attained an asymptotic height. The continued high investment in diameter growth at late stages and the asymptotic height point to low tree density and more frequent xylem embolism as the main drivers of tree allometric shape in DTW. This indicates that tree ontogenetic structure and allometric relationships depend on vegetation formation type.

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1. Introduction

During their life cycle plants go through a unidirectional sequence of developmental steps known as ontogenetic stages, each one characterized by discontinuous, discrete changes (Gatsuk et al., 1980). The changes that distinguish between ontogenetic stages can be qualitative and/or quantitative features that may differ among species, but duration of the stage is genetically determined and independent of chronological age (Gatsuk et al., 1980; Hutchings,

1997; Smirnova et al., 2002). Different ontogenetic stages have different ecological properties, thus having specific dynamics and playing different roles both in the population and the community (Smirnova and Bobrovskii, 2001). Since each ontogenetic stage interacts with the environment according to specific dynamics, resource use in time and space is complex, and this is an important component of species coexistence (Grubb, 1977).

During ontogenetic stages, individuals express different architectures that eventually reveal the architectural model of the species (Hallé et al., 1978). The architecture refers to the shape and position of the plant structures in space, which result from a compromise between the plant needs and constraints, and which enable light foraging, growth to canopy height, and reproduction (Iida et al., 2011; Poorter et al., 2005, 2006; Poorter and Rozendaal, 2008). When faced with constraints, adjustments in architecture

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can be made (Hallé et al., 1978), but a plant final architectural model is genetically determined and is the realization of just one of 23 mathematical models (Oldeman, 1979; Sterck and Bongers, 2001). Explicit examination of the sequence of ontogenetic stages and architectural changes during individual development adds biological meaning to population studies, since it constitutes a reliable background on which to infer the population life history (Souza et al., 2008). An ontogenetic structure with a greater proportion of individuals at the initial ontogenetic stages and fewer individuals at the final stages is a typical pattern in populations of shade-tolerant species, and can be observed in most tropical rainforest tree species where a seedling bank provides a survival strategy (Souza et al., 2000; Wright et al., 2003).

Describing the population structure based on size classes or ontogenetic stages is the first step towards understanding plant populations (Hutchings, 1997). For instance, a consistent lack of individuals of a given size or ontogenetic stage can be interpreted as evidence of a demographic bottleneck in recruitment, growth and/or survival, but population structure should only be used to make inferences about population viability or management if analyzed together with data on other demographic traits such as fecundity, recruitment, growth and mortality (Souza, 2007; Virillo et al., 2011). Morphological and biometric features are good descriptors of ontogenetic stages, and plant population structure based on ontogenetic stages has been studied widely in tropical species (Araújo et al., 2005; Carvalho et al., 1999; Souza et al., 2000).

Other measures, such as the way plants invest resources in vertical growth (to elevate photosynthetic and/or reproductive organs) and diameter growth (to support trunk weight) can be quantified by height–diameter allometric relationships according to biomechanical models (Rich et al., 1986). Three models have been proposed to describe the biomechanical blueprint of trees. In the geometric similarity model ($D \propto H^1$), diameter growth is directly proportional to height in such a way that the main structure remains geometrically similar (Norberg, 1988). The elastic similarity model ($D \propto H^{3/2}$) predicts that trunk diameter (D) grows at a proportion of height (H) raised to the power 1.5 to avoid weight-caused deformities (McMahon, 1973). In the constant stress model ($D \propto H^2$), diameter grows in a proportion of height squared, to resist wind-generated stress (Dean and Long, 1986). The geometric similarity model describes the growth pattern of fast-growing trees, such as young canopy and sub-canopy species (King, 1996; Niklas, 1995; Olesen, 2001) and adult pioneer trees (Alvarez-Buylla and Martinez-Ramos, 1992; Sposito and Santos, 2001). The elastic similarity and constant stress models have successfully explained patterns of canopy, understory and adult emergent trees (Alves and Santos, 2002; King, 1996; Niklas, 1995; O'Brien et al., 1995; Olesen, 2001; Rich et al., 1986). However, in some species, the growth pattern does not fit any of these models, and consequently their use has been criticized (e.g. Rich et al., 1986; Sterck and Bongers, 1998).

When variations in trunk allometry are investigated during ontogeny, different strategies of growth become evident (Rich et al., 1986). Allometric patterns of temperate and tropical rainforest trees can vary between species, or during the ontogeny of a single species due to different light requirements for growth, survival and reproduction, in response to variations in vertical light availability (King, 1996; Niklas, 1995; Olesen, 2001; Rich et al., 1986; Sterck and Bongers, 2001). Increments in diameter at final of ontogeny are a strategy of resource allocation to height that enables increased light capture at the initial developmental stages. Deviations from this pattern have been recorded in the juveniles of some pioneer trees, which invest heavily in diameter increases so that when tree-fall gaps appear they can undergo rapid height gain (Rich et al., 1986; Sposito and Santos, 2001).

In temperate and tropical rainforests, variations in trunk allometry during tree ontogeny are frequently associated with light availability, but how does allometry of a dominant tree in deciduous thorny woodland (DTW) vary during ontogeny? In tropical rainforests, trees are evergreen and tall, and competition for light in the understory is intense, and so investment in vertical and horizontal growth is vital for individual establishment (Poorter et al., 2006). In contrast, it has been speculated that light is not a limiting resource in dry formations due to the open physiognomy and short stature of the trees (Archibald and Bond, 2003; Martínez and Jorge, 2003). However, the germination dynamics, establishment and growth of plants in seasonal, dry environments occur in short rainy periods, when water and nutrients are available, but the quantity of light may be reduced and its quality at ground level modified (Rincón and Huante, 1993). Furthermore, even DTW is likely to have changes in the light distribution over the vegetation profile, with more light at the top, thus constituting a light gradient.

Is there enough light variation in DTW to induce the expression of allometric relationships similar to those found in shade-tolerant rainforest trees? If so, a DTW canopy tree should have the same ontogenetic structure and allometric relationships as observed in non-pioneer rainforest trees, that is: (1) a greater proportion of individuals at the initial ontogenetic stages and fewer individuals at the final ontogenetic stages; and (2) a greater investment in height growth in accordance with the geometric similarity model at the initial stages, and a greater investment in diameter in accordance with the elastic similarity model at the final stages. Although we are not aware of any studies of the light conditions in DTW, it is likely that the juvenile canopy trees of this environment thrive in conditions that are very different from those in the humid, shaded understory of the rainforest. If this is so, the ontogenetic structure and allometry of a DTW canopy species would be quite different to that of a rainforest canopy species. However, it is not yet known whether biomechanical models correspond well to the trunk allometry of DTW canopy species. In fact, biomechanical models have been tested often in temperate and tropical rainforest trees, but tests of their validity in seasonal dry tropical species is almost absent. One study (Dodonov et al., 2011) reported that these models do not apply to some woody species of the Brazilian savanna (Cerrado). Furthermore, if DTW canopy trees do have the same ontogenetic and allometric patterns as rainforest canopy trees, does this indicate that in both formations the light environments are similar or that tree growth is subject to similar biomechanical constraints (Niklas, 1995)?

Our aim was to address the hypothesis that tree growth is subject to the same biomechanical constraints wherever it occurs. If the hypothesis is correct, the ontogenetic trajectory of a DTW canopy tree should be similar to that of a rainforest canopy tree. To examine this prediction we investigated the ontogenetic structure and variation of the trunk diameter–height allometry during ontogeny of *Cordia oncocalyx* Allemão (Boraginaceae), a dominant canopy tree endemic to the DTW of northeastern Brazil. As we investigate our hypothesis we intend to discuss the ecological meaning of morphological and biometric changes during ontogeny in DTW canopy trees.

2. Methods

2.1. Study site and focal species

Our study area is located in the Natural Reserve *Serra das Almas* (5°6'58.1''S and 40°52'19.4''W) in Crateús municipality, Ceará state, in a tropical, semiarid region of northeastern Brazil. It is located 368 m above sea level on a crystalline basement landscape. According to the FAO soil classification system, the soil is a shallow,

rocky, fertile Lithosol. The local climate is BSh (hot semiarid with summer rains and a dry winter) according to Köppen–Geiger classification (Peel et al., 2007); it has defined wet and dry seasons with erratic, short rainy spells in the wet season and an unpredictable occurrence of dry years. The mean annual temperature is 27 °C, ranging from 25 °C in the coldest months (March–June) to 30 °C during the hottest months (October–December). The average annual rainfall of 683 mm is scattered over two to five months (January–May), which usually contributes >85% of the total annual rainfall. The total annual rainfall is variable; e.g. in 2010, total rainfall was 440 mm and in 2009 and 2011 it was 1107 and 843 mm, respectively. Climatic data was provided by the National Meteorology Institute (INMET).

The predominant vegetation in semi-arid northeastern Brazil is a type of woody savanna (Woodward et al., 2004), known regionally as *caatinga*, with physiognomies including savanna, scrubland and woodland. The area we studied is deciduous thorny woodland (DTW) with shrub and tree canopy cover between 61–88%. The majority of the vegetation is medium-height (3–4 m) with a few tall individuals reaching >8 m. There are many species in the herbaceous component, which is seasonal and mainly composed of therophytes. In the deciduous woody component, 25 phanerophyte species occur, of which *Croton blanchetianus* Baill., *Mimosa caesalpinifolia* Benth., *Croton adenocalyx* Baill., *Bauhinia cheilantha* Bong, and *Cordia oncocalyx* Allemão are the most abundant (Costa and Araújo, 2012).

C. oncocalyx Allemão, (Boraginaceae) is a mesophanerophyte that occurs in the shallow soils of crystalline basement lowlands (<500 m). It is endemic to semiarid northeastern Brazil (Silveira et al., 2005). It has a leafy crown during the rainy season and sheds its foliage in the dry season. Its flowers are arranged in racemes; the fruit is an indehiscent nuculanium wrapped in an accrescent calyx, with one to four seeds inside (Silva and Machado, 1997). *C. oncocalyx* has very regular phenodynamics and flowers annually between February and May (pers. obs.). It is locally known as “*pau-branco-preto*” (black–white wood), may have medicinal properties and is used for timber and landscaping as well as food for livestock (Lorenzi, 2009).

2.2. Data collection and analysis

A 1 ha area was divided in 100 permanent, adjacent 100 m² (10 × 10 m) sampling plots. All individuals in each plot, excluding seedlings, were sampled. To sample seedlings, we marked out a 25 m² (5 × 5 m) subplot at a corner of each 100 m² plot. We began sampling in April 2009 (rainy season), which was an atypical year in which 95% of the 1107 mm total rainfall fell between January and May. All rooted individuals in the plots and subplots were tagged and classified according to their ontogenetic stage. To classify ontogenetic stages we examined the presence or absence of external morphological traits according to Gatsuk et al. (1980): a) cotyledons; b) stem color (green or brown) c) orthotropic or plagiotropic branching; d) flowers and fruits. Seedlings were defined according to Garwood (1996), and the architectural model was determined according to the identification key proposed by Hallé et al. (1978). The number of seedlings, sampled in the 25 m² subplots, was multiplied by four, to allow for density comparisons with the other stages sampled in 100 m² sampling plots of the 1 ha area. Every tagged individual was examined monthly from April 2009 until March 2011. During this period we recorded the emergence of new seedlings, recruitment from one ontogenetic stage to the next, deaths and population phenodynamics. We used these data to support the distinction between ontogenetic stages, but the results are not presented here.

We used a digital caliper to measure stem diameter at ground level of small individuals and a measuring tape to measure stem circumferences larger than 150 mm. Circumference measurements were later converted to diameter (D). Aluminum poles up to 8 m long were used to measure plant height (H), defined as the vertical distance from the ground to the extremity of the plant's highest branch. To analyze the dispersion of diameter and height data in each ontogenetic stage we used the coefficient of variation (CV), given by the semi-amplitude of the confidence interval divided by the median. Plant height and diameter of the different ontogenetic stages were compared using box-plots.

Allometric relationships between height (H) and diameter (D) were described by model II regression (standardized major axis SMA) on log-transformed data for each stage separately and in all stages together. SMA is more suitable than “least squares” regression, (also called model I regression), and should be used when there is no clearly independent variable and/or when both variables are subject to error (Henry and Aarssen, 1999). We compared the slope coefficient of the allometric relationships among different ontogenetic stages through an analysis of post-hoc multiple comparisons across groups. We used the *F* test ($p > 0.05$) to compare the allometric coefficient (*b*) of the regression with the expected coefficients of the different models: geometric similarity ($b = 1.0$, Norberg, 1988), elastic similarity ($b = 0.66$, McMahon, 1973) or constant stress ($b = 0.5$, Dean and Long, 1986), obtained when diameter is plotted as the X axis and height is plotted as the Y axis. These analyses were performed with the software SMATR 2.0 (Falster et al., 2006), and the graphs were made in the R environment (R Development Core Team, 2010).

In order to investigate the existence of a vertical light gradient, we measured the active photosynthetic radiation at 1.30 m above ground, and at ground level with quantum sensors LI-191 linked to a data logger LI-1400. Measurements of photon flux density PFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$) in the active photosynthetic range were made during five days in the rainy season at five locations that were representative of the local vegetation. Representative locations had the lowest and highest plant density and biomass (Menezes, 2010). The percentage of incident light at each stratum was calculated as the difference between the incident light above canopy and that at 1.3 m above ground and at ground level. Above canopy PFD was represented by a measurement taken at an open location.

3. Results

3.1. Ontogenetic stages

Six stages were characterized in the *C. oncocalyx* population (Fig. 1):

Seedling: recently germinated individuals with soft, green, orthotropic and non-branched stems; cotyledons and leaves present or absent. Cotyledons and/or one to five leaves were present only during the rainy period. Leaves were simple, inserted alternately and obovate or oblanceolate in shape. Seedlings were phanero-epigeous-follicious (Garwood, 1996), as they had green, photosynthesizing cotyledons that were free of a seed coat and elevated above ground level.

Infant: characterized by a non-branched, brown, apparently lignified, orthotropic stem, with no cotyledons, and simple, obovate or oblanceolate leaves inserted in a spiral alternate phyllotaxy. Individuals at this stage had at least two leaves and scars indicating the loss of the first pair of leaves.

Juvenile: first-order branches appeared as plagiotropic axes, on which leaves assumed a horizontal position due to petiole twisting. Leaves maintained a spiral alternate phyllotaxy on the plagiotropic branches.

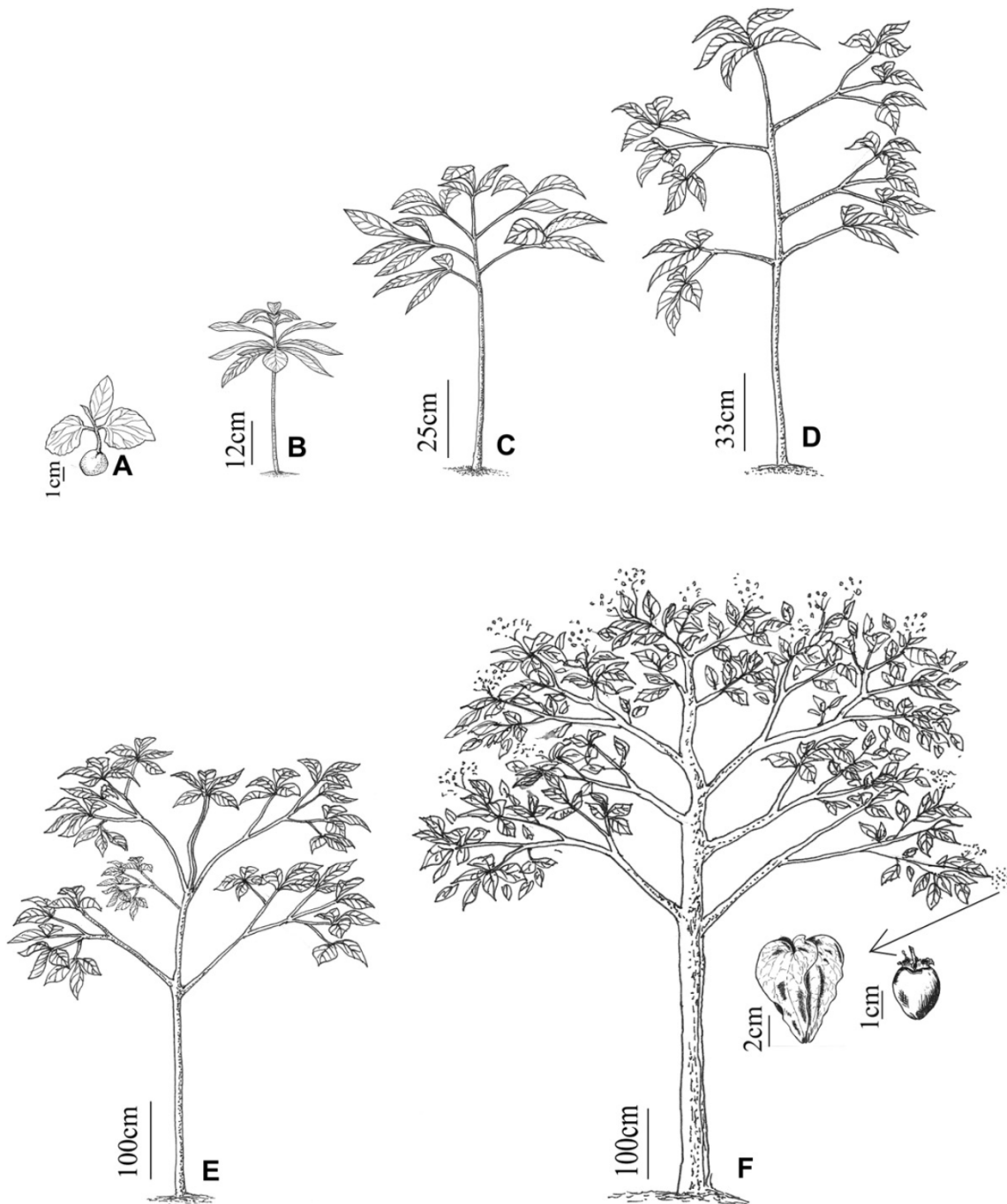


Fig. 1. Ontogenetic stages of *Cordia oncocalyx* Allemão. (A) Seedling with cotyledons and first leaves. (B) Infant with no cotyledons and with leaves in spiral alternate phyllotaxy. (C) Juvenile with first plagiotropic branches (D) Immature with second order branching (reiterations) displaying a Prévost architectural model. (E) Virginile with third or higher order branches. (F) Reproductive with third or higher order branches and infructescences. Detail: accrescent calyx and fruit indehiscent nuculanium.

Immature: verticils of plagiotropic axes appeared as second order branches (reiterations), and the distinction between trunk (orthotropic axis) and branches (plagiotropic axis) became apparent. At this stage the complete architectural model of the species, identified as Prévost was achieved. Thus, the immature stage was characterized by a modular architecture with two types of modules: one forming the trunk and the other forming branches. The trunk was simpodial, with defined growth on both trunk and branch modules. Branching of the plagiotropic axis was also modular, repeating the main trunk structure and resulting in successive repetitions of the model (Hallé et al., 1978).

Virginile: characterized by the appearance of third- or higher-order branches; individuals with typical adult traits, but no reproductive structures. From this stage on we observed individuals with three types of trunks: (1) single axis trunk; (2) single axis trunk with regrowth above ground; and (3) multiple trunks, with more than one axis emerging from the ground. In cases 2 and 3, up to three regrowths were observed.

Reproductive: third- or higher- order plagiotropic branches with reproductive structures (flowers and fruits) present seasonally. Reproductive structures were hapaxanthic, since after one period of vegetative activity the apical meristem was completely

transformed into the floral axis (Hallé et al., 1978). Individuals had up to four trunk regrowths.

C. oncocalyx individuals were found at high density (4.230 plants/ha⁻¹) in the population, with individuals at the initial infant (50.9%) and seedling (42.1%) stages predominating (Table 1). Size (both height and diameter) varied greatly among individuals of the same stage, especially in the immature, virginile, and reproductive stages, indicated by the variation coefficients (Table 1). Despite the observed overlap between individuals of successive ontogenetic stages, size increased progressively during ontogeny, i.e. the median diameter and height increased from the seedling to reproductive stage (Fig. 2).

3.2. Allometric relationships and biomechanical models

Allometric coefficients varied significantly among the ontogenetic stages ($F = 275.03$; $P = 0.001$). Seedling, infant and immature had a coefficient ~ 1.0 ; the virginile and reproductive stages had a coefficient ~ 0.5 ; and the juvenile stage had a coefficient ~ 1.5 and the juvenile stage had a coefficient ~ 1.5 (Table 2). These shifts indicate that energy investment was initially equally proportioned between height and diameter, then it was directed towards height during middle-life, and eventually changed to great diameter growth at the final ontogenetic stages.

Although the regression was statistically significant for each ontogenetic stage ($P < 0.005$), the determination coefficient was generally very small, but when all ontogenetic stages were analyzed together, a very high value of R^2 (0.942) was observed (Table 2, Fig. 3). Therefore, we concluded that the whole population had only one allometric form ($b = 0.966$). This means that although the allometric form of each stage could vary, it did not change during ontogeny, with diameter growth being a little greater than height growth throughout development. The allometric coefficient of the *C. oncocalyx* population was statistically different from that predicted by all three biomechanical models: geometric similarity ($F = 58.6$; $P = 0.000$), elastic similarity ($F = 7261.6$; $P = 0.000$) and constant stress ($F = 25,200.2$; $P = 0.000$).

We observed a vertical light gradient in the analyzed strata: 6.2% of the above canopy photon flux density reached the understory at 1.30 m above ground and 4.7% reached ground level. This is the first record of a vertical light gradient in the *caatinga*.

4. Discussion

4.1. Ontogenetic structure

Most previous studies of temperate and tropical rainforests did not adopt the ontogenetic approach we adopted here. For instance, most authors working with these systems have classified seedlings as any plant with ≤ 0.5 m height (e.g. Alvarez-Buylla and Martinez-Ramos, 1992; Wright et al., 2003). We think this introduces at least two potential problems: (1) it disregards ontogenetic development,

since similar-sized plants can attain different ontogenetic stages; and (2) it adds noise to allometric analyses, because placing individuals into different size classes in order to demonstrate that size relationship is different in each class violates the requirement for independence of the explanatory variables. The size overlap in different ontogenetic stages of *C. oncocalyx* shows that tree height and trunk diameter are not adequate for differentiating between ontogenetic stages. Overlap between ontogenetic stages seems to be a general phenomenon and has been observed in other tropical species (Araújo et al., 2005; Souza et al., 2000, 2008), reinforcing the idea that plant size is not directly correlated with ontogenetic stage.

Confirming our first expectation, we recorded a large proportion of *C. oncocalyx* individuals in the initial ontogenetic stages and fewer in the final stages. The high density of infants indicates that formation of an infant bank is an important part of the population turnover strategy, which also relies on the formation of a seed bank (data not shown). In tropical rainforests, seedling (ontogenetic concept) banks are the expected survival strategy for environments of low luminosity, and high seedling density is associated with mass fruiting patterns and a long seedling stage (Carvalho et al., 1999; Souza et al., 2000). In contrast, in seasonal dry vegetations, Araújo et al. (2005) and Miranda-Melo et al. (2007) have reported that seedling density is lower than infant (juvenile-1) density. According to these authors, this is due to supra-annual flowering and fruiting patterns, vegetative propagation, and a short seedling stage. Since vegetative reproduction does not occur in *C. oncocalyx*, and flowering and fruiting are annual, the large concentration of infants is likely to be due to previous recruitment of seedlings that have germinated from the seed bank, which have accumulated over many reproductive events. According to Araújo et al. (2005) and Cipriotti et al. (2008), hydric stress is the main cause of mortality in the initial ontogenetic stages of species of arid and semiarid climates. Therefore, the maintenance of both the seed (Baskin and Baskin, 1989) and the infant banks could be an efficient strategy for the regeneration of tree populations that do not reproduce vegetatively and which thrive in seasonal climates with erratic rainfall and inter-annual droughts.

We adapted the ontogenetic stage system to include an infant stage for *C. oncocalyx* because individuals that had already lost seedling traits, but had not yet acquired juvenile traits were observed. During tree development, in which a tree's architectural model is achieved, the step following seedling is adaptation to the model, followed by one or more steps of metamorphosis (Oldeman, 1990). Here, we considered adaptation to the architectural model to begin at the infant stage and for metamorphosis to start at the juvenile stage. Virginile and reproductive stages are mainly distinguished by the presence or absence of reproductive structures. Although these criteria could be difficult to apply to species with supra-annual flowering (Araújo et al., 2005; Souza et al., 2000), they were appropriate for *C. oncocalyx*, since it has regular annual flowering (pers. obs.). A number of studies (e.g. Gatsuk et al.,

Table 1
Ontogenetic structure and biometry of *Cordia oncocalyx* Allemão. N = number of individuals; (%) = percentage of individuals; Min = minimum; Max = maximum; M = median; CV = coefficient of variation (semi-amplitude of confidence interval/median).

	N (%)	Base diameter (cm)				Plant height (m)			
		Min.	Max.	M	CV	Min.	Max.	M	CV
Seedling ^a	1780 (42.1)	0.04	0.29	0.15	2.2	0.02	0.11	0.07	2.2
Infant	2152 (50.9)	0.11	1.53	0.42	2.2	0.05	1.14	0.16	3.4
Juvenile	86 (2.0)	0.85	2.08	1.23	4.0	0.44	2.00	0.97	5.9
Immature	16 (0.4)	1.49	3.81	2.43	13.0	1.19	3.00	2.25	12.5
Virginile	33 (0.8)	3.50	31.83	8.60	33.6	3.00	8.00	6.00	9.7
Reproductive	163 (3.8)	9.87	84.03	35.97	6.0	7.00	13.00	10.00	1.8

^a The number of seedlings (sampled in 0.25 ha) was multiplied by four for comparison with the other stages sampled in 1 ha.

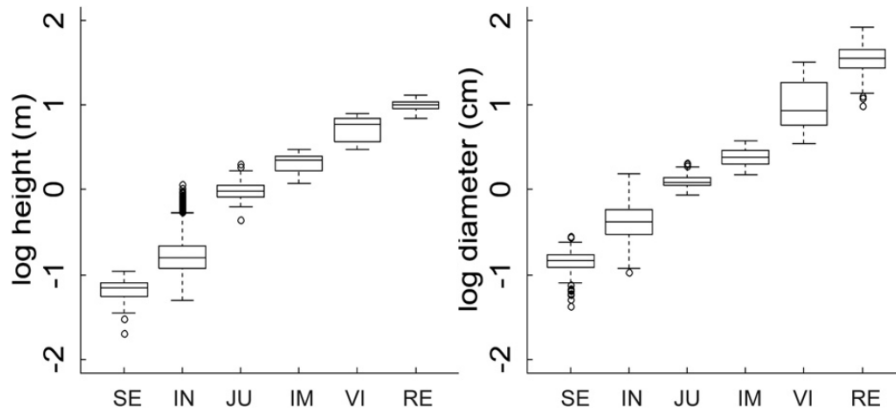


Fig. 2. Box-plots of height and diameter values of the ontogenetic stages of *Cordia oncocalyx* Allemão: SE = seedling, IN = infant, JU = juvenile, IM = immature, VI = virginile and RE = reproductive.

1980; Hutchings, 1997; Smirnova and Bobrovskii, 2001; Smirnova et al., 2002) reported that a senile stage is expected for fully developed, older populations. In the *C. oncocalyx* population we investigated, the absence of the post-reproductive period (sub-senile and senile stages) indicated that the population had full reproductive activity. Menezes (2010) observed that the presence of *C. oncocalyx* adults characterized the most stable sectors of the local community due to low mortality rates (only one individual died in six years). This suggests that our study population was young and that the oldest individuals were probably established during a recovery process that followed a recent past disturbance. The *caatinga* fragment we studied is considered to be well conserved, but it was only designated a conservation unit (Nature Reserve) in 2000 (IBAMA N. 51/00), and although historical records are absent, we observed signs of anthropic disturbances such as logging, which was common before the reserve was created.

4.2. Morphological changes and ecological significance

The variation in general allometric form of *C. oncocalyx* individuals at different ontogenetic stages reflects differences in resource allocation, as predicted by Gatsuk et al. (1980) and Grubb (1977). In *C. oncocalyx* infants, the non-overlapping leaves that result from spiral placement may be considered an optimized photosynthetic strategy due to non-branching at this stage. In juveniles, the twisting of petioles and the horizontal arrangement of leaves on the first plagiotropic branches may increase the photosynthetic efficiency and consequently favor biomass build-up, required for transition to the immature stage, when the species architecture is complete. These observations, together with adoption of the Prévost model, indicate that light may be a limiting factor at the initial stages of *C. oncocalyx* development. The modular

architecture of the Prévost model has been recorded for other *Cordia* species in tropical rainforests (Borchert, 1983). In this model, the plagiotropic orientation of branches, with a clear distinction between trunk and branches from the beginning of development, seems to favor survival in light-poor environments, such as the understorey of tropical rainforests (Hallé et al., 1978). This strategy has been confirmed, as trees in tropical rainforests with plagiotropic branching at the initial development stages had slower growth and were more tolerant to shade than trees with no such branching (Coomes and Grubb, 1998). The fact that Prévost architecture also occurs in species from DTW may indicate that this model is either intrinsic to taxonomic groups better adapted to rainforest environments (since the genus *Cordia* has few species in the *caatinga*), or it may indicate that even trees in dry woodlands can be influenced by light during their initial ontogenetic stages.

Light is a limiting resource in tropical rainforests, where approximately 1–2% of the radiation falling on the canopy reaches the forest floor, and successful establishment of a species chiefly depends on its form in response to light availability variations during ontogeny (Poorter et al., 2006; Sterck and Bongers, 1998). In seasonal dry tropical forests, light has not been considered

Table 2

Standardized major axis regression between height (H) and diameter (D) after log transformation ($\log H = \log A + B \log D$) for the ontogenetic stages of *Cordia oncocalyx* Allemão. B = allometric coefficient, CI = confidence interval, A = intercept, R^2 = coefficient of determination. The same letter indicates statistical similarity (F test, $p < 0.05$).

Stages	B	CI 95% (B)	A	CI 95% (A)	R^2
Seedling	1.055 ^a	0.965–1.154	-0.299	-0.379–0.218	0.086
Infant	1.102 ^a	1.080–1.124	-0.336	-0.345–0.327	0.784
Juvenile	1.497 ^b	1.279–1.753	-0.160	-0.191–0.130	0.469
Immature	1.096 ^{ab}	0.713–1.681	-0.107	-0.297–0.083	0.407
Virginile	0.486 ^c	0.354–0.665	0.234	0.071–0.397	0.235
Reproductive	0.296 ^d	0.256–0.342	0.537	0.471–0.604	0.138
Together	0.966	0.958–0.975	-0.379	-0.385–0.374	0.942

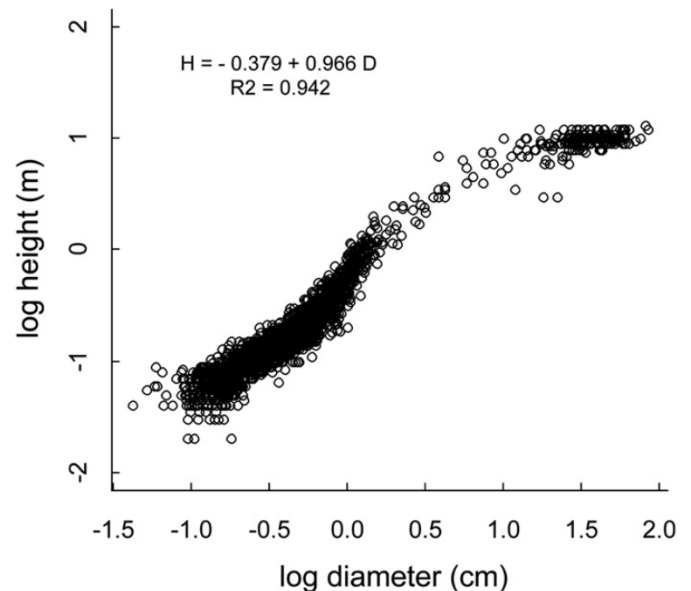


Fig. 3. Height–diameter relationship of *Cordia oncocalyx* Allemão. The allometric exponents were estimated through SMA regression. N = 2.895 individuals.

a limiting resource, and variations in growth patterns have been explained as responses to selective pressures from fire, large herbivores (Archibald and Bond, 2003), or water availability (Martínez and Jorge, 2003). However, in the short rainy season of seasonal dry forests, light quality and intensity are modified by the filtering influence of the canopy (Rincón and Huante, 1993). Lebrija-Trejos et al. (2010) showed that only 6% of the photosynthetically active radiation falling on the canopy arrived at the understory of a Mexican deciduous formation. We found that only 6.2% of photosynthetically active radiation falling on the canopy arrived 1.30 m above ground, and only 4.7% arrived at ground level. The light gradient we observed supports the idea that differences in light availability can also occur in woodlands of seasonal dry climates and that the abundant herbaceous and woody components of the rainy season may limit light availability and influence the early growth of woody *caatinga* plants. Therefore, the architecture of infant, juvenile and immature stages of *C. oncocalyx* may reflect strategies of photosynthetic optimization associated with different light conditions in understory. In consequence, habitat restoration with seedling and infant planting of *C. oncocalyx* should consider that excess light in the initial developmental stages may be harmful to plant establishment.

4.3. Allometric relationships and biomechanical design models

Contrary to our second expectation (greater investment in height at the initial stages and in diameter at the final stages), the allometric shifts in *C. oncocalyx* stages indicated a greater investment in height only at the intermediate (juvenile) stage, an equal investment in height and diameter at the initial stages, and a very large investment in diameter at the final stages. Initial investment in diameter was also recorded by Sposito and Santos (2001) for some pioneer species, and is a strategy that allows a strong trunk to form, providing support for rapid height growth when canopy openings appear. In general, pioneer rainforest trees exhibit the geometric similarity model throughout ontogeny, and are more prone to falls from mechanical failure (Alvarez-Buylla and Martínez-Ramos, 1992; Sposito and Santos, 2001). In seasonally dry forests death by trunk breakage is low due to a high root/shoot ratio, which provides mechanical stability, and consequently most trees die standing (Dickinson et al., 2001). In the DTW of north-eastern Brazil, standing trees form the largest fraction of dead trees (Menezes, 2010). The investment in diameter at the beginning of *C. oncocalyx* development may be associated with a need to support large leaves at the infant stage and is likely to reflect slow growth and shade tolerance. In addition, the high concentration of infants and the reduced density of juveniles suggest that abiotic (e.g. light, water) and/or biotic factors (e.g. competition, predation) affect infant growth and limit recruitment to the juvenile stage. Studies have revealed that typical shade-tolerant species (non-pioneer tropical rainforest trees), have slow growth strategies in shade and so are able to survive in the understory until they are capable of growing to canopy (Shukla and Ramakrishnan, 1986). In *C. oncocalyx* juveniles, resource allocation appears to be redirected from stem diameter growth to stem height growth. The marked decrease in diameter growth may indicate a strategy of both vertical and horizontal occupation, since plagiotropic branching starts at this stage. Sterck and Bongers (1998) highlighted that smaller individuals present a greater invest in height or branch formation to increase light capture. Hence, the occupation of vertical (height growth) and lateral space (branching) is a strategy adopted by *C. oncocalyx* to reach higher strata at the juvenile and immature stages, whereas the definitive occupation of vertical and horizontal space occurs at the final stages, when the highest investment in diameter growth occurs.

Henry and Aarssen (1999) claimed that greater investments in diameter at the final stages can minimize the risk of tumbling down associated with crown expansion. This seems to be the case in *C. oncocalyx*, as the allometric coefficient of the whole population did not adjust to any of the biomechanical models. Also, tree density is lower in DTW than in tropical rainforests, providing more space for larger growth increments in diameter relative to height (Henry and Aarssen, 1999). The small allometric coefficients ($b < 0.5$) we found for the virginile and reproductive stages indicate that they keep on growing in diameter even after reaching the canopy. This phenomenon (of continued diameter growth after a tree has reached maximum height) is described as an asymptotic height–diameter relationship (Thomas, 1996). In DTW, water shortage can lead to xylem embolism, especially high-up in the trunk, which can limit growth in height but not in diameter (Bullock, 2000). Considering our results, we suggest that the height–diameter relationships of DTW trees could be related to space availability and hydric constraints rather than mechanical failure. Future studies could investigate this hypothesis.

Our results reinforce the criticisms of the biomechanical models made by others (Dodonov et al., 2011; Rich et al., 1986; Sposito and Santos, 2001; Sterck and Bongers, 1998). In an allometric study of Brazilian *cerrado* trees, Dodonov et al. (2011) concluded that trees with greater height to diameter ratios were responding to recurrent fires, not to mechanical constraints. We are not aware of any study comparing fire frequency between the *caatinga* and the *cerrado*, but whilst fire has been considered a key evolutionary factor in the *cerrado* (Simon et al., 2009), it has not been connected to the *caatinga* (e.g. Dupont et al., 2010). Since the allometric growth pattern we found for *C. oncocalyx* differed from those observed in both *cerrado* and rainforest trees, our results did not confirm our hypothesis that tree allometric models would be independent of vegetation formation type.

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