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Germination, initial growth, and biomass allocation in three native *Cerrado* species

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ABSTRACT – (Germination, initial growth, and biomass allocation in three native *Cerrado* species). The parameters of germination, initial growth, and biomass allocation of three native plant species of *Cerrado* (*Copaifera langsdorffii*, *Dipteryx alata* and *Kielmeyera coriacea*) were established. The species had germination percentages above 88% and average germination times longer than 139 hours. The average time for the opening of the first leaf pair was more than 538 hours for all three species. The average root length of *C. langsdorffii* and *D. alata* seedlings after 80 days of growth was around 40 cm, four times larger than the average shoot length (< 10 cm), although the root and shoot biomasses were similar for both species. The average root length (> 20 cm) of *K. coriacea* seedlings was four times larger than the average shoot length (< 5 cm), and the root biomass was 243% greater than the shoot biomass. Increase in seedling biomass was sustained primarily by the cotyledons in *C. langsdorffii* and *D. alata*, which acted as reserve organs and showed progressive weight reductions. Increase in seedling biomass in *K. coriacea* was sustained primarily by photosynthesis, since the cotyledons showed no significant weight reduction, acting primarily as photosynthetic organs. The length of the root systems was at least four times larger than the length of the shoots parts in all three species. Higher investment in root length rather than in root biomass suggest that the initial growth of these species is primarily to ensure access to water resources, apparently putting off the function of the radicular system as storage organ.

Key words - biomass partitioning, *Copaifera langsdorffii*, *Dipteryx alata*, *Kielmeyera coriacea*, seedling growth

INTRODUCTION

The *Cerrado* vegetation (Brazilian savanna) is characterized by the seasonality of both temperature and precipitation during the year, with cold and dry winters and hot and humid summers (Eiten 1972, Ribeiro & Walter 2008). The climate is classified as Aw by the Köppen system (tropical rainy), with average annual rainfall near 1500 mm and average annual temperatures varying from 18 to 28 °C (Silva et al. 2008). The *Cerrado* shows a wide variety of physiognomies, including open field formations dominated by herbaceous species, savanna formations, with a well-developed herbaceous-shrub layer and sparse trees, to forest physiognomies formations with a well-developed arboreal component (Oliveira Filho & Ratter 2002). This gradient is affected and determined by diverse environmental agents such as temperature, water availability, depth of the water table, fire frequencies, anthropogenic disturbances, and edaphic factors (Coutinho 1978, Ribeiro & Walter 2008).

Among the factors limiting the initial establishment of *Cerrado* species the soil-water deficit is one of the most important. During the rainy season, the soil water

potential (ψ_s) remains very near the field capacity ($\psi_s = -0.06$ MPa) but can become much more negative during the *veranicos* (periods without rainfall during the rainy season), reducing water availability at depths up to 15 cm (Kanegae et al. 2000). During the dry season, the ψ_s is reduced considerably, reaching values up to -6.2 MPa at depths of 5 cm and -2.6 MPa at depths of 60 cm in the *campo sujo* (savanna-like vegetation) physiognomy. In the *cerradão* (forest-like vegetation) the minimum ψ_s at the same depths were -2.8 and -1.8 MPa respectively (Kanegae et al. 2000). These conditions restrict the establishment of drought-sensitive species, and consequently favor and select for species tolerant to water deficit.

Savanna species tend to invest more in deep roots, which make them less susceptible to soil water deficits than forest species (Hoffmann et al. 2004). Savanna species also tend to invest more in subterranean biomass than forest species, which gives them a greater resprouting capacity and therefore greater resistance to fires (Hoffmann 2000); savanna species usually invest more in subterranean biomass than in shoot biomass (Haridasan 2000). It has long been thought that the rapid root growth of savanna species and the formation of reserve organs are strategies that facilitate the survival of these plants during the long dry season (Labouriau et al. 1963).

The reserve tissues of the seedlings have a fundamental role in their initial growth, and these reserves can be determinant of the seedling recruitment

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under natural conditions, particularly in environments where the light intensity is low, or demand a rapid initial growth (Melo et al. 2004). Also, it is known that there is a direct relationship between diaspore reserve mobilization and the establishment of the photosynthetic apparatus in seedlings; indeed, if the cotyledons have a primary photosynthetic function they tend to remain for longer periods of time attached to the seedlings (Kitajima 1994, Melo et al. 2004, Ressel et al. 2004). For example, the cotyledons of *Kielmeyera coriacea* remain attached to the seedlings for approximately one year, suggesting that they have important role in the initial growth of this species (Nardoto et al. 1998). Despite their important role in the seedling growth, there is still relatively little information available about the physiological and biochemical aspects of cotyledons functions and the mechanisms of seed reserve mobilization for tree seedlings (Zaidan & Carreira 2008).

In a comparative study of species occurring in different *Cerrado* physiognomies, Moreira & Klink (2000) analyzed the patterns of initial growth and biomass allocation of species from *cerradão* and from *cerrado sensu stricto* physiognomies, as well as in species common to both phytophysiognomies. These authors did not identify any consistent differences between the *cerradão* and *cerrado sensu stricto* species in terms of the ratio of biomass allocation between the root and shoot parts (root shoot⁻¹ ratio); among the 10 species studied, five allocated more biomass to the roots (root shoot⁻¹ > 1.5) and five allocated similar biomasses to roots and shoots (root shoot⁻¹ ~ 1), or allocated less biomass to the roots than to the shoot parts of the plant (root shoot⁻¹ ≤ 1) (Moreira & Klink 2000). Although they could not determine any correlation of the ratios of biomass allocation between the roots and shoots with the physiognomies of occurrence of the species, these authors noted that all of the species showed accentuated elongation of the roots during their initial growth period (Moreira & Klink 2000). In particular, they found that *Kielmeyera coriacea*, a species typical of *cerrado sensu stricto* allocated considerably more biomass to the roots in relation to the shoot parts of the plants (root shoot⁻¹ ~ 9).

In order to contribute to a better understanding of the eco-physiology of the initial growth of *Cerrado* species, the present study examined the parameters of germination, initial growth, and biomass partitioning in three plant species widely distributed in the *Cerrado* vegetation: *Kielmeyera coriacea*, *Copaifera langsdorffii*, and *Dipteryx alata*. All of these species occur in *cerrado sensu stricto* and *cerradão*, although *K. coriacea* also occurs in *campo sujo* vegetation; *C. langsdorffii* and *D.*

alata also both occur in dry forests, and *C. langsdorffii* can also be found in gallery forests (Almeida et al. 1998, Silva Júnior 2005).

MATERIAL AND METHODS

Species characterization and seed collection and storage

Copaifera langsdorffii Desf. (Fabaceae – Caesalpinioideae) seeds were collected from at least five adult trees during November/2008 in the Darcy Ribeiro campus at the Universidade de Brasília, DF, Brazil (15°48'00" S; 47°51'50" W) and were stored at room temperature (22-24 °C) until April/2009. Before the beginning of the experiments the seeds were immersed in 2% sodium hypochlorite, stirred for 2 minutes, and subsequently rinsed with running tap water for 30 seconds.

Dipteryx alata Vogel (Fabaceae – Faboideae) fruits were collected from at least 10 adult trees between August and October/2008 in the municipality of Cavalcante, Goiás State (GO) (13°47'52" S; 47°51'50" W); the fruits were carefully broken in a vise to remove the seeds. The seeds were stored in cotton sacks at room temperature (22-24 °C) until April/2009. Before the beginning of the experiments the seeds were immersed in 2% sodium hypochlorite, stirred for 2 minutes, and subsequently rinsed in running tap water for 30 seconds.

Kielmeyera coriacea (Spreng.) Mart. (Clusiaceae) seeds were collected from the dehiscent fruits of at least 10 adult plants occurring in a preserved native area on the Darcy Ribeiro campus at the Universidade de Brasília, DF (15°48'00" S; 47°51'50" W) in August/2008. The seeds were stored at -18 °C until April/2009.

Dry weight, fresh weight, and seed germination

The fresh and dry weights and water content of the seeds were determined by drying them in a forced air drying oven at 90 °C for 24 hours (*N* = 20 seeds per species).

The experiments were initiated in April/2009. The germination tests were conducted in germination chambers (Marconi MA 403) under a 12 hour photoperiod at 30 °C (a temperature that lies within the temperature range appropriated for the germination of numerous *Cerrado* species) (Zaidan & Carreira 2008). It was employed threes replicates of 40 seeds for *K. coriacea*, two replicates of 80 seeds for *C. langsdorffii*, and two replicates of 50 seeds for *D. alata*. The seeds were considered as germinated if they emitted a radicle followed by its typical geotropic curvature (Labouriau 1983). Germination was evaluated daily to count and remove germinated seeds, and at the end of the experimental period the germinability (*G*, in percentage), the average germination time (AGT, in hours), and its standard deviations (SD, in hours) were calculated for each species (Labouriau 1983).

The germinated seeds were used for experiments examining the initial growth.

Initial growth

Field experiments were conducted in a small reserve area of *cerrado sensu stricto* located near the Laboratório de Termobiologia L. G. Labouriau and the seedlings were allowed to grow under natural conditions, without tree or shrub shading (table 1).

Table 1. Maximum and minimum temperatures, humidity, precipitation, and total illumination for the Federal District region from April to July/2009.

Averages	April	May	June	July
Max. temperature (°C)	28-31	25-28	25-28	28-31
Min. temperature (°C)	18-21	15-18	15-18	12-15
Humidity (%)	70-75	70-75	60-70	50-60
Precipitation (mm)	180-240	30-50	10-30	0
Total illumination (h)	150-180	180-220	220-250	250-300

Source: INMET.

The germinated seeds were transferred to PVC tubes 10 cm in diameter and 60 cm long filled with dystrophic Red Latosol (from 20 cm below the soil surface) gathered from the reserve area near the laboratory. The seedlings were watered daily. Samples of 20 individuals of each species were collected at intervals of 20, 30, 50 and 80 days after germination for biometric measurements. The average growth of the roots and shoots were measured, as well as the root and shoot dry weights (after drying at 80 °C/24h). Indeed, the average time required for the complete opening of the first pair of leaves (TLO, in hours) was calculated, as well as its standard deviation (SD, in hours). The criterion of initial growth was defined as the time between the beginning of the experiments (as the initial time) and the appearance of a fully expanded and completely formed leaf (final time).

RESULTS AND DISCUSSION

The seeds of *Copaifera langsdorffii* had average fresh weight of 0.94 grams and their water content was estimated to be 11.5%; the seeds of *Dipteryx alata* had fresh weight of 1.34 grams and their water content was estimated to be 7.6%; the seeds of *Kielmeyera coriacea* had fresh weight of 0.13 grams and their water content was estimated to be 3.9%. The seeds of the three species investigated can be classified in terms of their water contents as "orthodox" (Villela & Peres 2004). Although they have low water contents, seeds of *K. coriacea* have showed very short longevity; freezing them at -18 °C helped to maintain their germinability for more than six

months without significantly effect on their germination characteristics (unpublished results).

The seeds of all three species showed germinability above 88% under controlled conditions (table 2), indicating the absence of dormancy or restrictions to germination. All of the species showed average germination times (AGT) above 120 hours (more than five days) (table 2). The species that showed the smallest AGT and SD among the three species studied was *Dipteryx alata*, thus being classified as the species with the most rapid and uniform germination in respect to the other two species (Santana & Ranal 2004).

Table 2. Seed germination and initial growth parameters of *Copaifera langsdorffii* (copaíba), *Dipteryx alata* (baru), and *Kielmeyera coriacea* (pau-santo). Numbers of individuals per treatment (N), Germinability (G), Average germination time (AGT), Average time for opening of the first leaf pair (TLO) and their respective standard deviations (SD). Germination experiments were conducted at 30° C with a 12 hour photoperiod; initial growth was conducted under field conditions without shading. Average values in the same column, identified by the same letter, do not differ significantly according to the Kruskal-Wallis test followed by the Mann-Whitney test ($P < 0.05$).

Species	N	G (%)	AGT (h)	SD AGT (h)	N	TLO (h)	SD TLO (h)
Copaíba	160	89.4b	408.0b	120.3	80	956.40	58.34
Baru	100	96.0a	139.2a	25.0	80	538.50	55.18
Pau-santo	120	88.3b	260.1c	78.0	80	–	–

According to Ferreira et al. (2001), the average germination time is a good measure for evaluating the rapidity with which a given species can occupy a certain environment, and it can be used to classify seed germination into three general categories: rapid (AGT < 120hours), intermediate (120hours < AGT < 240 hours); and slow (AGT > 240 hours). So, in the present study (table 2), the germination of *D. alata* seeds can be classified as between rapid and intermediate; the germination of *K. coriacea* seeds as intermediate to slow; and the germination of *C. langsdorffii* seeds can be classified as slow (Ferreira et al. 2001).

Slow and spread germination over time is normally associated with species that occur in environments with unpredictable and/or seasonal climates, and this germination pattern has been considered as a strategy for plant establishment in environments where conditions are not always favorable (and/or predictable) to seedling growth (Leck et al. 1989, Doussi and Thanos 2002, Silva

et al. 2010). This germination pattern has been described as “bet-hedging” or “delayed germination” (Venable 2007, Ooi et al. 2009), and it is supposed to reduce the probability that an entire cohort of seeds germinate in response to an environmental stimuli at an inappropriate moment for the subsequent seedling growth (such as an erratic and sporadic rain during the dry season). Slow and time-spaced germination also contributes to persistence of seeds in the soil seed bank (Saatkamp et al. 2011), an important attribute for the recruitment of new individuals in environments characterized by an unpredictable climate.

In the *Cerrado* biome, savanna physiognomies are more often subject to environmental stress than are forest physiognomies; thermal amplitudes in forests tend to be smaller and water availability and soil humidity tend to be more stable than in open savanna areas (Kanegae et al. 2000). As such, the slow and/or temporally distributed germination of *C. langsdorffii* and *K. coriacea* seeds are apparently part of a germination strategy that contributes to successful recruitment of these species in savanna physiognomies of the *Cerrado*. In fact, both species are documented to be widely distributed in savanna formations of this large Brazilian biome (Almeida et al. 1998, Silva Júnior 2005).

Individuals of *C. langsdorffii* were shown to present greater root than shoot elongation during their first 80 days of growth. The seedling dry weight increased steadily but was essentially similar for both the shoot and root parts (figure 1). The shoot parts were quite uniform among the different specimens, with an average of eight leaflets per individual. The root system presented a long pivotal root and numerous lateral roots, these being shorter at shallow depths.

Seventeen-month-old individuals of *C. langsdorffii* exposed to different levels of shading were found to concentrate between 51 and 75% of their total biomass in the root system (Salgado et al. 2001). In the present study we found similar biomass partition between root and shoot parts during the first 80 days of growth, but the average root length was four times larger than the average shoot length, suggesting more investment in root elongation than in root biomass by this species.

A growth pattern similar to that described for *C. langsdorffii* was also seen in *D. alata* (figure 2). Morphologically, *D. alata* seedlings demonstrated homogeneity in the size of their shoot parts and in the quantities of leaves, with an average of 18 leaflets after 30 days and 24 leaflets after 80 days of growth. The roots were pivotal and long, and the lateral roots long, thick, and numerous along its entire extension. As *D.*

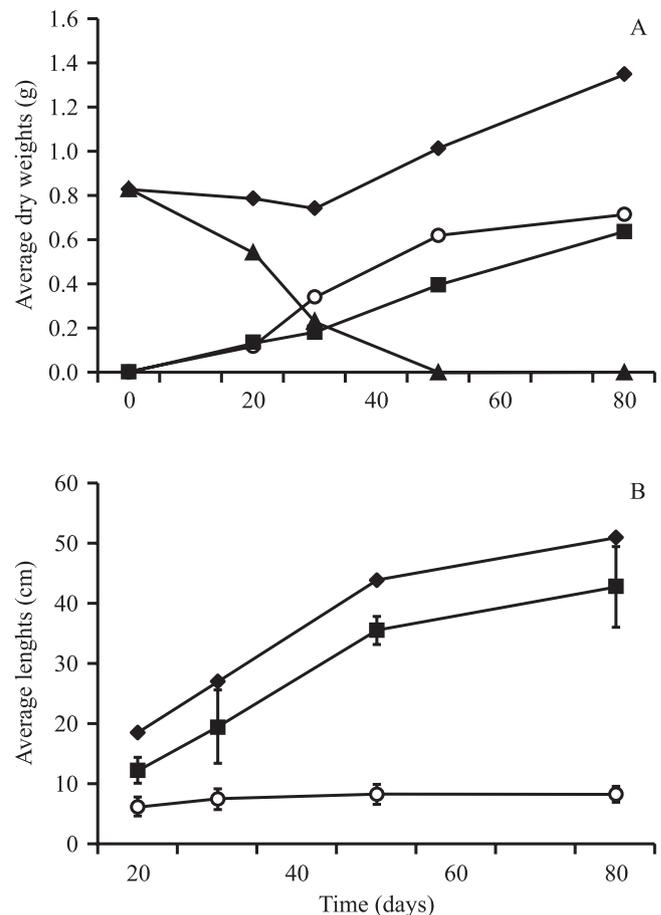


Figure 1. Average dry weights of the roots, cotyledons, shoots and of the entire plants (A), and average lengths of the roots, shoots and of the entire plants (B) of *Copaifera langsdorffii* grown on soil substrates under natural conditions between the months of April to July/2009. Vertical bars, when present, indicate the standard deviations. $N=20$ seedlings per date point (◆ = Total; ○ = Shoot; ▲ = Cotyledon; ■ = Root).

alata demonstrated the smallest average germination time, it also had the smallest average time required for the opening of the first leaf pair (TLO), as well as a more uniform initial growth (as judged by the small standard deviation of TLO) (table 2).

The biomasses of the shoot parts of both *C. langsdorffii* and *D. alata* increased without significant increase in plant height, indicating a greater initial investment in branching and leaf expansion. The reduction in the weight of the cotyledons in both species underline their principal function as food reserve organs, probably supporting shoot expansion as well as root elongation and lateral root differentiation (figures 1 and 2).

Kielmeyera coriacea did not show opening of the first leaf in any of the individuals examined during

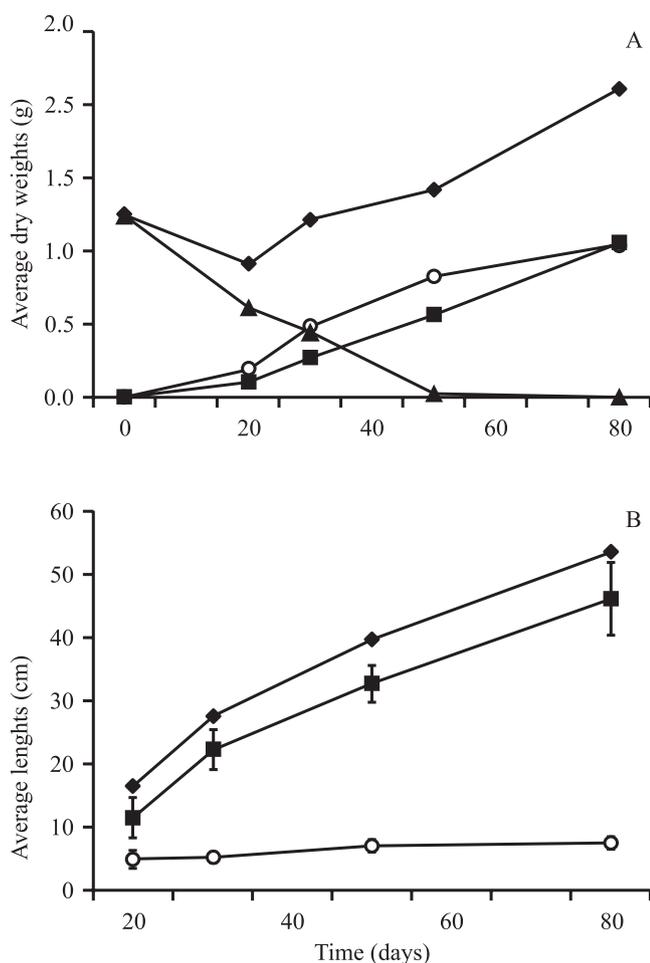


Figure 2. Average dry weights of the roots, cotyledons, shoots and of the entire plants (A), and average lengths of the roots, shoots and of the entire plants (B) of *Dipteryx alata* grown on soil substrates under natural conditions between the months of April to July/2009. Vertical bars, when present, indicate the standard deviations. $N = 20$ seedlings per date point. (—◆— = Total; —○— = Shoot; —▲— = Cotyledon; —■— = Root).

the first 80 days of growth, which made it impossible to calculate its TLO. This was probably due to the photosynthetic functions of the cotyledons (which remained green, intact, moderately thick, and attached to the seedlings during the entire experimental period) (figure 3). As such, it can be concluded that these organs were the principal plant structures responsible for the growth of the root system. The size and biomass of the shoot parts (the cotyledons) remained virtually the same over the entire period of seedling growth.

Morphologically, the root system presented a pivotal and large root, with long and thin lateral roots, these being more numerous in the central region of the main root. The region near the root/stem transition started to

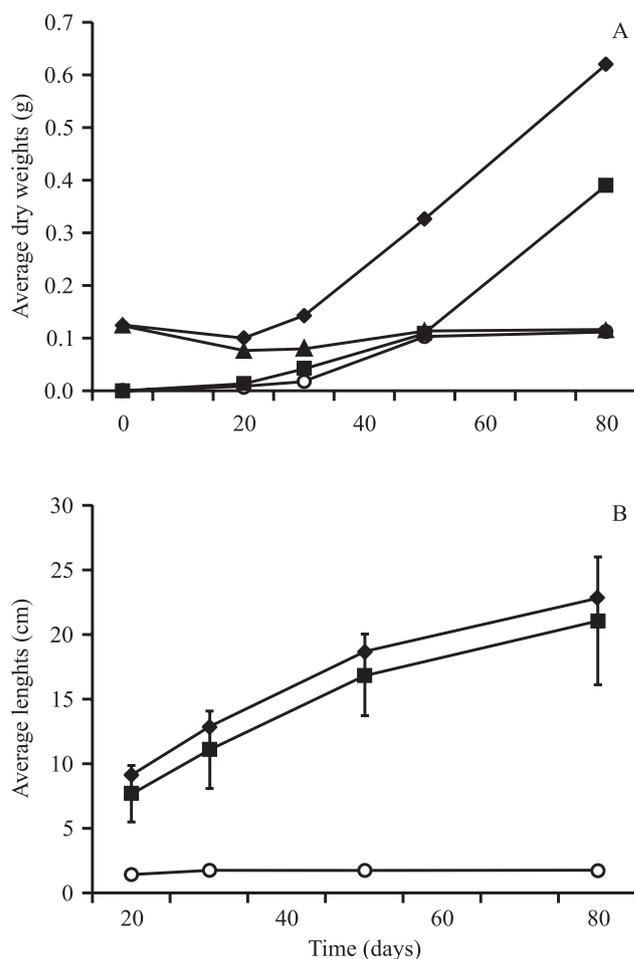


Figure 3. Average dry weights of the roots, cotyledons, shoots and of the entire plants (A), and average lengths of the roots, shoots and of the entire plants (B) of *Kielmeyera coriacea* grown on soil substrates under natural conditions between the months of April to July/2009. Vertical bars, when present, indicate the standard deviations. $N = 20$ seedlings per date point. (—◆— = Total; —○— = Shoot; —▲— = Cotyledon; —■— = Root).

intumescere as early as 30 days after germination in some individuals, and root intumescence was easily visible in all individuals after 50 days of initial growth, suggesting the formation of xylopodium. Under field conditions, six month-old individuals of *K. coriacea* were shown to present well-developed xylopodium (Oliveira & Silva, 1993), which represents an important strategy for the survival of young plants during the dry season in the *Cerrado* (Labouriau 1963).

The cotyledons of *D. alata* and *C. langsdorffii* acted mainly as reserve organs (Ressel et al. 2004), while those of *K. coriacea* acted mainly as photosynthetic organs (Ressel et al. 2004) – this strategy being associated with the more open savanna physiognomies of *Cerrado* biome

(Nardoto et al. 1998). The predominantly photosynthetic function of the cotyledons of *K. coriacea* may be among the factors that make the establishment of this species rather rare in forest environments in the *Cerrado* biome (Silva Júnior 2005) – as light availability in the forest understorey is quite reduced at soil level when compared to open savanna physiognomies (Nardoto et al. 1998). By contrast, individuals of *C. langsdorffii* and *D. alata*, whose cotyledons function predominantly as reserve organs, can be found in forest physiognomies of the *Cerrado* biome, as the gallery forests, dry forests, and *Cerradão* (Cavalcanti & Ramos 2001, Silva Júnior 2005).

In summary, *D. alata* and *C. langsdorffii* seedlings show similar shoot and root biomasses while *K. coriacea* seedlings have greater root than shoot biomasses, with precocious formation of xylopodium. For the three species the root length was at least four times larger than the shoot length. The higher investment in root length than in root biomass in the first 80 days of growth was noticeable, and suggests a strategy to ensure access to water instead of to establish reserves in the root system. This growth pattern has been for a long time considered as a survival strategy among plants occurring in environments subjected to recurring water-stress conditions, such as the savanna physiognomies of the *Cerrado* biome (Labouriau 1963).

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