ECOTROPICOS 13(1):43-51 2000
Sociedad Venezolana de Ecología

BIOMASS ALLOCATION AND GROWTH OF TREE SEEDLINGS FROM TWO CONTRASTING BRAZILIAN SAVANNAS

ASIGNACION DE BIOMASA Y CRECIMIENTO DE PLANTULAS DE ARBOLES EN DOS SABANAS BRASILERAS CONTRASTANTES

***Adriana G. Moreira*[1] and *Carlos A. Klink*[2]**

[1]*Banco Mundial, Edificio Corporate Financial Center, sala 603, Brasilia DF, Brazil.*
E-mail: amoreira@worldbank.org
[2]*Depto. de Ecologia, Universidade de Brasilia, C.P. 04631, Brasilia DF 70919-970, Brazil.*
E-mail: klink@unb.br

ABSTRACT

Growth and biomass allocation to roots and shoots of ten native trees of two contrasting savanna communities in central Brazil (Cerrado), differing in woody species density, was studied for up to seven months after germination. We compared three closed savanna woodland species with four open savanna species. Three other species were common to both savanna types. Root/shoot ratios differed greatly among species but no similar pattern of biomass allocation to roots and shoots was found between species of the same savanna type. After seven months of growth the woodland species *Alibertia edulis* Rich. had a root/shoot ratio smaller than one and the open savanna species *Kielmeyera coriaceae* (Spr.) Mart. a ratio equal to nine; the remaining species had values ranging from one to six, irrespective of savanna type. Relative growth rate (RGR) of early stage woodland seedlings (30-day old seedlings) was significantly different from open savanna seedlings (range between 0.059 and 0.192 mg mg^{-1} day^{-1} for the woodland species, and between 0.025 and 0.035 mg mg^{-1} day^{-1} for the open savanna species; common species had intermediate values). For older seedlings (150-day old seedlings) differences disappear (RGR ranging between 0.013 and 0.030 mg mg^{-1} day^{-1} espective of savanna type). The high values of root/shoot ratios and root elongation of most species is probably related to their capacity to withstand the dry season and resprout after fire.

Key words: biomass allocation, root/shoot ratios, seedling growth, tropical savanna, Cerrado, Brazil

RESUMEN

Se estudió la distribución de biomasa y crecimiento de tallos y raíces de diez árboles nativos de dos comunidades de sabana contrastantes in Brasil central (Cerrado), durante siete meses después de la germinación. Comparamos tres especies de sabana arbolada con cuatro especies de sabana abierta. Las otras tres especies fueron comunes a ambos tipos de sabana. La relación raíz/tallo mostró grandes diferencias entre especies, pero no se obsrevó lo mismo con la distribución de biomasa para especies del mismo tipo de sabana. Después de siete meses de crecimiento, la especie de sabana arbolada *Alibertia edulis* Rich. mostró una relación raíz/tallo menor que 1, mientras que para la especie de sabana abierta *Kielmeyera coriaceae* (Spr.) Mart. esa relación fue 9; el resto de las especies tuvieron valores en un rango de 1 a 6, independientemente del tipo de sabana. La tasa de crecimiento relativo (RGR) de los primeros estadíos de plátulas de sabana arbolada (30 días de edad) fue significativamente diferente de las de sabana abierta (rangos entre 0,059 y 0,192 mg mg^{-1} dia^{-1} para las especies de sabana arbolada, y entre 0,025 y 0,035 mg mg^{-1} dia^{-1} para las especies de sabana abierta; las especies comunes tuvieron valores intermedios). Las plántulas de más edad (150 días) no mostraron diferencias (RGR estuvo entre 0,013 y 0,030 mg mg^{-1} dia^{-1}, independientemente del tipo de sabana). Los altos valores obtenidos con la relación raíz/tallo y la elongación de raíces de la mayoría de las especies pprobablemente esté relacionado con su capacidad de resistir la época seca y rebrotar después de ocurrir el fuego.

Palabras clave: asignación de biomasa, relación raíz/tallo, crecimiento plántulas, sabana tropical, Cerrado, Brasil

INTRODUCTION

In a seasonal environment it can be expected that seedling establishment must occur when water and, indirectly, nutrients are not drastically limited in the top layers of the soil. Under these circumstances tree seedling growth forms, relative growth rate, and biomass allocation may affect establishment success. In particular, root characteristics appear to be important to exploit soil resources during the wet season, which enable the newly established seedling to endure the adverse conditions represented by the dry season.

The Cerrado savannas cover 2 million km^2 of central Brazil and have well defined wet and dry seasons (Klink *et al.* 1993). The Cerrado consists of a gradient of savanna communities, from pure grasslands to woodlands (Coutinho 1978). Generally four types of savanna are recognized: «campo limpo» (pure grassland), «campo sujo» (grassland with scattered shrubs), «cerrado *sensu stricto* «(cerrado *s.s.*, open savanna), and «cerradão» (savanna woodland), which differ from each other by the relative abundance of woody and herbaceous, mostly grasses, species. Dry season fires occur regularly in cerrado *sensu stricto* (*s.s.*) and are fueled by large amounts of dry grass biomass (Miranda *et al.* 1993). In contrast, fire is rare in most cerradão woodland areas, because of the absence of a fully developed grass layer.

For most Cerrado woody species, seed dispersal peaks at the end of the dry season (Oliveira and Moreira 1992), and the rainy season seems to be the most favorable time for seedling establishment (Labouriau *et al.* 1963, 1964, Oliveira and Silva 1993). The marked dry season, nutrient-poor soils and periodic fires have been regarded as constraints to seedling establishment of Cerrado woody species and specially adaptations are required for seedling survival (Oliveira and Silva 1993).

Some authors have demonstrated the presence of newly germinated seedlings in the Cerrado during the rainy season (Labouriau *et al.* 1963, 1964, Moreira 1987, Oliveira 1986) but studies on seedling establishment are still rare. There are some descriptive studies that show the ubiquitous distribution of «underground tuberized organs» among Cerrado plants (Rizzini and Heringer 1961, 1962, Labouriau *et al.* 1964, Rizzini 1965). These organs are related to the resprouting ability of these plants after damage to the above-ground part of the plant due to drought, fire or herbivory.

We hypothesized that seedlings of cerrado *s.s.* trees will have a high proportion of biomass allocated to roots in their early development and contrarily, cerradão woodland species will have a relatively higher proportion of biomass allocated to shoots since fire is rare in this community and competition for light can be an overriding factor for seedlings growing in a shadier environment (Osunkoya *et al.* 1993, Huante and Rincon 1998). Our objective in the research reported here was to determine the pattern of biomass allocation to roots and shoots and measure the growth rate of seedlings of cerrado *s.s.* savanna and cerradão woodland trees, in an attempt to answer the following question: Are there differences in biomass allocation to roots and shoots and in relative growth rate between species of these different savanna communities?

MATERIALS AND METHODS

The study was conducted during the wet season of 1990/1991 (from October 1990 to August 1991), in the Centro de Pesquisa Agropecuária dos Cerrados (CPAC) of the Brazilian Agricultural Research Institute (EMBRAPA) in Planaltina, Federal District, Brazil.

The Cerrado is a wet savanna (Frost *et al.* 1986) with two well defined seasons. The average annual precipitation in the region is 1500 mm, and more than 90% of the precipitation falls between October and April. In very dry years, rainfall can be zero for 3 to 4 months during the dry season (Adamoli *et al.* 1986). The monthly average maximum temperatures during the study period were never higher than 30°C and the average minimum never below 13°C. Cerrado soils are mainly yellow-red latossols (acrustox according to the American classification) and dark red latossols (haplustox) (Goedert 1983). Soils are acidic and distrophic with relatively high concentration of aluminum (Goedert 1983).

Ten tree species were chosen for this study based on seed availability and occurrence in different communities. None of them belong exclusively to a particular Cerrado community, but species were separated according to the one they are most abundant: three cerradão woodland species, *Alibertia edulis* Rich. (Rubiaceae), *Magonia pubescens* St. Hil. (Sapindaceae) and *Pseudobombax tomentosum* (St. Hil.) A. Robyns.(Bombacaceae); four cerrado *s.s.* savanna species: *Dalbergia miscolobium* Benth. (Leguminosae-Faboideae), *Eriotheca pubescens* (K. Schum.) A. Robyns (Bombacaceae), *Kielmeyera coriaceae* (Spr.) Mart. (Guttiferae) and *Stryphnodendron adstringens* (Mart.) Coville (Leguminosae-Mimosoideae); and three species that are common to both cerradão and cerrado *s.s.*: *Aspidosperma macrocarpon* Mart. (Apocynaceae), *Qualea grandiflora* Mart. (Vochysiaceae) and *Sclerolobium paniculatum* Vog. (Leguminosae-Caesalpinioideae). For a fuller description of Cerrado trees please refer to the site www.recor.org.br) .

Cerradão (woodland savanna) differs from cerrado *s. s.* (open savanna) in both botanical composition and community structure. The average number of trees per hectare in cerradão is 2,231 against 911 in cerrado *s. s.* , species richness is 81 against 66 respectively, and while tree cover in cerrado *s. s.* can be as high as 34%, it reaches 93% in cerradão (Ribeiro *et al.* 1985, Ribeiro and Walter 1998). Usually cerradão soils are not different from cerrado *s. s.* ; both are poor, acidic, deep and well drained. The levels of organic matter may be slightly higher in the cerradão due to the higher tree density (Rizzini 1965, Ribeiro *et al.* 1985, Villela and Haridasan 1994, Ribeiro and Walter 1998).

Mature seeds from a pool of several plants of all species were germinated in black sturdy plastic bags (20 x 60 cm), filled with recently collected cerrado soil. The soil was collected from the top 30 cm of the soil profile and all dead root fragments separated with a mesh. The soil collected was characterized as red latosol, with a pH of 5.3 and organic matter content of 3.3 %. The plastic bags were randomly set in a nursery with natural light and were watered once a day in the afternoon. Final seed germination varied from 41% to a maximum of 98%. The number of days to reach these values varied from 15 to 79 days.

After germination three to five seedlings were harvested at 15 day intervals for the first two months of growth, and every 30 days afterwards, until they reached 150 days of age, coinciding roughly with the wet season. Since seedlings were available, a final harvest was taken after 210 days after germination for *A. edulis*, *A. macrocarpon*, *K. coriaceae*, and *M. pubescens*. Soil was carefully washed from the root system, and shoots and roots carefully separated. Root length was also measured.

Roots and shoots were oven-dried at 80°C for 48 h. Dry weights were analyzed by the root-shoot ratio (R/S) and relative growth rate (RGR) according to Hunt (1982). We used the root/shoot ratio as an index of the balance of biomass allocation to below- and aboveground components of the plants. These ratios are indications of the ability of plants to withstand moisture stress (Gerhardt and Fredriksson 1995).

The mean relative growth rate (RGR) was measured as the dry weight increment per unit of total plant weight over time and was calculated for each species according to Hunt (1982). RGR was calculated for both roots and shoots.

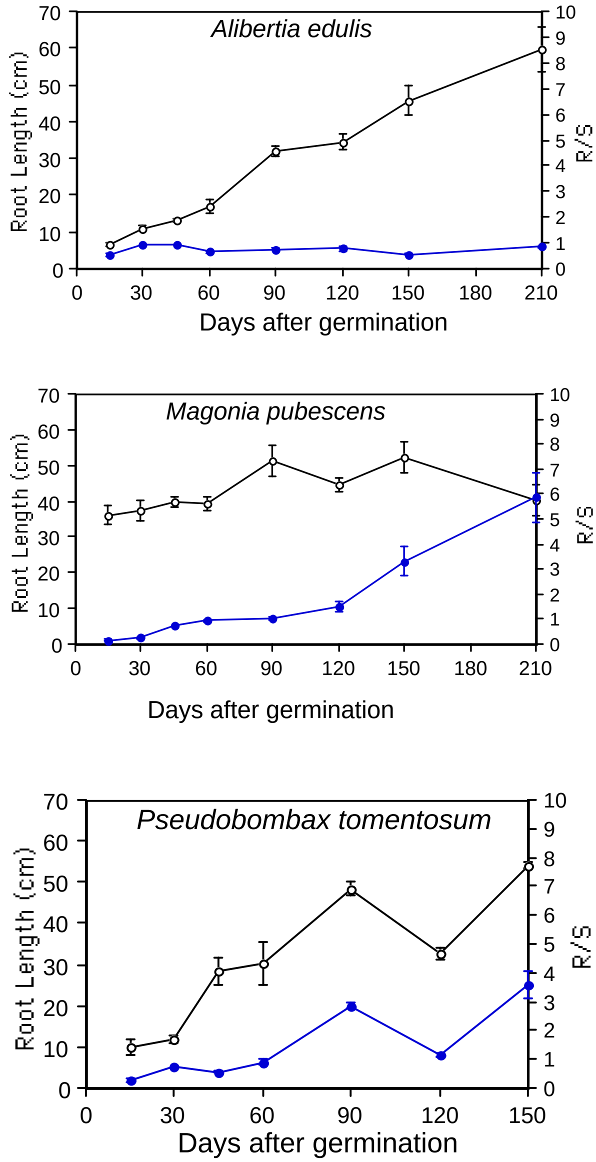

Figure 1. Root/shoot ratios (closed circles) and root length (open circles) over time of the three woodland savanna (cerradão) species (*Alibertia edulis*, *Magonia pubescens* and *Pseudobombax tomentosum*). Vertical bars represent one standard error.

Significant differences among the species for each measured parameter were tested by analysis of variance, using log transformed data when necessary to meet the assumptions of normality (Sokal and Rohlf 1981). Multiple comparisons among means (unplanned comparisons) followed the method described in Sokal & Rohlf (1981).

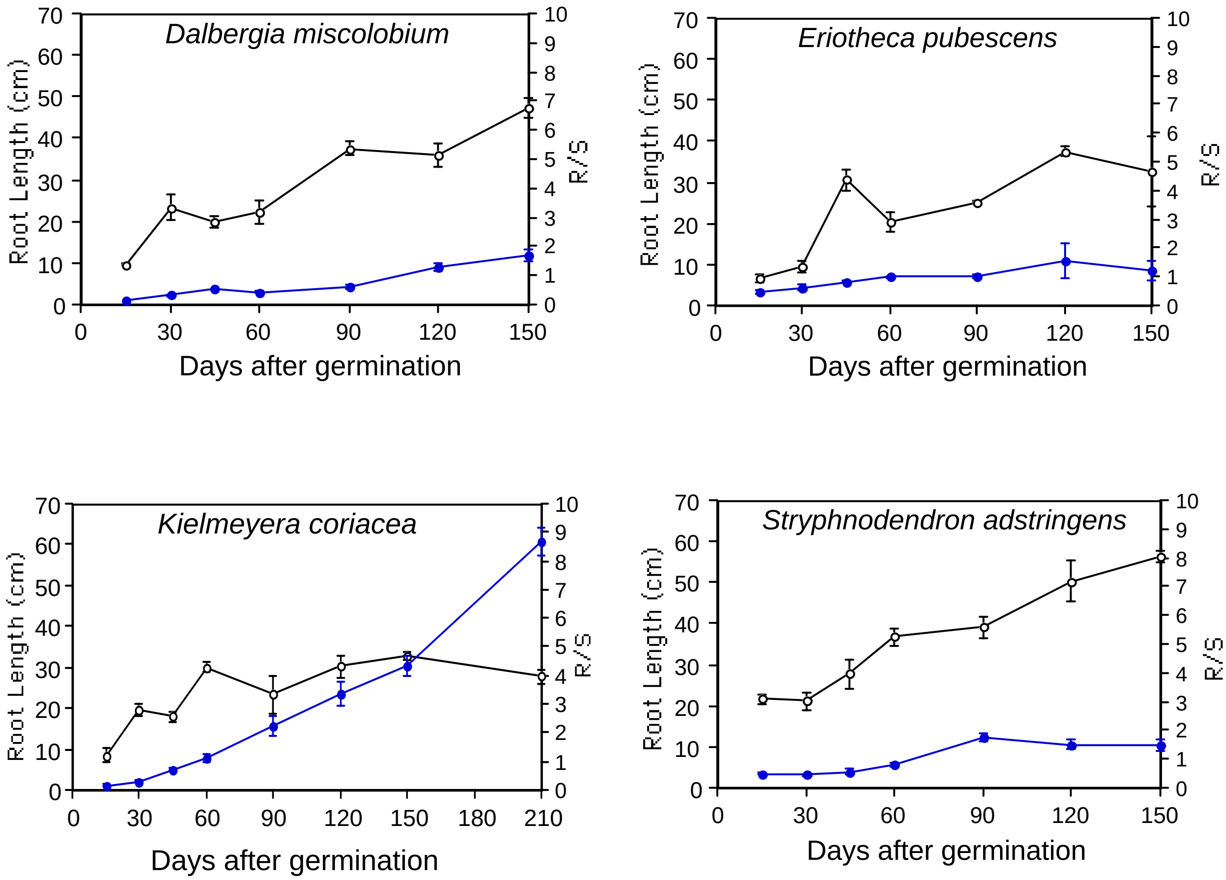

Figure 2. Root/shoot ratios (closed circles) and root length (open circles) over time of the four open savanna (cerrado *sensu stricto*) species (*Dalbergia miscolobium*, *Eriotheca pubescens*, *Kielmeyera coriaceae* and *Stryphnodendron adstringens*). Vertical bars represent one standard error.

RESULTS

The ten species had contrasting root morphologies, but two different types could be distinguished. *A. edulis*, *A. macrocarpon*, and *D. miscolobium*, had slender primary roots with a mesh of very fine lateral roots. By contrast *E. pubescens*, *K. coriaceae*, *M. pubescens*, *P. tomentosum*, *Q. grandiflora*, *S. paniculatum*, and *S. adstringens* presented a distinct, thickened primary root from the early stages and thinner lateral roots, with the exception of *K. coriaceae* that presented thickening of lateral roots.

Biomass allocation to roots and shoots was not consistent with our expectation that woodland species would allocate more biomass to shoots and open savanna species more to roots. Even though the root/shoot ratio of the woodland species *A. edulis* was never above one during the study period, the other two species from this community had a much higher allocation of biomass to roots than shoots: a ratio close to 4 in *P. tomentosum* and close to 6 in *M. pubescens* (Figure 1).

Only *K. coriaceae* allocated considerably more biomass to roots than shoots among the open savanna species. Its root/shoot ratio was close to 9 after 210 days of growth. The three other species had ratios between 1 and 2 (Figure 2). Two of the common species (*A. macrocarpon* and *S. paniculatum*) had ratios equal to one, while *Q. grandiflora* had a final root/shoot ratio of 3.5 (Figure 3).

Biomass allocation to roots was either diverted to root elongation or root thickening. The woodland species *A. edulis* (Figure 1), the open savanna species

D. miscolobium and *S. adstringens* (Figure 2), and the common species *Q. grandiflora* (Figure 3), all showed a constant increase in root length throughout the study period. Among these species root biomass was allocated to elongation in *A. edulis* and *S. adstringens*, while in *D. miscolobium* and *Q. grandiflora* root elongation occurred along with biomass accumulation.

In two species we observed root thickening but not root elongation. The woodland species *M. pubescens* had a very long root since the early stages of development but remained almost unchanged afterwards (Figure 1). In the open savanna species *K. coriaceae* root elongation occurred until 60 days after germination (Figure 2). In the remaining four species, the woodland species *P. tomentosum* (Figure 1), the open savanna species *E. pubescens* (Figure 2) and the common species *A. macrocarpon* and *S. paniculatum* (Figure 3), roots grew up to a point and remained unchanged after that.

Across all species, we found a 7.7-fold range in relative growth rate (0.025-0.192 mg mg^{-1} day^{-1}). The three woodland species had the highest values during the beginning of seedling growth (difference between 30-day and 15-day old seedlings) (Table 1). *A. edulis* had the highest rate (0.192 mg mg^{-1} day^{-1}). All other seedlings from both open savanna and common species had very low growth rate at this early stage, with the exception of the common species *A. macrocarpon* which did not differ significantly from *M. pubescens*, the woodland species with the lowest RGR (Table 1).

When growth was measured for the whole period (difference between 150-day and 15-day old seedlings) a 2.3-fold range was found accross species (0.030-0.013 mg mg^{-1} day^{-1}). *A. edulis* still had the highest growth rate, but it was not significantly different from two cerrado *s.s.* species, *D. miscolobium* and *K. coriaceae* (Table 1). Overall the ten species studied showed very low growth rates, irrespective of community type.

Comparing root and shoot RGR separately a different pattern emerges. 30-day old seedlings of *A. edulis* still had the highest growth rate for both roots and shoots, but they were not significantly different from the other woodland species (Table 1). In all but the open savanna species *S. adstringens*, root RGR was higher than shoot RGR in 30-day old seedlings. RGR of both roots and shoots decreased in 150-day old seedlings in all species, with the exception of *S. adstringens*, which showed an increase in root RGR (Table 1). For almost all species roots grew faster than shoots in both early and old seedlings since RGR of roots was higher than RGR of shoots.

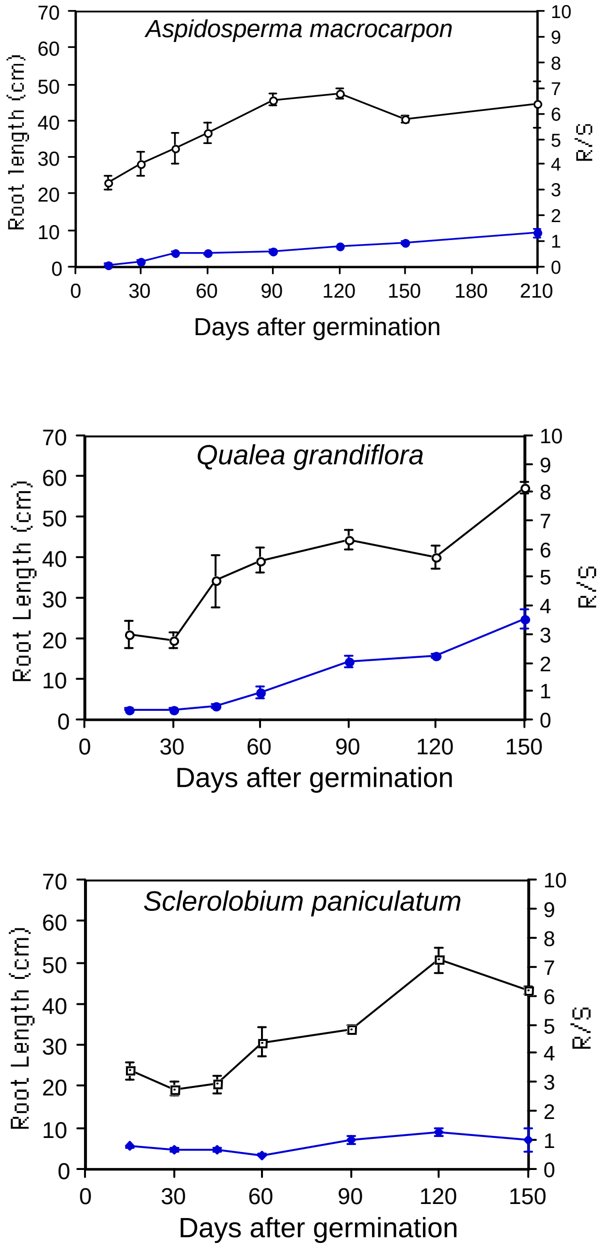

Figure 3. Root/shoot ratios (closed circles) and root length (open circles) over time of the three common species to both woodland and open savannas (*Aspidosperma macrocarpon*, *Qualea grandiflora* and *Sclerolobium paniculatum*). Vertical bars represent one standard error.

Table 1. Mean relative growth rate (RGR) of whole plant, roots and shoots of 30-day old seedlings and 150-day old seedlings of ten Cerrado tree species from two contrasting savanna communities. RGR of 30-day old seedlings refers to the difference between 30 and 15 days of age; likewise, RGR of 150-day old seedlings refers to the difference between 150 and 15 days of age. Significant differences (P<0.05) among species are indicated with letters for each column.

Specie	Whole Seedling		Roots		Shoots	
	30-day	150-day	30-day	150-day	30-day	150-day
Woodland savanna:						
Alibertia edulis	0.192 a	0.030 a	0.219 a	0.030 a,b	0.175 a	0.030 a
Magonia pubescens	0.059 c	0.020 b,c	0.083 b,c	0.032 a,b	0.055 b	0.011 b
Pseudobombax tomentosum	0.105 b	0.019 b,c	0.157 a,b	0.028 a,b	0.081 b	0.007 b
Open savanna:						
Dalbergia miscolobium	0.035 d	0.028 a	0.087 b,c	0.041 a	0.025 b	0.022 a,b
Eriotheca pubescens	0.033 d	0.019 b,c	0.057 b,c	0.023 gb	0.026 b	0.015 a,b
Kielmeyera coriaceae	0.035 d	0.026 a,b	0.083 b,c	0.043 a	0.031 b	0.016 a,b
Striphnodendron adstringens	0.025 d	0.021 b	0.021 c	0.033 a,b	0.027 b	0.021 a,b
Common Species:						
Aspidosperma macrocarpon	0.048 c,d	0.013 d	0.095 b,c	0.025 b	0.041 b	0.009 b
Qualea grandiflora	0.034 d	0.015 c,d	0.034 b,c	0.023 b	0.033 b	0.006 b
Sclerolobium paniculatum	0.038 d	0.015 c,d	0.048 b,c	0.023 b	0.034 b	0.014 a,b

DISCUSSION

Species from contrasting habitats often differ with respect to relative growth rate but differences are particularly noticeable during early stages, when soon after germination it attains a phase of more or less exponential growth (Grime and Hunt 1975). Comparisons of growth rate at later stages of plant development may be difficult because of morphological and developmental differences between species. Usually relative growth rates are measured only at the beginning of growth (Grime and Hunt 1975). In our study we did the comparisons among both young (the “exponential” phase) and old (150 days) seedlings, which represent the RGR for the whole period of growth.

The growth rate of the three woodland savanna seedlings at the early stage of growth was similar or even higher than rates reported for other tropical woody species. For instance, the relative growth rate of 28 Australian woody dicot species studied by Wright and Westoby (2000), ranged from a minimum of 0.0395 to a maximum of 0.1286 mg mg^{-1} day^{-1}, which is lower thant the maximum found in our study.

The main difference between this study and ours is regarding the range in relative growth rate across species that was found, a 3.3-fold range in theirs and a 7.7-fold range in ours. This difference is because in our study *A. edulis* had a very high rate of growth and six of our species had a growth rate smaller than the smallest found in their study. Therefore even though there are Cerrado plants that may reach high growth rates during early stage of seedling development, Cerrado species typically have low growth rates (Melhem 1975, Felippe and Dale 1990, Godoy and Felippe 1992, Sassaki and Felippe 1992) in comparison to other tropical woodlands.

We still do not have a full description of the growth process of Cerrado species, particularly a detailed comprehension of the balance between above and below-ground parts of the plant. For growth to occur, root and leaf functions must be co-ordinated and therefore a ‘functional balance’ between leaves and roots should exist (Wright and Westoby 2000). For instance, these authors measured the degree of variation in RGR that was accounted for mass allocation and morphology and leaf and root ´activity´ in 28 woody species in Australia, and found that at any time during growth, most species allocated greater mass to leaves than to roots. However, species with low RGR tended to partition a greater proportion of new biomass to roots instead of leaves and as a result a proportionally greater increase in root surface compared with leaf surface over time (Wright and Westoby 2000). If this finding is valid to all low growth rate woody species in tropical areas, that would explain, at least partially, the higher allocation of biomass to roots in most species in our study.

It was the initial contention of our study that seedlings of the more closed Cerrado woodland savanna should have a different pattern of biomass allocation when compared to seedlings of open savanna. Over time however, no consistent difference between woodland and open savanna species was found. As a whole five out of the ten species studied (*D. miscolobium*, *K. coriaceae*, *M. pubescens*, *P. tomentosum* and *Q. grandiflora*) allocated greater mass to roots than to aboveground parts. The remaining species (*A. edulis*, *A. macrocarpon*, *E. pubescens*, *S. adstringens* and *S. paniculatum*) accumulated equal amounts of biomass into roots and shoots over time but all had root elongation during seedling growth. With the exception of the woodland species *A. edulis*, all 150-day old seedlings had higher root RGR than shoot RGR, resulting in the overall trend of either mass allocation to roots or root elongation.

It has long been proposed that biomass allocation to roots and root elongation permit Cerrado seedlings to withstand the dry season during the first stages of life (Rizzini 1965) and allow plants to re-sprout from under-ground organs after fire (Dionelo-Basta and Basta 1984, Oliveira and Silva 1993, Franco 1998). Usually seed germination and establishment occur in the onset of the rains, even though short rain-free periods during the wet season had negative effects on establishment (Hoffmann 1996). Tree seedling mortality may be high a few months after germination in the field, but survivors can withstand the following dry season (Franco 1998, Franco *et al*. 1996). In many savannas fire favors species that have fire-resistant above-ground structures, such as thick bark, or species that have the ability to resprout from below-ground meristems or under-ground organs (Eiten 1972, Frost and Robertson 1987, Moreira 1991, 1996, 2000, San José and Fariñas 1991, Sato and Miranda 1996, Scholes and Archer 1997).

Our findings suggest that there is no general relationship between relative growth rate and biomass allocation across Cerrado woody species. For instance, the survivorship of seedlings of *Dalbergia miscolobium* has been attributed to its under-ground reserves that permitted resprouting after fire (Franco *et al*. 1996). On the other hand *Kielmeyera coriaceae* and *K. speciosa*, have a fast germination after the start of the wet season and early in development their root system swells forming a xylopodium (Oliveira and Silva 1993). This «establishment syndrome» recruit seedlings from a «seedling bank», plants with very small above-ground parts in comparison with large under-ground structures. Only when plants reach a certain size threshold, they can survive either fire or drought (Oliveira and Silva 1993). Even though this suggest that there is a possible balance between root and above-ground functions, we found no evidence that this varies with relative growth rate across the studied species.

ACKNOWLEDGMENTS

We thank José C.S. Silva, John D. Hay and Augusto C. Franco for commenting on earlier drafts of the manuscript. We are grateful to Embrapa-Cerrados Research Center in Planaltina, Brasília for the use of their facilities.

LITERATURE CITED

ADAMOLI, J., J. MACEDO, L. AZEVEDO and J. M. NETTO. 1986. Caracterização da região dos Cerrados. Pp 33-74, *in* W. Goedert (ed.): 'Solos dos Cerrados'. Nobel Press: São Paulo.

COUTINHO, L. M. 1978. O conceito de Cerrado. Revista Brasileira de Botânica 1: 17-23.

COUTINHO, L.M. 1982. Ecological effects of fire in Brazilian cerrado. Pp. 273-291, *in* B.Walker (ed.): Ecology of Tropical Savannas. Springer-Verlag: Berlin.

COUTINHO, L.M. 1990. Fire in the ecology of the Brazilian cerrado. Pp. 82-105, *in* J. Goldammer (ed.): Fire in the Tropical Biota. Springer-Verlag: Berlin.

DIONELO-BASTA, S. B. and F. BASTA. 1984. Estudos morfológicos das sementes e do desenvolvimento das plântulas de *Kielmeyera coriaceae* Mart. Brasil Florestal 58: 25-30.

EITEN, G. 1972. The cerrado vegetation of Brazil. Botanical Review 38: 210-341.

FELIPPE, G. M. and J. E. DALE. 1990. The effects of phosphate supply on growth of plants from the Brazilian Cerrado: experiments with seedlings of the annual weed *Bidens gardneri* Baker (Compositae) *Qualea grandiflora* (Mart.) (Vochysiaceae). Oecologia 82: 81-86.

FRANCO, A.C. 1998. Seasonal patterns of gas exchange, water relations and growth of *Roupala montana*, an evergreen savanna species. Plant Ecology 136: 69-76.

FRANCO, A.C., M. P. SOUZA and G. B. NARDOTO. 1996. Estabelecimento e crescimento de *Dalbergia* *miscolobium* em áreas de campo sujo e cerrado no Distrito Federal. Pp. 84-92, *in* H.S. Miranda, C. H. Saito and B. F. S. Dias (eds.): Impactos de Queimadas em Áreas de Cerrado e Restinga . University of Brasilia Press: Brasília.

FROST, P., E. MEDINA, J. C. MENAUT, O. T. SOLBRIG, M. SWIFT and B. WALKER. 1986. Response of savannas to stress and disturbance. Biology International 10, special issue.

FROST, P. and F. ROBERTSON. 1987. The ecological effects of fire in savannas. Pp. 93-140, *in* B. Walker. (eds.): Determinants of Tropical Savannas. IRL Press, Oxford.

GERHARDT, K. and D. FREDRIKSSON. 1995. Biomass allocation by broad-leaf Mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. Biotropica 27: 174-182.

GODOY, S.M.S. and G. M. FELIPPE. 1992. Crescimento inicial de *Qualea cordata*, uma árvore dos Cerrados. Revista Brasileira de Botanica 15: 23-30.

GOEDERT, W. J. 1983. Management of the Cerrado soils of Brazil: A review. Journal of Soil Science 34: 405-428.

GRIME, J.P. and R. HUNT. 1975. Relative growth-rate: its range and adaptive significance in a local flora. Journal of Ecology 63: 393-422.

HOFFMANN, W. 1996. The effects of fire and cover seedling establishment in a neotropical savanna. Journal of Ecology 84: 383-393.

HUANTE, P. and E. RINCÓN. 1998. Responses to light changes in tropical dedicuous woody seedlings with contrasting growth rates. Oecologia 11: 53-66.

HUNT, R. 1982. Plant Growth Curves. University Park Press, Baltimore.

KLINK, C.A., A. G. MOREIRA and O. T. SOLBRIG. 1993. Ecological impact of agricultural development in the Brazilian Cerrados. Pp 259-283, *in* M. D. Young and O. T. Solbrig (eds.): The world's savannas. Economic driving forces, ecological constraints and policy options for sustainable land use. MAB Series Volume 12 and Parthenon Publishing, London.

LABOURIAU, L. G., I. F. M. VALIO, M. L. SALGADO-LABOURIAU and W. HANDRO. 1963. Nota sobre a germinação de sementes de plantas de Cerrados em condições naturais. Revista Brasileira de Biologia 23: 227-237.

LABOURIAU, L. G., I. F. M. VALIO and E. P. HERINGER. 1964. Sobre o sistema reprodutivo de plantas dos Cerrados. Anais da Academia Brasileira de Ciências 36: 449-464.

MELHEM, T.S. 1975. Desenvolvimento da plântula de *Dipteryx alata* Vog. (Leguminosae - Lotoideae). Hoehnea 5: 91-121.

MIRANDA, A.C., H. S. MIRANDA, I. F. DIAS and B. F. DIAS. 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. Journal of Tropical Ecology 9: 313-320.

MOREIRA, A.G. 1987. Aspectos demográficos de *Emmotum nitens* (Benth) Miers. (Icacinaceae) em um cerradão distrófico do Distrito Federal. M.Sc. Thesis, Campinas State University, Brazil.

MOREIRA, A.G. 1992. Fire protection and vegetation dynamics in the Brazilian Cerrado. Ph.D. Thesis, Harvard University, USA.

MOREIRA, A.G. 1996. Proteção contra fogo e seu efeito na distribuição e composição de espécies de cinco fisionomias de Cerrado. Pp. 102-111, *in* H.S. Miranda, C.H. Saito, and B.F.S. Dias (eds.): Impactos de Queimadas em Áreas de Cerrado e Restinga. University of Brasilia Press, Brasília.

MOREIRA, A.G. 2000. Effects of fire protection on savanna structure in Central Brazil. Journal of Biogeography 27:1021-1029.

OLIVEIRA, P.E.A.M. 1986. Biologia de reprodução de espécies de *Kielmeyera* (Guttiferae) dos Cerrados de Brasília. M.Sc. Thesis, Campinas State University, Brazil.

OLIVEIRA, P.E.A.M., and A. G. MOREIRA. 1992. Anemocoria em espécies de cerrado e mata de galeria em Brasília. Revista Brasileira de Botânica 15: 163-174.

OLIVEIRA, P. E.A.M and J. C. S. SILVA. 1993. Reproductive biology of two species of *Kielmeyera* (Guttiferae) in the Cerrados of Central Brazil. Journal of Tropical Ecology 9: 67-79.

OSUNKOYA, O.O., J. E. ASH, A. W. GRAHAM and M. S. HOPKINS. 1993. Growth of tree seedlings in tropical rain forests of North Queensland, Australia. Journal of Tropical Ecology 9: 1-18.

RIBEIRO, J.F., J. C. S. SILVA and G. J. BATMANIAN. 1985. Fitossociologia de tipos fisionômicos de cerrado em Planaltina, Distrito Federal. Revista Brasileira de Botânica 8: 131-142.

RIBEIRO, J. F. and B. WALTER. 1998. Fitofisionomias do bioma Cerrado. Pp. 89-168, *in* S. Sano and S.P. Almeida (eds.): Cerrado: Ambiente e Flora. EMBRAPA Press, Brasília.

RIZZINI, C.T. 1965. Experimental studies on seedling development of cerrado woody plants. Annals of the Missouri Botanical Garden 52: 410-426.

RIZZINI, C.T, and E. P. HERINGER 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phyton 17: 105-124.

RIZZINI, C.T. and E. P. HERINGER. 1962. Underground organs of trees and shrubs from some southern Brazilian savannas. Anais da Academia Brasileira de Ciências 34: 235-247.

SAN JOSÉ, J. and M. FARIÑAS. 1991. Temporal changes in the structure of a *Trachypogon* savanna protected for 25 years. Acta Oecologica 12: 237-247.

SASSAKI, R.M. and G. M. FELIPPE. 1992. Desenvolvimento inicial de *Dalbergia miscolobium* em casa de vegetação e em Cerrado. Hoehnea 19: 75-83.

SATO, M.N. and H. S. MIRANDA. 1996. Mortalidade de plantas lenhosas do cerrado *sensu stricto* submetidas a diferentes regimes de queima. Pp. 93-101, *in* H.S. Miranda, C.H. Saito, and B.F.S. Dias (eds): Impactos de Queimadas em Áreas de Cerrado e Restinga. University of Brasilia Press, Brasília.

SCHOLES, R.J. and S. R. ARCHER. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517-544.

SOKAL, R.R. and J. ROHLF. 1981. Biometry. W.H.Freeman and Co, New York.

VILLELA, D.M. and M. HARIDASAN. 1994. Response of the ground layer community of a cerrado vegetation in central Brazil to liming and irrigation. Plant and Soil 163: 25-31.

WRIGHT, I.J. and M. WESTOBY. 2000. Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. Functional Ecology 14: 97-107.

Received September 28, 1999; revised March 04, 2000; accepted November 28, 2000.