

## Growth-survival tradeoff in the widespread tropical shrub *Baccharis dracunculifolia* (Asteraceae) in response to a nutrient gradient

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**Abstract:** *Baccharis dracunculifolia* DC. (Asteraceae) is a widely distributed species colonizing environments with a wide range of nutritional conditions, ranging from low fertility degraded areas to high fertility agriculture fields. The goal of this study was to evaluate the survival and early growth of *B. dracunculifolia* seedlings grown across a gradient of nutrient availability. This study was conducted in a greenhouse located at the Serra do Cipó, southeastern Brazil. Seedling survival, biomass partitioning and growth rate were recorded every 15 days, between 30 and 90 days after transplanting in soils with increasing nutritional availability. We found reduced seedling survival and higher biomass accumulation and growth rate with increasing nutrient availability indicating a clear trade-off between these parameters. There are evidences that the high phenotypic variability shown by *B. dracunculifolia* seedlings may play an important role in the capacity of this species to colonize disturbed areas with contrasting nutrient availability conditions.

**Resumen:** *Baccharis dracunculifolia* DC. (Asteraceae) es una especie de amplia distribución que coloniza ambientes con una gama amplia de condiciones nutricionales, desde áreas degradadas con fertilidad baja hasta campos agrícolas muy fértiles. El objetivo del estudio fue evaluar la supervivencia y el crecimiento temprano de plántulas de *B. dracunculifolia* que crecieron a lo largo de un gradiente de disponibilidad de nutrientes. El estudio se llevó a cabo en un invernadero ubicado en la Serra do Cipó, en el sureste de Brasil. Se hicieron registros de la supervivencia de las plántulas, la distribución de su biomasa y la tasa de crecimiento cada 15 días, entre 30 y 90 días después de haber sido trasplantadas a suelos que tenían una disponibilidad creciente de nutrientes. Encontramos una reducción en la supervivencia de las plántulas pero una mayor acumulación de biomasa y una mayor tasa de crecimiento conforme aumentó la disponibilidad de nutrientes, lo que indica una clara disyuntiva entre estos parámetros. Hay evidencias de que la variabilidad fenotípica alta que mostraron las plántulas de *B. dracunculifolia* puede jugar un papel importante en la capacidad de esta especie para colonizar áreas perturbadas con condiciones contrastantes de disponibilidad de nutrientes.

**Resumo:** *Baccharis dracunculifolia* DC. (Asteraceae) é uma espécie amplamente distribuída colonizando ambientes com uma ampla gama de condições nutricionais, que vão desde áreas degradadas de baixa fertilidade aos campos agrícolas de alta fertilidade. O objetivo deste estudo foi o de avaliar a sobrevivência eo crescimento inicial das plântulas de *B. dracunculifolia* crescendo através de um gradiente de disponibilidade de nutrientes. Este estudo foi conduzido numa estufa localizada na Serra do Cipó, sudeste do Brasil. A sobrevivência das plântulas, a partição da biomassa e a taxa de crescimento foram registradas em cada 15 dias,

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entre 30 e 90 dias após o transplante em solos com o aumento da disponibilidade nutricional. Encontramos uma reduzida sobrevivência das plântulas e maior acumulação de biomassa e taxa de crescimento com o aumento da disponibilidade de nutrientes, indicando um claro compromisso entre estes parâmetros. Há evidências de que a alta variabilidade fenotípica mostrada pelas plântulas de *B. dracunculifolia* podem desempenhar um papel importante na capacidade desta espécie para colonizar áreas perturbadas com condições de disponibilidade de nutrientes contrastantes.

**Key words** Cerrado, nutritional gradient, phenotypic variability, ruderal, rupestrian grasslands, seedling growth, stress resistance.

## Introduction

The Brazilian Savanna (Cerrado) and the Atlantic Rainforest stand out among priority biomes for conservation, due to an extraordinary species richness and high endemism, associated with intense rates of habitat loss (Myers *et al.* 2000). Deforestation, frequent fires and exotic species invasion are among the main impacts of anthropogenic origin that threaten the Cerrado biome (Klink & Machado 2005). In the disturbed areas resulting from these impacts the regeneration process begins with the dominance of pioneer species that often play a facilitating role in the establishment of species in the subsequent successional stages, and consequently assist in the regeneration of the plant community (Baider *et al.* 2001; Olson & Fletcher 2000).

The Cerrado and Atlantic Rainforest host many species of *Baccharis* (Asteraceae), among which *Baccharis dracunculifolia* is perhaps the most frequent. Several species of *Baccharis* are regarded as pioneers and play an important role in the regeneration and colonization of disturbed areas, such as *B. reticularia*, *B. glazioui* and *B. platypoda* (Safford 2001), *B. pilularis* (Ackerly 2004), *B. trinervis* (Quintana-Ascencio *et al.* 1996), *B. halimifolia* (Olson & Fletcher 2000), *B. linearis* (Holmgren *et al.* 2000), *B. salicina* (Skousen *et al.* 1990), *B. myrsinites* (Slocum *et al.* 2004), *B. cassinefolia* (Salimon & Negrelle 2001), *B. concinna* (Fernandes *et al.* 2007) and *B. dracunculifolia* (Baider *et al.* 2001; Galindez *et al.* 2009; Gomes & Fernandes 2002; Müller *et al.* 2007; Overbeck & Pfenhauer 2007; Tabarelli & Mantovani 1999). Furthermore, many species of *Baccharis* have been used in the rehabilitation of areas degraded by mining (Day & Ludeke 1980; Mendez & Maier 2008) and phytoremediation of contaminated soils (Haque *et al.* 2008) due to their capacity to adapt

to soils with low nutrient availability, high toxicity and contamination by heavy metals (Karrfalt & Olson 2008). In Brazil, although several authors have reported the importance of *B. dracunculifolia* in regenerating disturbed areas (Barbosa & Pizo 2006; Frenedo 2004; Santos *et al.* 2008), this species has not yet been used in ecological restoration programmes.

*Baccharis dracunculifolia* is an evergreen widespread dioecious perennial shrub native from southwestern and southern Brazil, Argentina, Paraguay, Uruguay and Bolivia (Barroso 1976). This species have traits commonly associated to colonizers and invasive plants, such as a large production of wind dispersed achenes and an efficient establishment and growth on disturbed habitats (Frenedo 2004; Gomes & Fernandes 2002). Besides this great capacity of dispersion, this species spontaneously colonizes environments with a wide range of nutrient conditions, ranging from extremely low fertility degraded areas due to mining (Santos *et al.* 2008) to high fertility agriculture fields (Macedo *et al.* 2003). Species adapted to environments with low resource availability have more “conservative” traits that enhance resource use efficiency and maximize survival at the expense of vegetative growth (Arendt 1997). Such species tend to show a stress resistance syndrome (Chapin *et al.* 1993) characterized by a set of traits such as an inherently slow growth rate, even when provided with optimal levels of nutrients (Aerts & Chapin 2000; Negreiros *et al.* 2009), and low phenotypic variation, which may manifest as a low response to differences in nutrient availability (Aerts & Chapin 2000; Bloom *et al.* 1985). These traits have important adaptive value, because they provide increased survival in conditions of resource (e.g., nutrients, water or light) limitation (Lortie & Aarssen 1996; Pearson *et al.* 2003). On the other

**Table 1.** Description of experimental treatments. Full-strength nutrient solution according to Novais *et al.* (1991).

Treatment	Substrate	Liming	Fertilization
Rupestrian	Rupestrian grasslands soil	No	No
Cerrado	Cerrado soil	No	No
Liming	Cerrado soil	Yes	No
Nutri (0.01x)	Cerrado soil	Yes	10 <sup>-2</sup> dilution of nutrient solution
Nutri (0.1x)	Cerrado soil	Yes	10 <sup>-1</sup> dilution of nutrient solution
Nutri (1x)	Cerrado soil	Yes	Full-strength nutrient solution
Nutri (2x)	Cerrado soil	Yes	Twice full-strength nutrient solution

**Table 2.** Chemical and physical properties of soils used as substrates for early growth of *Baccharis dracunculifolia*.

Parameters	Rupestrian grasslands soil	Cerrado soil
pH (H <sub>2</sub> O)	4.91	4.93
Organic matter content (%)	4.35	1.15
P (mg dm <sup>-3</sup> )	< 0.01	< 0.01
K (c mol <sub>c</sub> dm <sup>-3</sup> )	0.04	0.13
Ca <sup>2+</sup> (c mol <sub>c</sub> dm <sup>-3</sup> )	0.08	1.06
Mg <sup>2+</sup> (c mol <sub>c</sub> dm <sup>-3</sup> )	< 0.001	0.12
Al <sup>3+</sup> (c mol <sub>c</sub> dm <sup>-3</sup> )	0.10	0.87
Al saturation (%)	45.5	39.9
Base saturation (%)	1.8	20.4
Effective CEC (c mol <sub>c</sub> dm <sup>-3</sup> )	0.22	2.18
Zn (mg dm <sup>-3</sup> )	0.85	2.6
Fe (mg dm <sup>-3</sup> )	64.1	16.1
Mn (mg dm <sup>-3</sup> )	0.1	2.9
Cu (mg dm <sup>-3</sup> )	1.75	0.45
B (mg dm <sup>-3</sup> )	0.11	0.04
S (mg dm <sup>-3</sup> )	57.1	24.4
Sand (%)	49	27
Silt (%)	24	27
Clay (%)	27	46

hand, environments with high nutrient availability and subjected to frequent episodes of disturbance tend to favour the development of ruderal species. These plants have rapid growth and a consequent low investment in functions related to the conservative use of resources

acquired to ensure greater survival under adverse conditions (Grime *et al.* 1997). The ruderal strategy is attributed to plants with efficient colonizing capacity (Bullock *et al.* 2001), typically found during early successional stages (Körner & Jeltsch 2008).

Dalling & Hubbell (2002) reported a trade-off between growth and susceptibility to herbivores in Neotropical pioneer species. Other studies with woody species of tropical forests at seedling stage also showed a negative relationship between growth and survival (Gilbert *et al.* 2006; Pearson *et al.* 2003; Wright *et al.* 2010). While these studies documented this trade-off at the inter-specific context, it was rarely investigated within a species (but see Seiwa 2007). Since *B. dracunculifolia* colonizes efficiently a wide range of habitats (ranging from low to high soil fertility), we expect that this species is capable of responding differentially in widely contrasting conditions of nutrient availability, maximizing either survival or vegetative growth depending on the substrate fertility level. The goal of this study was to evaluate experimentally the survival and early growth of *B. dracunculifolia* seedlings exposed to a gradient of nutrient availability. Here three hypotheses were examined: (1) Seedlings of *B. dracunculifolia* show higher survival at lower nutrient availability. Since this species occur in sites with contrasting nutrient availability, it is expected that in conditions of low fertility it will show attributes that maximize survival at the expense of vegetative growth (Arendt 1997; Coley *et al.* 1985; Warembourg & Estelrich 2001). (2) Seedlings of *B. dracunculifolia* express a higher biomass and growth rate under higher nutrient availability conditions than low nutrient availability conditions. It is expected that *B. dracunculifolia* would display a higher growth rate under high fertility, due to its ruderal characteristics (Grime & Mackey 2002; Gutschick & BassiriRad 2003). (3) Biomass partitioning to the roots of seedlings is positively related to decreased nutrient availability. Under conditions of greater nutrient limitation, there must be higher biomass allocation to the roots, in order to optimize the growth process (Bloom *et al.* 1985; Lilienfein *et al.* 2001).

## Materials and methods

### *Study area*

This study was conducted in a greenhouse located at the Reserva Natural Particular Vellozia

**Table 3.** Concentration of applied nutrients (mg.kg<sup>-1</sup>) at each treatment of nutrient availability gradient.

	Rupestrian	Cerrado	Liming	Nutri (0.01x)	Nutri (0.1x)	Nutri (1x)	Nutri (2x)
N	-	-	-	1	10	100	200
P	-	-	-	3	30	300	600
K	-	-	-	1.5	15	150	300
Ca	-	-	209	209	209	209	209
Mg	-	-	110	110	110	110	110
S	-	-	-	0.4	4	40	80
Zn	-	-	-	0.04	0.4	4	8
Fe	-	-	-	0.015	0.15	1.5	3
Mn	-	-	-	0.036	0.36	3.6	7.2
Cu	-	-	-	0.013	0.13	1.3	2.6
B	-	-	-	0.008	0.08	0.8	1.6
Mo	-	-	-	0.0015	0.015	0.15	0.3

(lat 19° 16' 45.7" S, long 43° 35' 27.8" W), Serra do Cipó, Minas Gerais, southeastern Brazil. Serra do Cipó is located in the southern portion of the Espinhaço mountain range. The predominant vegetation type is the rupestrian grassland, a rocky montane savanna where plants are mainly sclerophyllous and herbaceous with scattered shrubs and trees comprising a mosaic of habitats (Giulietti *et al.* 1997). The soils are generally shallow, coarse textured, with high Al<sup>3+</sup>, very low nutrient content and varying amounts of organic matter (Negreiros *et al.* 2008). The climate is mesothermic with dry winters and rainy summers, the average annual temperature is 21°C and precipitation is 1600 mm (Marques *et al.* 2000).

#### *Early seedling growth along a soil nutrient gradient*

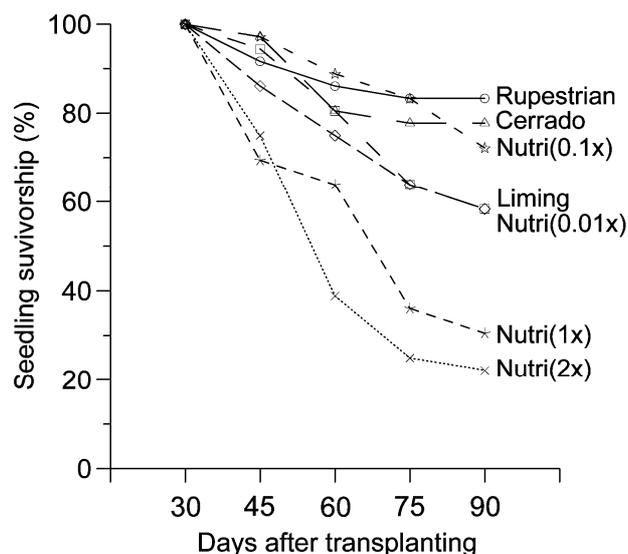
The achenes of *B. dracunculifolia* were obtained from six adult individuals found in the rupestrian grasslands near the study area, in February 2008. The achenes were germinated on a sand/vermiculite (1/1, v/v) under full sunlight. Seedlings with one pair of leaves were transplanted to the experimental plastic pots (4.8 dm<sup>3</sup>) filled with 4 kg of soil (see below), sixty days after germination.

The greenhouse-grown seedlings were exposed to a nutrient availability gradient, arranged in a complete randomized experimental design (7 treatments × 36 replicates). The applied treatments are detailed in Table 1. The substrate used in the Rupestrian treatment was a nutrient-poor soil, Lithic Ustorthents Entisols (Soil Survey Staff 1999) from an area of occurrence of adult *B.*

*dracunculifolia* plants, in a quartzitic rupestrian grassland, near the study site. Cerrado soil used for other treatments was a Typic Haplustox (Soil Survey Staff 1999). Soils of this treatment were obtained from a cerrado area 10 km away from the study area. Both soils were dried at air temperature and sieved (4 mm sieve) to remove large gravel fragments, and then subsampled for chemical and physical analyses (Table 2). The nutrient concentration applied on each treatment is detailed in Table 3.

Liming was performed 60 days before transplanting to improve base saturation values to 50 %. The phosphorus (P) source was applied 30 days after liming, and the other nutrients applied as solution immediately before transplanting. The nitrogen (N) and potassium (K) sources were applied three times at monthly intervals, beginning 30 days after transplanting (Novais *et al.* 1991). Manual weeding to remove invasive plants was performed twice a month. The greenhouse was covered by 30 % shade cloth and seedlings were irrigated by micro-dispersion for 5 min, two times a day, with a total of 3.9 mm of water per day.

Seedling survival was recorded every 15 days, between 30 and 90 days after transplanting. At the end of the experiment (90 days after transplanting), ten individuals of each treatment were randomly selected to evaluate biomass production of the plant components (leaf, stem and root). Since treatment Nutri (2x) did not have the minimum of 10 individuals, all individuals were sampled (n=8). A destructive biomass sample was made by splitting the aerial part into leaves and



**Fig. 1.** Percentage of seedling survival of *B. dracunculifolia* subjected to different treatments of soil fertility.

stems. For the root collection, a careful washing with running water was carried out until the substrate was completely removed. To determine the dry biomass production each plant component was bagged, frozen and then dried at 70 °C until constant weight. Finally, biomass was weighed in an analytical scale (0.001 g precision), following Chiariello *et al.* (1989).

To evaluate biomass partition between underground and aerial parts, root/shoot ratio was calculated following Hunt (1982). To evaluate the relative growth rate (RGR), non-destructive measures were made at the beginning and at the end of the experiment (30 and 90 days after transplanting, respectively). Primary shoot length and leaf number of each surviving individual were recorded on these two dates. Since the mortality differed between treatments, the number of replicates used to calculate the RGR was 30, 28, 21, 21, 26, 11 and 8 individuals respectively in the treatments Rupestrian, Cerrado, Liming, Nutri (0.01x), Nutri (0.1x), Nutri (1x) and Nutri (2x). The RGR was calculated according to Hunt (1982):

$$\text{RGR for leaf number: } \text{RGR} = (\ln N_2 - \ln N_1) / (t_2 - t_1)$$

$$\text{RGR for shoot length: } \text{RGR} = (\ln L_2 - \ln L_1) / (t_2 - t_1)$$

where,  $N$  = total leaf number;  $L$  = shoot length; and  $t$  = time.

### Statistical analysis

To evaluate whether there were differences

between treatments in the survival rate of seedlings, the chi-square test using contingency table was used (Zar 1996). The majority of the variables sampled did not fit the assumptions of the parametric tests, hence nonparametric Kruskal-Wallis was used followed by multiple comparisons with Bonferroni correction.

## Results

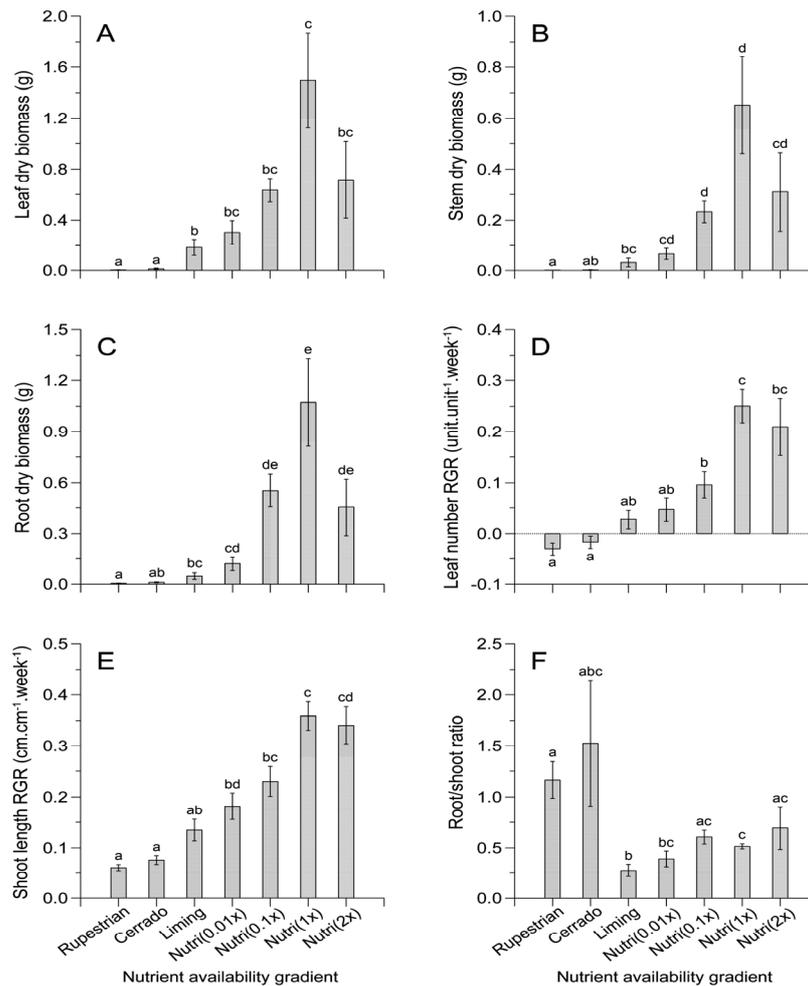
### Seedling survival experiment

Seedlings subjected to different fertilization treatments showed significant differences in survival rates at the end of the experiment ( $\chi^2 = 48.14$ ,  $P < 0.05$ ,  $n = 36$ ). Seedlings from the less fertile treatments (Rupestrian and Cerrado) exhibited the highest survival rates, 83 and 78 % respectively. Seedling mortality increased with higher soil nutrient availability (Fig. 1). Therefore, the results support the hypothesis of increased survival at lower nutrient availability.

### Seedling growth performance

Seedling growth and biomass production differed among treatments (Fig. 2). There was a tendency for seedling growth at higher nutrient availability treatments to show higher dry biomass of leaves (Kruskal-Wallis  $H^2 = 47.85$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2A), stems (Kruskal-Wallis  $H^2 = 49.66$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2B), and roots (Kruskal-Wallis  $H^2 = 50.45$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2C). Similarly, RGR in leaf number (Kruskal-Wallis  $H^2 = 50.16$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2D) and main shoot length (Kruskal-Wallis  $H^2 = 61.66$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2E) tended to increase with higher nutrient availability. Therefore, the results support the hypothesis of a higher accumulation of biomass and higher growth rate of *B. dracunculifolia* seedlings when exposed to more fertile substrates.

Despite some consistent differences between treatments (Kruskal-Wallis  $H^2 = 30.32$ ,  $df = 6$ ,  $P < 0.001$ , Fig. 2F) the partitioning of biomass to roots in the low-nutrient treatments (i.e., Rupestrian and Cerrado) did not differ statistically from treatments with higher nutrient availability (Fig. 2F). In other words, increasing dosages of fertilizers did not correspond to a significant decrease in the root/shoot ratio (Fig. 2F). Therefore, the results do not support the hypothesis of a negative relationship between biomass partitioning to roots and increased nutrient availability.



**Fig. 2.** Biomass production, partitioning and relative growth rate (RGR) in seedlings of *B. dracunculifolia* under different fertilization treatments. Bars represent the mean  $\pm$  standard error. (A) Leaf dry biomass (g); (B) Stem dry biomass (g); (C) Root dry biomass (g); (D) Leaf number relative growth rate (RGR) (unit.unit<sup>-1</sup>.week<sup>-1</sup>); (E) Shoot length RGR (cm.cm<sup>-1</sup>.week<sup>-1</sup>); (F) Root / shoot dry biomass ratio (g.g<sup>-1</sup>). Treatments followed by different letters are significantly different at probability < 0.05, according to the Kruskal-Wallis test followed by multiple comparisons with Bonferroni correction.

## Discussion

The reduced survival of *B. dracunculifolia* seedlings with increasing nutrient availability supports the predictions that species adapted to conditions of low soil fertility proportionally allocate more resources to functions that increase survival in adverse environments (Arendt 1997; Chapin *et al.* 1993; Coley *et al.* 1985). The negative effect of nutrient availability on the survival of seedlings on annual Asteraceae species was also reported by Milberg *et al.* (1999). On the other hand, Hastwell & Panetta (2005) reported higher survival rate of a ruderal weed species under conditions of greater nutrient availability.

Regarding biomass accumulation and growth rate, *B. dracunculifolia* seedlings showed a positive response to increased nutrient availability. In conditions of higher fertility, *B. dracunculifolia* seedlings had a shoot length RGR up to 4.5 times faster than the one year old rupestrian grasslands leguminous shrubs grown in high nutrient availability (Negreiros *et al.* 2009), emphasizing the ruderal characteristic of this species.

When analyzing both survival and growth of seedlings of *B. dracunculifolia*, the results of our study indicate a clear trade-off between these parameters. Espírito-Santo *et al.* (1999) found a negative relationship between production of secondary metabolites and the growth rate of branches

of *B. dracunculifolia*. Therefore, there is evidence that the trade-off between survival and growth exhibited by this species is related to a physiological adjustment in situations of nutritional stress that led to the conservative behaviour, while under high nutrient availability the seedlings direct most of the resources acquired into a rapid vegetative growth. Some studies in tropical forest systems have shown a negative relationship between survival and growth of seedlings based on inter-specific comparisons (e.g., Gilbert *et al.* 2006; Pearson *et al.* 2003; Wright *et al.* 2010). Inter-specific trade-off between growth and survival assumes that intra-specific variability is limited and that any particular species cannot achieve both good growth and high survival simultaneously. On the other hand, the intra-specific trade-off evidenced in the present study suggests a high phenotypic variability in *B. dracunculifolia*, indicated by its capacity to show distinct responses to the contrasted nutrient availability. This species can achieve both good growth (in nutrient rich conditions) and high survival (in nutrient poor conditions) depending on the substrate fertility level. Similarly to our results, Seiwa (2007) reported a negative correlation between survival and growth rate in the temperate tree species *Acer mono* (Sapindaceae) along a light availability gradient and associated this trade-off with the occurrence of this species in a wide range of habitats.

At low nutrient availability plants are assumed to show higher biomass partitioning to the roots. In spite of this fact, the gradient of increasing soil fertility did not cause a proportional reduction of biomass allocation to the roots, although that is expected when there is greater limitation of nutrients instead of light limitation (Bloom *et al.* 1985). Seedlings from Cerrado species usually have a root/shoot ratio greater than one (Moreira & Klink 2000). Higher biomass allocation to roots suggests adaptation strategies to low nutrient availability found in the Cerrado soils (Bucci *et al.* 2006; Lilienfein *et al.* 2001), drought stress caused by seasonal dry season (Hoffmann & Franco 2003) and frequent fires (Castro & Kauffman 1998).

*B. dracunculifolia* behaves as an obligate seeder species, since the adults do not resprout and survive after fire (Galindez *et al.* 2009; Müller *et al.* 2007). However, the passage of fire gives this species a competitive advantage over other species, as evidenced by the high seedling recruitment in recently burnt sites (Galindez *et al.* 2009; Overbeck & Pfadenhauer 2007; Tabarelli &

Mantovani 1999). The fast growth rate under conditions of high nutrient availability shown by *B. dracunculifolia* seedlings indicates that high recruitment of this species in disturbed areas may result from the temporary enrichment of nutrients in the soil after fire (Nardoto *et al.* 2006) and from large quantities of nutrients mobilized by human activities, such as road cutting (Gutschick & BassiriRad 2003). There are evidences that the high phenotypic variability shown by *B. dracunculifolia* in response to contrasting nutrient availability has a major role in the high capacity of colonization, both in processes of primary succession of low fertility degraded areas and secondary succession in environments of higher fertility after cutting and burning.

### Acknowledgements

We thank F. A. O. Silveira, J. C. Santos and two anonymous reviewers for critical comments on early versions of the manuscript. We are also grateful to J. S. Miranda, B. M. Rosa, L. A. C. Júnior, M. S. Belmiro and R. M. Lima for their field and laboratory support. We thank CNPq (56 1883/2010-6, 303352/2010-8, 141696/2009-5, 151817/2008-1), FAPEMIG (EDT - 465/07, APQ-01278/08, APQ-04105-10), CAPES (DRCI 002/2009), FAPEMIG/FAPESP/FAPESPA/VALE S.A. (RDP-00048-10), Reserva Vellozia and Com Cerrado for financial supports.

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(Received on 21.09.2012 and accepted after revisions, on 27.12.2012)