Original article

Seedling growth and biomass allocation of endemic and threatened shrubs of rupestrian fields

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ABSTRACT

The increasing anthropogenic pressure in the rare rupestrian fields in southeastern Brazil has led to the expansion of degraded areas on the extremely nutrient-deficient quartzitic soils. On the other hand, the use of rupestrian field native species in reclamation programmes has been hampered by the lack of studies involving seedling physiological ecology. The present study evaluated biomass allocation and seedling growth rate during early seedling growth of four Fabaceae shrubs: *Collaea cipoensis*, *Calliandra fasciculata*, *Chamaecrista ramosa*, and *Mimosa foliolosa*. The following hypotheses were tested: (i) species proportionally allocate higher biomass to the roots, presenting a high root/shoot ratio; and (ii) species exhibit low phenotypic variation because they have adapted to poor nutritional environments. A 12-month greenhouse experiment was carried out to evaluate seedling growth and biomass allocation performance in substrates with contrasting levels of soil fertility. The four species studied presented values of root/shoot ratio lower than one in both fertility conditions of the substrate. Growth parameters for *Collaea* and *Calliandra* increased with increasing soil fertility, while no differences were observed for *Mimosa* and *Chamaecrista*. Although the four species are naturally adapted to low nutritional quality soils, seedling development was not hindered by high fertility substrate conditions. Despite the remarkable differences in fertility between the substrates, the responsiveness in growth and allocation in *Chamaecrista* and *Mimosa* was lower than that expected if the species would exhibit high phenotypic variation. The implications for rupestrian field restoration are discussed.

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1. Introduction

A unique and rare vegetation physiognomy of the Brazilian Cerrado, a biodiversity hotspot (Myers et al., 2000; Marris, 2005), known as the rupestrian field, is exclusively found in the highlands of the Espinhaço mountain range and small disjunctions in southeastern and northeastern Brazil. The

rupestrian fields occur in areas above 900 m a.s.l., on shallow, Al-rich, water- and nutrient-deficient soils where rocky outcrops prevail (Giulietti et al., 1987; Benites et al., 2007). These plant communities also experience high daily thermal amplitudes, strong winds, high sun exposure and constant fires (Ribeiro and Fernandes, 2000; Jacobi et al., 2007). In this speciose physiognomy plants are mainly sclerophyllous and

herbaceous with scattered shrubs and trees comprising a mosaic of habitats (Giulietti et al., 1997). Most of the endangered species of the Brazilian Cerrado are endemic to the rupestrian fields (see Menezes and Giulietti, 2000), making this physiognomy especially important for plant conservation.

The survival of many of the rare species of the rupestrian fields is adversely affected by mining activities, road construction, pasture, uncontrolled fires, predatory tourism and unmanaged ornamental plant collection. The intense mining activities practiced for centuries on a large scale in the Espinhaço range keep impacting on its flora. Mining has resulted in bare areas with exposed subsoil or gravel (Giulietti et al., 1997; Menezes and Giulietti, 2000) and, even after being abandoned for decades, no natural recovery has been documented. In Serra do Cipó, at the southern portion of the Espinhaço range, extensive erosion due to mining can be easily observed, also as a result of careless construction or paving of existing highways (see Viana et al., 2005) where the high susceptibility to erosion of the quartzitic soils had not been taken into consideration. Furthermore, the impact of highway construction has increased the deposition of soils brought from different areas and caused the introduction of many exotic invasive species. Consequently, the need for restoration is urgent.

The selection of adapted species is a key step to rehabilitation of degraded areas and should focus on native rather than exotic species. In Brazil, most rehabilitation programmes employ exotic species such as Australian *Eucalyptus* and African grasses (mainly *Brachiaria* and *Melinis*) which have been shown to be an important threat to biodiversity (Pivello et al., 1999). The main attribute that plant species adapted to environments with low resource availability must have is an inherent low growth rate, even when exposed to optimal levels of resources (Parsons, 1968; Grime and Hunt, 1975; Chapin, 1980). These species allocate fewer resources to growth because a higher level of supply is needed for functions that increase survival rates in adverse environments (Coley et al., 1985; Chapin et al., 1993; Arendt, 1997). In such species, the slow growth rate is associated with several attributes that include high plant module longevity, a great capacity for photosynthate storage and the investment in anti-herbivory compounds (Chapin, 1980; Coley et al., 1985; Fernandes and Price, 1991; Grime, 1993). The combination of all these features has been described as stress tolerance by Grime (1977), in which selection favours traits that support retention and conservative use of acquired mineral nutrients (Grime, 1993; Warembourg and Estelrich, 2001).

The selection of species to restore degraded areas under quartzite-derived soils at the Espinhaço range must consider the optimal exploitation of the adaptive potential of rupestrian field native flora. In this harsh environment, traits such as survival and resistance to different types of stress should be favoured rather than simple fast growth and soil covering (see Elias and Chadwick, 1979; Bradshaw, 2000). The use of legume species in soil protection has been emphasized due to their increased capacity for water retention and, mainly, because of the soil fertility improvement provided by the interaction with N-fixing bacteria (Garg, 1999; Temperton et al., 2007). Fabaceae constitute one of the most well-represented families in

rupestrian fields and it is the third most represented family in Serra do Cipó, with 108 species (Giulietti et al., 1987). This study aimed to evaluate the biomass partitioning and growth responses of rupestrian field species when exposed to two levels of soil fertility. Information on restoration ecology of other Brazilian vegetation is available (Vieira and Scariot, 2006; Zamith and Scarano, 2006; Simões and Marques, 2007) but we are unaware of other studies addressing any aspect of rupestrian fields restoration. Studies on seedling growth and allocation patterns of rupestrian fields species are crucial for restoration since they will retrieve information on the ecophysiological adaptations to the harsh environment. Because restoration techniques strongly rely on seedling growth and survival, information on early seedling growth and allocation is required in order to accomplish successful programmes (Du et al., 2008).

Four native species were selected for the study. Three of them belong to the most speciose Fabaceae genera occurring in rupestrian fields: *Calliandra*, *Chamaecrista* and *Mimosa* (Giulietti et al., 1997; Menezes and Giulietti, 2000). The fourth species, *Collaea cipoensis* (Fortunato, 1995) is an endemic shrub of Serra do Cipó. Two hypotheses were tested in this study. The first hypothesis predicts that species proportionally allocate higher biomass to the roots. Being naturally adapted to poor soil environments with high light intensity, a high root/shoot ratio would be expected. High values of root/shoot ratio would be consistent with the expectation of the optimized growth process, where there is a great limitation for nutrients instead of light limitation (Chapin, 1980; Bloom et al., 1985; Wilson, 1988; Mooney and Winner, 1991; Moreira and Klink, 2000; Hoffmann and Franco, 2003). The second hypothesis predicts that species should exhibit low phenotypic variation. There is a trend for little responsiveness to the soil fertility variation in plants adapted to poor nutritional environments (Grime, 1977; Chapin, 1980; Bloom et al., 1985; Chapin et al., 1986, 1993). Hence, it is expected that growth performance and biomass partitioning will not differ in substrates with contrasting fertility conditions.

2. Materials and methods

2.1. Studied site and species

This study was conducted in a greenhouse located at the Reserva Natural Particular Vellozia (lat 19°16′45.7″S, long 43°35′27.8″W), Serra do Cipó, Minas Gerais, Brazil. Seeds were collected from plants occurring between 1060 and 1170 m a.s.l., where the climate is mesothermic, Cwb according to Köppen classification, with dry winters and rainy summers, with an average annual rainfall of 1500 mm and average temperature ranging from 17.4 to 19.8 °C (Galvão and Nimer, 1965).

Collaea cipoensis Fortunato (Papilionoideae) is a 2–4 m tall shrub, commonly found in grassy rupestrian fields (Fortunato, 1995). It occurs usually in soils with high organic matter accumulation, next to water courses. It has a very restricted area of distribution and is only known from Serra do Cipó (Fortunato, 1995). *Calliandra fasciculata* Benth. var. *bracteosa* (Bentham) Barneby (Mimosoideae), referred to as *Calliandra*, is a 0.4–2 m tall shrub. It occurs along and near the crest of

Espinhaço range, especially on outcrops associated with water courses, on rocky stream banks, and in rock-pockets of rupestrian fields between 820 and 1350 m a.s.l. (Barneby, 1998). It is endemic to upland northern and central Minas Gerais, between latitudes 16°30′–19°30′S (Barneby, 1998). *Chamaecrista ramosa* (Vog.) var. *parvifoliola* (Irwin) Irwin & Barneby (Caesalpinioideae), referred to as *Chamaecrista*, is a 0.3–0.8 m tall shrub. The species occur in montane regions, chiefly on white or gray sandy soils (Irwin, 1964), on stony fields and outcrops of Cerrado vegetation, between 250 and 1370 m a.s.l. (Irwin and Barneby, 1982). It has a wide distribution, being found in several Brazilian states (Irwin and Barneby, 1982). *Mimosa foliolosa* Benth. ssp. *pachycarpa* (Bentham) Barneby var. *pachycarpa* (Mimosoideae), referred to as *Mimosa*, is a 0.4–0.7 m tall shrub (Barneby, 1991). It occurs in sandy rupestrian fields and on the edges of sandstone outcrops, between 1100 and 1300 m a.s.l. It is known only from the Espinhaço range between latitudes 19°30′–20°S, Minas Gerais (Barneby, 1991). *Calliandra* and *Collaea* are strongly associated with mesic habitats whereas *Chamaecrista* and *Mimosa* occupy more xeric habitats.

2.2. Seedling growth in substrates with contrasting fertilities

To test the hypotheses of proportionally higher root biomass allocation and low phenotypic variation by the studied species, seedlings were grown in a greenhouse experiment in December 2002. Seeds of each species were obtained in a nearby area from mature fruits collected from at least 10 individuals per species. Parasitized or damaged seeds were discarded. Physical dormancy imposed by hard seed coat in *Chamaecrista* (Gomes et al., 2001), *Mimosa* (Silveira and Fernandes, 2006) and *Collaea* seeds (C. Louzada, 2002, personal communication) was broken by mechanical scarification by making a 2 mm long incision in the seed coat at the opposite side of the hilum (Orozco-Almanza et al., 2003). Physical dormancy was not reported for *Calliandra* seeds (Silveira et al., 2005). Afterwards, seeds were hydrated for 24 h and then directly seeded into the fertile and unfertile substrates, with one seed per bag. The greenhouse was covered by 50% shade cloth and seedlings were irrigated by micro-dispersion for 15 min, three times a day, with a total of 17.5 mm of water/day. Manual weeding to remove invasive plants was performed monthly.

The substrates used for plant growth were prepared to supply low (unfertile) versus high (fertile) fertility levels. The low fertility substrate was chosen to simulate the adverse chemical characteristics of soils found in degraded quartzite areas, while the substrate with high fertility had the characteristics of substrates used in commercial greenhouses for sapling production. The substrate used for the treatment called unfertile was obtained through 50 soil samples with 20 cm diameter × 20 cm depth, obtained through a random sampling at a degraded area nearby to the greenhouse, composed mostly of quartzite substrate. The collected soil was sieved through a 5 mm sieve to remove large gravel fragments. The soil was mixed until completely homogenised and then used to fill plastic bags of 12 cm diameter × 26 cm depth (3 L). The substrate used for the fertile treatment was

composed of equal parts of subsoil land, peat bog and an organic compound (with horse manure and sawdust at a 1:1 proportion). For acidity correction and nutritional enrichment, 2 L of $CaCO_3$ and 1 L of NPK (4:14:8) were added in 360 L of substrate. The resulting compound was mixed until completely homogenised and used to fill the bags. The chemical and physical properties of both treatments are provided in Table 1.

Seedlings were arranged in a complete randomized design (4 species × 2 substrate treatments × 5 replicates). To evaluate plant growth rate, non-destructive measures were made at the beginning and at the end of the experiment (3 and 52 weeks after seeding, respectively) to calculate the relative growth rate (RGR) for the interval. Primary shoot length, diameter and leaf number of each individual were recorded on these two dates. Primary shoot length was measured with a ruler (mm) while shoot diameter was measured with a digital caliper (0.01 mm precision). Leaves were counted with the help of a manual counter. Relative growth rate (RGR) was calculated according to Hunt (1982) and McGraw and Garbutt (1990):

- RGR for shoot length: $RGR = (\ln L_2 - \ln L_1)/(t_2 - t_1)$;
- RGR for diameter: $RGR = (\ln D_2 - \ln D_1)/(t_2 - t_1)$;
- RGR for leaf number: $RGR = (\ln N_2 - \ln N_1)/(t_2 - t_1)$;

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

To evaluate plant growth, the total lateral shoot number and crown volume, calculated by multiplying the three axes as shown in Fig. 1, were recorded at the end of the experiment for each individual. The leaf, stem, and root biomass production were recorded at the end of the experiment; a destructive biomass sample was made by splitting the aerial part into leaves and stems. For the root collection, a careful washing with running water was carried out until the substrate was completely removed. To determine dry biomass production,

| Table 1 – Chemical and physical properties of unfertile and fertile treatments.		
Parameter	Unfertile	Fertile
pH (H_2O)	5.15	6.54
Organic matter (%)	0.78	11.66
P (mg/dm^3)	0.10	99.00
K (mg/dm^3)	9.00	306.00
Ca^{2+} (cmol$_c$/dm^3)	0.09	6.87
Mg^{2+} (cmol$_c$/dm^3)	0.01	3.61
Al^{3+} (cmol$_c$/dm^3)	1.90	0.00
Al saturation (%)	93.92	0.00
Cation saturation (%)	3.59	84.90
Efective CEC (cmol$_c$/dm^3)	2.02	11.26
Zn (mg/dm^3)	1.66	16.02
Fe (mg/dm^3)	22.80	55.90
Mn (mg/dm^3)	1.20	23.80
Cu (mg/dm^3)	0.00	0.29
B (mg/dm^3)	1.66	4.89
S (mg/dm^3)	2.60	130.30
Sand (%)	49.00	28.00
Silt (%)	42.00	37.00
Clay (%)	9.00	35.00
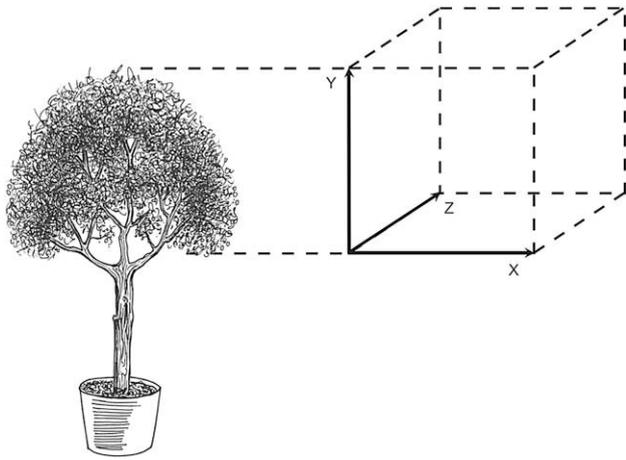
Fig. 1 – Schematic drawn of the three measured axes of seedling crown volume.

each component was bagged, frozen and then dried at 70 °C until constant weight was obtained. Finally, biomass was weighed in an analytical scale (0.001 g precision), following Chiariello et al. (1989).

To evaluate biomass partition among plant organs, parameters derived from dry biomass (root, stem, and leaf) were calculated, following Hunt (1982):

- root/shoot ratio: $RS = W_R/(W_L + W_S)$;
- root weight ratio: $RWR = W_R/(W_R + W_L + W_S)$;
- stem weight ratio: $SWR = W_S/(W_R + W_L + W_S)$;
- leaf weight ratio: $LWR = W_L/(W_R + W_L + W_S)$;

where, W_R = total root dry weight; W_S = total stem dry weight; and W_L = total leaf dry weight.

The hypothesis of higher biomass allocation to the roots was tested by the evaluation of the root/shoot ratio in the individuals for both treatments (fertile and unfertile). To test for low phenotypic variation, the values obtained by each species at the end of the experiment (size, biomass allocation ratios, and relative growth rate) were compared between fertile and unfertile treatments. The responsiveness of each species to the applied treatments is presented in the form of a proportion between the average of each measured variable in both treatments.

Most variables had neither a normal distribution nor could a normal distribution be achieved after transformation in order to meet the assumptions of parametric tests. In addition, variations of the residuals were not homogeneous for the groups studied (species and treatments). Hence, the data were analyzed by the non-parametric test of Mann–Whitney (Conover, 1980).

3. Results

3.1. Differential biomass allocation to roots

The fertile and unfertile substrates were very different in their chemical and physical properties. Striking differences were

observed in all parameters, but particularly in P, K, Ca^{2+}, Mg^{2+} and Al saturation (Table 1). The four species studied had root/shoot ratios lower than one in both treatments, indicating a higher biomass allocation for the aerial part of the seedlings, but the ratios were consistently higher for the unfertile treatment (Fig. 2A).

3.2. Growth performance in substrates with contrasting fertilities

Except for shoot length, all measured traits for the 1-year-old *Collaea* individuals were significantly lower under the unfertile treatment when compared with seedlings submitted to the fertile treatment (Table 2). Under the unfertile treatment, *Collaea* proportionally allocated less biomass to stems (Fig. 2) and presented a smaller RGR for shoot diameter and leaf number (Fig. 3).

All growth and allocation parameters of *Calliandra* had significantly lower values when seedlings were grown under the unfertile treatment (Table 2). On the other hand, no differences in root, stem and leaf biomass allocation (Fig. 2) and RGR for shoot length (Fig. 3) between treatments were found.

The contrasting conditions of the substrates did not affect the development of *Chamaecrista* individuals. No significant differences were found in any of the measured variables (Table 2), neither in RGR (Fig. 3). Seedlings of *Chamaecrista* significantly decreased biomass allocation to root and consistently allocated more biomass to aerial parts when grown under the fertile conditions (Fig. 2).

For *Mimosa*, variation between treatments was observed only in parameters related to stems with no lateral shoot production observed in any of the treatments (Table 2). There was a striking decrease in biomass allocation to stems under the unfertile treatment (Fig. 2C). No statistically significant differences were observed for other traits (Table 2; Figs. 2 and 3).

Interestingly, the species associated with water courses, *Collaea* and *Calliandra*, showed higher responsiveness to the substrate fertility as both size and biomass were significantly inferior in the unfertile substrate (Fig. 4A–I). On the other hand, the two species that occur in xeric habitats showed low responsiveness. *Chamaecrista* was not sensitive to substrate fertility conditions, excepting for allocation parameters (Fig. 4J–M) whereas *Mimosa* was partially affected as in the unfertile treatment (Fig. 4).

4. Discussion

It has long been suggested that biomass allocation to roots and root elongation permit Cerrado seedlings to withstand the dry season during the first stages of life and allow plants to resprout from underground organs after the passage of fires (Moreira and Klink, 2000). Paulilo and Felippe (1998) showed that four out of five species grown in the greenhouse had a root/shoot ratio higher than one, as should be expected for species adapted to water and nutrient poor environments. Moreira and Klink (2000) studied biomass allocation in Cerrado trees and found that only one species had a root/shoot ratio smaller than one, with most species having values ranging from one to six. Field estimates of root/shoot ratios of
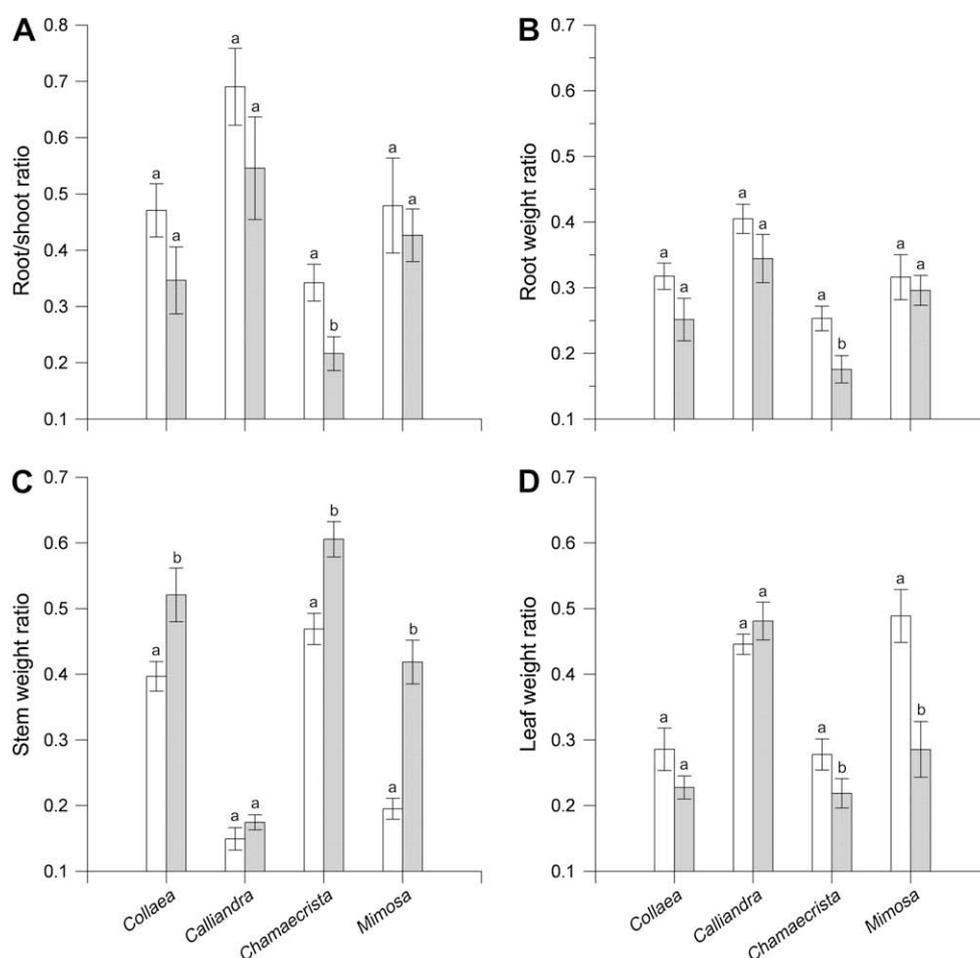
Fig. 2 – Biomass partition in *Collaea cipoensis*, *Calliandra fasciculata*, *Chamaecrista ramosa* and *Mimosa foliolosa* under unfertile (□) and fertile substrate (▨). Bars represent average values (±SE; $n = 5$). (A) root dry biomass/shoot dry biomass ratio; (B) root weight ratio; (C) stem weight ratio; (D) leaf weight ratio. In the same species, fertility treatments followed by different letters are statistically different at the probability level <0.05, according to the Mann–Whitney test.

tree-dominated Cerrado are typically greater than those found for Neotropical rainforests or dry forests (Hoffmann et al., 2003). The high root/shoot ratio of savanna species is therefore, considered to be an adaptation to an environment with deep and poor soils with low water retention capacity, where light is not a limiting resource, and probably explains the greater fire tolerance of savanna species (Hoffmann and Franco, 2003; Hoffmann et al., 2003).

The four species in this study showed low root/shoot ratio under both fertility conditions. These results were contrary to the expectation for native species inhabiting nutritionally poor environments (see Chapin, 1980; Bloom et al., 1985; Mooney and Winner, 1991; Chapin et al., 1993), but point to interesting new studies as this represents the first report on biomass allocation in species native to rupestrian fields. Most soils associated with rock outcrops in the Espinhaço range are shallow (Ribeiro and Fernandes, 2000; Benites et al., 2007) and therefore, low root/shoot ratios found for the studied species may be explained by the investment in aerial biomass because the shallow soils constrain root growth.

At Cerrado *sensu stricto*, Abdala et al. (1998) found, on average, a root/shoot ratio equal to one and state that this

value can be considered high in comparison to other savanna-like ecosystems. But despite having been grown under controlled conditions, the values of root/shoot ratio for *Lotus corniculatus* (0.34) and *Coronilla varia* (0.45) were considered high (Elias and Chadwick, 1979). These authors associated these values with the high capacity of these stress-tolerant Fabaceae species to restore low fertility degraded areas. Therefore, these data indicate that there is still controversy as to what should be considered a high root/shoot value. It is more reasonable to assume that the root/shoot ratio may be relative in different plant communities.

Several authors have investigated RGR in species from savanna-like formations (Wright and Westoby, 2000), cerrado *sensu stricto* and woodlands (Moreira and Klink, 2000; Hoffmann and Franco, 2003). However, because these authors expressed RGR on a biomass basis rather than as non-destructive data, comparisons with our data are impossible. Cerrado species typically have low growth rates in comparison to forest species (Moreira and Klink, 2000) because Cerrado is considered a more stressful, unproductive environment, where stress-tolerant species with traits such as low RGR are expected to have evolved (Grime, 1977; Chapin et al.,

Table 2 – Seedling size and biomass of the studied species measured for 1-year-old individuals on fertile and unfertile substrates.

	Collaea cipoensis		*Calliandra fasciculata*		*Chamaecrista ramosa*		*Mimosa foliolosa*	
	Unfertile	Fertile	Unfertile	Fertile	Unfertile	Fertile	Unfertile	Fertile
Shoot length (cm)	97.80 ± 8.27^a	154.70 ± 26.25^a	16.68 ± 1.40^a	25.70 ± 1.66^b	72.80 ± 2.63^a	76.20 ± 6.64^a	40.00 ± 3.70^a	70.00 ± 5.96^b
Shoot diameter (mm)	6.61 ± 0.53^a	10.21 ± 1.12^b	2.37 ± 0.16^a	5.10 ± 0.56^b	3.94 ± 0.46^a	5.34 ± 0.71^a	5.37 ± 0.67^a	7.72 ± 0.76^b
Crown volume ($m^3 \times 10^2$)	3.55 ± 0.67^a	34.24 ± 13.29^a	0.15 ± 0.02^a	1.43 ± 0.42^b	12.36 ± 2.59^a	12.30 ± 2.22^a	1.94 ± 0.45^a	3.05 ± 1.12^a
Number of leaves	23.40 ± 4.99^a	71.80 ± 12.99^b	15.60 ± 1.86^a	37.00 ± 3.86^b	487.20 ± 120.88^a	392.20 ± 60.26^a	17.80 ± 1.24^a	14.00 ± 2.30^a
Number of shoots	3.00 ± 1.00^a	9.00 ± 1.87^b	2.00 ± 0.95^a	4.20 ± 0.86^a	39.20 ± 7.39^a	45.80 ± 7.74^a	0^a	0^a
Total dry biomass (g)	9.32 ± 1.72^a	30.68 ± 9.13^b	1.21 ± 0.12^a	5.52 ± 1.10^b	7.40 ± 1.81^a	7.05 ± 1.20^a	4.58 ± 0.91^a	8.99 ± 2.01^a
Leaf dry biomass (g)	2.49 ± 0.23^a	6.65 ± 1.60^b	0.55 ± 0.07^a	2.57 ± 0.43^b	2.18 ± 0.59^a	1.48 ± 0.25^a	2.16 ± 0.43^a	2.66 ± 0.87^a
Stem dry biomass (g)	3.85 ± 0.98^a	17.12 ± 6.29^b	0.18 ± 0.02^a	0.93 ± 0.16^b	3.47 ± 0.91^a	4.39 ± 0.83^a	0.89 ± 0.19^a	3.72 ± 0.74^b
Root dry biomass (g)	2.98 ± 0.59^a	6.91 ± 1.52^b	0.40 ± 0.05^a	2.01 ± 0.58^b	1.75 ± 0.34^a	1.18 ± 0.22^a	1.52 ± 0.40^a	2.61 ± 0.55^a

Within species, means ($\pm SE$; $n = 5$) followed by different letters are statistically different at the probability level <0.05, according to the Mann–Whitney test.

1993). The low RGR for rupestrian field species is mostly explained by increased habitat harshness (Giulietti et al., 1997; Ribeiro and Fernandes, 2000; Benites et al., 2007; Jacobi et al., 2007) in comparison to other savanna/Cerrado vegetations. The documented association of low RGR with high root/shoot ratio (Wright and Westoby, 2000) was probably not observed here because of constraints in root growth as a result of shallow soil depths in the rupestrian fields.

With exception of *Calliandra* and *Collaea*, most growth and allocation traits were not significantly different between treatments. Given the large differences in substrate properties, differences in seedling performance were expected to be much larger for *Mimosa* and *Chamaecrista*. Therefore, the hypothesis that predicts little responsiveness to variation in soil fertility (Grime, 1977; Chapin, 1980; Chapin et al., 1986) holds only for *Mimosa* and *Chamaecrista*, the species that exhibited low responsiveness to soil fertilization.

The stress-tolerance syndrome was more evident in *Calliandra* because of the higher root/shoot ratio and lower RGR exhibited by this species. However, *Calliandra* has shown considerable sensitivity to substrate fertility, contradicting the expectations of stress-tolerant species (Chapin, 1980; Bloom et al., 1985; Chapin et al., 1993). On the other hand, although *Chamaecrista* was shown to be the most insensitive species to substrate fertility conditions it presented the lowest root/shoot ratio. The traits related to stress tolerance varied according to the species, suggesting that selection of these traits is species-specific and also that root/shoot ratio and growth rate may lack a direct relationship.

The low fertility, acidity and aluminum toxicity traits of the unfertile substrate were very similar to those found in several degraded quartzite areas located at Serra do Cipó (G.W. Fernandes, 2008, unpublished data). Conversely, the substrate used as fertile treatment resembles the substrates used for sapling production. The performance of the four studied species under the fertile substrate conditions suggests that the traditional techniques (pH correction and soil fertilization) used for propagation in conventional greenhouses could be applied to these species even though *Chamaecrista* and, in part, *Mimosa* do not require fertility and acidity corrections. There was no evidence of growth constraints due to high mineral toxicity for the four species in substrate with good nutrient

conditions although we do not know whether plants grown in fertile soil would survive transplantation to degraded areas compared to plants grown in unfertile soils. In fact, most native Cerrado woody species are capable of responding positively to acidity correction and soil fertilization in field and greenhouse conditions (Sassaki and Felippe, 1997; Haridasan, 2000).

In spite of the low variation observed for all studied species, there was a trend for the endemic species to present higher phenotypic variation in response to substrate fertility when compared to the widely distributed species, *Chamaecrista*. Plant endemism is very frequently related to soil specificity (Kruckeberg and Rabinowitz, 1985; Matthews et al., 1993; Ribeiro and Fernandes, 2000) and it has been argued that species with restricted distributions usually have a higher competitive advantage within the boundaries of their habitats (Matthews et al., 1993; Ribeiro and Fernandes, 2000; de Lange and Norton, 2004). Soil nutritional deficiency has been argued to favour only species adapted to nutritional stress (Grime, 1977; Chapin et al., 1986; Morghan and Seastedt, 1999). Although the three endemic species had better performance in the fertile substrate, under field conditions this probably would not happen since allochtonous competitive species (*sensu* Grime, 1977) would easily overwhelm them in growth, productivity and in fecundity. In general, the acid and poor quartzite soils have a rich flora and with high levels of plant endemism (Matthews et al., 1993). We argue that acidity correction and soil fertilization in quartzite degraded areas prior to revegetation should be made in a controlled way to maintain the properties naturally found in rupestrian fields soils since an increase in soil fertility usually results in a decrease in species diversity (Gough and Marrs, 1990). Road construction provides a way for the entrance of exotic species in these areas and therefore, in contrast to the traditional methods in degraded area restoration, maintaining the adverse soil conditions could prevent the invasion of exotic species in the area.

Natural regeneration is rarely observed in degraded areas on quartzite-derived soils in the Espinhaço range after being abandoned for decades (Giulietti et al., 1997; Menezes and Giulietti, 2000). Since these areas are surrounded by a flora adapted to adverse edaphic conditions, factors such as high seed predation and seedling herbivory (Holl et al., 2000), limited and incomplete seed rain (Buisson et al., 2006), soil
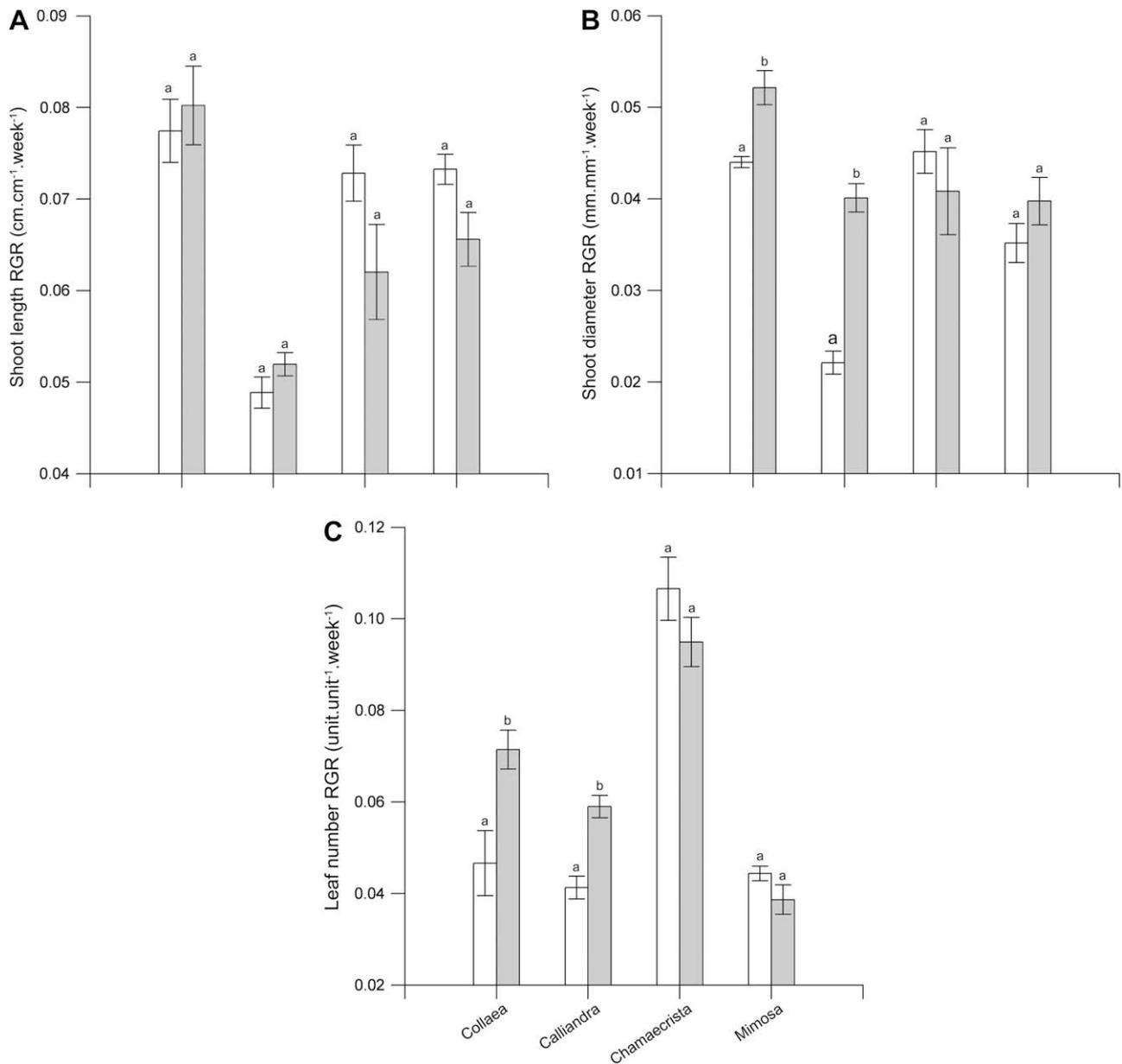
Fig. 3 – Relative growth rate in *Collaea cipoensis*, *Calliandra fasciculata*, *Chamaecrista ramosa* and *Mimosa foliolosa* under unfertile (□) and fertile substrate (▨). Bars represent average values (±SE; $n = 5$). (A) RGR for primary shoot length $(\text{cm cm}^{-1} \text{week}^{-1})$; (B) RGR for shoot diameter $(\text{mm mm}^{-1} \text{week}^{-1})$; (C) RGR for leaf number $(\text{unit unit}^{-1} \text{week}^{-1})$. In the same species, fertility treatments followed by different letters are statistically different at the probability level < 0.05, according to the Mann–Whitney test.

compacting (Teixeira and Lemos-Filho, 2002) and high susceptibility to erosion (Freitas and Silveira, 1977), absence of mycorrhiza inoculum and high soil surface temperature (as a result of lack of soil cover), may be the mechanisms accounting for limited recruitment, thus hindering natural regeneration in such areas.

5. Limitations and conclusions

The results shown by the studied species suggest an idiosyncratic trend, making it hard to draw any generalizations at present. However, alternative explanations accounting for low root/shoot ratios cannot be overlooked. The volume of the container used for seedling growth and the reduction of light intensity by 50% may also have been relevant for limited root development and the relative higher investment in aerial biomass (Bloom et al., 1985). In addition, ontogenetic variations may occur in root/shoot ratios (Wilson, 1988; Shipley and Peters, 1990). Hence, the results presented here could differ if the evaluation had been made on individuals growing in conditions similar to those experienced by the rupestrian field plant communities. Although it has been shown that light had no overall effect on RGR for Cerrado species (Hoffmann et al.,
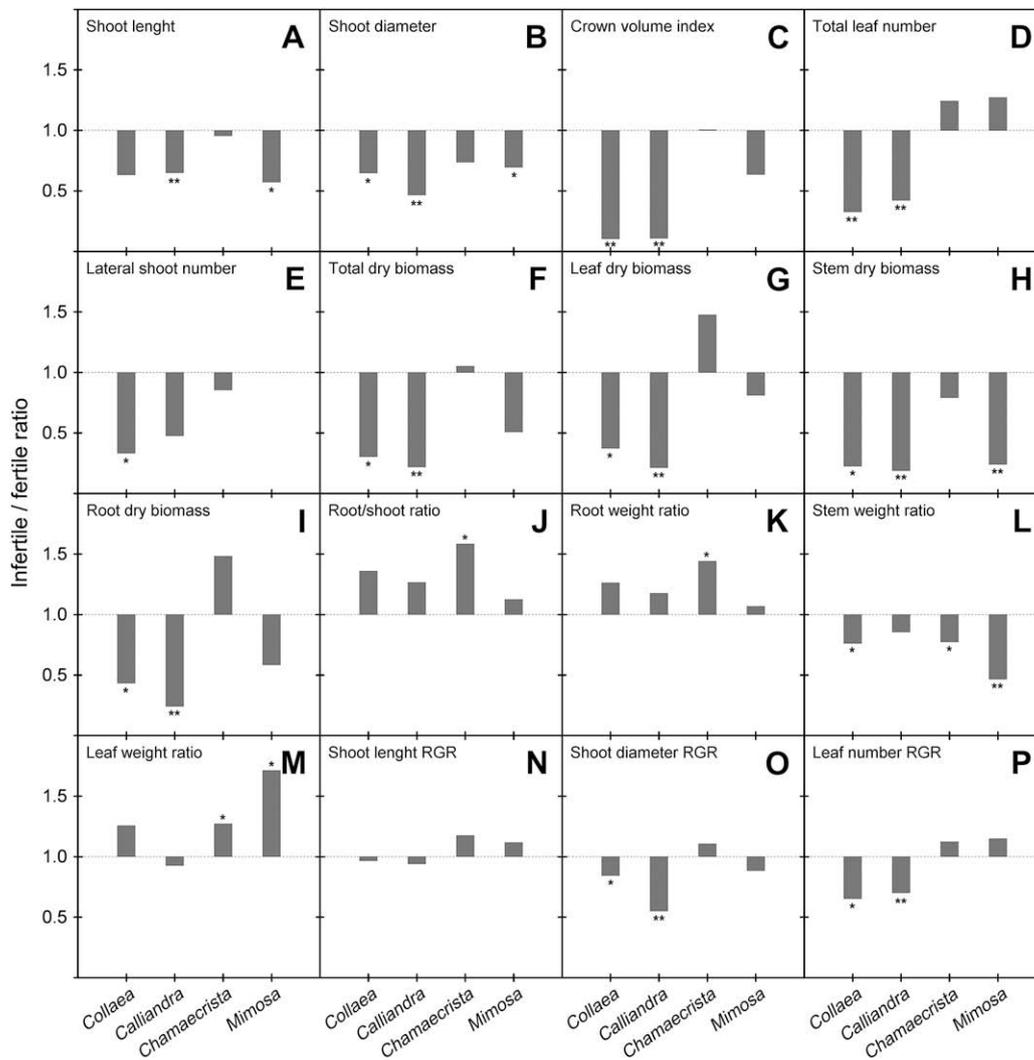
Fig. 4 – Differential performance of the studied species under contrasting substrate fertility conditions. The values are referred to the ratio between averages on unfertile treatments and fertile treatments for the following characteristics. (A) Primary shoot length (cm); (B) shoot diameter (mm); (C) crown volume (m^3); (D) total leaf number; (E) total lateral shoot number; (F) total dry biomass (g); (G) leaf dry biomass (g); (H) stem dry biomass (g); (I) root dry biomass (g); (J) root/shoot ratio; (K) root weight ratio; (L) stem weight ratio; (M) leaf weight ratio; (N) relative growth rate (RGR) for shoot length ($cm\,cm^{-1}\,week^{-1}$); (O): RGR for shoot diameter ($mm\,mm^{-1}\,week^{-1}$); (P) RGR for leaf number ($unit\,unit^{-1}\,week^{-1}$). For each species, the statistical difference between fertile and unfertile treatments is indicated by the value of P: $^*P < 0.05$; $^{**}P < 0.01$, according to the Mann–Whitney test.

2003), patterns of root/shoot ratio and growth are expected to be different if seedlings were grown in less fertile soils with low water availability.

Given the extremely adverse conditions of an unfertile substrate, the growth of the individuals provides support for the capacity to resist nutritional stress, providing evidence that the species are potential candidates for revegetation programmes in degraded quartzite-derived areas. They are also suggested for restoration ecology due to their high seed production and germinability (Gomes et al., 2001; Silveira et al., 2005; Silveira and Fernandes, 2006), and high establishment and N fixation capacity. Despite low growth rates presented by the studied species, the use of autochthonous flora should be preferred rather than fast-growing exotic

species. The low RGR is an inherent trait of stress-tolerant species and the use of native flora should be recommended in the long-term.

Using native species saplings (produced in greenhouse) could be an alternative to the restoration process of these areas. Fabaceae species planted this way could act as nurse plants in the recolonization process, through improvement of physical, chemical and biological soil conditions (Temperton et al., 2007). To better understand native species tolerance and nutritional needs, more specific evaluations as to how nutrients (and their combination) are more limiting to native species growth, as well as how isolated and combined effects of nutritional, hydric and light stress could influence the development and biomass partitioning in endemic plants of

this vegetation type, are required. These efforts would represent progress in the conservation of an endemic flora under increasing anthropogenic pressure.

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