- 1 Negreiros D., Fernandes G. W., Efremova A. A., Le Stradic S., Neves A. C. O. 2016 .Growth-survival
- trade-off in shrub saplings from Neotropical mountain grasslands. South African Journal of Botany.
- 3 106, 17-22. http://dx.doi.org/10.1016/j.sajb.2016.05.015

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Growth-survival trade-off in shrub saplings from Neotropical mountain grasslands

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ABSTRACT

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The growth-survival trade-off plays a central role in the coexistence of species-rich plant communities. While recurrently described in forest tree communities primarily limited by light availability, this trade-off is still poorly documented in grassland and savanna vegetation. In this comparative study we planted in a quartzitic degraded site eight-month-old saplings of eleven shrub species native from constrained mountain grassland (Brazilian rupestrian grassland). We measured the relative growth rate (RGR) during a 30-week time interval, leaf water potential under dry and wet conditions, and related these traits to the species survival. The interspecific comparison between the saplings performance clearly showed the classic growth-survival trade-off. The RGR expressed in stem diameter and aboveground biomass explained respectively 62 and 40% of the variation in saplings survival one year after planting, and respectively 65 and 44% of the variation in survival 4.5 years after planting. This trade-off was not related to either leaf water potential or final size in aboveground biomass and basal stem diameter. Our results corroborate the view that the growth-survival trade-off is universally applicable, even in non-forest communities such as grasslands and savannas subjected to severe nutritional deficiency, pronounced seasonal drought, and high light incidence. The environmental differences in micro-habitats that compose rupestrian grasslands should distinctly favour species with contrasting strategies of growth and survival, thus contributing to niche partitioning and coexistence in this speciesrich ecosystem.

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- Keywords: 'fast-slow' plant economics spectrum; relative growth rate; resource-use strategy;
- 45 rupestrian grasslands; sapling survival.

1. Introduction

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Growth rate and survival are two fundamental components related to plant fitness. Slow-growing plants exhibit generally a set of traits such as high longevity (at the individual and plant module level), well-developed capacity to accumulate reserves, more efficient resorption of nutrients during organ senescence, and major investments in secondary defensive compounds (Chapin et al., 1993; Aerts and Chapin, 2000; Willby, et al. 2001). In this sense, several lines of evidence point to the existence of a primary axis of specialization in the world flora that opposes, on the one hand, the ability to rapidly acquire resources and, on the other hand, the ability to retain and conserve these resources (acquisitive and conservative extremes, respectively), composing the world-wide 'fast-slow' plant economics spectrum (Grime et al., 1997; Wright et al., 2004; Ordoñez et al., 2009; Grime and Pierce, 2012; Reich, 2014). The trade-offs subjacent to this single economics spectrum are frequently invoked to explain coexistence in species-rich plant communities, allowing the partition of niches along multiple resource availability gradients (i.e., related to nutrients, water, luminosity, or space), thus favouring different strategies in heterogeneous environments (Kneitel and Chase, 2004; Baraloto et al., 2005; Sterck et al., 2006; Wright et al., 2010). The mechanisms behind these trade-offs vary depending on the overarching environmental factors to which plant communities are subjected (e.g. nutrient, light, or water limitation, and recurrent perturbation such as fire). However, while the trade-off between growth and survival seems to be universally applicable (see, Fine et al., 2006), this phenomenon is only widely and recurrently documented in tree species, and in forest communities primarily limited by light availability, such as tropical forest tree species (Kitajima, 1994; Dalling and Hubbell, 2002; Wright et al., 2003, 2010; King et al., 2006; Poorter and Bongers, 2006; Myers and Kitajima, 2007; Poorter et al., 2008; Russo et al., 2008; Suzuki et al., 2009), and in temperate forests (Walters and Reich, 1996; Seiwa, 2007;

Bigler and Veblen, 2009). The scarcity of such studies in ecosystems subjected to different selective pressures and dominated by herbaceous and shrubby life forms (e.g., grasslands and savannas) makes it uncertain whether the trade-off between growth and survival is a common phenomenon in systems which are distinct from closed-canopy forest communities.

Among the most ancient grassy ecosystem of the world are the rupestrian grasslands (also known as *campos rupestres*), which is a unique ecosystem that occurs mainly on the peaks and ridges of the mountains that comprise the Espinhaço mountain range in southeastern Brazil (Veldman et al., 2015; Silveira et al., in press). Rupestrian grasslands exhibit the classical features of OCBILs: very old, climatically buffered, infertile landscapes (Hopper et al., in press), and as such, this ecosystem is of recognized importance in the worldwide conservation scenario due to its enormous biodiversity (5011 vascular plant species distributed in 66,447 km²) and large proportion of endemism (some dominant families endemism rates ranging from 60 to 80%, such as Velloziaceae and Eriocaulaceae) (Silveira et al., in press). The vegetation that predominantly consists of a dominant herbaceous *stratum* interspersed with some small evergreen sclerophyllous shrubs is subjected to strong environmental stresses mainly due to the extremely infertile soils of quartzite and sandstone origin, pronounced seasonal drought, intense light, and strong and constant winds (de Carvalho et al., 2014; Negreiros et al., 2014b; Le Stradic et al., 2015; Oliveira et al., 2015; Silveira et al., in press).

The present study aimed to test the existence of a negative relationship between relative growth rate (RGR) and survival of shrubs species adapted to constrained environmental conditions occurring in rupestrian grasslands (i.e., high light incidence, extremely low nutrient availability, and recurrent fire; Veldman et al., 2015; Silveira et al., in press). It was expected that species with lower growth rate would have greater survival rates due to higher investments in functions that increase retention and conservative use of acquired

resources (Aerts and van der Peijl, 1993, Arendt, 1997; Grime and Pierce, 2012). In order to investigate the possible factors involved in the growth-survival trade-off, we examined the relationship between water stress resistance and the growth and survival rates of species. Since rupestrian grasslands are subjected to a pronounced seasonal dry period, we expected that drought tolerance could be a strong determinant of sapling establishment (Markesteijn and Poorter, 2009; Assis et al., 2011).

2. Material and methods

2.1. Study area and selected species

This study was carried out in the Reserva Natural Vellozia (19°17'46"S, 43°35'28"W, approximate altitude 1,200 m a.s.l.) located in the Morro da Pedreira Environmental Protection Area, Serra do Cipó, southern portion of the Espinhaço mountain range, Minas Gerais, Brazil, where rupestrian grasslands predominates. The local climate is considered mesothermal (Cwb according to Köppen classification), markedly seasonal, with two well-defined seasons: one hot and rainy (between November and April) and the other dry and colder (between May and October), with annual precipitation of 1,534 mm and a mean annual temperature ranging from 15.1 to 20.7°C (Alvares et al., 2013; data from Santana do Riacho municipality).

Among the sympatric and native shrubs from rupestrian grassland that occur in the vicinity of the study area, we selected eleven species belonging to six different families:

Dasyphyllum reticulatum (DC.) Cabrera (Asteraceae); *Jacaranda caroba* (Vell) A. DC.

(Bignoniaceae); *Chamaecrista semaphora* (HS Irwin & Barneby) HS Irwin & Barneby

(Fabaceae: Caesalpinioideae); *Calliandra fasciculata* Benth. var. bracteosa* (Bentham)

Barneby (Fabaceae: Mimosoideae); *Mimosa foliolosa* Benth. ssp. pachycarpa* (Bentham)

Barneby (Fabaceae: Mimosoideae); *Collaea cipoensis* Fortunato* (Fabaceae: Papilionoideae);

Diplusodon hirsutus (Cham. & Schltd) DC. and Diplusodon orbicularis Koehne (Lythraceae); Heteropterys byrsonimifolia A. Juss. (Malpighiaceae); Marcetia taxifolia (A. St.-Hil.) DC. (Melastomataceae); Tibouchina heteromalla (D. Don) Cogn. (Melastomataceae). These shrubs are relatively abundant in the study area, and produce a high number of viable seeds (see Le Stradic et al., 2014).

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2.2. Experiment preparation

Seeds of each species were collected manually in the field from mature fruits in more than ten adult individuals per species. Seeds that did not present signs of predation, pathogens, or malformation have been selected. At the end of November 2002 (Fig. 1), selected seeds were sown directly into prepared substrate (one seed per container) contained in black polyethylene bags (8 cm in diameter and 20 cm deep). For the four Fabaceae species dormancy breaking by mechanical scarification was necessary. The substrate used for growing the saplings was composed of equal parts of subsoil, peat, and an organic compound (consisting of tanned equine manure with sawdust at a 1:1 proportion), following Negreiros et al. (2009). For acidity correction and nutritional enrichment, 2 dm³ of CaCO₃ and 1 dm³ of NPK (4:14:8) in 360 dm³ of substrate were added. The resulting compound was thoroughly mixed until homogenized and used to fill the containers. For a detailed description of the greenhouse phase, and chemical and granulometric characterization of the saplings cultivation substrate, see Negreiros et al. (2009). During five months saplings grew in a greenhouse with 50% of shade and were irrigated by micro-aspersion for 15 minutes, three times a day, receiving a total of 17.5 mm of water per day. At the end of April 2003 (end of the rainy season; Fig. 1) saplings were transferred to the open air with gradual reduction of water supply in order to be acclimated before being planted in a permanent site.

At the end of July 2003 (peak of the dry season; Fig. 1), 96 saplings of each species were planted in an approximately 0.5 ha site degraded by the removal of gravel for road construction, and located close to the greenhouse (for chemical and granulometric details about the soil of the degraded area where the saplings were planted, see Negreiros et al., 2009). For each species, six 4 m² plots, positioned randomly in the degraded area, were allocated. In each plot, 16 saplings of the same species were planted in a regular spacing of 0.5 m between individuals, totalling 96 saplings per species. Four plots were designated for survival monitoring, while two plots were intended for destructive samplings of aboveground biomass and other measures (see details in section 2.3). Since the planting was carried out in the dry season, the plants were irrigated with sprinklers for 15 minutes every 10 days, during the first two months.

2.3 Evaluation of growth and water potential

For the calculation of RGR, destructive samplings were made in aboveground biomass of saplings in two dates: on the date of planting, and 30 weeks after planting (February 2004; Fig. 1). In each sampling, eight saplings of each species had their stem diameters at ground level measured with a digital calliper (0.01 mm of precision). In order to determine the shoot dry biomass, the aboveground parts of the plants were cut, dried in oven at 70°C until constant weight was reached, and weighted in analytic scale (precision of 0.001 g) according to Chiariello et al. (1989). The RGR in aboveground biomass (RGR biomass) and in stem diameter (RGR diameter) of each species was calculated according to Hunt (1982): RGR biomass ($\ln W_2 - \ln W_1$)/ ($t_2 - t_1$); RGR diameter ($\ln D_2 - \ln D_1$)/ ($t_2 - t_1$), where W_2 and D_2 are, respectively, the average aboveground dry weight, and the average stem diameter at the end of the evaluation (30 weeks after planting); W_1 and D_1 are, respectively, the average dry weight, and the average diameter on the date of planting; t_2 and t_1 are, respectively, the final and initial time of

evaluation (with a 30-week interval). The average values of aboveground dry biomass and stem diameter at 30 weeks after planting were used as indicators of the final plant size.

For determination of the plant water potential, the predawn leaf water potential (Ψ_{pd}) was measured in plants with a portable Scholander pressure bomb (PMS-600, Covalis, Oregon, USA) between 3 and 5 a.m. in vertically oriented leader twigs (Scholander et al., 1965). This technique has been widely used to infer plant water stress in different situations (Saha et al., 2008). The measurements were made in the field, on the main branch of eight saplings per species (immediately after cutting of the branch), at the end of the dry season (Ψ_{dry} ; early October 2003) and during the rainy season (Ψ_{wet} ; December 2003; Fig. 1). These two dates were chosen to compare the water potential of plants in conditions of apparent water stress (Ψ_{dry}), and in the absence of such stress (Ψ_{wet}). The difference between the water potential in the rainy and dry season (in MPa) was used as an indication of the degree of susceptibility of the species to water deficit, with higher values indicating greater stress.

2.4. Survival monitoring

In August 2004 (1 year after planting; Fig. 1) sapling survival of plants in the monitoring plots was recorded in the four plots dedicated to the survival monitoring per species. Additionally, we obtained the survival after 4.5 years of the planting (February 2008) from the study of Le Stradic et al. (2014), which reported the survival for the same plots after the completion of the initial study reported here. Survival monitoring was calculated as the percentage of living individuals relative to the total number of planted individuals (n = 64 per species).

2.5. Statistical analyses

To achieve the assumptions of normality, the values of final aboveground dry biomass and final basal stem diameter were transformed logarithmically. Since survival after 1 year and after 4.5 years showed a negative skewness, these variables were reflected prior to and after the transformation (square root), according to Quinn and Keough (2002). The values of survival after 1 and 4.5 years were treated as dependent variables. In order to identify the main axes of trait variation (RGR, final size, and water potential) a principal component analysis (PCA) was made. Varimax rotation was applied to the eigenvectors to simplify the interpretation of retained components. The correlation between the species coordinates in the two main axes and the dependent variables was examined. Additionally, linear regression analyses were employed to obtain the relationship between the measured plant traits and the dependent variables (Quinn and Keough, 2002).

3. Results

The 11 species assessed in this study showed a wide range of values in the measured traits (Table 1). The two main components of the PCA corresponded to 80.5% of the total trait variation measured in plants (Fig. 2). The positive side of PCA axis 1 corresponded to species with larger final size (i.e. greater biomass and diameter at 30 weeks after planting) and more resistant to water deficit (i.e. minor water potential variation between rainy and dry seasons). On the other hand, the PCA 2 axis separated on the positive side the species with larger RGR in biomass and diameter. This axis correlated negatively with the survival recorded after 1 year (r = -0.695; p < 0.05) and 4.5 years (r = -0.742; p < 0.01) of planting on degraded area (Fig. 2). Confirming this trend, we found a negative relationship between the survival (either 1 and 4.5 years after planting) and the RGR of plants (based on stem diameter and aboveground biomass). The RGR in diameter and biomass explained, respectively, 62.2 and 40.1% of the variation in sapling survival 1 year after planting (Fig. 3a-b). Similarly, the

RGR in diameter and biomass explained, respectively, 65.0 and 43.8 % of the variation in survival 4.5 years after planting (Fig. 3c-d).

4. Discussion

The interspecific comparison of growth and survival rates of the rupestrian grasslands shrubs planted in degraded area showed that, in general, slow-growing species had higher survival rates, whereas fast-growing species presented higher mortality rates. This observation is in agreement with the classical predictions of resource economics strategies (Aerts and van der Peijl, 1993; Grime et al., 1997; Reich, 2014) and confirms the central hypothesis of this study, that the growth survival trade-off is also evident in shrubs from low nutrient and high light environments.

There are a large number of examples of trade-off between growth rate and survival in animals (Mangel and Stamps, 2001) whereas almost all examples pertaining to this trade-off in plants are restricted to tree species' seedlings, saplings, and young plants from closed canopy ecosystems (e.g., Kitajima, 1994; Dalling and Hubbel, 2002; Wright et al., 2003, 2010; Poorter and Bongers, 2006; Poorter et al., 2008). In these environments, the dynamics of disturbances that create clearings lead to gradients of light availability that distinctly benefit species along a continuum ranging from shade-tolerant species (with slow growth and high survival rates in low light situation) to pioneer species (with rapid growth and high mortality rates in a situation of greater luminosity). The mechanisms underlying this trade-off relate to differences in the relative investment in defences against herbivores and pathogens, in the density of woody structures, and in traits related to the leaf economics spectrum (King et al., 2006; Poorter and Bongers, 2006; Sterck et al., 2006; Myers and Kitajima, 2007). Even in these forest environments where light availability plays a key role, there are indications that

factors related to moisture and soil fertility also influence the growth and survival rates of the species (Pearson et al., 2003; Russo et al., 2008).

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Since stressful conditions may be caused by a lack or excess of light, water, nutrients, or temperature (Grime, 1977), it is expected that in several habitats with different selective pressures it can be possible to detect this negative relationship between growth and stress tolerance. Correspondingly, Loehle (1998) reports a trade-off between the growth rate in height and tolerance to freezing as a probable cause of the northern and southern limits in tree species. Also, Perez-Ramos et al. (2013) reported greater survival and resistance to water stress in grasses from the conservative extreme of the plant economics spectrum. There are evidences that the plant economics spectrum is largely independent from the growth form, taxonomic affinity, characteristics of the environment, and geographic location (Reich et al., 1999; Wright et al., 2004, Díaz et al., 2016). Therefore, it is likely that the rarity of reports of trade-off between growth and survival in herbaceous or shrubby communities is simply a result of the scarcity of studies of this nature in open ecosystems (e.g., deserts, grasslands and savannas). Despite being rare, there are some scattered examples in the literature showing the trade-off between growth and survival in non-forest communities, such as in annual plants of the Sonoran Desert, USA (Angert et al., 2009), in perennial plants of smaller height that form rosettes (Metcalf et al., 2006) and in the shrub species of semi-arid Karoo, South Africa (Wiegand et al., 2000). Although the large-scale study of Lind et al. (2013) did not evaluate mortality of plants, it showed evidences that in grassland ecosystems, there is effectively a trade-off between growth and investment in anti-herbivore defences, thus reinforcing the universality of the growth-defence trade-off (Fine et al., 2006).

The precise factors that caused mortality in the saplings were not evaluated in this study, but the causes ranged from pathogens and insect herbivores to physiological stresses, since the saplings grew protected from disturbances such as trampling or burning. Therefore,

the survival of the evaluated shrubs may be linked to relative investments in conservative traits, with higher survival in species that maximize defensive traits and/or tolerance to stresses.

While seasonal water deficit was expected to act as a strong force in structuring rupestrian grasslands communities (Porembski & Brathlott, 2000; Negreiros et al., 2014b; Silveira et al.; in press), our study showed that water stress resistance plays a minor role in the survival of planted shrubs, which imply that other factors are involved to structure such plant communities. All evaluated species were relatively resistant to water deficit in the dry season, since these species showed a very low difference between the water potential in rainy and dry seasons. Other factors might play a more important role for structuring rupestrian grassland communities, such as phosphorus deficiency or fire (Le Stradic et al. 2015; Oliveira et al., 2015; Silveira et al., in press). However, since we measured only a small subset of rupestrian grassland flora, future studies including more species are needed to confirm this trend. The size of plants at the end of evaluation was also weakly coupled with the growth-survival trade-off. Accordingly, large-scale comparative studies (e.g. Pierce et al., 2013, Díaz et al., 2016) suggest that size related traits (both whole plant and leaf traits) vary independently in relation to plant economics spectrum traits (e.g. RGR, specific leaf area, leaf dry matter content, and leaf toughness).

The negative relationship between growth and survival has been well documented in a situation that compares survival in stressful conditions (lack of luminosity) and growth in favourable conditions (adequate luminosity). However, environmental heterogeneity is not a pre-requisite to the detection of the growth-survival trade-off, since this trade-off can also be detected in the same habitat and environmental condition (see, Russo et al., 2008). Similarly, in our study the sympatric shrubs adapted to chronic limited resources showed distinct growth and persistence abilities even though these shrubs grew in homogenous and semi-controlled

environment. On the other hand, the interplay between intraspecific variability and environmental heterogeneity allows the existence of the growth-survival trade-off even in the intraspecific scale (e.g., Seiwa, 2007; Negreiros et al., 2014a).

Strong environmental stresses (e.g., extreme nutritional deficiency, high luminosity, and pronounced seasonal drought) imply that plant species present variations in trait responses to these edaphic conditions. However, in addition to these life history singularities, there are countless variations in micro relief and soil texture that modify water, microclimatic, and nutritional regimes in reduced spatial scale that generate and support a very complex vegetation mosaics (de Carvalho et al., 2014; Le Stradic et al., 2015, Silveira et al., in press). Thus we argue here that the interaction between this rich environmental heterogeneity and the intrinsic position of rupestrian grassland species into the 'fast-slow' plant economics spectrum must play a fundamental role in the mechanisms responsible for niche partitioning and coexistence of the enormous diversity of species in this ecosystem (Silveira et al., in press).

Acknowledgments

We are grateful to G.E. Overbeck, M.A.R. Mello, C.P. Schlindwein and F.A.O. Silveira for critical comments on early versions of the manuscript, to A.M.O. Paiva, M.N.A. Pereira, M.L.B. Moraes, C. Louzada and C. Chalub for the field and laboratory support, to J.R. Pirani for the botanical identifications, to H.P. Dinsmore for language review, and to A.C. Franco for ecophysiological measurements suggestions. We thank Reserva Natural Vellozia for logistical support and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support.

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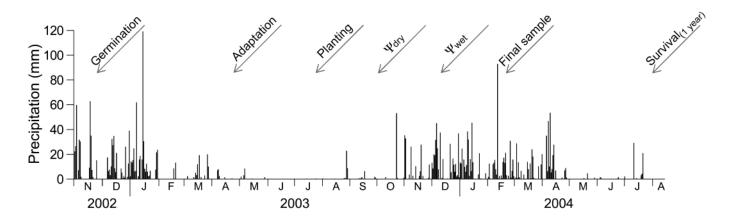


Fig. 1. Daily values of precipitation (mm) during the study period (October 2002 to September 2004), in Serra do Cipó, MG, Brazil. Data obtained from the Meteorological Database for Education and Research (BDMEP) of the National Institute of Meteorology (INMET), meteorological station of Conceição do Mato Dentro, MG, Brazil, located approximately 30 km away from the study area. Vertical dashed lines indicate the dates of the experimental main stages. Germination: seeds put in the greenhouse to germinate; Adaptation: sapling transferred from the greenhouse to open air; Planting: sapling planting in degraded areas and initial measurements of aboveground biomass and stem diameter; Ψdry and Ψwet: water potential measurements in the dry and rainy season, respectively; Final sample: measurements of aboveground biomass and stem diameter 30 weeks after planting; Survival_(1 year): evaluation of survival one year after planting.

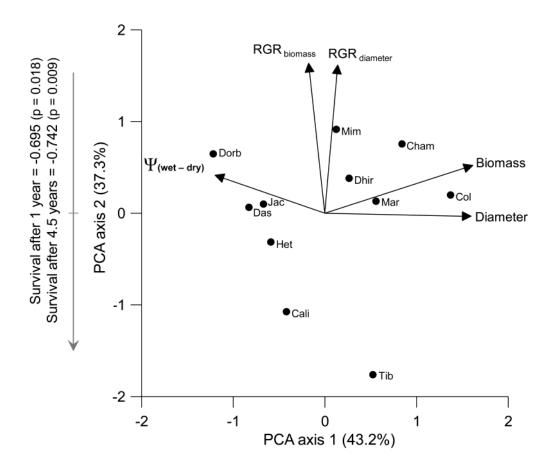


Fig. 2. Principal component analysis (PCA) on the matrix of 11 shrub species (points) × 5 mean traits (arrows) evaluated in plants grown in degraded quartzitic site in Serra do Cipó, MG, Brazil. Eigenvalues are indicated in brackets on each axis. Biomass and Diameter: average sapling final size in aboveground biomass and stem base diameter at 30 weeks after planting; Ψ_(wet-dry): difference between mean leaf water potential (predawn) in the rainy and dry seasons; Survival (1 year) and Survival (4.5 years): survival rate at 1 and 4.5 years after planting (n = 64 individuals per species); RGR biomass and RGR diameter: relative growth rate in biomass and diameter, respectively, estimated in the time interval between 0 and 30 weeks after planting. Transformation of variables was indicated where applicable. $\sqrt{\text{reft}}$: Square root applied to reflected variable (see details in section 2.5). Significant Pearson correlations (α = 0.05) between two principal axes retained in the PCA and dependent variables (survival after 1 and 4.5 years after planting) are shown. See Table 1 for species abbreviation codes.

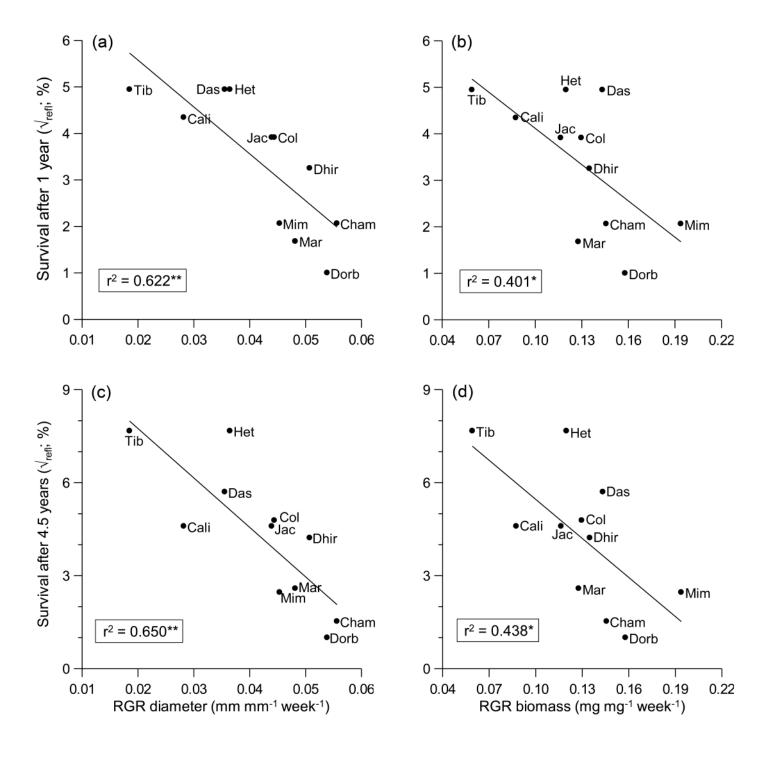


Fig. 3. Relationship between survival 1 year after planting in degraded quartzitic area and: (a) relative growth rate in stem diameter (RGR $_{diameter}$); (b) relative growth rate in aboveground biomass (RGR $_{biomass}$). Relationship between survival 4.5 years after planting and: (c) RGR $_{diameter}$ and (d) RGR $_{biomass}$. Transformation of the variables was indicated where applicable. $\sqrt{_{refl.}}$: Square root applied to reflected variable (see details in

section 2.5). The regression line, the coefficient of determination and significance of the relationship are shown. *: p < 0.05, **: p < 0.01. Points represent the mean trait value for each species (n = 11). See Table 1 for species abbreviation codes.

Table 1.

Parameters measured in rupestrian grassland shrubs saplings planted in a degraded quartzitic area in Serra do Cipó, MG, Brazil. The values refer to the mean \pm standard error (n = 8 individuals per species). **cod**.: species abbreviation codes. **Biomass** and **Diameter**: respectively, aboveground dry weight and stem diameter at ground level of the saplings 30 weeks after planting. Ψ_{dry} and Ψ_{wet} : Leaf water potential (pre-dawn) measured respectively, at the end of the dry season and at the peak of the rainy season. $\Psi_{(wet-dry)}$: difference between mean water potential in the rainy and dry seasons; **RGR** biomass and **RGR** diameter: respectively, relative growth rate in aboveground biomass and in stem diameter, estimated in the time interval between zero and 30 weeks after planting; **Survival** (1 year): percentage of survival one year after planting (n = 64 individuals per species).

Species	cod.	Biomass	Diameter	Ψ_{dry}	$\Psi_{ m wet}$	Ψ _(wet - dry)	RGR _{biomass}	RGR _{diameter}	Survival _(1 year)
		(g)	(mm)	(MPa)	(MPa)	(MPa)	(mg mg ⁻¹	(mm mm ⁻¹	(%)
							week ⁻¹)	week ⁻¹)	
Dasyphyllum reticulatum	Das	13.8 ± 1.4	5.5 ± 0.5	-0.72 ± 0.04	-0.20 ± 0.05	0.52	0.143	0.036	100.0
Jacaranda caroba	Jac	11.1 ± 2.2	8.7 ± 0.1	-1.04 ± 0.09	-0.32 ± 0.06	0.72	0.116	0.044	96.9
Chamaecrista semaphora	Cham	65.2 ± 12.5	10.3 ± 0.7	-0.37 ± 0.02	-0.23 ± 0.02	0.14	0.146	0.056	85.9
Calliandra fasciculata	Cali	8.2 ± 3.8	6.4 ± 1.1	-0.47 ± 0.04	-0.27 ± 0.01	0.20	0.088	0.028	98.4
Mimosa foliolosa	Mim	27.7 ± 11.7	8.8 ± 1.9	-0.43 ± 0.01	-0.15 ± 0.05	0.27	0.194	0.045	85.9
Collaea cipoensis	Col	106.3 ± 10.7	13.8 ± 0.5	-0.23 ± 0.03	-0.14 ± 0.01	0.09	0.130	0.044	96.9
Diplusodon hirsutus	Dhir	26.3 ± 3.5	8.5 ± 0.7	-0.47 ± 0.04	-0.29 ± 0.03	0.18	0.135	0.051	93.7
Diplusodon orbicularis	Dorb	5.5 ± 2.4	3.8 ± 0.6	-0.58 ± 0.06	-0.30 ± 0.06	0.28	0.158	0.054	76.6
Heteropterys byrsonimifolia	Het	11.6 ± 1.1	5.4 ± 0.8	-0.63 ± 0.06	-0.35 ± 0.10	0.28	0.120	0.036	100.0
Marcetia taxifolia	Mar	28.8 ± 3.4	9.0 ± 0.7	-0.30 ± 0.04	-0.28 ± 0.02	0.02	0.128	0.048	82.8
Tibouchina heteromalla	Tib	17.7 ± 3.1	9.8 ± 0.7	-0.14 ± 0.01	-0.13 ± 0.02	0.01	0.059	0.019	100.0