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Potencial de espécies nativas para revegetação de
campos rupestres

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Potencial of native species on rupestrian grassland revegetation

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Submetido a Restoration Ecology

Abstract

The introduction of plant species is a central topic in restoration research and a relevant active restoration technique for degraded areas in ecosystems with great biodiversity and low resilience, as are the rupestrian grasslands. Once implemented, the planting of native species is generally monitored for a limited time. Our pioneer study provides the first available information of the performance of 10 native rupestrian grassland species 8.5 years after transplanted into a degraded area. Survivorship, growth and recruitment were assessed in 2004, 2008 and 2012. For all species, analyzed parameters varied over time, and suggested a trade-off between different plant functions, as a response of the influences of environmental conditions, biotic interactions and ontogenetic changes. It was also observed a great ability of the species to resprouting. The studied species, in general, have shown remarkable capacity to overcome the extreme environment of the degraded area, persisting either through surviving or recruiting new individuals over the years.

Key words: restoration, trade-off, transplanting, harsh environment, resprout, Serra do Cipó

Introduction

The introduction and establishment of plant species are central topics in restoration research (Holzel et al. 2012). The re-establishment of the natural vegetation from a particular ecosystem is vital for ecological restoration, since only then the connectivity, ecosystem functioning and reconstitution of ecosystem services, such as nutrient cycling, soil protection and water purification are achieved (Resende et al. 2014). Native seedling favors the restoration process, improving microclimate conditions and contributing to greater organic matter and nutrients input (Vetaas 1992; Holl et al. 2000; Alday et al. 2014; Gomes et al. 2015). On the other hand, introduced seedlings in degraded areas present unique challenges due to the adverse environment found in these areas (Fernandes et al. 2015). To deal with it, is important to use native species, with plant materials obtained from the region of the area to be restored (Withrow-Robinson and Johnson 2006), ensuring better adaptation and development of the vegetation in degraded soil, and encourage ecological succession (Gomes et al. 2015; Nunes et al. 2015). Another important issue in selecting plant materials is maintaining genetic variation in the populations established in the restored area. Plant populations must be genetically variable to be able to adapt to new stresses (Robbinson and Johnson 2006; Reynolds et al 2012).

Old, climatically buffered, infertile landscapes (OCBILs) comprises ecosystems with unique features and high conservation value, like predominance of species with reduced dispersability, increased local endemism and common rarity; predominance of old lineages and old individuals; nutritional and other biological specialisations for resource acquisition; and high vulnerability to soil removal (Hopper 2009). Rupestrian grassland (also known as *campo rupestre*) found in the mountains of central and eastern Brazil,

more specifically in the Espinhaço Range, is an extremely old mountaintop ecosystem that fulfills the criteria for a classic OCBIL (Silveira et al 2016). The rupestrian grasslands are a vegetation mosaic associated to a diverse soil environments, with extremely high richness and endemism (Fernandes et al. 2016, in press). The richness comprises 14.7 % of the entire Brazilian vascular flora in an area corresponding to only 0.78 % of the country's land surface (Silveira et al. 2016). The combination of topography, substrate type and microclimate conditions is usually identified as the reason for the speciation and adaptation phenomena which provided the great biodiversity of this ecosystem (de Carvalho et al. 2012, 2014; Fernandes et al. 2016, in press). On the other hand, activities such as mining, quarrying, logging, road construction, frequent fires, grazing, uncontrolled tourism, and urban expansion have threatened this ecosystem (Fernandes et al. 2014; Nunes et al. 2015). Land use change has caused soil degradation and erosion, changing its physical and chemical structure and hindering the natural regeneration of the affected areas, as well as leaving the environment more susceptible to colonization of invasive species (Barbosa et al. 2010; Negreiros et al. 2011; Fernandes et al. 2014, 2015).

Natural restoration of rupestrian grassland becomes more unlikely given its extremely low resilience (e.g., Le Stradic et al. 2014a). Though well-adapted to constrained environmental conditions, such as shallow and nutrient-poor soils, rupestrian grasslands seem highly sensitive to land conversion, mainly because of their fine tuned adaptation to the original environment (Ribeiro & Freitas 2010; Negreiros et al. 2014). Mountain ecosystems are known to be poorly resilient to disturbances and therefore require restoration once they have been degraded (Urbanska & Chambers 2002; Negreiros et al. 2011). Seed availability and dispersal are the two first filters hampering plant community assembly (Lortie et al. 2004). Other biotic constraints, such as herbivory,

quality and dormancy of seeds, and abiotic constraints (e.g., physical and chemical soil alterations, and changes in fire regime) hinder the spontaneous establishment of native vegetation (Holl et al. 2000; Yuan et al. 2006; Le Stradic et al. 2014a,b).

Experimental knowledge about restoration of rupestrian grassland degraded areas is still incipient, although recent studies have shown a relative success in seedling establishment of some native species transplanted into degraded areas (Le Stradic et al. 2014b; Gomes et al. 2015). The introduction of native species is a relevant active restoration technique for species-rich grasslands (Holzel et al. 2012; Soliveres et al. 2012; Ma et al. 2015), and can overcome some filters that prevent natural regeneration, such as seeds arrival and germination (Maunder 1992). Although long-term monitoring of vegetation structure development and ecological processes are very importante in this kind of ecosystem (Korb & Fulé 2008; Fernandes et al. 2016, in press), restoration monitoring are usually time-limited (Wortley et al. 2013; Kollmann et al., unpublished data).

In this study, for the first time, we evaluated the performance of 10 plant species of rupestrian grasslands, 8.5 years after being transplanted to a degraded quartzitic area in Serra do Cipó, Brazil. We analysed species survivorship, growth and recruitment in two time intervals (2004 to 2008; and 2008 to 2012). The following questions were addressed: (1) How does species behave along time in the degraded area, concerning survivorship, growth, and recruitment? (2) Can species persist into the degraded area and overcome its harsh conditions after 8.5 years? (3) Is the performance different between time intervals for each species?

Methods

Study area

The study was conducted in a degraded area of approximately 0.5 ha in Reserva Vellozia (19°17'46"S, 43°35'28"W; 1,200m a.s.l.), in Serra do Cipó, MG, Brazil. This area, like others along the highway MG-010, was exploited for gravel and used to park machines during the road construction, leaving vegetation destroyed and soils strongly altered (Negreiros et al. 2011).

Serra do Cipó is located in the central region of Minas Gerais state, southeast Brazil, in the southern portion of the Espinhaço Range, a predominantly quartzitic range of mountains with approximately 1,200 km in length. The predominant climate is Cwb type at a tropical altitude with a pronounced dry season and wet summers (Alvares et al. 2013). The annual precipitation average during the study period (2004 to 2012) was 1522 mm, concentrated between November and February, according to the Instituto Nacional de Meteorologia (INMET), Banco de Dados Meteorológicos para Ensino e Pesquisa (BDMEP), Conceição do Mato Dentro weather station (83589), located approximately 30 Km of the study area. The landscape is predominantly formed by rupestrian grasslands. Its physiognomy is similar to that of other OCBILs, with the occurrence of sclerophyllous shrubs, ericaceous leaves, acaulescent rosettes, prostrate shrubs and herbs, erect herbs, and tussocks (Le Stradic et al. 2015). This vegetation type is adapted to extremely harsh abiotic conditions, such as high solar radiation, shallow and acidic soils, with high aluminum content, poor in nutrients and low water-holding capacity. The vegetation composition is strongly related to specific soil composition, with high spatial heterogeneity, which generates, in turn, a rich diversity even at small scales (de Carvalho et al. 2012, 2014; Negreiros et al. 2014; Le Stradic et al. 2015).

Studied species

Ten native shrub species of rupestrian grasslands (Table 1) were transplanted in the study area. Six of them are endemic to Espinhaço Range (*Dasyphyllum reticulatum*, *Chamaecrista semaphora*, *Collaea cipoensis*, *Mimosa foliolosa*, *Diplusodon hirsutus*, *Diplusodon orbicularis*), two of which (*Collaea cipoensis* and *Diplusodon orbicularis*) are endemic to Serra do Cipó. Four species are widely distributed: *Jacaranda caroba*, in the Cerrado biome of various Brazilian states; *Heteropterys byrsonimifolia*, in Cerrado formations and Semideciduous Forests; *Marcetia taxifolia*, from Brazilian coastal *restingas* to 3,000 m regions in Venezuela; and *Tibouchina heteromalla*, in Cerrado, Caatinga, Atlantic Forest and Amazonia biomes (in various states of Brazil and Venezuela; Guyana, and Colombia) (Barneby 1991; Fortunato 1995; Roque & Pirani 1997; Lohmann & Pirani 1998; Madeira & Fernandes 1999; Jacobi et al. 2000; Nunes et al. 2006; Martins et al. 2009).

Figura 1. List of transplanted species. SDS = síndrome de dispersão de sementes.

Espécie	Família	SDS
<i>Dasyphyllum reticulatum</i> (DC.) Cabrera	Asteraceae	Anemocórica
<i>Jacaranda caroba</i> (Vell) A. DC.	Bignoniaceae	Anemocórica
<i>Chamaecrista semaphora</i> H. S. Irwin and Barneby	Fabaceae: Caesalpinioideae	Autocórica
<i>Collaea cipoensis</i> Fortunato	Fabaceae: Papilionoideae	Autocórica
<i>Mimosa foliolosa</i> Benth. ssp. <i>pachyparpa</i> (Bentham) Barneby	Fabaceae: Mimosoideae	Autocórica
<i>Diplusodon hirsutus</i> (Cham. & Schltdl.) DC. (= <i>D. smithii</i>)	Lythraceae	Autocórica
<i>Diplusodon orbicularis</i> Koehne	Lythraceae	Autocórica
<i>Heteropterys byrsonimifolia</i> A. Juss	Malpighiaceae	Anemocórica
<i>Marcetia taxifolia</i> (A. St.-Hil.) DC.	Melastomataceae	Autocórica
<i>Tibouchina heteromalla</i> (D. Don) Cogn.	Melastomataceae	Autocórica

Seedlings production

In September to November 2002, seeds of all 10 species were collected in the field surrounding the degraded area. Mature fruits were collected from at least 10 individuals

of each species. For *Ch. semaphora*, *Mi. foliolosa* and *Co. cipoensis*, seed dormancy was broken by mechanical scarification (Gomes et al. 2001, Silveira et al. 2014). In November 2002, seeds were hydrated for 24 h and each seed was sown in black polythene bags (8cm diameter, 20cm deep) directly in the substrate composed of 1/3 soil from surrounding the degraded areas, 1/3 peat and 1/3 organic compost from confined cattle dung. To correct soil acidity and fertility, 2 L of dolomitic limestone and 1 L of NPK (4:14:8) were added to 360 L of substrate. Seedlings were placed in a greenhouse: 50% light, watering by micro-sprinklers for 15 minutes three times a day, equivalent to 17.5 mm/day. At the end of April 2003, seedlings (5 months aged) were transferred out of the greenhouse and exposed to ambient conditions, while watering with micro-sprinklers was gradually reduced.

At the end of July 2003 (peak of the dry season), we randomly assigned 64 eight-months-old seedlings of each species to be transplanted to the degraded area. As planting was carried out during the dry season, plants were irrigated with sprinklers for the first 2 months, receiving water for 15 minutes at every 10 days.

Planting and assessment

The study area was divided into plots of 4 m², separated by 50 cm. Each species was planted in four randomly assigned plots, with 16 individuals per plot, totaling 64 individuals per species. The individuals were planted 50 cm apart in each plot. The following parameters were measured for each individual: shoot length; stem diameter at ground level; and survival rate. These parameters were recorded on three occasions: 6 months after planting (2004), 4.5 years after planting (2008) and 8.5 years after planting (2012). Le Stradic et al. (2014b) showed results for survival and growth in 2004 and

2008. Shoot length was measured with a ruler and stem diameter, with a digital caliper (0.01 mm precision).

In addition, species recruitment was analyzed in 2008 (data from Le Stradic et al. 2014b) and in 2012, counting the number of new individuals of each species in study area. All plots with planted seedling were evaluated.

Data analyses

Plant survival was calculated as the percentage of living individuals in relation to the total number of planted individuals for each species (N=64). Minimum acceptable standards for species survival performance were adopted in accordance with Román-Dañobeytia et al. (2012): ‘excellent’ when survival was 76–100%, ‘good’ when 51–75%, ‘moderate’ when 26–50%, and ‘poor’ when less than or equal to 25%.

Relative Growth Rate (RGR) in shoot length and stem diameter (from now referred as length RGR and diameter RGR, respectively) were calculated for each species, comparing the first (2004 to 2008) and second (2008 to 2012) time interval. RGR was calculated according to Hunt (1982): $RGR = (\ln L_f - \ln L_i) / (t_f - t_i)$, where L_f and L_i denote, respectively, final and initial shoot length; and t_f and t_i , respectively, final and initial time, in year. The same was done for stem diameter, replacing respectively L_f and L_i for D_f and D_i in the formula, where D_f and D_i denote, respectively, final and initial stem diameter. For each species, a paired T-test was applied to compare RGR between the two time intervals (Quinn & Keough 2002).

A performance index (adapted from De Steven 1991) was calculated for each species for the first (2004 to 2008) and the second (2008 to 2012) time interval. To calculate the performance index, all variables (diameter RGR; length RGR; survival rate and number of recruited individuals) were standardized by the maximum value. The index value

(IRI) is the mathematical product of all parameters, after being standardized: diameter RGR x length RGR x survival rate x number of recruited individuals.

Additionally, a Pearson correlation analysis ($\alpha= 0.05$) was made among all parameters evaluated (survival, length RGR, diameter RGR and recruitment), for each time interval. To achieve normality assumptions, recruitment values were log transformed.

Results

All species presented a survival rate (S) over than 80% (Fig. 1) 0.5 year after planting (2004), with an ‘excellent’ initial survive performance standard (*sensu* Román-Dañobeytia et al. 2012). On the other hand, this pattern considerably changed over the years (Fig. 1). At the end of the first time interval (2008), 4.5 years after planting, half of the species (*H. byrsonimifolia*; *Di. reticulatum*; *T. heteromalla*; *J. caroba* and *Co. cipoensis*) maintained a survival rate above 80%; *Di. hirsutus* showed a survival rate of 78%; *Mi. foliolosa* and *Ma. taxifolia* showed a survival rate around 60%, with a 'good' survival performance standard; while the other two species (*Ch. semaphora*, $S= 47\%$ and *Di. orbicularis*, $S= 38\%$) showed a ‘moderate’ survival performance standard.

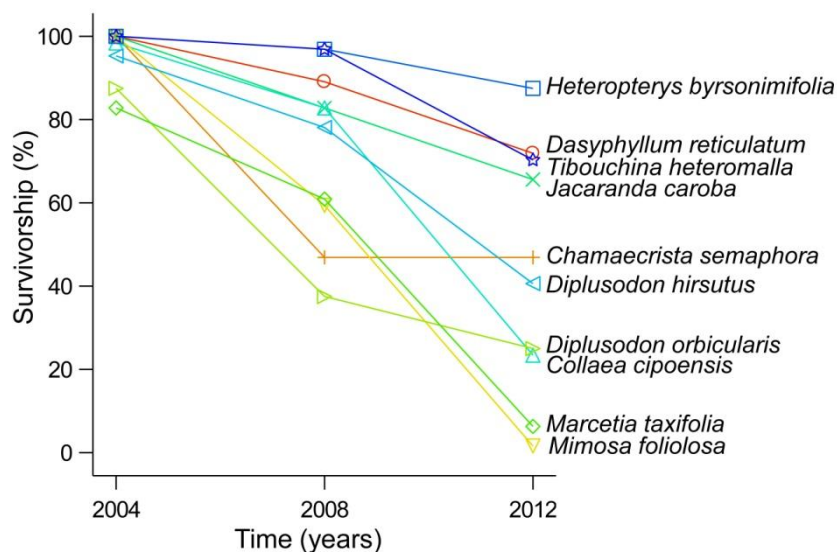


Figure 1. Survivorship of 10 rupestrian grassland species transplanted into a quartzitic degraded area in Serra do Cipó, Brazil.

At the end of the second time interval (2012), 8.5 years after planting, the survivorship of the plant species continued to decline. *Marcetia taxifolia* (S= 6%) and *Mi. foliolosa* (S= 2%) presented the lowest survival rate, while *Di. orbicularis* and *Co. cipoensis* reached approximately 20%. Therefore, these four species entered the category of 'bad' survival performance standard 8.5 years after being transplanted into a restoration site. *Diplusodon hirsutus* also presented a sharp reduction on survival rate, reaching 41% of its individuals being alive in 2012; therefore moving from 'excellent' to 'moderate' survival performance category. 47% of the *Chamaecrista semaphora* individuals remained alive in 2012. The other four species maintained a survival rate over 60%, with survival performance standard between 'good' (*Da. reticulatum*; *T. heteromalla* and *J. caroba*) and 'excellent' (*H. byrsonimifolia*).

Mean values of diameter RGR and length RGR were compared between the two different time intervals, for each species (Fig. 2). The species *Mi. foliolosa* and *Ma. taxifolia* were excluded from RGR analysis because the number of individuals alive in 2012 was very low (one and four individuals, respectively). Three species (*J. caroba*, *D. hirsutus*, *Di. orbicularis*) did not show a significant difference between time intervals on RGR in both growth parameters (shoot length and diameter). Three species showed significant differences between time periods on RGR of both growth parameters, with *Co. cipoensis* and *Ch. semaphora* exhibiting a great reduction on both length RGR and diameter RGR in the second time interval; while *He. byrsonimifolia* showed a great reduction on diameter RGR and an increase on length RGR. Only one species (*Da. reticulatum*) showed a significant increase on diameter RGR in the second time interval. The species *T. heteromalla* maintained their diameter RGR (without significant

difference between intervals), while length RGR was reduced in the second time interval, with negative values.

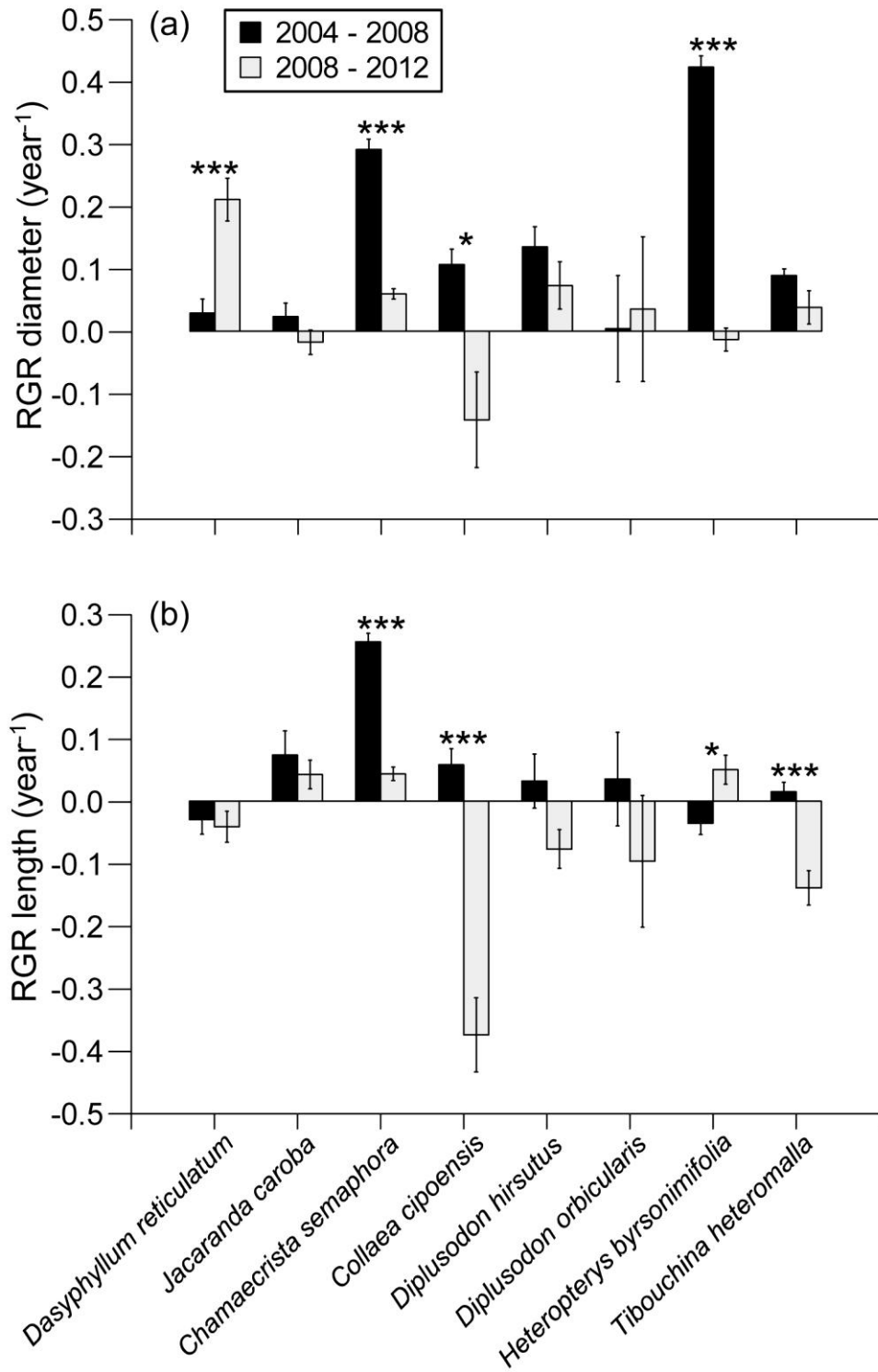


Figure 2. Relative growth rate (RGR) in stem diameter at ground level (a) and shoot length (b) on two different time intervals for eight native species of the rupestrian grasslands transplanted into a quartzitic degraded area, Serra do Cipó, Brazil. Bars denote the mean and vertical lines the standard error. Significant differences between periods are denoted by: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

The species showed, in general, a great intraspecific variation on diameter RGR and on length RGR in the second time interval. Except for *Ch. semaphora*, all species exhibited negative average RGR in the second time interval, or in diameter or in length (Fig. 2), and many individuals of each species exhibited negative RGR values in one or in both time intervals. It means a reduction of shoot length and/or diameter over time, demonstrating a loss of aboveground biomass. Some plants have lost part of the aerial shoots without reducing its diameter at ground level, resprouting from the base of the main branch (*Da. reticulatum*, in both time intervals; *Di. hirsutus*, *Di. orbicularis*, and *T. heteromalla*, in the second interval; *H. byrsonimifolia*, in the first time interval). Others have lost all the stem that existed until 2008, resprouting from the ground and, thus, showing a smaller diameter in 2012, with negative average of diameter RGR in the second interval (*J. caroba*, *Co. cipoensis*, *H. byrsonimifolia*). Some of those which resprouted from the ground, showed a positive average of length RGR in the second interval (*J. caroba* and *H. byrsonimifolia*), which can be explained by a fast growth in length after resprouting.

The number of recruited seedlings varied among time intervals for half of the species (Fig. 3). The other half has similar recruitment between intervals, including the three species (*H. byrsonimifolia*, *Da. reticulatum*, and *J. caroba*) that recruited zero individuals in one of the time interval and only one individual in the other interval (Fig. 3). Six species (*Ch. semaphora*, *Co. cipoensis*, *Mi. foliolosa*, *Di. hirsutus*, *Di. orbicularis*, and *Ma. taxifolia*) recruited 10 or more seedlings in one of the time intervals, while *Ch. semaphora* recruited the highest number of seedlings (Fig. 3), with 15 individuals in 2008 and 31, in 2012. The four species with the largest number of recruiting seedlings in 2012 (*Ch. semaphora*, *Di. orbicularis*, *Di. hirsutus*, and *Mi. foliolosa*) also showed low survival rates (<50%) in the same year (Fig. 1 & 3).

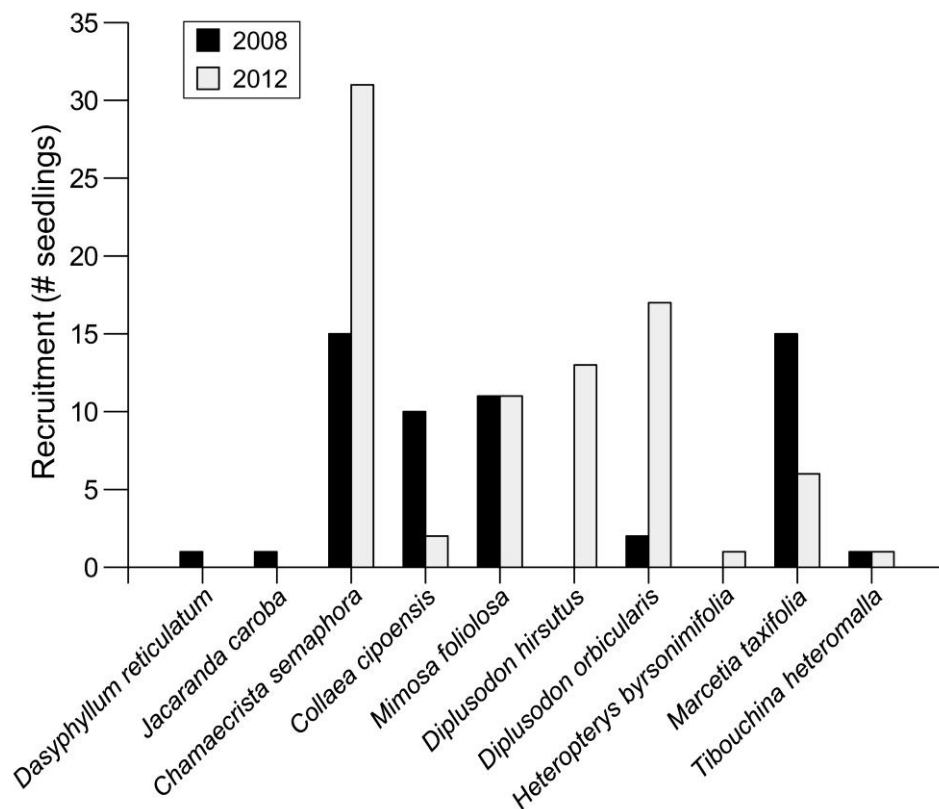


Figure 3. Recruitment of 10 native species of the rupestrian grasslands transplanted into a quartzitic degraded area, Serra do Cipó, Brazil, 4.5 (2008) and 8.5 (2012) years after planting. Recruitment is represented by number of individual seedlings.

The performance index was not calculated for *Mi. foliolosa* and *Ma. taxifolia*, since RGR are part of this calculation and RGR was not calculated for these two species due to the very low number of individuals alive in 2012. Four species (*Da. reticulatum*, *J. caroba*, *Di. orbicularis*, and *T. heteromalla*) exhibited very low performance index (<0.025), with little difference between time intervals (Fig. 4). There was a small increase in the performance index of the second time interval for *H. byrsonimifolia*, but in both intervals the index was less than 0.025 for this species. The other three species showed indexes markedly different between intervals, increasing (*Ch. semaphora*, *Di. hirsutus*) or decreasing (*Co. cipoensis*) index along time. The species *Ch. semaphora* stood out in relation to the performance index, with high values in both time intervals, but two times greater in second interval compared to the first. Most species exhibited little variation on performance over time, with similar index values between the two time intervals. An increase in a parameter was compensated by a decrease in another, with the product between them (performance index) not undergoing major changes through time.

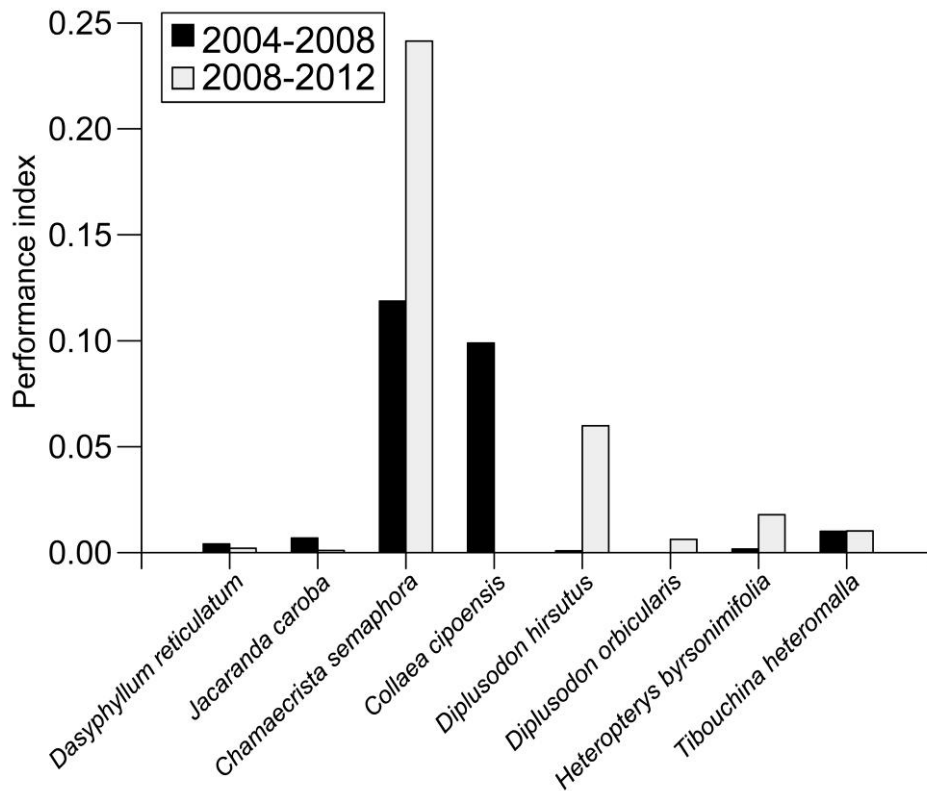


Figure 4. Performance index, adapted from De Steves (1991), for eight native species of the rupestrian grasslands transplanted into a quartzitic degraded area, Serra do Cipó, Brazil, at two different time intervals. Details in Methods section.

The pairwise correlation between all measured parameters resulted in two significant negative correlation: 1) between the survivorship in 2008 and the recruitment in 2012 ($r=-0.831$; $p=0.003$) and 2) between the survivorship in 2012 and the recruitment in 2008 ($r=-0.729$; $p=0.017$) (Fig. 5). Thus, species that poorly survived in 2008 showed a good recruitment in 2012, and species that recruited more seedlings in 2008 showed lower survivorship in 2012 (Fig. 5).

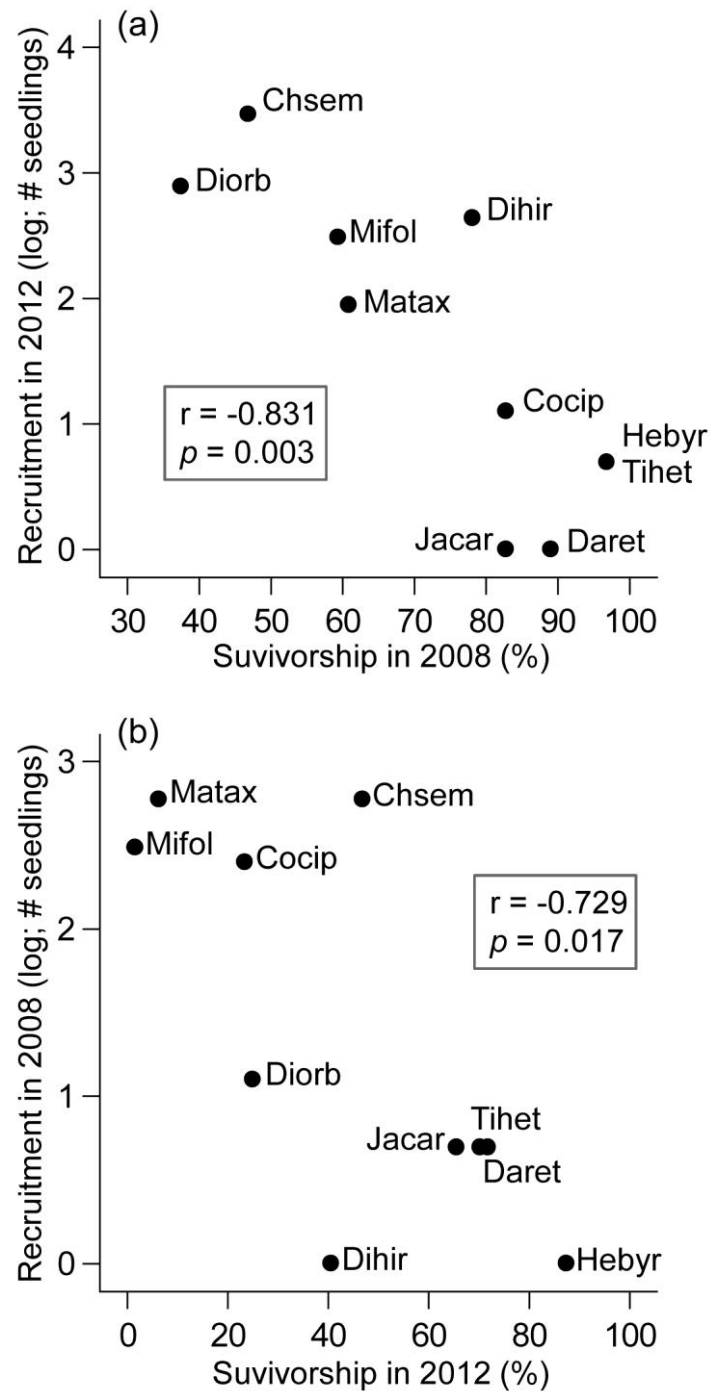


Figure 5. Negative correlation between survivorship in 2008 and recruitment in 2012 for eight native species of the rupestrian grasslands transplanted into a quartzitic degraded area, Serra do Cipó, Brazil. Daret= *Dasyphyllum reticulatum*, Jacar= *Jacaranda caroba*, Chsem= *Chamaecrista semaphora*, Cocip= *Collaea cipoensis*, Dahir= *Dipilusodon hirsutus*, Diorb= *Dipilusodon orbicularis*, Hebyr= *Heteropterys byrsonimifolia*, Tihet= *Tibouchina heteromalla*.

Discussion

The process of succession is generally long, taking decades or even centuries to reach an old state (Veldman et al. 2015). Revegetation is an intelligent management practice that provides a way for the ecosystem to reestablish or get back to the course of succession and ecosystem services such as water recharging and purification (Holzel et al. 2012; Resende et al 2014). Evaluate the performance of the introduced species is important to assess the revegetation success (Ma et al. 2015) and this may be even more important in extreme environments, such as tropical mountaintop savanna ecosystems, where there is no information on succession, and ecological restoration are at infancy. One such ecosystem is the fragile and low resilient rupestrian grassland in the mountaintops of the Espinhaço Range in Brazil (Silveira et al 2016; Fernandes et al. 2016, in press). Our pioneer study provides the first available information of performance of 10 native rupestrian grassland species 8.5 years after transplanted into a degraded area.

The growth, survival, and recruitment of the studied species varied considerably over the years. In all species, the performance of at least one of these parameters was very different between the time intervals, except for *J. caroba*, that showed similar growth and recruitment between time intervals (Fig. 2 & 3), and little difference on survival rate along years (always > 60%). Variation in performance parameters may reflect changes in the structural and physiological plant processes over time, according to their development (ontogeny). Different developmental stages have different requirements and resource allocation, as well as responds differentially to biotic and abiotic environmental interactions (Coleman et al. 1994; Roux et al. 2013). Moreover, interactions between distinct plant species in the area and among individuals of same species are also factors with strongly influence in species performance over time (Welk

et al. 2014; Tomiolo et al. 2015). In addition to species transplanted in the study area, other plant species were able to colonize the area, forming an herbaceous cover mainly composed by ruderal species that not occur in adjacent pristine rupestrian grasslands (Le Stradic et al. 2014b). Competition with these new species could also have had some effect on survival, growth and recruitment of transplanted species (Barbosa et al. 2010; Mangla et al. 2011; Fernandes et al. 2015). Furthermore, another aspect of major relevance is that of the interaction with other trophic levels. For instance, herbivory or even parasitism by mistletoes in the rupestrian grasslands are strong environmental filters (Bahia et al. 2015). But on the other hand, these were not evaluated in this study. Altogether, these aspects emphasize the importance of more wide and extensive monitoring periods in the harsh rupestrian grasslands, allowing the identification of species changes on survival, growth and recruitment over the years. While high survival rate in early years after planting is important for a species establishment (Derbel & Chaieb 2012), strong changes may be observed over time, such as that reported here for *Mi. foliolosa* and *Ma. taxifolia*. These species showed an excellent survival rate 0.5 year after planting, had a moderate survival after 4.5 years of planting, and almost disappeared after 8.5 years of planting, with very few living individuals. On the other hand, these species were capable to recruit more than 10 seedlings over the 8.5 years (Fig. 4), thus, persisting on the environment through producing new individuals despite their low survivorship.

In general, for each species, a better performance based in one parameter was accompanied by a worse performance based in another parameter, suggesting a trade-off in the resources investment between the different plant parts and functions. Plants commonly exhibit a trade-off between functions such as survival, growth and reproduction, depending on their ontogenetic stage and environmental conditions to

which they are submitted (Grime & Pierce 2012). The same trade-offs were postulated to occur with the dilemma to grow or defend (Mattson & Herms 1992). Species with high survival usually do not show a high growth rate and / or recruitment (Bond & Midgley 2001; Martins et al. 2004; Negreiros et al. 2014). Our results showed that species with great survival in 2008 had low recruitments in 2012, and species with great recruitment in 2008 had low survival in 2012, indicating a possible trade-off between survival and reproduction. Plants adapted to low resources environments promote a balance on energy and resource allocation. A function is developed at the expense of another, and investment to persist in the environment (survival) is often accompanied by late reproduction, as well as investment in reproduction can lead to a lower survival (Grime & Pierce 2012). Reproductive structures have high cost and divert reserves of plant functions that could provide greater resources feedback, substantially reducing the overall efficiency of resources gain and use by the plant, which, in turn, may have an impact on survival (Bloom et al. 1985). Bond and Maze (1999) observational studie of a sexually dimorphic dioecious shrub (*Leucadendron xanthoconus*) detected costs of reproduction in terms of survival. Forbis and Doak (2004) found a fecundity/mortality trade-off in two long-lived nonclonal alpine fellfield species (*Paronychia pulvinata* and *Minuartia obtusiloba*), using size-based population projection matrices. Aragón et al (2009) reported a survival cost of reproduction for a short-lived perennial subshrub of semiarid Mediterranean environments (*Helianthemum squamatum*) in an experimental approach. Wang et al (2013) studied the species *Rhamnus davurica*, which occurs as a shrub or small tree in a low-water content area in Northern China, and the results suggest a possible trade-off between reproduction and survival.

Regarding species growth, beside the expected variation in RGR over time, our results showed great ability of native species to overcome drastic environmental conditions. In

general, most species showed a strong reduction on main shoot length in the second time interval, but remained alive. These results indicate that these plants are able to lose much of their aboveground biomass and then resprout, depending on the damage that has caused the shoot loss, demonstrating the importance of the investment in underground organs in these species. Species adapted to low resource environments have a well developed capacity to accumulate reserves and developed efficient systems to minimize nutrients loss, such as high nutrient resorption rate (Chapin et al. 1986, 1993; Grime 1993). To be able to resprout after an injury, a plant needs survived meristem and stored reserves (Chapin et al. 1993; Bond & Midgley 2001). Many grassland and savana plants invest on underground organs that store starch and water to allow its resprout (Sarmiento 1984; Veldman et al. 2015) while other species are able to recover the biomass lost from epicornic gems (Barbosa et al. 2014). Rupetrian grassland plants are adapted to extreme environmental conditions such as high radiation and winds, seasonal rainfall distribution, nutritionally poor and shallow soils with low water holding capacity (Silveira et al. 2016). Theses adaptations increase the chances of these species in persisting in the even harsher environment found in degraded areas. Attributes related to stress-tolerant species suggest ways of natural selection that promoted characteristics consistent with conservative retention and use of acquired mineral nutrients (Wright et al. 2004; Grime & Pierce 2012; Negreiros et al. 2014).

Resprout vigor may be related to the amount and mobilization capacity of stored resources to recover aboveground biomass (Barbosa et al. 2014). Resource allocation for storage, in turn, has a balanced cost with growth and / or reproduction (Tilman 1990). As a response to disturbance, successful resprouting depends on diverting stored resources that could be invested in a future generation, through seed production (Bellingham & Sparrow 2000). Studies in Mediterranean fire prone shrublands have

documented indirect evidences that adult plants that vigorously resprout tend to recruit fewer seedlings (Bond & Midgley 2001). Something similar may occur in rupestrian grasslands, which must be investigated in more detailed studies about resprouting and reproduction of native species. On the other hand, balance between resprouting and seeding varies continuously along disturbance gradients, within and between species and cannot be interpreted effectively as a simple dichotomy. The plant species vegetative growth and seeding characteristics are both traded off against the physiological processes of resource acquisition determined by abiotic conditions of the site and the presence of other plants and animal consumers (Bellingham & Sparrow 2000).

Recruitment reflects the ability of plant species to reproduce and persist in the area and may be influenced by a trade-off between reproductive function and other plant functions, but also by other factors such as major pollinator lack or shortage, as well as lack of resources (e.g. water and nutrients), limiting fertility and interfering in seed quantity and quality (Cordeiro et al. 2009). Herbivory and competition are also factors that influence recruitment, and may affect establishment of emerged seedlings (Derbel & Chaieb 2012). Temporal response in plant recruitment is an integrated effect of biotic and abiotic environmental factors in processes related to seed production and germination, and seedling growth and survival (Weltzin & McPherson 1999). The characteristic environmental rigors of rupestrian grassland and, more intensely, the severity found in degraded area, with disturbed soil, should exert a great pressure in recruitment process. Rupestrian grassland seasonality, with a long dry season, makes the precipitation a limiting factor in vegetation development (Madeira & Fernandes 1999; Silveira et al. 2016; Scarano et al., unpublished data). Rainfall is a determinant factor in seedling emergence on dry environments, and survival is affected mainly by

humidity, high temperature and evaporation (DeSimone 2011; Derbel & Chaieb 2012). In addition, the huge daily variation in temperature of the rupestrian grassland ecosystem is another environmental filter that must be of major importance in seedling establishment and seed germination, but for which there is no data available (see Fernandes et al. 2016, in press). Therefore, to be able to recruit effectively in the harsh rupestrian grasslands, plants must overcome daily and seasonal variation of temperature and water availability.

Conclusion

Overall, the studied species showed a remarkable ability to overcome the extreme environment of the degraded area after 8.5 years from planting, either persisting in environment through recruiting new individuals, or maintaining its survivorship. Studied species are adapted to characteristic harsh soil conditions of rupestrian grasslands and to climatic conditions of the transplanting area, as they are native from rupestrian grassland ecosystem, and were produced with plant material from the region of the area. An example of a native species adaptation is described by Costa et al. (2013), in which the same *Ch. semaphora* plants transplanted into the present studied area showed no difference in levels of fluctuating asymmetry compared to plants on their natural environment, demonstrating stability in this species development even under the stressful conditions of degraded area.

Species selection for restoration of degraded areas in rupestrian grasslands should consider the adaptation potential of the native flora. In this harsh environment, survival and resistance to different kinds of stresses should be favored rather than simple and fast growing and ground cover (Bradshaw 2000, Negreiros et al. 2009, Gomes et al. 2015). Parameters evaluated in this study (survival, growth and recruitment) varied over

time, on a trade-off between different plant functions that they are linked, in response to influences of environmental severity, biotic interactions, and ontogenetic changes. Each species performance varied in a different way, showing an idiosyncratic pattern of plant performance over time. Finally, we emphasize the importance of long-term monitoring on evaluation of ecological restoration studies in order to better understand the results of processes dynamic involved in species performance over time.

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