The role of native woody species on the restoration of *campos rupestres* in quarries

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Abstract

Questions: Can shrub and tree seedlings be reintroduced in an extremely harsh environment by transplantation? Does the growth strategy of species affect their survival? What factors influence the transplantation success? Do transplanted species influence their immediate vicinity, e.g. promoting colonization by native species?

Location: *Campos Rupestres*, Espinhaço range, Minas Gerais, Brazil.

Methods*:* We studied the reintroduction of four native tree and 14 native shrub species. Their transplantation success (survival, growth, and reproduction) and their impacts on their immediate vicinity (understorey composition, soil surface indicators such as the cover of moss, biological crust, bare ground, litter, herbaceous cover, and soil characteristics) were assessed 4.5 years after transplantation.

Results*:* While some transplanted species had low survival (< 30%), half of them had a survival >78% 4.5 years after transplantation. Plant growth was barely correlated to the transplantation success in such harsh environment. Transplanted species did not influence soil and understorey plant composition but significantly impacted soil surface indicators. The shrub species with higher survival rates usually allowed the establishment of an understorey herbaceous cover which may increase soil erosion control. This is also true for some species for those the survival was <40%: *Diplusodon orbicularis* (survival: 39%) and *Lavoisiera campos-portoana* (37%). Crown volume had a direct effect on light reaching the soil (e.g. *Jacaranda caroba* or *Collaea cipoensis* had a less dense canopy more permeable to light allowing understorey species). On the other hand, crown volume was positively correlated to the amount of litter: Fabaceae species, such as *Chamaecrista semaphora* and *Mimosa foliolosa,* had denser canopy and produced a thick layer of litter, limiting herbaceous species establishment. Three tree species (*Enterolobium ellipticum, Kielmeyera petiolari,* and *Zeyhera tuberculosa*) neither had high survival nor did facilitate the establishment of the herbaceous cover. The layout and spacing of species and individuals must thus be considered carefully to insure recolonization by native shrub and herbaceous species.

Conclusion: This study demonstrates the practical efficiency of some native species to restore a harsh tropical ecosystem as the *campos rupestres* in terms of their transplantation success, their effects on both the establishment of herbaceous species and soil conservation.

Keywords*:* assessment of restoration success;, Cerrado; herbaceous understorey; neotropical mountain grasslands; Serra do Cipó; transplantation success.

Abbreviations*:* Dret : *Dasyphyllum reticulatum* ; Jcar : *Jacaranda caroba* ; Abon: *Actinocephalus bongardii;* Cfas: *Calliandra fasciculata;* Csem.: *Chamaecrista semaphora,* Mfol.: *Mimosa foliolosa;* Ccip.: *Collaea cipoensis;* Dhir.: *Diplusodon hirsutus;* Dorb.: *Diplusodon orbicularis;* Hbyr.: *Heteropterys byrsonimifolia;* Lcam.: *Lavoisiera campos-portoana;* Mtax.: *Marcetia taxifolia;* Thet.: *Tibouchina heteromalla;* Lpac.: *Lafoensia pacari;*

Kpet.: *Kielmeyera petiolaris;* Eell.: *Enterolobium ellipticum;* Edys.: *Eugenia dysenterica;* Ztub.: *Zeyhera tuberculosa.*

Nomenclature: Lista de Espécies da Flora do Brasil 2013 in *http://floradobrasil.jbrj.gov.br/*

Running head: *Campo rupestre* restoration

Introduction

Ecological restoration is the process of intentionally assisting the recovery of degraded ecosystems in order to repair ecosystem processes, productivity and services, as well as to re-establish the biotic integrity (SER 2004). Grassland restoration projects are often hampered by abiotic constraints, such as increased soil nutrients in case of degradation by intensive agriculture or the alteration of soil chemical and physical characteristics (i.e. limited nutrient availability, low water availability) in case of degradation by quarrying and mining activities (Ash et al. 1994, Jim 2001, Wong 2003, Yuan et al. 2006). Biotic constraints also affect seedling establishment through the lack of reliable seed sources, the limited dispersal of appropriate propagules or the presence of competitive exotic species (Ash et al. 1994, Bradshaw 1997, Bakker & Berendse 1999, Wilson 2002, Shu et al. 2005).

Open ecosystems, such as grasslands or savannas, represent more than 31% of world vegetation, but they have drastically decreased or have been highly altered throughout the world over the last decades (Gibson 2009), due to intensification of agricultural practices (Green 1990, Klink & Moreira 2002), land abandonment, invasive species, civil engineering and changes in disturbance regimes (Hoekstra et al. 2005, Gibson 2009). These ecosystems are important not only from the perspective of conserving biodiversity (FAO 1998), but also in maintaining ecosystem services, such as increased water quality or decreased soil erosion (Osborne et al. 1993, Berger & Rey 2004, MEA 2005 a, b). Moreover, since the process of natural succession is slow after degradation, especially by quarrying and mining activities (Bradshaw 1983, Davis et al. 1985, Bradshaw 1997), their restoration is often attempted.

The Cerrado is the richest tropical savanna in the world, representing the second largest vegetation formation of Brazil originally covering c.a. 2.2 million km^2 or 23% of the country (Oliveira & Marquis 2002) and due to anthropogenic pressures (e.g. intensive agriculture, mining, quarrying) is currently one of the most endangered biomes in South America (Klink & Machado 2005, Hoekstra et al. 2005). This has led to biodiversity losses, landscape fragmentation, biological invasions (Pivello et al. 1999), soil erosion, water pollution and land degradation (Klink & Moreira 2002). *Campos rupestres* are one of the physiognomies of the Cerrado biome, and are usually found above 900 meters high in altitude. They are composed of a more or less continuous herbaceous stratum with sclerophyllous evergreen shrubs and small trees growing between rocky outcrops, supporting a high biodiversity with one of the highest levels of endemism in Brazil (Giulietti et al. 1997, Carvalho et al. 2012). Such ecosystem is under extreme environmental conditions; their soils are coarse textured and shallow, with high Al^{3+} and low nutrient content (Benites et al. 2007). Few studies have been carried on such physiognomies of the Cerrado and they remain poorly documented while restoration ecology studies are urgently needed.

According to the level of degradation, restoration of quarries and mines may require seed addition (Cooper & MacDonald 2000, Turner et al. 2006, Kirmer et al. 2012, Ballesteros et al. 2012), native species transplants (Ash et al. 1994, Soliveres et al. 2012), turves or rhizomes transfer (Ash et al 1994, Cooper & MacDonald 2000). Currently in Brazil, many mine and quarry mitigation projects use exotic species for revegetation, such as the African grass *Melinis minutiflora* (Griffith & Toy 2001), to rapidly reach specific goals, e.g. to reduce soil erosion. Exotic species are one of the major threats to local diversity, particularly when degraded areas are close to roads where propagation and invasion risks are higher (Hansen & Clevenger 2005; Barbosa et al. 2010).

Spontaneous regeneration of woody as well herbaceous campo rupestre species does not seem to occur on degraded *campos rupestres* or is extremely slow (Le Stradic 2012) in contrast with the seasonal deciduous forests (Sampaio et al 2007). Several non-mutually-exclusive hypotheses could explain the lack of spontaneous recruits in degraded areas (Bradshaw 2000): i) species produce viable seeds but they do not disperse far enough to reach degraded sites; ii) dispersed seeds arrive to degraded areas but do not germinate due to the high temperature and dryness of the bare and nutrient poor and/or toxic substrate; iii) dispersed seeds are able to germinate but further development of saplings does not take place due to the extreme harshness of the degraded site, the stress caused by natural enemies, or lack of symbiotic interactions with facilitating arbuscular mycorrhizal fungi. The first two reasons and sometimes the third one can be overcome by reintroduction which consists in the re-establishment of taxa in part of their native range from where they had disappeared or had drastically declined (Maunder 1992; Young 2000). Transplantation of native species may thus be a suitable substitute (Maunder 1992; Bradshaw 1997, Byers et al. 2006, Hölzel et al. 2012), ensuring that a desired panel of species are introduced and avoiding limited seedling establishment (Bradshaw 1997).

For practical reasons, restoration by reintroduction often involves a single species; restoring full communities is often costly and difficult to implement (Sampaio et al. 2007). Usually species are selected as they are keystone, structuring, dominant or rare species (Maunder 1992; Byers et al. 2006). Recent interest in the outstanding biodiversity of *campos rupestres* has led to germination studies of some native plants which is a necessary step to perform restoration projects (Gomes et al. 2001, Silveira et al. 2012). Species propagation and their performance under controlled conditions in greenhouses represented the next crucial step for restoration programs (Negreiros et al. 2009). The third step consists in a pilot field study.

It is now widely accepted that monitoring should be carefully planned prior, during and after all restoration projects (Holl & Cairns 2002). In order to provide a common basis for the assessment of restoration success, numerous measurements (i.e. ecosystem attributes) were proposed (SER 2004). However, most projects consider one or two measurements among the three major ecosystem attributes: (1) species diversity; (2) vegetation structure; and (3) ecological processes (Ruiz-Jaen & Aide 2005). When restoration projects are based on (single-) native species reintroduction, monitoring and evaluation of success is often restricted to survival and growth of these reintroduced species (Maunder 1992; Guerrant & Pavlik 1998). Nevertheless, introduced species can drastically change ecosystem functioning (Simberloff et al. 2005) and monitoring should therefore assess the impact of introduced species on their environment (SER 2004); 1) by measuring reintroduced species survival, growth and recruitment ability and 2) by measuring the impacts of reintroduced species on their direct environment. While short-term monitoring is needed to document the survival and establishment of reintroduced species, mid-term and long-term monitoring is essential to understand induced changes in ecosystem functioning (Maunder 1992; Sutter 1996).

In this context, we studied the reintroduction of 18 native *campo rupestre* tree and shrub species to degraded areas. The questions raised by this study were: (1) can shrub and tree seedlings be reintroduced in an extremely harsh environment by transplantation? ; (2) does the growth strategy of species affect their survival?; (3) what factors influence the transplantation success?; and finally (4) do transplanted species influence their environment, i.e. the herbaceous understorey, the soil properties, and the soil surface indicators in their immediate vicinity? In this experiment, we expected the ideal to-be-transplanted species to be able to survive and to grow on harsh environments and to allow herbaceous species, cryptogams and biological crust to colonize the understorey in order to increase total vegetation cover and thus soil conservation.

Methods

STUDY SITE

Campos rupestres are encountered along the Espinhaço mountain range (states of Minas Gerais and Bahia) in Brazil. Our study area is located in the southern portion of the

Espinhaço Range. Fieldwork was conducted in the Vellozia Private Reserve (19°16’45.7”S, 43°35’27.8”W; elevation 1200 m) in the buffer zone of the Serra do Cipó National Park (Minas Gerais). The climate is classified as Cwb according to the Köppen’s system, which is characterized by warm temperature, dry winter and warm summer. It is markedly seasonal, with a rainy season during summer. The mean annual precipitation is 1622 mm and the annual temperature is 21.2°C (Madeira & Fernandes 1999).

A study reported the presence of degraded areas along the highway MG010 in 1996 (Negreiro et al. 2011) which dated back from 1990. They were exploited for gravel and/or were used to park machines. These small quarries are common in the region: vegetation is destroyed and soils are disturbed and when exploitation stops, soils are not returned entirely and construction debris may be added resulting in a high-altered soil. All of these degraded areas are surrounded by pristine *campos rupestres*, that is why we chose them as the reference ecosystem. Two experimental degraded areas, with a sandy altered substrate, were selected. Sites were located a few tens of meters apart, thus, for both sites, exploitation stop at the exact same time and the mixed soil horizons were put back in the same way in order to have true site replicates. Indeed, sites further apart may have different soil granulometry due to the way that soil horizons are mixed after exploitation.

EXPERIMENTAL DESIGN

Eighteen native species were planted: fourteen shrub species and four tree species (Table 1). In 2002, seeds of all eighteen species were gathered in the field in areas surrounding the degraded areas. Mature fruits were collected from at least ten individuals of each species. For *Chamaecrista semaphora, Mimosa foliolosa, Collaea cipoensis* and *Enterolobium ellipticum*, seed dormancy was broken by mechanical scarification (Gomes et al. 2001). In November 2002, seeds were hydrated for 24 hours and each seed was sown in black polythene bags (8cm diameter and 20cm deep) directly in the substrate, composed of

1/3 of soil from around the degraded areas, 1/3 of peat and 1/3 of organic compost of confined cattle dung. To correct for soil acidity and nutrients, 2L dolomitic limestone and 1L NPK (4:14:8) were added for 360L 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 were transferred out of the greenhouse and exposed to ambient conditions, while watering by micro-sprinklers was gradually reduced.

Between 20 Jul 2003 and 26 Jul 2003, we randomly assigned 64 eight month-old seedlings (except *Lavoisiera campos-portoana:* 27 months-old) of each species to be transplanted to the degraded areas. Shrubs were transplantated on both degraded areas; while trees were transplantated on only the largest degraded area. Seedling transplantation was carried out according to the experimental design explained in Figure 1. As planting was carried out during the dry season, plants were irrigated by sprinklers during the first two months. Plants received water for 15 minutes at every other 10 days.

MONITORING OF THE SURVIVAL AND GROWTH OF PLANTED SPECIES

Survival was recorded for each individual in August 2003 (date of transplantation), September 2003, February 2004, April 2006 and February 2008 (4.5 years after transplantation). Some individuals were considered dead one year, but they had to be considered alive after due to resprouting. At each date, growth was evaluated by measuring the height of the main stem, crown volume (calculated using the largest crown diameter, the largest perpendicular diameter to the first one and crown height) and basal diameter of each individual. These variables are known to reflect the growth of both roots and shoot systems (Niklas 1993; Negreiros et al. 2009). Relative Growth Rates (RGRs) were calculated for diameter, height and volume as: RGR= $(\mathrm{Ln}\ x_{t\mathrm{j}} - \mathrm{Ln}\ x_{t\mathrm{i}}) / (t_\mathrm{j} - t_\mathrm{i})$ where x denotes the variable measured at two different dates t_i and then t_j. Since it is important to assess the sustainability of a species in a restored area through its reproductive ability, we recorded the occurrence of new sprouts, individuals with flowers or fruits and new seedlings in February 2008.

UNDERSTOREY AND SOIL SAMPLING

In February 2008, on each plot, four 20×20cm quadrats were set randomly to assess soil surface indicators and the composition of species colonizing the understorey (understorey composition and richness). Percent of cover of each understorey species was recorded. Monitored soil surface indicators were: (I) cover of moss (%); (II) biological crusts (thin organic layer formed by cyanobacteria, green algae, lichens, fungus and heterotrophic bacteria (Belnap & Lange 2001)); (III) cover of bare ground (%); (IV) litter cover (%); and (V) herbaceous plant cover (%) (hereafter named herbaceous cover). In order to assess the influence of transplanted species on light reaching the ground, canopy closure (named shade) was estimated based on the vertical projection of the crown area weighted by an index of foliage density (Daubenmire 1959). This index was calculated from the analysis of four canopy pictures for each species using an image processing software which assessed the percentage of the picture with foliage.

In order to determine whether species influence soil chemical properties, one soil sample was collected on each plot, resulting from four sub-samples which were mixed and homogenized, dried and sieved prior to chemical analyses. The following chemical analyses were performed: P and K in mg/dm^3, N and C in dag/kg, Mg^{2+}, Al^{3+}, Ca^{2+} in $cmol_c/dm^3$, Organic Matter (OM) in dag/kg – P, Na, K with the Mehlich 1 extraction method, Ca^{2+}, Mg^{2+}, Al^{3+} with 1 mol/L KCl extraction, OM = C.Org x 1.724 following the Walkley-Black method).

DATA ANALYSIS

The effects of the qualitative variables “sites” and “plots” on survival (0 or 1 at the individual level) at the end of the survey were tested using GLM (Generalized Linear Models) with a binomial distribution and a logit link function (Crawley 2007). Then, the effect of the variables “initial size of individuals” (size when transplanting) and “RGR” on individual survival were analyzed with GLM procedures (binomial distribution and logit link function) by setting the “plot” and “site” effects as an *offset* component of the GLM. An *offset* specifies an *a priori* known component to be included in the linear predictor during fitting (using the R package stats) (Crawley 2007). Differences in survival according to the plant family and plant stature levels were tested at the different times of the survey (2004, 2006 and 2008) using χ^2 tests.

Similar treatments being expected to lead to similar effects in both sites, multivariate analyses were performed to assess the co-structure of their variables. Three co-inertia analyses were thus ran between site 1 and 2 considering: (i) soil surface indicators (2 matrices of 30 plots × 6 soil surface indicator), (ii) soil chemistry (2 matrices of 30 plots × 9 soil variables) and understorey composition data (2 matrices of 30 plots x 81 understorey species) separately (Chessel et al. 2009). The significance of the coinertia coefficient was estimated with 999 Monte Carlo permutations.

Then, as a co-structure was found only for soil surface indicators, we further explored the effects of transplanted species on these indicators, by running an inter-class Principal Component Analysis (76 transplanted and control plots × 6 soil surface indicators; PCA-between; ade4 R package, Chessel et al. 2009). Simple ANOVAs, followed by post-hoc tests (Tukey HSD: Honestly Significant Difference) were performed: herbaceous cover and understorey richness were treated as dependent variables and species and control plots as categorical predictors. Normality and homoscedasticity assumptions were checked and a square root transformation was applied (Sokal & Rohlf 1998). Species morphology especially the crown volume was expected to impact on the amount of light reaching the soil. In order to assess the relationship between crown volume at the end of the survey and soil surface indicators, tests for association between paired samples using Spearman's ρ were carried out. All statistical analyses were performed using the software R (R Development Core Team 2009).

Results

SURVIVAL AND GROWTH OF PLANTED SPECIES

Differences in terms of survival and growth were observed. Four and a half years after transplantation, some species were characterized by a fairly high survival (above 78%): *Calliandra fasciculata, Collaea cipoensis, Jacaranda caroba, Dasyphyllum reticulatum, Heteropterys byrsonimifolia, Tibouchina heteromalla*, *Eugenia dysenterica, Diplusodon hirsutus* and *Lafoensia pacari*. On the contrary survival was lower than 50% for *Actinocephalus bongardii*, *Chamaecrista semaphora, Diplusodon orbicularis, Enterolobium ellipticum*, *Lavoisiera campos-portoana* and *Zeyhera tuberculosa* (Table 2). In addition, survival of seven species significantly differed depending on the plot and/or the site: *A. bongardii, C. fasciculata, C. semaphora, D. hirsutus, D. orbicularis, J. caroba* or *Kielmeyera petiolaris*. Individuals growing in the site 2 generally presented a higher survival (Table 2).

Beyond their simple survival, some species were able to colonize available sites: *Chamaecrista semaphora, C. cipoensis, Marcetia taxifolia* and *M. foliolosa* recruited more than 10 seedlings. Others expanded through resprouting, such as the majority of individuals of *C. cipoensis, D. reticulata, D. hirsutus, H. byrsonimifolia, L. pacari,*and *T. heteromalla* (Table 2). Finally no signs of reproduction were observed in *Z. tuberculosa, E. dysenterica* and *E. ellipticum* (Table 2).

Species appeared to differentially survive according to their families at different dates (respectively χ^2=319.8, *df*=4, P<0.001 in 2006, χ^2=21.8, df=4, P<0.001 in 2008). Melastomataceae suffered higher mortality (at least of the aboveground parts) than the other families at the beginning and during the first years, as 39% of their individuals died during the first six months and 76% after 2.5 years, especially *L. campo-portoana* (Table 2 & Table 3). Melastomataceae species were able to resprout, thus increasing their survival rates 4.5 years after the transplantation (Table 3) compared to the two first years after the transplantation. At the end of the survey, Fabaceae and Bignoniaceae were the families with the highest mortality rate (respectively 59.69% and 54.69% of survival) (Table 3). Shrubs presented higher mortality than trees at the beginning and during the first years of the transplantation (respectively 10% *vs.* 6% respectively for 2004; χ^2=3.7, *df*=1, *P*=0.052 and 29% *vs.*14% respectively for 2006; χ^2=21.9, *df*=1, *P*<0.001), while at the end of the survey shrubs were characterized by a lower mortality than trees (31% *vs.* 45% respectively; χ^2=15.6, *df*=1, *P*<0.001).

For most species, the RGR did not appear to significantly reflect the final survival probability. However, when such effects where observed, a faster growth was associated with a higher survival, excepted for *C. semaphora* (Table 4). Survival 4.5 year after the transplantation was positively related to the initial size of individuals for *A. bongardii, D. reticulatum* and *M. taxifolia* and to a lesser extent for *E. dysenterica* and *C. fasciculata* (Table 4). For only two species, *E. ellipticum* and *M. taxifolia,* the survival 6 months after the transplantation was positively related to the RGR during the first month (Table 4). The RGR during the first 6 months was positively linked to the survival 2.5 years after the transplantation (in 2006) for five species: *C. fasciculata, D. orbicularis, K. petiolaris, M. taxifolia* and *M. foliolosa*. Finally, for just three species, *C. fasciculata*, *D. reticulatum* and *Z. tuberculosa,* the RGRs during the first years, between 2004 and 2006, were positively correlated with the survival at the end of the survey, 4.5 years after the transplantation, while it was negatively correlated with the survival of one species: *C. semaphora* (Table 4).

UNDERSTOREY RECOLONISATION

Similar treatments should lead to similar effects; we then expected that the factor "species" lead to some co-structure between the two sites. However among the three co-inertia analyses run between site 1 and 2, a significant co-structure was found only for soil surface indicators ($RV=0.390$, $P<0.05$ Monte-Carlo permutations), and not for soil or understorey composition data ($RV=0.136$, $P=0.17$ and $RV=0.595$, $P=0.34$ respectively). A first PCA was carried out and indicated that *C. semaphora* was highly correlated with percent cover of litter masking other effects (Inertia = 0.42, $P<0.001$- Monte-Carlo permutations). Another PCA was thus carried out, without *C. semaphora* (Inertia = 0.35, P <0.01- Monte-Carlo permutations), indicating on the axis 1 (45% of the total inertia) that *Eugenia dysenterica* (8%), *Z. tuberculosa* (9%) and *K. petiolaris* (10%) were characterized by bare ground (axis contribution: 23%) while *C. fasciculata* (29%) *M. foliolosa* (26%) and *L. campos-portoana* (9%) were correlated with high cover of litter and shade (axis contribution: 38% and 34% respectively) (Fig. 2). Axis 2 (38% of the total inertia) underlined that *Actinocephalus bongardii* (6%), *D. hirsutus* (10%), *L. campos-portoana* (13%) and control plot (27%) were characterized by a dense cover of biological crust (39%) and to a lesser extent by a cover of moss (11%) and herbaceous vegetation (18%) contrary to *E. ellipticum* (8%) and *K. petiolaris* (10%) which were distinguished by a higher cover of bare ground (21%).

The transplanted species appeared to influence both species richness and the herbaceous cover of the understorey. *Calliandra fasciculata*, *J. caroba*, *D. reticulatum*, *D. orbicularis*, *L.campos-portoana*, *A. bongardii* and control plots had significantly higher understorey richness than that of other species ($F=3.33$, $P<0.001$). Moreover the pre-cited species as well as *D. hirsutus*, *C. cipoensis* and control plots had significantly higher herbaceous cover than that of other species ($F = 2.78$, $P<0.001$). The floristic survey of the herbaceous understorey led to the identification of 69 species, of which the majority were represented by ruderal species which were likely to be dispersed from the road and that did not occur on the surrounding savannas. The most represented family was Poaceae (21 species), followed by Fabaceae (15) and Asteraceae (8). Two invasive species were identified: *Melinis repens* (from Africa; Starr et al. 2006) and *Euphorbia hirta* (from India, USDA 2008).

Crown volume, was positively correlated with the cover of litter (Spearman's ρ=0.65, P<0.01) and, since it influenced the amount of light reaching the soil, with shade (Spearman's ρ=0.74, P<0.001). Crown volume was negatively correlated with the cover of bare ground (Spearman's ρ=-0.54, P<0.05). No significant correlations between crown volume and biological crust, moss and herbaceous cover were found.

Discussion

The restoration success typically depends on multiple criteria. In this survey of a transplantation experiment, we considered two crucial aspects: (i) the capacity of transplanted species to settle and reproduce in the degraded area; (ii) the effect of the re-introduced species on their immediate environment which may result in an increased re-colonization of the site by other species. This study represents a landmark in the restoration of this type of tropical mountain savannas. We report one of the first conclusive restoration projects on these highly threatened ecosystems and emphasise that transplantation in degraded sites is a very good way to reintroduce native species and increase plant cover in harsh environments.

SURVIVAL AND GROWTH OF PLANTED SPECIES

Prior to the analysis of the efficiency of transplanted species to modify their environment, the first step in restoration using transplants is to identify species characterized by a high survival. Although some native species transplanted in this study was characterized by a low survival (<50%), half of our species panel showed a high survival (>78%) 4.5 years after transplantation in highly degraded areas. Those species, *C. fasciculata, C. cipoensis, J.*

caroba, D. reticulatum, H. byrsonimifolia, T. heteromalla, E. dysenterica, D. hirsutus and *L. pacari*, are therefore excellent candidates to restore degraded areas of highland savannas. While native trees presented a low survival compared to the native shrubs, the tree species *E. dysenterica* was also successfully transplanted (survival > 96%) and could be reintroduced with success, even if its contribution to recruitment would probably occur in the longer term.

Beyond survival, planted species, were able to reproduce vegetatively and/or sexually and therefore initiate the self-recolonisation of the degraded sites. This was also true concerning some species presenting low survival and in another hand 1) which are able to recruit numerous seedlings, such as the Fabaceae species: *Mimosa foliolosa* or *Chamaecrista semaphora*, or, 2) which are able to resprout like Melastomataceae species. This is particularly interesting since most of the transplanted species do not seem to fastly re-colonize degraded sites. They are not generally found in disturbed areas which have been abandoned for years (Le Stradic 2012), and their seeds are not detected in the seed bank (Medina & Fernandes 2007).

In addition, species lifespan should balance any evaluations exclusively based on the survival of transplanted individuals. *Actinocephalus bongardii* presented the lowest survival of all planted species (< 10%), but this species commonly lives only three to four years (Oriani et al. 2008) and the transplanted individuals survived well during the first two years. *Actinocephalus bongardii* has bloomed every year and has produced a large number of seeds although few recruitements are currently found. *A. bongardii* thus participated in degraded area stabilization during the first years. Moreover, dead individuals produced a fine litter which may have played a role in increasing soil organic matter and nutrients and in allowing colonisation by herbaceous species.

Plant growth did not appear to be a generic predictor of individual survival. Early survival, reflecting the species ability to establish on degraded sites, was poorly related to early RGR. In the same way, for only five species, i.e. *C. fasciculata*, *D. orbicularis, D.*

hirsutus, K. petiolaris, M. foliolosa and *M. taxifolia*, the growth rate partially reflected the ability of an individual to persist in degraded areas. In a majority of the species, survival at the end of the survey was not related to the RGR measured on shoots which might be the result of an investment in root growth.

However, if growth is not a critical factor determining the survival in degraded areas, we can expose some hypotheses explaining the low survival of some species. First edaphic conditions on degraded sites are more stressful than on their non-degraded counterparts. Abiotic conditions could limit the early stage of plant establishment (Maestre et al. 2006); maladjustment to the physical and chemical conditions of the degraded sites, critical in the short-term, may lead to a high mortality during the early stage (e.g., as observed for Melastomataceae). Establishment of tree and shrub seedlings in Neotropical savannas is highly constrained by drought, fire and competition with herbaceous species and thus depends on seedling ability to access water (Medina & Silva 1990).

In addition, on degraded sites, species distribution is less dense which modify species interactions compared to pristine areas. Fabaceae species bring, for the plant community, the potentially important feature of fixing atmospheric nitrogen. Unfortunately, two tested Fabaceae (*M. foliolosa* and *C. semaphora*) recorded high late mortality, possibly due to the effects of intra-specific competition occurring at the relatively small experimental plot scale. In a different way, *Enterolobium ellipticum* recorded a high mortality rate during the last year due to the parasitism of all individuals by *Struthanthus flexicaulis* Mart. (Loranthaceae).

COMMUNITY RESTORATION

Candidate species for future restoration projects can be listed on the basis of survival but the next step must be to assess the efficiency of transplanted species to modify their environment (i.e. nurse species, Padilla & Pugnaire 2006). Our work shows that transplanted species, even if they did not significantly influence soil properties and understorey plant composition, affected significantly their immediate vicinity modifying soil surface indicators, potentially increasing the establishment of recruits or future colonization by other species. A large fraction of our species (i.e. *C. fasciculata, C. cipoensis, J. caroba, D. reticulatum, D. orbicularis, D. hirsutus L. campos-portoana* and *A. bongardii*) allowed the establishment of an herbaceous strata participating to the soil stabilisation. We, however, did not find a potential nurse effect of our species, as an equal herbaceous cover was also present on control plots. In addition, large part of the new herbaceous cover is composed by ruderal species, which were not encountered on pristine highland savannas, underlining the real limitation of savanna species to immigrate on degraded areas.

Colonization of the understorey by herbaceous species is partly influenced by the amount of light reaching the ground and therefore by the canopy density and morphology of transplanted shrubs and trees. *Jacaranda caroba* and *C. cipoensis* have a canopy which is more permeable to light. They thus favour colonisation by herbaceous species, by contrast with *C. semaphora*. Canopy opening influences regeneration of herbaceous understorey under tree and shrub cover (Cusack & Montagnini 2004; Hobbs & Mooney 1986), especially since savannah species are not shade tolerant (Hoffmann & Franco 2003).

Denser plant cover should increase soil stability (Snelder & Bryan 1995) but according to Rey (2003) vegetation cover of 30% is already effective to control erosion and to trap sediments. *Marcetia taxifolia*, characterized by an average cover of the herbaceous understorey (23.8% ± 7.3), has significant cryptogam cover (30% ± 9.5) which also participates in erosion control. The ground does not necessarily have to be covered with shrubs; if their establishment is promoted, biological crusts and cryptogams can also play a major role in erosion control (Belnap & Lange 2001).

On the contrary, we highlighted that some species can limit re-colonisation by understorey species. For example, in this study, we showed that Fabaceae species (i.e. *C. semaphora, M. foliolosa, C. fasciculate*) were characterized by a high production of a thick litter. Leaves of plants of the genus *Chamaecrista* are rich in secondary compounds such as tannins (e.g. Madeira et al. 1998); tannin-rich litter decomposes very slowly and it has been shown that grasses may be sensitive to tannins released during leaf decomposition (Facelli 1991). This litter thus induced a strong inter-specific competition not favourable to colonisation by herbaceous understorey. In addition species of the genus *Mimosa* are often competitive (Braithwaite et al. 1989; IUCN 2002) due to their architecture, dense foliage and the shade they create.

A bad planting protocol can thus also lead to some re-colonization limitation, beyond a higher mortality by intra-specific competition, as we have just mentioned with the example of Fabaceae which should be planted far apart from one another due to their plant architecture and physiology. Therefore, when designing planting protocols, intra- and inter-specific competition and the effects of shade and litter have to be taken into account. To increase bare ground colonization by herbaceous species, plantation should be spaced out, as previously stated, and various types of plant architecture must be combined.

Conclusion

This work shows that the reintroduction of native species into a harsh environment is possible using seedling transplantation. Species, such as *C. fasciculata, C. cipoensis, J. caroba, D. reticulatum* and *D. hirsutus*, are excellent candidate to restoration project since they were able to settle and reproduce in the degraded area and they allowed the re-colonization of the site by understorey species. Our work emphasise that plant growth did not seem a good criterion to determine the transplantation success in such harsh environment. Intra-specific competition, leading to higher mortality, was observed especially for Fabaceae species. Therefore, a particular attention should be taken when planning restoration. A suitable planting design, including space between competitive species, is necessary to avoid mortality due to competition and to allow recolonisation.

Botanical and ecological knowledge of these ecosystems is still poor and needs to be improved in order to provide a better basis for selection of species to be transplanted. Monitoring is important to measure herbaceous understorey colonization (herbaceous, moss or biological crust cover and richness of herbaceous understorey) and to assess the efficiency of recruitment of transplanted species. Long-term monitoring is necessary; the influence of transplanted species on soil properties and understorey plant composition might occur on a longer time.

Acknowledgements

We are grateful to A.M.O. Paiva, M.N.A. Pereira and M.B.L. Moraes for their field and laboratory support and to two anonymous referees for their valuables comments. We also thank CNPq (558250/2009-2, 563304/2009-3, 303352/2010-8, 561883/2010-6), FAPEMIG (EDT-465/07, APQ-04105-10) and the Conseil Général du Morbihan for financial support.

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Table 1: List of transplanted species. Abbrev: abbreviations used in tables and figure. Stature: is the stature of the plant in the study. *Actinocephalus bongardii* is an herb but was considered as a shrub due to its stature

Species	Abbrev.	Family	Stature
Dasyphyllum reticulatum (DC.) Cabrera	Dret	Asteraceae	Shrub
Jacaranda caroba (Vell) A. DC.	Jcar	Bignoniaceae	Shrub
Actinocephalus bongardii A. St.-Hil Sano	Abon	Eriocaulaceae	Shrub
Calliandra fasciculata Benth. *var. bracteosa* (Bentham) Barneby	Cfas	Fabaceae	Shrub
Chamaecrista semaphora HS. Irwin & Barneby	Csem	Fabaceae	Shrub
Mimosa foliolosa Benth. ssp. *pachycarpa* (Bentham) Barneby var. *pachycarpa*	Mfol	Fabaceae	Shrub
Collaea cipoensis Fortunato	Ccip	Fabaceae	Shrub
Diplusodon hirsutus (Cham & Schlecht) DC	Dhir	Lythraceae	Shrub
Diplusodon orbicularis Koehne	Dorb	Lythraceae	Shrub
Heteropterys byrsonimifolia A. Juss	Hbyr	Malpighiaceae	Shrub
Lavoisiera campos-portoana Mell. Barr	Lcam	Melastomataceae	Shrub
Marcetia taxifolia A. St.-Hil DC	Mtax	Melastomataceae	Shrub
Tibouchina heteromalla (D. Don) Cogn.	Thet	Melastomataceae	Shrub
Lafoensia pacari A. St.-Hil	Lpac	Lythraceae	Shrub
Kielmeyera petiolaris Mart.	Kpet	Clusiaceae	Tree
Enterolobium ellipticum Benth.	Eell	Fabaceae	Tree
Eugenia dysenterica DC.	Edys	Myrtaceae	Tree
Zeyhera tuberculosa Bureau	Ztub	Bignoniaceae	Tree

Table 2: Overall and site-specific survival (%) in February 2008. Reproduction was recorded as the percentage of individuals with flowers and/or fruits, the number of seedlings recruiting and the percentage of individuals using vegetative reproduction. For species abbreviations, see Table 1. Site and plot effects were assessed using GLM procedures. / : no data, empty cell: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ (2 plots in each site with 16 plants in each plot)

	Survival 2008 (%)						
Species	Overall	(Site 1 - Site 2)	Site effect	Plot effect	Individuals with flowers or/and fruits (%)	Number of seedlings recruiting for 64 transplanted plants	Individuals using vegetative reproduction (%)
Lafoensia pacari	100	(100.0 - 100.0)			0	0	100
Eugenia dysenterica	96.9		/		0	0	0
Heteropterys byrsonimifolia	96.9	(100.0 - 93.8)			0	0	96.9
Tibouchina heteromalla	96.9	(96.9 - 96.9)			32.8	1	95.3
Dasyphyllum reticulatum	89.1	(87.5 - 90.6)			39.1	1	89.1
Collaea cipoensis	82.8	(90.6 - 75.0)			46.9	10	82.8
Calliandra fasciculata	81.3	(65.6 - 96.9)	***	**	40.6	3	0
Jacaranda caroba	81.3	(84.4 - 78.1)		**	0	1	0
Diplusodon hirsutus	78.1	(62.5 - 93.8)	**	***	34.4	0	78.1
Kielmeyera petiolaris	67.2		/	**	6.3	0	0
Marcetia taxifolia	60.9	(56.3 - 65.6)			53.1	15	0
Mimosa foliolosa	59.4	(65.6 - 53.1)			40.6	11	0
Chamaecrista semaphora	46.9	(28.1 - 65.6)	**	*	46.9	15	0
Diplusodon orbicularis	39.1	(25.0 - 53.1)	*	*	12.5	2	0
Lavoisiera campos-portoana	37.5	(28.1 - 46.9)			29.7	0	37.5
Enterolobium ellipticum	28.1		/		0	0	0
Zeyhera tuberculosa	28.1		/		0	0	0
Actinocephalus bongardii	10.9	(18.8 - 3.1)	*	*	9.4	1	0

Table 3: Number and percentage of dead individuals in 2004, 2006 and 2008 according to their families. Resprouting individuals were taken into account, which increased survival rate for some families (e.g. Melastomataceae species)

2004	Number of dead individuals	% of survival	Total number of individuals
Other families	8	97.50%	320
Bignoniaceae	0	100.00%	128
Fabaceae	11	96.56%	320
Lythraceae	11	94.50%	200
Melastomataceae	75	60.94%	192
2006			
Other families	40	87.50%	320
Bignoniaceae	9	92.70%	128
Fabaceae	60	81.25%	320
Lythraceae	39	80.50%	200
Melastomataceae	146	23.06%	192
2008			
Other families	89	72.19%	320
Bignoniaceae	58	54.69%	128
Fabaceae	129	59.69%	320
Lythraceae	53	73.50%	200
Melastomataceae	67	65.10%	192

Table 4: Effects of the early RGR (between August 2003 and September 2003), the mid-term RGR (between September 2003 and February 2004) and the late RGR (between February 2004 and April 2006) on respectively the survival in 2004, 2006 and 2008, using GLM procedures. Effects of the initial plant size (diameter, height and volume in 2003) on the survival in 2008 using GLM procedures. / : no data, empty cell: non-significant, +: significant positive GLM coefficient value with $P < 0.05$, ++: with $P < 0.01$, +++: with $P < 0.05$, - -: significant negative GLM coefficient value with $P < 0.01$, - - -: with $P < 0.001$

	Effect of early RGR on survival in 2004 (transplantation + 6 months)			Effect of mid RGR on survival in 2006 (transplantation + 2.5 years)			Effect of late RGR on survival in 2008 (transplantation + 4.5years)			Effect of initial plant size on survival in 2008		
Species	Diameter	Height	Volume	Diameter	Height	Volume	Diameter	Height	Volume	Diameter	Height	Volume
Abon											+	+
Cfas					+	+		++	+++	+		
Csem							- - -					
Ccip												
Dret							++	+++	++	+		+
Dhir						+						
Dorb				++	++	+++						
Eell	+											
Edys										+		
Hbyr												
Jcar												
Kpet				+		++						
Lpac												
Lcam				/	/	/	/	/	/			
Mtax	+++		++	++							+	+
Mfol				+++	+++	+++						
Thet							/	/	/			
Ztub							+++	+				

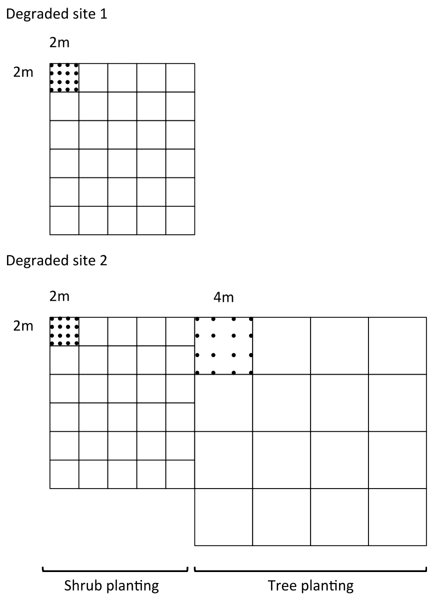

Figure 1: sketch of the experimental design: two sites were assigned to shrub transplantation. In each site, 30 4-m² plots were defined and two plots were randomly assigned to each shrub species (14 species x 2 plots); only two 4-m^2 plots remained unplanted as controls for the study of species influence on soil surface indicators. Because of the small size of both sites, we could not place 28 control plots with nothing planted on them, as it would be an ideal scenario. One site was assigned to tree transplantation, sixteen 16-m² plots were assigned for tree species plantation (4 species x 4 plots). In each plot, 16 individuals of one species were transplanted 1m apart for tree species and 0.5m apart for shrub species.

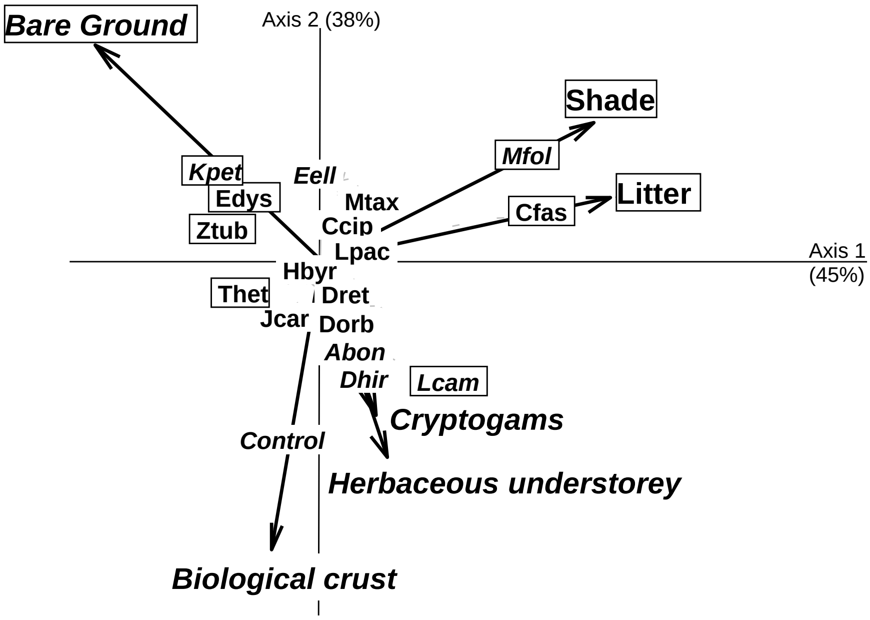

Figure 2: Inter-class PCA carried out on various soil surface indicators and shade, projection of two first principal components [72 points × 6 variables]. Variables and species contributing to axis 1 are framed and to axis 2 are in italics. Monte-Carlo permutations: inertia = 0.35, $P < 0.01$. *Chamaecrista semaphora* was not included in the analysis. Abbreviations refer to Table 1.