

## Rehabilitation of degraded areas in northeastern Patagonia, Argentina: Effects of environmental conditions and plant functional traits on performance of native woody species (Postprint)

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**Date:** 2020-10-20T00:00:00+00:00

### Abstract

Degradation processes affect a vast area of arid and semi-arid lands around the world and damage the environment and people's health. Degradation processes are driven by human productive activities that cause direct and indirect effects on natural resources, such as species extinction at regional scale, reduction and elimination of vegetation cover, soil erosion, etc. In this context, ecological rehabilitation is an important tool to recover key aspects of the degraded ecosystem. Rehabilitation trials rely on the use of native plant species with characteristics that allow them to obtain high survival and growth rates. The aim of this work was to assess the survival and growth of native woody species in degraded areas of northeastern Patagonia and relate them to plant functional traits and environmental variables. We observed high early and late survival rates, and growth rates in *Prosopis flexuosa* DC. var. *depressa* F.A. Roig and *Schinus johnstonii* F.A. Barkley, and low values in *Condalia microphylla* Cav. and *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart. Early survival rates were positively associated with specific leaf area (SLA) and precipitation, but negatively associated with wood density, the maximum mean temperature of the warmest month and the minimum mean temperature of the coldest month. Late survival rates were positively associated with SLA and soil organic matter, but negatively associated with plant height and precipitation. The temperature had a positive effect on late survival rates once the plants overcame the critical period of the first summer after they were transplanted to the field. *Prosopis flexuosa* and *S. johnstonii* were the most successful species in our study. This could be due to their functional traits that allow these species to acclimatize to the local environment. Further research should focus on *C. microphylla* and *G. decorticans* to determine how they relate to productive conditions, acclimation

to environmental stress, auto-ecology and potential use in ecological rehabilitation trials.

## Full Text

### Rehabilitation of Degraded Areas in Northeastern Patagonia, Argentina: Effects of Environmental Conditions on Performance of Native Woody Species

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**Abstract:** Degradation processes affect vast areas of arid and semi-arid lands worldwide, damaging both the environment and human health. These processes are driven by human productive activities that cause direct and indirect effects on natural resources, including species extinction at regional scales, reduction and elimination of vegetation cover, soil erosion, and more. In this context, ecological rehabilitation serves as an important tool to recover key aspects of degraded ecosystems. Rehabilitation trials rely on the use of native plant species with characteristics that enable high survival and growth rates. This work aimed to assess the survival and growth of native woody species in degraded areas of northeastern Patagonia and relate them to plant functional traits and environmental variables. We observed high early and late survival rates and growth rates in *Prosopis flexuosa* DC. var. *depressa* F.A. Roig and *Schinus johnstonii* F.A. Barkley, and low values in *Condalia microphylla* Cav. and *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart. Early survival rates were positively associated with specific leaf area (SLA) and precipitation, but negatively associated with wood density, the maximum mean temperature of the warmest month, and the minimum mean temperature of the coldest month. Late survival rates were positively associated with SLA and soil organic matter, but negatively associated with plant height and precipitation. Temperature had a positive effect on late survival rates once plants overcame the critical period of the first summer after transplantation. *Prosopis flexuosa* and *S. johnstonii* were the most successful species in our study, likely due to functional traits that allow them to acclimatize to local environmental conditions. Further research should focus on *C. microphylla* and *G. decorticans* to determine their relationships with productive conditions, acclimation to environmental stress, auto-ecology, and potential use in ecological rehabilitation trials.

**Keywords:** arid lands; *Condalia microphylla*; *Geoffroea decorticans*; *Prosopis flexuosa*; *Schinus johnstonii*; survival rates; height growth; basal diameter

growth

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Received 2019-12-15; revised 2020-06-08; accepted 2020-06-23

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## Introduction

Degradation processes affect vast areas of arid and semi-arid lands around the world, which are inhabited by  $2.5 \times 10^9$  people (UNCCD, 2011). Most of these lands are located in developing countries and display several degradation symptoms, affecting the health of both people and ecosystems (James et al., 2013). Ecosystem degradation is caused by human activities, evidenced by loss of soil fertility and vegetation cover, soil erosion, and diminishing land productivity (Abraham et al., 2009; Vallejo et al., 2009; Cortina et al., 2011). In this scenario, ecological rehabilitation represents a key strategy to recover degraded ecosystems (Aronson et al., 1993; Maestre et al., 2001; Delgado-Baquerizo et al., 2013).

Ecological rehabilitation involves interventions on natural systems to return some of their lost structural and functional attributes. To achieve this objective, practitioners should remove disturbance factors and take actions to increase vegetation cover (Aronson et al., 1993; Hobbs and Kramer, 2008). Techniques for improving vegetation cover include sowing seeds of native or exotic species in bare soils, transplanting plants to the field, and applying soil amendments to improve physical and chemical soil properties (Peláez et al., 1996; de Villalobos and Peláez, 2001; Maestre et al., 2001; Novak and Prach, 2003; de Villalobos et al., 2005; Milgrom, 2008; Dalmasso, 2010; Landi and Renison, 2010; Neri and Sánchez, 2010; Delgado-Baquerizo et al., 2013; Meli et al., 2013; Gasch et al., 2014; Soteras et al., 2014; Torres et al., 2015; Mcadoo et al., 2016; Plaza Behr et al., 2016; Pérez et al., 2019). Active plantation of species produced in nurseries is one of the most frequently used techniques in rehabilitation trials (Pérez et al., 2019). Additionally, it is desirable to initiate ecological rehabilitation processes using genetic material from the intervened area because native plant species are adapted to dominant environmental conditions (Aronson et al., 1993; Cortina et al., 2006; Hobbs and Kramer, 2008).

The success of rehabilitation projects depends largely on selected species (Cortina et al., 2006). The functional traits framework has recently emerged as a useful tool to identify the most suitable species for rehabilitation programs (Martínez-Garza et al., 2013; Laughlin, 2014; Ostertag et al., 2015; Engst et al., 2016; Zirbel et al., 2017). This approach helps us understand and predict species trait responses to environmental conditions and determine how these traits may affect ecosystem functions (Lavorel and Garnier, 2002; Zirbel et al., 2017). For example, wood density shows a significant positive relationship with resistance to cavitation, and specific leaf area (SLA) relates to competitive ability and stress tolerance. Species with high SLA have faster growth rates

and are less stress-tolerant (Westoby and Wright, 2006). Plant height predicts root system depth and its ability to explore deep soil layers. Tall plants have deep roots, while dwarf shrubs have extended, shallow root systems (Weiher et al., 1999).

Our study area is located in northeastern Patagonia, Argentina—an ecotonal environment between the Monte and Espinal phytogeographic regions. Structurally, it is a shrubby steppe with isolated trees surrounded by tall grasses and herbaceous species. Plant communities develop across a wide variety of soils and reliefs (Leon et al., 1998; Bran et al., 2000; Godagnone and Bran, 2009; Morello et al., 2012; Oyarzabal et al., 2018).

Northeastern Patagonian ecosystems show obvious signs of degradation and fragmentation (Zeberio, 2012, 2018; Abraham et al., 2016). The dominant land use in this area is extensive livestock production and rainfed agriculture. Crops have been abandoned due to loss of profitability caused by periodic drought (Zeberio et al., 2018). Ecological restoration studies in this area have different scopes and are not always accessible (Bran et al., 2007; Gaitán et al., 2007, 2008; Kropff et al., 2011; Funk et al., 2012; Peter et al., 2012; Zeberio, 2018). Additionally, research on the performance of native woody species in rehabilitation projects in this area is particularly scarce (Torres Robles et al., 2015; Zeberio et al., 2018). To our knowledge, no previous studies have related the functional traits of these species to their performance in the harsh environmental conditions of degraded northeastern Patagonia.

We developed a structural equation model (SEM) based on hypothesized relationships among environmental conditions, plant functional traits, and species responses. SEM is a useful tool for understanding direct and indirect effects of predictors in complex multivariate systems (Grace et al., 2010). Therefore, this work aimed to assess the survival and growth of native woody species in degraded areas of northeastern Patagonia and link these plant responses to plant functional traits and environmental variables.

## 2.1 Site Selection

We identified degraded areas in northeastern Patagonia based on geomorphological units as defined by Godagnone and Bran (2009). According to Morello et al. (2012), the study area is located in the eco-region known as Monte of plains and plateaus.

We selected sites for rehabilitation trials according to two criteria: (1) they share a common land-use history (Table 1), but (2) have differential geomorphological characteristics representative of the high heterogeneity of the area (Table 2; Fig. 1 [Figure 1: see original paper]). We selected three sites named after the landowners' last names: Erripa (Err) and Iturburu (Itu) in Adolfo Alsina district (Río Negro Province), and Bosero (Bos) in Patagones district (Buenos Aires Province). Degraded lands represent 40% of the total surface of these districts (Pezzola and Winschel, 2004; Zeberio, 2012).

**Table 1** Location and land use in each rehabilitation trial site

Site	Latitude	Longitude	Land use	Age of clearing (a)
Err	41°09' 11'' S	63°25 19 W	Rainfed agriculture	15
Itu	41°01' 04'' S	63°01 40 W	Extensive livestock	20
Bos	40°39' 30'' S	62°52 00 W	Rainfed agriculture	10

**Table 2** Characteristics of rehabilitation trial sites

Site	Geomorphology	Soil texture	Depth (cm)	EC (dS/m)	BD (g/cm <sup>3</sup> )	OM (mg/g)	TN (mg/g)	P (mg/g)
Err	Loess plateau	Sandy	>100	0.31	1.35	1.63	0.08	0.02
Itu	Loess plateau	Sandy-loamy	>100	0.28	1.38	1.21	0.06	0.01
Bos	Interfluvial plateau	Loamy	60	0.35	1.42	0.46	0.03	0.01

Note: EC, electrical conductivity; BD, bulk density; OM, organic matter; TN, total nitrogen; P, phosphorus.

Three 100 m<sup>2</sup> plots were established at each site. The plots were at least 75 m apart from each other and fenced with 60-cm-high plastic mesh to actively protect planted species against potential damage from livestock and small mammal herbivores.

Climate data were obtained from the WorldClim database (Fick and Hijmans, 2017). Mean annual precipitation during 2013–2016 presented a bimodal behavior with two maxima. Rainfall peaked in April at all three sites, with a second peak in September at Bos and in October at the other two sites. Accumulated annual precipitation at Bos, Itu, and Err sites was 443.0, 460.3, and 455.3 mm, respectively. The highest precipitation in autumn and winter was recorded at Bos and Err sites, while the highest precipitation in spring and summer was observed at Err, the site closest to the sea (Fig. 2 [Figure 2: see original paper]). The maximum mean temperature for January (the warmest month) ranged from 27.2°C to 25.8°C, and the minimum mean temperature for July (the coldest month) ranged from 0.6°C to -0.2°C, depending on the site.

Soil chemical properties were estimated from composite soil samples (30 cm depth) collected from the center of each plot. We estimated soil organic matter (OM) by the Walkley and Black method, total nitrogen (TN) by the micro-Kjeldahl method, and total phosphorus (P) by the Olsen method. We also recorded soil depth at each site until lithic contact and extracted a core to determine soil density (de Inalbon, 2005).

## 2.2 Species Selection

We selected the most frequent woody species in non-degraded areas (Zeberio et al., 2018): the shrubs *Prosopis flexuosa* DC. var. *depressa* F.A. Roig, *Condalia microphylla* Cav. and *Schinus johnstonii* F.A. Barkley, as well as the tree *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (Table 3).

Seeds of the selected species were collected from the study area to produce individuals in a greenhouse. Seeds were collected from plants meeting selection criteria by Ffolliott and Thames (1983) and stored in paper bags until sowing. Seeds were sown between May and July 2012 in the greenhouse of the experimental station of the National Institute of Agricultural Technology, Argentina.

The most adequate pre-germination treatments were conducted for each species. *Condalia microphylla*, *G. decorticans* and *P. flexuosa* seeds were scarified with sulphuric acid (98% P/V) for 32 min. For *S. johnstonii*, we removed the exo- and mesocarp of the seeds (Zeberio and Calabrese, 2013). Seeds were sown in plastic trays of 60 cm × 48 cm × 15 cm containing a mixed substrate with equal parts sand and peat to facilitate seedling removal. A month later, seedlings were placed in individual pots.

**Table 3** Summary of plant characteristics used in rehabilitation trial sites

Woody species	SLA (cm <sup>2</sup> /g)	WD (g/cm <sup>2</sup> )	Foliage	Height (cm)	Life form
<i>C. microphylla</i>	45.2	0.78	Evergreen	150	Shrub
<i>G. decorticans</i>	112.5	0.52	Deciduous	500	Tree
<i>S. johnstonii</i>	72.3	0.55	Evergreen	200	Shrub
<i>P. flexuosa</i>	58.4	0.58	Deciduous	300	Shrub

*Note:* SLA, specific leaf area; WD, wood density.

Each individual pot contained a substrate of soil extracted from the experimental sites (50%), commercial earthworm castings (25%), and peat (25%). Plants were grown in the greenhouse for about seven months with periodic irrigation (twice a week). After that, an acclimation process was developed (Cortina et al., 2006). A month before transplanting to the field, plants were gradually exposed to natural environmental conditions, including direct sunlight and wind, with decreased irrigation (once a week).

## 2.3 Experimental Design

Plants were transplanted to the experimental sites between April and May 2013. For each species, nine individuals were planted in two rows, except for *C. microphylla* (five plants in one row). This species showed high mortality during the

acclimation phase, preventing us from obtaining enough individuals. Rows were arranged 2 m apart. Plant holes were 15 cm in diameter and 20 cm deep, with 1200 cm<sup>3</sup> of commercial earthworm castings added at the bottom to prevent compaction. The remaining space in the holes was filled with extracted soil and manually compacted. To improve moisture retention, we dug a basin around each plant to capture and retain natural moisture.

In December 2013, we recorded the survival of individuals of each species (early survival rate), plant height, and basal diameter. Three years later, in February 2016, we recorded the late survival rate and measured plant height and basal diameter of each surviving plant. Growth was estimated as the difference between initial and final measurements of height and basal diameter. Plant functional traits (SLA, wood density, and plant height) were obtained from the TRY plant trait database (Kattge et al., 2011) (Table 3).

## 2.4 Data Analyses

Generalized linear models were performed to evaluate plant survival and growth, assuming binomial distribution for survival data and normal distribution for growth data. Site and species were considered predictor variables. Site-species interaction was estimated to evaluate differential species performance at each site. Means were compared using the LSD (least significant difference) test. Data were analyzed using Infostat software (di Rienzo et al., 2008).

Causal relationships between environmental variables and plant functional traits were analyzed to determine their effects on early survival rates, late survival rates, plant height, and basal diameter. Environmental variables and plant functional traits were selected by linear correlation with plant survival and growth rates. Structural equation models (SEM) synthesize path analysis, factor analysis, and maximum likelihood techniques, serving as causal inference tools in ecological science. This analysis can prove the plausibility of causal models based on a priori information about relationships between variables of interest. We used SEM to evaluate the relative importance and direct/indirect effects of climate, soil variables, and plant functional traits on plant survival and growth. We used the normed fit index and root mean square error of approximation index as measures of model fit (Grace, 2006). Path coefficient estimates were obtained using maximum-likelihood estimation, equivalent to standardized partial regression coefficients and interpreted as relative effects of one variable upon another (Grace et al., 2010).

## 3.1 Early Survival Rate

Early survival rate was estimated seven months after transplanting to restoration trial sites. *Prosopis flexuosa*, *G. decorticans* and *S. johnstonii* presented high survival rates (near 100%) (n=288; df=6; F=124.4; P<0.001). *Condalia microphylla* presented lower survival rate (50%) than other species (P<0.001) (Fig. 3 [Figure 3: see original paper]). Bos and Err sites showed higher survival

rates (85% and 95%, respectively) than Itu (75%) ( $P=0.046$ ). Species $\times$ site interaction for early survival rate was significant only for *C. microphylla* ( $P=0.09$ ). This species showed higher survival rate at Err (70%), but lower at Bos (50%) and Itu (20%).

### 3.2 Late Survival Rate

Late survival rate was recorded three years after transplantation, in summer 2016. Survival rates decreased over time, as late survival rate was lower than early survival rate ( $n=224$ ;  $df=6$ ;  $F=296.6$ ;  $P<0.001$ ). *Prosopis flexuosa* and *S. johnstonii* presented higher survival rates (70% and 75%, respectively) than *C. microphylla* and *G. decorticans* (15% and 35%, respectively) ( $P=0.0003$ ) (Fig. 4 [Figure 4: see original paper]). Late survival rate at Itu (60%) was higher than at Bos and Err sites (42% and 38%, respectively) ( $P=0.0074$ ). Species $\times$ site interaction was not significant ( $P=0.186$ ). Transplanted specimens of *G. decorticans* were severely browsed by the Patagonian hare (*Dolichotis patagonum*), with stems felled at ground level.

### 3.3 Species Growth

Three years after transplantation, plant height ranged from 25.50 cm (*C. microphylla*) to 38.54 cm (*S. johnstonii*) ( $n=224$ ;  $df=6$ ;  $F=113.0$ ;  $P<0.001$ ). Height increase of *P. flexuosa* (9.76 cm) and *S. johnstonii* (9.58 cm) was higher than that of *G. decorticans* (5.99 cm). *Condalia microphylla* showed the smallest height increase (1.04 cm;  $P=0.0002$ ) (Fig. 5 [Figure 5: see original paper]). Height increase was higher at Itu than at Bos and Err sites ( $P<0.0001$ ). Species $\times$ site interaction was significant ( $P=0.047$ ) because *G. decorticans* and *S. johnstonii* showed greater height increase at Itu than at other sites.

Basal stem diameter varied from 0.47 cm (*G. decorticans*) to 0.96 cm (*S. johnstonii*) ( $n=288$ ;  $df=6$ ;  $F=125.6$ ;  $P<0.001$ ). The highest basal diameter increase was found for *S. johnstonii* (0.29 cm) and *P. flexuosa* (0.21 cm) ( $P<0.001$ ) (Fig. 6 [Figure 6: see original paper]). Itu showed greater basal diameter increase than the other two sites ( $P<0.001$ ). Species $\times$ site interaction showed significant differences ( $P<0.001$ ). *Schinus johnstonii* showed higher basal diameter increase at Itu, but *C. microphylla*, *G. decorticans* and *P. flexuosa* showed no differences among sites.

### 3.4 Effects of Environmental Variables and Plant Functional Traits on Survival and Growth

A structural equation model was built to evaluate relationships between environmental variables and functional plant traits on early survival rate, late survival rate, and growth ( $\chi^2=43.5$ ;  $P=0.18$ ;  $df=28$ ; normed fit index=0.87). This model explained 91% of variation in early survival rate, height growth, and diameter growth, and 95% of late survival rate (Fig. 7 [Figure 7: see origi-

nal paper]). The graphs show only statistically significant positive and negative effects ( $P < 0.05$ ). Wood density was negatively associated with late survival rate. SLA was positively associated with both early and late survival rates. Mean plant height had a negative effect on late survival rate.

Minimum and maximum temperatures had negative effects on early survival rate but positive effects on late survival rate. Accumulated seasonal precipitation during the study period positively affected early survival rate but negatively affected late survival rate and height growth.

Soil OM and soil depth to lithic contact were the edaphic variables showing statistical significance. Soil OM had a positive effect on late survival rate, while soil depth had negative effects on early survival rate and height growth.

#### 4 Discussion

In this study, selected species showed high early and late survival rates related to prevailing strategies in arid and semi-arid environments. Two contrasting plant strategies have been identified: the acquisitive strategy, involving functional attributes that facilitate rapid resource acquisition and high growth rates; and the conservative strategy, involving attributes that allow plants to retain acquired resources at lower growth rates (Poorter, 1990; Lambers and Poorter, 1992; Reich et al., 1997; Aerts and Chapin, 2000; Wright and Westoby, 2002; Díaz et al., 2004). SLA values of woody species used in this study positively impacted their early and late survival rates. Plant species with low SLA values tend to have sclerophyllous leaves. Their thick epidermal walls retain moisture more efficiently, and they have lower canopy height and small xylem vessels that prevent cavitation and high specific wood density (Wright and Westoby, 2002; Díaz et al., 2004; Westoby and Wright, 2006). Prevailing plant strategies are associated with environmental characteristics of the regions where they are established (Díaz et al., 2004). In the arid and semi-arid regions of Argentina, species have relatively low SLA values (Díaz et al., 1999).

This applies to species in our study because their leaves have anatomical structures that protect photosynthetic tissues from desiccation and herbivory, such as thick cuticles, spines, and anti-herbivore compounds (Peláez et al., 1994; Kraus et al., 2003; Bucci et al., 2004; Villagra et al., 2011). Therefore, these species may be considered conservative according to their low SLA values. These conservative strategies could have helped selected species achieve high or moderate survival rates under harsh environmental conditions at our study sites.

SLA negatively correlated with wood density. Wood density is considered a proxy for vulnerability to embolism, which can endanger plant growth and survival under water stress conditions. Higher wood density relates to greater resistance to cavitation (Westoby and Wright, 2006; Chave et al., 2009). Thus, we expected a positive relationship between wood density and survival rate. However, wood density was negatively associated with early survival rate. We believe this result was conditioned by the high mortality rate of *C. microphylla*,

which had the highest wood density among species used in this study. The high mortality of *C. microphylla* may relate to its ecophysiological characteristics. Peláez et al. (1996) reported low *C. microphylla* survival rate (25%) in the semi-arid region of Argentina, where rainfall shortage impaired establishment of transplanted individuals. In our work, in addition to environmental constraints, the older age of transplanted individuals may have harmed their survival rates. *Condalia microphylla* specimens used in this rehabilitation trial showed high mortality during the acclimation phase (unpublished data), and older specimens had to be used to complete the required number of plants. Cortina et al. (2006) indicated that to obtain high survival rates, woody species specimens destined for ecological restoration should be transplanted in their first vegetative stage.

Maximum and minimum temperatures may indicate effects of extreme temperature on plants. These temperatures showed negative effects on early survival rate of plant species in this study but positive effects on late survival rate. These results likely associate with the critical threshold plants must overcome during the first year after field transplantation and the acclimation process (Cortina et al., 2006; Maestre et al., 2006).

Recorded rainfall had positive effects on early survival rate but negative effects on late survival rate and plant height in all transplanted individuals. Godagnone and Brand (2009) indicated precipitation tendencies coincident with our precipitation record. Northeastern Patagonia is characterized by inter-annual and intra-annual precipitation variability (Godagnone and Bran, 2009). For the period measured in this study, the rainiest seasons were autumn (80 mm) and spring (71 mm), with the lowest rainfall recorded in summer (25 mm). Early plant survival was estimated in spring, one of the rainiest periods, but three years later, plants were exposed to summer rainfall shortages. Plant transpiration demands are highest during summer, and drought could have negatively affected late survival rate and limited plant growth.

Soil OM values obtained at each study site (0.46 to 1.63 mg/g) coincided with those reported by Godagnone and Bran (2009) for northeastern Patagonia. However, low soil OM values had positive effects on late survival rate of plant species in our study. This might relate to adaptation of native species and their ability to obtain scarce soil resources and use them efficiently. Additionally, sites in this study shared a common land-use history of rainfed agriculture. Grman et al. (2013) found that residual nutrients from previous cropland use may positively affect plant survival and establishment in restoration areas.

Mean plant height of species used in this study negatively affected late survival rate. This links to the lowest survival rate of *G. decorticans*, the only tree in this study. Plant height growth related to soil depth. Schenk and Jackson (2005) indicate that woody plant height is a good predictor of root system depth. When root systems are limited by physical soil impediments, plants show lower development of above-ground organs (Peláez et al., 1994; Bucci et al., 2004). Bos site had the lowest soil depth due to a sub-superficial calcium carbonate layer that acts as a barrier to root system development. Differences in plant

height growth registered at study sites indicate that soil depth had a sharp effect on transplanted plants, regardless of species identity. Height growth was higher in plants grown in deeper soil sites.

In our study, *P. flexuosa* and *S. johnstonii* were the most successful species because they exhibited the highest survival and growth rates. Both species have a dimorphic root system, with deep roots that allow water uptake from deep soil layers and shallow roots that capture surface water from occasional rainfall (Villagra, 2000; Bucci et al., 2009; Jobbágy et al., 2011; Villagra et al., 2011). The high early survival rate of *P. flexuosa* obtained in this study was similar to that obtained by López Launstein et al. (2012) in northwestern Argentina, where *P. flexuosa* showed 100% early survival under moderate water stress and 70% survival under severe water stress. In northwestern Patagonia, Pérez (2013) found lower survival in *S. johnstonii* (75%) than in our study. Both *P. flexuosa* and *S. johnstonii* had different SLA values but similar wood density and root system morphology. Dimorphic root systems are absent in other species in this rehabilitation trial. *Condalia microphylla* presents a shallow root system extended in the first 60 cm of soil depth, making it compete with grasses for rainfall water (Peláez et al., 1994). In contrast, *G. decorticans* presents a pivoting, deep root system (Kraus et al., 2003), making it less able to take advantage of superficial soil water. The dimorphic root system of *P. flexuosa* and *S. johnstonii* allows them to obtain water from both superficial and deep soil layers, which may explain their persistence under water stress conditions (Díaz and Cabido, 1997; Whitford, 2002). Additionally, *P. flexuosa* and *S. johnstonii* are shrubs, while *G. decorticans* is a tree. As *G. decorticans* was severely damaged by Patagonian hare in the field, we could not obtain conclusive data.

## 5 Conclusions

The structural equation models used in this study related the performance of native woody species to functional traits and environmental variables in an ecological restoration trial in deforested semi-arid lands. *Prosopis flexuosa* and *S. johnstonii* were the most successful species in our study. These species overcame rainfall shortages and high-temperature stress. The presence of a dimorphic root system may provide them competitive advantages regardless of other functional traits, potentially related to their ability to use both deep soil water and shallower soil layers.

Due to damage caused by Patagonian hare, future field studies should focus on survival and growth of *G. decorticans* to evaluate its inclusion in ecological rehabilitation projects in deforested areas of northeastern Patagonia. Similarly, as *C. microphylla* is a frequent species in northern Patagonia, auto-ecology studies should determine whether this species may be included in rehabilitation projects.

**Acknowledgements:** This work was funded by the National University of Río Negro, Argentina (PI40c658, PI40c654). We thank the staff and owners of the

study sites Bosero, Iturburu, and Erripa. Two anonymous reviewers greatly improved the quality of this work.

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