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## *Polylepis australis*' regeneration niche in relation to seed dispersal, site characteristics and livestock density

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### Abstract

Establishment of *Polylepis* forests endemic to the mountains of South America may be affected by seed dispersal, site characteristics and livestock density. *Polylepis australis* (“tabaquito”) grows in the high mountains of central Argentina, where we set up 76 square study plots of 900 m<sup>2</sup>. To determine dispersal distance, we distributed 6 seed traps per plot in and around 20 plots. To determine the best site characteristics and livestock stocking rates, at two river basins differing in historic stocking rates, we analyzed the presence of seedlings in 56 plots and recorded topography, vegetation types and indicators of livestock activity. We also measured microsite characteristics in a sample of 32 comparable pairs of 1 m<sup>2</sup> quadrats, with and without seedlings. Maximum recorded dispersal distance of *P. australis* seeds was 6 m, and seedlings were found no more than 10 m from seed trees. The numbers of seedlings and seed trees were 3.5 and 4 times higher, respectively, in the basin with less livestock. At the 900 m<sup>2</sup> plot scale, a Poisson regression indicated a positive relationship between seedling number and *P. australis* canopy cover. At the quadrat scale (1 m<sup>2</sup>), seedlings were found in quadrats with significantly lower evidence of soil erosion than comparison quadrats without seedlings. We conclude that the main limitations to recruitment are short seed dispersal distances, lack of seed trees and extreme soil erosion. Management should therefore aim at preserving seed trees and reducing livestock density to prevent erosion.

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**Keywords:** Forest cover; Erosion; Mesohabitat; Microsite; “Tabaquito”; Seedling establishment

### 1. Introduction

Dispersal and establishment are two critical stages for many plant species, as seeds are often dispersed to inappropriate sites for germination, and the newly emerged seedlings do not have the ability to withstand the adverse conditions tolerated by adult plants (Fenner and Thompson, 2005). Abiotic stress factors such as shade, excess light, heat, water stress and flooding may prevent seed germination, kill seedlings or lower their tolerance to biotic mortality agents such as neighboring vegetation or herbivory. For example, the type and density of neighboring vegetation may influence seedling establishment directly, through competition for resources or the production of allelopathic substances, and indirectly through influence on

predator behavior (George and Bazzaz, 1999; Kitajima and Fenner, 2000). In addition, herbivory is known to be one of the most hazardous factors affecting newly germinated seedlings (Harmer, 2001; Bellingham and Allan, 2003).

Variability in seedling recruitment may be especially accentuated in mountain ecosystems due to their heterogeneous abiotic and biotic environmental conditions, such as water availability or livestock browsing intensity (Ellenberg, 1979; Ferreyra et al., 1998; Körner, 2002). In the mountains of South America, human activities such as livestock rearing, anthropogenic fires, cutting and cultivation have converted extensive areas of forest to grasslands or open woodlands. The new vegetation types may have highly altered microclimate conditions, which could be a barrier to the restoration of mountain forests due to reduced dispersal, germination and establishment of tree species (Aide et al., 1996; Fjeldså and Kessler, 1996; Rivera and Aide, 1998; Körner, 2002).

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Studies on seed dispersal and regeneration niche are important in determining management strategies that favor forest restoration (Aide and Cavelier, 1994; Spies and Turner, 1999). Here, we analyze seed dispersal and regeneration niche of *Polylepis australis* BITTER, also called “tabaquillo” or “queñoa”, endemic to the high cloud forest areas of central and north-western Argentina. Previous studies suggested that long term livestock rearing has produced important soil degradation, decreases in *P. australis* seed viability and reductions in juvenile growth and *P. australis* canopy cover (Renison et al., 2004, 2005, 2006; Teich et al., 2005). Restoration of South American *Polylepis* mountain forests is fundamental due to the large proportion of endemic species they harbor, and because of their important function in protecting the catchments of rivers that provide water to populations in the lowlands (Fjeldså and Kessler, 1996).

We evaluated whether the first stages of *P. australis* seed regeneration in the Córdoba Mountains are limited by seed dispersal and/or relevant site conditions. Our objectives were: (1) to determine seed rain and dispersal distances, and (2) to study how the availability of seed sources, topography, substrate, vegetation characteristics and anthropogenic degradation relate to the presence of seedlings at the plot (900 m<sup>2</sup>) and quadrat (1 m<sup>2</sup>) scales.

## 2. Methods

### 2.1. Study area and species

The present-day vegetation of the Córdoba Mountains (central Argentina, north–south orientation, 1400–2800 m a.s.l., 31°34'S, 64°50'W; 124,700 ha) consists of a mosaic of tussock grasslands, grazing lawns, granite outcrops, eroded areas with exposed rock surfaces and *P. australis* forests, woodlands or shrublands. These woody *P. australis* formations occupy around 12% of the area and are generally restricted to steep slopes and ravines at mid to low topographic positions (Cingolani et al., 2004; Renison et al., 2006). The main economic activity is livestock rearing (cattle, sheep, horses and goats). Winds are predominantly easterly or westerly, but due to local topography may vary considerably. Mean temperatures of the coldest and warmest months at 2100 m a.s.l. are 5.0 and 11.4 °C, respectively, with no frost-free periods (Cabido, 1985). Mean annual precipitation is 840 mm, with 83% of all rainfall concentrated in the warmer months (Renison et al., 2002a). *P. australis* shrubs or trees reach 3–14 m in height, and annually produce 8–10 mm long winged nutlets (hereafter referred to as seeds), which disperse in January and February by gravity and wind. Clonal growth is possible but does not play an important role in regeneration (Enrico et al., 2004).

We used 76 permanent square sample plots of 900 m<sup>2</sup> each, established throughout the Córdoba Mountains as part of a larger project. We randomly chose areas within vegetation units, which were expected to contain forests or sparse shrublands and stratified the sampling to obtain an even distribution of samples within each altitudinal belt (1400–2500 m a.s.l.). In the field, we located plots using GPS and

selected them for the study when: (1) there was at least one seed tree (defined as individuals 2 m or taller) and (2) all occurring individuals were accessible for measuring (as in Renison et al., 2006). As we intended to monitor regeneration over time – and seed traps affect regeneration – we used separate plots for seed dispersal and regeneration niche studies.

### 2.2. Seed dispersal

In December 2004, we distributed 6 seed traps per plot in and around 20 plots. Seed trap location was random, with the constraint that distances to the stem of the closest seed tree had to be less than 13 m. We considered larger distances unnecessary, as in a preliminary survey we found no seeds in traps further than 6 m from seed trees. Seed traps consisted of a mesh bag of 706 cm<sup>2</sup> circular area, posted 50 cm above the ground. We collected the traps in May 2005, when seed dispersal was over, and discarded 13 broken or fallen traps; so our total sample size was 107 traps. For each trap, we measured the distance to the stems of the three closest seed trees, height of the trees and slope from the trap to the trees.

### 2.3. Regeneration niche

Regeneration was evaluated in two basins (30 and 26 plots, not coincident with the seed trap plots), which differed in their historic land use and conservation status. The first was the well-preserved Los Molles river basin (hereafter called “preserved basin”; 468 ha; 31°58'S, 64°56'W), with no roads or houses and where human activities had been restricted to livestock rearing (mainly cattle and a few goats) at relatively low stocking rates. The second was the Mina Clavero river basin (hereafter called “degraded basin”; 8925 ha; 31°42'S, 64°51'W), which was traversed by a large highway and populated by more than 40 houses—most inhabited by owners of the cattle, sheep, horses and goats, which graze the area at quite high stocking rates (Cáceres, 2001; Cingolani et al., 2004).

Seedling presence was registered in quadrats of 1 m<sup>2</sup>. Five quadrats had fixed locations at the corners and centre of each plot and were used for both plot and quadrat scale analyses (see below). Another five quadrats were randomly located within the plot and were used to better quantify seedling numbers within the plots, and were used only for the plot scale analysis. *P. australis* seedlings were defined as individuals 5 cm or shorter. To determine the relationship between plot characteristics ( $n = 56$  plots) and seedling presence, we registered as indicators of grazing-related disturbance: (1) dung frequency, as estimated by randomly placing 50 squares of 900 cm<sup>2</sup> and registering the presence of fresh cattle, horse, goat and sheep dung; proportional cover of (2) grazing lawn and (3) rock exposed by soil erosion. As topographic variables, we measured: (4) altitude above sea level; (5) slope; (6) aspect and (7) proportion of natural rock outcrop. We also measured the following vegetation characteristics: proportion of (8) thick tussock grassland (*Poa stuckertii*); (9) thin tussock grassland (*Festuca* spp., *Deyeuxia hieronymii* and *Stipa* spp.); (10) ferns and (11) *P.*

*australis* (see Cingolani et al., 2003, 2004 for a detailed vegetation description).

To determine whether seedling occurrence was associated with certain types of microsite characteristics, at the quadrat scale (1 m<sup>2</sup>), we registered: (1) soil erosion in three categories, 0 = no clear presence of erosion, 1 = less than 50% exposed soil, 2 = more than 50% exposed soil. Soil exposed by erosion could be recognized by the presence of bare roots and stones at its surface; (2) local slope inclination (°); (3) sun incidence—visually estimated in the field as the sun's trajectory (°) that directly illuminates the quadrat (i.e. in a flat plateau with no obstacles, the value would be 180, rock outcrops and canopy trees reduced the value); height (cm) of: (4) litter; (5) dead; (6) live vegetation at four randomly chosen points; proportion of (7) mosses; (8) ferns; (9) thick tussocks (*P. stuckertii*); (10) thin tussocks (*Festuca* spp., *D. hieronymii* and *Stipa* spp.); (11) distance (m) to the closest seed tree.

#### 2.4. Data analysis

As seed traps could catch seeds from several seed trees, to derive a seed rain model we selected 50 traps for which seed rain was presumably influenced by only one seed tree. As no seeds dispersed more than 6 m, this included traps with none, or only one tree closer than 6 m. We used Poisson multiple regression with the number of captured seeds/m<sup>2</sup> (ln transformed) as a response variable, and distance, slope to and height of the seed tree as predictor variables. The seed rain predictive model was tested by predicting the number of seeds captured by the 57 remaining traps, which were influenced by more than one seed tree (which we subsequently took into account by adding the contribution of the three closest seed trees). We calculated root mean squared error as  $RMSE = (\sum(OSR_i - PSR_i)^2/n)^{0.5}$  and the average bias of the model as  $BIAS = \sum(OSR_i - PSR_i)/n$ , where  $OSR_i = \ln(\text{Observed Seed Rain}_i + 1)$ ;  $PSR = \ln(\text{Predicted Seed Rain}_i + 1)$ ;  $n$  = number of samples (57 seed traps).

Many of the grazing-related and vegetation variables measured to study the regeneration niche were correlated both at the plot and quadrat scale. We therefore reduced their number to the most relevant variables, performing a principal components analysis (PCA, on a correlation matrix) for each scale, and selecting variables best correlated to as many axes of variation as were needed to explain at least 70% of the loadings. Slope and aspect were used to calculate an index of sun incidence by multiplying slope by the cosine of the aspect. This variable ranged from highly positive values for northerly exposed steep slopes (maximum sun incidence), to highly negative values for southerly exposed steep slopes (minimum sun incidence).

To determine differences between the two basins at the 900 m<sup>2</sup> plot scale ( $n = 30/26$  plots), we used Wilcoxon tests. To determine whether the variance in number of seedlings (mean of the 10 quadrats per plot, ln transformed) was related to altitude above sea level, index of sun incidence, percentage of natural rock outcrop and grazing-related or vegetation variables selected by the PCA, we used Poisson regression. Because

regeneration could be most abundant at intermediate altitudes above sea level, we also included the quadratic term of altitude in the model (Affi and Clark, 1984).

For the analysis at the quadrat scale, as the overall number of quadrats with seedlings was low (34 out of 280), we selected pairs of quadrats with and without seedlings to determine differences in microsite characteristics using paired Wilcoxon tests. For each quadrat with seedlings, we randomly chose a quadrat without seedlings from the database, with the constraints that both quadrats should be comparable in terms of distance to seed tree (<20 cm deviance) and altitude above sea level (<100 m deviance). Priority was given to quadrat pairs from the same plot. To maintain independence, only one quadrat with seedlings was considered for each plot. Using Poisson regressions and step-wise selection procedures we obtained similar results as using the above procedures, but models were somewhat unstable. We used Infostat (2006) statistical package for all analyses and present means  $\pm$  standard deviation (S.D.). Residuals of regression were checked for normality and homocedasticity. Most Wilcoxon tests could have been replaced by *T*-tests, but the results of both tests were similar and for simplicity we report Wilcoxon throughout.

### 3. Results

#### 3.1. Seed rain

Almost 50% of the traps captured at least 1 seed (53 out of 107 traps) with the highest catch being 565 seeds (8003 seeds/m<sup>2</sup>). No seeds were found in traps more than 6 m away from seed trees. Seed rain was negatively associated to distance to nearest seed tree and positively associated to height and slope to the seed tree in the following way:  $\ln(CS + 1) = e^{((-0.336D) + (0.010S) + (0.004H))}$ , where  $CS$  = captured seeds/m<sup>2</sup>,  $D$  = distance to nearest seed tree (m),  $S$  = slope to the nearest seed tree (°) and  $H$  = height of seed tree (cm); all *P*-values were <0.001.

This model explained 66% of the variation in ln transformed captured number of seeds/m<sup>2</sup> (Poisson linear regression:  $R^2 = 0.66$ ;  $\chi^2 = 75.5$ ;  $P < 0.0001$ ). When we used the model to predict seed rain rates for the 57 seed traps influenced by more than one seed tree, and compared them to observed values, the root mean squared error was 3.46 and the bias  $-1.91$ .

#### 3.2. Regeneration niche

We registered a total of 269 *P. australis* seedlings in 560 m<sup>2</sup> (distributed in 56 plots). Seedlings were highly aggregated, as we found no seedlings in 43% of the plots and a record plot of 2.6 seedlings/m<sup>2</sup>. *P. australis* canopy cover and number of seedlings were 3.5 and 4 times higher in the preserved basin than in the degraded basin. Dung frequency and proportion of rock exposed by soil erosion were lower in the preserved basin, while plots in either basin did not significantly differ in altitude above sea level, index of sun incidence or natural rock outcrop (Table 1).

Table 1  
Differences at the plot scale (900 m<sup>2</sup>) between the degraded and the well-preserved river basins

Variable	Degraded <i>n</i> = 26	Preserved <i>n</i> = 30	Wilcoxon test value	<i>P</i>
Density of seedlings (m <sup>-2</sup> )	0.2 ± 0.5	0.7 ± 0.8	615.5	0.030
<i>P. australis</i> canopy cover (%)	7.6 ± 4.2	30.8 ± 31.9	561.5	0.002
Dung frequency	5.7 ± 4.4	4.0 ± 6.8	903.5	0.007
Rock exposed by soil erosion (%)	6.3 ± 5.6	3.5 ± 5.6	887.0	0.011
Altitude above sea level (m)	1927 ± 142	1896 ± 275	736.0	0.935
Index of sun incidence	-9.4 ± 4.5	3.4 ± 3.9	629.0	0.066
Natural rock outcrop (%)	17.7 ± 13.6	21.0 ± 14.3	682.0	0.327

Means ± S.D., test and *P*-value are reported for each measured variable.

Table 2  
Poisson regression between number of seedlings and site variables at the 900 m<sup>2</sup> plot scale

Variable	Regression coefficient	Wald's $\chi^2$ test value	Probability level
<i>P. australis</i> canopy cover	0.0120	4.76	0.03
River basin (categorical)	-0.4707	1.37	0.24
Dung frequency	-0.0791	2.70	0.10
Rock exposed by soil erosion	0.0079	0.05	0.82
Altitude above sea level	0.0007	0.52	0.47
Altitude above sea level <sup>2</sup>	0.0000	0.79	0.37
Index of sun incidence	-0.0101	2.01	0.16
Proportion of natural rock outcrop	0.0064	0.34	0.56

The variable name, regression coefficient, test value and probability level are indicated.

Plot scale grazing-related and vegetation variables could be reduced to three PCA axes, which explained 70% of the variation in the data and were best correlated to the proportion of *P. australis* cover, dung frequency and rock exposed by soil erosion (variables used in the following analyses). At the plot scale, variation in seedling number was significantly associated to the proportion of *P. australis* canopy cover (Poisson regression:  $r^2 = 0.35$ ,  $n = 56$ ,  $P = 0.03$ ), while river basin, dung frequency, rock exposed by soil erosion, altitude above sea level and its quadratic term, index of sun incidence and proportion of natural rock outcrop were not significant (Table 2).

At the quadrat scale, in accordance with seed rain data, seedlings were not found more than 10 m away from seed trees, even though 122 of the 280 quadrats were located at distances greater than 10 m. Microsite soil erosion categories were significantly lower in quadrats with seedlings than in quadrats without seedlings (indexes  $0.53 \pm 0.84$  and  $0.91 \pm 1.05$ , respectively, Wilcoxon paired test,  $n = 64$ ,  $Z = -2.11$ ,  $P = 0.03$ ). No significant differences were found for local slope ( $Z = -0.14$ ,  $P = 0.89$ ) or visual estimation of sun incidence ( $Z = -0.08$ ,  $P = 0.93$ ). Vegetation variables in quadrats with and without seedlings could be reduced to four PCA axes, which explained 80% of the variation in the data and were best correlated to proportion of thin tussocks, height of dead vegetation, proportion of thick tussocks and proportion of mosses. None of the relevant vegetation variables differed significantly between quadrats with or without seedlings (thin tussocks:  $Z = -0.20$ ,  $P = 0.98$ , height of dead vegetation:  $Z = -1.92$ ,  $P = 0.06$ , proportion of thick tussocks:  $Z = -1.00$ ,  $P = 0.32$  and proportion of mosses:  $Z = -0.05$ ,  $P = 0.96$ ).

#### 4. Discussion

We believe our results are representative of the Córdoba Mountains, as the two chosen study basins represent fairly typical habitats, and no conspicuous inter annual variations in seed production have been reported or observed in 9 years of seed collection for reforestation purposes (Renison et al., 2005). Our seed trap experiment showed that *P. australis* seed dispersal was restricted to the close proximity of seed bearing trees and influenced by tree height and slope. As seed number was positively related to tree height, factors which retard growth such as fire use and livestock browsing (Teich et al., 2005; Renison et al., 2006), seem to be the main factors limiting seed rain in our study areas. Higher seed capture rate down slope of seed trees is probably explained by larger fall distances. The model taking into account proximity to seed bearing trees, tree height and slope predicted fairly well seed rain rates (ln seed rain) as shown by values of root mean squared error and the bias. The ln transformation means higher seed rain values are less well predicted, probably due to inter-tree variation in seed productivity due to factors not taken into account in this study, like soil humidity and nutrients, soil compaction and others.

A major methodological problem with seed dispersal studies using traps is that seed traps do not detect long distance dispersal events (Clark et al., 1999; Bullock and Clarke, 2000; Cain et al., 2000). Although we did not measure long distance dispersal events, in concurrence with our seed trap results, the distance between *P. australis* seedlings and the next seed-bearing tree did not exceed 10 m. Still, this result does not rule out the possibility of long distance dispersal events, but shows that these are indeed rare and probably associated with extremes in wind speed, turbulence or updrafts (Tackenberg et al., 2003), or by means of secondary dispersal such as flowing water along streams (personal observation). Our results are in accordance with those of other studies showing that in plants dispersed by wind the pattern of seed rain density is more influenced by the distance to the seed sources than by other factors (Greene and Johnson, 1989; Willson and Traveset, 2000).

Seedlings were more abundant in the preserved basin than in the degraded basin, where *P. australis* canopy cover was lower and indices of historic and current grazing impact were clearly higher. At the 900 m<sup>2</sup> plot scale, seedling number was only associated with *P. australis* canopy cover, a variable mainly



affected by periodic fires and long-term overgrazing, which reduces the transition rates of seedlings to adults due to browsing (Renison et al., 2002b, 2006; Teich et al., 2005). At the 1 m<sup>2</sup> quadrat scale, besides distance to the closest tree, reduced seedling numbers were best explained by presence of soil erosion. Seeds falling in areas with soil erosion are probably washed off before they can germinate. Moreover, surface erosion due to livestock activity in *P. australis* forests leads to increased soil compaction and diminished soil organic matter content (Renison et al., unpublished data), both processes resulting in lower water-holding capacity. Water deficiency is known to reduce germination probability (e.g. Wilson and Witkowski, 1998; Elmarsdottir et al., 2003) and to increase seedling mortality (Williams and Hobbs, 1989; Gobbi and Schlichter, 1998; Topoliantz and Ponge, 2000). In addition, Renison et al. (2005) found lower growth rates of planted *P. australis* seedlings in eroded sites, providing evidence to suggest that soil degradation is indeed a negative factor for seedling establishment. Excluding areas with soil erosion, we found *P. australis* seedlings in a variety of microsites, showing that they may germinate and establish on most surfaces, provided seed rain is abundant. Further work is needed to determine the relative contribution of fires and domestic livestock browsing in each stage of *P. australis* life cycle, and thus be able to determine what livestock managements are compatible with forest conservation.

We conclude that *P. australis* seedling recruitment is highly dependent on the presence of seed trees. In reforestation areas with a lack of such trees, sowing could represent an easy-to-perform measure to enhance seedling emergence, as shown by Cierjacks et al. (2007) for *P. incana* and *P. pauta* in Ecuador. Alternatively, planting could be carried out (Renison et al., 2005). Furthermore, seed trees must be protected by reducing fires and their seedling growth into adults must be promoted by reducing or excluding livestock stocking rates (Renison et al., 2002b; Teich et al., 2005).

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