



Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina

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Abstract

Polylepis australis woodlands range from northern to central Argentina. They support a high number of endemisms (both plants and animals) and constitute the main cover type in watersheds contributing to retain soil and catch water. Natural regeneration of *P. australis* in the Córdoba mountains, Argentina, was studied in two communities dominated by *P. australis*: shrublands and woodlands. The main objectives of the study were: (1) to characterize shrublands and woodlands in terms of physical (physical and chemical soil properties) and biological (*Polylepis*' growth form, fern and moss cover) characteristics; (2) to describe *P. australis*' soil seed bank and compare seedling and sapling establishment between both communities. The presence of seedlings as well as saplings was quantified, and soil samples were taken so as to characterize the seed bank.

Results showed significant differences in habitat conditions between shrublands and woodlands. Seedlings' density was higher in the shrublands, while no differences appeared regarding the sapling numbers. A negative correlation was found between seedling numbers and total community cover as well as mosses and ferns cover. Seed density in the soil bank was higher in the woodlands, but overall seed viability was less than 5%. In the shrublands, the most critical stage of the species regeneration cycle was the transition from seedling to sapling, while in the woodlands the main "filter" occurred during seed germination. The low number of saplings observed in both units suggests a stagnation of *P. australis* regeneration, which could be translated into an unlikely expansion of the species throughout the Córdoba mountains.

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1. Introduction

The understanding of natural regeneration of plant species is an important topic in conservation and management (Guariguata and Pinard, 1998). Regeneration involves several stages of the life cycle of plants, such as seed production and seedling or sapling

establishment and survival. Seed (e.g. seed dispersal or seed bank) and seedling (or sapling) stages have been recognized as the most important stages in the regeneration (Houle, 1991, 1994; Kitajima and Fenner, 2000). Many factors, both biotic and abiotic exert the primary control of seedling recruitment (Kitajima and Fenner, 2000). Soil properties (Facelli, 1994), light availability (Rooney et al., 2000), plant cover (Kitzberger, 1995; Dobrowolska, 1998), the presence of bryophytes and ferns (St. Hilaire and Leopold, 1995; Gobbi and Schlichter, 1998) and the formation of a soil

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seed bank (Harper, 1977) have been considered important factors in the establishment and survival of tree seedlings. In some temperate woodlands the dominant tree species do not seem to maintain a persistent reserve of seeds in the soil (Pickett and McDonnell, 1989; Houle, 1992, 1994; Moles and Drake, 1999).

Seed production/viability and seedling/sapling establishment may show difficulties in tree populations growing above the timber-line (Crawford, 1989; Wardle, 1971; Wardle and Coleman, 1992) or at the latitudinal boundary of the species' range (García et al., 1999) where temperature and water availability often limit the viability of plant populations. Temperature and water availability can have marked effects on mortality of individuals, especially those in juvenile stages, and by depressing reproductive capacity due to severe reduction in the production of fertile, filled seeds (García et al., 1999, 2000; and references therein).

The genus *Polylepis* (Rosaceae) comprises 20 species of trees distributed in South America, in Andean and extra-Andean mountains from Venezuela to Argentina. In many areas of the Andes, these species are the major or even the only component of the tree canopy above the treeline (Hensen, 1994; Fjeldså and Kessler, 1996). Some of these taxa are the tree species inhabiting the highest altitudes in the world (Hensen, 1994). The southernmost species of the genus is *Polylepis australis* ("tabaquillo"), that ranges from northern (Jujuy province) to central (Córdoba province) Argentina (Cantero and Bianco, 1987). *P. australis* woodlands comprise rather isolated patches located in deep ravines (locally known as *quebradas*) where microclimatic conditions are more favourable; more open patches of shrublands occur in more exposed sites near summits (Cabido and Acosta, 1986). *Polylepis* woodlands are important because they support a high number of endemisms (both plants and animals) and also because they are the main cover type in watersheds contributing to retain soil and catch water (Fjeldså and Kessler, 1996). Despite their importance, these forests have been reduced to isolated patches as a consequence of intentional burning, browsing by livestock and logging for timber and fuel (Cabido and Acosta, 1985; Fjeldså and Kessler, 1996). The protection and restoration of *Polylepis* forests and woodlands has been declared as a priority by the "World Conservation Monitoring Center" (Hjarsen,

1997). However, no study has yet evaluated the natural regeneration of this species in order to promote the conservation and management of its populations.

Taking into account the floristic composition and structure, Cabido and Acosta (1985) recognized two communities where *P. australis* is the dominant species: shrublands and woodlands. In general, shrublands are more exposed to wind and frosts than woodlands, which occur in protected quebradas. Besides their habitats, woodlands and shrublands also differ in species composition. Cabido and Acosta (1985) suggested successional relationships between woodlands and shrublands sharing similar habitats. It is likely that shrublands result after disturbance (fire and logging) on mature woodlands. However, different environmental conditions in ravines and exposed sites may preclude the establishment of woodlands or shrublands. Those differing conditions should affect *Polylepis*' regenerative characteristics. This paper addresses the following questions concerning the regenerative characteristics of *P. australis* at the southern limits of its range: (1) Is there a difference in seedling establishment and recruitment strategies in the woodlands and shrublands of *P. australis*? (2) Are those differences related to site differences and nature of associated vegetation growing in different sites? We specifically aimed to: (1) characterize shrublands and woodlands in terms of physical (e.g. soil properties) and biological (e.g. *Polylepis*' growth form) characteristics; (2) describe the seed bank and the recruitment of seedlings and saplings in populations of *P. australis* in shrublands and woodlands.

2. Methods

2.1. Study area

The study area is located in the National Park Quebrada del Condorito, in the Córdoba mountains, central Argentina (approximately 31°35'S, 64°45'W, 2100 m a.s.l.). The climate is subhumid, with short, cool summers and long, cold winters (Capitanelli, 1979). The mean annual temperature is 8 °C, and the annual rainfall (mostly concentrated in the warm season) is 840 mm (Cabido et al., 1987).

The vegetation consists of a mosaic of different plant communities. Tall-tussock grasslands and grazing

lawns predominate in the more exposed “pampas” (local name for high altitude plains) while *Polylepis* woodland is the main cover type in deep ravines (“quebradas”) (Cabido et al., 1987). In these woodlands individuals of *P. australis* up to 5–7 m tall may conform an almost continuous canopy with cover

ranging from 90 to 100%. In more exposed sites in upper slopes and rocky summits, shrublands with individuals of “tabaquillo” of 1–3 m tall and cover ranging from 50 to 90% are found (Cabido and Acosta, 1985, 1986; Acosta, 1986). Stands information and tree characteristics are outlined in Fig. 1.

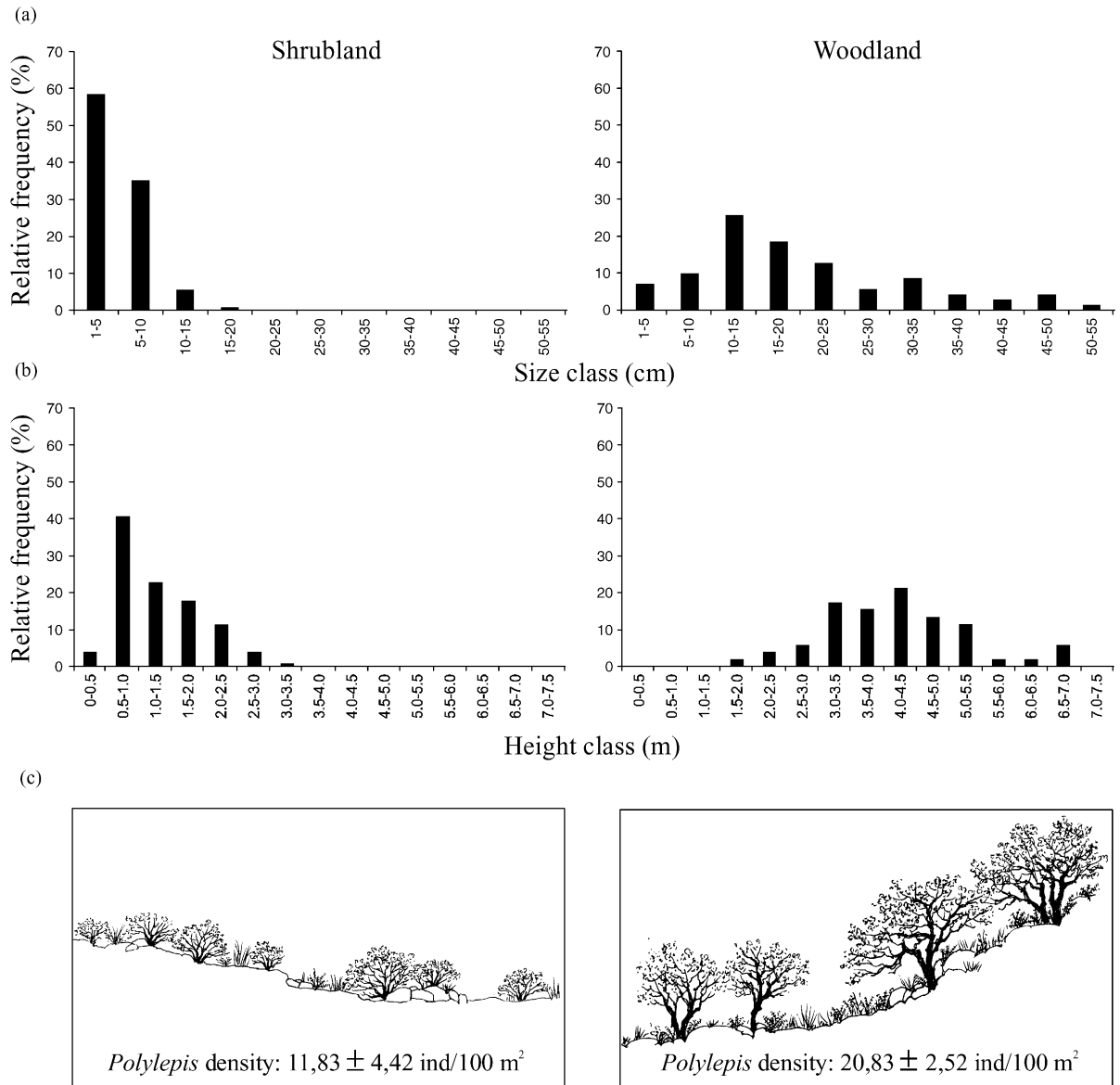


Fig. 1. Structural characteristics of *P. australis* shrublands and woodlands in the mountains of central Argentina: (a) size classes, (b) height classes, and (c) schematic profile showing the characteristic physiognomy of *P. australis* shrublands (left) and woodlands (right).

2.2. Data collection

We arbitrarily positioned twelve 10 m × 10 m replicates (six in woodlands and six in shrublands stands) so as to maximize ecologic and floristic homogeneity in quadrat characteristics. Stands selected were located at similar altitudes, under the same macroclimate. Since all the sites are located within a National Park, they are excluded to grazing by domestic herbivores.

2.3. Soil and stands characteristics

Ten composite soil samples (10 cm depth) were collected from each 10 m × 10 m quadrat. Samples were taken with a soil corer 5 cm in diameter. For each soil sample, texture (percent of sand, silt and clay) (Day, 1986) and organic matter content (Nelson and Sommers, 1996) were estimated. Samples were subjected to the following chemical analyses (Sparks, 1996): organic C (Walkley–Black); total N (Kjeldahl); pH in water 1:25; Ca⁺⁺, Mg⁺⁺, Na⁺ and K⁺ and total P (Bray and Kurtz). *Polylepis* foliage cover (projection of canopy cover) was also recorded. In order to characterize *Polylepis* growth form in both woodland and shrubland units, total height and height of first branch for all individuals within each 10 m × 10 m quadrat was recorded. Due to the obvious differences in total height between shrublands' and forests' trees, number of stems per individual was measured at 0.5 m height in shrublands and 1.3 m height in forests, as a more descriptive indicator of growth habit.

In order to correlate seedling abundance with biotic characteristics, fern and moss cover and total community cover were recorded within each of sixty 2 m × 2 m (five in each 10 m × 10 m quadrat), using the following scale—1: 1–20%, 2: 21–40%, 3: 41–60%, 4: 61–80% and 5: 81–100% cover. Within these same quadrates, seedlings and saplings were counted (see below).

2.4. Population regeneration

Polylepis' species can regenerate vegetatively as well as by seeds (Hensen, 1994; Renison and Cingolani, 1998). In the study site, the percentage of asexual reproduction was estimated by counting vegetative seedlings and saplings ("ramets"). However, asexual reproduction was finally not considered because of its

low incidence in population regeneration (less than 5% of total seedlings plus saplings established).

According to Acosta (1986) in our study area height correlates significantly with age and size classes in *P. australis*. Hence, height was used to establish the regenerative classes (sapling and seedling) in this study. Saplings (individuals ≤50 cm but >15 cm tall) and seedlings (individuals ≤15 cm tall) were inventoried in five quadrats (2 m × 2 m) positioned in the corners and the centre of each of the 10 m × 10 m quadrats.

In order to describe the seed bank, adjacent to each of the 4 m² quadrats, soil samples (10 cm diameter, 10 cm depth) were taken. The seed bank was collected in autumn (after the seed rain) and in spring (after seed germination and before new seed dispersal). The soil samples were sieved through a 1 cm mesh sieve, in order to remove plant fragments and stones. The soil was then sorted under a magnifying glass (5×) in order to separate the *Polylepis* seeds. These seeds were tested for viability through two treatments. Firstly, all seeds were placed in a controlled-environment chamber (alternating temperatures of 20 °C/30 °C and 12 h/12 h photoperiod) and watered during 1 month for germination. Seeds were treated with a solution of fungicide in order to prevent fungal infection. Secondly, the remaining seeds (those that did not germinate) were divided into two groups. One set of 400 seeds (100 for shrublands and woodlands from autumn and spring) were dissected by hand in order to detect the development of embryo (apparently intact or empty). All the remaining seeds (65 and 34 for shrublands in autumn and spring, respectively, and 100 for woodlands both in autumn and spring) were tested for viability through the flotation/sink method. Seeds were placed in a recipient with water for 1 week. This is appropriated to estimate seed viability in *Polylepis* since the viable seeds sink (Kopta, 1986).

The presence of a seed bank was assumed if the majority of the seeds in the soil were viable. The seed banks were classified according to Thompson and Grime (1979), taking into account their annual dynamics through the comparison of autumn and spring viable seed densities in the soil.

2.5. Data analysis

Differences in stand characteristics (soil properties, *Polylepis* cover and height of first branch) between

shrubland and woodland were tested using the Mann–Withney non-parametric test (Sokal and Rohlf, 1995). Differences in sapling, seedling and seed (both dates) densities between shrubland and woodland and within each community were also tested using the Mann–Withney non-parametric test. Spearman correlation (Sokal and Rohlf, 1995) was used to relate the seedling density and habitat characteristics (community cover and fern and bryophyte cover).

3. Results

3.1. Stand characteristics

There were differences in soil physical and chemical properties between shrublands and woodlands. The sand percentage in the soil was significantly higher in the shrublands than in the woodlands. The proportions of lime, clay, organic matter, N, P, Ca, Mg and K were significantly higher in the woodlands (Table 1). There were also differences in *Polylepis* growth form and

cover between units. *Polylepis* cover and height of the first branch were significantly higher in woodland stands, but the number of stems per individual was higher in the shrublands (Table 1).

3.2. Population regeneration

Seedlings and saplings density were higher in shrublands than in woodlands. However, significant differences were only detected in seedling density (Table 2). A negative correlation was found between seedling number and total community cover ($r = -0.4606$, $P < 0.0001$) and fern and bryophytes cover ($r = -0.5048$, $P < 0.0001$, Spearman correlation). In shrublands the 90.44% of seedlings were present under an adult individual of *Polylepis*.

The total soil seed density (viable plus non-viable seeds) of *Polylepis* was significantly higher in the woodland, both in autumn and spring (Fig. 2). However, very low percentage of viable seeds was found in both units and dates (Table 3). Both in shrublands and woodlands and in both dates, the majority of seeds

Table 1
Major abiotic and biotic characteristics of the stands of *P. australis* shrublands and woodlands in the mountains of Córdoba, central Argentina^a

	Shrublands	Woodlands	Significant
Sand (%)	80.63 ± 1.09	52.88 ± 1.65	**
Lime (%)	13.43 ± 0.78	33.67 ± 0.92	**
Clay (%)	5.93 ± 0.39	13.45 ± 0.77	**
Organic matter (%)	5.97 ± 0.93	12.12 ± 0.85	**
Organic C (%)	3.47 ± 0.54	7.05 ± 0.49	**
N, total (%)	0.24 ± 0.06	0.69 ± 0.1	*
P (mg kg ⁻¹)	16.6 ± 2.25	37.65 ± 4.57	**
pH	4.49 ± 0.18	4.36 ± 0.08	NS ^b
Ca ²⁺	6.83 ± 1.03	14.2 ± 1.71	*
Mg ²⁺	0.94 ± 0.27	4.61 ± 0.67	**
Na ⁺	0.32 ± 0.02	0.28 ± 0.01	*
K ⁺	0.36 ± 0.05	0.78 ± 0.08	**
<i>Polylepis</i> cover (%)	40 ± 11.11	85.83 ± 7.24	**
Height first branch (cm)	0.88 ± 0.26	33.42 ± 3.92	***
Number of stems per individual	23.63 ± 0.97	3.72 ± 0.32	***

^a Mean values ± S.E. ($n = 6$, except height for first branch and stem number $n = 125$ in shrublands, $n = 71$ in woodlands).

^b Not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

Table 2
Seedlings and saplings density (no. per meter square) ± S.E. ($n = 30$) of *P. australis* in shrublands and woodlands in the mountains of central Argentina

	Shrublands	Woodlands	Significant
Seedling (no. per meter square)	1.133 ± 0.355	0.025 ± 0.018	***
Sapling (no. per meter square)	0.043 ± 0.025	0.008 ± 0.008	NS ^a

^a Not significant.

*** $P < 0.001$.

Table 3
Percentage of *P. australis* viable seeds in soil samples collected in shrublands and woodlands in autumn and spring^a

	Autumn		Spring	
	Shrublands	Woodlands	Shrublands	Woodlands
Germination (%)	1.5 (201)	2.4 (942)	0 (147)	1.2 (557)
Sink (%)	1.5 (65)	3 (100)	3 (34)	5 (100)

^a Total number of seeds indicated in parentheses. Details of methods in the text.

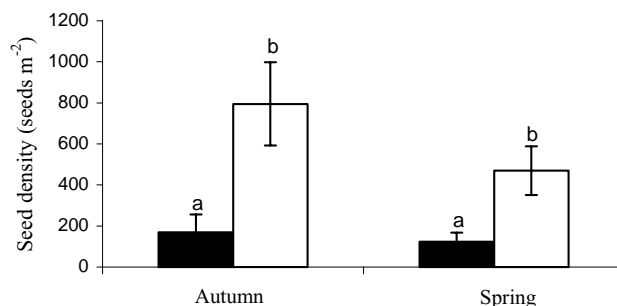


Fig. 2. Seed bank density (no. of seeds per meter square), plus S.E. ($n = 30$) of *P. australis* from shrublands and woodlands in autumn and spring. Different letters indicate significant differences ($P < 0.01$) in the mean values of seed banks between shrublands (■) and woodlands (□).

were empty (71 and 72% in shrublands and 68 and 73% in woodlands for autumn and spring, respectively).

4. Discussion

Environmental conditions differ in *P. australis* shrublands and woodlands. Soils of shrublands showed a higher percentage of sand and lower percentage of lime, clay and organic matter than woodlands as well as N, P, Ca, Mg and K. Taking into account these characteristics, shrubland habitats could be considered as less suitable for the development of *P. australis*. This is in agreement with the results reported by Cabido and Acosta (1985) with respect to the unfavourable conditions prevailing in shrubland habitats.

The presence of basal branches may have adaptive value in individuals growing under water stress (Gibson, 1996) and in habitats more exposed to wind, snow and frosts like timber-lines where they develop as stunted or twisted trees referred to as *Krummholz* (German, *krumm* = twisted, *Holz* = wood) (Wardle, 1971; Wardle and Coleman, 1992; Crawford, 1989; Archibold, 1995). Barrera et al. (2000) have reported differences in growth form of *Nothofagus pumilio* in Tierra del Fuego, Argentina, that quite resemble those we have seen for *P. australis*. They attributed these growth form differences to factors, which affect water availability, length of the growing period, occurrence of early frosts, mechanical impact of snow and biological processes such as foliar phenology, radial growth and decomposition rates. Moreover, Jóbbagy and Jackson (2000) in an integral study of forest line elevation in northern and southern hemispheres, pointed that

temperature during the cold part of the year is the main factor affecting the dominant life form of trees.

Woodlands and shrublands showed differences in regeneration characteristics. The seedling density was higher in shrublands. This may be explained in part by the high cover of mosses and ferns in woodlands, where we found a low number of seedlings. Marrs and Lowday (1992) and Lowday and Marrs (1992) reported an enhancement in the establishment of new species after the removal of *Pteridium* individuals or litter from the community in a *Calluna* heath and a grass heath in Breckland (UK). Gliessman and Muller (1978) reported inhibition of growth in many southern California's plant species under the presence of ferns, probably related to the liberation of allelopathic compounds. Water extracts from bracken fern significantly reduced growth, germination, or both in competing herbaceous vegetation (Gliessman and Muller, 1972). The phytotoxic principle was suspected to be a phenolic compound. On the other hand, Den Ouden (2000) showed that the inhibition of tree regeneration by bracken (*Pteridium aquilinum*) in Dutch forest habitats was due to a combination of factors, especially structural and mechanical properties of bracken vegetation and the habitat function of bracken for seed predated rodents. On the other hand, it is well known that dense litter can inhibit colonization by other species (Grime, 1979). In the woodland unit, there is a dense deposit of litter of Pteridophytes mainly composed of *Polystichum montevidense* and *Blechnum penna-marina* (Cabido and Acosta, 1985). This high litter deposition could be due to the slow leaf decomposition rate showed by both fern species, perhaps related to the presence of qualitative

secondary compounds with specific effects on decomposition processes (Pérez-Harguindeguy et al., 2000). Thus, in woodlands sites there could be an effect of chemical inhibition as well as physical inhibition of *Polylepis*' germination by ferns.

Most of the seedlings were found beneath adult individuals of *Polylepis* which may exert a nurse effect. Nurse effect of adult trees on seedlings of the same species is characteristic of dry or stressing habitats (Kitzberger, 1995; Callaway and Davis, 1998). Thus, in temperate timber-lines of the southern Andes as well as in New Zealand, regeneration can only take place under the parent's canopy, due to a higher sensitivity of seedlings than adults to adverse conditions (Crawford, 1989).

Sapling density did not differ significantly between shrublands and woodlands. This suggests a high seedling mortality in shrublands, probably due to the abiotic characteristics of these stands. Sudden freezing and severe drought, may diminish the survival of seedlings (Wardle, 1971; Wardle and Coleman, 1992; Kitajima and Fenner, 2000). Therefore, the passage from seedling to sapling could be a "filter phase" (Houle, 1996; Houle et al., 2001) which limits the recruitment of *Polylepis* in shrublands.

The soil seed density was higher in woodland sites both in autumn and spring. This might be related to two factors. Firstly, seed production should be higher in woodlands taking into account the greater size of individuals, in relation to smaller individuals in shrublands. Crawley (1997) reported a positive relation between the size of individuals and the production of seeds for several plants species. In *P. australis*, Renison and Cingolani (1998) have determined that trees growing in woodlands provide better seeds than those growing isolated. Secondly, pre- and post-dispersal seed predation has been reported as the more important factor responsible for seed bank depletion (Hulme, 1998; Crawley, 2000). Moreover, according to the findings of Santos and Tellería (1994), pre- and post-dispersal seed predation should be higher in the shrubland stands where seeds are supposed to be more accessible for predators. Shrublands are in more tight contact with tall-tussock grasslands where rodents (murids, ctenomyds and cavid) live. Mice are the main responsible for post-dispersal seed predation and seed banks depletion (Edwards and Crawley, 1999; Crawley, 2000).

We found that most of the seeds from woodlands and shrublands were not viable. Renison and Cingolani (1998) have reported low viability (6–16% viability) for a neighbouring site. Taking into account these results, the potential effect of seed banks on population regeneration could be minimized. This pattern of high non-viable or empty seeds is characteristic of tree populations growing above the timberline (Crawford, 1989) or at the limit of a species range (García et al., 2000). In the case of *P. australis*, this high percentage of non-viable seeds could be the expression of its latitudinal and altitudinal range.

The seed phase of the life cycle is especially important because seeds may be the means by which new areas are colonized (by seed dispersal or from the seed bank) and because seed production (or viable seeds produced) may limit population growth (Valverde and Silvertown, 1995). The knowledge of this characteristic is very important for the conservation and management of plant species. It is known that abiotic and biotic factors act as a series of filters operating sequentially from the seed to the adult stage, and that the environmental filters acting on the germination stage are those that determine the spatial patterns of recruitment (Houle, 1996). In the case of *P. australis*, our results show that there are different "filtering" phases in population regeneration, both in woodlands and shrublands. In both communities the seed-to-seedling transition appears as the more crucial "filter" phase. Besides, the passage from seedling to sapling (apparent seedling mortality) is critical in shrublands. In conclusion, taking into account the relative lack of natural recruitment from seed bank and relatively low density of seedlings and saplings mainly in woodlands, we strongly recommend promoting reforestation activities in the region, in order to conserve the populations of *P. australis* at the boundary of its geographic range, with the subsequent preservation of habitats for endemisms and protection of watersheds in Córdoba mountains.

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References

- Acosta, A., 1986. Estructura poblacional de *Polylepis australis*. In: MAB 6, Programa de investigación integrada y entrenamiento en la región andina y montañas extra-andinas. UNESCO/MAB-PNUMA-CERNAR, pp. 392–402.
- Archibald, O.W., 1995. Ecology of World Vegetation, 1st ed. Chapman & Hall, London.
- Barrera, M.D., Frangi, J.L., Richter, L.L., Perdomo, M.H., Pinedo, L.B., 2000. Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina. *J. Veg. Sci.* 11, 179–188.
- Cabido, M., Acosta, A., 1985. Estudio fitosociológico en bosques de *Polylepis australis* Bitt. (Tabaquito) en las Sierras de Córdoba, Argentina. *Documents Phytosociol.* 9, 385–400.
- Cabido, M., Acosta, A., 1986. Bosques de *Polylepis australis*. In: MAB 6, Programa de investigación integrada y entrenamiento en la región andina y montañas extra-andinas. UNESCO/MAB-PNUMA-CERNAR, pp. 384–392.
- Cabido, M., Breimer, R., Vega, G., 1987. Plant communities and associated soil types in a high plateau of the Córdoba mountains, central Argentina. *Mountain Res. Dev.* 7, 25–42.
- Callaway, R.M., Davis, F.W., 1998. Recruitment of *Quercus agrifolia* in central California: the importance of shrub dominated patches. *J. Veg. Sci.* 9, 647–656.
- Cantero, J.J., Bianco, C.A., 1987. El límite austral de *Polylepis australis* Bitt. (Tabaquito) en la R. Argentina. *Parodiána* 5, 65–71.
- Capitanelli, R., 1979. Clima. In: Vázquez, J., Miatello, R., Roque, M. (Eds.), Geografía Física de la Provincia de Córdoba. *Bol. Buenos Aires*, pp. 213–296.
- Crawford, R.M.M., 1989. Studies in plant survival. In: *Ecological Case Histories of Plant Adaptation to Adversity*. Blackwell, Oxford, Chapter 4, 296 pp.
- Crawley, M.J., 1997. Sex. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell, Oxford, pp. 156–213.
- Crawley, M.J., 2000. Seed predators and plant population dynamics. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 167–182.
- Day, P.R., 1986. Particle fractionation and particle-size analysis. In: Black, C.A. (Ed.), *Methods of Soil Analysis. Part I*. American Society of Agronomy/Soil Science Society of America, Madison, WI, USA, pp. 545–567.
- Den Ouden, J., 2000. The role of bracken (*Pteridium aquilinum*) in forest dynamics. Ph.D. Thesis. Wageningen University, Wageningen, 218 pp.
- Dobrowolska, D., 1998. Structure of silver fir (*Abies alba* Mill.) natural regeneration in the 'Jata' reserve in Poland. *For. Ecol. Manage.* 110, 237–247.
- Edwards, G.R., Crawley, M.J., 1999. Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 91, 360–364.
- Facelli, J.M., 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* 75, 1727–1735.
- Fjeldsá, J., Kessler, M., 1996. Conserving the Biological Diversity of *Polylepis* Woodlands of the Highland of Peru and Bolivia, 1st ed. Nordeco, Denmark, 250 pp.
- García, D., Zamora, R., Hódar, J.A., Gómez, J.M., 1999. Age structure of *Juniperus communis* L. in the Iberian peninsula: conservation of remnant populations in Mediterranean mountains. *Biol. Conserv.* 87, 215–220.
- García, D., Zamora, R., Gómez, J.M., Jordano, P., Hódar, J.A., 2000. Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J. Ecol.* 88, 436–446.
- Gibson, A.C., 1996. Structure–Function Relations of Warm Desert Plants. Springer-Verlag, Berlin, 216 pp.
- Gliessman, S.R., Muller, C.H., 1972. The phytotoxic potential of bracken, *Pteridium aquilinum* (L.) Kuhn. *Madroño* 21, 299–304.
- Gliessman, S.R., Muller, C.H., 1978. The allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. *J. Chem. Ecol.* 4, 337–362.
- Gobbi, M., Schlichter, T., 1998. Survival of *Austrocedrus chilensis* seedlings in relation to microsite conditions and forest thinning. *For. Ecol. Manage.* 111, 137–146.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester, 222 pp.
- Guariguata, M.R., Pinard, M.A., 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: implications for natural forest management. *For. Ecol. Manage.* 112, 87–99.
- Harper, J.L., 1977. *Population Biology of Plant*. Academic Press, London.
- Hensen, I., 1994. Estudios ecológicos y fenológicos sobre *Polylepis bessi* Hieron en la Cordillera Oriental Boliviana. *Ecología en Bolivia* 23, 21–32.
- Hjarsen, T., 1997. The effects of plantations in the Andes. *Trop. For. Update* 7, 15.
- Houle, G., 1991. Regenerative traits of tree species in a deciduous forest of northeastern North America. *Holarctic Ecol.* 14, 142–151.
- Houle, G., 1992. The reproductive ecology of *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in the Taranté Ecological Reserve, Québec. *J. Ecol.* 80, 611–623.
- Houle, G., 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species—*Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. *J. Ecol.* 82, 39–53.
- Houle, G., 1996. Environmental filters and seedling recruitment on a coastal dune in subarctic Quebec (Canada). *Can. J. Bot.* 74, 1507–1513.
- Houle, G., McKenna, M.F., Lapointe, L., 2001. Spatiotemporal dynamics of *Floerkea proserpinacoides* (Limnanthaceae), an annual plant of the deciduous forest of eastern North America. *Am. J. Bot.* 88, 594–607.
- Hulme, P., 1998. Post-dispersal seed predation and seed bank persistence. *Seed Sci. Res.* 8, 513–519.

- Jóbbagy, E.G., Jackson, R.B., 2000. Global controls of forest line elevation in the northern and southern hemispheres. *Glob. Ecol. Biogeogr.* 9, 253–268.
- Kitajima, K., Fenner, M., 2000. Ecology of seedling regeneration. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CAB International, Wallingford, UK, pp. 331–359.
- Kitzberger, T., 1995. Fire regime variation along a northern patagonian forest steppe gradient: stand and landscape response. Ph.D. Thesis. University of Colorado, Boulder, 203 pp.
- Kopta, R., 1986. Estudios sobre la germinación de *Polylepis australis*. In: MAB 6, Programa de investigación integrada y entrenamiento en la región andina y montañas extra-andinas. UNESCO/MAB- PNUMA-CERNAR, pp. 402–403.
- Lowday, J.E., Marrs, R.H., 1992. Control of bracken and the restoration of heathland. III. Bracken litter disturbance and heathland restoration. *J. Appl. Ecol.* 29, 212–217.
- Marrs, R.H., Lowday, J.E., 1992. Control of bracken and the restoration of heathland. II. Regeneration of the heathland community. *J. Appl. Ecol.* 29, 204–211.
- Moles, A.T., Drake, D.R., 1999. Potential contributions of the seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *NZ J. Bot.* 37, 83–93.
- Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Sparks, D.L. (Ed.), *Methods of Soil Analysis. Part 3. Chemical Methods*. ASA/SSSA/CSSA, Madison, WI, Chapter 34, pp. 961–1010.
- Pérez-Harguindeguy, N., Vendramini, F., Díaz, S., Cabido, M., Cornelissen, J.H.C., Gurvich, D., Castellanos, A., 2000. Descomposición y caracteres foliares de especies de Pteridófitas y angiospermas del Chaco Serrano de Córdoba, Argentina. *Kurtziana* 28, 35–44.
- Pickett, S.T.A., McDonnell, M.J., 1989. Seed bank dynamics in temperate deciduous forest. In: Leck, M.A., Parker, V.P., Simpson, R.L. (Eds.), *Ecology of Soil Seed Banks*. Academic Press, San Diego, pp. 123–147.
- Renison, D., Cingolani, A.M., 1998. Experiencias en germinación y reproducción vegetativa aplicadas a la reforestación con *Polylepis australis* (Rosaceae) en las Sierras Grandes de Córdoba, Argentina. *Agroscientia* 15, 47–53.
- Rooney, T.P., McCormick, R.J., Solheim, S.L., Waller, D.M., 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper great lakes, USA. *Ecol. Appl.* 10, 1119–1132.
- Santos, T., Tellería, J.L., 1994. Influence of forest fragmentation on seed consumption and dispersal of Spanish juniper. *Biol. Conserv.* 70, 129–134.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*. Freeman, New York.
- Sparks, D.L., 1996. *Method of Soil Analysis. Part 3. Chemical Methods*. ASA/SSSA/CSSA, Madison, WI.
- St. Hilaire, L., Leopold, D.J., 1995. Conifer seedling distribution in relation to microsite conditions in a central New York forested minerotrophic peatland. *Can. J. For. Res.* 25, 261–269.
- Thompson, K., Grime, J.P., 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.* 67, 893–921.
- Valverde, T., Silvertown, J., 1995. Spatial variations in the seed ecology of a woodland herb (*Primula vulgaris*) in relation to light environment. *Funct. Ecol.* 9, 942–950.
- Wardle, P., 1971. An explanation for alpine timberlines. *NZ J. Bot.* 9, 371–402.
- Wardle, P., Coleman, M.C., 1992. Evidence for rising upper limits of four native New Zealand forest trees. *NZ J. Bot.* 30, 303–314.