
The Restoration of Degraded Mountain Woodlands: Effects of Seed Provenance and Microsite Characteristics on *Polylepis australis* Seedling Survival and Growth in Central Argentina

Daniel Renison,^{1,2} Ana M. Cingolani,³ Ricardo Suarez,⁴ Eugenia Menoyo,⁴ Carla Coutsiere,⁴ Ana Sobral,⁴ and Isabell Hensen⁵

Abstract

South American high-mountain ecosystems are greatly influenced by human disturbance. In the mountains of Córdoba, Argentina, *Polylepis australis* (Rosaceae) woodlands are currently highly fragmented and subject to extensive burning and livestock grazing, resulting in severe changes of habitat characteristics, which hamper natural regeneration. In order to find out how to achieve successful reforestation, we compared *P. australis* seedling survival and growth and the development of a shrubby habit for two seed provenances and different planting microsites. Survival of planted seedlings after 5 years was 70%, with most deaths (19%) in the first year and declining mortality with ongoing establishment. Survival did not show any relationship with seed provenance or microsite characteristics. Height growth averaged 34.6 ± 1.2 cm in

5 years. Seedlings produced from seeds collected in a well-preserved woodland grew taller and showed a higher tendency for development of shrubby habit than those produced from seeds collected in a degraded woodland. Seedlings planted in more degraded microsites with exposed soil or rock due to past grazing pressure grew less and developed a more shrubby habit than those planted in better preserved microsites. Our results show that restoration of degraded areas with *P. australis* is possible and that there is potential to improve restoration success with a careful selection of seed provenance and planting microsites.

Key words: microsite variation, mountain woodlands, *Polylepis australis*, reforestation, seed provenance, seedling growth, seedling survival, shrub habit.

Introduction

Humans have greatly changed the appearance of mountain forest ecosystems, reducing and fragmenting the forest landscape through burning, cutting, and livestock rearing (Ellenberg 1979; Spies 1998; Zak & Cabido 2002). Forest reduction and fragmentation is usually accompanied by changes in floral and faunal composition, loss of litter cover, compaction of soils, reduction in soil moisture, and increases in soil erosion. As a consequence, the forest ecosystem functions of retaining and cycling limiting resources, such as water and nutrients, and the maintenance of biodiversity may be seriously affected. In these cases, the recovery of the forest is desirable (Yates et al. 2000; Kauffman et al. 2003).

When anthropogenic modifications are long-lasting and widespread, there may be little potential for a natural or assisted recovery due to the following causes: (1) if seed dispersal is limited, seed rain can be diminished due to the low density of the remaining trees (Holl & Kappelle 1999); (2) anthropogenic transformations of the habitat may prevent seedling establishment because environment and soil characteristics are no longer adequate for the original species (Amaranthus & Perry 1987; Aide & Cavellier 1994; Fiedler & Laven 1996; Yates et al. 2000); (3) seeds developed in degraded and/or highly grazed areas may be smaller or lighter (Cierjacks & Hensen 2004), which in turn can negatively influence seedling establishment and growth rate (Tripathi & Khan 1990; Hendrix et al. 1991; Milberg et al. 1996, 1998); and (4) seed viability can be diminished with the degradation of the soil around the mother plant (Renison et al. 2004).

Consequently, degraded areas are commonly planted with alien tree species, which are often more successful. The advantages aliens can have over natives are that they grow more rapidly in a wide range of sites, they are easier to manage silviculturally, their seeds are genetically improved and readily available, and they are better studied

¹ Cátedra de Ecología General, Universidad Nacional de Córdoba, Argentina

² Address correspondence to D. Renison, email drenison@com.uncor.edu

³ Instituto Multidisciplinario de Biología Vegetal, CONICET-UNC, Argentina

⁴ Proyecto Conservación y Reforestación de las Sierras de Córdoba, Argentina

⁵ Martin-Luther-University Halle-Wittenberg, Institute of Geobotany and Botanical Garden, Germany

than native trees (Richardson 1998). However, alien tree species often do not supply the ecosystem services provided by natives and may negatively affect the environment and biodiversity (Poore & Fries 1987) or may invade non-planted areas (McEvoy & Coombs 1999). If native species are to be established in degraded areas, it is necessary to develop appropriate techniques. In particular, quick and effective restoration procedures are especially important in most degraded South American mountains, where human populations depend on the mountains for livestock rearing and water supply.

Restoration of the high-mountain *Polylepis* woodlands of South America has been highly recommended by the World Conservation Monitoring Centre because they belong to one of the most endangered woodland ecosystems in the world (UNEP-WCMC 2004). Moreover, *Polylepis* woodlands provide important ecosystem services and contain a high proportion of endemic species (Fjeldså 1993; Hensen 1995; Fernández & Ståhl 2002). With the objective of contributing to their conservation, we began a reforestation project in the high Córdoba mountains, Argentina, in an anthropogenically degraded *Polylepis australis* woodland area. Since the beginning of the project, techniques to optimize the restoration process have been developed (Renison & Cingolani 1998, 2002; Renison et al. 2002a). In the present communication we further develop restoration techniques by (1) characterizing the microsites where we planted the seedlings according to natural and human-induced habitat variation; (2) determining the combined effects of seed provenance and seedling microsite characteristics on reforestation success; and (3) discussing the implications of these studies for the restoration of *P. australis* woodlands. Because restoration of degraded mountain forests using native species is still rare in the Neotropics (Pedraza & Williams-Linera 2003), we hope that our study will serve as a model for restoring other high-altitude mountain forests.

Materials and Methods

Study Species and Area

The southernmost stands of *Polylepis australis* (Rosaceae, locally called tabaquillo or queñoa) are located in the high Córdoba mountains of central Argentina (1,200–2,884 m above sea level [a.s.l.]). *Polylepis australis* grows in either a shrubby or tree habit (Enrico et al. 2004), can reach 14 m in height, and is characterized by a striking red-colored bark, which defoliates in many layers.

Mean temperatures of the coldest and warmest months in the Córdoba mountains are 5.0 and 11.4°C, respectively, and there is no frost-free period. Mean annual precipitation is 840 mm, with 83% of the rainfall occurring between October and April (Cabido 1985). The landscape consists of a mosaic of granitic outcrops, woodlands, different types of tussock grasslands, grazing lawns, and eroded

areas with exposed soil and rock surfaces colonized by annuals, mosses, and lichens (Cabido 1985; Cabido & Acosta 1986; Funes & Cabido 1995; Cingolani et al. 2004). Woodlands are largely dominated by *P. australis*, with other less abundant woody species like the tree *Maytenus boaria* (Celastraceae), the shrubs *Berberis hieronimii* (Berberidaceae) and *Satureja* spp. (Lamiaceae), and the dwarf shrub *Gaultheria poepigii* (Ericaceae). Due to its intrinsic fragility (steep slopes, no frost-free month, intense rains) and four centuries of domestic grazing, the high Córdoba mountains are severely degraded (Cingolani et al. 2003). Around 20% of the mountains now consists of exposed rock that was formerly covered by soil, including large areas in steep ravines and valleys, the most typical habitat of *Polylepis* woodlands (Cingolani et al. 2004). Erosion control and vegetation restoration are urgently needed in the area.

Seed Provenance and Seedling Production

We collected seeds during January–February 1998 from two woodland areas: (1) 40 trees distributed in four degraded woodlands or patches of trees in “Los Gigantes” (2,000 m a.s.l., lat 31°25’S, long 64°48’W; hereafter called “degraded woodland”) and (2) 40 trees in a relatively well-preserved woodland 30 km south-southeast of Los Gigantes, within “Quebrada del Condorito” National Park (1,900 m a.s.l., lat 31°40’S, long 64°42’W; hereafter called “well-preserved woodland”). At each location, we chose *P. australis* trees or shrubs (hereafter called “trees”) that were more than 100 m apart. Because tree height and growth habit could influence height and growth habit of their progeny (Renison & Cingolani 2002; Mahmood et al. 2003), we first collected seeds from the degraded woodlands and then selected trees in the well-preserved woodland with height and number of basal stems (as a growth habit measure) similar to those of trees in the degraded woodland. To characterize provenance locations, in a subsample of 23 trees in the degraded woodland and 25 trees in the well-preserved woodland, we visually estimated percent cover of *Polylepis* to a distance of 100 m around each tree, percent rock cover, and slope under the tree canopy. We sowed seeds in germination trays in a greenhouse in May 1998, transplanted them to individual tubes 5 cm in diameter and 15 cm in height in July, and planted them in a mountain enclosure (see below) at the start of the summer (November–December) when they were 6–7 months old (more details in Renison et al. 2002a). We did not plant older seedlings because they do not survive the hot summer in the lowlands (Renison et al. 2002a) and we had no facilities in the mountains.

Seedling Transplantation and Microsite Characteristics

The reforestation area occupied part of the degraded woodland area in Los Gigantes that has a general south aspect.

In the past the area was used for firewood extraction, livestock rearing, and tourism. Firewood extraction stopped in the 1970s, when no more accessible trees remained, and livestock was excluded in September 1998 when we built a 10-ha enclosure. At present the only human economic activity in the area is tourism (one tourist lodge and a trekking trail). We visually estimated that one-third of the soil in the enclosure has been lost, as evidenced by erosion gullies, edges, and exposed rock surfaces that had soil over them in the past. Most of the remaining vegetation consisted of grazing lawns with variable degrees of soil degradation (Cingolani et al. 2003). After exclusion, short grasses and forbs began to be replaced by large tussocks, and some shrubby species increased their cover, as described in Pucheta et al. (1998) for a similar situation. The natural regeneration of *P. australis* was poor, limited to an increase in size of a few seedlings already present but which before livestock exclusion grew very slowly due to browsing, and the emergence of a few seedlings in sites very close to one big tree present in the area, with no regeneration being observed under or near the 15 remaining trees of the reforestation area probably due to their low or null seed viability (Renison et al. 2004).

Before planting *P. australis* seedlings in the reforestation area, we first marked 655 sites using labeled metal pins. Sites were chosen in a random manner regarding field pattern, but always at least 3 m apart, and were selected for the largest possible variety of microsites with respect to aspect, slope, substrate, and surrounding vegetation. During November and December 1998 (the beginning of the growing season), we carried the seedlings to the area in backpacks (3-hr walk) and planted them beside

the pins in a random manner with respect to provenance. The number of seedlings per microsite type and provenance is shown in Table 1. We watered the seedlings and measured their initial height the day they were planted. Seedlings were never watered or attended to after planting. Every winter (June–August 1999–2003) we assessed survival for all seedlings ($n = 655$) and measured shoot height in a subsample of 455 seedlings (out of which 339 lived for the five seasons of the study). In 2003 we also determined the number of basal stems and canopy widths from two perpendicular diameters.

For all 655 planted seedlings, microsite characteristics were measured in a radius of 30 cm around the seedling and included:

- (1) sun incidence measured as the trajectory of the sun not covered by mountains, rock outcrops, or other obstacles (in a flat area with no obstacles, 180°);
- (2) soil depth, by hammering a 1-m iron bar into the soil until rock was reached (deeper soils are rare); depth was estimated from three locations per seedling and then averaged;
- (3) substrate type visually estimated at the surface as the percentage of massive rock (>200 mm), stones (200–5 mm), sand (5–2 mm), black soil, and red clay;
- (4) vegetation cover: percentage of lawns (perennial short graminoids and forbs), degraded lawns (sparse annuals, mosses, and lichens), tussocks less than 30-cm tall, tussocks more than 30-cm tall, and ferns;
- (5) proportion of bare soil; and
- (6) slope inclination and aspect (degrees); slope and aspect were reduced to two variables: relative north

Table 1. Mean characteristics of the eight microsite types as classified by *K*-means clusters nonhierarchical method (Norušis 1992), and number of microsites planted with seedlings from degraded and well-preserved provenances (*N*: degraded–well preserved).

Plant Cover	Low			Intermediate			High	
	1.1	1.2	1.3	2.1	2.2	2.3	3.1	3.2
<i>Microsite</i>								
Sun trajectory (degrees)	111.4	130.4	119.5	124.1	114.8	103.4	107.5	114.1
Soil depth (cm)	75.7	19.3	15.5	54.9	64.1	32.8	35.7	87.3
Massive rock (%)	1.2	9.7	65.9	0.8	5.8	12.2	1.0	1.0
Stones (%)	6.3	22.9	5.9	0.8	2.0	2.5	0.6	0.4
Sand (%)	9.9	35.4	8.3	24.2	12.7	9.6	7.9	7.8
Red soil (%)	82.5	7.4	0.3	48.8	1.2	0.4	0.0	0.1
Black soil (%)	0.1	24.6	19.7	25.4	78.3	75.4	90.5	90.8
Lawn (%)	1.9	5.2	6.8	61.7	13.8	59.2	92.0	88.2
Degraded lawn (%)	9.2	15.5	3.6	18.5	38.1	5.4	0.3	2.0
Ferns (%)	0.0	0.4	1.5	0.0	1.2	1.2	0.3	0.0
Tall tussocks (%)	0.0	0.1	0.1	3.2	0.8	1.0	0.3	0.9
Short tussocks (%)	0.3	0.3	0.8	0.7	1.0	1.1	0.8	1.9
Bare soil (%)	81.3	46.2	15.7	14.3	37.4	17.7	4.8	5.7
Slope (degrees)	14.2	5.3	10.2	8.4	9.0	8.4	9.9	7.8
Relative north aspect	–3.3	–3.7	–5.3	–5.0	–5.9	–4.7	–6.9	–5.3
Relative east aspect	5.6	–1.7	–1.7	–3.8	–3.8	–4.6	–3.4	–2.8
<i>N</i>	17–41	27–41	26–39	16–21	58–80	26–45	63–64	55–56

Microsite types correspond to: 1.1, bare soil; 1.2, sand and stones; 1.3, massive rock; 2.1, lawns on red and/or sandy soils; 2.2, lawn with bare black soil; 2.3, lawn with bare soil and massive rock; 3.1, lawn on black and shallow soil; 3.2, lawn on deep black soils.

and relative east aspects through cosine and sine transformations, multiplied by the slope inclination (according to Cingolani et al. 2002; Cushman & Wallin 2002).

Data Analysis

To compare provenance woodland characteristics we used *t* tests. We classified microsites where we planted the seedlings into eight groups that we considered appropriate to describe microsite variability. We used the *K*-means clusters nonhierarchical method (Norušis 1992), with the 16 variables detailed in Table 1. Because many of the 16 variables were correlated, we summarized the variability among microsite types using principal component analysis (PCA), according to the mean values detailed in Table 1. In this way, we obtained three axes (compound variables) that summarized the main variations in the average characteristics of the microsites.

Five seedling response variables were analyzed. The first (1) was survival ($n = 655$ seedlings), which was compared among two provenances and eight types of microsites using a Chi-square test. The remaining four response variables (see below) were compared among provenances and microsite types with a two-way analysis of variance (ANOVA) on 339 seedlings. The variables were (2) total growth, estimated as final height (July 2003) – height when planted (November–December 1998); (3) shape of the growth curve, estimated by arbitrarily dividing the 5 years into two periods, 1998–2001 and 2001–2003, and calculating a shape index as (second growth period – first growth period)/total growth; and two shrubbiness indices, (4) number of basal stems, which was square root transformed to better approximate normality of residuals, and (5) $s = (w1 + w2)/2 \times h$ where s is the shrubbiness index, $w1$ and $w2$ are the two estimates of crown width, taken at perpendicular angles, and h is the height.

In all cases we tested for interactions between provenance and microsite. We considered post hoc comparison among microsite types not to be meaningful because we classified microsites in types whose characteristics varied in a continuous fashion, and which can be described by three PCA axes. Hence, when we found significant differences with the ANOVA, we performed multiple regressions among mean values of the dependent variables for each type of microsite, with the mean position of each microsite type in the three PCA axes as independent variables. In this way we determined what microsite properties were relevant in explaining the differences among them. We preferred this approach rather than directly analyzing all data with ordination and regressions because microsite categories are easier to identify in the field than continuous variables, and thus more useful for applying the information. All means are reported \pm their standard errors. All residuals were checked for normality and homogeneity of variances.

Results

Seed Provenance and Microsite Description

The surroundings of trees from the degraded woodland were characterized by less *Polylepis* cover ($14 \pm 2\%$ compared to $58 \pm 4\%$, $t = 10.0$; $p < 0.001$), more rock cover ($59 \pm 6\%$ compared to $35 \pm 7\%$, $t = -2.6$; $p < 0.013$), and steeper slopes ($40 \pm 5^\circ$ compared to $22 \pm 3^\circ$, $t = -2.8$; $p = 0.01$) than the surroundings of trees from the well-preserved woodland.

Microsites around the planted seedlings were classified into eight groups (described in Table 1), which the PCA procedure arranged in three main axes according to the mean values of their abiotic and biotic variables (Fig. 1). Axis 1 (explaining 37% of variance) was related to total plant cover, varying from types with low vegetation cover, generally highly degraded, at the negative end, to non-degraded microsite types with high vegetation cover at the positive end. Axis 2 (22% of variance) was determined by topography and substrate, with sunny types with gentle rocky slopes at the negative end, and steeper types with deeper soils and more clay at the positive end. Axis 3 (17% of the variance) was determined by the contrast between habitats with high massive rock proportion and shallow soils at the negative end and habitats with deep soils with low massive rock cover and higher insolation at the positive end.

Effects of Microsite and Provenance on Seedling Survival and Growth

Seedling survival over five seasons averaged 70% and no significant differences were found between seedling microsite or seed provenance ($\chi^2 = 20.9$, $df = 15$, $p = 0.14$). Highest seedling mortality was observed during the first season after planting (19%), whereas postestablishment mortality was clearly lower (5, 4, 4, and 2%, respectively) in the next four seasons.

Seedlings were planted with an average height of 3.9 ± 0.1 cm. Growth averaged 34.6 ± 1.2 cm during the five growing seasons (6.9 cm per season, $n = 339$ seedlings), and was fairly similar between seasons, ranging from a minimum of 5.37 ± 0.41 cm for the second growing season to a maximum of 7.88 ± 0.42 cm for the fifth season. Total growth differed significantly both between seed provenance and between microsite types (ANOVA: $F = 4.14$, $df = 15$, $p < 0.001$) and there was no interaction ($p = 0.43$). During the five seasons after planting, seedlings from the well-preserved woodland grew on average 8 cm more than those from the degraded woodland (Fig. 2). The multiple regression procedure with the three PCA axes as independent variables showed that growth was positively associated with PCA axis 1 ($r^2 = 0.72$, $p < 0.001$), whereas axes 2 and 3 were not significant, indicating that seedling growth increased with vegetation cover and decreased with site degradation. Mean growth per microsite type ranged from an average of 25 cm in degraded

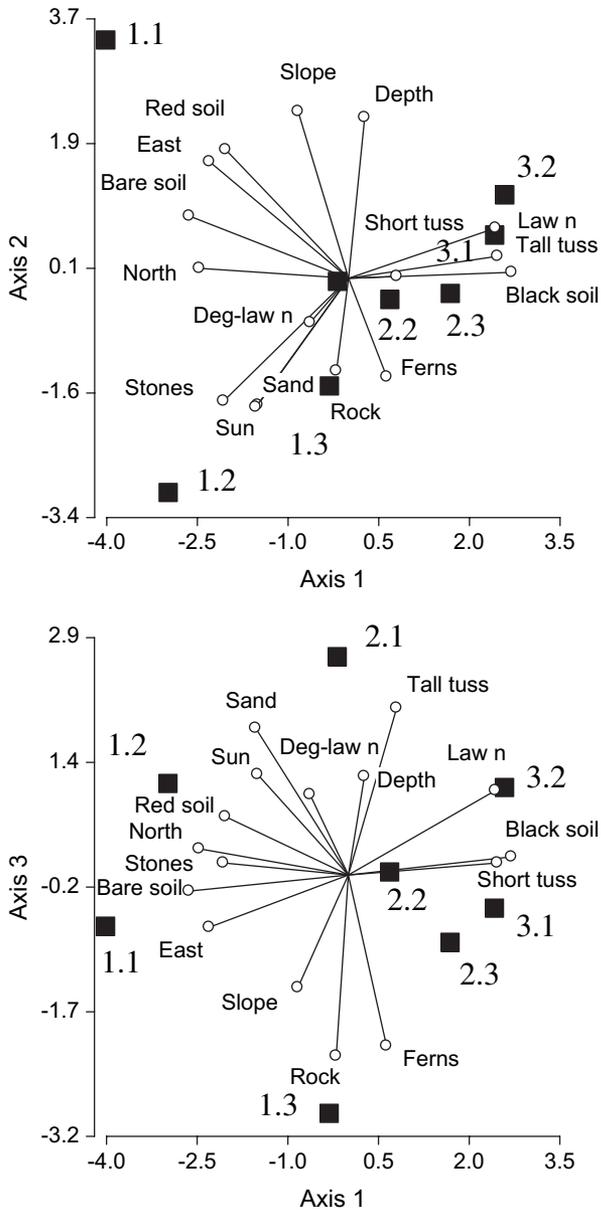


Figure 1. Diagram of PCA ordination where average microsite location is represented with filled squares and microsite variables with open circles joined to the origin with a line. Numbers of microsite types as in legend of Table 1.

microsite types 1.1 and 1.2 to almost double in microsite type 3.1 with more vegetation (Fig. 2). The shape of the growth curves did not differ significantly between provenance and microsite types (ANOVA: $F = 1.26$, $df = 15$, $p = 0.22$).

Both shrubbiness indices gave the same pattern of results, so we only report the results on the number of basal stems. This variable differed significantly between provenances and microsities (ANOVA: $F = 3.02$, $df = 15$, $p < 0.001$), and no interaction between both factors was detected ($p = 0.62$). The number of stems was greater for

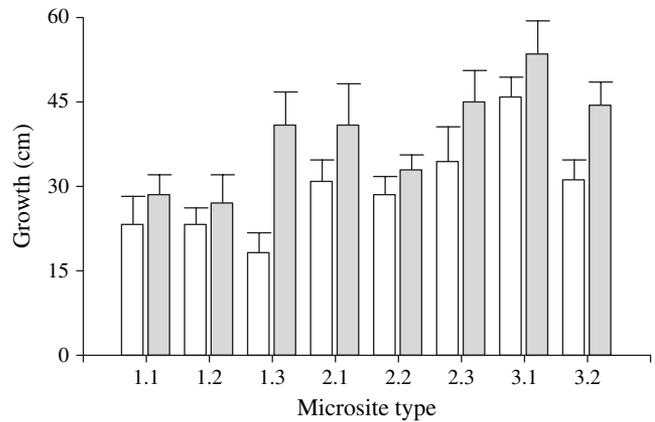


Figure 2. Mean *Polylepis australis* growth in height after five growing seasons, for seedlings planted in eight microsite types and which belonged to a degraded forest provenance (white columns) and a well-preserved forest provenance (gray columns). Numbers of microsite types as in legend of Table 1.

seedlings whose provenance was the well-preserved woodland (Fig. 3). The multiple regression procedure showed that mean number of basal stems per habitat type was negatively associated with axis 1 and positively associated with axis 3 ($r^2 = 0.76$, $p = 0.01$), indicating that the development of a shrubby habit is favored by microsite degradation, rockiness, and shallow soils. Axis 2 was not significant.

Discussion

In terms of seedling survival, *Polylepis australis* reforestation in the Córdoba mountains was particularly successful, because 70% of the planted seedlings survived the first five seasons, even though they were only 6–7 months old and on average 3.9 cm high when transplanted to the

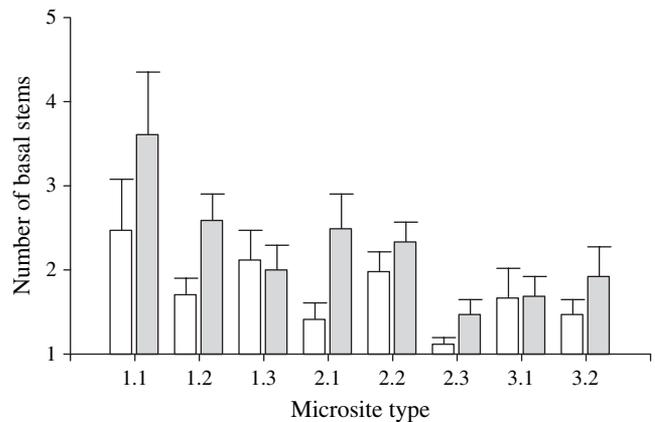


Figure 3. Number of *Polylepis australis* basal stems after five growing seasons, for seedlings planted in eight microsite types and which belonged to a degraded forest provenance (white columns) and a well-preserved forest provenance (gray columns). Numbers of microsite types as in legend of Table 1.

mountains. Survival appeared not to be affected by provenance or seedling microsite but was lowest in the first season probably due to stresses associated with transplanting (Pakkard et al. 2003). In the following years, however, survival was as high as that reported for commercial tree species (e.g., *Pinus sylvestris* and *Pinus nigra*; Castro et al. 2002).

The growth rates we measured for *P. australis* seedlings were similar to those of Hensen (1994), who measured height growth of *P. besseri* juveniles in Bolivia to be 3–7 cm/year (3,500 m a.s.l.). Unfortunately, these rates are rather low compared to commercial reforestation with *Pinus* sp. in the high Córdoba mountains, which grow an average of 25–30 cm/year (1,620 m a.s.l.; personal observation). Fast-growing trees provide more rapid protection to bare soils, are a quick source of firewood, and are more likely to achieve acceptance as a reforestation species. More importantly, fast-growing trees need to be protected from livestock for a shorter time because they can more quickly reach a height above which at least parts of the tree remain unaffected by browsing (approximately 2 m). Domestic grazing is the most important economic activity in high-mountain ecosystems, and browsing greatly affects *Polylepis* seedling and juvenile growth as well as survival (Fjeldså & Kessler 1996; Hensen 2002).

Growth has been enhanced through provenance selection in several forest species (e.g., Montenegro et al. 1997; Hodge et al. 2002; Mantovan 2002; Mahmood et al. 2003; Nielsen & Jørgensen 2003; Sotelo Montes et al. 2003). *Polylepis australis* also appears to have potential for improved growth rates through provenance selections, and our data suggest that even better provenances may be found in a larger scale provenance trial. Reduced seedling growth from the degraded woodland provenance may be explained by factors such as water shortage or lack of nutrients, which diminish seed reserves and quality (Vaughton & Ramsey 1998), and which in turn could affect seedling growth. We did not measure seed weight, but in other species, larger and heavier seeds have been shown to enhance shoot growth rates (Bonfil 1998; Chacón et al. 1998). The influence of genetic factors such as a reduced effective population size in the degraded woodland and concomitant genetic impoverishment might be a further explanation (Morgan 1998; Cascante et al. 2002; Reed & Frankham 2003). All these explanations are highly speculative but of conservation interest, because if true they imply that woodland degradation reduces recovery potential of the species.

The well-preserved woodland provenance showed a higher tendency for basal ramification than that of the degraded woodland. The difference in growth habit between provenances is not unique to *P. australis* because this factor was found to differ between provenances in other species (i.e., *Alnus glutinosa*, DeWald et al. 1983; *Pinus oocarpa*, Moura et al. 1998; *Prosopis juliflora*, Ræbild et al. 2003). However, all these studies included provenances that were more geographically separated than those of our study. A possible explanation is that

there are genetic differences in growth habit between provenances, even though our provenances were only 30 km apart, and even though shrubbiness in *Polylepis* is a phenotypic trait commonly caused by nongenetic causes such as browsing, resprouting from fires (Renison et al. 2002b), or microsite type (this study). Supporting the genetic hypothesis, although we selected parents with a similar number of basal stems in both seed provenances, the percentage of multistemmed trees in the well-preserved woodland was clearly higher than in the degraded woodland (personal observation). Maternal carryover effects could be another explanation for differences in growth habits as observed in *Senecio vulgaris* for other traits (Aarssen & Burton 1990). Further studies are needed to determine the causes of differences in growth habit between seed provenances.

The association between *P. australis* growth and microsite type is similar to the association reported by Bonfil and Soberón (1999) for *Quercus rugosa* and Camargo et al. (2002) for *Caryocar villosum* and *Parkia multijuga*. Slower growth rates in degraded microsites are probably due to nutrient and moisture deficiency because the degraded microsites are characterized by high evaporation rates and run-off due to shallow or missing topsoil (Cingolani et al. 2003). Consequently, we suggest further research on enhancing degraded site quality by adding aboveground obstructions to rainwater such as plant debris and/or stones to increase water infiltration (Whisenant et al. 1995; Yates et al. 2000), seeding (Montalvo et al. 2002) or planting legumes and/or other nurse-plants, which could facilitate *Polylepis* seedling establishment (Castro et al. 2002), or using fertilizers. Basal ramification of *P. australis* seedlings seems to be an adaptation to adverse growing conditions.

High vegetation cover in more favorable sites was associated with faster seedling growth, and vegetation did not appear to negatively influence *P. australis* survival and growth through competition. Tall tussock grass coverage was still relatively low in the restoration area when we planted the seedlings; however, it remains to be determined if seedlings planted in microsites with high tussock cover could be outcompeted.

Because growth curves did not differ between provenances and microsites, we expect the observed differences among provenances and microsites to remain constant in the next few years. However, microsite differences are in part related to characteristics such as vegetation cover, nutrients, and water-holding capacity, which in the long term should improve relatively more in degraded areas and eventually become less different with time.

Implications for Restoration of *Polylepis* Woodlands

Where permanent livestock exclusion is a possibility, the restoration of *Polylepis* woodlands appears to be possible. In this manner, and with a large dependence on conservation funding, we have so far expanded our reforestation area to 30 ha, promoted the restoration of degraded areas around three local rural schools (5 ha), and are

collaborating with the reforestation of degraded areas of Quebrada del Condorito National Park established in 1997. Around 20% of the Córdoba mountains consists of eroded rock surfaces or soils that are being lost due to low vegetation cover (Cingolani et al. 2004). Much of this large area could potentially benefit from the establishment of *Polylepis* woodlands and is of low value to livestock producers so livestock exclusion per se should not be an issue. Due to government incentives directed to commercial tree species, forestations with exotic commercial trees (mainly *Pinus*) have been performed successfully in several hundred hectares of the Córdoba mountains (Vischi et al. 2004) including very degraded areas, suggesting stronger incentives could help promote reforestation with native tree species for conservation purposes. Research on promoting *P. australis* growth in degraded areas is still desirable.

At present, most of the Córdoba mountains are used for livestock rearing (Cingolani et al. 2003) and permanent livestock exclusion is likely not an option in the near future. So a relevant consideration is whether woodland restoration and livestock rearing are compatible. If we extrapolate from our data using an average overall growth in height of 6.9 cm/year, *P. australis* trees in our restoration area are going to take 28 years to average a height of 2 m, which would be high enough to allow low livestock use and avoid severe damage by browsing. This is too long a period for most producers who need their pasture to make a living, and our feeling is that livestock reintroduction into rehabilitated areas should be a very well-studied process to make sure erosion and woodland retraction is not triggered once again.

However, the high variability in growth according to provenance and microsite shows a potential to reduce exclusion periods. Selection of the best provenance-microsite combination of our study would reduce the period of livestock exclusion to 20 years (average growth in height of 10.6 cm/year; Fig. 2). The exclusion period may be further reduced by selection of the best seeding trees within a provenance (Renison & Cingolani 2002), by further experimentation to identify even faster growing provenances, or by planting larger seedlings. Also, *Polylepis* juveniles may grow faster when older (Hensen 1994) so the scenario might be better than predicted with the first 5 years of data. Thus, we see some potential to implement reforestation using native *Polylepis* trees, with reasonable exclusion times, in areas where soil loss has not been widespread. Nevertheless, reduction of the current stocking rates is necessary if certain areas are going to be excluded for several years, and this is not likely to happen without appropriate economic incentives.

Acknowledgments

We are very grateful to Professors S. Zingoni and O. Berté and their students of the Umberto Illia School,

D. Schinner, M. Caselles, E. Galli, F. Diprieto, R. Renison, and numerous volunteers for collaboration in the field work and/or greenhouse. Club Andino Córdoba and Villa Carlos Paz provided lodging in the field. Diego Gurvich, David Lamb, and two anonymous reviewers helped improve the manuscript. Los Algarrobos Association, Agencia Córdoba Ambiente S.E., Whitley Laing and Volkswagen foundations helped fund this study throughout the years. The authorities of Quebrada del Condorito National Park provided seed collection permits.

LITERATURE CITED

- Aarssen, L. W., and S. M. Burton. 1990. Maternal effects at four levels in *Senecio vulgaris* (Asteraceae) grown on a soil nutrient gradient. *American Journal of Botany* **77**:1231–1240.
- Aide, M. T., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* **2**:219–229.
- Amaranthus, M. P., and D. A. Perry. 1987. Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. *Canadian Journal of Forest Research* **17**:944–950.
- Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *American Journal of Botany* **85**:79–87.
- Bonfil, C., and J. Soberón. 1999. *Quercus rugosa* seedling dynamics in relation to its re-introduction in a disturbed Mexican landscape. *Applied Vegetation Science* **2**:189–200.
- Cabido, M. 1985. Las comunidades vegetales de la Pampa de Achala, Sierras de Córdoba, Argentina. *Documents Phytosociologiques* **9**:431–443.
- Cabido, M., and A. Acosta. 1986. Variabilidad florística a lo largo de un gradiente de degradación en céspedes de la Pampa de Achala, Sierras de Córdoba, Argentina. *Documents Phytosociologiques* **10**:289–304.
- Camargo, J. L., I. D. Ferraz, and A. M. Imakawa. 2002. Rehabilitation of degraded areas of central Amazonia using direct sowing of forest tree seeds. *Restoration Ecology* **10**:636–644.
- Cascante, A., M. Quesada, J. J. Lobo, and E. A. Fuchs. 2002. Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. *Conservation Biology* **16**:137–147.
- Castro, J., R. Zamora, J. A. Hódar, and J. M. Gómez. 2002. Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. *Restoration Ecology* **10**:297–305.
- Chacón, P., R. Bustamante, and C. Henriquez. 1998. Effect of seed size on germination and seedling growth in *Cryptocarya alba* (Lauraceae). *Revista Chilena de Historia Natural* **71**:189–197.
- Cierjacks, A., and I. Hensen. 2004. Variation of stand structure and regeneration of Mediterranean holm oak along a grazing intensity gradient. *Plant Ecology* **173**:215–223.
- Cingolani, A., J. Anchorena, S. Stoffella, and M. Collantes. 2002. A landscape-scale model for optimal management of sheep grazing in the Magellanic steppe. *Applied Vegetation Science* **5**:159–166.
- Cingolani, A. M., M. Cabido, D. Renison, and V. Solís Neffa. 2003. Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *Journal of Vegetation Science* **14**:223–232.
- Cingolani, A. M., D. Renison, M. Zak, and M. Cabido. 2004. Mapping vegetation in a heterogeneous mountain rangeland using Landsat

- data: an alternative method to define and classify land-cover units. *Remote Sensing of Environment* **92**:84–97.
- Cushman, S. A., and D. O. Wallin. 2002. Separating the effects of environment, spatial and disturbance factors on forest community structure in the Russian Far East. *Forest Ecology and Management* **168**: 201–215.
- DeWald, L. E., K. C. Steiner, and K. K. Carter. 1983. Juvenile performance in three black alder provenance plantations in the northeast. *Proceedings of the Northeast Forest Tree Improvement Conference* **28**:37–39.
- Ellenberg, H. 1979. Man's influence on tropical mountain ecosystems in South America. *Journal of Ecology* **67**:401–416.
- Enrico, L., G. Funes, and M. Cabido. 2004. Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. *Forest Ecology and Management* **190**:301–309.
- Fernández, E., and B. Ståhl. 2002. Diversity and phytogeography of the vascular flora of the *Polylepis* forests of the Cordillera de Cochabamba, Bolivia. *Ecotropica* **8**:163–182.
- Fiedler, P. L., and R. D. Laven. 1996. Selecting reintroduction sites. Pages 157–170 in D. A. Falk, C. I. Millar, and M. Olwell, editors. *Restoring diversity: strategies for reintroduction of endangered plants*. Island Press, Washington, D.C.
- Fjeldså, J. 1993. The avifauna of the *Polylepis* woodlands of the Andean highlands: conservation priorities based on patterns of endemism. *Bird Conservation International* **3**:37–55.
- Fjeldså, J., and M. Kessler. 1996. Conserving the biological diversity of *Polylepis* woodlands of the highland of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes. NORDECO, Copenhagen, Denmark.
- Funes, G., and M. Cabido. 1995. Variabilidad local y regional de la vegetación rupícola de las Sierras Grandes de Córdoba, Argentina. *Kurtziana* **24**:173–188.
- Hendrix, S. D., E. Nielsen, T. Nielsen, and M. Schutt. 1991. Are seedlings from small seeds always inferior to seedlings from large seeds? Effects of seed biomass on seedling growth in *Pastinaca sativa* L. *New Phytologist* **119**:299–305.
- Hensen, I. 1994. Estudios ecológicos y fenológicos sobre *Polylepis besseri* Hieron. en la Cordillera Oriental Boliviana. *Ecología en Bolivia* **23**:21–32.
- Hensen, I. 1995. Die vegetation von *Polylepis*-Wäldern der Ostkordillere Bolivians. *Phytocoenologia* **25**:235–277.
- Hensen, I. 2002. Impacts of anthropogenic activity on the vegetation of *Polylepis* woodlands in the region of Cochabamba/Bolivia. *Ecotropica* **8**:183–203.
- Hodge, G. R., W. S. Dvorak, H. Uruña, and L. Rosales. 2002. Growth, provenance effects and genetic variation of *Bombacopsis quinata* in field tests in Venezuela and Colombia. *Forest Ecology and Management* **158**:273–289.
- Holl, K. D., and M. Kappelle. 1999. Tropical forest recovery and restoration. *Trends in Ecology and Evolution* **14**:378–379.
- Kauffman, J. B., M. D. Steele, D. L. Cummings, and V. J. Jaramillo. 2003. Biomass dynamics associated with deforestation, fire, and conversion to cattle pasture in a Mexican tropical dry forest. *Forest Ecology and Management* **176**:1–12.
- Mahmood, K., N. E. Marcar, M. H. Navqui, R. J. Arnold, D. F. Crawford, S. Iqbal, and K. M. Aken. 2003. Genetic variation in *Eucalyptus camaldulensis* Dehnh. for growth and stem straightness in a provenance-family trial on saltlands in Pakistan. *Forest Ecology and Management* **176**:405–416.
- Mantovan, N. G. 2002. Early growth differentiation among *Prosopis flexuosa* D.C. provenances from the Monte phytogeographic province, Argentina. *New Forests* **23**:19–30.
- McEvoy, P. B., and E. M. Coombs. 1999. Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications* **9**:387–401.
- Milberg, P., L. Andersson, C. Elfverson, and S. Regner. 1996. Germination characteristics of seeds differing in mass. *Seed Science Research* **6**:191–197.
- Milberg, P., M. A. Pérez-Fernández, and B. B. Lamont. 1998. Seedling growth response to added nutrients depends on seed size in three woody genera. *Journal of Ecology* **86**:624–632.
- Montalvo, A. M., P. A. McMillan, and E. B. Allen. 2002. The relative importance of seeding method, soil ripping, and soil variables on seeding success. *Restoration Ecology* **10**:52–67.
- Montenegro, F., V. Meneses, and J. A. Wright. 1997. Growth of *Pinus muricata* provenances in the highlands of Ecuador. *Forest Ecology and Management* **99**:291–294.
- Morgan, J. W. 1998. Effects of population size on seed production and germinability in an endangered, fragmented grassland plant. *Conservation Biology* **13**:266–273.
- Moura, V. P., W. S. Dvorak, and G. R. Hodge. 1998. Provenance and family variation of *Pinus oocarpa* grown in the Brazilian cerrado. *Forest Ecology and Management* **109**:315–322.
- Nielsen, C. N., and F. V. Jørgensen. 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: variation between and within provenances. *Forest Ecology and Management* **174**:233–249.
- Norušis, M. J. 1992. SPSS for Windows base system user's guide. Release 5.0. SPSS Inc., Chicago, Illinois.
- Pakkard, G., F. Torre, S. Elliott, and D. Blakesley. 2003. Selecting seed trees for a forest restoration program: a case study using *Spondias axillaris* Roxb. (Anacardiaceae). *Forest Ecology and Management* **182**:363–370.
- Pedraza, R. A., and G. Williams-Linera. 2003. Evaluation of native tree species for the rehabilitation of deforested areas in a Mexican cloud forest. *New Forests* **26**:83–99.
- Poore, M. E., and C. Fries. 1987. Efectos ecológicos de los eucaliptos. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Pucheta, E., M. Cabido, S. Díaz, and G. Funes. 1998. Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina. *Acta Oecologica* **19**:97–105.
- Ræbild, A., L. Graudal, and P. C. Fernandes. 2003. Evaluation of a provenance trial of *Prosopis juliflora* at Petrolina – PE, Brazil. Trial no. 4 in the arid zone series. Results and documentation no. 15. Danida Forest Seed Centre, Humlebaek, Denmark.
- Reed, D. H., and R. Frankham. 2003. Correlation between fitness and genetic diversity. *Conservation Biology* **17**:230–237.
- Renison, D., and A. M. Cingolani. 1998. Experiencias en germinación y reproducción vegetativa aplicados a la reforestación con *Polylepis australis* (Rosaceae) en las Sierras Grandes de Córdoba, Argentina. *AgriScientia* **15**:47–53.
- Renison, D., and A. M. Cingolani. 2002. Optimización del crecimiento del tabaquillo (*Polylepis australis*, Rosaceae): selección de las mejores plantas semilleras. *AgriScientia* **19**:63–66.
- Renison, D., A. M. Cingolani, and D. Schinner. 2002a. Optimizing restoration of *Polylepis australis* woodlands: when, where and how to transplant seedlings to the mountains? *Ecotropica* **8**:219–224.
- Renison, D., A. M. Cingolani, and R. Suarez. 2002b. Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba, Argentina. *Revista Chilena de Historia Natural* **75**:719–727.
- Renison, D., I. Hensen, and A. M. Cingolani. 2004. Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. *Forest Ecology and Management* **196**:327–333.
- Richardson, D. M. 1998. Forestry trees as invasive aliens. *Conservation Biology* **12**:18–26.
- Sotelo Montes, C., H. Vidaurre, and J. Weber. 2003. Variation in stem-growth and branch-wood traits among provenances of *Calycoophyllum spruceanum* Benth. from the Peruvian Amazon. *New Forests* **26**:1–16.

- Spies, T. 1998. Forest stand structure, composition, and function. Pages 11–30 in K. A. Kohm, and J. F. Franklin, editors. *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, D.C.
- Tripathi, R. S., and M. L. Khan. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* **57**:289–296.
- UNEP-WCMC. 2004. United Nations Environment Programme, World Conservation Monitoring Center (available from: www.unep-wcmc.org).
- Vaughton, G., and M. Ramsey. 1998. Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *Journal of Ecology* **86**:563–573.
- Vischi, N., E. Natale, and C. Villamil. 2004. Six endemic plant species from central Argentina: an evaluation of their conservation status. *Biodiversity and Conservation* **13**:997–1008.
- Whisenant, S. G., T. L. Thurow, and S. J. Maranz. 1995. Initiating autogenic restoration on shallow semi-arid sites. *Restoration Ecology* **3**:61–67.
- Yates, C. J., D. A. Norton, and R. J. Hobbs. 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. *Austral Ecology* **25**:36–47.
- Zak, M. R., and M. Cabido. 2002. Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. *Applied Vegetation Science* **5**:213–226.