Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina

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Abstract

South American *Polylepis* mountain forests belong to the most endangered forest ecosystem in the world. Reforestation measures have been strongly recommended but may be hampered due to the very low seed germination rates reported for several *Polylepis* species. In order to determine the causes behind reduced seed germination we analysed seed viability of *Polylepis australis* trees in the mountains of central Argentina. We picked seeds from seven heterogeneous areas (4–5 well-separated trees per area totaling 29 trees) with high within and between variation in degradation status. At the landscape scale we measured altitude above sea level and forest fragmentation in a radius of 1000 m around seven areas. At the mesohabitat scale we measured vegetation types and amount of soil erosion in a square of 90 m × 90 m around each study tree. At the microhabitat scale we assessed site characteristics under the tree canopy. Additionally, we measured some individual characteristics of each tree. Average percentage of viable seeds was 23.0 ± 15.7 S.D. and lack of an embryo was the main reason for seeds not being able to germinate. Landscape variables were not related to seed viability. At the mesohabitat scale, a multiple regression procedure showed that seed viability was positively associated with relatively undisturbed soils supporting tussock grasslands (38.7% of variance) and negatively associated with soil erosion (18.8% of the variance). Microhabitat variables and individual *Polylepis* characteristics were also related to seed viability, but explained less variability than mesohabitat characteristics. In order to improve seed viability, our data suggests that livestock pressure and burning practices should be reduced, as these are the main causes for erosion and other forms of soil destruction. For reforestation purposes, we recommend collecting seeds from undisturbed areas.
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1. Introduction

Forests of the genus *Polylepis* are restricted to the higher mountain regions of South America where land use history has fundamentally changed the vegetation. Burning to promote grass re-growth, domestic animal browsing, and the extraction of timber has greatly reduced forest areas. Many forest remnants are now restricted to rocky outcrops, where they are protected from livestock and burning, and soil erosion is widespread in the mountain slopes which were previously

occupied by *Polylepis* forests (Ellenberg, 1979; Fjeldså and Kessler, 1996; Kessler, 1995, 2000; Lauer et al., 2001; Hensen, 1995, 2002; Renison et al., 2002a). Today, *Polylepis* forests are one of the most endangered forest ecosystems in the world (Walter and Gillett, 1998; UNEP-WCMC, 2004). In Bolivia, more than 90% of the original forest area is thought to have been destroyed (Kessler, 2002). In other countries, the extent of *Polylepis* forest loss is unknown but likely to be equally high. Consequently, the conservation of the last remaining stands and reforestation of areas formerly occupied by *Polylepis* forests is a conservation priority (Fjeldså and Kessler, 1996; Renison et al., 2002b; Enrico et al., 2004).

Reforestation protocols for *Polylepis* species frequently propose vegetative reproduction through cuttings because of the low rate of seed germination (Pretell et al., 1985; Brandbyge and Holm-Nielsen, 1987; Reynel and Leon, 1990). As is the case with species of other genera (e.g. *Samanea saman*, Cascante et al., 2002; *Podocarpus falcatus*, Negash, 2003), seed germination could be diminished due to forest fragmentation and/or soil degradation. This was also suggested for *Polylepis australis* by Renison and Cingolani (1998), who documented that seeds germinate fairly well when collected from a relatively undisturbed area within a large forest, while seeds from isolated trees, in an area with a long history of human influence, tended not to germinate at all. Further supporting this possibility, Hensen (unpublished) found a high percentage of empty and nonviable seeds in several severely anthropogenically influenced Bolivian *Polylepis* species (*P. hieronymi* 80%, *P. tomentella* 84%, *P. besseri* 90–100%, *P. racemosa* 100%, *P. tarapacana* 100%). It is important to understand the causes of low germination rates since they hamper reforestation and could affect natural regeneration. Furthermore, low germination rates promote the use of cuttings which grow slower than trees produced from seedlings (for *P. australis* Renison and Cingolani, 1998) and do not contribute to genetic diversity.

Considering the varying extent of degradation in the mountains of central Argentina (Cingolani et al., 2003a), the aim of this study was to determine whether seed viability of *P. australis* is associated with degree of land degradation and forest fragmentation, measured at the landscape, mesohabitat and microhabitat

scales. *P. australis* is the only native species that forms forests in the higher mountains of central Argentina and its conservation is especially important because of its ecological benefits regarding the regional water cycle, associated endemic species, control of soil erosion, and supply of firewood for the local inhabitants.

2. Methods

2.1. Study area

The study was carried out in the Cordoba mountains, central Argentina. Annual precipitation is 840 mm and mean temperature of the coldest and warmest months are 5.0 and 11.4 °C, respectively (Cabido, 1985). The landscape is a mosaic of different types of tall tussock grasslands, grazing lawns, natural granitic outcrops, exposed rock surfaces produced by anthropogenic soil erosion, and forests dominated almost exclusively by *P. australis* (Rosaceae) trees (Cabido and Acosta, 1985; Cingolani et al., 2003a). The landscape is very heterogeneous and patches of the different community types can vary within a few dozen meters due to relief, rock outcrops disposition and accessibility to livestock (Cingolani et al., 2003a).

Human intervention and forest fragmentation probably started around 8000 years ago when the first Amerindians colonised the area and used fire for hunting (Berberián, 1999; Pastor, 2000). Europeans settled in the area around 400 years ago (Díaz et al., 1994) and forests declined further due to burning, livestock grazing and utilisation for timber and fuel. Such land use practices still persist (Cabido and Acosta, 1985; Kopta, 1999; Renison et al., 2002a), and many areas previously occupied by forests now consist of isolated *Polylepis* trees which have managed to escape human exploitation.

2.2. Seed collection and assessment of viability

We collected seeds from seven areas distributed within 60 km of each other during February and March 2001 when fruit set was at its optimum (Los Gigantes S 31°24′, W 64°48′; Las Lomitas S 31°36′, W 64°48′; Altas Cumbres S 31°36′, W 64°49′; Río del Sur S 31°41′, W 64°43′; Ceferino S 31°48′, W 64°46′;

Yatán S 31°49′; W 64°47′; Paso Garay S 31°50′, W 64°45′). Areas were chosen in order to represent varying forest fragmentation states, and a wide geographic range within the Cordoba mountains. We were unable to find large forests on degraded sites, but we specifically incorporated two areas (Las Lomitas and Altas Cumbres) with isolated trees in the relatively undisturbed land within the ''Quebrada del Condorito'' National Park. In each area we selected 4–5 trees (totaling 29 trees) which were larger than 2 m tall (seed bearing size), at least 100 m apart from each other, and situated in varying levels of soil degradation states. Individual tree locations were recorded using a global positioning device (GPS12, Garmin Corporation, USA). We collected approximately 150 seeds per individual (range = 116 to 201 seeds), opened the seeds to determine whether they had an embryo, and tested viability using tetrazolium (according to Baskin and Baskin, 1998).

2.3. Habitat and tree characteristics

Habitat characteristics varied at different scales which we classified into three categories: the landscape and mesohabitat scales which were measured using a land cover map of the Cordoba mountains and the microhabitat scale which was measured in the field in the area under the canopy or each study tree. Variables which were relatively constant within study areas were defined as landscape variables while meso- and microhabitats varied considerably within areas. The vegetation map was based on Landsat-ETM+ satellite imagery and distinguished eight land cover types with an overall precision of 85%. Because of the highly heterogeneous landscape, each land cover type consisted of a mosaic of community types of known proportions. In order to determine the percent cover of a particular community (e.g. *Polylepis* forest) in a given area, we averaged the proportion of that community in each cover type weighed by the proportion of each cover type in the area (Cingolani et al., 2003b).

At the landscape level we defined (1) a fragmentation indicator as the proportion of *Polylepis* forests in an area of 1000 m around the centroid of the study trees in each of the seven study areas (2) altitude above sea level. The mesohabitat scale covered an area of 90 m × 90 m (3 × 3 pixels) surrounding each individual tree. Here, we calculated the proportion of (1) tussock grassland, (2) *Polylepis* forest, (3) natural rock outcrop, and (4) bare rock exposed due to soil erosion. At the same scale, we estimated (5) general slope (%) and aspect (degrees from North) from a topographic map. Aspect was used to calculate two variables: (6) the relative North–South and (7) the relative East–West component of the slope by multiplying slope (%) by the cosine (for North–South) or sine (for East–West) of the aspect. These variables range from highly positive values (North or West aspect with steep slopes) to highly negative values (South or East aspect with steep slopes).

In the field, we estimated the following microhabitat variables and tree characteristics: (1) sun incidence as the sun's trajectory (in degrees) which directly illuminates individual tree canopies (i.e. in a flat plain with no obstacles the value would be 180°, rock outcrops and other obstacles reduce the value); (2) percent rock under the individual tree canopy; (3) number of basal stems (one in trees, more than one in shrubs); (4) height; and (5) circumference at the base of the stem. We did not use breast height circumference because most *P. australis* individuals have branches below breast level. When individuals had several basal stems, we chose the stem with the largest circumference (Acosta, 1986).

2.4. Data analysis

The relationship between seed viability and variables at the landscape ($N = 7$ areas), mesohabitat and microhabitat/individual ($N = 29$ trees) scales were analysed separately with stepwise multiple regressions ($P < 0.05$). A fourth multiple regression between seed viability and all selected variables was carried out to determine if a combination of variables measured at different scales explains seed viability better than each scale by its own. We tested for normality of residuals using Kolmogorov–Smirnov test ($P > 0.05$). We verified that significant variables were not highly correlated as this would cause instabilities in the regression procedure (Afifi and Clark, 1984).

3. Results

Mean percentage of viable *P. australis* seeds was 23.0 ± 15.7 S.D. ($N = 29$ trees). The range of
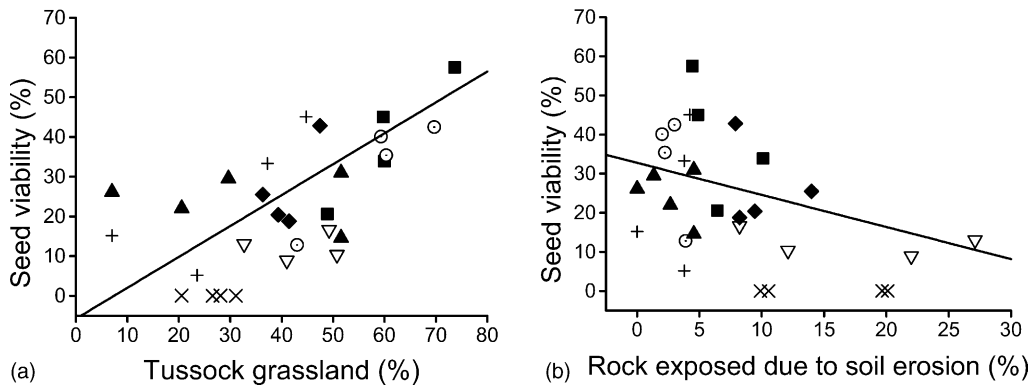
Fig. 1. Relationship between *P. australis* seed viability and the two most important mesohabitat variables: (a) % tussock grasslands surrounding the individual tree, and (b) % rock exposed by soil erosion, according to the forward stepwise regression procedure (viability = $0.529 + 0.778 \times$ % tussock grassland $- 0.820 \times$ % exposed rock $- 0.316 \times$ East aspect). For each plot the regression line was drawn leaving the remaining explanatory variables as constants equivalent to their average (rock exposed due to soil erosion = 8.0%, relative East–West component of aspect = -0.8, tussock grassland = 41.1%). Symbols represent areas: ($\times$) Los Gigantes; ($\triangledown$) Las Lomitas; ($\blacklozenge$) Altas Cumbres; ($+$) Río del Sur; ($\blacksquare$) Ceferino; ($\blacktriangle$) Yatán; ($\bigcirc$) Paso Garay.

viability was from 0 to 57.5%. An average of $94.5 \pm 5.3\%$ of the non-viable seeds were "empty", which implied that their pericarp had grown to full size but no embryo growth had occurred.

At the landscape scale, neither altitude nor forest fragmentation were selected by the multiple regression procedure ($N = 7$, $P > 0.05$). At the mesohabitat scale, seed viability increased with tussock cover (38.7% of the variance, $P < 0.0001$) and decreased with rock exposed by soil erosion (18.8% of the variance, $P = 0.015$, Fig. 1). An additional 6.7% was explained by East aspect, indicating that trees on East-facing slopes had less viable seeds than trees on West-facing slopes ($P = 0.04$). All selected variables together explained 64% of the variance in viability ($r^2 = 0.64$, $N = 29$). Natural rock outcrops, forest proportion, general slope and North aspect were not selected by the regression procedure. Pairwise correlations between selected variables were not significant (tussock grasslands and exposed rock: $r = -0.12$, $P = 0.54$; tussocks grasslands and relative East aspect: $r = 0.34$, $P = 0.07$; exposed rock and relative East aspect: $r = 0.29$, $P = 0.13$).

At the scale of microhabitat and individual characteristics, seed viability decreased with the percentage of rock under the canopy (23.2% of the variance, $P = 0.003$, Fig. 2a) and increased with tree height (10.5% of the variance, $P = 0.05$, Fig. 2b). Total explained variance ($r^2 = 0.34$, $N = 29$) was

lower than in the analysis at the mesohabitat scale. Sun incidence, number of trunks, and basal trunk perimeter were not selected, and there was no correlation between the selected variables "rock under the canopy" and "individual height" ($r = 0.13$, $P = 0.50$).

When we considered all significant variables together to determine their relative importance, the multiple regression procedure selected the same variables which had been selected at the mesohabitat scale (% tussock grassland, % rock exposed by soil erosion and relative East aspect), with no microhabitat or individual variables (hence $r^2 = 0.64$ as at the mesohabitat scale).

4. Discussion

In the mountains of central Argentina, *P. australis* develops a high percentage of empty or otherwise non-viable seeds. Fruit set and subsequent fruit growth do not seem to be dependent on the presence of a growing embryo, which contrasts with other species of Rosaceae (Stephenson, 1981). Well developed fruits containing empty seeds may result either from post-fertilisation embryo abortion due to lack of nutrients, or from parthenocarpy, in absence of pollination (Stephenson, 1981; Campbell and Halama, 1993). It is difficult to determine which of the two causes
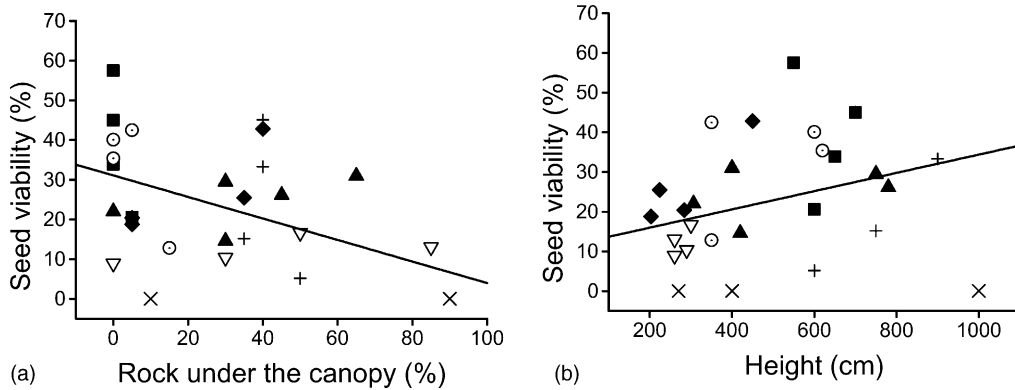
Fig. 2. *P. australis* seed viability and (a) % rock under the canopy, (b) tree height, according to the forward stepwise regression procedure (viability = 19.701 − 0.271 × % rock + 0.023 × height). For each plot the regression line was drawn leaving the remaining explanatory variables as constants equivalent to their average (height = 495 cm, rock under the canopy = 30.7%). Symbols represent areas as in Fig. 1.

initiates the seedlessness of fruits without employing manipulative experiments. However, the best viability for *P. australis* trees growing in tussock grasslands habitats with no soil erosion suggests a connection to nutrients and/or water stress. In the Cordoba mountains, large tussock grasslands occur in relatively flat areas where burning and livestock grazing have been a relatively minor disturbance factor for at least two decades. Soils where these communities occur are characterized by a relatively high water absorption capacity, and high nutrient content, as opposed to eroded or naturally rocky areas (Cabido et al., 1987; Pucheta et al., 1998; Cingolani et al., 2003a). In accordance with our results, Cierjacks and Hensen (in press) demonstrated that increasing grazing intensity is positively correlated with the percentage of aborted acorns of Mediterranean holm oaks (*Quercus ilex*) and that it negatively influences acorn quality. Jordano (1988) and Verdú and García-Fayos (1998) found evidence that water is the limiting factor which accounts for the high production of parthenocarpic fruits in *Pistacia lentiscus*.

Also in line with the resource deficiency hypothesis, in this study individuals with a higher percentage of rock substrate under their canopy produced a lower percentage of viable seeds. In the Cordoba mountains, rocky and inaccessible deep ravines and cliffs are usually covered by extensive *Polylepis* forests (i.e. the largest populations of our study) and for many decades these habitats were thought to be the most favourable for growth and reproduc-

tion (discussion in Fjeldså and Kessler, 1996). However, evidence exists that forests on rocky and inaccessible deep ravines and cliffs are relict fragments that have survived man-made fires, livestock browsing and firewood cutting and are not necessarily the best habitat for the natural growth and reproduction of *Polylepis* (Fjeldså and Kessler, 1996; Renison et al., 2002a,b). The significant association between slope aspect and seed viability could be due to West-facing slopes being warmer than slopes facing East (Price, 1981). In cold regions, higher radiation intensity and warmth may benefit growth and seed production directly, or indirectly by accelerating decomposition rates and thereby increasing availability of nutrients (Seastedt et al., 1983; Yang et al., 1998; Posse et al., 2000).

P. australis forest fragmentation was not related to seed viability, suggesting that pollination inefficiency is not a main factor affecting seed viability in isolated trees. This result corresponds with the results of ongoing studies on pollen fertility and pollination efficiency of *P. australis* which suggest that post-fertilisation embryo abortion is more likely to be the reason for non-viability than absence of pollination (Seltmann et al., personal communication). *P. australis* flower structure indicates wind pollination (Simpson, 1979) and preliminary studies with pollen traps suggest that *P. australis* pollen is dispersed at least several hundred meters from the flowers (Seltmann et al., personal communication). Moreover, studies in other wind pollinated trees have found that

out-crossing rates are usually high (e.g. *Quercus chrysolepis*, Montalvo et al., 1997), further supporting the hypothesis that pollination inefficiency in *P. australis* is not a main factor affecting seed viability.

Mesohabitat characteristics were more important than microhabitat and individual characteristics when considered together in the multiple regression. This suggests that nutrient and/or water deficiency might be widespread on degraded sites and that even small patches with apparently good soil conditions are affected by lack of nutrients and/or water when surrounded by degraded areas. A high percentage of exposed rock due to erosion and low coverage of tussock grasses, indicates that the site suffered periodic burning and overgrazing over many years with a consequential permanent low vegetation ground cover (Cingolani et al., 2003a).

The results of this study suggest that a reduction of livestock and burning practices would be necessary in order to prevent further soil destruction (Cingolani et al., 2003a) and losses in *P. australis* seed viability. For reforestation purposes seeds should be collected from undisturbed areas with well preserved soils. We suggest that similar studies be carried out with other *Polylepis* species and be replicated during several seeding seasons to determine possible interactions with climatic variability. We also propose long term fertilisation and irrigation experiments to confirm whether nutrients and/or water are responsible for low seed viability.

Acknowledgements

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