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Age–size–habitat relationships for *Polylepis australis*: dealing with endangered forest ecosystems

Ma. Laura Suarez · Daniel Renison · Paula Marcora · Isabell Hensen

Abstract   Assessing tree ages is important for the understanding of forest recruitment patterns and tree growth. However, little experience exists in the subtropics and accurate aging usually involves potentially damaging techniques such as tree coring or even the use of entire cross sections, which is not recommendable in endangered species or ecosystems. We provide an example of how age may be predicted on the basis of tree size and site conditions, using *Polylepis australis* of Central Argentina. Our study was conducted in two entire river basins where 96 independent trees were successfully cored for age analysis. Site and tree characteristics were registered and tree age determined through standard dendrochronological techniques. The multiple regression procedure selected tree circumference and proportion of rock under the tree canopy as significant variables explaining 48% of the variation in number of growth rings. Trees surrounded by rock clearly grew slower than those surrounded by a higher proportion of soil and vegetation. A comparison with a one site study shows that the ability to predict *P. australis* age is clearly reduced when geographical range is extended but the explanatory power of our model is still high enough for certain applications and within the range of other one site studies. We suggest that tree size and site characteristics may be used to predict age in other subtropical mountain forests with a well marked growth season.

Keywords   Age–size relationship · Site characteristics · Rock cover · Endangered ecosystems

Ma. L. Suarez
Laboratorio Ecotono, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Quintal 1250, 8400 Bariloche, Argentina

D. Renison (✉) · P. Marcora
Cátedra de Ecología, FCEFyN, Universidad Nacional de Córdoba,
Av. Vélez Sarsfield 299, X5000JJC Cordoba, Argentina
e-mail: drenison@com.uncor.edu

I. Hensen
Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg,
Am Kirchtor 1, 06108 Halle, Germany

Introduction

Assessing data on tree ages is extremely important in determining forest recruitment patterns, tree growth and the responses of forests to climate change, human and natural disturbances. However, few studies exist in the subtropics (Grau et al. 2003) and the task of obtaining accurate tree ages is not easy. During the last two decades several studies have attempted to improve the accuracy of tree age estimation, but all involved techniques such as extraction of increment cores or entire cross-sections (Norton et al. 1987; Villalba and Veblen 1997; Wong and Lertzman 2001; Gustell and Johnson 2002; Rozas 2003). These proceedings are unsuitable for endangered forest ecosystems, for which the development of less destructive methodologies is urgently needed.

A potential lower impact procedure, and one which would also be less time-consuming, involves the prediction of age on the basis of stem size (Morey 1936; McConnell and Smith 1963; Lieberman et al. 1985; Acosta 1986; O'Brien et al. 1995; Loewenstein et al. 2000). Although age and size are generally correlated, data are highly variable, not only between individuals, but also between sites. This is a consequence of the amount of resources allocated to growth, which in turn is determined by several related factors including climate, soil conditions, topography, internal growth regulators, stored nutrients, competition and disease (Fritts 1971, 1976). On average, when considering a specific study area, size explains only half of the variance in the age of a tree (McConnell and Smith 1963; Loewenstein et al. 2000; Perryman and Olson 2000). However, few studies that have considered size for age prediction have included other environmental or tree related variables to improve age estimation (as in Echeverría and Lara 2004). In addition, tree age–size relationships are generally developed for one specific site (McConnell and Smith 1963; Lieberman et al. 1985; Acosta 1986; Perryman and Olson 2000), and cannot be easily extrapolated to other sites. Thus, a single age by size estimation derived from a specific site could lead to a misinterpretation of age distribution and, consequently, stand dynamics.

Here we attempt to predict *Polylepis australis* age on the basis of stem diameter and site conditions. Forests dominated by *Polylepis* belong to the most endangered tropical and subtropical mountain forest ecosystems of the world (UNEP-WCMC 2004). They are restricted to the high mountains of South America where the use of fire to promote grass re-growth, domestic animal grazing, removal of timber and firewood, and soil erosion have reduced these forests to isolated patches (Ellenberg 1979; Hensen 1995, 2002; Fjeldså and Kessler 1996; Kessler 2000, 2002; Lauer et al. 2001; Teich et al. 2005; Renison et al. 2006). However, very little is known about the ecology, growth, structure, regeneration and dynamics of *Polylepis* forests, and data on age-class distributions of populations are urgently needed to develop suitable management strategies. Three *Polylepis* species have already been successfully used for dendrocronological studies, suggesting the genus is well suited for this kind of study (Acosta 1986; Roig et al. 2001; Argollo et al. 2004; Morales et al. 2004).

Polylepis australis, the southernmost species of this genus, dominates the canopy of open-canopy forests (also called woodlands) in Northern and Central Argentina. It is characterized by well marked growth rings. A first *P. australis* age–size relationship was demonstrated by Acosta (1986) who, using entire cross-sections found that an amazing 95% of the variation in age was explained by stem diameter, suggesting great potential for the use of stem diameter as a proxy for age. However, this study was conducted in a very restricted geographical area and the largest studied tree had a circumference of only 75 cm. It was therefore not known whether the predictive value of the model derived by Acosta (1986) is transferable to other areas, whether site characteristics could improve the estimation, or

whether the predictive model can be used for trees with larger circumferences. Therefore, the main objective of our study was to develop a more general age prediction model which incorporated site characteristics for *P. australis* in the Córdoba Mountains of Central Argentina. We believe this approach could be useful for other mountain tree species with well defined summer growth seasons.

Methods

Study area

The landscape of the Córdoba Mountains, Argentina is a mosaic of different types of tall tussock grasslands, grazing and hydromorphic lawns, natural granitic outcrops, exposed rock surfaces produced by soil erosion as a consequence of excessive livestock densities, and open-canopy forests, which are dominated by *P. australis* (Rosaceae) trees (Cingolani et al. 2004, 2007). The forests are often associated with steep areas with rock outcrops, because these sites are less affected by browsing and fires (Renison et al. 2002; Teich et al. 2005; Renison et al. 2006). Annual precipitation is 840 mm and mean temperature of the coldest and warmest months are 5.0 and 11.4°C, respectively (at 2,100 m asl., Cabido 1985).

Data collection

This study was conducted within the "Condorito" (31°37/40′ S, 64°40/46′ W) and "Tabaquillo" (32°02/04′ S, 64°49/56′ W) river basins (37,400 ha—linear distance between both basins was approximately 45 km) where *P. australis* individuals are found both in protected rocky areas and in areas with more favourable soil conditions but with greater interference by livestock and fires (Cingolani et al. 2004; Renison et al. 2006). We sampled 140 trees separated by a distance of between 0.5 and 10 km, and we made an effort to select as wide a range of tree sizes and site characteristics as possible. We excluded trees growing under the canopies of other trees, thereby ensuring that all cored individuals were dominant trees. Trees were cored as low down the trunks as possible; to minimize damage due to core extraction we only selected trees with basal circumferences of >0.30 m (ca. 0.10 m diameter at basal height). According to Acosta (1986), tree rings are always complete. However, as *P. australis* stems have irregular shapes, two cores were sampled in each tree (at opposite sides) to augment the probability of reaching the centre. When the tree had more than one basal stem, we cored the stem with the largest circumference (as in Acosta 1986). We followed Stokes and Smiley's (1968) standard dendrochronological methods to mount, sand, measure and count growth rings.

In order to obtain the best age predictor, we assessed circumference at the coring level. In addition, we registered tree height, number of basal stems per tree, crown exposition (by sun trajectory on the crown of the tree), and distance to the nearest conspecific neighbour of equal or greater height. We also recorded topographic and site variables including altitude above sea level, slope, proportion of bare soil, and proportion of rock under the tree crown (in accordance to Renison et al. 2006).

Data analysis

Unfortunately, available climatic data for the study area were scarce and cover only the last 15 years, and there were no chronologies available for *P. australis* in sites covered by

climate data. Because reliable cross-dating of tree-ring series should not be expected for sequences of less than around 40 or 50 years, cross-dating was made using pointer years. Thus, we used "narrow years" that were coincident in several samples—but were unable to detect missing years. *P. australis* apparently does not tend to form packages of micro-rings or extremely narrow rings, which normally results in uncounted years (see Acosta 1986 for details of annual ring formation in *P. australis*).

In samples that reached the pith, total age was considered equal to the number of total tree-rings dated in the sample. However, as *P. australis* wood is fairly dark and the limit of growth rings is usually not visible without smoothing, the presence/absence of pith was impossible to determine in the field. Thus, not until after smoothing sample sections in the laboratory did it become evident that in many cases the cores did not reach the centre. In such cases, age was estimated by Duncan's (1989) geometrical procedure, setting a maximum of 10 estimated missing rings, above which, age was not estimated (e.g. broken cores, trees with rotten centres). To perform the extrapolations we measured width of the five innermost rings using a computer compatible increment tree ring measurer (0.01 mm resolution) and a stereomicroscope. We always considered age at coring height instead of true age (or date of tree establishment), as the latter would imply the use of destructive methods to estimate time taken by the young trees to reach sampling height (Norton et al. 1987; Villalba and Veblen 1997).

To obtain the best set of predictors of *P. australis*' coring age, we used the forward procedure of multiple linear regression analysis. Independent variables included circumference at coring height, tree height, number of basal stems per tree, distance to the nearest tree of the same or larger height, altitude above sea level, sun trajectory, slope, aspect, proportion of rock, and proportion of bare soil under the tree canopy. We also added coring height to determine if this variable was influencing the predictions, and checked whether altitude above sea level had a unimodal response (larger growth at intermediate altitudes where Polylepis forests are more frequent) by including its squared term in the model. After checking residuals, number of growth rings and circumference were log transformed to meet normality and homocedasticity assumptions, and two outliers had to be deleted (both trees clearly older than would have been predicted by our model). Proximity to the nearest tree was also log transformed considering that short distances mattered more than large distances. Slope aspect was transformed to a relative north and east aspect (calculated through cosine and sine transformations, respectively).

Results

Our sample encompassed a total of 218 increment cores (radii) corresponding to 140 *P. australis* trees. However, for 42 of the 140 trees it was either impossible to count rings due to decomposed pith (25%), or neither of the two cores per tree met the criteria of ≤10 estimated missing rings (3.5%). None of the remaining 98 trees showed microring packages or extremely narrow rings, and in all cases, the innermost part of tree growth (younger stages) showed wide rings, thus the number of estimated missing rings was always low (on average: 3 years). After deleting two outliers (see statistical analysis), our final sample size was $n = 96$.

Tree and site characteristics

Table 1 summarizes data on coring height, tree and site characteristics. In general, *P. australis* trees were not exceedingly tall (average tree height was 3.4 m) and grew under

Table 1 Summary statistics for *P. australis* coring, tree and site characteristics (*N* = 96 trees)

Variable	Mean ± SD	Range
Coring height (cm)	30.6 ± 6.5	10–40
Circumference at coring height (cm)	52.0 ± 22.1	30–160
Tree height (m)	3.4 ± 1.1	1.9–8.0
Number of basal stems per tree	2.6 ± 1.6	1.0–9.0
Distance to the nearest tree (m)	6.5 ± 17.3	1–>100
Proportion of rock under the canopy (%)	33.2 ± 30.4	0–100
Proportion of bare soil under the canopy (%)	9.9 ± 17.0	0–80
Altitude above sea level (m asl.)	1,911 ± 406	905–2,700
Slope (°)	22.2 ± 16.7	0–70
Sun incidence (°)	112.8 ± 32.9	40–170

a variety of site characteristics. Only one tree reached 8 m in height and was also one of the oldest ones. Tree circumference at coring height of our samples ranged from 30 to 160 cm, with a predominance of smaller sizes (Fig. 1). This pattern coincided with a high predominance of younger trees (Fig. 2; piths of trees with a larger circumference of up to 3.65 m were always decomposed).

Age–size–site relationships

The multiple regression procedure selected tree circumference and proportion of rock under the canopy as significant explanatory variables of number of growth rings ($F = 23.04$, adjusted $r^2 = 0.48$, $P < 0.0001$). Tree height, number of basal stems per tree, sun trajectory, distance to the nearest tree, slope inclination and aspect, proportion of bare soil under the tree canopy, coring height, altitude above sea level and its quadratic term were not selected. Tree circumference explained 44% of the variance in age, while
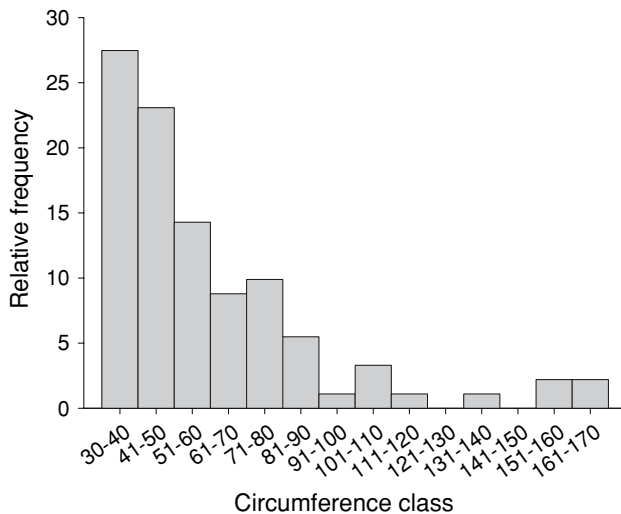

Fig. 1 Size (circumference at coring height) distribution of 96 *P. australis* trees
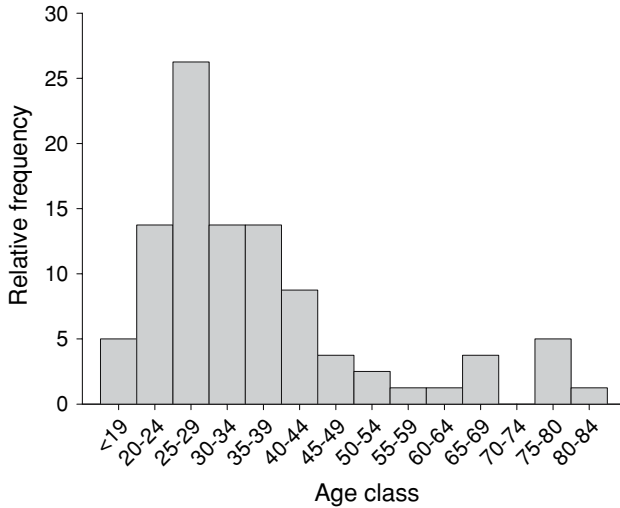
Fig. 2 Age (at coring height) distribution of 96 cored *P. australis* trees
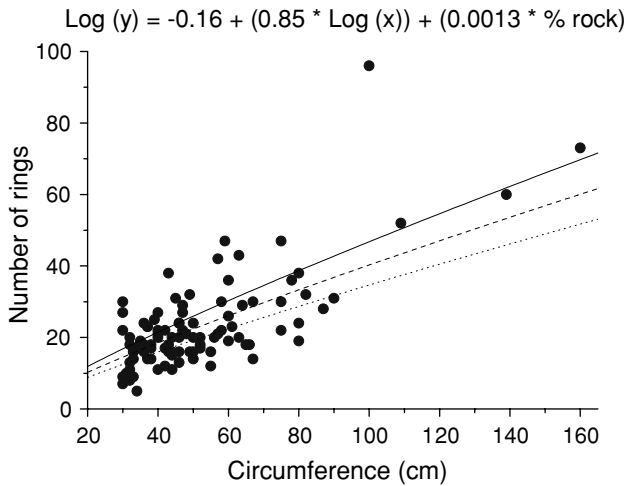

Fig. 3 Number of *P. australis* growth rings in relation to circumference and proportion of rock under the canopy. The lines indicate the best-fit regression model with log transformations for number of rings and perimeter; lower to upper lines correspond to 0%, 50% and 100% rock under the canopy, respectively. The four trees with the largest perimeter and number of rings are above the middle line because the log transformation reduces the importance of large values and thus have not influenced the regression model as much as its observation at a linear scale would suggest

proportion of rock under the canopy only explained a further 4%. The model which best-explained *P. australis* age was: $\text{Log}(y) = -0.16 + (0.85 \times \log(\text{circumference in cm})) + (0.0013 \times \% \text{ rock})$. As both circumference and proportion of rock were positively associated to age, trees with a higher proportion of rock under their canopies were older (as determined by number of growth rings) than would have been predicted by their circumference alone (Fig. 3).

Discussion

Circumference and proportion of rock under the tree canopy were significant predictors in estimating the number of tree rings at coring height of dominant *P. australis* in Central Argentina, even when using a large area as that encompassed by our study. The model we derived to predict *P. australis* age of dominant trees was very similar to that calculated by Acosta (1986); log *y* = −0.36 + 0.78 log (circumference in cm), which we presume also consisted of dominant trees, as the forests of her study area—and most of the mountains of central Argentina—consist of relatively small trees which have re-sprouted after fires and do not reach a competition stage where clear dominant and sub-dominant trees coexists (Renison et al. in press). Thus, the main result of our study reveals that the predictive power of circumference in estimating *P. australis* age is still fairly high when individuals are sampled under differing site characteristics and the measurement of the proportion of rock may add a little more explanatory power (a total of 48% of the variance explained in our study compared to 95% in Acosta 1986). In addition, the utilization of increment cores instead of fully destructive cross-sections (used in Acosta 1986) seemed to be an appropriate method for determining the number of tree rings for *P. australis*.

The results of our survey are remarkable as only a few studies have reported reasonable age–size relationships for tree individuals. Total variations in age explained by stem diameter ranged between 34% to 86% for individuals within particular stands (McConnell and Smith 1963; Brotherson et al. 1984; Veblen 1986; Tyrrell and Crow 1994; O'Brien et al. 1995). In all cases, the regression models were not transferable to other scales. Generally, the given relationship between age and size was valid only within a given stand of one particular site, and it must be re-determined for different sites. However, Perryman and Olson (2000), found regression models that were consistent across stands and at different geographical scales. In that study, as in ours, total variability explained by stem diameter decreased as a predictable response when combining data sampled from areas that varied in several characteristics (soil type, precipitation amount, vegetation, etc.).

Our data shows that tree age–size relationships can be slightly improved by taking site characteristics into account, in particular the proportion of rock under the canopy. Many *P. australis* trees are restricted to rocky sites where they survive fires and livestock browsing (Renison et al. 2002, 2006), but our data shows that these sites are of lower quality for tree growth. In concurrence, *P. australis* growth was found to be clearly reduced in rocky microsites in other studies (Renison et al. 2005; Marcora et al. in press). Thus, diminished soil water-holding capacity and nutrient levels may constitute the most important limiting factor for *P. australis* seedling and tree growth, as already pointed out by Fritts (1976). In addition, differences in soil physical and chemical properties between different *P. australis* stands, exposure to wind and other variables not included in this study may explain another part of the variation in growth. For example, Enrico et al. (2004) found the proportions of lime, clay, and organic matter, as well as the contents of N, P, Ca, Mg and K to be significantly higher in a woodland area in a steep ravine than in an exposed shrubland area where *P. australis* growth was reduced. Also Villalba et al. (1994) named slope aspect and steepness—which mainly influence air temperature and soil moisture—to be the most critical site factors for the growth of subalpine trees. In a recent study Marcora et al. (in press) found a small portion of the variability in *P. australis* ring-width to be associated to altitude above sea level, with the widest rings at intermediate altitudes. Although the trees of our study had a similar trend, we suppose the relation was not significant because our trees were more heterogeneous in sizes, microsite characteristics and geographical range, thus blurring the influence of altitude.

We conclude that for threatened ecosystems like subtropical *Polylepis* forests, a preliminary study of the relation between age, circumference and site characteristics may later be used to interpret stand structure and development, facilitating the drawing up of adequate management plans. In addition, our results present further evidence supporting the theory that the current distribution of *Polylepis* forests, at least in our study area, is attributable to human impact (Ellenberg 1979; Hensen 2002; Kessler 2002; Renison et al. 2002, 2006; Cingolani et al. 2007) as tree growth is clearly reduced at microsites with a high proportion of rock, to where they have been restricted due to fires and long term grazing pressure.

References

Acosta A (1986) Estructura poblacional de *Polylepis australis*. In: MAB 6: Efecto de las actividades humanas sobre los ecosistemas montañosos y de tundra. MAB-PNUMA, pp 392–401

Argollo J, Soliz C, Villalba R (2004) Potencialidad dendrocronológica de *Polylepis tarapacana* en los Andes Centrales de Bolivia. Eco Bol 29:5–24

Brotherson JD, Carman JG, Szyska LA (1984) Stem-diameter age relationships of *Tamarix ramosissima* in Central Utah. J Range Manage 34:362–364

Cabido MR (1985) Las comunidades vegetales de la Pampa de Achala, Sierras de Córdoba, Argentina. Doc Phytosociol 9:431–443

Cingolani AM, Cabido MR, Renison D, Solís Neffa V (2004) Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. J Veg Sci 14:223–232

Cingolani A, Renison D, Tecco P, Gurvich D, Cabido M (2007) Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. J Biogeog. doi: 10.1111/j.1365-2699.2007.01807.x

Duncan RP (1989) An evaluation of errors in tree age estimates based on increments cores in Kahukatea (*Dacrycarpus dacrydioides*). N Z J Nat Sci 16:31–37

Echeverría C, Lara A (2004) Growth patterns of secondary *Nothofagus oblique—N. alpina* forests in southern Chile. For Ecol Manage 195:29–43

Ellenberg H (1979) Man's influence on tropical mountain ecosystems in South America. J Ecol 67:401–416

Enrico L, Funes G, Cabido MR (2004) Regeneration of *Polylepis australis* Bitt. in mountains of central Argentina. For Ecol Manage 190:301–309

Fjeldså J, Kessler M (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

Fritts HC (1971) Dendroclimatology and dendroecology. Quaternary Res 1:419–449

Fritts HC (1976) Tree rings and climate. Academic Press, London

Gustell SL, Johnson EA (2002) Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. J Ecol 90:153–166

Grau HR, Easdale TA, Paolini L (2003) Subtropical dendroecology-dating disturbances and forest dynamics in northwestern Argentina montane ecosystems. For Ecol Manage 177:131–143

Hensen I (1995) Die vegetation von *Polylepis*-Wäldern der Ostkordillere Boliviens. Phytocoenologia 25:235–277

Hensen I (2002) Impacts of anthropogenic activity on the vegetation of *Polylepis* woodland in the region of Cochabamba, Bolivia. Ecotropica 8:183–203

Kessler M (2000) Observations on a human-induced fire event at a humid timberline in the Bolivian Andes. Ecotropica 6:83–93

Kessler M (2002) The "*Polylepis* problem": where do we stand? Ecotropica 8:97–110

Lauer W, Rafiqpoor MD, Theisen I (2001) Physiogeographie, Vegetation und Syntaxonomie der Flora des Páramo de Papallacta (Ostkordillere Ecuador). Erdwissenschaftliche Forschung 39, Stuttgart

Lieberman D, Lieberman M, Hartshon G, Peralta R (1985) Growth rates and age–size relationships of tropical wet forest trees in Costa Rica. J Trop Ecol 1:97–109

Loewenstein EF, Johnson PS, Garrett HE (2000) Age and diameter structure of a managed uneven-aged oak forest. Can J For Res 31:1060–1070

Marcora P, Hensen I, Renison D, Seltmann P, Wesche K The performance of *Polylepis australis* trees along their entire altitudinal range: implications of climate change for their conservation. Divers Distrib, in press

McConnell BM, Smith JG (1963) Estimation of bitterbrush age from stem-diameter measurements. Ecology 44:579–581

Morales MS, Villalba R, Grau HR, Paolini L (2004) Rainfall-controlled tree growth in high-elevation subtropical treelines. Ecology 85:3080–3089

Morey HF (1936) Age–size relationships of hearts content, a virgin forest in northwestern Pennsylvania. Ecology 17:251–257

Norton DA, Palmer JG, Odgen J (1987) Dendroecological studies in New Zealand. 1. An evaluation of tree age estimates based on increment cores. N Z J Bot 25:373–383

O'Brien ST, Hubbell SP, Spiro P, Condit R, Foster RB (1995) Diameter, height, crown, and age relationship in eight neotropical tree species. Ecology 76:1926–1939

Perryman BL, Olson RA (2000) Age-stem diameter relationships of big sagegrush and their management implications. J Range Manage 53:352–346

Renison D, Cingolani AM, Suarez R (2002) Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba, Argentina. Rev Chil Hist Nat 75:719–727

Renison D, Cingolani AM, Suarez R, Menoyo E, Coutsiers C, Sobral A, Hensen I (2005) The restoration of degraded mountain forests: effects of seed provenance and microsite characteristics on *Polylepis australis* seedling survival and growth in Central Argentina. Rest Ecol 13:129–135

Renison D, Hensen I, Suarez R, Cingolani AM (2006) Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? J Biogeogr 33:876–887

Renison D, Bellis L, Guzmán GF, Grau R, Pacheco S, Rivera L, Politi N, Martin E, Cuyckens E, Marcora P, Robledo G, Cingolani AM, Perasso L, Cornell F, Dominguez J, Landi M, Hensen I Estado de conservación de los bosques Argentinos de *Polylepis* y su avifauna. In: "Una Contribución al Conocimiento de los Bosques Altoandinos de *Polylepis*: Distribución, Diversidad y Estado Actual de los Bosques más Altos del Mundo". American Bird Conservancy—Comunidad Andina, Lima, Perú, in press

Roig F, Fernández M, Gareca E, Altamirano S, Monge S (2001) Dendrochronological studies in the humid puna environments of Bolivia. Rev Bol Ecol 9:3–13

Rozas V (2003) Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecol 167:193–212

Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. University of Chicago Press, Chicago

Teich I, Cingolani AM, Renison D, Hensen I, Giorgis M (2005) Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? For Ecol Manage 219:229–241

Tyrrell LE, Crow TR (1994) Structural characteristics of old-growth Hemlock-Hardwood forests in relation to age. Ecology 75:370–386

UNEP-WCMC (2004) United Nations Environment Programme. World Conservation Monitoring Center; http://www.unep-wcmc.org

Veblen TT (1986) Age and size structure of subalpine forests in the Colorado Front Range. Bol Torr Bot Club 113:225–356

Villalba R, Veblen TT (1997) Improving estimates of total tree ages based on increment core samples. Ecoscience 4:534–542

Villalba R, Veblen TT, Ogden J (1994) Climatic influences on the growth of subalpine trees in the Colorado front range. Ecology 75:1450–1462

Wong C, Lertzman P (2001) Errors in estimating tree age: implications for studies of stand dynamics. Can J For Res 31:1262–1271