

# Seed production in *Polylepis australis* (Rosaceae) as influenced by tree size, livestock and interannual climate variations in the mountains of central Argentina

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Received: 15 August 2011 / Accepted: 10 February 2012  
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**Abstract** The expansion of tree species within a grassland-woodland matrix relies heavily on an abundant seed crop, which may be affected by many factors; among these, browsing by livestock has gone largely ignored. Here we explore how seed production is affected by tree size, grazing by large domestic herbivores and interannual climate fluctuations in a small-sized tree (*Polylepis australis*, Rosaceae), which dominates the remnant forests in the high mountains of central Argentina. Seed number and seed mass per tree were quantified in 100 different-sized trees located in areas with and without livestock. Using seed traps we also determined seed rain variation in 15 plots between 2005 and 2008. The estimated number of seeds per tree ranged from 0 to 224,000 and increased with tree height (power relation); for trees smaller than 354 cm in height, seed production was lower in areas with livestock and higher in areas without livestock. Mass per seed increased with tree height, with no significant livestock effect. The largest seed rain was recorded in 2008, probably due to growth of seed trees and not in response to climate. To promote seed production and forest expansion, livestock should be excluded from areas with small trees, such as forest edges.

**Keywords** Mountain forest · Large herbivores · Seed mass · Browsing · Seed rain · Plant reproduction

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## Introduction

Seed production and dispersal to sites of favorable conditions are essential components in regeneration, expansion and migration of tree populations (Spies and Turner 1999; Kramer et al. 2006; Du et al. 2007; Van Do et al. 2011). In particular, low seed capital limits the number of seedling recruits and might limit population growth (Turnbull et al. 2000; Brown et al. 2003). Moreover, yearly variations in seed production in response to environmental and demographic events might affect population dynamics, particularly in species that do not form soil seed banks and that have infrequent asexual reproduction (Turnbull et al. 2000). Thus, knowing the factors influencing seed production is important to understand tree population dynamics (Caswell 1989; Brown et al. 2003; Van Do et al. 2011).

Seed production may be affected by a large array of factors, such as substrate type, interannual climate variations, altitude and slope aspect (Young and León 2007; Torres et al. 2008; Wesche et al. 2008). In high mountain areas worldwide, livestock breeding is one of the principal economic activities (Price 1981), tree height is reduced due to harsh climate conditions and tree biomass is therefore made more available to consumption by livestock. Reduced seed production in trees within reach of livestock may be caused by flower and seed predation (Haase et al. 1995) or indirectly by consumption of vegetative tissues, which reduces resources that could otherwise be assigned to seed production (Bergström and Danell 1987; Fenner and Thompson 2005). However, in woody plant species tolerant to browsing, herbivory can have an indirect positive effect by eliminating competition or modifying fire regimes (Asner et al. 2004; Cingolani et al. 2005; Katjiua and Ward 2006). Some woody plants have developed tolerance to herbivory by partially compensating or even over-compensating the lost tissues through rapid regrowth (Stowe et al. 2000; Cingolani et al. 2005; Stevens et al. 2008). This response has been interpreted as an expression of a mutualistic relationship between herbivores and plants (Agrawal 2000). Thus, the effects of herbivores on seed production and other aspects of tree performance are not easy to predict (Sankey et al. 2006a, b; Cingolani et al. 2005). Moreover, individuals are not evenly affected by livestock. Small trees are more accessible whereas large trees are usually out of reach of domestic herbivores; and even if reached by herbivores, large trees have more abundant seed crops due to their higher photosynthetic surface, better competitive ability and accessibility to water and other nutrients than small trees, although notable exceptions have been reported (Guariguata and Pinard 1998; Greenberg 2000).

In the mountains of South America, introduced domestic livestock (cattle, goats, sheep, mules and horses) have substantially reduced the extent and structural complexity of *Polylepis* forests (Hensen 1995; Purcell and Brelsford 2004; Cingolani et al. 2008; Giorgis et al. 2010; Renison et al. 2010, 2011). As livestock rearing is one of the principal economic activities in most mountain regions in the world (Price 1981), understanding its effects on mountain forests is both economically and ecologically important (García et al. 2008; Renison et al. 2010). In these regions, livestock might influence the development of several stages of the tree plant cycle and might affect the dynamics of several processes including forests expansion. Knowing how and to what extent livestock might affect seed production is important to understand the dynamics of woody species populations, specially in the southern hemisphere where this aspect has received little attention. Moreover, knowing which stages of the plant cycle are the most seriously affected might contribute to management decision making. Additionally, to promote seed production and forest development, managing livestock may be easier than managing other potentially involved factors.

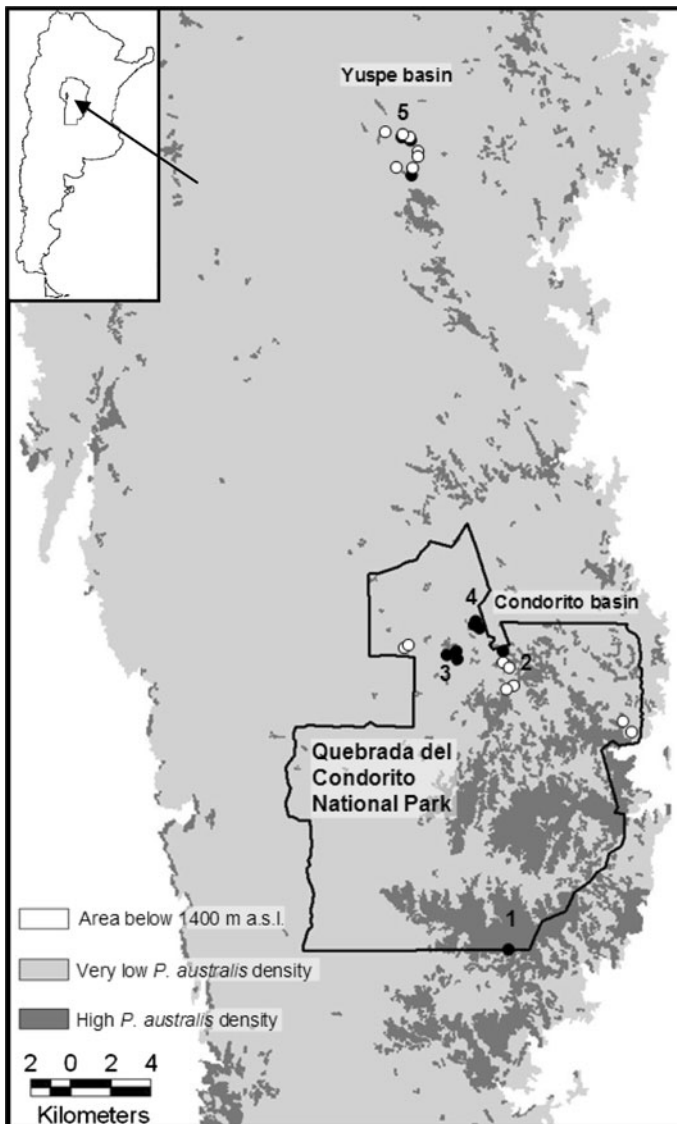
The effect of livestock on different stages and processes of the life cycle of *Polylepis australis* Bitter (Rosaceae) has been intensively studied to generate information for management decision makers and to promote the needed regeneration of these forests. Thus, we know that moderate grazing promotes *P. australis* seedling recruitment due to reduced competition from ground vegetation (Torres et al. 2008; Zimmerman et al. 2009). However, subsequent livestock exclusion is needed to accelerate the growth of the established seedlings, because continuous browsing of juveniles, even at relatively low livestock densities, prevents the recruitment of adult reproductive trees (Giorgis et al. 2010), as occurs in other woody species (Close et al. 2009). In addition, livestock-induced soil erosion reduces *P. australis* seed viability indirectly (Renison et al. 2004, 2010). Enhanced seedling recruitment in two *Polylepis* species was also found in Ecuador in areas with heavier livestock use than in the mountains of central Argentina (Cierjacks et al. 2007, 2008). However, to the best of our knowledge, there are no studies quantifying seed production of *P. australis* per tree or relating this trait to livestock. Moreover, most studies on seed production have focused on seed rain using traps but not on seed production per tree, for which there is scarce information, particularly in the southern hemisphere (Peinetti et al. 2001; Kelly and Sork 2002).

In an attempt to contribute to ongoing efforts to understand the effects of livestock rearing, our main objective was to determine how *P. australis* seed production is influenced by tree size, livestock and interannual climatic fluctuations. In particular, we: (1) quantified *P. australis* seed productivity (in terms of seed number and mass) across a wide range of tree heights, (2) compared *P. australis* seed productivity between areas with and without livestock, (3) compared seed productivity in branches of the same tree that were within or out of reach of livestock browsing, and (4) compared seed rain among years and in relation to interannual climatic fluctuations. We used a combination of seed trap data and direct estimation of seed production. Through seed counts we obtained a model that predicts seed crop on the basis of livestock presence or absence and tree size, which provides useful information to integrate seed production with other important life stages (Caswell 1989). Because a large proportion of the accessible *P. australis* biomass is consumed by livestock (Teich et al. 2005; Giorgis et al. 2010), we expect that domestic livestock will reduce seed production in small trees and that the effect of livestock will decrease with tree size.

## Materials and methods

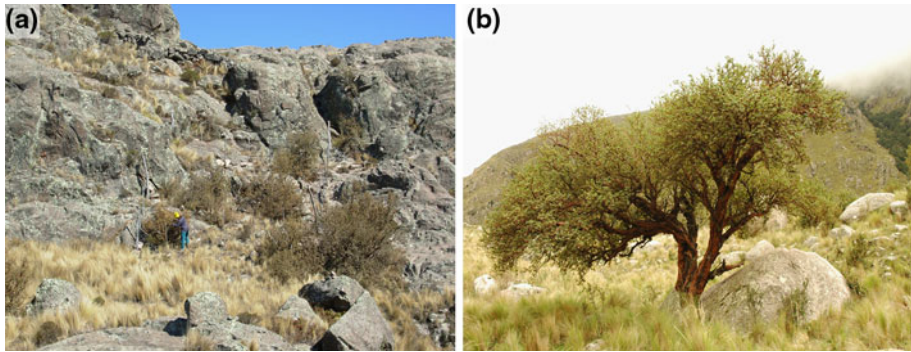
### Study area and species

The study was conducted in the mountains of central Argentina (North–South direction, maximum altitude 2,884 m a.s.l., 31°34'S, 64°50'W), where the Quebrada del Condorito National Park (37,000 ha) was created in 1996. The vegetation consists of a mosaic of tussock grasslands, grazing lawns, areas where soils have been lost and are now exposed rock surfaces, granite outcrops, and closed and open *P. australis* forests (2.5 and 9.4% of the area, respectively; Cingolani et al. 2004) (Figs. 1, 2a). The mean temperature for the coldest and warmest months is 5.0 and 11.4°C, respectively, with no frost-free period (data recorded at 2,100 m a.s.l., Cabido 1985). Mean annual precipitation is 920 mm, with 83% of the rainfall concentrated in the warmest months, between October and April (Colladon 2000).



**Fig. 1** Map of the mountains of central Argentina, with the relative location of study sites, in Pampa de Achala Provincial Hydric Reserve (area above 1,400 m a.s.l.). Black circles indicate sites used for studying livestock effects and white circles indicate sites used for studying seed rain. Numbers (1) and (2) indicate Quebrada del Condorito National Park S and NE boundaries, respectively; three experimental livestock exclosures were built in each of the three following sectors: (3) Las Lomitas (4) Las Ensenadas and (5) Yusepe basin. Sites with high and low *P. australis* cover are represented in grey scale

Like other South American mountains, the mountains of central Argentina have a long history of large herbivore grazing. Before the massive extinctions of the Pleistocene, this area was inhabited by glyptodon (*Glyptodon* sp.), milodon (*Scelidotherium* sp.), several camelids (like *Lama*, *Paleolama* and *Macrauchenia* spp.), horse predecessors (*Equus* sp.) and the toxodon (*Toxodon* sp.). Later, the mountains were grazed by guanacos (*Lama*



**Fig. 2** Study site and study species. **a** One of the experimental livestock exclosures in Las Ensenadas sector, used for estimating livestock effects on seed production, in a typical landscape of *P. australis* low cover, and **b** an individual of *P. australis*

*guanicoe*), rheas (*Rhea pennata*) and an unknown kind of deer, all of which were observed in the region until the 1920 s, when they became locally extinct (Díaz et al. 1994; Pucheta et al. 1998; Medina et al. 2011). Domestic livestock (cattle, goats, sheep, mules and horses) were introduced in the 1600 s and since the 1920 s they have been the only large herbivores in the area.

*Polylepis australis* altitudinal range varies from 900 to 2,700 m a.s.l., with most extensive forests occurring at about 1,850 m a.s.l., where the species finds optimal growing conditions (Cingolani et al. 2008; Marcora et al. 2008). *P. australis* sprouts after browsing and fires, and is tolerant to herbivory only at low rates of browsing (Giorgis et al. 2010). This species can grow as a shrub or a tree; trees can sometimes reach 14 m in height (Fig. 2b, Renison et al. 2011). Vegetative reproduction is very rare (Enrico et al. 2004). Sexual reproduction consists of an annual production of fruits (hereafter referred to as “seeds”), of approximately  $5 \times 3 \times 2$  mm in size. The fruits are wind-dispersed and do not form a persistent seed bank (Enrico et al. 2004). The seed capsules are dry, generally bearing one seed, and can be found on the tree during the austral summer, from December to March (Demaio et al. 2002). The seeds are not selected by livestock (personal observation); however, they might be occasionally consumed during livestock browsing of stems.

### Tree size, livestock and seed production

To examine whether tree size and livestock browsing affect seed production, we compared 50 pairs of trees of height ranging between 82 and 690 cm. Each pair consisted in one tree located in an area without livestock and another tree located in an area with livestock. Trees were selected from five sectors where fences divided areas with livestock from areas without livestock. The sectors were (1) Quebrada del Condorito National Park S boundary ( $31^{\circ}46'S$ ,  $64^{\circ}44'W$ —4 trees), (2) Quebrada del Condorito National Park NE boundary ( $31^{\circ}37'S$ ,  $64^{\circ}44'W$ —20 trees), and three experimental livestock exclosures built in each of the three following sectors: (3) Las Lomitas ( $31^{\circ}36'S$ ,  $64^{\circ}48'W$ —31 trees), (4) Las Ensenadas ( $31^{\circ}35'S$ ,  $64^{\circ}45'W$ —18 trees) and (5) Yuspe basin ( $31^{\circ}24'S$ ,  $64^{\circ}48'W$ —27 trees). Areas with livestock had traditional stocking rates ranging from 0.4 to 2.2 livestock equivalents  $ha^{-1}$  (Giorgis et al. 2010), whereas livestock was excluded in 1998 from the

two sectors within the National Park boundaries and at the beginning of 2004 from the nine exclosures distributed in sectors (3) to (5).

To best isolate the effects of tree size and livestock, we selected trees located in areas browsed or not by livestock and that were similar in other aspects we considered important in *P. australis* performance (Renison et al. 2004, 2006; Marcora et al. 2008; Suarez et al. 2008). For this purpose, we measured several tree attributes: height (cm), number of stems and stem basal circumference (in trees with several stems, we chose the largest one) and crown cover (often mentioned by its converse: crown transparency) as the proportion of the tree crown that covered the sky (% visual estimation). We also measured microsite variables: altitude above sea level (m a.s.l.), proportion of rock under the tree crown (%), topographic position (1 = valley; 2 = mid slope, 3 = summit), slope inclination (°) and slope aspect (degrees with respect to the North). We did not measure distance to the closest dominant tree because our study sectors had relatively isolated trees and previous studies showed that under these conditions no significant effect of competition could be demonstrated (Suarez et al. 2008). We estimated relative livestock densities by calculating dung frequency, following Cingolani et al. (2003). For that purpose, we haphazardly threw 40 quadrats (30 × 30 cm) in the surroundings of each tree and calculated the percentage of quadrats with dung in relation to the total quadrats thrown. We also estimated intensity of browsing by counting the number of browsed buds of 100 randomly chosen buds per tree.

Seeds were harvested from selected trees between December 2005 and January 2006. We divided each tree into four quarters using ropes and we randomly chose two quarters to collect all seeds manually (adapted from Kay 1995). When we were unable to harvest all the seeds of the two selected quarters in a tree, we estimated visually the proportion of harvested seeds. To estimate seed production per tree, for each quarter we weighed the collected seeds, counted and weighed a sub-sample of 1,000 seeds and estimated the total number of collected seeds. We estimated the average seed mass per tree by weighing the 1,000 seeds in 10 groups of 100 seeds per tree (mg).

As an additional evaluation of livestock effects, we performed a within-tree comparison in 20 trees situated in exclosures but with branches that were within reach of browsing by livestock from adjacent paddocks. There were trees in this situation in four of the five study sectors. We selected trees that were less than 2 m tall because trees of this size are more susceptible to browsing (in terms of growth, Teich et al. 2005). From each tree we selected a branch within livestock reach and a similar branch out of livestock reach. We collected and counted all seeds from each branch. Branches were characterized by measuring their length (cm), basal circumference (cm) and proportion of browsed growth buds.

### Seed rain variation among years

To determine interannual variations in seed production, we estimated seed rain using traps at fixed locations during four consecutive years (2005–2008). We selected 15 pre-established 900 m<sup>2</sup>-plots in forests dominated by *P. australis* in Yuspe and Condorito river basins (Fig. 1). There were plots in areas with and without livestock in both basins. Seed trees in areas with livestock were out of reach of browsing by livestock (i.e., in ravines not accessible to livestock, personal observation). Thus, we assumed that seed rain would not be affected by livestock browsing. As *P. australis* seeds have short dispersal distances (<10 m; Torres et al. 2008), six seed traps were randomly distributed in each plot at a distance of up to 13 m from seed trees. Seed traps consisted of a mesh bag of 706 cm<sup>2</sup> circular area, posted 50 cm above the ground. Traps were posted every season in December before the start of seed rain and collected in May when seed dispersal was

completed. To evaluate if climatic variables contribute to explain variations in seed rain among years we used temperature data from Córdoba city, located 60 km from our study area, and precipitation data from Las Ensenadas station, located in Condorito river basin.

### Data analyses

To determine the variables that influenced seed number and mass, we performed two stepwise multiple linear regression procedures using backward selection. Response variables were (1) number of seeds (Ln-transformed) and (2) mass per seed (Ln-transformed). Predictor variables were: (1) livestock situation (categorical fixed factor with two levels: with and without livestock), (2) sector (categorical random factor with five levels or study sectors); and the continuous variables: (3) tree height (Ln-transformed), (4) proportion of rock under the tree crown, and (5) slope inclination. We also modeled the interaction term livestock situation  $\times$  tree height. We included the terms: sector, proportion of rock under the tree crown and slope inclination in the procedure because previous studies found differences in *P. australis* tree performance for these variables (Seltmann et al. 2007; Marcora et al. 2008; Suarez et al. 2008). To assess differences in number of seeds per branch (Ln-transformed) and branch attributes for branches with and without livestock, we performed *T* tests for paired samples.

For descriptive purposes, we compared tree and sector attributes, livestock presence and intensity of browsing on trees located in areas with and without livestock by means of Mann–Whitney non-parametric tests. For this comparison, relative North and East aspect was calculated through cosine and sine transformations, respectively, of slope aspect, multiplied by the slope inclination, following Cingolani et al. (2004).

To assess differences in seed rain among years, we performed an ANOVA for repeated measures and pairwise comparisons. Seed rain per plot (Ln-transformed) was calculated as the average of seeds  $\text{m}^{-2}$  of all traps per plot. We calculated the coefficient of variation ( $\text{CV} = \text{SD}/\text{mean}$ ) of seed rain per plot over the 2005–2008 period to identify masting years with a CV larger than 1 (Kelly and Sork 2002; Fenner and Thompson 2005). In all the parametric tests, we checked residuals for normality and homoscedasticity (Underwood 1997).

## Results

### Tree size, livestock and seed production

The estimated number of seeds  $\text{tree}^{-1}$  ranged between 0 and 224,000 units. The smallest seed trees for areas with and without livestock were 107 and 87 cm tall, respectively, whereas the average number of seeds ( $\pm \text{SE}$ ) for trees with and without livestock was 8,393 ( $\pm 4,269$ ) and 11,180 ( $\pm 2,628$ ) seeds  $\text{tree}^{-1}$ , respectively. The backward stepwise procedure showed that variation in number of seeds  $\text{tree}^{-1}$  was best explained by tree height, livestock situation and the interaction between these variables, explaining 84% of the variation in seed production ( $p < 0.001$ ). The procedure did not select study sector, proportion of rock under the tree crown or slope inclination as explanatory variables. Number of seeds  $\text{tree}^{-1}$  is a power function of tree height (i.e., linear in an Ln–Ln scale). The interaction indicates a lower production of seeds for trees located in areas with livestock than for trees in areas without livestock only for small trees of up to 354 cm (Fig. 3). In addition, browsed branches had significantly fewer seeds than similar branches of the same



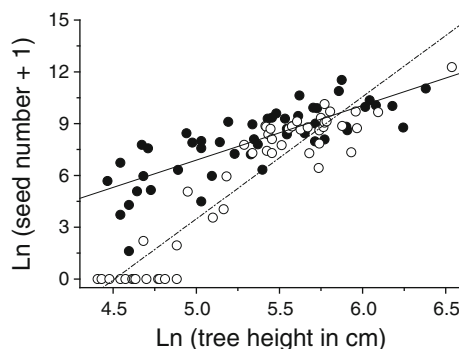
tree that were not browsed ( $169.65 \pm 69.58$  compared to  $249.5 \pm 110.98$  seeds; Paired  $T$  test, Ln-transformed,  $p = 0.014$ ).

Average ( $\pm$ SE) seed mass was  $4.9 \pm 1.8$  mg ( $n = 88$ ), with average tree values ranging from 2.3 to 10.5 mg per seed. Mass per seed (Ln-transformed) increased linearly only with tree height (Ln-transformed), and this trait explained 19% of the variation in mass per seed ( $p < 0.05$ ). The procedure did not select livestock situation, study sector, rock under the tree crown or slope inclination to explain the variation in seed mass. Unlike results obtained for seed number per tree, there were no significant differences for seed mass per tree between areas with and without livestock ( $n = 37$  and 50 trees, respectively, Fig. 4).

Tree characteristics, microsite variables and indicators of livestock presence (proportion of browsed buds and dung) of the studied trees are shown in Table 1. We confirmed no biases in tree selection because tree height, number of stems and stem perimeter did not differ between livestock treatments (Mann–Whitney test, all  $p > 0.05$ ). However, trees in areas with livestock had approximately 20% less crown cover than trees in areas without livestock ( $p < 0.001$ ). For microsite variables, trees in areas with and without livestock did not differ significantly in altitude, topographic position, proportion of rock under the tree crown, slope inclination, or slope aspect (both N–S and E–W components, Mann–Whitney test, all  $p > 0.05$ ). Trees in areas with livestock had almost 40% of their buds browsed and 10% of the quadrats thrown around trees had livestock dung, whereas trees in areas without livestock, as expected, had no signs of browsing or presence of dung in the surroundings.

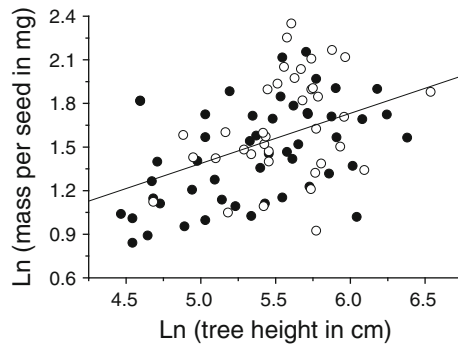
### Seed rain variation among years

Average seed rain per plot per year varied between 0 and 3,280 seeds  $m^{-2}$ . No seeds were captured in 22 (27%) of the traps during the 4 years of study and seeds were never trapped more than 10 m away from seed trees. By contrast, the highest catch per trap was 897 seeds ( $27,200$  seeds  $m^{-2}$ ). While the ANOVA for repeated measures did not find significant differences in seed rain among years ( $p = 0.5$ ), pairwise comparisons between years showed that the largest seed rain was in 2008 (all  $p < 0.05$ ;  $p = 0.022$ ;  $p = 0.018$ ;



**Fig. 3** Relationship between number of seeds per *P. australis* tree and tree height. Empty circles and the dashed and dotted line represent trees in areas with livestock, and solid circles and continuous line represent trees in areas without livestock. Trend lines indicate the best linear fits (adjusted  $r^2 = 0.84$ ;  $p < 0.001$ ; without livestock:  $\text{Ln}(\text{number of seeds} + 1) = -8.941 + (3.166 \times \text{Ln tree height in cm})$ ; with livestock:  $\text{Ln}(\text{number of seeds} + 1) = -31.916 + (7.08 \times \text{Ln tree height in cm})$





**Fig. 4** Relationship between *P. australis* average mass per seed (mg Ln-transformed) and tree height (cm, Ln-transformed). Empty and solid circles represent seed trees in areas with and without livestock, respectively ( $n = 37$  and  $51$ ). The continuous line represents the best linear fit for an overall single model including trees with and without livestock (adjusted  $r^2 = 0.19$ ;  $p < 0.05$ ;  $\text{Ln (mass per seed in mg)} = -0.338 + (0.345 \times \text{Ln tree height in cm})$ )

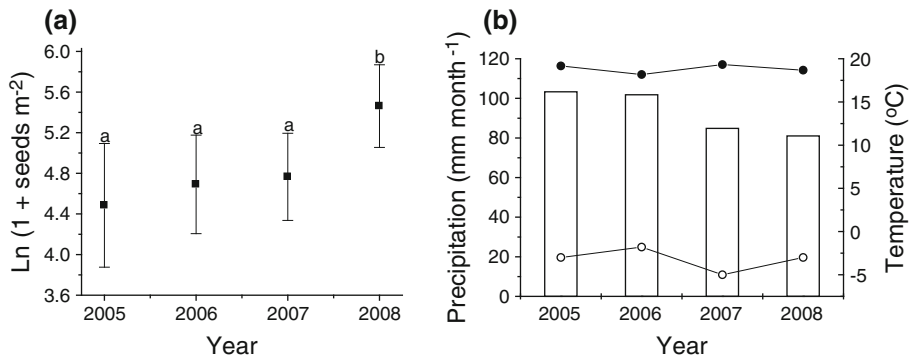
**Table 1** Attributes of *P. australis* trees of areas with and without livestock (mean  $\pm$  SE,  $n = 50$  and  $50$  trees, respectively)

Attribute	Livestock presence	Livestock exclusion	<i>p</i>
Tree			
Height (cm)	233 $\pm$ 17	241 $\pm$ 17	0.860
Crown cover (%)	56 $\pm$ 3	79 $\pm$ 1	<0.001
Number of stems	3.4 $\pm$ 0.3	3.1 $\pm$ 0.3	0.673
Largest stem circumference (cm)	43.0 $\pm$ 3.8	44.1 $\pm$ 4.7	0.756
Microsite			
Altitude (m a.s.l.)	2,101 $\pm$ 14	2,105 $\pm$ 15	0.994
Rock under the crown (%)	41 $\pm$ 5	33 $\pm$ 4	0.135
Topographic position <sup>a</sup>	1.9 $\pm$ 0.1	2.0 $\pm$ 0.1	0.521
Slope inclination (°)	27.0 $\pm$ 0.9	27.3 $\pm$ 0.7	0.706
Slope aspect (N–S component)	−0.09 $\pm$ 0.06	0.01 $\pm$ 0.82	0.504
Slope aspect (E–W component)	−0.04 $\pm$ 0.13	0.280 $\pm$ 0.11	0.142
Indicators of livestock presence			
Proportion of browsed buds (%)	37.38 $\pm$ 1.90	1.48 $\pm$ 0.39	<0.001
Proportion of dung (%)	10.35 $\pm$ 0.95	0	<0.001

*p* values of non-parametric Mann–Whitney test are indicated in the last column

<sup>a</sup> Topographic position, 1 valley, 2 mid slope, 3 summit

$p = 0.002$  for comparison with 2005, 2006 and 2007, respectively) as shown in Fig. 5(a). CV per plot (SD/Mean) of seed rain among years ranged between 0.285 and 1.528, and CV of all plots was 0.392. Interannual variations in seed rain of each plot did not show a synchronous pattern. No relation was observed between yearly seed rain and average monthly precipitation, or between absolute minimum and average monthly temperatures recorded from August to January, during the flowering and fruiting periods of *P. australis* (Fig. 5a, b).



**Fig. 5** Interannual variation (2005–2008) of **a** *P. australis* seed rain; and **b** precipitation (bars) together with mean and absolute minimum temperatures (lines with solid and empty circles, respectively). In **a** the means and SD correspond to a mean tree height of 290 cm; different letters indicate significant differences at 0.005 level

## Discussion

Seed production was mainly related to tree size (through tree height) and was reduced by livestock browsing. The reduction in seed production was not a response to climate or other tested variables, but largely to livestock browsing, especially in small-sized trees. These findings make a key contribution to the knowledge of the life cycle of this species and serve as baseline information for the design of management guidelines to promote *P. australis* forests cover restoration. In addition, these results provide useful information for the study and management of other forest woody species present in mountain areas devoted to livestock rearing worldwide, particularly in the southern hemisphere, where studies are scarce.

Seed production in *P. australis* trees was found to be extremely prolific as compared to other species. Trees as small as 87 cm produced seeds and the estimated record seed production of 224,000 seeds for a 690-cm tall tree is higher than the seed/fruit/nut production of other species, such as *Betula* spp., with reported values of 120,000, *Fagus* with 18,000 and *Quercus* 15,000 (Kramer et al. 2006). Hence, *P. australis* produces large amounts of seeds, a trait that should be taken into account in the study of the species fitness and strategies of resource allocation.

*Polylepis australis* seed production increases with tree height, as commonly observed in other woody species, such as *Pinus nigra* from the European Mediterranean area (Ordóñez et al. 2005), shrubby *Acacia* species from the south-east of Australia (Brown et al. 2003), and *Prunus virginiana* and *Prushia tridentata* in North America (Kay 1995). Bigger trees produce a higher number of seeds than smaller trees because they have greater ability to capture sunlight and produce compounds, and because they may assimilate more nutrients through the root system (Allison 1990; Snook et al. 2005). Therefore, the power and the direction of the relation between tree height and seed production should be taken into account to select the most productive *P. australis* trees for management and restoration purposes.

Our results showed that *P. australis* seed production is reduced when seed trees are accessible to browsing by livestock, with the greatest impact on the smallest trees (Fig. 3). The comparison of branches of the same tree that could or could not be reached by

livestock supports the assumption of the negative effect of browsing on seed production, and it was useful to discard the effect of genetic variability among trees. Species with a long history of herbivory, such as *P. australis*, can develop tolerance or mutualistic relationships, such as compensation or over-compensation (McNaughton 1983; Strauss and Agrawal 1999). Notwithstanding the long evolutionary grazing history of the area (Díaz et al. 1994) and multiple mechanisms of tolerance to browsing exhibited by *P. australis* (Giorgis et al. 2010), livestock has a negative effect on seed production of the smallest *P. australis* trees, and we did not detect compensation or over-compensation processes (Strauss and Agrawal 1999). A similar negative effect on seed production was reported in a *Nothofagus* species, in which the influence of livestock on seed production is important in young forests (Soler-Esteban et al. 2010). Similar effects on seed production were found for *Pinus sylvestris*, whose fast-growing trees were more strongly affected by herbivory than slow-growing trees (Edenius et al. 1995); and for *Acer pensylvanicum*, in which simulated herbivory reduced seed production, but only in buds with leaves directly subtending infructescences, and during some of the study years (Marquis 1988).

*Polylepis australis* seeds are lowly palatable; hence, it is unlikely that livestock select them for consumption. Most probably, seed crop reductions are due to the reduction of photosynthetic tissues. Plants assign their limited reserves to reproduction, survival and growth (Fenner and Thompson 2005). The smallest and most heavily browsed plants have even fewer resources for reproduction. Moreover, browsing of buds by livestock is heavier during winter, when availability of grasses is low (Giorgis et al. 2010). Typically, browsed buds will not produce seeds in the next reproductive season (personal observation), as occurs in other species (Marquis 1988; Bellocq et al. 2005). In addition, the hormone system may be altered by browsing, with a consequent decrease in flowering and competitive ability (Bergström and Danell 1987). Therefore, seed production seems not to be favored by livestock browsing through the mechanisms such as elimination of the vegetation surrounding *P. australis* trees, or by increasing its fitness through compensation or overcompensation in response to browsing.

Seed mass was similar to previously reported values (Seltmann et al. 2007; Marcora et al. 2008), increased with tree height, which only explained 19% of variation, and was not significantly affected by livestock exclusion. Seed mass is highly variable at any particular plant size (Rees and Venable 2007). In addition, several studies have found no relationship between seed mass and resource availability or climatic conditions (Sautu et al. 2006), suggesting that mass per seed would be a stable genetic character (Körner 1999). This may explain the lack of significant differences found for seed mass of *P. australis* trees between areas with and without livestock. Similar results were found for *Trigobalanus doichangensis*, a woody species that produces seeds whose seed mass is not correlated with geo-climatic variables (Zheng et al. 2009). On the other hand, our results show that livestock browsing caused a reduction in seed number but not in seed mass, suggesting that when resources are limited, seed quality would be favored over seed number (Fenner and Thompson 2005).

The largest seed rain occurred in 2008 and was probably caused by growth of seed trees (data not shown) and not by climatic conditions. Interannual variations in seed rain were not important ( $CV > 1$ ), suggesting that pulses of reproduction are not likely in *P. australis*, unlike findings reported in other mountain tree species (Cuevas 2000; Fenner and Thompson 2005). This result is supported by 14 years of field observations during seed collection for reforestation purposes (1997–2011; D. Renison, unpublished results), and by the fact that masting events have not been reported in other *Polylepis* species studied in Andean regions (Cierjacks et al. 2007, 2008). At the plot scale, interannual seed rain

variation was large, without showing a consistent pattern among plots. Moreover, inter-annual variability in seed rain at the plot scale was not associated with regional climatic variables during flower and seed formation because temperatures (average and absolute minimum) were similar among years and because precipitations did not follow the same pattern as seed rain.

The present results show that seed production of *P. australis* is prolific but is affected by livestock browsing on the smallest trees. Seed production and seed rain seem to be very prolific and stable over the years. The lack of a persistent seed bank and of asexual reproduction (Enrico et al. 2004) make seed production and seed rain the main and direct source of natural seedling establishment, as shown by Van Do et al. (2011) for two woody species in Vietnam. Hence, in a population at the establishment stage, the influence of livestock browsing on seed production would be higher than in a population in steady state conditions, as has been determined for other forest species (Soler-Esteban et al. 2010). At present, *P. australis* forests in central Argentina cover less than 5% of their potential estimated range (Cingolani et al. 2008; Renison et al. 2010), and these remnant forests are degraded and in areas with livestock (Renison et al. 2011). Although the relative contribution of seed production stage to total population growth in comparison to other stages is an issue that has not been elucidated in this study, we highlight that the impact of livestock on overall seed production is probably high at the patch scale, because most of the individuals in the remnant patches are shorter than 300 cm (Renison et al. 2011). However, the highest impact of livestock on *P. australis* is probably on juvenile growth, which is almost completely interrupted by browsing (Teich et al. 2005; Giorgis et al. 2010).

The present study suggests that livestock browsing would affect *P. australis* forest dynamics and probably forest distribution through its influence on sexual reproduction and other vital traits. We have elucidated an important issue that until this moment was unknown and controversial, because of the ambiguous effects of browsing on different stages of *P. australis* life cycle; negative in juvenile growth (Teich et al. 2005; Giorgis et al. 2010), and positive in establishment stages at intermediate livestock rates (Torres et al. 2008; Zimmerman et al. 2009).

Forest expansion into grasslands would be slow, because most of the seeds fall less than 10 m away from the seed tree. Consequently, most *P. australis* remnant forest edges and large isolated trees are surrounded by a 10-m boundary where seedlings and juveniles have established in the surrounding grasslands but remain as dwarf trees due to browsing (Torres et al. 2008; Giorgis et al. 2010). The information obtained in the present work shows that if dwarf trees are protected, they can produce an abundant seed crop that will cause another 10-m forest advance into the grasslands. These results stress the role of livestock and the need to include this factor in future studies and management decisions.

**Acknowledgments** We are very grateful to the Volkswagen Foundation (Germany), IAI and CONICET (Argentina) for financial support. CIRSA provided temperature and precipitation data. We especially thank all the volunteers who spent many hours picking and counting seeds. To the Quebrada del Condorito National Park authorities and to J. Nores, N. Bazan, A. Moreno and J. Cuello, who allowed us to carry out part of the study on their lands. To Ana M. Cingolani, who improved our manuscript and made Fig. 1. J. Brasca revised the English style.

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