

# The performance of *Polylepis australis* trees along their entire altitudinal range: implications of climate change for their conservation

Paula Marcora<sup>1\*</sup>, Isabell Hensen<sup>2</sup>, Daniel Renison<sup>1</sup>, Peggy Seltmann<sup>2</sup> and Karsten Wesche<sup>2</sup>

<sup>1</sup>Cátedra de Ecología, FCEFYN, Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina, <sup>2</sup>Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchor 1, 06108 Halle/Saale, Germany

\*Correspondence: Paula Marcora, Cátedra de Ecología, FCEFYN, Universidad Nacional de Córdoba, Avenida Vélez Sarsfield 299, 5000 Córdoba, Argentina.  
E-mail: paulamarcora@yahoo.com.ar

## ABSTRACT

Altitudinal gradients are expected to heavily influence the general performance of mountain tree species. For this study we evaluated vitality, radial growth and reproductive efficiency in *Polylepis australis* (Rosaceae) throughout its complete altitudinal range in central Argentina. We selected seven forest fragments ranging from 900 to 2700 m a.s.l. In the field, we subjectively assigned vitality and seed productivity indexes to 12 *P. australis* trees per fragment. In addition, we cored and assessed for radial growth 10–18 trees per altitudinal level. In the laboratory, we individually weighed seeds from four or five trees from each altitudinal level and divided into two seed mass classes (light and heavy). We then tested for germination and monitored their seedlings for survival. Seedlings of three trees per altitudinal level were harvested after 40 days and assessed for dry mass. Seedlings of one to two trees per altitudinal level were monitored for survival until both leaves and roots had died. Our main results showed two types of responses to altitude: a unimodal relationship with an optimum at intermediate altitudes of around 1800 m a.s.l. for tree vitality, radial growth, seed productivity and seed mass; and an increase with altitude for in-vitro seed germination and seedling survival. A rise in temperature due to climate change could restrict *P. australis* to the upper most altitudes, where conservation of these forests will be a priority.

## Keywords

Central Argentina, Córdoba Mountains, altitudinal gradient, seed mass, germination, reproductive efficiency, radial growth.

## INTRODUCTION

The underlying factors explaining the altitudinal ranges of tree species are of major concern in ecology. Altitude may affect both growth and reproduction and thus determine species distribution limits (García *et al.*, 2000). Tree growth is mainly influenced by precipitation and temperature (Morales *et al.*, 2004), the latter being the most likely limiting factor near the upper treelines (Hoch & Körner, 2005). Lower distribution limits have been less well studied but it is assumed that high-altitude plants are out competed by other species better adapted to higher temperatures and lower humidity, which may result in a loss of accumulated carbohydrates due to photorespiration (Bruehlheide & Lieberum, 2001; Argollo *et al.*, 2004).

Reproductive efficiency is one of the major constraints in high mountain ecosystems, as several studies have reported decreasing sexual reproduction at the upper altitudinal limit of tree species

(Tranquillini, 1979; Pigott & Huntley, 1981; Holm, 1994; Cierjacks *et al.*, 2007, 2008). At such altitudes, unfavourable climatic conditions, including the short duration of the growing season, might constrain seed development and seedling establishment or may reduce seed mass or quantity (Crawford, 1989; García *et al.*, 2000; Pluess *et al.*, 2005). Thus, altitude is likely to be a factor associated with variation in reproductive efficiency among populations (Lord, 1994). In light of this, several authors (e.g. Dorne, 1981; Angosto & Matilla, 1993; Holm, 1994; Lord, 1994; Vera, 1997) have documented differing germination responses in relation to altitude; and Cierjacks *et al.* (2008) found a negative relationship between altitude and seedling survival of two Ecuadorian *Polylepis* treeline species.

The genus *Polylepis* (Rosaceae) includes approximately 30 tree species (Schmidt-Lebuhn *et al.*, 2006) endemic to the South American high mountains, where they inhabit the uppermost forests and dominate the canopy at higher altitudes and along the

upper treeline. They often form woodland patches far above a more continuous treeline and controversy has existed whether this patchy distribution is natural or due to human-caused fires, pasturing, or agriculture (Hensen, 1995; Fjelds  & Kessler, 1996; K rner, 2003; Renison *et al.*, 2006). The natural limitations defining the occurrence of *Polylepis* are still poorly understood (Kessler, 2002; Kessler *et al.*, 2007). Here, we present a study of growth variation and reproductive efficiency for *P. australis* along a transect representing the widest altitudinal gradient known for the species in central Argentina (900–2700 m a.s.l.). Previous studies have already revealed that *P. australis* seeds are often empty or otherwise non-viable, a fact that Renison *et al.* (2004) found to be related to the extent of soil degradation around the parental tree. Enrico *et al.* (2004) suggest that this high percentage of non-viable seeds could represent an expression of its latitudinal and altitudinal range. Taking these findings into account, we explored the following questions: Do altitude and site conditions influence *P. australis* seed productivity, tree radial growth, and tree vitality? Is there an influence of altitude on seed mass, seed germination, seed viability, in-vitro seedling survival, and subsequent biomass development? Knowing what is the influence of altitude on the response of tree species is crucial to better understand vegetation altitudinal gradients, the response of tree species to human disturbances at varying altitudes, and for the prediction of possible consequences of climate change.

## METHODS

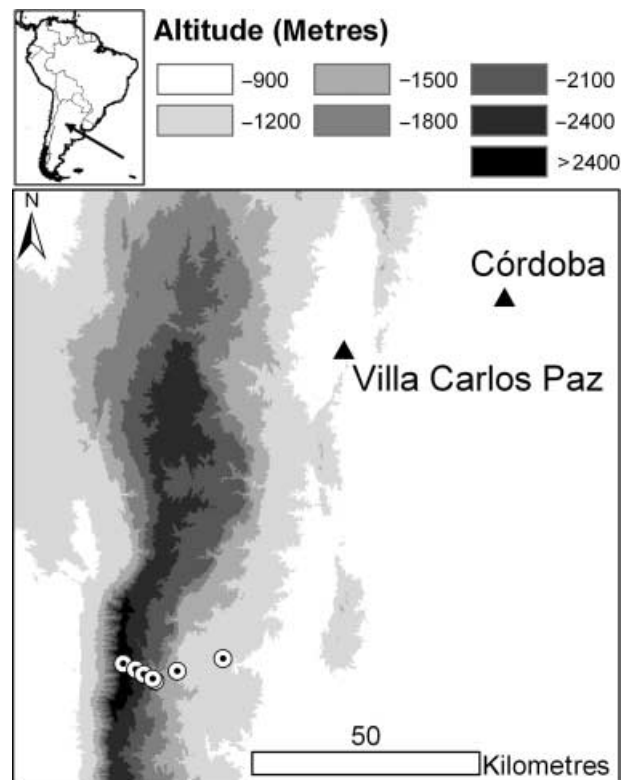
### Study area and species

The C rdoba Mountains in central Argentina (31 4' -S, 64 52' -W; Fig. 1) rise up to 2884 m a.s.l., and are formed by a mosaic of different types of tall tussock grasslands, pasture lands, granite outcrops, exposed rock surfaces created by soil erosion, and woodland fragments dominated almost exclusively by *P. australis* (Cingolani *et al.*, 2004). At 2100 m a.s.l., annual precipitation fluctuates around 840 mm. Mean temperatures of the coldest and warmest months are 5.0  C and 11.4  C, respectively (Cabido, 1985).

*Polylepis australis* is the southernmost *Polylepis* species, endemic to Argentina where it occurs in the central and north-western parts of the country (Simpson, 1979). The fruits are mostly single-seeded nutlets (in this paper referred to as seeds) dispersed between January and March. Seeds germinate readily and without any dormancy-breaking treatment when subjected to adequate water and temperature conditions (Renison & Cingolani, 1998). The species is known to develop well-marked growth rings with almost no false rings due to the long cold and dry winters prevailing in the area (Acosta, 1986).

### Sampling and experimental design

Our study areas represented seven woodland fragments distributed along an altitudinal gradient (900, 1200, 1500, 1800, 2100, 2400, and 2700 m a.s.l.; Fig. 1). Temperature was recorded hourly 1 m above ground level by Hobo data loggers stationed in



**Figure 1** Map of study area. The position of the mountains of central Argentina in South America is shown in the upper left. A detail of the mountains of central Argentina and their altitudinal levels are shown in gray scales. Circles represent study areas. Two of the regionally most important cities are indicated.

the seven altitudinal levels between 6 September 2004 and 6 September 2005. To minimize exposure to the sun, data loggers were stationed on the south/centre of a tree and under a cone-shaped green plastic that provided additional shading from sun specks. In December 2004 we assigned a vitality index (1 = more than 50% of the stems dry and/or with yellowish leaves; 2 = intermediate, 3 = all stems vital with abundant and dark green leaves), and an index of seed productivity (between 1 = few seeds and 6 = many seeds) to 12 *P. australis* individuals per altitudinal level which were between 2 and 4 m tall. We used this quick method of evaluating seed productivity because there were very obvious differences among trees (i.e. *P. australis* higher than 2 m in height can produce between 200 and 200.000 seeds – J. Pollice, unpublished data). Both indices were always designated by the same person (PM). In addition, we cored 10–18 trees per altitudinal level. Coring was performed below 0.4 m above ground level in trees which had a basal circumference of > 0.3 m using a 5 mm stem corer. As *P. australis* stems have irregular shapes, two to four cores at opposite sides were sampled in each tree to increase the probability of reaching the centre. Where the tree had more than one basal stem, we cored the stem with the greatest circumference (in accordance with Acosta, 1986). Cores were mounted and sanded, and tree ring widths were measured using a stereomicroscope with a precision of 0.1 mm. For analysis we used a total of 128 cores from 82 trees.

To determine whether site variables influence *P. australis* growth and seed productivity, we measured slope inclination, slope aspect, and proportion of rock under the canopy (%). We also measured sun incidence in the field as the trajectory of the sun not covered by mountains, rock outcrops, or other obstacles (in a flat area with no obstacles: 180 degrees).

In January and February of 2004, we collected 200 seeds from between six to 12 *P. australis* individuals per altitudinal level. Mean seed mass was determined after a 5-month storage period under ambient laboratory conditions (mean temperature 20 °C). Seeds of four (2700 m a.s.l.) to five individual trees (all other altitudes) were randomly selected and weighed individually to the nearest 0.1 mg. As the results of a former study (Seltmann *et al.*, 2007) revealed that lighter *P. australis* seeds often lack embryos, seeds were divided evenly into two seed mass classes: light and heavy seeds. Replicates of three Petri dishes, each containing 30–35 seeds, were taken from these two fractions.

Germination of *P. australis* seeds was tested in a climate chamber with a warm white light source at temperatures of 20 °C/10 °C (12 h of light/12 h of darkness), which are known to reflect optimum temperatures (Seltmann *et al.*, 2007). Seeds were laid on filter paper and kept moist with deionized water for 50 days, after which time the germination rate reached zero. The viability of non-germinated seeds was assessed using the tetrazolium test (Baskin & Baskin, 1998). All germinated seeds were subsequently placed into Petri dishes (up to four seedlings each), kept moist, and their survival was monitored. The surviving seedlings of three trees per altitudinal level were terminated after 40 days, and their dry mass was assessed to an accuracy of 1 mg (balance Sartorius MC1 – AC 210S, Sartorius, Göttingen, Germany). Seedlings of one (2700 m a.s.l.) to two trees per altitudinal level were monitored over a further 20-week period until they died (complete dryness of roots and leaves) in order to analyse survival potential under conditions of severe nutrient deprivation.

### Data analysis

We analysed vitality index (range 1–3) using Kruskal–Wallis ANOVA. Linear regressions were performed to assess the relationship between altitude and (1) average width of tree rings, (2) seed productivity index, (3) seed mass, (4) seed germination, (5) seedling mass after 40 days, and (6) seedling survival after 40 days. Following a visual inspection of the corresponding graphics, where appropriate, we added the term ‘altitude squared’ to determine whether variables had an optimum at intermediate altitudes. For seed productivity and tree ring growth, we also included site variables as a predictor variable and performed backward selection procedures to identify the most explanatory set of variables. Due to the relatively low sample sizes, we used ANOVA and Tukey–Kramer multiple-comparison posthoc test to determine the relationship between altitudes and mean days of seedling survival produced by the heavier seeds. Altitudinal levels were grouped as follows: 1200/1500 m a.s.l., 1800/2100 m a.s.l., and 2400/2700 m a.s.l. Percentages were arcsin square-root transformed and average tree ring width was log<sub>10</sub> transformed before analysis. To better explore the role of

**Table 1** Means and absolute minimum/maximum temperatures 1 m above ground level as provided by climatic data loggers (Hobo H8) stationed between 6 September 2004 and 6 September 2005 in the seven study sites along the altitudinal gradient. To minimize exposure to the sun, data loggers were stationed on the south/centre of a tree and under a cone-shaped green plastic which provided additional shading from sun specks. Days mean > 5 °C is number of days with a mean temperature higher than 5 °C.

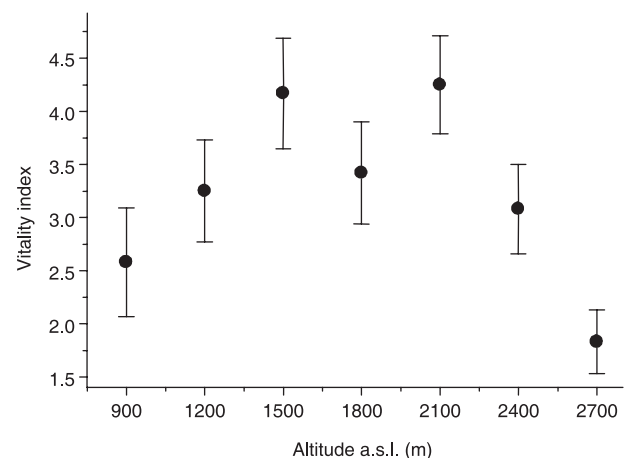
Altitude a.s.l. (m)	Mean (°C)	Absolute minimum (°C)	Absolute maximum (°C)	Days mean > 5 °C
900	15.7	−3.4	43.4	357
1200	13.7	−3.4	32.8	339
1500	13.2	−2.0	34.4	331
1800	11.2	−6.3	29.5	313
2100	10.6	−5.8	27.1	308
2400	9.0	−8.9	24.0	288
2700	7.4	−11.7	23.6	261

temperature, in the final models we successively replaced altitude by (1) annual mean temperature; (2) days of the year with a mean temperature higher than 5 °C; (3) absolute maximum temperature; and (4) absolute minimum temperature (Table 1). For analysis, temperatures were converted to the Kelvin scale to avoid invalid product operations. All residuals were tested for normality and homocedasticity.

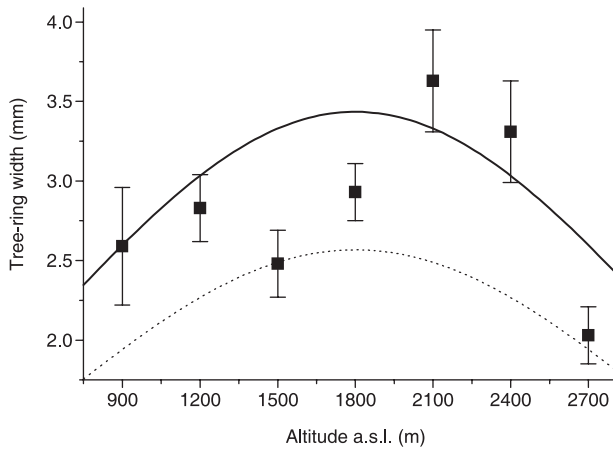
## RESULTS

### Tree vitality, growth, and seed productivity

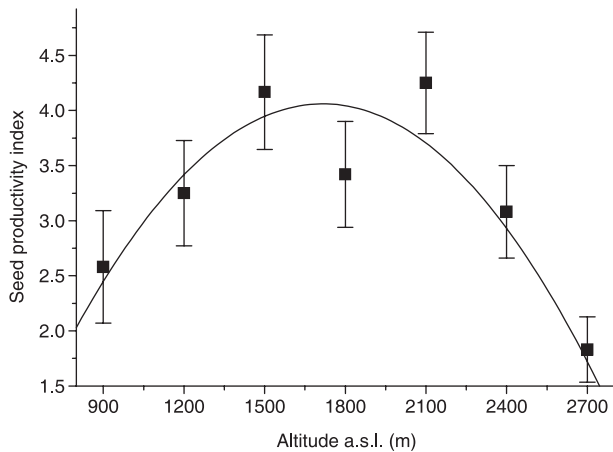
*Polylepis australis* vitality index was highest at intermediate altitudes and lowest in the extremes of the species distribution (Kruskal–Wallis ANOVA:  $\chi^2 = 18.41$ ,  $P = 0.005$ ; Fig. 2). Correspondingly, ring widths had a similar unimodal pattern



**Figure 2** Relation between altitude and mean *Polylepis australis* vitality index ( $\pm$  SE;  $n = 12$  trees per altitude). Vitality index was (1) when more than 50% of the stems were dry and/or with yellowish leaves, (2) intermediate, and (3) when all stems were vital, with abundant and dark green leaves.



**Figure 3** Altitude and mean *Polylepis australis* tree-ring width ( $\pm$  SE;  $n = 82$ , 9–17 trees per altitude). The trend lines indicate the best fit quadratic model, assuming a constant slope of 5° and 30° inclination (solid and dotted line, respectively) and 10% and 90% rock under the canopy (solid and dotted line, respectively).

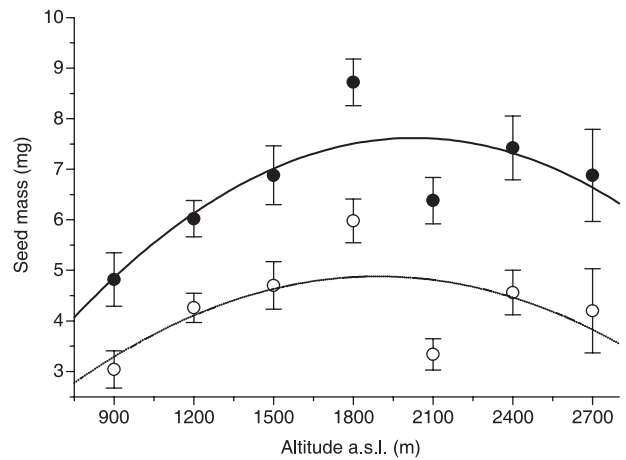


**Figure 4** Altitude and mean *Polylepis australis* seed productivity index ( $\pm$  SE;  $n = 12$  trees per altitude). The trend line indicates the best fit quadratic model.

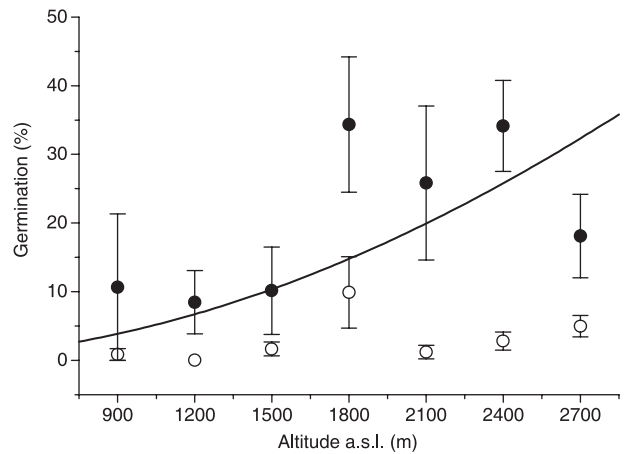
(ANCOVA: overall model, adjusted  $r^2 = 0.11$ ,  $P = 0.0001$  for altitude and its squared term; Fig. 3). Ring widths were also negatively related to the percentage of rock under the canopy ( $P = 0.001$ ) and to slope inclination ( $P = 0.02$ ). Seed productivity indices were also largest at intermediate altitudes (adjusted  $r^2 = 0.16$ ,  $P = 0.0002$ ; Fig. 4), and no other site variable was selected by our procedures.

### Seed mass, germination, and seedling survival

Seed mass was significantly higher at intermediate altitudes for both lighter and heavier seeds (lighter seeds  $P = 0.01$  and  $P = 0.02$ ; heavier seeds  $P = 0.003$  and  $P = 0.007$  for altitude and its square term, respectively; Fig. 5). Seed germination was generally low, highly variable among trees, and all seeds of several trees failed to germinate. As expected, heavier seeds always



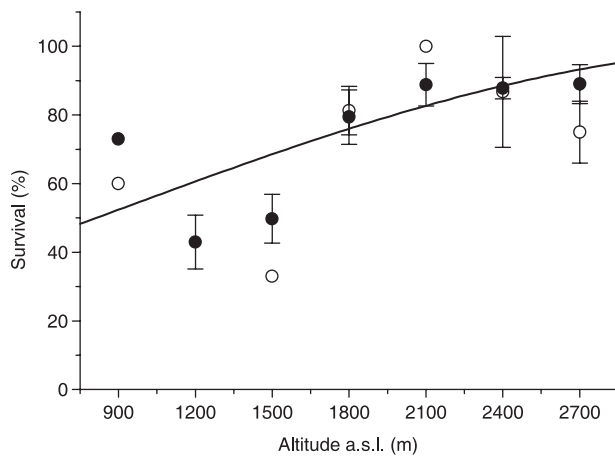
**Figure 5** Altitude and mean *Polylepis australis* seed mass ( $\pm$  SE) for light (open circle) and heavy (solid circle) seeds ( $n = 4$  for 2700 m a.s.l., otherwise  $n = 5$ ). The trend lines indicate the best fit quadratic model.



**Figure 6** Altitude and mean *Polylepis australis* germination percentage ( $\pm$  SE) of light (open circle) and heavy (solid circle) ( $n = 4$  for 2700 m a.s.l., otherwise  $n = 5$ ). The trend line indicates the best fit linear model for the arcsin square-root-transformed data.

germinated better than lighter seeds. Altitude was positively and significantly related to seed germination of the heavier seeds (adjusted  $r^2 = 0.23$ ,  $P = 0.004$ ; for light seeds  $P = 0.67$ , Fig. 6). Altitude squared was not selected by our regression model underlining the fact that this relationship is not unimodal, as could be expected by the distribution of seed masses. The final Tetrazolium test showed that non-germinated seeds were always empty or otherwise unviable.

The 40-day survival percentages of seedlings varied between 0 and 100% and were not significantly different between heavier and lighter seeds. However, survival of seedlings produced by the heavier seeds was positively related to altitude (adjusted  $r^2 = 0.49$ ,  $P = 0.05$ , for light seeds  $P = 0.2$ , Fig. 7). After 40 days of growth, seedlings from the heavier *P. australis* seeds were slightly heavier (mean dry mass  $3.3 \text{ mg} \pm \text{SD } 1.44$ ;  $n = 363$ ) than those of the lighter seeds (mean dry mass  $3.0 \text{ mg} \pm \text{SD } 1.59$ ;  $n = 40$ ). However,



**Figure 7** Altitude and mean *Polylepis australis* survival percentages ( $\pm$  SE) of 40-day-old seedlings produced by light (open circle) and heavy (solid circle) seeds. The trend line indicates the best fit linear model for the arcsin square-root-transformed data.

this result was neither significant, nor was there any effect of altitude on seedling mass (linear regression: adjusted  $r^2 = 0.14$ ,  $N = 2, 7$ , seed mass  $P = 0.83$ ; altitude  $P = 0.48$ ).

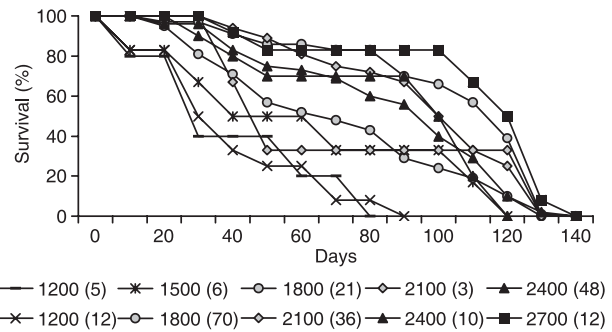
Seedlings survived up to 135 days under conditions of severe nutrient deprivation (Fig. 8). Means were between 37 and 97 days for the lighter seeds and 49–110 days for the heavier seeds. Seedlings survival rates of heavier seeds were higher, the higher the collection site (ANOVA:  $F = 6.51$ ,  $GL = 2$ ,  $n = 10$ ,  $P = 0.025$ ). Differences of mean days of survival were significant between seedlings of seeds collected at 1200/1500 m a.s.l., and those collected at 2400/2700 m a.s.l.

As expected, mean, absolute minimum, and maximum temperatures gradually became lower at upper altitudes and days of the year with a mean temperature  $> 5^\circ\text{C}$  became fewer (Table 1). When we sequentially replaced altitude in the regression models with temperature related variables we always obtained a model with similar or lower explained variance.

## DISCUSSION

Few comparative studies on plant performance have included the complete altitudinal range of a species. In this sense our study represents an important contribution to the understanding of how a species responds to the climatic changes that occur with altitude. Interestingly, we found two types of responses to altitude: an optimum at intermediate altitudes for tree vitality, radial growth, seed productivity, and seed mass; and an increase with altitude for in-vitro seed germination and seedling survival.

In the high mountains of temperate/subtropical central Argentina environmental conditions are cold and damp, whereas with decreasing altitude the climate becomes warmer (Table 1) and drier, with vegetation becoming increasingly xeromorphic (Cingolani *et al.*, 2003). Thus, climate-related growth limitation at the lower and upper extremes of the gradient might be the reason for the unimodal responses in *P. australis* tree vitality, radial growth, seed productivity, and seed mass. At the upper



**Figure 8** Survival curves of *Polylepis australis* seedlings produced by heavier seeds from different altitudes and trees (initially  $n = 1$  tree for 2700 m a.s.l., otherwise  $n = 2$ ; both trees from 900 m a.s.l. and one tree from 1500 m a.s.l. failed to germinate). In brackets number of seedling per tree.

limit, tree growth is in all likelihood primarily determined by low temperatures, limiting the investment possibilities of assimilates (Körner, 1999, 2003). At the lower limit, high-altitude plants may generate high transpiration rates and suffer from water stress, reducing accumulated carbohydrate reserves (Norton, 1984; Bruelheide & Lieberum, 2001; Mäkinen *et al.*, 2002).

Not surprisingly, *P. australis* vitality and ring width followed a similar unimodal pattern. The same pattern for tree growth was found for *Nothofagus solandri* and *Picea abies* (Norton, 1984; Mäkinen *et al.*, 2002). Norton (1984) assumed that radial tree growth probably does not start until apical stem growth is completed, which signifies a drawback for trees growing under low temperatures. Low temperatures were also found to reduce  $\text{CO}_2$  assimilation of *Polylepis sericea* (Arteaga, 2002) and to inhibit tissue growth of *Polylepis tarapacana*, leading to smaller tree ring widths towards its upper distribution limit (Hoch & Körner, 2005). We also found that *P. australis* ring width was negatively related to the proportion of rock under the canopy, which supports Renison *et al.* (2004), who revealed a similar relationship for *P. australis* seed viability and attributed this to a reduction in the availability of water and nutrients. These results further support the hypothesis that the existing association between *Polylepis* and rocks is due to the protection rocks provide from human-caused fires and not caused by a more favourable microclimate (Renison *et al.*, 2002, 2006).

A unimodal response to altitude was also found for *P. australis* seed productivity and seed mass, even with our rough seed productivity index; a pattern found in other species (Pigott, 1992; Cuevas, 2000; Bruelheide & Lieberum, 2001). Our results are also in line with those of a comparative study on *Juniperus communis* reproduction along a latitudinal gradient, which revealed a reduction of seed productivity towards the outer distribution limits (García *et al.*, 2000). Other authors have reported continuously decreasing seed productivity with altitude (Cuevas, 2000; Miller & Cummins, 2001; Cierjacks *et al.*, 2008), or even a general reduction in within-species seed mass with latitude (Moles & Westoby, 2003). As *P. australis* seed production and seed mass were found to decline at the extremes of their distribution, loss of carbohydrates at the lower limit and low temperature

combined with a short growing season at the upper limit can probably explain the pattern. The fact that we found seeds to be lightest at the lowest altitude again suggests a strained water balance.

In contrast to the unimodal response of *P. australis* growth, seed production, and seed mass, we found increases with altitude for seed germination (equal to seed viability), seedling survival, and seedling longevity under conditions of nutrient deprivation. The fact that altitude affects seed germination is in line with Vera (1997) – who found seeds of *Calluna vulgaris* and *Erica cinerea* collected at the highest altitudes to germinate best – and with Lord (1994) who reported a similar correlation for *Festuca novae-zelandiae*. However, several authors (e.g. Ellison, 2001; Ter Borg, 2005) found no differences in seed germination for various plant species collected at different latitudes and altitudes; and Holm (1994) and Miller & Cummins (2001) even revealed a contrasting relationship.

The fact that altitude was positively related to *P. australis* seed germination/viability as well as seedling survival and longevity is not easily explained. We assume that seeds at higher altitudes might ripen more slowly under the influence of lower temperatures, and the longer filling period as well as the higher soil moisture allow for greater total assimilation resulting in seeds of higher quality (Fenner & Thompson, 2005). In contrast, at 900 m a.s.l., *P. australis* grows at the lowest margin of its altitudinal distribution and thus under suboptimal environmental conditions that might impose increased stress on reproductive plants resulting in a reduced investment of maternal energy into the offspring (Oostermeijer *et al.*, 1995). Correspondingly, seed germination/viability was extremely low between 900 and 1500 m a.s.l., compared to the higher altitudes. In general, failure of sexual reproduction at the edges of a tree species' distribution is common (e.g. Pigott & Huntley, 1981; Pigott, 1992; Holm, 1994; Cierjacks *et al.*, 2008) and we assume that the influence of longer periods of drought might affect embryo development and seed mass at lower altitudes.

Our data reveal a clear climatically driven lower distribution limit for *P. australis* in central Argentina due to the decline in all the indicators of plant performance we measured. No clear upper limit was apparent, as important parameters of seed quality such as viability, germination, and seedling development improved with altitude, while tree vigour, growth, and productivity gradually declined with altitude. Studies integrating all stages of the *P. australis* life cycle are necessary in order to gain a clear picture of its overall performance at increasing altitudes. Interestingly, during the year of our study, none of the measured parameters completely limited high-altitude performance, and the exclusion of fires and livestock in the upper Córdoba Mountains has facilitated the establishment of *P. australis* where they 'typically' do not grow (P.M., pers. obs.). This evidence, plus the fact that radial growth is lower in trees restricted to rocks by fires, further support the findings of Cingolani *et al.* (2007) that human impact is the main reason for present day reduced forest extension. With regard to climate change, our findings indicate that any rise in temperature will further restrict *P. australis* to its uppermost distributional altitudes. Thus, it is of vital importance that human impact at these higher altitudes is reduced in order to

curb the decline of the already heavily compromised habitat available for the species.

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