

## Variation of seed mass and its effects on germination in *Polylepis australis*: implications for seed collection

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**Abstract** South American *Polylepis* mountain forests are recognised as being one of the most endangered forest ecosystems in the world. Reforestation measures have been strongly recommended but may be hampered due to the very low seed germination reported for several *Polylepis* species. In order to facilitate reforestation we analysed the influence of seed mass on germination probability for *Polylepis australis* seeds in the Córdoba mountains (central Argentina). We collected seeds from 43 trees distributed throughout five woodland fragments located within two regions differing in size, topographical position, and altitude (1,900 m a.s.l. and 2,200 m a.s.l.). Seeds of *Polylepis australis* exhibited a great variation in terms of mass and percent seed germination among individual trees and among geographical regions. The results of logistic regression showed that germination probability was highly correlated with seed mass. However, the explained deviance significantly increased by including the region, the woodland fragment and especially the individual tree in addition to seed mass in the regression models. We conclude that selecting seeds on the basis of mass is an appropriate way to enhance germination prospects for reforestation projects. However, no absolute mass values are applicable in this context as the highest germination probabilities were reached at varying seed mass values depending on geographical region, woodland fragment or individual tree. We suggest collecting the relatively heaviest available seeds, even though the absolute seed mass may be low.

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## Introduction

The genus *Polylepis* (Rosaceae) includes approximately 20 tree species (Kessler 1995) endemic to the South American high mountains, where land use history has fundamentally changed the vegetation due to the influence of pasturing, burning, and agriculture. Currently, many *Polylepis* woodland remnants are restricted to unproductive or inaccessible areas such as rocky outcrops or steep slopes and soil erosion is widespread (e.g., Ellenberg 1979; Kessler 1995; Fjeldså and Kessler 1996; Renison et al. 2002a). Today, *Polylepis* forests are one of the most endangered forest ecosystems in the world (Walter and Gillett 1998; UNEP-WCMC 2004). Consequently, the conservation of the last remaining stands and reforestation of areas formerly occupied by *Polylepis* forests is a conservation priority (Fjeldså and Kessler 1996; Renison et al. 2002b; Enrico et al. 2004). However, reforestation attempts may be hampered due to the low seed germination that has been frequently observed for several *Polylepis* species (e.g., Hensen 1994; Renison and Cingolani 1998; Renison et al. 2004). In this context, Renison et al. (2004) demonstrated that *P. australis* seed viability was correlated to anthropogenic habitat degradation. In accordance, Hensen (unpublished) found a high percentage of empty and non-viable seeds in several severely anthropogenically influenced Bolivian *Polylepis* species (*P. hieronymi* 80%, *P. tomentella* 84%, *P. besseri* 90–100%, *P. racemosa* 100%, *P. tarapacana* 100%).

Seed mass is an important parameter of plant fitness as it may highly influence the regeneration process of a population (Hendrix et al. 1991; Fenner 1992; Leishman 2001). Extensive variation in seed mass has frequently been demonstrated within plant populations (e.g., Hendrix et al. 1991; Leishman et al. 1995). Increasing seed mass within species has been shown to correlate with an increase in seed germination (e.g., Vera 1997; Shaukat et al. 1999; Cordazzo 2002); establishment success (e.g., Kidson and Westoby 2000; Chacón and Bustamante 2001); growth rate (e.g., Leishman 1999; Cordazzo 2002); and survival (e.g., Hendrix et al. 1991; Vera 1997). Nevertheless, published results are lacking in consistency and several authors report no, or even negative, relationships between seed mass and seed germination as well as seedling performance parameters (e.g., Stamp 1990; Cordazzo 2002).

*Polylepis australis* seeds are often empty or otherwise non-viable. Although there is a correlation to habitat degradation (Renison et al. 2004), many aspects of *P. australis* regeneration appear to vary geographically (Renison and Cingolani 1998; Renison et al. 2004) and we do not know if seed mass can be used as a quick evaluation of seed viability over a wide range of habitats. Thus, the aim of the present study was to determine: (1) whether *P. australis* seed mass varies within individuals, woodland fragments and geographical regions, and (2) whether seed mass correlates to seed viability. Such information will be useful to future reforestation efforts and for further studies on the regeneration of *Polylepis* species.

## Methods

### Study area and species

The study was carried out in the Córdoba mountains, central Argentina (S 31° 34', W 64° 50'). Mean temperatures of the coldest and warmest months are 5.0°C and 11.4°C, respectively, and there is no frost-free period. Mean annual precipitation is 840 mm, with most rainfall concentrated in the warmer months between October and April (Cabido 1985). The landscape is a mosaic of different types of tall tussock grasslands, pasture land, granite outcrops, exposed rock surfaces produced by soil erosion, and woodland fragments dominated almost exclusively by *P. australis* (Cingolani et al. 2004) whose stands are located between 900 m a.s.l. and 2,884 m a.s.l. *Polylepis australis* flowers from September to November with a peak in October (pers. obs.). Its racemiform pendulous inflorescences are produced annually and may carry up to 12 inconspicuous anemogamous flowers (Simpson 1979). Fruits are mostly single seeded nutlets (hereafter referred to as seeds) dispersed between January and March.

### Seed collection

We collected *P. australis* seeds from five woodland fragments distributed in two regions (two fragments in Los Gigantes (LG): 1,900 m a.s.l.; S 31° 24', W 64° 48'; three fragments in Pampa de Achala (PA): 2,200 m a.s.l.; S 31° 34', W 64° 50') during January and February 2003 when fruit set was at its optimum. In each woodland fragment we randomly selected 10 trees, except in one fragment where we only found three trees; totalling 43 trees. As both regions have been largely used for livestock rearing over the last 400 years (Díaz et al. 1994), more than 20% of the areas consist of rock exposed by soil erosion (Cingolani et al. 2003, 2004). Los Gigantes is characterised by steep rock outcrops and deep ravines where small remaining *P. australis* woodlands find refuge from human activities. Pampa de Achala is a flat plateau with a few *P. australis* individuals associated to rock outcrops. We collected up to 30 ripe seeds per individual and stored them under room temperature conditions for 1 month. Each seed was then weighed individually to the nearest 0.1 mg in the laboratory.

### Germination and viability tests

Germination ability of individual seeds ( $n = 586$ ) was tested in petri dishes at a temperature of 20°C/10°C (12 h of light/12 h of darkness) in a climate chamber with a warm white light source. The experiments were ceased after 50 days when germination was zero. The viability of ungerminated seeds was assessed using the Tetrazolium Test (Baskin and Baskin 1998).

### Data analysis

Statistical analyses were performed using SPSS 12.0 (2003) and R-DCT (2003). “Nested ANOVA” and “Analysis of Variance Components” were used to test differences and variances of individual seed mass and percent seed germination per tree (arcsin-transformed data) among geographical regions, woodland fragments,

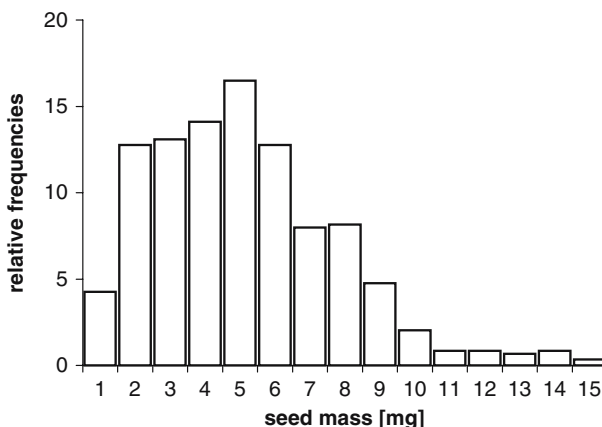
and individual trees. The germination probability in relation to seed mass, geographical regions, woodland fragments, and individual trees was determined by logistic regression (ter Braak and Looman 1995; Crawley 2003). We tested whether germination probability follows a linear or a unimodal model in relation to seed mass, and if an interaction term for the combinations of seed mass and region, seed mass and woodland fragment and seed mass and individual tree needed to be included in the model. The significance of a chosen model in comparison with the null model or a different model (e.g., sigmoid against unimodal; seed mass against seed mass + region; seed mass + region against seed mass + region + interaction term) was tested by the explained deviance using a “Chi-square” test. The deviance estimates the goodness of fit of the model and is defined as  $-2$  times the difference in log likelihood between the current model and a saturated model (Crawley 2003).

## Results

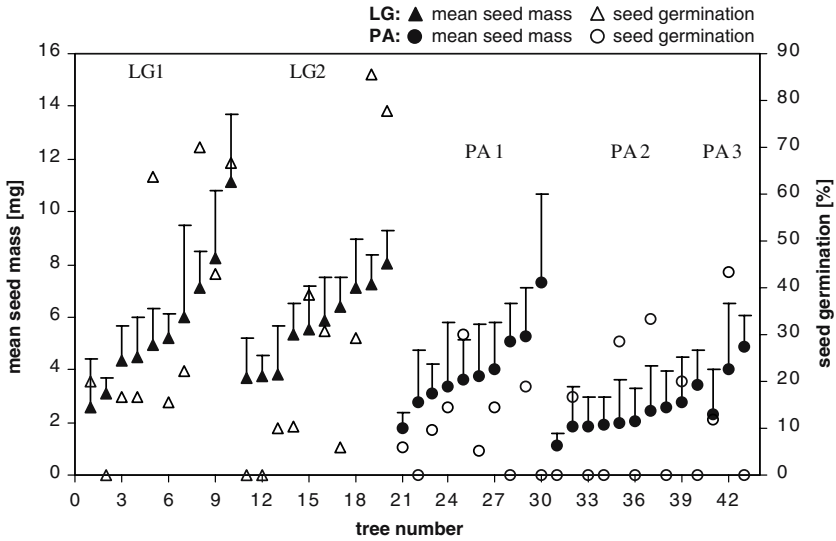
### Seed mass

*Polylepis australis* seeds exhibited a great variation in mass, ranging from 0.2 mg to 14.7 mg with a mean of 4.6 mg ( $n = 586$ ; SD 2.7) with a coefficient of variation of 58.17%. Distribution of seed masses was skewed to the right (Fig. 1). Mean seed mass for individual trees ranged from 1.1 mg to 11.1 mg (Fig. 2). Within individual trees, seeds varied in mass from 1.6-fold to 23.5-fold. This variation is reflected further in the large coefficients of variation, which ranged from 18% to 62% and averaged 42%.

A “nested ANOVA” indicated that both variation among trees within fragments and variation among regions contributed significantly to the observed variation in seed mass, while variation among fragments within regions did not (Table 1). Most of the variation occurred among trees within fragments and among regions, each of which contributed roughly equally to the overall variation in seed mass, while variation among fragments within regions accounted for the remaining 5% (Table 1). Mean seed mass in the Pampa de Achala region was 2.5 mg less than the mean seed



**Fig. 1** Histogram of *Polylepis australis* seed masses



**Fig. 2** Variation in mean seed masses (+SD, closed symbols) and percent seed germination (open symbols) among all sampled *Polylepis australis* trees (ordered by geographical regions (triangle = LG, Los Gigantes; circle = PA, Pampa de Achala) and woodland fragments within regions). For an easier visual interpretation, trees were ranked by mean seed mass within each woodland fragment ( $n = 10$  for LG1, LG2, PA1, PA2, and  $n = 3$  for PA3)

mass in the Los Gigantes region, although there was a significant variability between trees from each region (Fig. 2).

### Seed germination

Seeds began to germinate 7 days after initiation of the experiment, with a peak after 10–15 days, followed by occasional germinations thereafter. Ninety-eight percent of the seeds that did not germinate were found to be empty (without embryo) and 2% were otherwise unviable.

Seed germination from the 43 sampled trees ranged from 0% to 86% (Fig. 2) with a mean of 20.3% and great variability among individual trees (SD 23.1, Fig. 2) with a coefficient of variation of 86.6%. In contrast to variation among fragments within regions, variation among regions contributed significantly to the observed variation in percent seed germination (nested ANOVA, Table 2). Most of the variation occurred among trees within fragments followed by variation among regions, whereas

**Table 1** Variance and distribution of variance in seed mass in *Polylepis australis* among regions, among fragments within regions and among trees within fragments

Source of variation	df	Sum of squares	F-ratio	Significance (P)	Variance component	Percent of variance added at each level
Regions (A)	1	770.42	13.76	<0.05	3.15	47.74
Fragments B(A)	3	167.98	1.42	>0.05	0.35	5.27
Trees C(AB)	38	1,500.25	12.32	<0.0001	3.1	46.99

**Table 2** Variance and distribution of variance in percent seed germination in *Polylepis australis* among regions, among fragments within regions and among trees within fragments

Source of variation	df	Sum of squares	F-ratio	Significance ( <i>P</i> )	Variance component	Percent of variance added at each level
Regions (A)	1	0.9	31.42	<0.05	0.04	27.27
Fragments B(A)	3	0.09	0.3	>0.5	0	0
trees C(AB)	38	3.65			0.1	72.73

variation among fragments within regions did not contribute to the overall variation in percent seed germination (Table 2). Mean seed germination in the Pampa de Achala region was 20.2% lower than that in the Los Gigantes region. Similar to mean seed mass, there was a great variability in percent seed germination among individual trees (Fig. 2).

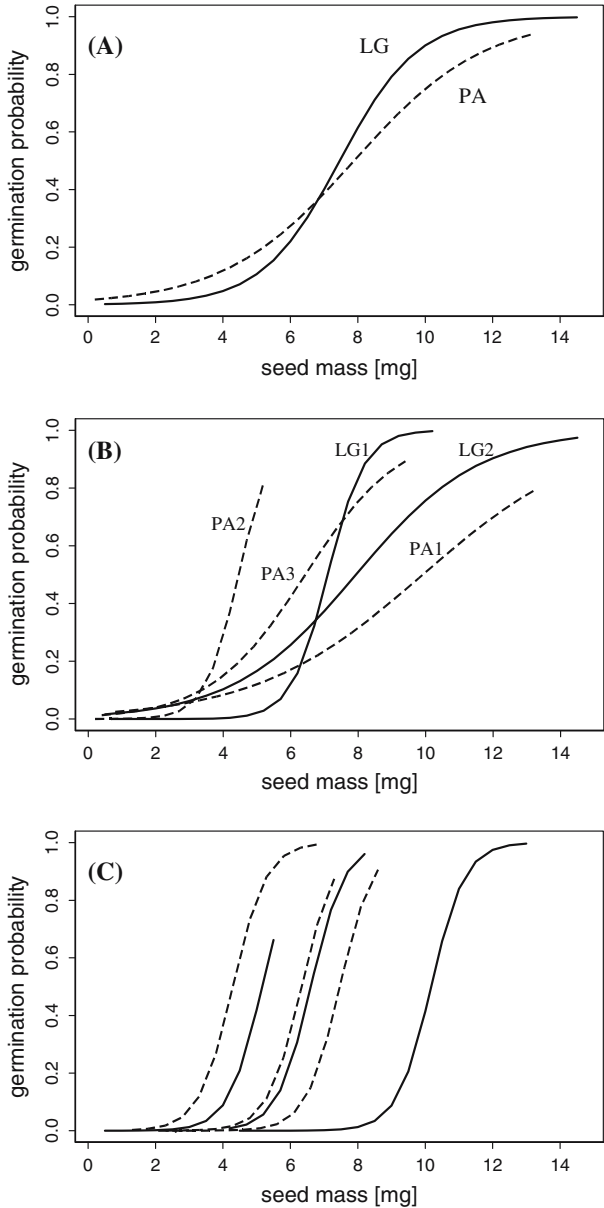
### Seed mass—seed germination probability associations

When pooling all data, the effect of individual seed mass on germination probability of *P. australis* seeds was found to be highly significant (explained deviance 31.8%,  $P < 0.0001$ , linear relationship, Table 3). The germination probability increased with increasing seed mass (Fig. 3). The explained deviance was significantly higher when the variable region (with interaction term) was additionally included in the model and as such indicated the regional effect on the germination success (explained deviance 33.1%,  $P < 0.05$ , tested against the model in which seed mass is solely included, Table 3, Fig. 3A). For light seeds, the germination probability was higher in Pampa de Achala than in Los Gigantes, while for heavier seeds germination probability was lower in Pampa de Achala and higher in Los Gigantes. Logistic regression revealed considerable differences in germination probability–seed mass relationships among woodland fragments (explained deviance 39.9%,  $P < 0.0001$  in comparison to the seed mass model, interaction term included, Table 3, Fig. 3B). In all fragments, the highest germination probability was reached by the heavier seeds. However, in fragment PA2, high germination probability occurred at relatively lower seed masses (at similar masses germination probability was almost zero in fragment LG1 (about 4.6 mg) and low in all other fragments (Fig. 3B)).

**Table 3** Deviance table of logistic regression for the seed germination probability in relation to different variables: model seed mass was tested against the Null model, all other models against the seed mass model

Null model	df	Total deviance	
	585	596.9	
Model seed mass	df	Explained deviance (%)	$P < 0.0001$
	584	31.8	
Model seed mass × regions	df	Explained deviance (%)	$P < 0.05$
	582	33.1	
Model seed mass × fragments	df	Explained deviance (%)	$P < 0.0001$
	576	39.9	
Model seed mass × trees	df	Explained deviance (%)	$P < 0.0001$
	500	79.5	

**Fig. 3** Probability of germination in relation to the combination seed mass with the variable (A) geographical region, (B) woodland fragment and (C) individual tree (for clarity only six trees are illustrated; solid lines: trees in LG; shaded lines: trees in PA)



The explained deviance was highest if seed mass, in combination with the tree variable, was included in the model (71.1%,  $P < 0.0001$ , tested against the seed mass model, interaction term included, Table 3, Fig. 3C). The individual trees were characterized by quite different germination probability–seed mass relationships, such as was observed among different fragments. Germination probability was always positively associated to seed mass, but the highest ones were reached by quite different seed mass values in the different trees (Fig. 3C).

## Discussion

### Effect of seed mass, geographical region, woodland fragment, and individual tree on germination

The results of this study revealed that *P. australis* seed mass varies significantly among different regions and trees. Furthermore, seed mass is positively correlated to seed germination probability, albeit the highest germination probabilities were reached at quite different seed mass values depending on geographical region, woodland fragment, or tree. Several authors address the issue of high variabilities in seed masses (e.g., Vera 1997; Leishman and Westoby 1998; Cordazzo 2002) and the significance of seed mass for seed germination (e.g., Shaukat et al. 1999; Gómez 2004).

The results of our study are striking in the sense that *P. australis* seeds that did not germinate were almost always empty. The seedlessness in well-developed fruits may either result from: post-fertilisation embryo abortion due to lack of water or nutrients; the absence of pollination; or from low pollen vigour (Stephenson 1981; Campbell and Halama 1993; Arista et al. 2001). In *P. australis*, Renison et al. (2004) established a positive relationship between seed viability and soil conditions, and a negative one between seed viability and soil erosion, which suggests a connection to nutrient availability and/or water stress rather than to problems of pollination. Furthermore, Seltmann (unpublished) showed a significant decrease in filled seeds from young to mature seeds. Thus, all current data clearly indicate that post-fertilisation embryo abortion is more likely to be the reason for empty seeds among *P. australis* than are problems of pollination. The degree to which post-fertilisation embryo abortion occurs is thought to be determined by the degradation status of a certain habitat (Renison et al. 2004).

The great variability of seed masses among *P. australis* trees within a woodland fragment shown in this study is in line with the hypothesis that environmental factors, rather than genetic differences, influence seed mass and germinability. The woodland areas are a mosaic of different vegetation types (Cabido and Acosta 1985; Cingolani et al. 2003) that can vary within a few dozen meters due to relief, rock outcrops, disposition, and accessibility for livestock (Cingolani et al. 2003). Thus, the observed differences in seed masses may be the result of differences in small-scale habitat conditions to which the mother trees are subjected (Renison et al. 2004). Accordingly, the results of several studies demonstrated the significance of parental environment on seed mass (e.g., Lacey 1996; Lacey et al. 1997; Galloway 2001; Griffen et al. 2004).

Differences in several seed attributes, such as mass and germinability, among geographical regions have been reported by several authors. For instance, seed germinability of *Juniperus communis* is controlled by the general macroclimate in a given geographical region (Garcia et al. 2000). Concerning the relationship between seed mass and germination, published results have been rather inconsistent, although the majority of the studies report positive effects of seed mass on germination. For example, the germinability of heavier seeds was found to be higher in *Acacia nilotica* subsp. *indica* (Shaukat et al. 1999) and *Quercus ilex* (Gómez 2004), whereas no significant correlation between seed mass and germinability was reported for *Calluna vulgaris* (Vera 1997). In contrast, germinability of heavier seeds



of *Erodium brachycarpum* was reported to be lower by Stamp (1990; see Milberg et al. 1996 for details).

### Implications for restoration purposes

Our results can be used to provide implications for seed collection in woodland restoration projects and future studies. Due to the fact that we demonstrated a clear relationship between seed mass and germination probability, our study suggests that weighing seeds could be a quick way to assess seed viability. As heavier seeds are also larger, an alternative, less time-consuming way would be picking out the larger seeds in the field. However, it is important to consider that the relatively heavier seeds can reach high probabilities of germination even if the absolute seed mass within a region, or an individual tree for that matter, is low. It is important to note therefore that not absolute, but relative seed masses are important in this context. For other mountain ranges where seed mass is not yet known, to optimize germination success we suggest regarding the relatively heaviest available seeds, even if the absolute seed mass may be low. In addition to selecting the relatively highest seed masses, following Renison et al. (2004) we recommend that seeds should be collected in the least degraded areas where they found percent seed germination to be higher. In order to optimise germination probabilities and to select the heaviest available seeds in a particular area, seeds should be sieved or seeds that float should be eliminated. This knowledge is important because low seed viability often deters producers from using seeds in favour of reproduction through cuttings (e.g., Reynel and Leon 1990), which, at least in *P. australis*, grow slower than saplings produced from seeds (Renison and Cingolani 1998) and results in lower genetic diversity of the population that may cause reduced reproductive fitness. However, as it is possible that there are genetic differences between large and small seeds, using only large seeds for reforestation could result in a reduction in genetic diversity. Thus, in case of selecting seeds according to their masses, genetic studies should precede reforestation projects.

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