



Is the benefit of larger seed provisioning on seedling performance greater under abiotic stress?



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ABSTRACT

Seed size is a relevant predictor of seed survival, seedling phenotype and species recruitment and it is generally accepted that larger seeds give rise to seedlings with improved performance. In pioneer tree species the success in seedling survival is strongly determined by resource availability, which largely varies at diverse spatial scales. Here, using a pioneer Mediterranean pine species as a model (Maritime pine, *Pinus pinaster* Ait.), we hypothesized that the positive effect of seed provisioning on seedling establishment and early performance may be stronger under environmental harassment, and that the progeny of lineages investing in bigger seeds would be favored in such stressful conditions. We explored the effect of seed mass on seedling traits related to germination, survival, growth and biomass partitioning by sowing pre-weighted seeds of known genetic background and culturing the seedlings under a range of abiotic stress conditions by experimentally modifying phosphorus (four levels, 5260 seeds) and water availability (three levels, 975 seeds) in two independent experiments. Phenotypic variation in seed mass was extremely large, with more than a tenfold change between the smallest and the largest seed. Seed mass variation showed a strong genetic component with large and significant variation both between and within populations. As expected, seed mass was a positive predictor of germination time and early seedling performance. However, contrary to our expectations, populations from more stressful sites produced smaller seeds, and the positive effect of seed mass on seedling performance was not magnified under resource limitation. Our results thus does not support that early seedling performance is favored by greater seed provisioning under resource limiting conditions.

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1. Introduction

Seed mass is a relevant life history trait with well-documented effects on early seedling phenotype, affecting crucial processes of species recruitment such as dispersal (Debain et al., 2003), germination (Cendán et al., 2013; Mishra et al., 2014), seedling growth (Zas et al., 2013), seedling survival (Larson et al., 2015; Lebrija-Trejos et al., 2016; Moles and Westoby, 2004), seed predation (Fricke and Wright, 2016) and tolerance to different stressors, including shade (Paz and Martínez-Ramos, 2003; Quero et al., 2007), drought (Khurana and Singh, 2000; Metz et al., 2010), limited nutrient availability (Bergholz et al., 2015; Hanley et al., 2007), or fire (Calvo et al., 2016; Escudero et al., 2000). Because of these large effects on the transition across generations, seed mass is considered to be a crucial functional trait linked to plant life history (Leishman et al., 2000).

Although comparatively much less studied than in annual plants, seed mass is also known to affect the offspring performance of long-lived plants, at least during the early establishment (Bladé and Vallejo, 2008; Castro, 1999; Cendán et al., 2013; Gómez, 2004; Milberg and Lamont, 1997; Parker et al., 2006; Ramirez-Valiente et al., 2009; Surles et al., 1993; Wennstrom et al., 2002; Zas et al., 2013). Because seedling establishment is the most critical life stage of trees, during which extremely large mortality rates can occur (Petit and Hampe, 2006), seed mass is also assumed to have high adaptive relevance in trees (Zas and Sampedro, 2015). Particularly, seed size effects are expected to be especially relevant in sun-loving pioneer tree species, in which regeneration usually occurs at high densities in large forest gaps over a short period of time, resulting in a high competitive environment. Any little advantage at the establishment can, thus, have strong fitness consequences (Castro, 2006). Previous results on pine trees have confirmed the relevance of seed mass on recruitment processes (Castro, 1999; Cendán et al., 2013; Parker et al., 2006; Zas et al., 2013). However, empirical evidences are not completely conclusive, with a number of studies failing to detect significant effects of seed mass on

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germination rate, germination time or seedling performance (Bladé and Vallejo, 2008; Calvo et al., 2016; Escudero et al., 2000; Wahid and Bounoua, 2013). Differences in the species considered, the age at which seedling traits are assessed or the environmental conditions in which seeds were tested, all can contribute to this variability.

Of particular relevance is the potential effect of the abiotic environment as a potential modulator of the relationship between seed mass and seedling performance: seedlings developing from larger seeds, containing more nutrients and carbon-based reserves, could take advantage of a better provisioning leading to an improved ability to uptake the scarce resources and support respiration longer under carbon starvation (Leishman et al., 2000; Westoby et al., 1992, 2002). Consequently, the effect of seed mass on seedling survival and performance may be more evident under conditions of abiotic stress or limited resource availability. This prediction has been reported for tolerance to shade (Paz and Martínez-Ramos, 2003; Quero et al., 2007) and intraspecific competition (Lebrija-Trejos et al., 2016). However evidences in the case of nutrient limitation and drought are limited and almost restricted to annual grasses (Bergholz et al., 2015; Hanley et al., 2007).

A larger effect of seed mass on seedling performance under stressful conditions may impose a positive selection pressure on seed mass, leading to heavier seeds when resources are scarce (Leishman et al., 2000; Westoby et al., 1992). This has been widely studied at the interspecific level, searching for abiotic gradients in seed mass, in which large-seeded species are commonly associated with unfavorable environmental conditions (Dainese and Sitzia, 2013; Metz et al., 2010; Moles et al., 2007; Qi et al., 2014). However, whether the intraspecific variation in seed mass across populations or lineages may influence the ability of the emerging seedlings to survive and grow under stressful conditions has received comparatively much less attention (Gorden et al., 2016; Khurana and Singh, 2000; Quero et al., 2007; Völler et al., 2012). Populations from harsher environments have been reported to provide heavier seeds (Guo et al., 2010; Konarzewski et al., 2012; Völler et al., 2012) suggesting that this could be relevant also within species. However, opposite results, with seed mass decreasing across populations as the environmental conditions become more stressful have also been reported (Lázaro and Traveset, 2009; Pluess et al., 2005). In the particular case of pine trees, seed mass is known to largely vary both within (Bilir et al., 2008; Zas and Sampedro, 2015) and across populations (Calvo et al., 2016; Correia et al., 2014; Wahid and Bounoua, 2013), with some authors relating the variation in seed mass across populations with the variation in their ability to cope with different stresses. For example, Wahid and Bounoua (2013) suggested that heavier *P. pinaster* seeds are better adapted to drought conditions, while Correia et al. (2014) found *P. pinaster* seeds from high-altitude origins to be larger and germinate earlier than seeds from low-land origins.

The aim of the present study was to test, using a pioneer pine species (*Pinus pinaster* Ait.) as a model, i) whether the effect of seed mass on seedling performance is more relevant when seedlings experience reduced resource availability, and ii) whether populations from abiotic stressed environments bear larger seeds in order to help seedlings to cope with that stress. We explored the effect of seed mass on seedling traits related to germination, survival, growth and biomass partitioning by sowing pre-weighted seeds of known genetic background and culturing the seedlings under a range of abiotic stress conditions by manipulating nutrient (four levels of phosphorous availability, 5260 seeds) and water availability (three levels, 975 seeds) in two independent experiments. We hypothesize that i) seeds from origins experiencing more abiotic stress will be heavier than seeds from origins with more favorable environmental conditions. And that ii) the

influence of seed mass will be more relevant under conditions of limiting resource availability, or, in other words, that seedlings developing from large seeds will be less dependent on the availability of soil nutrients and water.

2. Materials and methods

This study includes two independent greenhouse experiments. In the first one, *P. pinaster* seedlings derived from pre-weighted seeds of 39 half-sib families of one population were submitted to four different levels of phosphorous availability. In the second, seeds from 18 half-sib families of 3 contrasting populations, which are known to strongly differ in their tolerance to drought (Corcuera et al., 2011, 2012), were grown under different levels of water availability, from full field capacity to severe water deficiency. After one growing period subjecting the seedlings to the stress treatments, we measured different seedling traits in order to analyze how seed mass affected seedling performance under abiotic stress.

Maritime pine (*Pinus pinaster* Ait.) is a species with a high level of population differentiation (González-Martínez et al., 2002) and for which seed mass is known to be extremely variable (Wahid and Bounoua, 2013; Zas and Sampedro, 2015) and to have important impacts on seedling traits (Cendán et al., 2013; Escudero et al., 2000; Zas et al., 2013). Drought is a main limiting factor and a major driver of population differentiation for this Mediterranean pine species (Gaspar et al., 2013; Lamy et al., 2014). Phosphorus limitation is one of the most important factors limiting pine productivity in the Atlantic and humid area of Northwest Spain (Martíns et al., 2009).

2.1. Experiment 1: nutrient stress experiment

2.1.1. Plant material

Open pollinated seeds from 39 mother trees selected within the Atlantic Coastal-Galicia (CGAL) population (Northwest Spain) were used in the nutrient stress experiment. The region has a temperate humid climate with mean annual precipitation around 1500 mm, low summer drought, and mean annual temperatures of about 11°, typically ranging between 4° and 25 °C (min and max daily means). Soils in this area are thin, sandy and acidic, with high organic matter content, high total nitrogen and very low phosphorous concentration. Soil phosphorus availability has been identified as one of the most relevant drivers of forest productivity in the region (Martíns et al., 2009; Zas and Serrada, 2003).

2.1.2. Experimental design

The greenhouse experiment followed a randomized split-plot design replicated in four blocks, with four levels of phosphorus availability (complete fertilization, and three levels of phosphorus-limited fertilization) as the whole factor and 39 open-pollinated half-sib families as the split-plot factor. In total we sowed 5260 seeds, approximately 135 of each family, of which 3389 finally germinated. During this germination phase, we maintained common environmental conditions for all the seeds. Approximately one month after sowing we arranged the plants following the final experimental design and began the fertilization treatments. A total of four plants per family, randomly selected among the available germinated seedlings, were included in each whole plot (phosphorus treatment by block combination). The experiment included, thus, a total of 2496 seedlings (4 blocks × 4 phosphorus treatments × 39 families × 4 plants).

2.1.3. Greenhouse conditions and nutrient availability treatments

Individually weighed seeds (at 0.0001 g) were sown in 2 L pots filled with sterilized perlite and covered with 1 cm layer of sand. In

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