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The role of seed provenance in the early development of *Arbutus unedo* seedlings under contrasting watering conditions

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ABSTRACT

In the last decades, several studies have reported the increase of land degradation and desertification in the Mediterranean Basin. Depending on degradation severity, ecological restoration might be needed in order to promote ecosystem recovery. The ecology of the selected species and intra specific variability should be considered in order to improve restoration options, especially facing climate change.

The present study tested the hypothesis that seedlings from drier provenances would be better adapted to low water content conditions. Seeds were germinated under controlled temperature after which seedlings were grown in a phytotron under two contrasting watering regimes. Seedling performance was analysed using morphological and physiological parameters.

Low water content had a clear negative effect on the seedlings' aboveground biomass (total dry weight, root collar diameter, leaf dry weight and leaf weight ratio) and a positive effect on belowground biomass (root weight and root:shoot ratio). This response was not unequivocal, since provenances differed in morphological adaptations to low water content. Seedlings from the wettest provenance revealed a higher relative growth rate under high water content but a poor adaptation to limited water availability when compared to the other two provenances. This was observed by the absence of a significant belowground investment in this provenance. Seedlings from the wettest provenance also presented a significant reduction of total leaf area that was not observed in the other two provenances. This can however be hardly considered as a successful adaptation to cope with drought since this provenance produced less sclerophyllous leaves, less belowground biomass and also lower sapwood to leaf area ratio independently from the water content conditions. By contrast, seedlings from the dry provenance with the hottest summer had similar root collar diameter, leaf dry weight and physiological performance under both watering regimes.

The observed adaptations to water regimes seem to be related with the climate of the seed source and highlighted the importance of seed provenance in ecological restoration actions using Mediterranean species. This knowledge could improve early establishment success predictions for different plant populations, allowing more reliable and cost-effective management decisions under climate change scenarios.

1. Introduction

In the past decades, the Mediterranean Basin has suffered a considerable increase in the area affected by land degradation and desertification (Díaz-Delgado et al., 2002; Pausas et al., 2008). The principal underlying causes are land abandonment and poor management of forest areas, which then result in recurrent and high-intensity wildfires (Vallejo et al., 2012). Although Mediterranean plant communities are well adapted to fire, recurrent wildfires tend to favour fire-prone species, i.e. species that accumulate large amounts of dead biomass and, thereby, not only increase fire hazard but also fire intensity (Baeza et al., 2011).

Abbreviations: HWC, high water content; LWC, low water content; H_s, shoot height; TDW, total dry weight; RCD, root collar diameter; TLA, total leaf area; SLA, specific leaf area; LDW, leaves dry weight; SDW, stem dry weight; RDW, root dry weight; LWR, leaf weight ratio; RWR, root weight ratio; R:S, root to shoot ratio; SW:LA, sapwood to leaf area ratio; A, net photosynthesis; Gs, stomatal conductance; IWUE, Intrinsic Water Use Efficiency; Ci, Transpiration; Φ PS II, Yield Photosystem II; Ci, substomatal CO_2 concentration; SW:LA, Sapwood to Leaf Area.

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The Mediterranean climate is typically seasonal, with a summer period of warm temperatures and the bulk of rainfall occurring in spring and autumn. Water is considered as the main factor regulating plant activity and plant survival. In forest seedling plantations, plant survival is strongly influenced by the intensity and duration of drought periods right after plantation (Vallejo and Alloza, 1998). According to climate change projections, the frequency and intensity of drought is expected to increase in the Mediterranean region (Solomon et al., 2007). Although Mediterranean plants are well adapted to post-fire regeneration and summer drought, these adaptations may not be sufficient to ensure plant regeneration under extreme land degradation scenarios (Pausas et al., 2008).

In general, plants respond to stressful environmental conditions by shifting carbon allocation to the organs collecting the most limiting resource (Chambel et al., 2005). It is therefore expected that under drought conditions, plants increase belowground biomass allocation to improve water uptake capacity. However, drought-induced adjustments usually involve complex adaptation mechanisms, such as leaf area reduction, osmotic regulation and heat dissipation (Chaves, 2002). In addition, different plant species have different strategies to cope with drought, i.e. drought avoidance in the case of winter and spring annuals or drought resistance in the case of sclerophyllous Mediterranean species (Chaves, 2002).

In the past decades, our understanding of plant water relations and plant adaptation mechanisms was considerably improved through research focused on genetic determinants and environmental triggering factors that regulate plant activity of economically relevant species (Price and Courtois, 1999; Hamanishi and Campbell, 2011).

It is now increasingly recognised that wild species play a key role in ecosystem resilience under climate change scenarios. In this context, the intra-specific variability in plant functional traits can be determinant to improve species' fitness (Bischoff et al., 2006, 2008). This variability can result from ecotypic differentiation caused, in its turn, by specific morphological and physiological adaptations to different habitats (Hufford and Mazer, 2003).

Depending on the degree of plant regeneration impairment, the implementation of ecological restoration actions by sowing or planting can be crucial to prevent the disruption of ecosystem resilience. Among other management practices, the selection of local-specific low flammable and high resilient species, can contribute to interrupt the established degradation processes by promoting resilience against major perturbations (Vallejo et al., 2012).

The first studies on the genetic variation of forest tree provenances date back to the beginning of the 19th century. Under the concept of ecological distance, the benefits of matching seed source and target site conditions have been widely reported for tree production purposes (Matyas, 1994; O'Neill et al., 2008).

Though ecological protocols address the importance of local gene pool conservation (SER, 2004), the role of intra-specific variability and seed source adequacy has only been addressed recently for a limited number of herbaceous species (Bischoff et al., 2008; Mijnnsbrugge et al., 2010). In this context, the improvement on the knowledge base of provenance-related adaptations might not be set aside in plant performance predictions following restoration actions.

The strawberry tree (*Arbutus unedo*) is an evergreen shrub, native to South Europe, North Africa, Palestine, Ireland and Macaronesia. It is widely spread in Portugal and commonly present in understory of oak and pine forests. This species presents several characteristics that justify its selection as a case study for the improvement of knowledge based for ecological restoration protocols, namely: low standing death biomass, being catalogued as low to intermediate flammable (Liodakis and Kakardakis, 2008); strong resprouting ability after fire, contributing to ecosystem resilience (Vallejo et al., 2012); late successional, whose recruitment is often compromised by recurrent wildfires (Mesléard and Lepart, 1991) and, finally an intermediate resistance to drought, in comparison to other Mediterranean species (Gratani and Varone, 2004).

Few decades ago, *A. unedo* was used as a model species to study environmental factors limiting CO_2 assimilation in Mediterranean species (Harley et al., 1986). Previous studies with *A. unedo* reported a conservative water use strategy, through Gs reduction or increase in root investment under drought conditions (Castell and Terradas, 1994; Navarro-García et al., 2011). Water stress resistance mechanisms, such as anti-oxidative protection were also reported for this species (Munné-Bosch and Penuelas, 2004). In spite of this, Ogaya et al. (2003) and Ogaya and Peñuelas (2004) reported a higher growth reduction and phenophase delay in *A. unedo* than in other co-existent species, such as *Phillyrea latifolia* and *Quercus ilex*. Gratani and Varone (2004) also compared these species and found a higher reduction of photosynthesis and stomatal conductance in *A. unedo* after drought. These results suggest a higher sensitivity to drought in *A. unedo* than in other pre-mediterranean species and therefore enhance its potential as an indicator of early drought effects following ecological restoration actions.

The main objective of the present study was to analyse the effect of seed provenance on the short-term development in *A. unedo* seedlings. The hypothesis tested is that seedlings from drier provenances would be better adapted to low water content conditions. With this objective, seeds were harvested in three distant provenances in mainland Portugal, representing different climates. Two different water regimes were simulated and plant response during early stages of development was assessed through several eco-physiological and morphological traits, using 10 mother plants from each provenance.

2. Materials and methods

2.1. Seed harvesting: sites and procedure

Seeds were harvested at three different locations in mainland Portugal, at distances of at least 150 km, with latitudinal-related climate differences and also between coastland and inland provenance regions (Table 1). The aridity index of Martonne (De Martonne, 1926) however distinguishes the Aljezur location as semi-dry from the humid Gerês and Pesqueira locations. This reflects both the higher annual temperature and lower annual rainfall at Aljezur than the other two locations.

Between October and December 2010, the three different locations were visited to harvest ripe fruits of *A. unedo*. In each site, 30 plants with ripen fruits were selected randomly, according to the nearest neighbour method, ensuring a minimum distance of at least 5–10 m between plants. At the mother-plant level, 30 fruits were harvested, ensuring its even distribution over the canopy. Fruits were then depulped and seeds were washed, dried and stored in glass bottles with silica. Seeds were then placed in the fridge at 4–5 °C for approximately 14 months before the beginning of the experiment.

2.2. Experimental setup: germination and growth system

Seeds were soaked in distilled water for 2 h and, after excluding those that floated, were set to germinate on Petri dishes over moist filter paper. Three Petri dishes were used as replicates and a total of approximately 30 seeds of one mother-plant were sown on each per Petri-dish. Seeds were then placed in a germination chamber with 12:12 hour's photoperiod at a constant temperature of 15 °C. Germination was monitored two times per week and