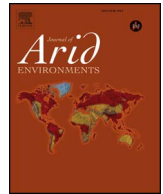




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## Intraspecific leaf shape at local scale determines offspring characteristics

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### ABSTRACT

Identifying the degree of adaptation to particular environmental constraints at small geographical scales (e.g., intra-population variability) is particularly valuable to select plant reproductive material in restoration projects. We analyzed possible differences among progeny characteristics of *Quercus coccifera* L. a species of interest in forest restoration under Mediterranean climates. The differences were tested among seeds and seedlings from two phenotypic groupings (small and large leaves) within one provenance under semi-arid climate. In addition, these seeds and seedlings were compared with those from a near population under contrasted climate (i.e., subhumid climate). We analyzed differences in germination, growth and seedling morphological traits (height, number of leaves and canopy area). We considered the different characteristics of the progeny across different parent individuals, intra- and inter-population levels. We found seed provenance effects on germination and seedling morphology at different scales. Progenies from semi-arid populations and from parent plants with a smaller leaf size showed lower germination rates and lower development of above-ground structures (shoots and leaves). Our results suggest that intrapopulation variability for phenotypic traits, such as leaf size, could influence offspring fitness. In addition, these morphological traits are easily identifiable by stakeholders and could be a useful tool to ensure early plant establishment in reforestation programs.

### 1. Introduction

Despite the high number of resources and efforts invested, afforestation under Mediterranean conditions often render poor results, mainly because of harsh and unpredictable environmental conditions and a marked summer drought (Cortina et al., 2011; Vallejo et al., 2012). It has been argued that selecting material from locally adapted populations can enhance the success of restoration efforts, as local adaptation increases the fitness of a population in response to environmental limiting factors (Hufford and Mazer, 2003). Using local provenance material should be the normal practice in most situations, especially when there is not enough knowledge to assess the genetic consequences of introducing genotypes from elsewhere (Sackville Hamilton, 2001). Non-local provenance seeds may hamper successful establishment and generate unfavorable effects, such as founder effects, genetic swamping and outbreeding depression (Hufford and Mazer, 2003). In general, a negative relationship between spatial distance from the source population and the level of adaptation to a given site has been found (Keller and Kollman, 1999) and restoration managers always recommend the use of local seeds for reforestation projects

(Chazdon, 2008). For example, in assisted colonization projects where it may supplement an existing population in a site where their numbers are dwindling (McLachlan et al., 2007).

However, strong adaptive genetic differentiation can also occur at small geographical scales (i.e., within populations) and may be more related to environmental than to spatial distances (Montalvo and Ellstrand, 2000). Indeed, local adaptation is not always prevalent in wild populations, especially in small ones (Leimu and Fischer, 2008), and the usage of local populations is not always guarantee of restoration success (Lampej-Bucharová et al., 2017). Therefore, alternative ways of selecting plant material could substantially improve the chances to succeed in restoration efforts under harsh conditions (Bischoff et al., 2008). For example, phenotypic differences within populations modulate how species respond to current and future climatic constraints (Valladares et al., 2014), and may have an important influence on seedling quality and restoration success (Langlet, 1971). Despite this potential, the performance of plant selection based on phenotypic differences has been poorly explored. Additionally, the scale at which local adaptation occurs may be more important to determine the restoration success of the selected plant material (Bischoff

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et al., 2006). However, our ability to predict the spatial and temporal scale of variation in adaptive traits differs among populations and species (Linhart and Grant, 1996). Thus, using visually detectable traits in the selection of plant material might be helpful to identify transfer zones able to ensure establishment success under a given environment (Bognounou et al., 2010).

To compare the effect of within and across population adaptation in the potential success of plant material for restoration, we analyzed the influence of provenance (parent individual, different leaf phenotypes and populations from contrasting climates) on germination, growth and seedling morphological traits (height, number of leaves and canopy area). These morphological traits are the most common to evaluate plant stock quality in reforestation projects as they are related to how plants respond to the environment when introduced in the field (Shimono and Kudo, 2003; Villar-Salvador et al., 2012; Vasques et al., 2013). We focused the study on *Quercus coccifera* L. a species native to the western Mediterranean region which is particularly interesting for restoration because of its resprouting ability after fires, the protection against erosion, and the shelter it provides for wild and domestic animals (Cañellas and San Miguel, 2003; Vallejo et al., 2012).

## 2. Materials and methods

### 2.1. Study area

Two locations were selected in the SE of the Iberian Peninsula (Crevillente: 38° 15' 20'' N; 00° 50' 07'' W, and Tárbenas: 38° 42' 00'' N; 00° 06' 17'' W), with mean annual temperature and rainfall of 18 °C and 271 mm for Crevillente (semiarid climate), and 16.5 °C and 833 mm for Tárbenas (subhumid climate). These areas were selected based on their contrasted climatic conditions. They cover a wide range of environmental conditions under which *Q. coccifera* grows. Soils in both locations are classified as *Lithic calciorthid* (Soil survey staff 1994), these shallow soils have a high content of calcium carbonate and low percentage of organic matter.

### 2.2. Effects of different provenances on the progeny germination and growth

Three parental provenances were selected. Two of them were located in.

Crevillente, whose parent plants' mean leaf area was  $0.70 \pm 0.02 \text{ cm}^2$  and  $3.29 \pm 0.37 \text{ cm}^2$  (mean  $\pm$  SE;  $n = 8$ ; referred to as C-SL and C-BL, respectively). The third parental provenance was located in Tárbenas, with a mean leaf area of  $1.38 \pm 0.13 \text{ cm}^2$  (mean  $\pm$  SE;  $n = 8$ ; hereafter TAR). In the latter population, we could not find enough parent individuals with contrasted leaf size to establish different phenotypic groupings (See details in Supplementary Material).

In November 2002, acorns were collected from eight different individuals of each parental provenance (C-SL, C-BL and TAR). To ensure sufficient genetic diversity within each of them, parent plants were randomly chosen at least 150 m apart from each other. Acorns were transported to a public nursery (Santa Faz, Alicante, Spain; 38°23'N; 0°26'W; 80 m.a.s.l.), where they were stored at 4 °C until the beginning of the experiment. In January 2003, acorns were floated in water, those that did not sink or those with some damage were discarded. Finally, 40–80 acorns per each parent plant were selected, accounting for a total of 400 acorns per parental provenance ( $n = 1200$  acorns). These acorns were wetted for 48 h. The 400 acorns of each parental provenance were distributed in four replicates (four plastic trays filled with peat:coco-peat [1:1] substrate). Emergence was monitored every day for two months, when an acorn showed radicle emergence (2 mm), it was removed from the tray and placed in a 300 cm<sup>3</sup> plastic pot. These pots were filled with peat:coco-peat (1:1) substrate with slow-release fertilizer (Plantacote; dose of  $1.5 \text{ g l}^{-1}$  of substrate).

Differences in environmental conditions experienced by parent plants, as well as seed position in the canopy or phenology, among

other factors, may lead to nongenetic differences in seed size (e.g., Donohue and Schmitt, 1998). Generally, bigger seeds, regardless of their genetic similarity, contain more nutrient reserves for seed germination than small ones, often showing greater germination rates (Westoby et al., 1992). To evaluate possible effects of seed size on germination, the length of all acorns were measured before wetting them and included as a covariate in the models (see Statistical analyses below). Seed length is easier to measure by restoration practitioners than seed weight and was directly related to the latter ( $R^2 > 0.60$ ; see details in Supplementary Material).

The number of germinated seedlings of each parent individual varied according to acorns germination rate and their survival (7–55 seedlings/parent individual;  $n = 392$  seedlings in total). Finally, only five out of eight parent individuals per provenance were chosen because the rest did not produce enough seedlings. Seedlings were grown outdoors under homogeneous and optimal environmental conditions (no water restriction, uniform light and nutrient supply). In July 2003 (after 6 months of growth under optimal conditions), the seedling height, major and minor canopy diameters and the number of leaves were measured on each seedling. Diameters were used to calculate the canopy area assuming the shape of the canopy as an ellipse. Apart from analyzing these morphological traits separately, we also analyzed “plant form” as an integrative variable including the three together as a complex morphological structure present greater hereditary capacity than individual variables (Alía, 2006). Different plant forms could also be more related to the ability of seedlings to respond to the environment when introduced in field than isolated morphological variables (Shimono and Kudo, 2003; Villar-Salvador et al., 2012).

### 2.3. Statistical analyses

The provenance effects on the shape of germination curves were assessed by using the Kaplan-Meier procedure, where “parental provenance” (population [TAR vs CRE] and within-population phenotypic differences [CRE-BL vs CRE-SL], added as a single factor with three levels) and “parent individual” were considered as factor and strata, respectively. Non-parametric Log-Rank tests were used to perform pairwise comparisons (Pyke and Thompson, 1986). Differences in germination rates were analyzed by using Generalized Linear Models (GLM). We could not introduce “parent individual” as a random factor in our model because the optimal model did not accomplish homocedasticity and normality assumptions when introducing this factor. Hence, the proportion of germination events scored for each “parent individual” (Y successes out of n independent trials) was calculated to avoid pseudoreplication (Crawley, 2007). A quasibinomial approach was used to perform the GLM to avoid the effect of overdispersion in the data (Crawley, 2007; Zuur et al., 2009).

Acorn length was used as a covariate in this model, with “parental provenance” treated as fixed factor. The full model including “acorn length” was compared to a reduced model without the covariate, using F-tests with an empirical scale parameter instead of chi-squared (Crawley, 2007). Residuals of this final model fulfilled the assumptions of normality and homocedasticity.

Seedling height and canopy area were analyzed with GLMMs with a Gaussian distribution of the errors. The number of leaves was analyzed by using the same technique, but with a Poisson distribution (recommended for count data; Zuur et al., 2009). “Parental provenance” and “parent individual” were treated as fixed and random factors, respectively. The same steps-procedure as for the analyses of germination was used to select the best model. Residuals fulfilled the assumptions of normality and homocedasticity. Since these three variables (height, canopy area and number of leaves) were correlated ( $r > 0.4$  in all cases), we applied the Bonferroni correction to avoid multiple testing problems (corrected  $\alpha = 0.05/3 = 0.017$ ). The effect of origin (the parental provenance and the parent individual) on the plant form was evaluated from the conversion of these morphological variables into

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