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Original article

Effects of waterlogging on seed germination of three Mediterranean oak species: Ecological implications

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ABSTRACT

Soil water saturation during prolonged periods of time generates a negative impact on nearly all terrestrial plants. In Mediterranean woodlands, precipitation can be very abundant during the wet season, inducing temporary soil waterlogging, coinciding with the seed dispersal and germination time of many species. We investigated the effects of waterlogging on seed germination and early root growth of three coexisting oak species (*Quercus canariensis*, *Q. suber* and *Q. pyrenaica*), by completely flooding of seeds for various periods of time. The three oak species showed a certain level of tolerance to waterlogging, only being affected those seeds subjected for long periods of submersion (over 30 days). Waterlogging during prolonged periods of time decreased the probability of seed germination in the three oak species, lengthened the time to germination, and hampered root development in two of the studied species. The main differences between oak species occurred in terms of root growth (*Q. canariensis* being the less affected, and *Q. suber* the most); these differential responses could be related to a species rank of waterlogging tolerance. Thus inter-specific differences in germination responses to waterlogging could contribute to explain, at least partially, species habitat and distribution patterns across landscapes. Seed mass also played an important role on different aspects of germination, though its relative importance varied as function of species and waterlogging treatment. The tolerance to stress induced by waterlogging increased with seed mass, but only in the case of *Q. canariensis*.

1. Introduction

Soil water saturation over prolonged periods of time generates a negative impact on nearly all terrestrial plants, as a consequence of the slow diffusion rates of gases in water (Jackson, 1985; Armstrong, 2002), which hampers oxygen supply to roots and reduces respiration and photosynthesis rates (Pezeshki, 1994; Voesenek et al., 2006). Several studies have shown that soil waterlogging as a result of periodic-to-continuous flooding of bottomland is the major factor affecting tree regeneration in many temperate forested wetlands (e.g., Streng et al., 1989; Kevin and Brooks, 2003; Sakio, 2005; Trowbridge et al., 2005; Battaglia and Sharitz, 2006). Mediterranean ecosystems experience contrasting two-phase precipitation dynamics, receiving almost all of their yearly rainfall during the autumn–spring cold period (which can lead to pulses of over-abundant water levels), in contrast with the prolonged, warm dry summer. Water shortage during the summer has commonly been claimed to be a major limiting factor for seedling recruitment in this type of ecosystems (e.g., García, 2001; Herrera et al., 1994; Sack et al., 2003; Marañón et al., 2004; Pulido and Díaz, 2005; Gómez-Aparicio et al., 2004; Castro et al., 2005), but potential negative effects of excess water during the wet period have been overlooked. Precipitation can be very abundant in autumn–spring, with frequent events of soil waterlogging that can be more prominent and persistent in clayey soils of low permeability.

Tree species can show important differences in tolerance to waterlogging during early stages of regeneration, even within the same genus, depending on the environmental conditions of their habitats. Several authors have reported that seeds of tree species occurring in potentially flooded sites are not affected by waterlogging (Guo et al., 1998) or they are able to keep under water during long periods of time without significant loss of viability (Hosner, 1957; DuBarry, 1963). Contrarily, other studies have shown that excess water affects negatively the capacity of seed germination in species that are less adapted to flooding (Guo et al., 1998; Walls et al., 2005). Inter-specific differences in tolerance to waterlogging may determine the structure and composition of the community along a gradient of soil humidity. For example, in forested wetlands, plant community changes occur primarily as the result of variation in

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flood-tolerance among plants and the effect of flooding on growth rates (Megonigal et al., 1997). However, ecological implications of differences between species in the responses to soil waterlogging are still unknown in Mediterranean woodlands.

In a recent field study in a mixed oak woodland located in southern Spain, we demonstrated that soil waterlogging was one of the main factors limiting initial stages of seedling recruitment in the three dominant oak species (*Q. canariensis*, *Q. suber*, and *Q. pyrenaica*) (Urbieta et al., 2008a). Over-abundant water levels during the wet season reduced the probability of germination and emergence and lengthened time-to-emergence of seedlings, which in turn decreased their survivorship during summer drought. However, the mechanisms by which soil waterlogging affects initial stages of oak species recruitment are not clear.

In this study, we specifically investigated the effects of waterlogging on different aspects of seed germination in three Mediterranean oak species. We carried out a laboratory experiment, where groups of seeds of each species were completely submerged under water (with measures to prevent fungal infections) for different periods of time. We wanted to answer the following specific questions: (1) does waterlogging – and the consequent restriction of oxygen supply – decrease the probability of seed germination? (2) How long can seeds stay viable under submersion conditions? (3) What is the relative importance of seed mass on tolerance to submersion? (4) How does waterlogging affect root growth? (5) Are there differences between the three oak species in their responses to waterlogging? If so, how are such inter-specific differences related to species distribution patterns?

2. Materials and methods

2.1. Study species and area

Quercus suber L. (cork oak) is an evergreen tree dominating forests in sub-humid Mediterranean-type climate, on acidic soils. Its distribution range covers the western half of the Mediterranean Basin (France, Italy, Spain, Portugal, Morocco, Algeria, and Tunisia). Its seed is one of the largest in the Mediterranean forest, and its dispersal is restricted to the autumn/early winter season (between October and February).

Quercus canariensis Willd. is a semi-deciduous oak, locally abundant in moister sites, and usually mixed with *Q. suber*. The distribution range is restricted to the Iberian Peninsula (Spain and Portugal) and NW Africa (Morocco and Algeria). The seeds are somewhat smaller than those of *Q. suber*, and their dispersal is earlier (September–December).

Q. pyrenaica is a deciduous oak distributed from SW France to N Morocco. Its seeds are usually larger than those of the other two oak species, and dispersal timing is similar to *Quercus canariensis*.

The three studied species coexist in the mixed oak forests of the Aljibe Mountains, near the Strait of Gibraltar, in southern Spain (see a detailed description of the experimental site in Quilchano et al., 2008 and Pérez-Ramos et al., 2008). The dominant bedrock in the area is Oligo–Miocenic sandstone, with rugged terrain and a highest peak of 1094 m a.s.l. Climate is subhumid Mediterranean-type, with cool and wet winters, alternating with warm and dry summers. Mean annual temperature ranges from 14.6 to 18.48 °C, with a mean monthly maximum of 36.8 °C (July) and mean monthly minimum of 2.8 °C (January). Mean annual rainfall varies from 701 to 1331 mm (mean of 1056 for 15 weather stations), depending on the effects of the local orographic relief. Overstorey canopy of these forests is co-dominated by *Q. suber* and *Q. canariensis*, whereas *Q. pyrenaica* is only present in scarce populations at higher altitudes (>900 m). Most of the forested area has been protected within *Los Alcornocales* (meaning cork oak forests) Natural Park, covering about 1700 km^2.

2.2. Experimental design

To encompass intra-specific variation, more than 1000 seeds of *Q. suber* and *Q. canariensis* were collected from various trees (at least 10 of each species) in the surroundings of the study area, when seed-drops of both species overlap (late November 2005). Seeds of *Q. pyrenaica* (with scarce seed production in Aljibe mountains) were brought from Sierra Morena stands, an inland area also located at southern Spain. A sample of healthy, normal-sized seeds (i.e., discarding aborted acorns) was made, using the floating method to discard those infected by moth or beetle larvae (Gribko and Jones, 1995). The selected seeds were stored on a moist substrate at 2–4 °C until used in the experiment (with a storage timing below 15 days). Subsequently, selected seeds were buried in a moist sand (pure silica) bed on plastic trays, and completely submerged in distilled water (at 5 cm of depth) for different periods of time. We used distilled water to avoid the possible effects of nutrient content on seed germination and early root growth. Three waterlogging treatments were established as a function of the submersion time (W_{15}, W_{30}, and W_{60} for groups of seeds submerged for 15, 30, and 60 days, respectively) and another treatment (W_0) for non-submerged seeds. The duration of W_{15} and W_{30} treatments is comparable to field observations of soil waterlogging timing at the study site, especially during rainy years (Fig. 1). The W_{60} treatment was also selected for this experiment in order to check how long seeds of the three species are able to stay viable under submersion conditions. The trays used for seed submersion were set up within a germination chamber at constant temperature (≈20 °C).

After waterlogging treatment, four groups of 20 seeds (per treatment and species) were randomly selected and set to germinate semi-buried, separated from each other by approx. 7 cm, in a new bed of sand (pure silica), 8 cm deep covering the bottom of 48 × 33 × 10 cm plastic trays. Previously (just after submersion), the selected seeds were washed with sodium hypochlorite (2%) and then treated with a commercial fungicide based on copper oxychloride (50%) to prevent fungal infections. All selected seeds were initially weighed to the nearest 0.01 g. Mean ± SD (standard deviation) seed fresh mass (g) was 3.11 ± 0.71 for *Q. canariensis*, 3.19 ± 1.13 for *Q. suber*, and 6.32 ± 1.55 for *Q. pyrenaica*. We used acorn fresh weight as a surrogate of seed mass, according to Quero et al. (2007).

Trays for germination monitoring were set up within a germination chamber, where they stayed for 28 days at constant temperature (≈20 °C) and in darkness, which have been

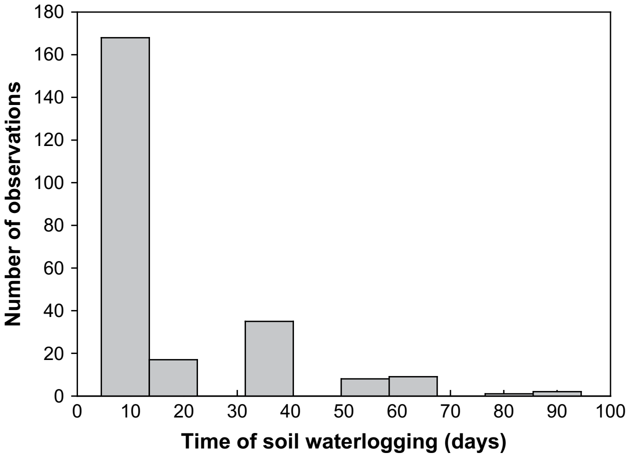

Fig. 1. Histogram of frequencies of soil waterlogging timing, based on field observations at the study site during the wet season (2004 year). See Urbieta et al. (2008) for methodological and analytic details.