

# Soil water content and emergence time control seedling establishment in three co-occurring Mediterranean oak species

Itziar R. Urbietta, Ignacio M. Pérez-Ramos, Miguel A. Zavala, Teodoro Marañón, and Richard K. Kobe

**Abstract:** Tree species can differ in their responses to resource availability during the critical phase of establishment, which could influence forest dynamics. In Mediterranean forests, most of the attention has focused on the effects of shade and summer drought on seedling survival, but little is known about the effect of autumn to spring rains on earlier stages of recruitment. A sowing experiment was set up along natural light and water gradients with three co-occurring oak species (*Quercus suber* L. (cork oak), *Quercus canariensis* Willd. (Algerian oak), and *Quercus pyrenaica* Willd. (Pyrenean oak)) that show limited natural regeneration in southern Spain. Recruitment stages were monitored for 1 year. Models of seed germination, seedling emergence, and seedling survival as well as of overall recruitment patterns were developed as functions of light, soil moisture, and soil compaction. The influence of intraspecific variation in seed mass and emergence time were also tested. Excess soil water levels during the winter reduced germination and emergence and lengthened time to emergence (in waterlogged open areas), which in turn decreased seedling survival during the dry season. Seedlings from larger seeds were more likely to germinate and emerge. The results suggest that temporal and spatial variability of soil water content, mediated by emergence time and seed size, play a crucial role in the regeneration dynamics of Mediterranean oak forests.

**Résumé :** Les espèces d'arbre peuvent avoir des réactions différentes face à la disponibilité des ressources pendant la phase critique d'établissement, ce qui peut influencer la dynamique forestière. Dans les forêts méditerranéennes, on s'est surtout préoccupé des effets du manque de lumière et de la sécheresse estivale sur la survie des semis, mais les effets de la pluie qui tombe de l'automne au printemps sur les premiers stades de recrutement sont peu connus. Une expérience d'ensemencement a été établie le long de gradients naturels de disponibilité de lumière et d'eau avec trois espèces de chêne sympatriques (*Quercus suber* L., *Quercus canariensis* Willd. et *Quercus pyrenaica* Willd.) dont la régénération naturelle est peu abondante dans le sud de l'Espagne. Les stades de recrutement ont été suivis pendant une année. Des modèles de germination, d'émergence et de survie de même que des patrons généraux de recrutement ont été établis en fonction de la lumière, de l'humidité du sol et de la compaction du sol. L'influence de la variation intraspécifique du poids des semences et de l'émergence des semis a aussi été testée. Un excès d'eau du sol pendant l'hiver a diminué la germination et l'émergence et allongé la période de temps nécessaire à l'émergence (dans les endroits ouverts et saturés en eau), ce qui a diminué le taux de survie des semis pendant la saison sèche. Les semis issus de grosses semences avaient plus de chances de germer et d'émerger. Ces résultats indiquent que la variabilité temporelle et spatiale de la teneur en eau du sol, par l'intermédiaire de la période d'émergence et de la taille des semences, joue un rôle important dans la dynamique de régénération des forêts méditerranéennes de chêne.

[Traduit par la Rédaction]

## Introduction

Resource competition and stress tolerance are important drivers of plant community structure and dynamics (Grime 1979; Tilman 1982). Plant species can differ in their responses to both resource abundance and scarcity during the

critical phase of establishment (Sher et al. 2004). Differences in regeneration requirements and responses to environmental heterogeneity define regeneration niches that influence community composition (Grubb 1977; Beckage and Clark 2003). Therefore, the assessment of stress tolerance and survival in early stages of life cycles and during

Received 15 December 2007. Accepted 24 June 2008. Published on the NRC Research Press Web site at [cjfr.nrc.ca](http://cjfr.nrc.ca) on 12 August 2008.

**I.R. Urbietta.**<sup>1</sup> IRNA, CSIC, P.O. Box 1052, Sevilla 41080, Spain and Departamento de Ecología, Universidad de Alcalá, Edificio de Ciencias, Ctra. Madrid-Barcelona km 33.6, E-28871 Alcalá de Henares, Spain.

**I.M. Pérez-Ramos<sup>2</sup> and T. Marañón.** IRNA, CSIC, P.O. Box 1052, Sevilla 41080, Spain.

**M.A. Zavala.** Departamento de Ecología, Universidad de Alcalá, Edificio de Ciencias, Ctra. Madrid-Barcelona km 33.6, E-28871 Alcalá de Henares, Spain and Centro de Investigación Forestal (CIFOR), INIA. Carretera de la Coruña km 7, 28040 Madrid, Spain.

**R.K. Kobe.** Department of Forestry, Michigan State University, East Lansing, MI 48824-1222, USA.

<sup>1</sup>Corresponding author (e-mail: [itziar.rodriguez@gmail.com](mailto:itziar.rodriguez@gmail.com)).

<sup>2</sup>Present address: Centre d'Écologie fonctionnelle et évolutive, CNRS, 1919 Route de Mende, 34293 Montpellier 5, France.

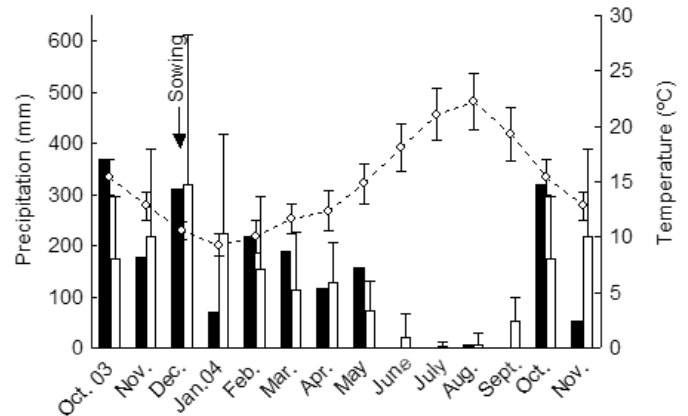
periods of resource variability could be important to understanding forest community dynamics.

In seasonally dry environments, rainfall is too scarce to support the closed canopy that normally drives plants to compete for light; instead, belowground resources such as water and nutrients can be more limiting (Coomes and Grubb 2000). Rainfall variability coupled with site factors such as microtopography, soil type, or vegetation cover translates into spatially and temporally heterogeneous soil moisture content that can provide axes of ecological differentiation among species (Joffre and Rambal 1993; Chesson and Huntly 1997). In Mediterranean ecosystems, for example, interactions between water and light availability can lead to differential regeneration strategies in tree species in response to variability in these factors (Sack 2004; Sánchez-Gómez et al. 2006; Quero et al. 2006), thereby influencing forest composition and dynamics (Zavala and Zea 2004). Most of the attention in Mediterranean forests has centered on the effects of water shortage on forest regeneration. In particular, summer drought is commonly thought to be a major limiting factor for seedling survival (Espelta et al. 1995; Pulido and Díaz 2005), with shade alleviating drought stress in seedlings but potentially leading to light limitation (Quero et al. 2006). In contrast, effects of wet-period rains, which could be a critical bottleneck to earlier stages of recruitment (i.e., seed germination and emergence), remain rather uncertain.

Predictions of forest regeneration patterns must account for discordant microsite effects on seedling recruitment stages (Jordano and Herrera 1995), since environmental conditions that are optimal in one stage can be suboptimal in others, causing demographic conflicts (Schupp 1995). The timing of seasonal precipitation and the wide range of light conditions in the understory of Mediterranean forests require quantitative studies that match detailed demographic sequences of seedling establishment with fine-scale spatiotemporal variation in resources. In this study, we conducted a sowing experiment of three co-occurring Mediterranean oaks, *Quercus suber* L. (cork oak), *Quercus canariensis* Willd. (Algerian oak), and *Quercus pyrenaica* Willd. (Pyrenean oak), along field gradients of water and light, with an emphasis on wet- and dry-period water effects on seedling recruitment stages (from seed germination to 1 year establishment). We focused on the most southern European oak forests located in the mountains north of the Strait of Gibraltar, where both seedlings and saplings are scarce (Pérez-Ramos 2007; Urbieto 2008). All yearly rainfall is concentrated from autumn to spring (causing frequent soil waterlogging locally), followed by a pronounced summer drought. Thus, this ecosystem provides a natural model system for examining the effects of three important and widespread environmental drivers for vegetation (i.e., drought, waterlogging, and shade) on forest regeneration (see Niinemets and Valladares (2006) for a review of these stress factors).

Recruitment stages (germination, emergence, and 1 year seedling survival) of oaks were monitored regularly. Seed mass can influence seedling performance during early establishment (Seiwa 2000) and thus was treated as a covariate in our analyses. In addition, seedling emergence time was monitored because together with strong seasonality in pre-

**Fig. 1.** Climate diagram for the study area (data from La Saucedá meteorological station). Monthly precipitation values recorded during the experiment, from autumn 2003 to winter 2004 (solid bars), are compared with the monthly mean precipitation ( $\pm$  1SD) registered from 1985 to 2004 (open bars). Monthly mean temperature is represented by the values ( $\pm$ 1 SD) from 1985 to 1997 (broken line).



cipitation, emergence time could influence seedling survival and hence plant fitness (Verdú and Traveset 2005). We calibrated species-specific models of seed germination, seedling emergence, and seedling survival as well as 1-year-old seedling establishment models to address the following questions: (i) How do contrasting soil water availability (during wet and dry seasons) and light availability in the understory influence the success of oak species during each recruitment stage (seed germination, seedling emergence, and seedling survival)? (ii) Could local waterlogging produced by autumn to spring rains reduce oak regeneration? (iii) Do initial seed mass and emergence timing mediate responses to light and water heterogeneity? (iv) Over gradients of resource availability, do co-occurring oak species differ in their responses?

## Materials and methods

### Study site and species

The study was conducted in La Saucedá forest (530 m a.s.l.; 36°31'54"N, 5°34'29"W) in Los Alcornocales Natural Park, a mixed mountain-oak woodland of ~1700 km<sup>2</sup> in southern Spain. The dominant bedrock is Oligo-Miocenic sandstone, giving rise to acidic and sandy soils with small inclusions of loam and clay soils. The climate is subhumid Mediterranean, with mild temperatures (annual mean of 17 °C) and frequent mists year-round, due to the proximate confluence of the Mediterranean Sea and the Atlantic Ocean. Annual mean rainfall varies from 900 to 1800 mm, with the heaviest rainfall in autumn, winter, and spring, followed by dry summers (see mean 1985–2004 data from La Saucedá meteorological station in Fig. 1). Forests are codominated by evergreen *Q. suber* and winter-deciduous *Q. canariensis*, which is more abundant in stands located near streams (Urbieto et al. 2008), whereas deciduous *Q. pyrenaica* occurs in small stands at the highest altitudes. There is little natural regeneration of the three oak species as revealed by forest inventory surveys (Urbieto 2008), but the causes remain rather uncertain. See Quilchano et al.

(2008) and Pérez-Ramos et al. (2008b) for a description of the experimental forest site.

### Experimental design and data collection

To encompass intraspecific variation, we collected acorns from several trees (at least 10 of each oak species) during the fruiting season (October–December 2003). Acorns of these species are mainly dispersed by gravity, but a significant proportion is dispersed by birds, rodents, or even insects and then buried (Pérez-Ramos et al. 2007). Acorns of *Q. suber* and *Q. canariensis* were collected from local stands near the experimental site, whereas acorns of *Q. pyrenaica* (with scarce reproduction in the area) were brought from Sierra Morena stands (inland area also in southern Spain). Acorns infected by moths or beetle larvae were culled through flotation. Selected acorns were stored on a moist vermiculite bed in plastic trays at 2–4 °C until used in the experiment; they were individually weighed to the nearest 0.01 g. Mean  $\pm$  SD acorn fresh mass (grams) was  $4.36 \pm 1.63$  g for *Q. suber*,  $4.48 \pm 1.38$  g for *Q. canariensis*, and  $5.56 \pm 1.04$  g for *Q. pyrenaica*. We used acorn fresh mass as a surrogate of seed mass, justified by their high correlation (Quero et al. 2007). Acorns were buried 2–3 cm in the soil and distributed haphazardly, covering a wide and continuous gradient of water and light availability, from open habitats (up to 90% full sun) to deeper shade under shrubs and trees (down to 5% full sun). Sampling points were separated from each other by at least 10 m and consisted of four wire cages (25 cm  $\times$  25 cm  $\times$  25 cm, 1.3 cm mesh size) to avoid attack by predators ( $N = 240$  cages). Ten acorns of *Q. suber*, 10 acorns of *Q. canariensis*, and 8 acorns of *Q. pyrenaica* were sowed (5 acorns of either *Q. canariensis* or *Q. suber* and 2 acorns of *Q. pyrenaica* inside each cage). A total of 600 seeds of each of *Q. suber* and *Q. canariensis* were sown on 23 December 2003 and 480 seeds of *Q. pyrenaica* were sown on 5 February 2004, when they became available.

Individuals were censused regularly for 1 year. We tracked seedling emergence above ground through biweekly monitoring. Seedling survival and cause of mortality were monitored biweekly through spring–autumn (until October 2004) with an additional census in February 2005 (1 year after emergence). We considered seedlings to be dead if they lacked green leaves and had brittle stems. In some cases, apparently dead seedlings (by shoot dieback) recovered and resprouted after summer; these seedlings were re-categorized as live. Germination was assessed indirectly. After summer, we unearthed acorns from cages without emerged seedlings and inspected the seeds for radicles (indicating germination). Thus, we were able to estimate germination probability (those emerged + those non-emerged but germinated / total seeds sown). The very few unearthed acorns (38 in total) that showed signs of predation by rodents, beetles, or insect larvae were excluded from the analyses.

We estimated species responsiveness to episodic summer rains by watering half of the seedlings (two of the four cages per sampling point). During the summer season (July–September) we added 2 L of water per cage (equivalent to  $\sim 33$  mm rainfall) biweekly. Percent soil volumetric water content (SVWC) was measured at each sampling point (four readings, one per cage, for a total of 240), using time

domain reflectometry (TDR; Campbell Scientific, Inc., Logan, Utah) with stainless steel rods inserted 12 cm into the soil. Measurements were taken in winter (29 January and 4 March 2004), early spring (2 April), and summer (4 August) to characterize soil moisture during wet and dry periods. We calculated minimum, maximum, and mean SVWC values as well as the mean value of the wet period (winter and spring) and oscillation range (difference between the means of the wet period and summer). We also recorded visual evidence of soil waterlogging (i.e., standing pools of water) in the cages during biweekly monitoring. Light availability at the seedling level was measured at each of the sampling points with hemispherical canopy photographs (two per sampling point) using a Nikon Coolpix 4500 camera with fish-eye lens (F8 Nikon) and then analyzing the images with Hemiview canopy analysis software (Delta-T Devices Ltd. 1999, version 2.1). All photographs were taken in October 2004, before *Q. canariensis* trees began to drop their leaves. We selected global site factor (GSF), given in units of percent full sun, as an estimate of understory light availability (e.g., see Quilchano et al. 2008). Soil compaction (expressed in megapascals) was measured with a penetrometer (Penetrologger, Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) in early spring (March 2005). Two measurements were taken per sampling point, to characterize the soil profile to 60 cm depth, which could influence seedling rooting through aeration or mechanical limitation. We calculated minimum, maximum, and mean compaction along the profile as well as compaction of the first 20 cm and at maximum depth (60 cm); we recorded maximum soil depth when reaching bedrock.

### Statistical analysis

Each recruitment stage (seed germination, seedling emergence, and seedling survival) was modelled independently as function of abiotic factors (light, soil water content, and soil compaction) and seed mass. In this demographic sequence, germination was analysed for all sowed acorns, excluding those that germinated during storage ( $N = 526$  for *Q. suber*,  $N = 552$  for *Q. canariensis*,  $N = 462$  for *Q. pyrenaica*); seedling emergence was analysed for all germinated acorns ( $N = 414$  for *Q. suber*,  $N = 288$  for *Q. canariensis*,  $N = 337$  for *Q. pyrenaica*); and seedling survival was analysed for all the emerged seedlings ( $N = 303$  for *Q. suber*,  $N = 220$  for *Q. canariensis*,  $N = 205$  for *Q. pyrenaica*). Furthermore, overall seedling establishment models (the total proportion of sown seeds that survived to 1 year) were developed. Different models were fit to the data, with the objective of studying the full level of variability among individuals (see below) and thus values of soil water, soil compaction, and light availability measured at the cage level were assigned to each acorn and (or) seedling. Because our goal was to develop individual seedling-based models of performance, we considered each acorn and (or) seedling as the unit of analysis rather than mean seedling performance in each cage.

### Seed germination and seedling emergence models

With maximum likelihood techniques we fitted linear and non-linear models of germination and emergence for each species. These processes were described by a binomial dis-

tribution, with each independent trial resulting in one of two possible final outcomes, that is, seed survival (germinated or emerged) or seed failure (non-germinating or non-emerging). For each species, we specified germination and emergence probabilities ( $p_i$ ), as functions of abiotic factors: light, soil water content, and soil compaction. In addition, seed mass was tested as a covariate in all models. Different functional responses that covered a wide range of possible forms were fitted: linear, exponential, logistic, Michaelis–Menten-type, and power functions (see S1 Appendix for equations).<sup>3</sup> We first tested models for each factor and functional response independently. Then, we tested for two- and three-factor models using the factors and functional responses that yielded the best fit when evaluated singly. Three-factor models did not considerably improve two-factor model fits and thus for simplicity they were not considered further.

In addition, we fitted regression models to test how abiotic factors affected emergence times. Based on exploratory analyses of potential distributions that best fitted our data, a gamma distribution of emergence times was assumed. This distribution has a flexible shape defined by a shape parameter ( $n$ ), which varies from exponential-like to bell-shaped but left-skewed probability distributions (Evans et al. 2000). We specified the mean of the gamma distribution as a function of abiotic factors and seed mass using the above-mentioned functional responses, that is, linear, exponential, logistic, Michaelis–Menten, and power and fitting one- and two-factor models.

**Seedling survival models**

Survival analysis and maximum likelihood methods were combined to parameterise survival models (for all emerged seedlings) as a function of resources (according to Kobe et al. 2002). Analogous to the distribution function for a binomial random variable, the likelihood function for a continuous distribution of survival times is

$$[1] \quad L = \prod_{i=1}^D f(t_i; \phi) \prod_{i=1}^{N-D} S(c_i; \phi)$$

where the contribution to the likelihood of a seedling observed to die at time  $t$  is  $f(t_i; \phi)$  (i.e., the density of failure at time  $t$ ), and the contribution to the likelihood of an individual surviving beyond time  $c$  is  $S(c_i; \phi)$  (i.e., the survivor function),  $\phi$  is a vector of parameters,  $D$  represents the number of individuals dying, and  $N - D$  is the number of individuals surviving beyond time  $c$ , both indexed by  $i$  to represent individual seedlings (Cox and Oakes 1984).

We examined survival time distributions of seedlings, and generally the exponential provided the best fits from among the distributions tested (e.g., the exponential resulted in a maximum log-likelihood that was  $\sim 7$  log-likelihood units higher than the normal distribution for *Q. suber*). Although mortality often decreases as seedlings age and grow, first-year mortality risk was relatively constant (an assumption of the exponential distribution)

during this study, especially after accounting for environmental influences on mortality (see below). Using an exponential distribution of survival times, the likelihood becomes

$$[2] \quad L = \prod_{i=1}^D M(x_i, \phi) e^{-t_i M(x_i, \phi)} \prod_{i=1}^{N-D} e^{-c_i M(x_i, \phi)}$$

where  $M(x_i, \phi)$ , or the hazard function, is composed of a vector of explanatory variables,  $x_i$ , and set of parameters  $\phi$ .

We specified the hazard,  $M(x_i, \phi)$ , as a function of abiotic factors (light, soil water content, and soil compaction), and we also tested the effects of seed mass and emergence times. The same procedure as for the other stages was followed, fitting several functional responses and testing models with all combinations of factors. The effect of the summer watering treatment on seedling survival was tested by first using the complete data set (without respect to the watering treatment, i.e., general model) to identify the factors that were best predictors of seedling survival. Second, we compared the general model fit versus a model that included parameters specific to the watering treatment (i.e., saturated model) with Akaike’s information criteria (AIC; see model selection criteria below).

**One-year-old seedling establishment models**

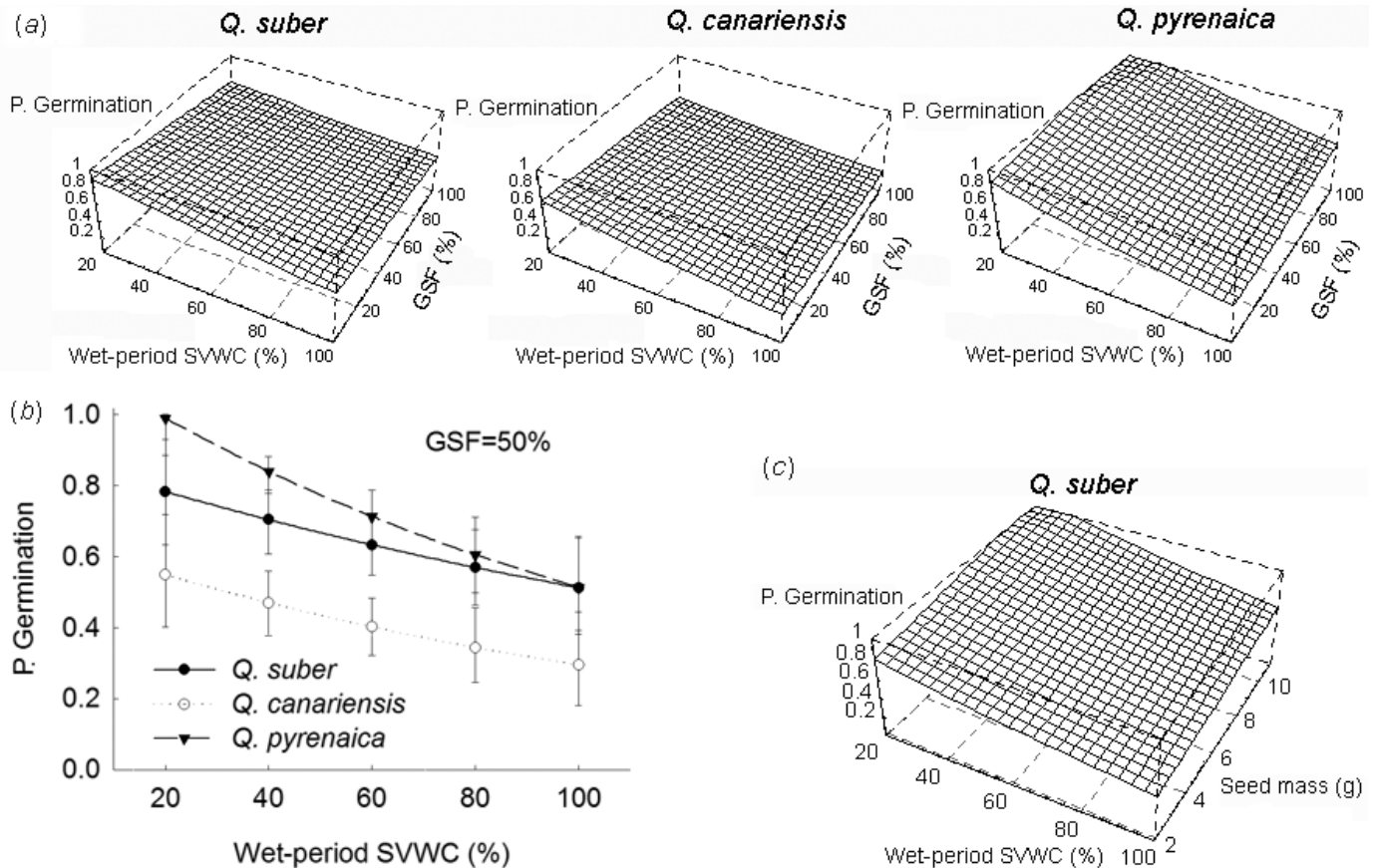
Seedling establishment was characterized as a binomial distribution, with each independent trial resulting in one of two possible final outcomes: seedling establishment or failure to establish. For each species, we specified the establishment probability ( $p_e$ ) as function of abiotic factors: light, soil water content, and soil compaction. In addition, seed mass was tested as a covariate in all models. Different functional responses were used and one- and two-factor models were fitted. The effect of the summer watering on seedling establishment was analysed by first using the complete data set (i.e., general model) to identify the factors that were best predictors of species establishment, which was then compared with a model that included parameters specific to the watering treatment (i.e., saturated model) using AIC.

**Model selection and goodness-of-fit**

Models were parameterised with maximum likelihood (Edwards 1992), using a simulating annealing algorithm (Metropolis et al. 1953). To test for the influence of predictors in each regeneration stage, fitted models were compared with a null model of no factor effect using likelihood ratio tests (LRTs) (Edwards 1992). We estimated 95% support regions (equivalent to 95% CIs but used in conjunction with likelihood methods) by likelihood profile (Hilborn and Mangel 1997). All the models and numerical algorithms were implemented in programs we wrote in C (Borland C++, Borland International Inc. 1996, version 5.01). Fitted models were compared with AIC, specifically  $\Delta AIC$ , which is defined for each Model $_i$  as  $AIC_i$  minus  $AIC_{\text{minimum}}$  (Akaike 1992). The model with the strongest empirical support has the minimum AIC and thus its  $\Delta AIC$  equals 0. Models with  $\Delta AIC$  between 0 and 2 were considered to have equivalent

<sup>3</sup>Supplementary data for this article are available on the journal Web site (cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3804. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub\_e.html.

**Fig. 2.** (a) Probability of germination ( $P$ . germination) of the three oaks (*Quercus suber*, *Quercus canariensis*, and *Quercus pyrenaica*) exponentially declined as soil volumetric water content (SVWC) of the wet period increased and light availability (GSF) increased (except for *Q. pyrenaica*). (b) Interspecific differences in responses to wet-period SVWC for a given point of the light gradient (GSF = 50%). Bars denote 95% support regions. (c) Germination probability of *Q. suber* as function of wet-period SVWC and seed mass.



and substantial empirical support,  $\Delta\text{AIC}$  between 4 and 7 indicated less support, and models with  $\Delta\text{AIC} > 10$  were dismissed, as they had negligible empirical support (Burnham and Anderson 2002).

## Results

Soil water content in winter and spring was very high and spatially heterogeneous, with waterlogging in some experimental units (Mean  $\pm$  SD SVWC (%) was  $46.8 \pm 18$  in January,  $45.3 \pm 20$  in March, and  $53.7 \pm 22$  in April). However, very dry and homogeneous water conditions were found in summer ( $9.3\% \pm 3\%$  SVWC in August). GSF was positively correlated with mean wet-period SVWC ( $r = 0.33$ ,  $p < 0.05$ ) as well as with the SVWC oscillation between winter and summer ( $r = 0.35$ ,  $p < 0.05$ ). Thus, open areas tended to suffer more winter waterlogging but dried out in summer, reaching similar minimum SVWC values as more shaded areas. Mean  $\pm$  SD soil compaction was  $2.27 \pm 0.75$  MPa and mean  $\pm$  SD soil depth was  $35.4 \pm 11.7$  cm.

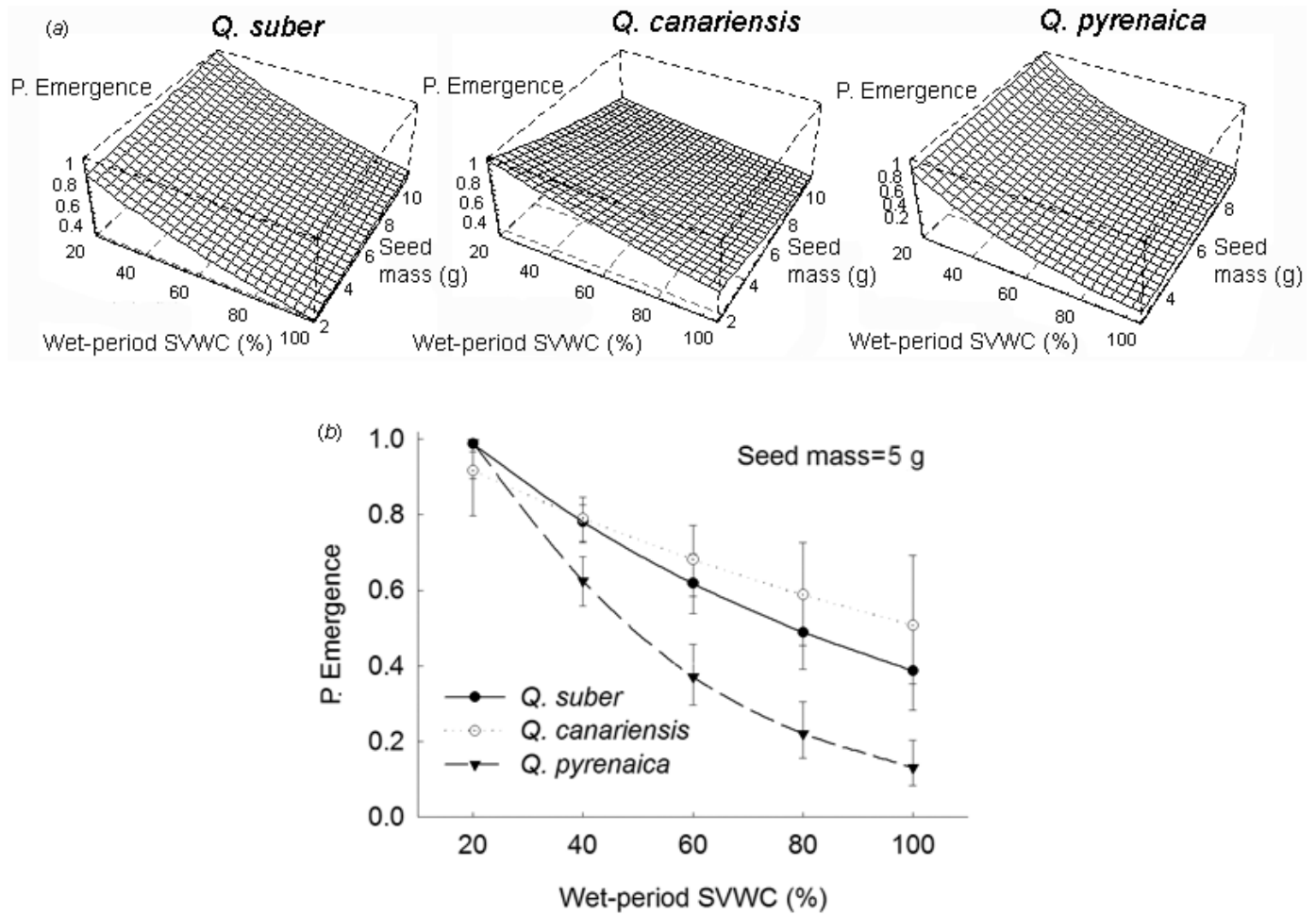
The three oak species diverged substantially in each of the studied recruitment stages: *Q. canariensis* had the lowest seed germination rate (47%) compared with *Q. suber* (71%) and *Q. pyrenaica* (75%). In contrast, *Q. pyrenaica* had a lower percentage of emerged seedlings (61%) than *Q. suber* (74%) and *Q. canariensis* (76%). *Quercus suber* seedlings

had lower survival rates (37%) than *Q. canariensis* (47%) and *Q. pyrenaica* (44%) 1 year after emergence. Seedling mortality of all the species was mainly due to desiccation and started with warm and dry conditions (early June; Fig. 1) until the first autumn rains (October). Shoot dieback was frequent in *Q. pyrenaica* seedlings (61%), recovering in autumn after losing all leaves in summer but less frequent (approximately 12%) in the other two species. Seedling mortality during the subsequent cool and wet period (October–February) was low. The overall proportion of 1-year-old seedlings established was similar ( $\sim 18\%$ ) for the three oak species.

## Seed germination

In all three species, probability of germination declined exponentially with mean SVWC during the wet period, as indicated by the best-supported germination models (see SSAppendix S1 for parameter estimates of all models and LRT results).<sup>3</sup> In addition, light availability and seed mass influenced some species (see below and SSAppendix S1).<sup>3</sup> Light availability intensified the negative effect of wet-period SVWC on germination of *Q. suber* and *Q. canariensis*, but light had a small positive effect on *Q. pyrenaica* (Fig. 2a). The model including wet-period water and light availability had strong empirical support for *Q. pyrenaica* ( $\Delta\text{AIC} = 0$ ) and *Q. canariensis* ( $\Delta\text{AIC} =$

**Fig. 3.** (a) Probability of emergence of the three oaks exponentially declined as wet-period SVWC increased and seed mass decreased (except for *Q. canariensis*). Note the different scales on the axes. (b) Interspecific differences in responses to wet-period SVWC for a mean seed mass of 5 g. Bars denote 95% support regions.



0.3) and lower support for *Q. suber* ( $\Delta AIC = 5.6$ ; SSAppendix S1).<sup>3</sup> Species differed in their response to SVWC at any level of the light gradient. Fixing light to its mean value of the gradient (i.e., GSF = 50%), species response to SVWC showed a similar trend (slope), but *Q. canariensis* had lower germination probability than the other two species along the gradient (Fig. 2b). We also tested for the effects of light over a narrower range of conditions (5%–30% full sun) to control for possible confounding effects with waterlogging. However, estimated models still showed negative light effects for *Q. suber* and *Q. canariensis*.

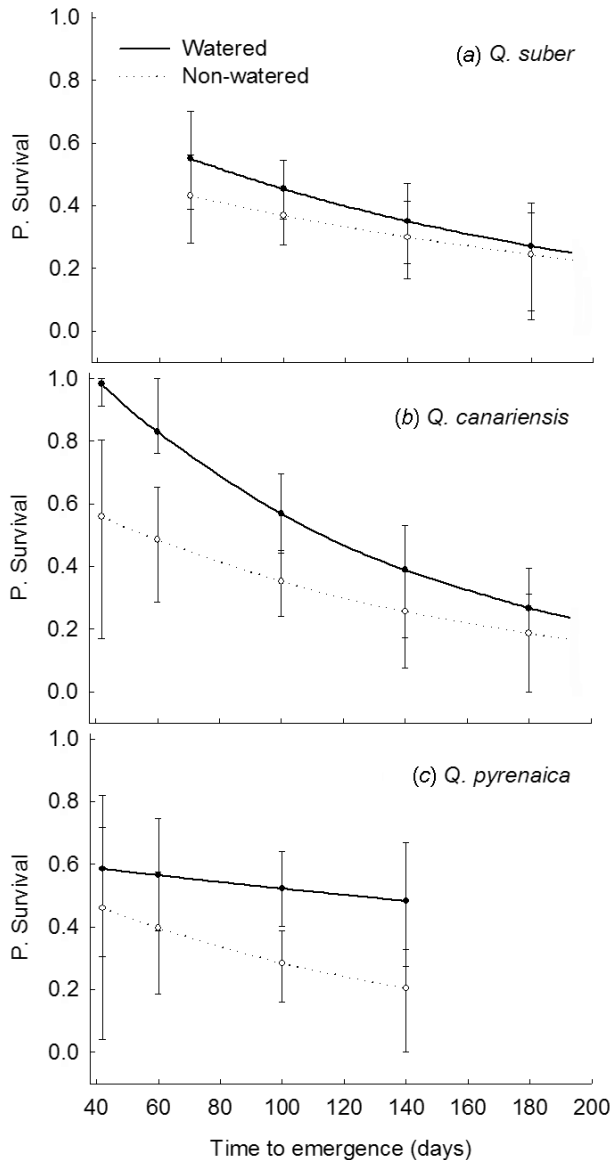
For *Q. suber*, in addition to the negative effects of wet-period SVWC, seed mass had positive effects on germination (Fig. 2c), as indicated by the model with the greatest empirical support (SSAppendix S1).<sup>3</sup> Other factors such as soil depth and compaction had an effect on species germination but with considerably less empirical support (SSAppendix S1).<sup>3</sup>

**Seedling emergence**

For all three species, probability of emergence also declined exponentially with wet-period SVWC, as indicated by the models with the strongest empirical support (SSAppendix S1).<sup>3</sup> Models including SVWC of the wet period

alone showed the greatest empirical support ( $\Delta AIC = 0$ ) for *Q. suber* and *Q. pyrenaica*, but for both species models that included seed mass or light availability also had substantial support (within 2 AIC units of the best supported model). For *Q. canariensis*, emergence probability declined with increases in both wet-period SVWC and seed mass, and no other models were within 2 AIC units. Thus, common among all three species, models that included SVWC of the wet period and seed mass had strong empirical support. However, in contrast with *Q. canariensis*, larger seeds of *Q. suber* and *Q. pyrenaica* had higher probabilities of emergence (Fig. 3a). Species differed in their responses to SVWC. For a mean value of seed mass (i.e., 5 g), probability of emergence declined as SVWC increased, especially for *Q. pyrenaica* seedlings (Fig. 3b). SVWC and light availability (GSF) equivalently explained emergence of *Q. suber* and *Q. pyrenaica*. An increase of soil water content and light availability diminished the emergence probability of *Q. suber* and *Q. canariensis*, whereas a small positive effect of light was found on *Q. pyrenaica*'s emergence. When examining factor effects over a restricted light gradient (5%–30% full sun) that excluded the more open waterlogged sites, models including light still showed negative effects on seedling emergence for *Q. suber* and *Q. canariensis*.

**Fig. 4.** Models resulting from the best fit for seedling survival. Responses of watered and non-watered (control) individuals are differentiated. Probability of survival in summer was lower for those seedlings that delayed their emergence. *Quercus suber* seedlings did not respond to the water treatment (a). Watering significantly increased seedling survival in *Q. canariensis* (b) and *Q. pyrenaica* (c).



### Seedling survival

Time to emergence, that is, number of days elapsed from sowing to when seedlings emerged above ground, was the best predictor of seedling survival for all three species (SSAppendix S1).<sup>3</sup> Individuals that emerged earlier had a higher probability of survival during the dry period (Fig. 4). Water addition during the dry summer did not improve seedling survival of *Q. suber* (Fig. 4a) but reduced mortality of the two deciduous species. The beneficial effect of summer watering was stronger for *Q. canariensis* seedlings that emerged earlier, that is, watered and non-watered curves converged for late emergence (Fig. 4b). *Quercus pyrenaica* watered seedlings showed a similar probability of survival

(but always greater than non-watered individuals) whenever they emerged (Fig. 4c). Parameter 95% support regions of the three oaks overlapped for non-watered individuals (figure not shown); thus, there was no strong difference among species in their survival responses to emergence times under field conditions.

### Emergence time

Because seedling survival during the dry period was best predicted by emergence time, we also analysed how abiotic factors and seed mass affected species emergence times. In general, emergence times followed a decreasing distribution, with a greater number of seedlings emerging in March–April (70–80 days after sowing) and reaching lower percentages as summer approached. The start of emergence time was earlier for *Q. canariensis* and *Q. pyrenaica* (40 days after sowing) than for *Q. suber* (70 days), and the total emergence length was shorter for *Q. pyrenaica* (up to 140 days) than for the other two species (up to 195 days). Mean SVWC during the wet period was the key factor influencing species emergence time, as indicated by the models with the strongest empirical support (SSAppendix S1),<sup>3</sup> with higher SVWC being associated with later emergence times. In addition, variability among individual emergence times was higher in the wettest soils. Seedlings of *Q. suber* needed, on average, a longer time to emerge compared with the other species at any level of the water gradient. For all three species, additional factors influenced emergence time, as indicated by the best-supported models (SSAppendix S1).<sup>3</sup> Wet-period SVWC and seed mass explained emergence timing of *Q. pyrenaica*, with larger seeds being associated with a more delayed emergence. For *Q. suber* and *Q. canariensis*, light availability intensified the effect of wet-period soil moisture on delaying seedling emergence.

### One-year-old seedling establishment

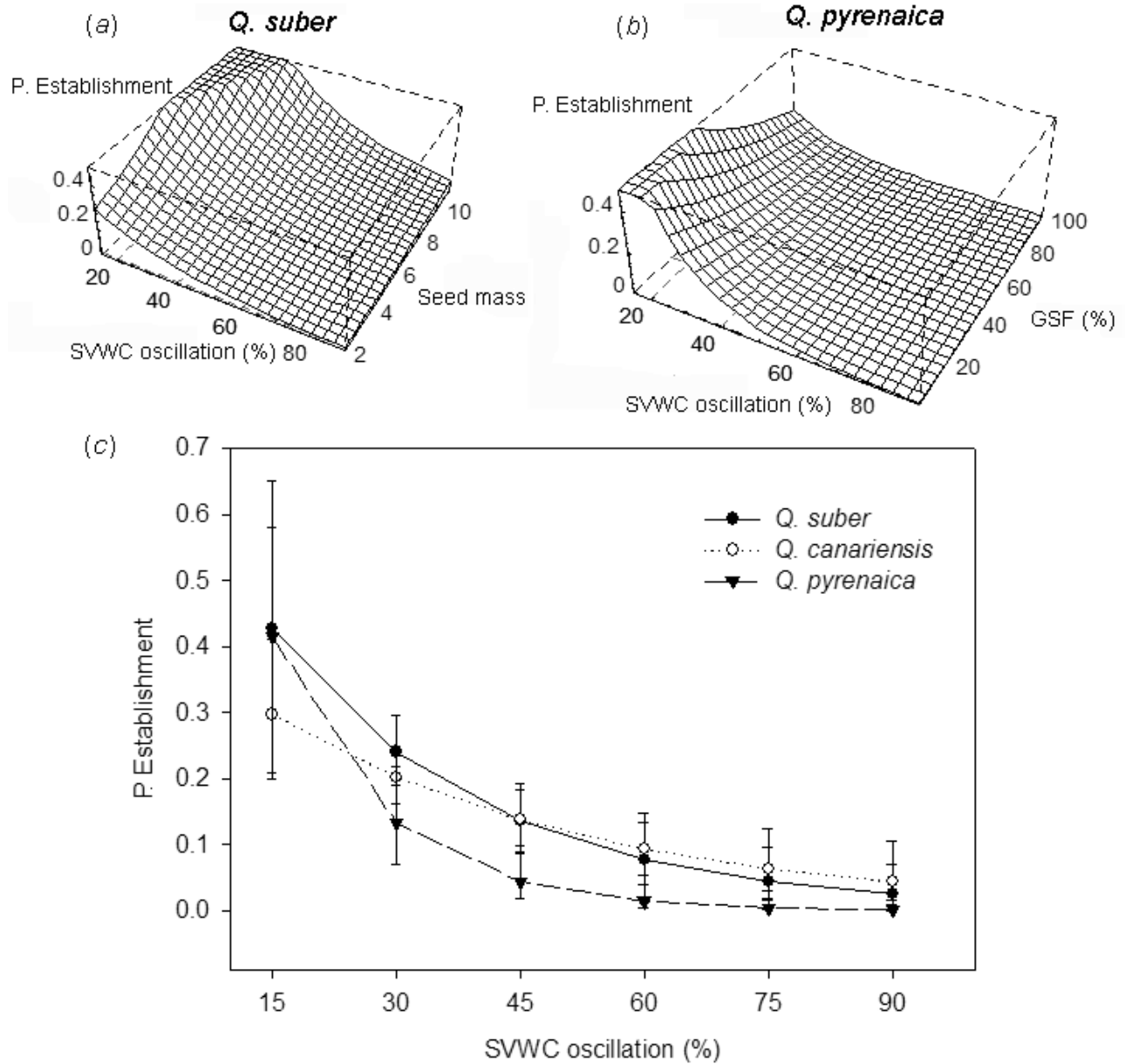
For all three species SVWC oscillation (i.e., SVWC difference between wet and dry periods) had a negative effect on seedling establishment, according to best model fits (SSAppendix S1).<sup>3</sup> Furthermore, light availability and seed mass influenced some species. For *Q. suber*,  $p_e$  exponentially declined with SVWC oscillation and increased with seed mass (Fig. 5a); no other models were within 2 AIC units. Establishment of *Q. pyrenaica* yearlings decreased with SVWC oscillation and light availability (Fig. 5b). For *Q. canariensis*, the model including SVWC oscillation alone had the greatest empirical support (Fig. 5c). Parameter support regions of the three oak species overlapped along the SVWC oscillation gradient; seedlings of all species could only establish in areas that had relatively low water oscillation levels (Fig. 5c). Watering in summer had a positive effect on seedling establishment for *Q. canariensis* and *Q. pyrenaica*, whereas *Q. suber* seedlings did not benefit from watering (SSAppendix S2).<sup>3</sup>

## Discussion

### Resource availability and oak establishment

Spatial and temporal soil water variability (from waterlogged to very dry conditions) was the major factor controlling, either directly or indirectly through emergence time,

**Fig. 5.** Overall 1 year seedling establishment models for the three species according to best model fits (using the complete data set). (a) Seedling establishment probability of *Q. suber* as function of SVWC oscillation (difference between wet and dry periods) and seed mass. (b) Seedling establishment probability of *Q. pyrenaica* as function of SVWC oscillation and light availability (GSF). (c) Seedling establishment probability of *Q. canariensis* as function of SVWC oscillation. Interspecific differences in responses to SVWC oscillation are represented in (c), where bars denote 95% support region. Note that to facilitate the comparison between species, *Q. suber* response is represented for a mean seed mass of 5 g and *Q. pyrenaica*'s response is represented for a given point of the light gradient (GSF = 50%). See SSAppendix S2<sup>3</sup> for the effect of watering treatment on seedling establishment.



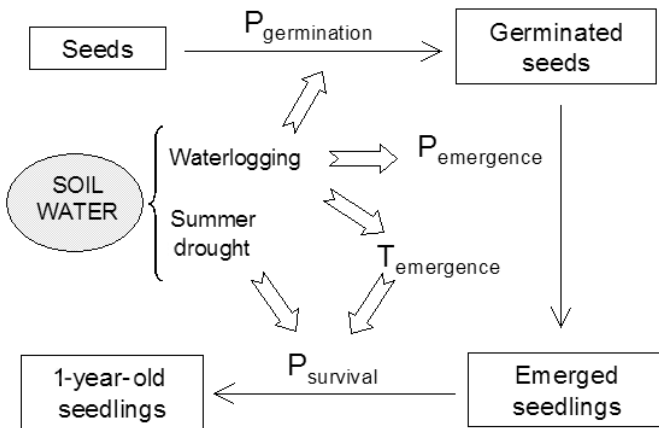
seedling establishment in this subhumid Mediterranean forest. Soil water deficit (i.e., drought) is commonly reported to be the primary limiting resource of seedling establishment in the Mediterranean (Rey Benayas 1998; Gómez-Aparicio et al. 2005); however, here we found evidence of two seasonal water-related constraints primarily affecting seedling establishment: water excess in the wet period and water shortage during the dry summer. The stress caused by over-abundant water during the wet season greatly limited seedling establishment by reducing germination and emergence. Moreover, high soil water levels lengthened time to emer-

gence of seedlings, which in turn decreased their survival rates during summer drought (Fig. 6). The importance of this factor (local waterlogging) for tree regeneration has been mostly overlooked under Mediterranean conditions.

Some recruitment stages were influenced by the combined effects of both soil water content and light. In general, light availability was found to have a negative effect on most of the stages (i.e., lower probability of germination and emergence in more open areas). This effect partly arose from the positive correlation between GSF and wet-period SVWC, which indicates that relatively open areas tended to suffer



**Fig. 6.** Oak regeneration cycle with the main factors controlling each of the studied stages. High levels of soil water content (waterlogging) recorded during the wet period (autumn–spring) reduced species germination and emergence. Moreover, seedling survival was indirectly (through emergence time) affected by soil water excess, which delayed seedling emergence and shortened the time window of the growing season. Seedlings with delayed emergence had higher probabilities of mortality during summer drought.  $P_{\text{germination}}$ , probability of seed germination;  $P_{\text{emergence}}$ , probability of seedling emergence;  $T_{\text{emergence}}$ , time of seedling emergence;  $P_{\text{survival}}$ , probability of seedling survival.



more waterlogging, owing to higher soil water retention and the absence of rainfall interception by vegetation. However, the negative effect of irradiance was still present even when developing models under a restricted range of light conditions. In the mosaic of soils found in the studied forests, more clayey patches have poorer drainage, leading to conditions less suited for the colonization and establishment of woody species. These conditions are reflected in sparse woody vegetation and greater light availability. Winter waterlogging was associated with the presence of low permeability clayey soils, which show strong redoximorphic features in the profile (L.V. García, personal communication, 2007) that are indicative of seasonal soil saturation (Jacobs et al. 2002). We hypothesize that seedlings may have experienced low oxygen concentration (hypoxia) while in seasonally waterlogged soil, potentially curtailing respiration and impeding radicle and shoot development (e.g., Schnull and Thomas 2000). In a parallel study, submerging acorns of these three oak species for prolonged periods (>30 days) in controlled conditions (to prevent fungal infection) resulted in reduced and delayed germination and hampered root development.<sup>4</sup> Similar negative effects of clayey hydromorphic soils, which suffer temporal waterlogging and sporadic dry periods, have been found in declining stands of Atlantic temperate oak forests (Thomas and Hartmann 1998; Vincke and Delvaux 2005).

Our results suggest that water can act as a double factor of stress (by excess and deficit), during the initial stages of seedling recruitment in forest ecosystems with contrasting seasonal rainfall regimes. Nevertheless, other factors not recorded here—soil nutrients or herbivory—might also

influence the multidimensional regeneration niche (Canham et al. 1996) of these oak species.

### Effects of seed size and emergence time on seedling establishment

We confirmed that initial seed mass and time of emergence mediated the response of seedlings to waterlogging and light availability. For germination of *Q. suber* and emergence of all three oak species, models that included soil conditions (water content) and seed mass provided best fits. This might be due to the important role played by seed reserves in large-seeded species such as oaks during early development (Bonfil 1998; Quero et al. 2007), principally under resource stress (Moles and Westoby 2004). Within the same oak species (especially for *Q. suber*), seedlings with larger seeds generally showed higher probabilities of germination and emergence, which resulted in an improved overall seedling establishment. In contrast, a negative seed size effect was found for *Q. canariensis*, which would merit further study. Positive effects of seed size were more apparent in non-waterlogged microsites. In a parallel study, larger seeds experienced a higher probability of removal by rodents (Pérez-Ramos et al. 2008a), which may have been predated or dispersed. Similarly, Gómez (2004) found conflicting selective pressures between a positive effect of (*Quercus ilex* L.) acorn size on most fitness components related to seedling establishment and direct negative effect of acorn size on surviving predation.

Early seedling emergence had a strong positive effect on seedling survival for all three oak species. Differences among emergence dates may be controlled either by phenotypic and genetic effects related to seeds or by environmental conditions experienced by the germinating seed (Jones et al. 1997). In this study, seedlings that did not suffer waterlogging emerged earlier and could benefit from growing season (spring) resources for a longer period of time. Thus, intraspecific differences in emergence times were primarily due to differences in environmental conditions of the germinating seed. Similarly, Castro (2006) found that emergence time determined establishment success (higher probability of seedling survival and growth) of *Pinus sylvestris* L. seedlings in southeastern Spain across microhabitats and irrespective of the intensity of summer drought. In Mediterranean plant communities, seedling survival of different species during the dry period is positively correlated with mass allocation to roots (Lloret et al. 1999). Thus, with a better phenological match to resource availability and avoidance of waterlogging, seedlings that emerged earlier likely developed root systems more fully, which enabled greater seedling survival during the dry period (Nicotra et al. 2002).

### Oak regeneration ecology and forest dynamics

Identification of seedling functional responses along resource gradients is critical to achieving a mechanistic understanding of vegetation dynamics (Pacala et al. 1996; Kobe 1999). In the present study, the same functional responses and factors (mainly soil water oscillation between the wet

<sup>4</sup> Pérez-Ramos, I.M., and Marañón, T. Effects of soil waterlogging on seed germination of three Mediterranean oak species: ecological implications. *Acta Oecol.* In review.

and dry seasons) characterized the responses of three oaks, but mortality peaks occurred in different life stages for different species. *Quercus canariensis* had the lowest germination rate among species. However, germinated *Q. canariensis* acorns succeeded most in seedling emergence and survival (especially if they could emerge early and were watered in summer). In contrast, *Q. pyrenaica* had the highest probability of germination, regardless of soil water level, but waterlogging sharply reduced probability of emergence. *Quercus pyrenaica*'s emergence times (despite their delayed planting) were similar to those of *Q. canariensis*. Seedlings of both deciduous species responded positively to watering during the dry period, supporting previous studies showing the benefits of summer rains on seedling survival (Castro et al. 2005) and growth (Castro-Díez et al. 2006). *Quercus suber* had an intermediate response in germination (equivalent to *Q. pyrenaica*) and emergence (similar to *Q. canariensis*), but had higher mortality in summer, primarily because seedlings emerged later and thus experienced a shorter time window between when soils were too wet and when they were too dry. In addition, evergreen *Q. suber* had a weak response to watering during the summer, which is consistent with a greenhouse study in which watering increased stomatal conductance, photosynthesis, and respiration in deciduous *Q. pyrenaica* and *Q. canariensis* but not in *Q. suber* (Quero et al. 2006).

The intensity and timing of rainfall, and hence variation in soil water content, may be critical in driving forest structure and dynamics. Seasonal water variability (with waterlogging and drought events) captured during the experiment typified long term climatic data for the study region (see Fig. 1). Consequently, in most years, tree seedlings experience contrasting high soil water content during the wet season versus dry soil conditions in summer, in which emergence time must be critically balanced between avoiding waterlogging and growing large enough to resist drought to establish. Interannual climatic variation can alter the quality of microhabitats for seedling establishment in heterogeneous Mediterranean forests (Gómez-Aparicio et al. 2005). Thus, between-year variation in precipitation (i.e., drier winters or sporadic rains in summer) and differences in rainfall timing (i.e., early versus late) could differentially impact species establishment patterns.

Our modelling approach can help elucidate how oak establishment might change over time, because species-specific responses were parameterised across broad light availability and soil water content gradients. Although we must be cautious in extrapolating a 1 year study to longer time scales, we speculate that in a moderately wet winter (without waterlogging) *Q. suber* would benefit disproportionately among these species, since it had higher germination and emergence rates at the driest part of the water gradient. Conversely, *Q. suber* would be negatively affected by wet winter conditions and late rains, owing to its later seed-drop timing compared with *Q. canariensis* (Pérez-Ramos 2007) and its greater delay in emergence under waterlogged conditions, which would then shorten its time window for growing before summer. We also speculate that sporadic summer rain events would provide greater benefit to deciduous species (especially *Q. canariensis*) because their seedling survival improved with

summer watering and thus they could gain an advantage over *Q. suber* in nutrient-rich, more mesic habitats. These qualitative predictions are consistent with the species landscape distributions; *Q. canariensis* is more abundant near stream beds, whereas *Q. suber* is more abundant under drier conditions (Urbieto et al. 2008).

We hypothesize that if autumn–spring rainfall regimes persist (with waterlogging) but the onset of summer drought advances, there may no longer be an adequate time window for oak seedlings to develop the root systems necessary to tolerate summer drought, thereby intensifying problems with oak regeneration. The sensitivity of early seedling life history stages to soil water suggests that changes in the precipitation regime or temperature-mediated effects on water balance could have major impacts on regeneration dynamics in Mediterranean oak forests.

## Acknowledgements

We thank the Andalusian Government and Felipe Oliveros for providing the facilities to carry out the field work. We thank Maite Domínguez, Carmen Navarro, Rocío Sánchez, Paco Rodríguez, and Rafael Villar for their assistance at different stages. Stephen W. Pacala, Drew Purves, and Frederic Bartumeus provided helpful comments on earlier versions of the manuscript. This study was supported by FPI and FPU-MEC grants to the first and second authors, respectively, and by project grants Heteromed (REN2002-04041-C02) and Dinamed (CGL2005-05830-C03). This research is part of the GLOBIMED ([www.globimed.net](http://www.globimed.net)) network on forest ecology.

## References

- Akaike, H. 1992. Information theory and an extension of the maximum likelihood principle. *In* Breakthroughs in statistics. Vol. 1. Edited by S. Kotz and N. Johnson. Springer-Verlag, London. pp. 610–624.
- Beckage, B., and Clark, J.S. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology*, **84**: 1849–1861. doi:10.1890/0012-9658(2003)084[1849:SSAGOT]2.0.CO;2.
- Bonfil, C. 1998. The effects of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). *Am. J. Bot.* **85**: 79–87. doi:10.2307/2446557.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., and Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Can. J. For. Res.* **26**: 1521–1530. doi:10.1139/x26-171.
- Castro, J. 2006. Short delay in timing of emergence determines establishment success in *Pinus sylvestris* across microhabitats. *Ann. Bot. (Lond.)*, **98**: 1233–1240. doi:10.1093/aob/mcl208. PMID:17056614.
- Castro, J., Zamora, R., Hódar, J.A., and Gómez, J.M. 2005. Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: an experimental approach. *Plant Ecol.* **181**: 191–202. doi:10.1007/s11258-005-6626-5.
- Castro-Díez, P., Navarro, J., Pintado, A., Sancho, L.G., and Maestro, M. 2006. Interactive effects of shade and irrigation on

- the performance of seedlings of three Mediterranean *Quercus* species. *Tree Physiol.* **26**: 389–400. PMID:16356909.
- Chesson, P., and Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* **150**: 519–553. doi:10.1086/286080.
- Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* **70**: 171–207.
- Cox, D.R., and Oakes, D. 1984. *Analysis of survival data*. Chapman and Hall, New York.
- Edwards, A.W.F. 1992. *Likelihood*. Revised edition. Johns Hopkins University Press, Baltimore, Md.
- Espelta, J.M., Riba, M., and Retana, J. 1995. Patterns of seedling recruitment in west Mediterranean coppiced holm-oak (*Quercus ilex* L.) forests as influenced by canopy development. *J. Veg. Sci.* **6**: 465–472. doi:10.2307/3236344.
- Evans, M., Hastings, N., and Peacock, B. 2000. *Statistical distributions*. 3rd ed. Wiley-Interscience, New York.
- Gómez, J.M. 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, **58**: 71–80. PMID:15058720.
- Gómez-Aparicio, L., Gómez, J.M., and Zamora, R. 2005. Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. *J. Ecol.* **93**: 1194–1202. doi:10.1111/j.1365-2745.2005.01047.x.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley & Sons, New York.
- Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Camb. Philos. Soc.* **52**: 107–145. doi:10.1111/j.1469-185X.1977.tb01347.x.
- Hilborn, R., and Mangel, M. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, N.J.
- Jacobs, P.M., West, L.T., and Shaw, J.N. 2002. Redoximorphic features as indicators of seasonal saturation, Lowndes County, Georgia. *Soil Sci. Soc. Am. J.* **66**: 315–323.
- Joffre, R., and Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology*, **74**: 570–582. doi:10.2307/1939317.
- Jones, R.H., Allen, B.P., and Sharitz, R.R. 1997. Why do early-emerging tree seedlings have survival advantages?: a test using *Acer rubrum* (Aceraceae). *Am. J. Bot.* **84**: 1714–1718. doi:10.2307/2446470.
- Jordano, P., and Herrera, C.M. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience*, **2**: 230–237.
- Kobe, R.K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology*, **80**: 187–201.
- Kobe, R.K., Likens, G.E., and Eagar, C. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminium in a northern hardwood forest. *Can. J. For. Res.* **32**: 954–966. doi:10.1139/x02-018.
- Lloret, F., Casanovas, C., and Peñuelas, J. 1999. Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Funct. Ecol.* **13**: 210–216. doi:10.1046/j.1365-2435.1999.00309.x.
- Metropolis, N., Rosenbluth, A.W., Rosenbluth, M.N., and Teller, A.H. 1953. Equation of state calculations by fast computing machines. *J. Chem. Phys.* **21**: 1087–1092. doi:10.1063/1.1699114.
- Moles, A.T., and Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* **92**: 372–382. doi:10.1111/j.0022-0477.2004.00884.x.
- Nicotra, A.B., Babicka, N., and Westoby, M. 2002. Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. *Oecologia (Berl.)*, **130**: 136–145.
- Niinemets, Ü., and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* **76**: 521–547. doi:10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* **66**: 1–43. doi:10.2307/2963479.
- Pérez-Ramos, I.M. 2007. Factores que condicionan la regeneración natural de especies leñosas en un bosque mediterráneo del sur de la Península Ibérica. Ph.D. dissertation. University of Seville, Spain.
- Pérez-Ramos, I.M., Marañón, T., Lobo, J.M., and Verdú, J.R. 2007. Acorn removal and dispersal by the dung beetle *Thorectes lusitanicus*: ecological implications. *Ecol. Entomol.* **32**: 349–356. doi:10.1111/j.1365-2311.2007.00874.x.
- Pérez-Ramos, I.M., Urbieto, I.R., Marañón, T., Zavala, M.A., and Kobe, R. 2008a. Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. *Oikos*. doi:10.1111/j.2008.0030-1299.16370.x.
- Pérez-Ramos, I.M., Zavala, M.A., Marañón, T., Díaz-Villa, M.D., and Valladares, F. 2008b. Dynamics of understorey diversity following shrub-clearing of cork oak forests: a five-year study. *For. Ecol. Manage.* **255**: 3242–3253. doi:10.1016/j.foreco.2008.01.069.
- Pulido, F.J., and Díaz, M. 2005. Regeneration of a Mediterranean oak: a whole-cycle approach. *Ecoscience*, **12**: 92–102. doi:10.2980/i1195-6860-12-1-92.1.
- Quero, J.L., Villar, R., Marañón, T., and Zamora, R. 2006. Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytol.* **170**: 819–834. doi:10.1111/j.1469-8137.2006.01713.x. PMID: 16684241.
- Quero, J.L., Villar, R., Marañón, T., Zamora, R., and Poorter, L. 2007. Seed mass effect in four Mediterranean *Quercus* species (*Fagaceae*) growing in contrasting light environments. *Am. J. Bot.* **94**: 1795–1803. doi:10.3732/ajb.94.11.1795.
- Quilchano, C., Marañón, T., Pérez-Ramos, I.M., Noejovich, L., Valladares, F., and Zavala, M.A. 2008. Patterns and ecological consequences of abiotic heterogeneity in managed cork oak forests of Southern Spain. *Ecol. Res.* **23**: 127–139. doi:10.1007/s11284-007-0343-6.
- Rey Benayas, J.M. 1998. Growth and survival in *Quercus ilex* L. seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural lands. *Ann. For. Sci.* **55**: 801–807. doi:10.1051/forest:19980704.
- Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos*, **107**: 110–127. doi:10.1111/j.0030-1299.2004.13184.x.
- Sánchez-Gómez, D., Valladares, F., and Zavala, M.A. 2006. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytol.* **170**: 795–806. doi:10.1111/j.1469-8137.2006.01711.x. PMID: 16684239.
- Schmull, M., and Thomas, F.M. 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Liebl., *Fagus sylvatica* L.) to waterlogging. *Plant Soil*, **225**: 227–242. doi:10.1023/A:1026516027096.
- Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and

- patterns of plant recruitment. *Am. J. Bot.* **82**: 399–409. doi:10.2307/2445586.
- Seiwa, K. 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. *Oecologia (Berl.)*, **123**: 208–215. doi:10.1007/s004420051007.
- Sher, A.A., Goldberg, D.E., and Novoplansky, A. 2004. The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. *Oecologia (Berl.)*, **141**: 353–362. doi:10.1007/s00442-003-1435-9.
- Thomas, F.M., and Hartmann, G. 1998. Tree rooting patterns and soil water relations of healthy and damaged stands of mature oak (*Quercus robur* L., and *Quercus petraea* [Matt.] Liebl.). *Plant Soil*, **203**: 145–158. doi:10.1023/A:1004305410905.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- Urbieta, I.R. 2008. Estructura, dinámica y regeneración de los bosques mixtos de alcornoque (*Q. suber* L.) y quejigo moruno (*Q. canariensis* Willd.) del sur de la Península Ibérica: una aproximación multiescala. Ph.D. dissertation. University of Alcalá, Spain.
- Urbieta, I.R., Zavala, M.A., and Marañón, T. 2008. Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. *J. Biogeogr.* doi:10.1111/j.1365-2699.2008.01914.x.
- Verdú, M., and Traveset, A. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology*, **86**: 1385–1394. doi:10.1890/04-1647.
- Vincke, C., and Delvaux, B. 2005. Porosity and available water of temporarily waterlogged soils in a *Quercus robur* (L.) declining stand. *Plant Soil*, **271**: 189–203. doi:10.1007/s11104-004-2388-4.
- Zavala, M.A., and Zea, G.E. 2004. Mechanisms maintaining biodiversity in Mediterranean pine-oak forests: insights from a spatial simulation model. *Plant Ecol.* **171**: 197–207. doi:10.1023/B:VEGE.0000029387.15947.b7.