

Capítulo 5

La heterogeneidad del agua en el suelo y el tiempo de emergencia controlan el establecimiento de plántulas de tres especies de *Quercus*

Este capítulo reproduce el texto del siguiente manuscrito:

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Resumen

La diferente respuesta de las especies arbóreas a la disponibilidad de recursos durante la fase crítica de establecimiento de plántulas puede influir en la dinámica forestal. Los estudios en bosques mediterráneos se han centrado fundamentalmente en el análisis de los efectos de la sombra y de la sequía estival en la supervivencia de plántulas. Sin embargo, no se conocen los efectos de las lluvias que caen desde el otoño hasta la primavera sobre las etapas más tempranas (germinación y emergencia) del reclutamiento de plántulas. A tal fin, se llevó a cabo un experimento de siembra de bellotas a lo largo de gradientes naturales de disponibilidad de luz y agua (durante los periodos húmedo y seco) con tres especies de *Quercus* (*Q. suber*, *Q. canariensis*, *Q. pyrenaica*) que coexisten y que muestran una limitada regeneración natural al sur de la Península Ibérica. Las etapas del reclutamiento de plántulas se monitorizaron durante un año. Se construyeron modelos de germinación, emergencia y supervivencia (por máxima verosimilitud) para cada especie en función de la luz, el contenido de agua en el suelo durante la época húmeda y seca, y la compactación del suelo. También se analizó la influencia de la variación intraespecífica del tamaño de la semilla y de los tiempos de emergencia en cada fase. Los resultados muestran que el exceso de agua en el suelo durante el invierno (debido a las fuertes lluvias) causó una menor germinación y emergencia de plántulas sobre todo en las zonas más abiertas y encharcadas. Asimismo, el encharcamiento provocó un retraso en el tiempo de emergencia de las plántulas, lo que se tradujo en una menor probabilidad de supervivencia durante la época seca. Por tanto, durante el establecimiento de plántulas el agua actuó como un doble factor de estrés: por exceso en la época lluviosa y por defecto en la época seca. En general, un mayor tamaño de semilla contribuyó a una mayor probabilidad de germinación y emergencia de plántulas. Estos resultados muestran que la heterogeneidad temporal y espacial del contenido de agua en el suelo, mediada por los tiempos de emergencia de plántulas, juega un papel determinante en la dinámica de la regeneración de los bosques mediterráneos de *Quercus*.

Soil water heterogeneity and emergence time control seedling establishment in three co-occurring oak species

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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 (germination and emergence). A sowing experiment was set up along natural gradients of light availability and water content (during wet and dry periods) with three co-occurring oak species (*Quercus suber*, *Q. canariensis* and *Q. pyrenaica*), that show limited natural regeneration in the south of the Iberian Peninsula. Recruitment stages were monitored for one year. Using maximum likelihood, models of germination, emergence, and survival were developed as functions of light, soil moisture during wet and dry periods, and soil compaction. The influence of intra-specific variation in seed mass and emergence time were also tested. Over-abundant soil water levels during the winter (due to heavy rains) reduced germination and emergence and lengthened time to emergence (in waterlogged open areas), which in turn decreased seedling survivorship during the dry season. Thus, water acted as a double factor of stress (by excess and deficit) during seedling establishment. Seedlings from larger seeds had overall increased probabilities of germination and emergence. Results suggest that temporal and spatial heterogeneity of soil water content, mediated by emergence time and seed size, play a crucial role in the regeneration dynamics of Mediterranean oak forests.

Keywords: light heterogeneity; Mediterranean forest; *Quercus suber*; regeneration niche; resource effect; seed germination; seedling survival; waterlogging.

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 periods of resource variability could be important to understand 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, translate into a 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 among 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), thereby influencing forest composition and dynamics (Zavala and Zea 2004). Most of the attention in Mediterranean forests has centred 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 conditions alleviating drought stress in seedlings, but potentially leading to light limitation (Quero *et al.* 2006). Nonetheless, 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 during one stage can be sub-optimal for 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), *Q. canariensis* Willd., and *Q. pyrenaica* Willd., along field gradients of water and light, with emphasis on wet and dry period water effects on seedling recruitment stages (from seed germination to one-year establishment). We focused on the most southern European oak forests (mountains north of the Strait of Gibraltar). Natural dynamics have been little studied, but both oak seedlings and saplings are scarce. All yearly rainfall concentrates 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 factors of stress].

Specifically, recruitment stages (germination, emergence and one-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-

precipitation, emergence time could influence survival and hence plant fitness (Verdú and Traveset 2005). We calibrated species-specific models of seed germination, seedling emergence and survival, in order to address the following questions: (1) How do contrasting soil water availability (during wet and dry seasons) and light availability in the understorey influence the success of oak species during each recruitment stage (germination, emergence and survival)? (2) Could local waterlogging produced by autumn to spring rains reduce oak regeneration? (3) Do initial seed mass and emergence timing mediate responses to light and water heterogeneity? (4) Over gradients of resource availability, do co-occurring oak species differ in their response?

Material and methods

Study area and species

The study was conducted in La Saucedá forest (530 m above sea level, 36°31'54'' N, 5°34'29'' W) in Los Alcornocales Natural Park, a mixed mountain oak woodland of ~ 1700 km² in the south of the Iberian Peninsula. 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 sub-humid 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 average 1985-2004 data from La Saucedá meteorological station in Fig. 5.1). Forests are co-dominated by evergreen oak *Q. suber* and winter-deciduous *Q. canariensis*, which is more abundant in stands located near streams (Urbieta *et al.* in press, chapter 3); while deciduous *Q. pyrenaica* occurs in small stands at the highest altitudes. See Quilchano *et al.* (2008) for a description of the experimental forest site.

Experimental design and data collection

To encompass intra-specific variation, we collected acorns from several trees (at least ten 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 insects, and then buried (Pérez-Ramos *et al.* 2007). Acorns of *Q. suber* and *Q. canariensis* were collected from local stands near the experimental plot, while acorns of *Q. pyrenaica* (with scarce reproduction in the area) were brought from Sierra Morena stands (inland area also in S 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 standard deviation (SD) acorn fresh weight (g) was: 4.36 ± 1.63 for *Q. suber*, 4.48 ± 1.38 for *Q. canariensis* and 5.56 ± 1.04 for *Q. pyrenaica*. We used acorn fresh weight as a surrogate of seed mass, justified by their high correlation (Quero *et al.* 2007). Acorns were buried 2-3 cm into the soil and distributed haphazardly across 60 experimental units (minimum distance of 10 meters between units), which spanned 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 %). Experimental units were separated from each other at least by 10 m. Each unit consisted of 4 wire cages (25 x 25 x 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 at each unit (5 acorns of either *Q. canariensis* or *Q. suber*, and 2 of *Q. pyrenaica* inside each cage). A total of 600 seeds each of *Q. suber* and *Q. canariensis* were sown on 23 December 2003 and 480 seeds of *Q. pyrenaica*

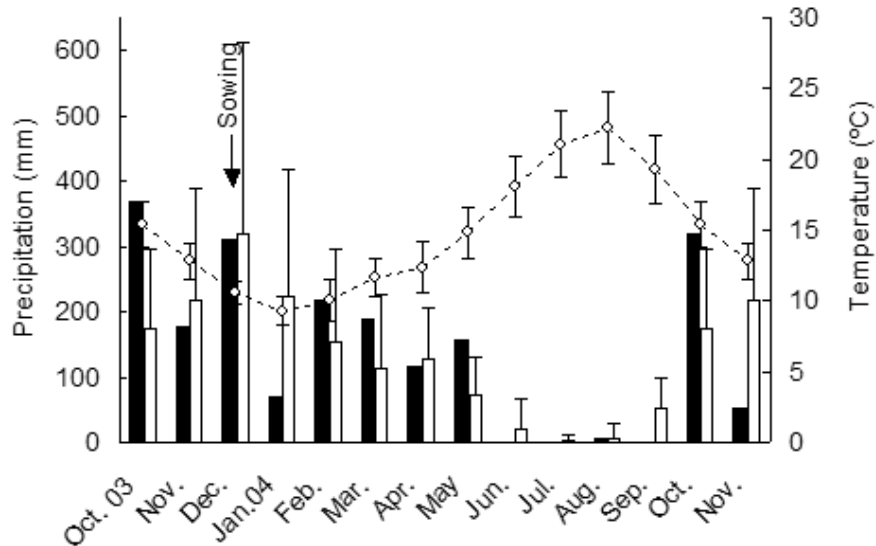


Figure 5.1 Climate diagram for the study area (data from La Sauceda meteorological station). Monthly precipitation values registered during the experiment, from autumn 2003 to winter 2004 (black bars), are compared to the monthly mean \pm SD registered from 1985-2004 (white bars). Monthly temperature is represented by the mean \pm SD of the values for the period 1985-1997 (dashed line).

were sown on 5 February 2004 when they became available.

Experimental units were censused regularly for one year. We tracked seedling emergence above ground through bi-weekly monitoring. Survival of seedlings and cause of mortality were monitored bi-weekly through spring-autumn (until October 2004) with an additional census in February 2005 (one 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 the summer; these seedlings were re-categorized as live. Germination was assessed indirectly. After the 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 plus those non-emerged but germinated / total seeds sown). The very few unearthed acorns (38 in

total) that had 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 unit). During three summer months (July-September) we added two litres of water per cage (equivalent to \sim 33 mm rainfall) bi-weekly. Percent soil volumetric water content (SVWC) was measured at each experimental unit (four readings, one per cage, total of 240), using Time Domain Reflectometry (TDR) (Campbell Scientific, Inc., Logan, Utah, USA) 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), in order to characterize soil moisture during wet-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 experimental units during bi-weekly monitoring. Light availability at the seedling level was measured at each of the 60 experimental units with hemispherical canopy photographs (two per experimental unit), 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, v. 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 understorey light availability. Soil compaction (expressed in MPa) was measured with a penetrometer (Penetrologger, Eijkelpamp Agriserch Equipment, Giesbeek, The Netherlands) in early spring (March 2005). Two measurements were taken per experimental unit in order 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 survival) was modelled independently as functions of abiotic factors, seed mass and emergence time. 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 for all the emerged seedlings (N=303 for *Q. suber*, N=220 for *Q. canariensis*, N=205 for *Q. pyrenaica*). Values of soil water and light level measured at the cage level were assigned to each acorn / seedling.

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 can be described by a binomial distribution with likelihood function:

$$[1] \quad L = \prod_{i=1}^{N-D} p_i \prod_{i=1}^D (1 - p_i)$$

where, N is the number of individuals starting each stage, D is the number of seeds failing (non germinating or non emerging), and p_i is the probability of germination or emergence for the individual i .

For each species, we specified germination and emergence probabilities (p_j), 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 Appendix 5.1 for equations). We first tested models for each factor and functional response independently. Then, we tested for two factor models using the factors and functional responses that yielded the best fit when evaluated singly.

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, i.e. 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 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:

$$[2] \quad L = \prod_{i=1}^D f(t_i; \phi) \prod_{i=1}^{N-D} S(c_i; \phi)$$

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), ϕ 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 loglikelihood that was ~ 7 loglikelihood units higher than the normal distribution for *Q. suber*). Although mortality often decreases as seedlings age and grow larger, during this study's focus on first-year seedling establishment, mortality risk was relatively constant (an assumption of the exponential distribution), especially after accounting for environmental influences on mortality (see below). Using an exponential distribution of survival times, the likelihood becomes:

$$[3] \quad L = \prod_{i=1}^D M(x_i, \phi) e^{-t_i M(x_i, \phi)} \prod_{i=1}^{N-D} e^{-c_i M(x_i, \phi)}$$

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

We specified the hazard, $M(x_i, \phi)$, as a function of abiotic factors (light, soil water content, and soil compaction), and we also explored the effects of seed mass and emergence times. The same procedure as for germination and emergence was followed, fitting several functional responses (i.e., linear, exponential, logistic, Michaelis-Menten and power), and testing single-factor and two-factor models. The effects of the summer watering treatment on seedling survival was tested by first using the complete data set to identify the factors that were best predictors, and secondly by comparing a general model fit to all the data (without respect to the watering treatment), versus models that were specific to the watering treatment.

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 to a null model of no factor effect using Likelihood Ratio Tests (LRTs) (Edwards 1992). We estimated 95% support regions (equivalent to 95% confidence intervals 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 International Inc. 1996, v.5.01). Fitted models were compared with Akaike's Information Criteria, specifically ΔAIC , which is defined for each Model $_j$ as: $AIC_j - AIC_{\text{minimum}}$ (Akaike 1992). The model with the strongest empirical support has the minimum AIC and thus its $\Delta AIC = 0$. Models with ΔAIC between 0-2 were considered to have equivalent and substantial empirical support, ΔAIC between 4-7 indicated less support and models with $\Delta AIC > 10$ 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 ± 18 in January, 45.3 ± 20 in March, and 53.7 ± 22 in April). However, very dry and homogeneous water conditions were found in summer (9.3 ± 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.

The three oak species diverged substantially in each of the studied recruitment stages: *Q. canariensis* had the lowest seed germination rate (47%), compared to *Q. suber* (71%) and *Q. pyrenaica* (75%). On the contrary, *Q. pyrenaica* had a lower percentage of emerged seedlings above ground (61%) than *Q. suber* (74%) and *Q. canariensis* (76%). *Q. suber* seedlings had lower survival (37%) than *Q. canariensis* (47%) and *Q. pyrenaica* (44%) one year after emergence. Seedling mortality of all the species was mainly due to desiccation and started with warm and dry conditions (late May- early June, Fig. 5.1), until the first autumn rains (October). Shoot dieback was frequent in *Q. pyrenaica* seedlings (61%), recovering in autumn after losing all the leaves in summer, but less frequent (about 12%) in the other two species. Seedling mortality during the subsequent cool and wet period (October-February) was low.

Models were formulated to test alternative hypotheses regarding main factors controlling germination, emergence and seedling survival. Among the tested models, those with the strongest empirical support are described below for each recruitment stage (see Appendixes 5.1 and 5.2 for parameter estimates of all models, and LRTs results).

Seed germination

In all three species, probability of germination declined exponentially with increasing mean SVWC during the wet period, as indicated by the best-supported germination models (Appendix 5.1). Light availability intensified the negative effect of wet-period soil moisture on germination of *Q. suber* and *Q. canariensis*, but light had a small positive effect for *Q. pyrenaica* (Fig. 5.2a). The model including wet-period water and light availability had strong empirical support for *Q. pyrenaica* (Δ AIC= 0) and *Q. canariensis* (Δ AIC= 0.3), and lower support for *Q. suber* (Δ AIC= 5.6) (Appendix 5.1). 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. 5.2b). 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. 5.2c), as indicated by the model with the greatest empirical support (Appendix 5.1). Other factors such as soil depth and compaction had an effect on species germination but with considerably less empirical support (Appendix 5.1).

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 (Appendix 5.1). Models including SVWC of the wet period alone showed the greatest empirical support (Δ AIC= 0) for *Q. suber* and *Q. pyrenaica*, but for both species, models that included seed mass or light availability also had substantial support

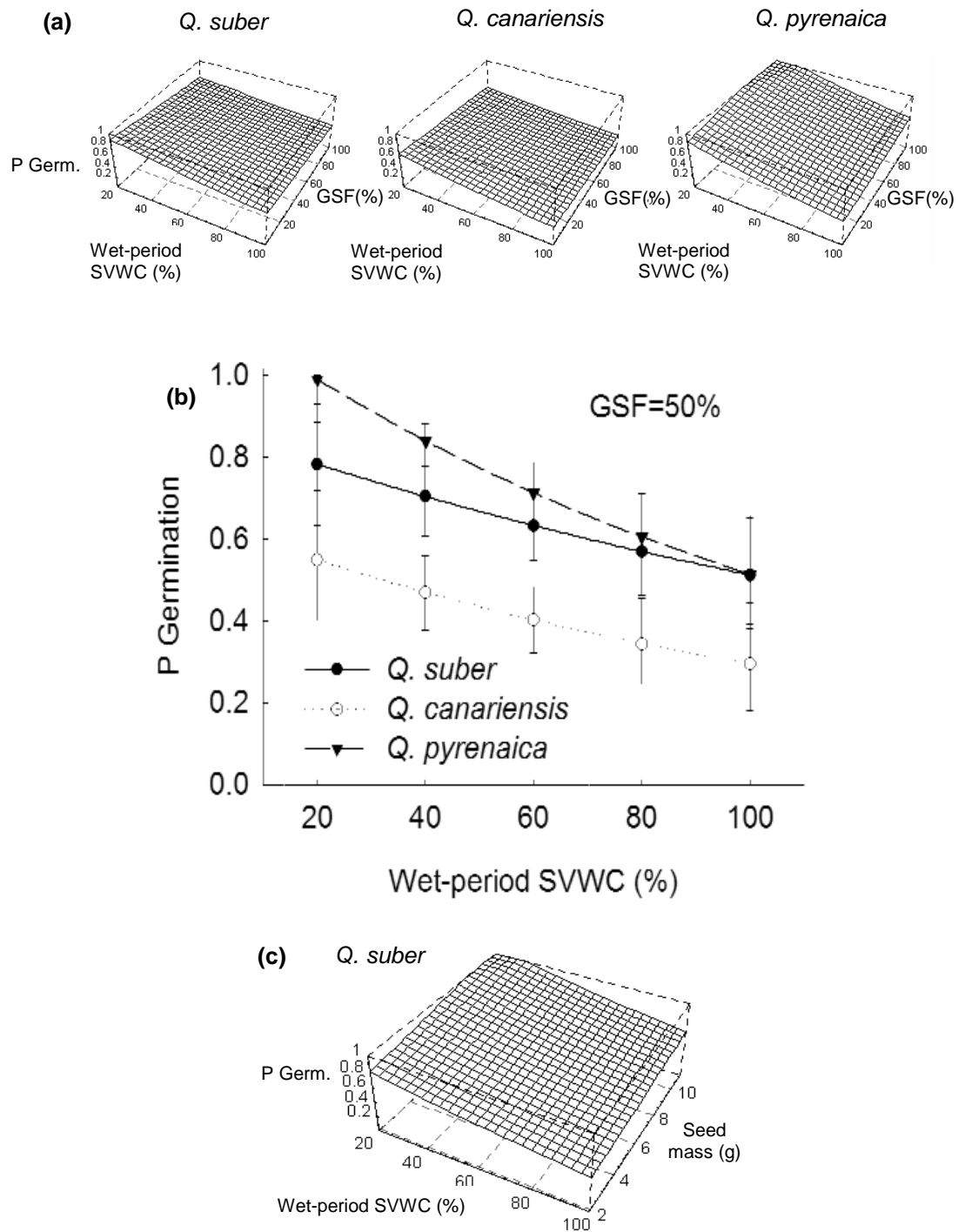


Figure 5.2 (a) Probability of germination of the three oaks exponentially diminished as soil volumetric water content (SVWC) of the wet period increased and light availability (GSF) increased (except for *Q. pyrenaica*). (b) Interspecific differences in responses to wet-period SVWC for a given point 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.

(within two 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 to *Q. canariensis*, larger seeds of *Q. suber* and *Q. pyrenaica* had higher probability of emergence (Fig. 5.3a). Species differed in their response to SVWC. For a mean value of seed mass (i.e., 5g), probability of emergence diminished as SVWC increased, especially for *Q. pyrenaica* seedlings (Fig. 5.3b). SVWC and light (GSF) equivalently explained emergence of *Q. suber* and *Q. pyrenaica*. A simultaneous increase of soil water content and light availability diminished the emergence probability of *Q. suber* and *Q. canariensis*, while a small positive effect of light was found for *Q. pyrenaica*'s emergence. When examining factor effects over a curtailed 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*.

Seedling survival

Time to emergence, i.e. number of days elapsed from sowing until seedlings emerged above ground, was the best predictor of seedling survival for all three species (Appendix 5.1). Individuals that emerged earlier had a higher probability of survival during the drought period (Fig. 5.4). Water addition during the dry summer did not improve seedling survival of *Q. suber* (Fig. 5.4a), but did reduce mortality of the two deciduous species. The beneficial effect of summer watering was stronger for *Q. canariensis* seedlings that emerged earlier, i.e., watered and non-watered curves converged for late emergence (Fig. 5.4b). *Q. pyrenaica* watered seedlings showed a similar probability of survival (but always greater than non-watered individuals) whenever they emerged (Fig. 5.4c). 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 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 soil moisture (SVWC) during the wet period was the key factor influencing species emergence time, as indicated by the models with the strongest empirical support (Appendix 5.2), with higher SVWC 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 to 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 (Appendix 5.2). Wet-period SVWC and seed mass explained emergence timing of *Q. pyrenaica*, with larger seeds 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.

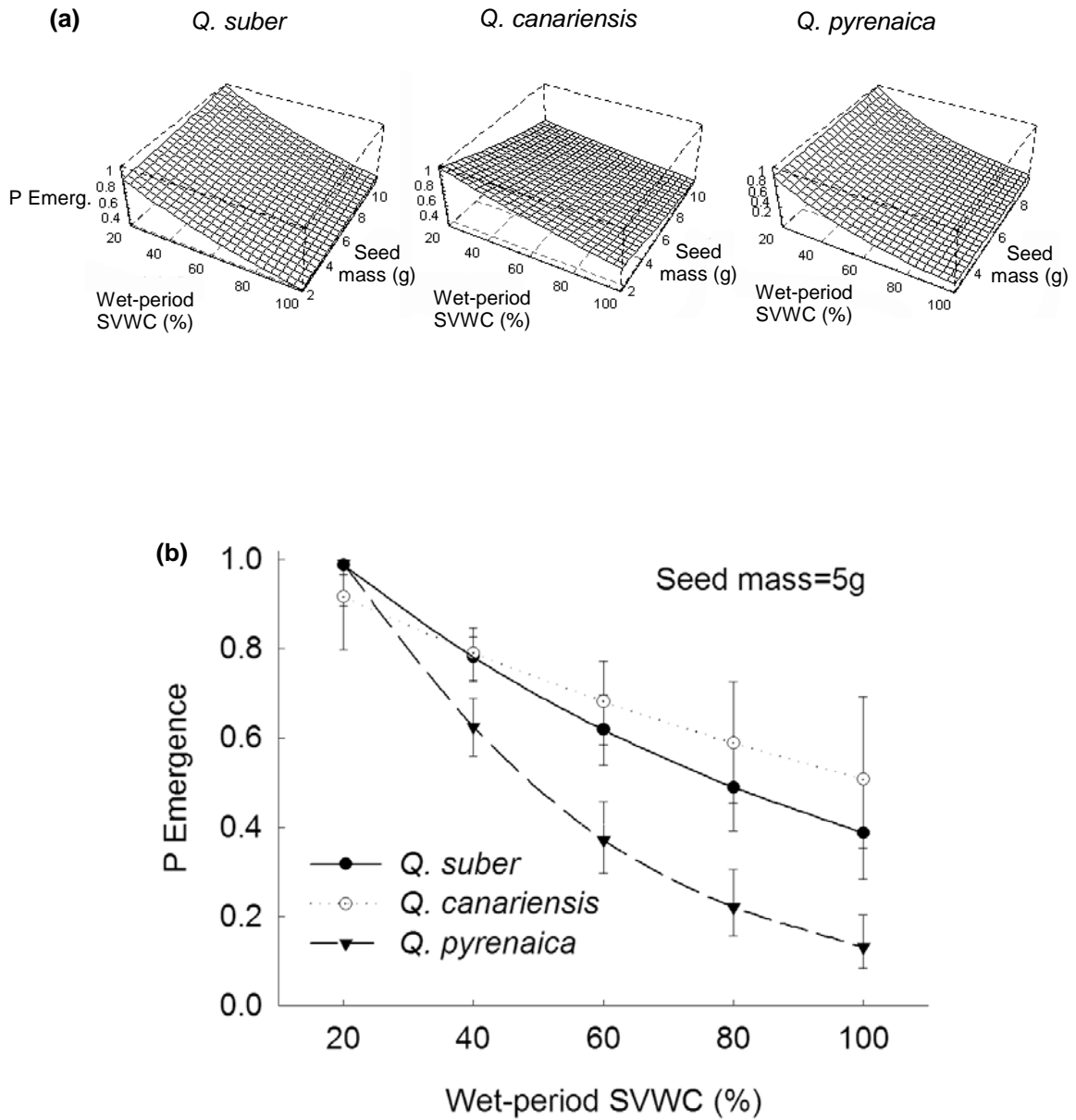


Figure 5.3 (a) Probability of emergence of the three oaks exponentially diminished as wet-period soil volumetric water content (SVWC) increased and seed mass decreased (except for *Q. canariensis*). Notice different scales in the axes. (b) Interspecific differences in responses to wet-period SVWC for an average seed mass of 5 g. Bars denote 95% support regions.

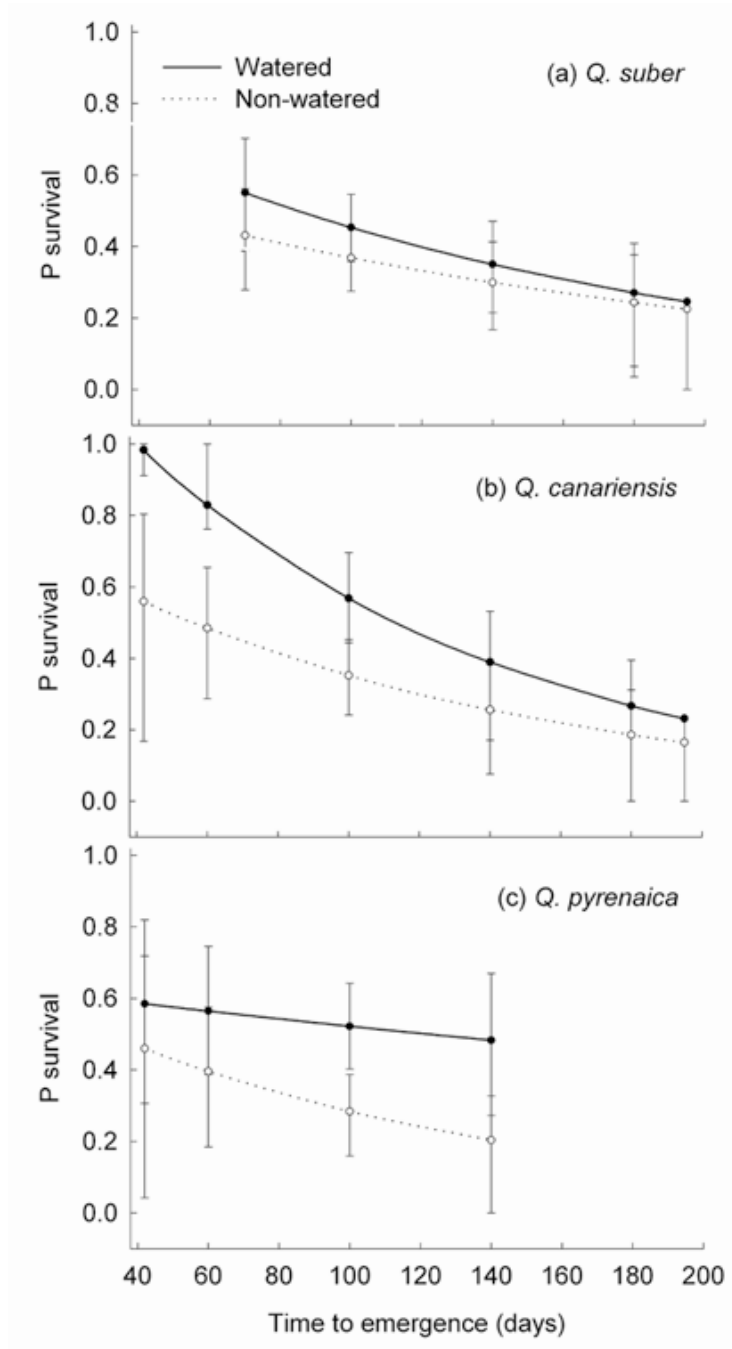


Figure 5.4 Models resulting from the best fit for seedling survival. Responses of watered and non-watered (control) individuals are differentiated. Probability of survival in summer was lower for those seedlings that delayed their emergence. *Q. suber* seedlings did not respond to the water treatment (a). Watering significantly increased *Q. canariensis'* (b) and *Q. pyrenaica's* (c) survival.

Discussion

Resource availability and oak establishment

Spatial and temporal soil water heterogeneity (from waterlogged to very dry conditions) was the major factor controlling, either directly or indirectly through emergence time, seedling establishment in the studied sub-humid Mediterranean forest. Drought (i.e., soil water deficit) primarily limiting seedling establishment has been commonly reported by previous studies 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 through reducing germination and emergence. Moreover, high soil water levels lengthened time to emergence of seedlings, which in turn decreased their survivorship during summer drought (Fig. 5.5). 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 effect of both soil water and light. In general, a negative effect of light availability was found for 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 more waterlogging due to higher soil water retention and the absence of rainfall interception by vegetation. However, the negative effect of irradiance was still present even when looking at a curtailed 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

higher 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, pers. com.) that are indicative of seasonal soil saturation (Jacobs *et al.* 2002). We hypothesise 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., Schull 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 (Pérez-Ramos 2007). 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), rather than as a resource, 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 emergence timing 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

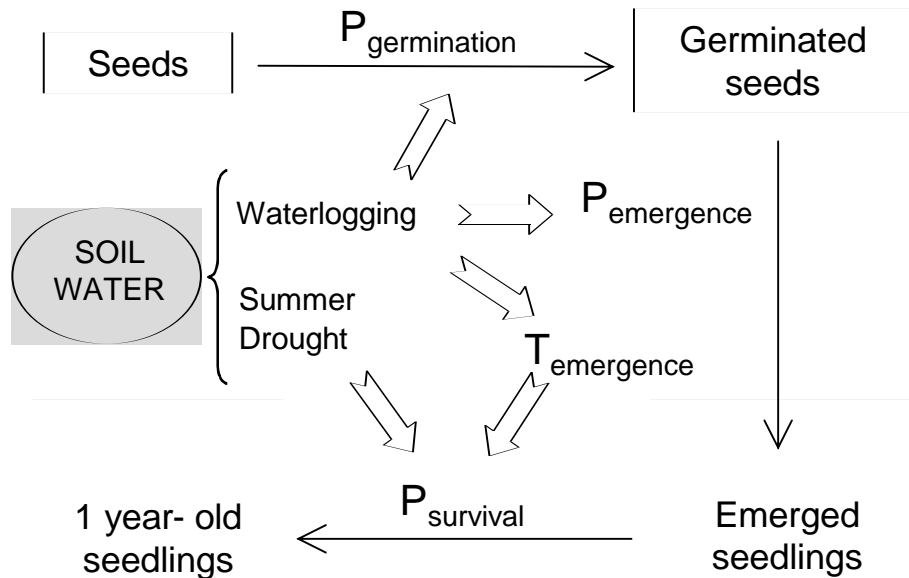


Figure 5.5 Diagram of oak's regeneration cycle with the main factors controlling each of the studied stages. High levels of soil water content (waterlogging) registered during the wet period (autumn to spring) reduced species germination and emergence. Moreover, seedling survival was indirectly (through emergence time) affected by soil water excess, which delayed seedling emergence and shorted the time window of the growing season. Seedlings with delayed emergence had a higher probability of mortality during the summer drought.

Westoby 2004). Within the same oak species, seedlings with larger seeds showed in general higher probabilities of germination and emergence, with the exception of those of *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 (see chapter 4), which may have been predated or dispersed. Similarly, Gómez (2004) found conflicting selective pressures between a positive effect of (*Q. ilex*) acorn size on most fitness components related to seedling establishment, and direct negative effect of acorn size on survival to predation.

Early seedling emergence had a strong positive effect on 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, those seedlings that did not suffer waterlogging emerged earlier and could benefit from growing season (spring) resources for a longer period of time. Thus, intra-specific 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 survival and growth) of *Pinus sylvestris* seedlings in SE 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 root allocation (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 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 achieve 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 during the wet period) characterized the responses of three oaks, but mortality peaks occurred in different life stages for different species. *Q. canariensis* had the lowest germination rate among species. However, germinated acorns of *Q. canariensis* succeeded most in emergence and survival (especially if they could emerge early and were watered in summer). On the contrary, *Q. pyrenaica* showed the highest probability of germination, whatever the soil water level, but waterlogging sharply reduced probability of emergence. *Q. pyrenaica*'s emergence times (despite their delayed planting) were similar to those of *Q. canariensis*. Seedlings of both deciduous species responded positively to water addition 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). *Q. suber* had an intermediate response in germination (equivalent to *Q. pyrenaica*) and emergence (similar to *Q. canariensis*), but suffered higher mortality in summer, primarily because seedlings emerged later and 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 water addition during the summer, which is consistent with a greenhouse study where 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 heterogeneity (with waterlogging and drought events) captured during the experiment typified long term climatic data for the study region (see Fig. 5.1). Consequently, in most years, tree seedlings suffer an excess-deficit water cycle, in which emergence time must be critically balanced between avoiding waterlogging and being large enough to resist drought, in order to establish. Inter-annual 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 spatially and across years, because species-specific responses were parameterised across broad light and water gradients. Although we must be cautious in extrapolating a one year study to longer time scales, we speculate that under a drier 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 due to its later seed drop compared to *Q. canariensis* (Pérez-Ramos 2007), and its greater delay in emergence under waterlogged conditions, which would then shorten its time window for growing before the summer. We also speculate that sporadic summer rain events would provide greater benefit to deciduous species (especially *Q. canariensis*), because their survival improved when watered in summer, and thus, they could gain an advantage over *Q. suber* in nutrient-rich and more mesic habitats. These qualitative predictions are consistent with the species landscape distributions, *Q. canariensis*

being more abundant near stream beds, while *Q. suber* under drier conditions (Urbietta *et al.* in press; chapter 3).

We hypothesise 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. On the other hand, decreased rainfall during the wet period could alleviate waterlogging in clayey soils, promoting seedling establishment in areas that currently do not support woody vegetation. 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.

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Appendix 5.1

Table 5.1 Maximum likelihood parameter estimates for germination, emergence and survival models. Models are ranked from best to poorest fits.

GERMINATION										
	Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	ΔAIC
<i>Q. suber</i>	Wet-period SVWC (%)	Seed mass (g)	EXP+	0.86	-0.0069	0.0340	-301.1	28.5***	608.2	0.0
	Max. SVWC (%)		EXP	0.99	-0.0059		-304.4	21.9 ***	612.8	4.6
	Wet-period SVWC (%)	GSF (%)	EXP+	1.00	-0.0053	-0.0028	-303.9	22.9***	613.8	5.6
	Wet-period SVWC (%)	GSF (%)	EXP*	0.83	0.0000	-2.5642	-304.3	22.4***	614.6	6.5
	Wet-period SVWC (%)		EXP	0.98	-0.0068		-305.4	19.9 ***	614.8	6.6
	GSF (%)		EXP	0.83	-0.0048		-308.6	13.3 ***	621.3	13.1
	Seed weight (g)		EXP	0.59	0.0454		-311.7	7.3 **	627.4	19.2
	Max. depth (cm)		LIN	0.57	0.0040		-312.6	5.4 *	629.3	21.1
	Null model			0.71			-315.3		632.7	24.5
<i>Q. canariensis</i>	Wet-period SVWC (%)		EXP	0.73	-0.0093		-375.4	13.0***	754.8	0.0
	Wet-period SVWC (%)	GSF (%)	EXP+	0.74	-0.0078	-0.0029	-374.5	14.7***	755.1	0.3
	Wet-period SVWC (%)	GSF (%)	EXP*	0.57	-0.0386	0.0033	-374.6	14.6***	755.2	0.4
	Wet-period SVWC (%)	Seed mass (g)	EXP+	0.75	-0.0092	-0.0068	-375.4	13.1**	756.8	1.9
	Max. SVWC (%)		EXP	0.68	-0.0067		-376.6	10.7**	757.1	2.3
	GSF (%)		EXP	0.56	-0.0054		-378.5	6.7 **	761.0	6.2
	Mean compact. (MPa)		MM	0.68	0.7574		-379.4	5.0 *	762.8	8.0
	Max. compact. (MPa)		MM	0.59	0.6000		-379.8	4.2 *	763.6	8.8
	Null model			0.47			-381.9		765.8	11.0
<i>Q. pyrenaica</i>	Wet-period SVWC (%)	GSF (%)	EXP+	1.00	-0.0081	0.0029	-239.4	37.4***	484.8	0.0
	Wet-period SVWC (%)		EXP	1.10	-0.0081		-244.4	27.5 ***	492.7	7.9
	Max. SVWC (%)		EXP	1.07	-0.0063		-245.2	25.8 ***	494.4	9.6
	Wet-period SVWC (%)	Seed mass (g)	EXP+	1.13	-0.0081	-0.0041	-244.4	27.5***	494.7	9.9
	Superf. compact. (MPa)		MM	0.95	2.1390		-253.6	9.0 **	511.2	26.4
	Mean compact. (MPa)		MM	0.91	2.1220		-255.2	5.8 *	514.5	29.6
	GSF (%)		LIN	0.70	0.0018		-256.2	3.8 *	516.4	31.6
	Null model			0.75			-258.1		518.3	33.5

Table 5.1 Continued

EMERGENCE									
Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	ΔAIC
Wet-period SVWC (%)		EXP	1.25	-0.0117		-213.4	46.4 ***	430.7	0.0
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.16	-0.0116	0.0150	-212.7	47.6***	431.0	0.3
Wet-period SVWC (%)	GSF (%)	EXP+	1.25	-0.0106	-0.0018	-212.6	47.8***	431.3	0.6
Max. SVWC (%)		LIN	1.09	-0.0065		-214.1	44.8 ***	432.3	1.6
Wet-period SVWC (%)	GSF (%)	EXP*	0.91	0.0034	-0.0462	-218.5	36.1***	443.0	12.3
GSF (%)		EXP	0.89	-0.0064		-228.2	16.7 ***	460.4	29.7
Wet-period SVWC (%)	Seed mass (g)	EXP*	0.97	-0.0508	0.0270	-227.5	18.1***	461.0	30.3
Superf. compact. (MPa)		MM	0.98	1.8178		-232.1	9.0 **	468.1	37.4
Max. compact. (MPa)		LOGI	0.31	0.1643		-233.6	5.9 *	471.2	40.5
Null model			0.74			-236.6		475.1	44.4
Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	ΔAIC
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.39	-0.0070	-0.0627	-146.1	22.7***	298.1	0.0
Wet-period SVWC (%)	Seed mass (g)	EXP*	1.10	-0.2595	0.0071	-147.8	19.1***	301.7	3.6
Max. SVWC (%)		EXP	1.05	-0.0060		-150.4	14.0 ***	304.8	6.7
Wet-period SVWC (%)		EXP	1.06	-0.0074		-151.0	12.7 ***	306.1	7.9
Wet-period SVWC (%)	GSF (%)	EXP+	1.08	-0.0068	-0.0014	-150.6	13.7**	307.1	9.0
Wet-period SVWC (%)	GSF (%)	EXP*	0.86	0.3494	-0.0002	-152.4	9.9**	310.8	12.7
Seed mass (g)		EXP	1.02	-0.0660		-154.1	6.6 *	312.2	14.0
GSF (%)		LOGI	1.56	-0.0124		-155.2	4.4 *	314.4	16.2
Null model			0.76			-157.4		316.8	18.7
Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	ΔAIC
Wet-period SVWC (%)		EXP	1.77	-0.0261		-170.0	111.2 ***	344.0	0.0
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.52	-0.0250	0.0205	-169.2	112.8***	344.3	0.3
Wet-period SVWC (%)	GSF (%)	EXP+	1.74	-0.0267	0.0014	-169.4	112.4***	344.8	0.7
Max. SVWC (%)		EXP	1.58	-0.0200		-171.6	108.1 ***	347.1	3.1
Wet-period SVWC (%)	Seed mass (g)	EXP*	1.24	0.0747	-0.0416	-186.2	78.8***	378.4	34.4
Wet-period SVWC (%)	GSF (%)	EXP*	0.84	0.0180	-0.0132	-206.6	38.1***	419.1	75.1
Superf. compact. (MPa)		LIN	0.29	0.1632		-212.0	27.2 ***	428.0	84.0
Mean compact. (MPa)		LIN	0.22	0.1669		-213.3	24.6 ***	430.6	86.5
GSF (%)		EXP	0.71	-0.0052		-222.4	6.5 *	448.7	104.7
Null model			0.61			-225.6		453.2	109.2

Table 5.1 Continued

SURVIVAL										
	Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	Δ AIC
Q. suber	Time to emergence (days)		LIN	0.02	0.0004		-692.1	20.3***	1388.1	0.0
	Oscillation SVWC (%)	Seed mass (g)	LIN+	0.07	0.0008	-0.0065	-694.0	16.4***	1394.0	5.9
	Seed mass (g)		EXP	0.14	-0.1700		-695.5	13.5***	1395.0	6.9
	Oscillation SVWC (%)		LIN	0.04	0.0010		-698.2	8.0**	1400.5	12.4
	Oscillation SVWC (%)	GSF (%)	LIN+	0.04	0.0010	-0.00004	-698.2	8.0*	1402.4	14.3
	Mean SVWC (%)		LIN	0.03	0.0010		-699.3	5.8*	1402.6	14.5
	Null model				0.07		-702.2		1406.4	18.3
Q. can.	Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	Δ AIC
	Time to emergence (days)		LIN	-0.002	0.0006		-444.1	24.3***	892.2	0.0
	Null model				0.06		-456.2		914.5	22.3
Q. pyrenaica	Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT (x²)	AIC	Δ AIC
	Time to emergence (days)		LIN	0.04	0.0003		-415.9	32.1***	835.8	0.0
	Oscillation SVWC (%)	GSF (%)	LIN+	-0.02	0.0019	0.0013	-417.2	29.6***	840.3	4.5
	GSF (%)		LIN	0.03	0.0014		-421.1	21.7***	846.2	10.4
	Mean SVWC (%)		LIN	-0.02	0.0030		-423.3	17.3***	850.6	14.8
	Oscillation SVWC (%)		LIN	-0.002	0.0024		-424.5	14.8***	853.1	17.3
	Oscillation SVWC (%)	Seed mass (g)	LIN+	0.01	0.0024	-0.0030	-424.3	15.3***	854.6	18.8
	Min. SVWC (%)		EXP	0.03	0.1004		-428.2	7.6**	860.3	24.5
Null model				0.06		-431.9		865.9	30.1	

Note: Models are noted as LIN (Linear), LOGI (Logistic), MM (Michaelis-Menten), EXP (Exponential), and POW (Power). A and S are parameters estimated in the models (see equations below). D is the estimated parameter when Factor 2 was added to the functional response that yielded the best fit when evaluated singly. Additive interactions between two factors are noted as (+) and multiplicative as (*).

LogLike. corresponds to the maximum log-likelihood: $\log(Lq|data, model)$. Factors' effects are evaluated through loglikelihood ratio test (LRT, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). AIC (Akaike's Information Criteria) is calculated as: $AIC = -2\log(Lq|data, model) + 2K$, being K the number of parameters in the model. Model fits are evaluated through ΔAIC ($AIC_i - AIC_{min}$). Bold font denotes models with equivalent empirical support (i.e., $\Delta AIC < 2$).

Linear: $A + SFactor_i$

Exponential: $Ae^{(SFactor_i)}$

Power: $AFactor_i^S$

Logistic: $\frac{e^{(A+SFactor_i)}}{1+e^{(A+SFactor_i)}}$

Michaelis-Menten: $\frac{AFactor_i}{\frac{A}{S} + Factor_i}$

Appendix 5.2

Table 5.2 Maximum likelihood parameter estimates for best-fitted models that relate emergence time of three oak species with seed mass and abiotic factors. Models are ranked from best to poorest fits.

TIME TO EMERGENCE											
	Factor 1	Factor 2	Fit	n	A	S	D	LogLike.	LRT (x²)	AIC	Δ AIC
<i>Q. suber</i>	Wet-period SVWC (%)	GSF (%)	EXP+	12.0	77.6	0.0055	0.0025	-1463.7	45.6***	2935.4	0.0
	Wet-period SVWC (%)		EXP	11.7	79.9	0.0065		-1468.2	36.6***	2942.5	7.1
	Wet-period SVWC (%)	Seed mass (g)	EXP+	11.8	85.1	0.0063	-0.0126	-1467.3	38.4***	2942.6	7.2
	GSF (%)	Seed mass (g)	EXP+	11.2	102.5	0.0038	-0.0161	-1475.1	22.9***	2958.1	22.7
	GSF (%)		EXP	11.2	95.3	0.0038		-1476.4	20.2***	2958.8	23.4
	Null model				10.4	105.7			-1486.5		2977.0
<i>Q. canariensis</i>	Wet-period SVWC (%)	GSF (%)	EXP+	12.3	66.7	0.0069	0.0015	-1019.1	42.2***	2046.1	0.0
	Wet-period SVWC (%)		EXP	12.2	68.8	0.0071		-1020.2	39.9***	2046.4	0.3
	Wet-period SVWC (%)	Seed mass (g)	EXP+	12.1	67.2	0.0071	0.0054	-1020.2	40.0***	2048.3	2.2
	GSF (%)		MM	10.8	106.6	44.5312		-1033.9	12.6***	2073.7	27.6
	GSF (%)	Seed mass (g)	EXP+	10.6	84.3	0.0028	0.0079	-1036.2	7.9**	2080.4	34.3
	Null model				10.2	94.5			-1040.2		2084.3
<i>Q. pyrenaica</i>	Wet-period SVWC (%)	Seed mass (g)	EXP+	12.5	66.6	0.0049	0.0286	-922.8	14.8***	1853.6	0.0
	Wet-period SVWC (%)		EXP	12.5	78.0	0.0049		-924.1	12.2**	1854.2	0.6
	Wet-period SVWC (%)	GSF (%)	EXP+	12.4	77.9	0.0048	0.0002	-924.1	12.2**	1856.2	2.6
	GSF (%)	Seed mass (g)	EXP+	12.2	75.6	0.0014	0.0316	-926.8	6.8*	1861.7	8.1
	Seed mass (g)		LIN	12.1	77.4	2.9367		-927.9	4.6*	1861.8	8.2
	GSF (%)		EXP	12.1	90.3	0.0013		-928.3	3.9*	1862.6	8.9
Null model				11.9	93.8			-930.2		1864.4	10.8

Note: Models are noted and evaluated as in Table 5.1. *n* is the shape parameter of the gamma distribution of emergence times, where *n*>1 indicates bell-shaped but left skewed probability distribution.