

Seedling growth and morphology of three oak species along field resource gradients and seed mass variation: a seedling age-dependent response

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Abstract

Question: What is the relative importance of seed mass and abiotic factors in species-specific seedling growth and morphology during the first and the second growing season? How do oak species respond along gradients of these factors?

Location: Mediterranean oak forest in southern Spain.

Methods: We analysed seedling growth components and morphology of three co-occurring *Quercus* species (two deciduous and one evergreen). Oak seeds with a wide variety of sizes were sown along broad gradients of abiotic conditions. Intra- and inter-specific differences were evaluated by calibrating maximum likelihood estimators of seedling growth during the first two years of life.

Results: We found multiple resources and conditions affecting seedling morphology and biomass allocation. However, the integrative variables of seedling growth – total aboveground biomass and relative growth rate (RGR) – were affected by two main factors: seed mass and light conditions. The relative contribution of these two factors depended strongly on seedling age. Seed mass explained most of the growth and morphological variables during the first year, while light conditions were the best predictor in the second growing season. In contrast, soil factors did not play an important role in seedling growth. We found some evidence of regeneration niche partitioning between oak species along the

light gradient, a reflection of their distribution patterns as adults at the study site.

Conclusions: We conclude that inter-specific differences in seedling growth, arising from seed size variability and microsite heterogeneity, could be of paramount importance in oak species niche segregation, driving stand dynamics and composition along environmental gradients.

Keywords: Leaf life-span; Mediterranean forest; *Quercus canariensis*; *Quercus pyrenaica*; *Quercus suber*; Regeneration niche; Relative growth rate.

Introduction

The seedling stage is crucial for plant population dynamics due to its higher vulnerability to environmental constraints in comparison with seed and adult stages (Harper 1977; Silvertown & Charlesworth 2001). Studies on plant growth during this demographic phase and how resources affect this process are critical for understanding tree recruitment patterns (Poorter 2001; Villar et al. 2008; Gómez-Aparicio et al. 2008), which in turn largely drive forest composition and dynamics (e.g. Pacala et al. 1996; Zavala et al. 2000; Kobe 2006).

Most studies on seedling growth components have been carried out under controlled conditions and have focused on the effect of a low number of factors (e.g. Grubb et al. 1996; Walters & Reich 2000; Espelta et al. 2005; Quero et al. 2006, 2008; Sánchez-Gómez et al. 2006). Although greenhouse experiments provide very valuable information, they do not allow a representation of the complex scenario to which plants are exposed in nature. Natural conditions where plant species regenerate constitute a multidimensional space where many abiotic and biotic factors act simultaneously and interactively (Ibañez & Schupp 2001; Gómez 2004; Puerta-Piñero et al. 2007). However, there are very few published examples identifying the main factors – and their interactions – that drive seedling growth along wide, natural environmental gradients.

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In natural conditions, the amount of light intercepted for photosynthesis is one of the most important environmental factors affecting seedling growth in the understorey, and plants acclimate to this resource through morphological and physiological changes (Poorter 2001; Quero et al. 2008). Plant species may respond not only to light availability, but also to its spectral quality. Many plants are sensitive to changes in the red:far-red light ratio (R:FR), which can be considered a signal of shading and proximity to other plants (Gilbert et al. 1995; Aphalo & Lehto 2001), and usually respond to this factor by modifying certain morphological and physiological traits as mechanisms of shade avoidance (Ammer 2003; Tegelberg et al. 2004).

The variation in soil resource availability, mainly of water and nutrients, can also modulate seedling and sapling performance (Kobe 2006). The importance of soil water for seedling growth has been well documented for Mediterranean plants (e.g. Di Castri et al. 1981; Blondel & Aronson 1999; Valladares & Sánchez-Gómez 2006). However, scant information is available on how growth and morphology of Mediterranean tree species vary along natural gradients of nutrients.

In addition to external abiotic factors, seedling growth can vary according to some intrinsic traits of the plant species, such as seed mass and leaf lifespan. On one hand, seed mass represents the amount of reserves provided for the young plant during its early life, being one of the main characters influencing seedling early growth (Long & Jones 1996; Quero et al. 2007; Turnbull et al. 2008). On the other hand, seedlings with short-lived leaves (deciduous species) tend to show a higher efficiency for assimilation of light and CO₂, and thus grow faster than related evergreen species (Reich et al. 1992; Cornelissen et al. 1998; Antúnez et al. 2001; Wright et al. 2004). Leaf lifespan can therefore be related to species habitat and distribution patterns across landscapes (Reich et al. 1992; Ruíz-Robledo & Villar 2005).

The changes in seedling biomass through time – i.e. the relative growth rate (RGR) – can be broken down into a morphological component, the leaf area ratio (LAR), which indicates the plant investment in leaves, and a physiological component, the net assimilation rate (NAR) or plant mass increment per leaf area. In general, the morphological component (LAR) is the biggest contributor to RGR variation in tree species (Reich et al. 1992; Huante et al. 1995; Cornelissen et al. 1998; Antúnez et al. 2001). However, most of these studies are greenhouse experiments that usually use limiting light conditions. The few studies that have explored these

relationships under field conditions suggest that the physiological component (NAR) also plays an important role, especially in high light environments (Poorter 1999; Shipley 2002).

This study is part of a general research programme on the regeneration ecology of three co-occurring *Quercus* species – two deciduous (*Quercus canariensis* Willd. and *Quercus pyrenaica* Willd.) and one evergreen (*Quercus suber* L.) – that dominate the tree canopy in forests of southern Spain. In the selected study area (Aljibe Mountains), the studied oak species segregate along environmental gradients of soil moisture and canopy cover. Thus, *Q. suber* tends to dominate in habitats with a lower availability of water and nutrients, where the overstorey canopy is usually sparse (Pérez-Ramos 2007). In contrast, *Q. canariensis* is more abundant in moister habitats, where the overstorey canopy is denser (Urbietta et al. 2008b). *Q. pyrenaica* is less frequent in the study area, and restricted to scarce populations at higher altitudes (>900 m). We hypothesise that differences in the adult distribution of these species should be reflected as differential responses to environmental factors at the seedling stage: for example, *Q. canariensis* seedlings being more shade-tolerant and water-demanding than *Q. suber* seedlings.

These three oak species, which are protected by a European Union Directive (Habitat Directive 92/43EEC), frequently exhibit problems of natural regeneration (Pérez-Ramos 2007). In previous studies, we explored the effects of seed size and vegetation cover on seed removal (Pérez-Ramos et al. 2008a), and the effects of soil conditions and light availability on seed germination, seedling survival and plant biomass (Gómez-Aparicio et al. 2008; Urbietta et al. 2008a). Specifically, in this paper we analyse in detail seedling growth (both RGR and its two growth components) and morphology in a field experiment by sowing seeds of the three oak species along wide gradients of abiotic factors, with a broad range of seed mass for each species. All measurements were made during the first 2 years of seedling life, which enabled us to evaluate whether species responses along resource gradients changed depending on the time scale. Most previous studies have focused on first-year seedlings, but the influence of environment is expected to change drastically with time, since seed reserves are mainly depleted during the first months of seedling life (Quero et al. 2007).

The main aims of this study are (i) to examine the relative importance of seed mass and abiotic factors (light, soil water and nutrient content, soil texture and soil compaction) on species-specific seedling growth and morphology; (ii) to test whether seedling growth

and morphology are more dependent on seed mass during the first year, while they are more affected by environmental conditions during the second growing season; (iii) to explore the intrinsic causes of variation in growth rates (LAR versus NAR); (iv) to investigate whether oak species or functional groups (deciduous versus evergreen) respond differently along gradients of these factors; and (v) to infer whether their distribution patterns across landscapes are a reflection of inter-specific differences in seedling response to environment, and to discuss the ecological implications of all these findings for forest stand dynamics and species coexistence.

Methods

Study site and experimental design

The study was conducted in La Saucedá forest (530 m above sea level, 36°31'54"N, 5°34'29"W), located in the mixed oak forests of the Aljibe Mountains, near the Strait of Gibraltar, in southern Spain (for a detailed description of the experimental site, see Pérez-Ramos et al. 2008b; Quilchano et al. 2008). The climate is sub-humid Mediterranean, with mild wet winters alternating with hot dry summers. Annual mean temperature is 17°C, and annual mean rainfall is 1265 mm (based on 1985–2004 yearly data from La Saucedá meteorological station). The overstorey canopy of this forest is co-dominated by the evergreen *Q. suber* and the deciduous *Q. canariensis*, whereas the deciduous *Q. pyrenaica* is present only in scarce populations at higher altitudes (> 900 m).

Acorns of *Q. suber* and *Q. canariensis* were collected from several trees (at least ten of each species) in the surroundings of the study area during the fruiting season (October–December) of 2003. Acorns of *Q. pyrenaica* (with scarce seed production in the Aljibe Mountains) were brought from stands in the Sierra Morena (an inland area also in southern Spain). We selected healthy, normal-sized acorns and discarded those infected by moth or beetle larvae using a flotation method (Gribko & Jones 1995). Selected acorns were individually weighed to the nearest 0.01 g and stored on a moist substrate at 2–4°C until used in the experiment. Mean \pm SD (standard deviation) acorn fresh weight was 4.36 ± 1.63 g for *Q. suber*, 4.48 ± 1.38 g for *Q. canariensis* and 5.56 ± 1.04 g for *Q. pyrenaica*. We used acorn fresh weight as a surrogate for dry seed mass, justified by their high correlation (with R^2 values ranging from 0.93 to 0.99, Quero et al. 2007). In December 2003,

seeds from the three species were sown horizontally, 1–3-cm deep in the mineral soil, simulating biotic acorn dispersal by European jays (Kollmann & Schill 1996), rodents (Gómez et al. 2008) or dung beetles (Pérez-Ramos et al. 2007). Seeds were randomly distributed among 60 experimental units (with a size of about 2 m² and a minimum distance of 10 m between them), which spanned a wide, continuous gradient of soil conditions and light availability, from open habitats (up to 90% full sun) to deeper shade under shrubs and trees (down to 10% full sun). Ten acorns of *Q. suber*, ten acorns of *Q. canariensis*, and eight acorns of *Q. pyrenaica* were sown in each unit, protected by wire cages (25×25×25 cm, 1.3-cm mesh size) to exclude seed predators.

Characterisation of abiotic factors

Aboveground (light availability and R:FR) and belowground (soil water and nutrient content, soil compaction and soil pH) factors were quantified in each of the 60 experimental units; a list of the 17 abiotic factors measured is given in Table 1.

Light availability was estimated by means of hemispherical canopy photography. Photographs were taken at the seedling level in the centre of each experimental unit, using a horizontally levelled digital camera (Coolpix 4500, Nikon, Tokyo, Japan) with a fish-eye lens and 180° field of view (FCE8, Nikon). Photographs were taken before dawn, after sunset, or at other times of day when the sun was blocked by clouds, ensuring homogeneous condi-

Table 1. Environmental variability of the 60 experimental microsites. Mean, standard deviation and range of the 17 abiotic factors considered in the study.

Abiotic Factor	Mean \pm SD	Range
Light availability – GSF – (%)	31.7 \pm 23.7	8.0–88.9
Light spectral quality – R:FR –	0.64 \pm 0.34	0.09–1.30
Soil volumetric water content – VWC – (%)		
Minimum	9.3 \pm 2.8	5.0–17.5
Maximum	56.3 \pm 22.5	27.0–90.7
Mean	38.3 \pm 14.0	20.0–79.0
Soil compaction (MPa)		
Maximum	4.63 \pm 1.33	2.10–8.19
Superficial	1.89 \pm 0.62	0.96–3.36
Soil depth (cm)	35.68 \pm 9.16	13.50–49.00
Soil pH	6.22 \pm 0.58	5.39–8.30
Soil clay (%)	36.6 \pm 10.8	13.7–62.6
Soil organic matter – OM – (%)	10.5 \pm 3.7	4.8–20.6
Soil nutrients		
Nitrogen (%)	0.33 \pm 0.12	0.12–0.75
Ammonium (mg kg ⁻¹)	30.7 \pm 29.1	6.8–160.9
Phosphorus (mg kg ⁻¹)	1.9 \pm 1.8	0.2–8.9
Calcium (mg kg ⁻¹)	2903 \pm 1749	477–7925
Potassium (mg kg ⁻¹)	191 \pm 69	89–419
Magnesium (mg kg ⁻¹)	261 \pm 100	69–530

tions of illumination at the understorey and a correct contrast between canopy and sky. We used Hemiview Canopy Analysis software (Delta-T Devices Ltd. 1999, v. 2.1) to analyse the images and calculate the Global Site Factor (GSF), which represents the fraction of total radiation above the canopy that penetrates below the canopy (Anderson 1964). Spectral quality of light (R:FR) was measured at each experimental unit using an SKR 110 sensor (Skye Instruments Llandrindod Wells, UK). Measurements of R:FR were taken around midday (11.00–13.00) on a sunny day to avoid errors derived from variations in sun height and cloud cover.

Soil volumetric water content (VWC) was measured using a time-domain reflectometer (TDR, Campbell Scientific Inc., Logan, UT, USA) with 12-cm depth rods. Measurements were taken at each experimental unit (four readings per unit) every 2 months (from January until September) in order to characterise soil moisture during wet–dry periods. For each experimental unit, we calculated minimum, maximum and mean VWC values.

Soil compaction was estimated using a penetrometer (Penetrologger, Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands), which provides a value of resistance to soil penetration at every cm in depth. Two measurements were taken in early spring (March 2005) per experimental unit in order to characterise the soil profile to 60-cm depth. From these profiles, we derived three variables that can affect rooting penetration and, consequently, seedling growth: maximum soil resistance in the profile (maximum soil compaction, MPa), superficial soil resistance (superficial soil compaction, mean value of the upper 20 cm of soil), and maximum depth at which soil resistance was measured, which provides an estimation of soil depth (cm).

To analyse soil physico-chemical properties, we sampled the upper 20 cm of the soil using an auger (3 cm in diameter) at 3–7 points located inside each experimental unit, and mixed them to produce one composite soil sample per unit. Samples were dried, crushed and sieved, and the <2-mm fraction was analysed for standard chemical and physical properties (Sparks 1996). Nine soil properties were determined: acidity (with a pH meter), total organic matter (OM, by calcination at 540°C), available phosphorus (using the Bray-Kurtz method), total nitrogen (using a Kjeldahl digestion and distillation–titration of the produced ammonium), ammonium-N (extracted with KCl 2N and determined by distillation–titration), available calcium, magnesium and potassium (extracted with ammonium acetate 1N and determined by atomic

emission spectroscopy) and percentages of sand, silt and clay (using the Bouyoucos hydrometer method). Of the three variables related to soil particle size distribution, only percentage clay was used in the statistical analyses as a representative measurement of textural characteristics.

Seedling growth and morphology measurements

From the total number of seedlings emerged in the different experimental units, a sample was randomly selected (one seedling per species for each available unit, to avoid problems of pseudo-replication) in order to span a broad range of soil resources and light availability. The total number of marked and measured seedlings was 56 for *Q. canariensis*, 47 for *Q. pyrenaica* and 56 for *Q. suber* during the first growing season, and had to be reduced to 36 for *Q. canariensis*, 29 for *Q. pyrenaica* and 36 for *Q. suber* during the second growing season due to high seedling mortality. Thus, mean survival rates after 2 years were 28% for *Q. canariensis*, 14% for *Q. pyrenaica* and 11% for *Q. suber* (Gómez-Aparicio et al. 2008). For each seedling, non-destructive measurements in stems and leaves were taken repeatedly over time. Length and diameter at three marked positions (at the base, at 4 cm from the base, and at the top) were measured for stems and branches. Diameters were taken in two perpendicular directions, using a caliper with precision of 0.001 cm. The number of leaves was counted and measurements of length and width were recorded for each leaf. To estimate the RGR of the aboveground part of the seedling (RGR_a), these non-destructive measurements were taken at the beginning (April–May 2004) and end (June 2004) of the growing season, until there was no longer any evidence of seedling growth. Surviving marked seedlings were re-measured 12 months later (June 2005) in order to estimate RGR_a during the second growing season.

To estimate stem biomass and leaf area from the non-destructive measurements, additional seedlings were harvested and measured in a representative sample of the same experimental units. The number of selected seedlings for destructive measurements ranged between 15 and 20 per species at each sampling date (at the beginning and end of the growing season). Once the samples were in the laboratory, all the non-destructive measurements described above were taken, and then each seedling was separated into leaf and stem fractions. Each fraction was oven-dried at 60°C for 48 h and weighed to the nearest 0.0001 g. Linear regressions between volume and dry weight of the stem were calculated per species and sampling

date ($R^2 > 0.86$) using the harvested seedlings. These regressions were used to estimate stem biomass from the non-destructive measurements.

To calculate total leaf area per seedling, all fresh leaves were scanned and their areas measured using an image analysis programme (Image Pro-plus 4.5, Media Cybernetic Inc., USA). An allometric relationship per species and growing season was established between leaf area and individual measurements of leaf length and width ($R^2 > 0.97$), and applied to estimate total leaf area for each seedling based on individual non-destructive leaf measurements taken in the field. In addition, relationships between total leaf area and leaf dry weight in harvested seedlings were used to calculate specific leaf area (SLA) values per species and sampling date. The ratio between the estimated total leaf area and SLA mean values provided good estimates of leaf biomass for the seedlings monitored in the field.

The sum of the leaf and stem biomass provided an estimate of the total aboveground biomass for each seedling monitored in the experiment.

The aboveground relative growth rate (RGR_a) was calculated for each seedling as $RGR = (\ln M_1 - \ln M_0)/t$, in which M_0 and M_1 are the aboveground biomass values at the beginning and end of each growing season, respectively, and t is the time interval between the two dates. For the first year, we calculated the seasonal growth (RGR_a in $g \cdot g^{-1} \cdot d^{-1}$) during 66 days (from April to June 2004, for *Q. canariensis* and *Q. suber* seedlings) or 31 days (from May to June, for *Q. pyrenaica*, due to its later seedling emergence). For the second year, we calculated the annual growth (RGR_a in $g \cdot g^{-1} \cdot y^{-1}$) between June 2004 and June 2005. The RGR_a was separated into its two main components: the leaf area ratio (LAR_a , leaf area per unit aboveground biomass, $cm^2 g^{-1}$) and the NAR_a (net aboveground biomass growth per unit leaf area, $g \cdot cm^2 \cdot d^{-1}$ or $g \cdot cm^2 \cdot y^{-1}$), which were calculated according to formulas given by Hunt (1978). In addition, we calculated other morphological variables such as the specific stem length (SSL, stem length per unit stem biomass, $cm g^{-1}$), or total leaf area (cm^2). Finally, the leaf mass ratio (LMR_a , proportion of aboveground biomass assigned to leaves) was included in the statistical analyses as a representative measurement of biomass allocation.

Data analyses

Analyses of abiotic factors

Variation trends of the 17 abiotic variables were explored using two complementary approaches: first,

a principal components analysis (PCA) on all abiotic factors, and second, Pearson's correlation analyses among the main variables defining each PCA axis. Previously, all variables were standardised and, if necessary, log-transformed to fulfill assumptions of normality and homoscedasticity. Normality was tested using the Shapiro-Wilk test. These analyses were carried out using Statistica (v. 6, StatSoft Inc., 2001).

Models of seedling growth

We fitted linear and non-linear models of seedling growth for each oak species using maximum likelihood techniques. The different variables related to seedling growth were modelled independently as functions of seed mass and each of the 17 abiotic factors considered in the study (Table 1). We tested three alternative functions (linear, exponential and Michaelis-Menten), which cover a wide range of possible forms (see equations in Appendix S1). We first tested models for each factor and function independently, and the best of the three models was compared with a fourth model (the null model) that assumes no effect of any factor. Second, to test for joint limitation (i.e. more than one factor being limiting at once), we fitted bivariate and trivariate models using those factors that had an effect on different variables of seedling growth when evaluated singly. We tried alternative models in which the second and the third abiotic factor were added either additively or multiplicatively. Models including more than three factors were not considered due to their lower empirical support compared with the others. In total, more than 4000 different models were individually run for this study. This modelling approach is suitable to identify strategic axes along which species differentiate (e.g. Pacala et al. 1996; Kobe 1999, 2006; Gómez-Aparicio et al. 2008; Urbietta et al. 2008a).

Parameter estimation and model comparison

Models were parameterised with maximum likelihood (Edwards 1992), using a simulating annealing algorithm. Based on exploratory analyses, we assumed a Poisson distribution for the response variable "number of leaves" and a normal distribution for the rest of the seedling growth variables. The alternative models were compared using the Akaike Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002) – the lower the AIC_c value, the better the model. The absolute magnitude of the differences in AIC_c (ΔAIC) between alternative models provides an

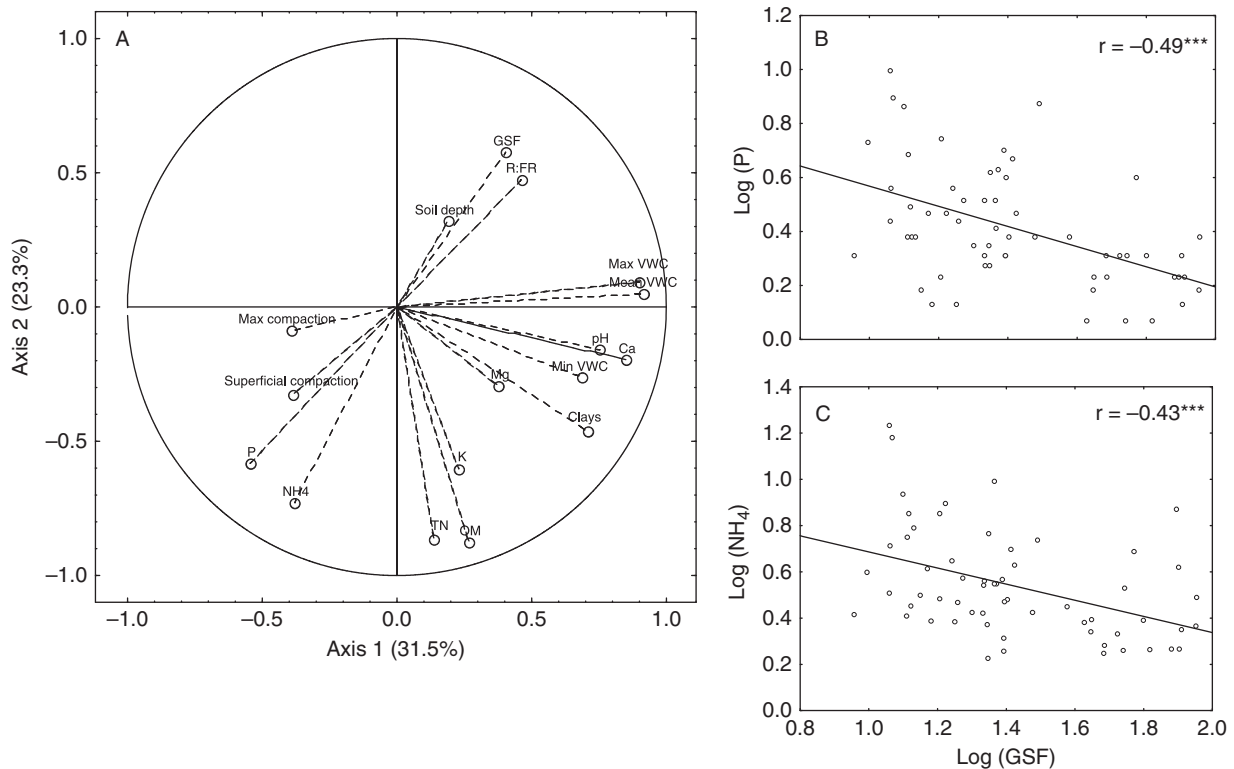


Fig. 1. Projection of the 17 measured abiotic variables on the plane defined by the two main axes resulting from the Principal Components Analysis (a). Relationships between light availability (GSF) and the two main key nutrients, phosphorus (b) and ammonium (c).

objective measurement of the strength of empirical support for the competing models. Models with ΔAIC between 0 and 2 were considered to have equivalent and substantial empirical support (Burnham & Anderson 2002). We used asymptotic two-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). The R^2 of the regression of observed versus predicted was used as a measurement of goodness of fit of each alternative model. All models were implemented using the *likelihood* package version 1.1 for R and software written specifically for this study in R v 2.5.0 (R Development Core Team 2006).

Results

Variation in abiotic factors

The high environmental heterogeneity of environmental conditions and resource availability was reflected in the wide variation shown by the 17 variables measured for the 60 microsites where oak

seedlings grew (Table 1). For example, light availability (GSF) varied between 8% and 89%, mean soil water content ranged from 20% to 79%, superficial soil compaction from 0.96 to 3.36 MPa, soil ammonium from 7 to 161 mg kg⁻¹ and soil phosphorus from 0.2 to 9 mg kg⁻¹.

Under field conditions, abiotic factors were correlated – either positively or negatively – as shown by the PCA results (Fig. 1a). The first axis (31.5% of the total variance) represented a combined gradient of soil moisture and calcium availability, while the second axis (23.3% of variance) was clearly defined by a light availability gradient joined to a decreasing soil nutrient content (mainly ammonium and phosphorus). Therefore, soils in open microsites were poorer in nutrients, especially phosphorus ($r_{\log \text{GSF} - \log \text{P}} = -0.49$; $P < 0.001$; Fig. 1b) and ammonium ($r_{\log \text{GSF} - \log \text{NH}_4} = -0.43$; $P < 0.001$; Fig. 1c), the two key resources being highly correlated ($r_{\log \text{P} - \log \text{NH}_4} = 0.76$; $P < 0.001$). In addition, soils in moister microsites were more clayey ($r = 0.5$; $P < 0.001$), more basic ($r = 0.64$; $P < 0.001$) and richer in calcium ($r = 0.74$; $P < 0.001$).

Factors affecting seedling growth and morphology

In general, there was a wide variation within and between species with regard to seedling growth (Table 2). Light conditions (both light availability and spectral quality) and seed mass were the main factors explaining seedling growth, but their relative importance varied depending on seedling age. The seed mass effect was more evident in the first growing season than in the second, this factor appearing as one of the best predictors in 68% and 35% of the 27 modelled variables (nine per species) for the first and the second year, respectively (Tables 3 and 4). In contrast, factors related to light conditions were better represented within the best models for the second growing season (86% of the modelled variables) than for the first (56%; Tables 3 and 4). Several soil variables, such as compaction, pH, water content, and nutrient content (phosphorus and nitrogen), were also good predictors of certain morphological variables, with a similar relative contribution for the 2 years of seedling life (Tables 3 and 4). However, none of them had an important effect on the integrative variables of seedling growth (total aboveground biomass and RGR_a , Tables 3 and 4).

First-year seedlings

The average aboveground total biomass was much lower for *Q. pyrenaica* than for *Q. suber* and *Q. canariensis* (support intervals for the intercept – *a* parameter – in the null models overlapped for these two latter species, see Table 2 and Appendix S2). Seed mass was the best predictor of aboveground biomass, but the functional relationship between the two variables differed for the three species (linear for *Q. canariensis*, exponential for *Q. pyrenaica*, and Michaelis-Menten for *Q. suber*; Fig. 2a).

The RGR_a was similar for the three species (Table 2), but inter-specific differences appeared along gradients of seed mass and R:FR. Along a gradient of seed mass, *Q. suber* was exceeded by the two deciduous species only when seedlings arose from bigger seeds (Fig. 2b). Along a gradient of light quality, *Q. pyrenaica* and *Q. suber* showed a higher RGR_a than *Q. canariensis* for low values of R:FR, whereas the opposite occurred for high values of R:FR (Fig. 2c). For the first two species, RGR_a decreased linearly with R:FR, but no effect was found for *Q. canariensis* (Fig. 2c).

For the three oak species, total aboveground biomass was explained by the variation in RGR_a (Table 4). In all cases, RGR_a depended strongly on NAR_a , whereas the influence of LAR_a was evident

only in the case of *Q. suber* (Fig. 3). As a result, the total aboveground biomass of the seedlings was mainly determined by NAR_a (Table 5).

Light variables were the best predictors for biomass allocation of the three species. Leaf mass ratio (LMR_a) increased with GSF for *Q. suber* (linearly) and *Q. canariensis* (Michaelis-Menten function). In the case of *Q. pyrenaica*, LMR_a increased linearly with R:FR and decreased with soil pH (Table 3).

The three species showed marked differences in average stem height – *Q. suber* seedlings being the tallest, followed by *Q. canariensis* and finally by *Q. pyrenaica* (the support intervals did not overlap for the *a* parameter in the null models, Appendix S2). The three species had a high plasticity of stem elongation, with seed mass and light conditions (GSF or R:FR) again being the main predictor variables (Table 3). Stem height increased with seed mass (linearly for *Q. canariensis* and exponentially for *Q. suber*) and decreased with GSF or R:FR, depending on the oak species (Table 3). There was also evidence of a negative effect of superficial soil compaction on stem height in the case of *Q. canariensis* (Table 3).

Seed mass and light conditions were also the main factors influencing the variation of other morphological variables (Table 3). Larger seeds produced seedlings with a higher total leaf area, a higher number of leaves and lower values of LAR_a and SSL (Table 3). Regarding light conditions, higher values of GSF and/or R:FR induced oak seedlings with a higher number of leaves and lower values of LAR_a and SSL (Table 3). The inclusion of several soil variables into multivariate models (bivariate or trivariate) provided the strongest empirical support for certain morphological variables. For example, a higher soil compaction reduced linearly the total leaf area (for *Q. canariensis*) and exponentially the number of leaves (for *Q. canariensis* and *Q. suber*); in the case of *Q. canariensis*, the number of leaves increased exponentially with soil depth. Soils with a higher nitrogen content (total or ammonium) favoured the development of seedlings with higher values of SSL (for *Q. canariensis*) and LAR_a (for *Q. suber*). Finally, maximum soil moisture was correlated negatively with other morphological and physiological variables, such as SSL or NAR_a , in the case of *Q. canariensis* (Table 3).

Second-year seedlings

After two growing seasons, the average aboveground biomass remained much lower for *Q.*

Table 2. Mean \pm SD and range (in brackets) of the nine growth variables measured in the study, during the first and second growing seasons. RGR_a, Relative growth rate; NAR_a, Net assimilation rate; LAR_a, Leaf area ratio; LMR_a, Leaf mass ratio; SSL_a, Specific stem length.

Growth variable	First year			Second year		
	<i>Q. canariensis</i>	<i>Q. pyrenaica</i>	<i>Q. suber</i>	<i>Q. canariensis</i>	<i>Q. pyrenaica</i>	<i>Q. suber</i>
Total aboveground biomass (g)	0.44 \pm 0.17 [0.15-0.89]	0.30 \pm 0.08 [0.12-0.53]	0.51 \pm 0.22 [0.05-1.1]	0.67 \pm 0.36 [0.16-2.1]	0.38 \pm 0.18 [0.05-0.62]	0.55 \pm 0.36 [0.15-1.86]
RGR _a (1st year: g · g ⁻¹ · d ⁻¹ ; 2nd year: g · g ⁻¹ · y ⁻¹)	0.011 \pm 0.006 [0.001-0.028]	0.012 \pm 0.012 [-0.004 to 0.045]	0.013 \pm 0.007 [-0.009 to 0.033]	0.31 \pm 0.33 [-0.59 to 0.96]	0.08 \pm 0.42 [-0.9 to 0.8]	-0.06 \pm 0.51 [-0.94 to 1.06]
NAR _a (1st year: g · cm ² · d ⁻¹ ; 2nd year: g · cm ² · y ⁻¹)	0.12 $\times 10^{-3}$ \pm 0.09 $\times 10^{-3}$ [0.01 $\times 10^{-3}$ - 0.44 $\times 10^{-3}$]	0.12 $\times 10^{-3}$ \pm 0.13 $\times 10^{-3}$ [-0.05 $\times 10^{-3}$ to 0.61 $\times 10^{-3}$]	0.13 $\times 10^{-3}$ \pm 0.07 $\times 10^{-3}$ [-0.09 $\times 10^{-3}$ to 0.32 $\times 10^{-3}$]	0.004 \pm 0.004 [-0.009 to 0.016]	0.002 \pm 0.004 [-0.008 to 0.01]	-0.0006 \pm 0.005 [-0.009 to 0.011]
LAR _a (cm ² g ⁻¹)	95.47 \pm 22.11 [57.24-157.84]	108.26 \pm 14.08 [55.4-139.17]	109.78 \pm 15.45 [68.06-140.58]	85.19 \pm 25.40 [0-147.28]	60.17 \pm 29.07 [0-103.58]	95.52 \pm 22.79 [59.21-159.79]
LMR _a	0.53 \pm 0.13 [0.23-0.77]	0.67 \pm 0.12 [0.28-0.86]	0.64 \pm 0.11 [0.44-0.88]	0.51 \pm 0.16 [0-0.78]	0.44 \pm 0.23 [0-0.87]	0.60 \pm 0.18 [0.29-0.89]
Total leaf area (cm ²)	40.64 \pm 13.71 [17.84-79.84]	33.07 \pm 9.89 [9.53-58.81]	56.03 \pm 21.33 [3.6-105.35]	57.39 \pm 29.74 [0-121.94]	21.34 \pm 11.69 [0-38.06]	51.77 \pm 34.26 [13.14-173.85]
Number of leaves	6.0 \pm 2.7 [3-15]	5.1 \pm 1.5 [2-9]	12.6 \pm 5.9 [1-35]	8.4 \pm 6.5 [0-40]	3.7 \pm 2.0 [0-6]	14.3 \pm 11.9 [3-57]
Stem height (cm)	11.16 \pm 3.50 [3.75-21.97]	8.31 \pm 3.49 [2.62-17.31]	14.73 \pm 6.92 [1.03-41.06]	14.48 \pm 5.14 [7.34-31.09]	14.43 \pm 8.01 [4.57-36.20]	17.0 \pm 8.54 [5.52-38.7]
SSL (cm g ⁻¹)	60.62 \pm 21.23 [31.34-136.15]	88.24 \pm 23.63 [39.78-136.31]	93.08 \pm 23.68 [40.82-137.99]	59.32 \pm 20.55 [25.41-125.32]	84.71 \pm 35.33 [22.78-178.83]	101.53 \pm 52.10 [28.41-307.84]

Table 3. Summary of the models analysing the response of first-year seedling growth to seed mass and abiotic factors. Differences in AIC_c (ΔAIC) between alternative models represent an objective measure of the strength of empirical support for each model. Only the models with the best empirical support (lowest AIC) are shown. Additive interactions between two or three factors are noted as (+) and multiplicative as (*). The sign of the relationship (positive or negative) between response variables and the selected predictors is also indicated. Functional Forms (FF): LIN, Linear model; EXP, Exponential model; MM, Michaelis-Menten model; NULL, Null model.

Species	Growth variable	Predictors	FF	Relation	R^2	ΔAIC
<i>Q. canariensis</i>	Total aboveground biomass	Seed mass	LIN	+	0.357	0.000
			NULL			22.497
	RGR_a	Seed mass	LIN	+	0.115	0.000
			NULL			4.599
	NAR_a	Seed mass+maximum VWC	MM	+, +	0.234	0.000
			NULL			10.362
	LAR_a	Seed mass+R:FR	EXP	-, -	0.249	0.000
			NULL			11.471
	LMF_a	GSF	MM	+	0.273	0.000
			LIN			1.361
			NULL			15.619
	Total leaf area	Seed mass+superficial compaction	LIN	+, -	0.356	0.000
			NULL			20.124
	Number of leaves	Seed mass+superficial compaction	EXP	+, -	0.283	0.000
			EXP			0.251
NULL			11.663			
Stem height	Seed mass+superficial compaction+GSF	LIN	+, -, -	0.306	0.000	
		NULL			13.465	
		LIN			0.353	
SSL	Seed mass+NT+MAXIMUMVW C	LIN	-, +, -	0.353	0.000	
		NULL			17.43	
<i>Q. pyrenaica</i>	Total aboveground biomass	Seed mass	EXP	+	0.184	0.000
			NULL			7.275
	RGR_a	Seed mass+R:FR	LIN	+, -	0.305	0.000
			NULL			12.386
	NAR_a	Seed mass+R:FR	EXP	+, -	0.379	0.000
			NULL			17.687
	LAR_a	pH	LIN	-	0.096	0.000
			NULL			2.473
	LMF_a	pH+R:FR	LIN	-, +	0.525	0.000
			NULL			30.259
			LIN			0.251
	Total leaf area	Seed mass+pH	LIN	+, -	0.251	0.000
			NULL			8.92
	Number of leaves	GSF	EXP	-	0.417	0.000
			NULL			23.044
EXP			0.244			
Stem height	GSF	EXP	-	0.244	0.000	
		NULL			10.83	
<i>Q. suber</i>	Total aboveground biomass	Seed mass	MM	+	0.150	0.000
			NULL			6.873
	RGR_a	R:FR	LIN	-	0.168	0.000
			NULL			7.484
	NAR_a	R:FR	LIN	-	0.161	0.000
			NULL			7.076
	LAR_a	Seed mass+R:FR+NH4	LIN	-, -, +	0.439	0.000
			NULL			25.445
	LMF_a	GSF	LIN	+	0.473	0.000
			NULL			33.657
	Total leaf area	Seed mass	MM	+	0.112	0.000
			NULL			4.389
	Number of leaves	GSF+superficial compaction	EXP	+, -	0.153	0.000
			NULL			15.249
	Stem height	Seed mass+R:FR	EXP	+, -	0.380	0.000
NULL			22.182			

pyrenaica than for the other two species (support intervals for the intercept – a parameter – in the null models overlapped for these two species, Table 2 and Appendix S3). None of the measured factors were selected as predictors of total aboveground

biomass and RGR_a for the two deciduous species (Table 5). In contrast, *Q. suber* seedlings were highly affected by seed mass and light conditions (Table 5). Consequently, *Q. suber* outgrew its co-dominant oak species (*Q. canariensis*) at high values of seed

Table 4. Summary of the models analysing the relations among growth parameters for the three oak species during the two growing seasons. The R^2 values and the best functional forms (LIN, Linear; EXP, Exponential; MM, Michaelis-Menten) are showed for all the possible combinations. The strength of empirical support (based on the absolute magnitude of the differences in AIC_c with the null model) is indicated as follows: $*2 \leq \Delta AIC \leq 7$; $**7 \leq \Delta AIC \leq 14$; $***14 \leq \Delta AIC$. The type of relationship between growth parameters was always positive.

Species	Growth parameters	First growing season					Second growing season				
		Total Ab. Biomass	RGR _a	NAR _a	LAR _a	LMR _a	Total Ab. Biomass	RGR _a	NAR _a	LAR _a	LMR _a
<i>Q. canariensis</i>	Total Ab. Biomass	–	0.12* [LIN]	0.15** [LIN]	0.25** [LIN]	0	–	0.47*** [LIN]	0.60*** [LIN]	0	0.07
	RGR _a	–	–	0.87*** [LIN]	0	0	–	0.76*** [LIN]	0.23* [LIN]	0.38** [LIN]	
	NAR _a	–	–	–	0.06	0	–	–	0.02	0.1	
	LAR _a	–	–	–	–	0.12* [MM]	–	–	–	–	0.48*** [MM]
						0.08	–	0.60** [LIN]	0.59** [LIN]	0.08	0.06
<i>Q. pyrenaica</i>	Total Ab. Biomass	–	0.11* [EXP;LIN]	0.12* [EXP;LIN]	0	0.08	–	0.60** [LIN]	0.59** [LIN]	0.08	0.06
	RGR _a	–	–	0.74*** [EXP]	0	0.07	–	0.98*** [LIN]	–	0	0.02
	NAR _a	–	–	–	0	0.08	–	–	–	0	0.02
	LAR _a	–	–	–	–	0.42*** [MM]	–	–	–	–	0.94*** [MM]
<i>Q. suber</i>	Total Ab. Biomass	–	0.19** [LIN]	0.26** [LIN]	0.02	0.01	–	0.57*** [LIN]	0.60*** [LIN]	0.01	0.13
	RGR _a	–	–	0.89*** [LIN]	0.16** [LIN]	0	–	0.99*** [LIN]	–	0.15	0.53*** [LIN]
	NAR _a	–	–	–	0.05	0.02	–	–	–	0.12	0.33** [LIN]
	LAR _a	–	–	–	–	0.06	–	–	–	–	0.57*** [MM]

mass and GSF, whereas *Q. pyrenaica* was exceeded by these two species across most seed ranges and light conditions (Fig. 4a and b).

The mean annual RGR_a was highest for *Q. canariensis*, followed by *Q. pyrenaica* and then *Q. suber* (Table 2); however, the support intervals for the intercept (a parameter) in the null models overlapped for the three species, indicating the lack of strong support for inter-specific differences in the mean RGR_a (Appendix S3). In contrast to the first year, *Q. suber* seedlings had a higher RGR_a than the other two species in the most open microsites (i.e. high values of GSF and R:FR), and the opposite was true for the most shaded microsites (i.e. low values of GSF and R:FR), where RGR_a even reached negative values (Fig. 4c). This was probably a consequence of leaf shedding in those *Q. suber* seedlings growing in the most shaded microsites (data not shown).

Similar to the first growing season, total above-ground biomass was largely explained by the variation in RGR_a (Table 4) for the three oak species. RGR_a was again strongly correlated with the physiological component (Table 4 and Fig. 3). In this case, the morphological variables had greater

influence on RGR_a than in the first year, LAR_a and LMR_a appearing as marked predictors of RGR_a for *Q. canariensis* and *Q. suber* (Table 4 and Fig. 3).

Regarding biomass allocation, light conditions (GSF and R:FR) were again the best predictors of LMR_a for the three species (Table 5). In addition, there was evidence of a negative relationship with soil phosphorus in the case of *Q. canariensis* (Table 5).

After two growing seasons, *Q. suber* seedlings continued to be taller than the other two species (Table 2); however, the support intervals for the intercept (a parameter) in the null models overlapped for the three species (Appendix S3). Stem height was affected by the same predictor variables as during the first year (mainly seed mass and light conditions), although this time superficial soil compaction exerted a negative effect on *Q. pyrenaica* but not on *Q. canariensis* (Table 5).

Finally, the main factors explaining the rest of the morphological variables for second-year seedlings were seed mass, light conditions and soil compaction (especially in the case of *Q. canariensis*), which exerted a similar effect to that in the first year (Table 5). The relationships between growth para-

Table 5. Summary of the models analysing the response of second-year seedling growth to seed mass and abiotic factors. Only the models with the best empirical support (lowest AIC) are shown. Models are noted and evaluated as in Table 3.

Species	Growth variable	Predictors	FF	Relation	R ²	ΔAIC	
<i>Q. canariensis</i>	Total aboveground biomass		NULL				
		RGR _a	NULL				
		NAR _a	NULL				
		LAR _a	NULL				
		LMF _a	GSF	LIN	+	0.129	0.000
			P	LIN	–	0.119	0.434
			R:FR	LIN	+	0.116	0.561
				NULL			2.598
	Total leaf area	Superficial compaction	LIN	–	0.156	0.000	
			NULL				3.725
	Number of leaves	Superficial compaction+GSF	EXP	+, –	0.552	0.000	
			NULL				62.446
	Stem height	Seed mass+GSF	EXP	+, –	0.468	0.000	
			NULL				17.798
SSL	Max. Compaction+minimum VWC	EXP	+, +	0.340	0.000		
		NULL				10.020	
<i>Q. pyrenaica</i>	Total aboveground biomass		NULL				
		RGR _a	NULL				
		NAR _a	NULL				
		LAR _a	P	EXP	–	0.194	0.000
			GSF	LIN	+	0.173	0.767
		NH4	EXP	–	0.166	1.019	
		R:FR	EXP	+	0.153	1.442	
			NULL				3.769
	LMF _a	GSF	MM	+	0.398	0.000	
			NULL				12.211
	Total leaf area		NULL				
	Number of leaves		NULL				
	Stem height	R:FR+superficial compaction	EXP	–, –	0.740	0.000	
			NULL				33.824
SSL		NULL					
<i>Q. suber</i>	Total aboveground biomass	Seed mass+GSF	LIN	+, +	0.650	0.000	
			NULL				26.357
	RGR _a	GSF	LIN	+	0.405	0.000	
		R:FR	LIN	+	0.386	0.711	
			NULL				9.012
	NAR _a		NULL				
	LAR _a		NULL				
	LMF _a	GSF	MM	+	0.497	0.000	
			NULL				18.154
	Total leaf area	Seed mass+GSF	LIN	+, +	0.632	0.000	
			NULL				24.826
	Number of leaves	GSF	EXP	+	0.702	0.000	
			NULL				154.578
	Stem height	Seed mass+R:FR	EXP	+, –	0.630	0.000	
		NULL				24.679	
SSL	Seed mass+R:FR	LIN	–, –	0.544	0.000		
		NULL				18.390	

meters and the main factors considered in this study (seed mass, light conditions and soil variables) are summarised in Fig. 5 for the two growing seasons.

Discussion

Factors affecting seedling growth and morphology

Seedling growth and morphology may be affected by a large number of resources and environmental conditions; however, results from our modelling approach showed that the integrative

variables of seedling growth – RGR_a and total aboveground biomass – were affected by two main factors: light conditions and seed mass. Interestingly, the relative contribution of these two factors depended strongly on seedling age. Light affected seedling performance of 2-year-old seedlings, whereas during early growth, younger seedlings were more dependent on seed mass. Several soil factors, such as compaction, pH, water content and nutrient content (phosphorus and nitrogen), were also good predictors of certain morphological variables, but none of them had an important effect on the integrative variables of seedling growth (Fig. 5).

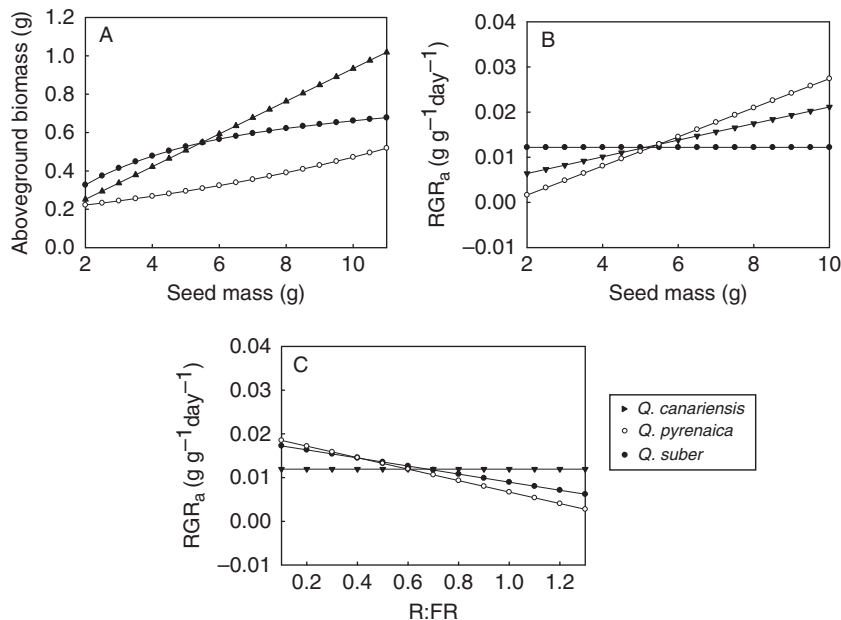


Fig. 2. Predicted variation in seedling aboveground biomass and relative growth rate (RGR_a) as a function of the best predictors (Table 3) for the first growing season. (a) Seedling aboveground biomass along the seed mass range; (b) RGR_a as a function of seed mass for intermediate values of red:far red ratio (R:FR = 0.65); (c) RGR_a along the gradient of R:FR for an average seed mass of 5 g. Straight lines denote no effect of the considered factor on first-year RGR_a , but are included for comparative purposes.

Light conditions

Light was the best environmental predictor of many variables related to seedling morphology for the three studied oak species, especially during the second year. However, its influence on seedling growth varied according to the species and the growing season. Seedling growth and morphology depended not only on light availability (GSF), but also on its spectral quality (R:FR), which highlights the importance of this factor as a mediator of seedling performance in tree species (Lee et al. 1997; Ammer 2003; Tegelberg et al. 2004). In shade conditions (i.e. in microsites with lower values of R:FR and GSF), seedlings of the three studied species were taller, sometimes at the expense of increased thinness of their stems (higher SSL). This pattern is typical of plants growing in microsites where the R:FR is reduced, that increase stem height as a mechanism of shade avoidance (Ammer 2003; Tegelberg et al. 2004). The enhanced stem height with shade could be one of the main contributors to the negative linear relationship found between RGR_a and R:FR for *Q. suber* and *Q. pyrenaica* during the first growing season (Fig. 2c). The non-sensitivity of *Q. canariensis* to R:FR, which can be considered a typical response of shade-tolerant species (Kwesiga & Grace 1986; Kitajima 1994), reveals its higher degree of tolerance to low light environ-

ments in comparison with the other two studied species.

During the second year, the three oak species retained the same response of higher stem elongation in shaded microsites, but seedling growth was independent of light conditions for the two deciduous species. In contrast, in the evergreen *Q. suber* seedlings, biomass increased with light (Fig. 4b), and RGR decreased to negative values in deep shade microsites (Fig. 4c). The net carbon balance for this species probably became negative under limiting light conditions, when seed reserves were depleted and seedlings were more dependent on external resources. This hypothesis is supported by the marked leaf shedding (net carbon loss) in many *Q. suber* seedlings in these low light microsites during the second year. These results are in accordance with Cardillo & Bernal (2006), who classified *Q. suber* as a species of intermediate tolerance to shade. The observed pattern of enhanced seedling growth with increasing light is consistent with previous studies (Pacala et al. 1994; Sack & Grubb 2002; Quero et al. 2006; Sánchez-Gómez et al. 2006), but contrasts with others that have documented maximum values of RGR in intermediate (Veenendaal et al. 1996; Poorter 1999; Puerta-Piñero et al. 2007; Quero et al. 2008) or even low light conditions (Holmgren 2000). The absence of a negative response to light scarcity

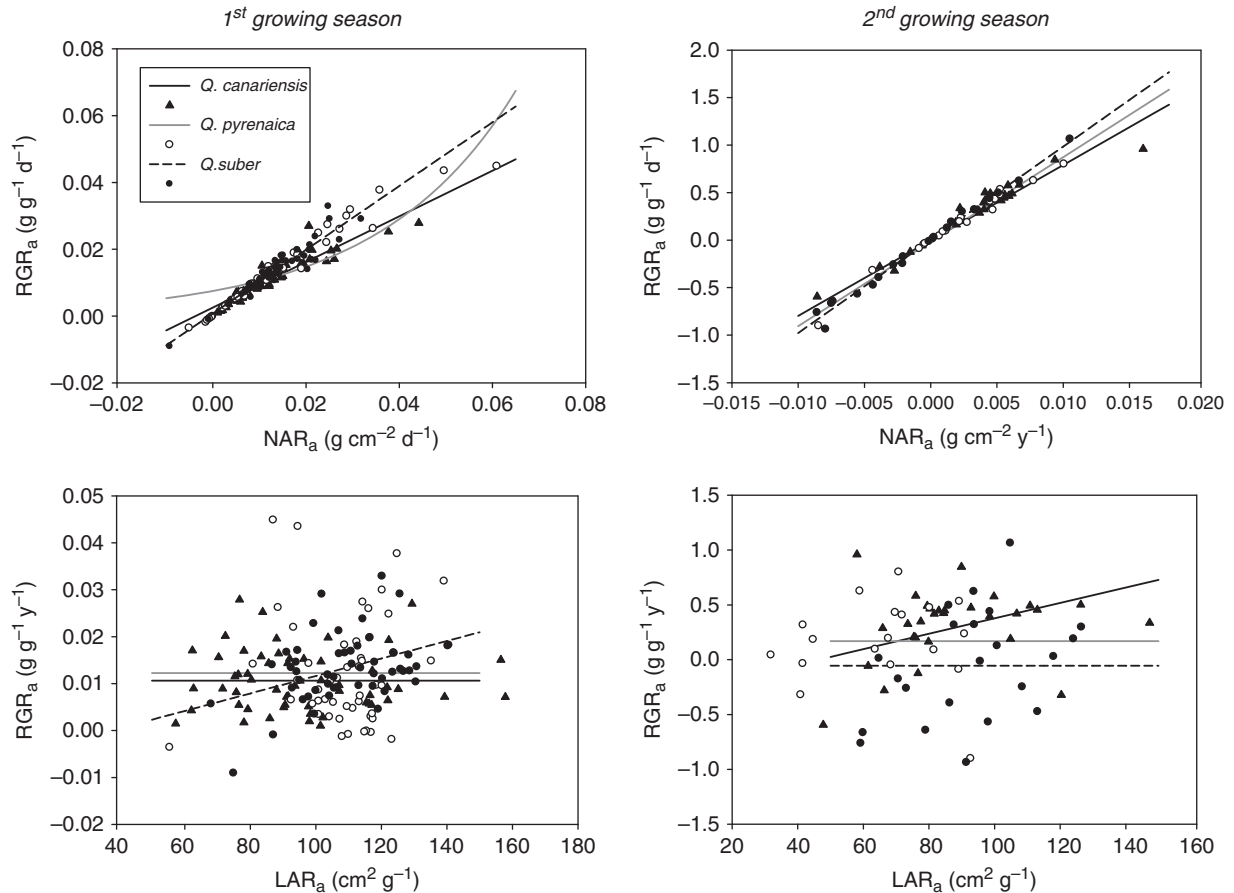


Fig. 3. Relationships between the relative growth rate (RGR_a) and its two main components (NAR_a and LAR_a) for the two growing seasons, following the models in Table 4.

for the two deciduous species could be a consequence, at least partially, of their high tolerance to shade during early life stages (Gómez-Aparicio et al. 2006; Quero et al. 2006). In addition, the proportion of deep shade microsites (<10% full sunlight) was relatively low at the study site, which is typical of Mediterranean forests (Gómez et al. 2004; Quilchano et al. 2008). Therefore, the type of relationship between seedling growth and light is strongly variable, and appears to be affected by several factors, including the study system, the target species and the explored light gradient.

The three studied species also showed a high capacity of response to light conditions across the modification of certain structural plant and leaf traits. On one hand, oak seedlings usually had higher values of LAR_a in low light environments, probably for maximising the light interception (Poorter 1999; Castro-Díez et al. 2005; Cardillo & Bernal 2006). On the other hand, in the most open microsites, seedlings developed a higher number of leaves, usually of lower SLA. As a result of these

opposing tendencies, the total leaf area remained constant over the range of observed light values. A similar total leaf surface of higher biomass in open microsites, together with a lower investment in stem height, were probably the main causes explaining the positive relationship between LMR_a and light that was detected for the three species during the two growing seasons.

Soil factors

Surprisingly, none of the soil factors considered in this study (nutrient and water availability, texture or compaction) exerted an important effect on the integrative variables of oak seedling growth. Nevertheless, several morphological traits of the seedling were affected by soil factors.

Superficial compaction exponentially reduced the number of leaves for two of the studied species, and linearly the total leaf area in the case of *Q. canariensis*. In addition, stem height was negatively correlated with soil compaction for the two deciduous species. In general, higher soil compaction

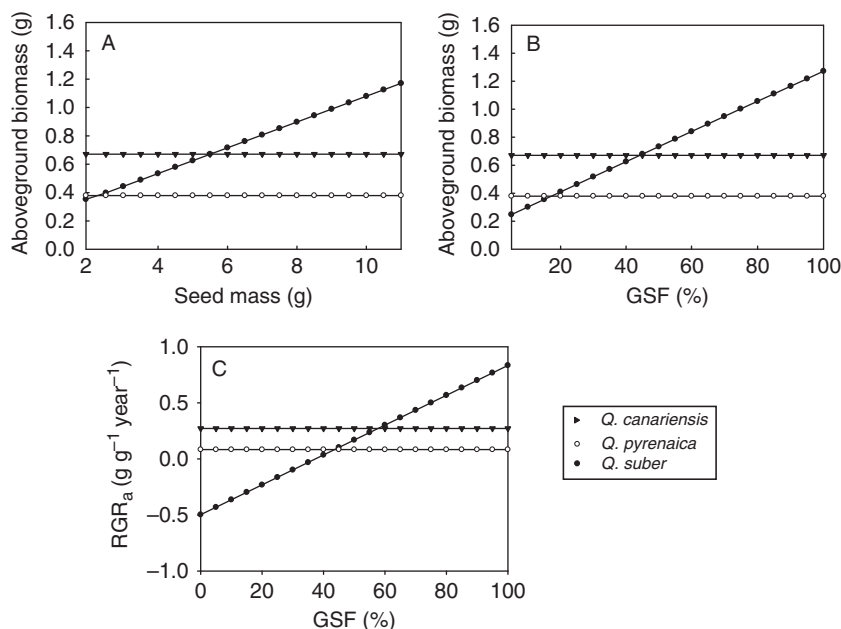


Fig. 4. Predicted variation in seedling aboveground biomass and relative growth rate (RGR_a) as a function of the best predictors (Table 4) for the second growing season. (a) Seedling aboveground biomass along the seed mass range for intermediate values of global site factor (GSF = 40%); (b) seedling aboveground biomass as a function of GSF for an average seed mass of 5 g; (c) RGR_a along the gradient of GSF. Straight lines denote no effect of the considered factor on second-year RGR_a, but are included for comparative purposes.

means stronger resistance of the substrate to penetration by the fine radicle of the growing seedling (Kozłowski 1999; Basset et al. 2005). A compacted soil could limit root growth of the seedling (Verdú & García-Fayos 1996), reduce its capacity for nutrient assimilation (Lloret et al. 1999) and, therefore, negatively affect some of its aboveground growth variables (e.g. Basset et al. 2005; Alameda & Villar 2009). The effect of soil compaction was more marked for *Q. canariensis* than for the other two species, probably as a consequence of the smaller root system developed by this species during the first months of its life (demonstrated in a parallel study under laboratory conditions; Pérez-Ramos & Marañón 2009).

Soil moisture also affected other morphological and physiological variables of the seedling in the case of *Q. canariensis*. However, excess water during the rainy season – and not water shortage in summer – was selected as a negative and better predictor of certain variables related to seedling growth. This could be due to the fact that high soil water levels lengthened time to emergence of seedlings (Urbieta et al. 2008a), which in turn reduced the time available for growth before the end of the favourable season. The apparent lack of response to summer water deficit was probably a direct consequence of the uniformly low values of soil VWC recorded

during the dry season along the whole explored light gradient (Table 1).

Models that incorporated several soil nutrients, such as nitrogen or phosphorus, had higher empirical support for some morphological variables than did models based only on seed mass or light. For example, oak seedlings growing in soils with a higher nitrogen content showed higher values of SSL (for *Q. canariensis*) or LAR_a (in the case of *Q. suber*) during the first growing season. The importance of soil nutrients on tree seedling growth has been amply reported in other studies that document positive effects of nursery fertilisation (e.g. Van den Driessche 1982; Villar-Salvador et al. 2004). However, the three studied oak species exhibited, under field conditions, a very limited response to nutrient availability in comparison with seed mass or light. In general, this low leaf-level responsiveness to nutrients in Mediterranean woody plants is considered part of a conservative resource-use strategy (Valladares et al. 2000), including a reduced demand for resources (Sack et al. 2003). In addition, the counteracting gradients of light and soil nutrients (Fig. 1) – mainly derived from the relationship between canopy density and litter accumulation (García et al. 2006) – may counterbalance oak seedling performance in microsites with high light availability but nutrient-poor soils, in comparison with shaded mi-

crossites that are richer in nutrients but limited in light.

Seed mass

The amount of reserves contained in the seed was the main factor affecting seedling growth for the three oak species during the first year of life. During the second year, seedling aboveground biomass was still highly dependent on the initial seed mass in the case of *Q. suber*, but this factor did not affect its RGR, or exert any effect at all in the other two species. The differential importance of seed size with oak seedling age confirms the strong dependence on seed reserves during early growth (Long & Jones 1996; Quero et al. 2007, 2008). Other studies have also shown that the strength of correlation between growth variables and seed mass declines over time, and tends to disappear after several years (Castro 1999; Poorter & Rose 2005; Quero et al. 2007).

Seed mass also affected other morphological variables. In general, the larger-seeded seedlings had a larger total leaf area, a higher number of leaves and a lower LAR_a . Regarding variables related to the stem, the bigger the seed the taller the resulting seedling, and, sometimes, the lower its SSL. The negative relationships with LAR_a and SSL could be interpreted as mechanisms for maximising light interception, and thus seedling growth; the smaller-seeded seedlings would achieve greater leaf photosynthetic surface and greater stem height at the expense of having thinner leaves and stems.

Inter-specific differences in seedling growth along resource gradients

The specialisation along resource availability gradients during seedling establishment, as part of the regeneration niche, is one of the frequently hypothesised mechanisms for species coexistence in plant communities (Grubb 1977; Silvertown 2004). Specifically, how resources influence seedling growth could affect forest dynamics and species distribution across resource gradients (Kobe 2006). The results of this study provide some evidence of regeneration niche partitioning between oak species along the light gradient. However, these inter-specific differences were variable for the first 2 years of seedling life. Although *Q. canariensis* had a higher RGR than the other two species in the most open microsites (i.e. high values of R:FR and GSF) during the first growing season (Fig. 2c), the following year *Q. suber* outgrew the two deciduous species in high light environments (Fig. 4b and c). When light availability was scarce, many *Q. suber* seedlings lost

a large amount of their leaves, reduced their growth rates (even reaching negatives values of RGR_a , probably as a consequence of a reduced carbon gain) and were thus exceeded by the other two species.

The differential species responses in second-year seedling growth along the light gradient are consistent with the observed seedling survival pattern, where the two deciduous species also exceeded the evergreen *Q. suber* in low light environments (Gómez-Aparicio et al. 2008). These results support the low light survival versus high light growth trade-off previously reported in other forest systems (Kobe et al. 1995; Pacala et al. 1996; Sánchez-Gómez et al. 2006). This pattern of seedling performance can be related to species habitat and distribution patterns in the study area, and supports the initial hypothesis proposing a higher shade tolerance for *Q. canariensis* seedlings in comparison with the co-dominant *Q. suber*. On the other hand, *Q. pyrenaica* was outperformed by the two dominant species along almost the whole light gradient. At the study site, this species appears as an accompanying species, frequently restricted to scarce populations at higher altitudes.

Seed mass also played a crucial role in inter-specific differences, affecting the competitive hierarchies between oak species (Figs. 2b and 4a). Inter-specific differences in seedling growth, arising from seed size variability and microsite heterogeneity, could be of paramount importance in oak species niche segregation, driving stand dynamics and composition along environmental gradients.

Concluding remarks

This study represents an example of an innovative combination of field experiments and statistical modelling, used here to identify the main factors affecting seedling growth and morphology in three oak species coexisting in a Mediterranean forest, and how species-specific responses vary along wide gradients of resources and environmental factors. Seedling growth – RGR_a and total aboveground biomass – was affected by two main factors: light conditions and seed mass. The relative contribution of each factor depended highly on seedling age, supporting previous studies defining ontogenetic changes between seedlings and saplings (Cavender-Bares & Bazzaz 2000) or among juveniles of different ages (Espelta et al. 1995).

For the two growing seasons, NAR_a was the biggest factor contributing to RGR variation in the

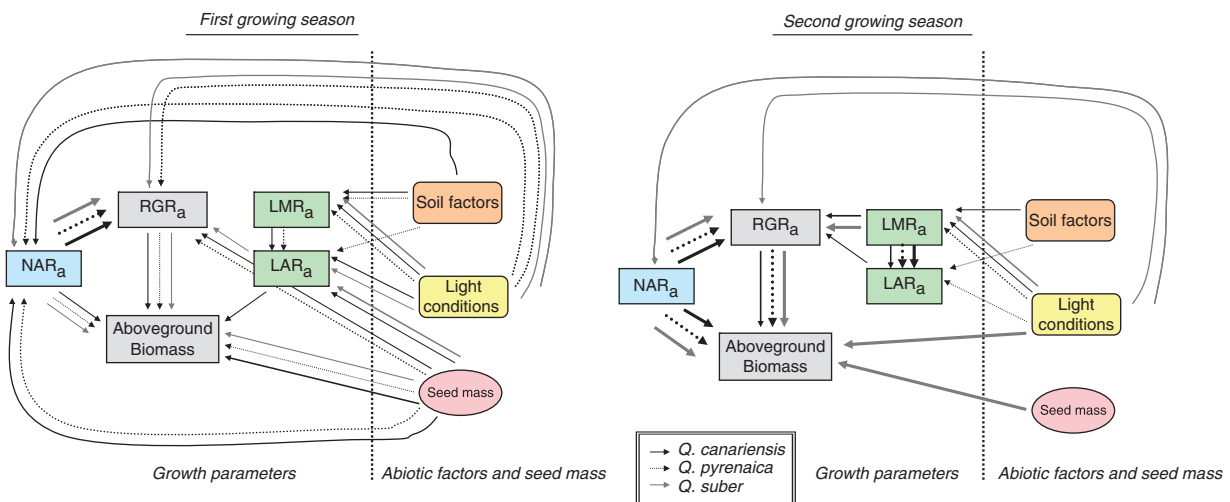


Fig. 5. Summary diagram on relationships among growth parameters and the main factors (seed mass, light conditions and soil variables) affecting them during the two growing seasons. The thickness of the arrows indicates the strength of the empirical support for the relationships between pairs of variables (see Tables 3–5).

three oak species (Figs. 3 and 5). These results are consistent with previous studies (Popma & Bongers 1988; Poorter 2001), but contrast with others identifying the morphological component (LAR) as the primary factor explaining the high variability in RGR (e.g. Reich et al. 1992; Huante et al. 1995; Cornelissen et al. 1998; Antúnez et al. 2001).

The results of this study provide some evidence of regeneration niche partitioning between oak species along light gradients. Differences between leaf longevity functional groups depended strongly on the light environment explored; deciduous species outgrowing the evergreen species only at low light microsites. The information provided by our modelling approach is another necessary step towards the development of a mechanistic model that integrates species-specific responses for all recruitment stages (seed production and predation, seed germination and seedling emergence, survival and growth) in order to analyse general patterns of regeneration niche partitioning and species coexistence, and thus predict forest dynamics.

Acknowledgements. We thank the Consejería de Medio Ambiente (Andalusian Government) and Felipe Oliveros, then Director of Los Alcornocales Natural Park, for the facilities and support to carry out our fieldwork. We also thank Fernando Valladares for giving advice on light and R:FR measurements, J. L. Quero for unpublished data on *Q. pyrenaica*, and Semillas Silvestres (<http://www.semillassilvestres.com>) for providing seeds of *Q. pyrenaica*. We are tremendously grateful to Maite Domínguez, Itziar Rodríguez, Lola Vega, Eduardo Gutiérrez, Ana Polo and

Rocío Sánchez for invaluable field and lab assistance. This study was supported by a FPU-MEC grant to IMPR, a Juan de la Cierva contract to LGA and by the Spanish MEC projects Heteromed (REN2002-4041-C02-02), Dinamed (CGL2005-5830-C03-01/02) and Interbos (CGL2008-4503-C03-01/02). This research is part of the Globimed (<http://www.globimed.net>) network in forest ecology.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Equations of the different functions fitted in the models calibrated for this study.

Appendix S2. Estimates of equation parameters (a, b, c, d) and associated two-likelihood unit support intervals (in brackets) for the best supported first-year growth models shown in Table 3. Functional forms (FF): LIN, Linear; EXP, Exponential; MM, Michaelis-Menten; NULL, Null model.

Appendix S3. Estimates of equation parameters (a, b, c, d) and associated two-likelihood unit support intervals (in brackets) for the best supported second-year growth models shown in Table 5. Functional forms (FF): LIN, Linear; EXP, Exponential; MM, Michaelis-Menten; NULL, Null model.

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Received 24 July 2009;

Accepted 7 December 2009.

Co-ordinating Editor: Dr. Lindsay Turnbull.

1 **Supporting information**

2 **Appendix 1.** Equations of the different functions fitted in the models calibrated for this study.

3

4 **Appendix 2.** Estimates of equation parameters (a, b, c, d) and associated 2-likelihood-unit
5 support intervals (in brackets) for the best-supported 1st-year growth models shown in Table 3.

6 Functional forms (FF): LIN, Linear; EXP, Exponential; MM, Michaelis-Menten; NULL, Null model.

7

8 **Appendix 3.** Estimates of equation parameters (a, b, c, d) and associated 2-likelihood-unit
9 support intervals (in brackets) for the best-supported 2nd-year growth models shown in Table 5.

10 Functional forms (FF): LIN, Linear; EXP, Exponential; MM, Michaelis-Menten; NULL, Null model.

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1 **Appendix 1.**

2 [i] Linear additive: $a + bFactorA_i + cFactorB_i + dFactorC_i$;

3 [ii] Linear multiplicative: $a + bFactorA_i * cFactorB_i * dFactorC_i$;

4 [iii] Exponential additive: $ae^{(bFactorA_i + cFactorB_i + dFactorC_i)}$;

5 [iii] Exponential multiplicative: $ae^{(bFactorA_i * cFactorB_i * dFactorC_i)}$;

6 [iii] Michaelis- Menten multiplicative:

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$$\frac{aFactorA_i * FactorB_i}{\left(\frac{a}{b} + FactorA_i\right) * \left(\frac{a}{c} + FactorB_i\right) * \left(\frac{a}{d} + FactorC_i\right)}$$

8

9 where a, b, c and d are parameter estimates that maximized the likelihood function, and *Factors*

10 A_i, B_i and C_i are the selected predictor variables for each seedling "i".

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1 Appendix 2.

Species	Growth variable	Predictors	FF	a	b	c	d	
<i>Q. canariensis</i>	Total abov. biomass	Seed mass	LIN	8.12 [4.39-11.61]	8.52 [7.67-9.38]			
			NULL	44.48 [39.58-49.37]				
	RGR _a	Seed mass	LIN	2.72 [1.12-4.38]	1.84 [1.48-2.23]			
			NULL	10.63 [8.93-12.43]				
	NAR _a	Seed mass*Maximum WVC	MM	4999.35 [3699.76-5000]	94.34 [77.52-112.26]	54.62 [41.73-69.97]		
			NULL	118.91 [95.13-142.69]				
	LAR _a	Seed mass+R.FR	EXP	138.33 [130.03-146.63]	-0.05 [-0.06 to -0.04]	-0.29 [-0.39 to -0.21]		
			NULL	95.50 [88.82-102.19]				
	LMF _a	GSF	MM	69.46 [64.60-74.32]	13.15 [10.52-17.12]			
			LIN	53.99 [50.75-57.23]	17.42 [12.71-21.77]	-0.23 [-0.29 to -0.17]		
		R.FR+Maximun WVC	NULL	53.36 [49.62-57.09]				
	Total leaf area	Seed mass+Superficial compaction	LIN	26.29 [23.40-29.45]	6.01 [5.35-6.73]	-5.63 [-6.90 to -4.24]		
			NULL	606.40 [545.76-668.21]				
	N leaves	Seed mass+Superficial compaction	EXP	4.45 [3.96-4.98]	0.15 [0.12-0.17]	-0.17 [-0.23 to -0.12]		
			EXP	3.71 [3.30-4.15]	1.10 [0.87-1.32]	0.003 [0.002-0.003]		
		NULL	5.98 [5.32-6.70]					
	Stem height	Seed mass+Superficial compaction+GSF	LIN	117.3 [109.09-125.51]	8.99 [7.19-10.79]	-14.46 [-17.88 to -10.91]	-0.61 [-0.86 to -0.35]	
			NULL	111.65 [101.60-121.70]				
	SSL	Seed mass+NT+Maximum WVC	LIN	917.06 [860.38-966.04]	-68.13 [-79.36 to -59.03]	489.19 [360.27-601.14]	-4.12 [-5.17 to -3.31]	
			NULL	606.4 [545.76-668.21]				
EXP			18.38 [16.91-19.86]	0.09 [0.08-0.11]				
<i>Q. pyrenaica</i>	Total abov. biomass	Seed mass	EXP	30.5 [27.75-32.94]				
			NULL	3.7 [0.85-6.59]	3.22 [2.68-3.77]	-13.12 [-17.09 to -9.4]		
	RGR _a	Seed mass+R.FR	LIN	12.26 [8.71-15.82]				
			EXP	40.49 [32.39-49.4]	0.32 [0.29-0.35]	-1.25 [-1.8 to -0.83]		
	NAR _a	Seed mass+R.FR	EXP	125.02 [85.02-165.02]				
			NULL	166.06 [161.08-171.05]	-9.76 [-10.42 to -9.12]			
	LAR _a	pH	LIN	108.26 [103.93-112.59]				
			NULL	111.48 [108.14-114.83]	-9.68 [-10.09 to -9.28]	20.14 [16.69-23.36]		
	LMF _a	pH+R.FR	LIN	67.26 [63.23-71.3]				
			NULL	70.37 [67.56-73.18]	2.76 [2.29-3.22]	-8.77 [-9.18 to -8.35]		
	Total leaf area	Seed mass+pH	LIN	33.07 [30.09-36.05]				
			NULL	5.15 [4.48-5.87]				
	N leaves	GSF	EXP	124.06 [112.9-135.23]	-0.01 [-0.02 to -0.01]			
			NULL	83.17 [72.36-93.99]				
	SSL	GSF	EXP	1061.12 [988.07-1138.68]	-0.006 [-0.008 to -0.004]			
			NULL	882.55 [811.94-958.42]				
			EXP	88.91 [74.69-104.92]	25.86 [19.91-33.62]			
	<i>Q. suber</i>	Total abov. biomass	Seed mass	MM	51.50 [45.32-57.68]			
				NULL	18.18 [16.36-20.0]	-9.22 [-12.17 to -6.32]		
		RGR _a	R.FR	LIN	13.42 [11.41-15.44]			
NULL				179.81 [161.83-197.79]	-90.69 [-119.92 to -61.94]			
NAR _a		R.FR	LIN	132.96 [113.01-152.9]				
			NULL	127.78 [123.95-131.61]	-1.95 [-2.51 to -1.4]	-23.94 [-28.86 to -18.95]	1.42 [0.68-2.19]	
LAR _a		Seed mass+R.FR+NH4	LIN	109.79 [105.40-114.18]				
			NULL	54.00 [51.30-56.70]	0.42 [0.34-0.49]			
LMF _a		GSF	LIN	64.02 [60.82-67.22]	11.35 [9.47-13.96]			
			NULL	84.77 [72.90-97.49]	35.00 [26.60-47.60]			
Total leaf area		Seed mass	MM	56.04 [49.88-62.21]				
			NULL	13.92 [12.81-15.04]	0.007 [0.005-0.01]	-0.15 [-0.19 to -0.11]		
N leaves		GSF+Superficial compaction	EXP	12.61 [11.6-13.62]				
			NULL	166.64 [148.31-181.64]	0.06 [0.044-0.077]	-0.93 [-1.18 to -0.75]		
Stem height		Seed mass+R.FR	EXP	147.29 [128.14-166.44]				
			NULL	930.86 [885.70-1001.55]				

1 Appendix 3.

Species	Growth variable	Predictors	FF	a	b	c	d
<i>Q. canariensis</i>	Total abov. biomass		NULL	67.1 [55.03-79.18]			
			NULL	271.44 [127.57-415.15]			
	RGR _a		NULL	3.59 [1.98-5.18]			
	NAR _a		NULL	85.21 [76.69-93.73]			
	LMF _a	GSF	LIN	43.84 [38.58-49.1]	0.27 [0.13-0.41]		
			LIN	57.73 [52.53-62.92]	-2.44 [-3.81 to -0.99]		
			LIN	41.43 [36.05-46.41]	16.32 [8.91-23.36]		
	Total leaf area	Superficial compaction	NULL	51.33 [45.68-56.97]			
			LIN	86.69 [77.16-96.23]	-12.94 [-16.52 to -9.18]		
			NULL	57.4 [47.06-67.7]			
	N leaves	GSF+Superficial compaction	EXP	10.62 [9.34-11.89]	0.01 [0.01-0.02]		-0.32 [-0.38 to -0.27]
			NULL	8.44 [7.43-9.51]			
	Stem height	Seed mass+GSF	EXP	97.45 [88.68-106.22]	0.15 [0.13-0.17]		-0.01 [-0.01 to -0.008]
			NULL	144.67 [127.31-162.03]			
	SSL	Max. compaction+Minimum VWC	EXP	236.12 [212.51-258.49]	0.08 [0.07-0.1]		0.06 [0.04-0.06]
			NULL	593.63 [522.39-661.75]			
			NULL	37.87 [31.05-44.44]			
<i>Q. pyrenaica</i>	Total abov. biomass		NULL	82.89 [0-264.44]			
			NULL	37.87 [31.05-44.44]			
	RGR _a		NULL	82.89 [0-264.44]			
	NAR _a		NULL	82.89 [0-264.44]			
	LAR _a	P	EXP	78.44 [65.89-90.99]	-0.11 [-0.2 to -0.06]		
			LIN	45.02 [35.12-54.93]	0.54 [0.27-0.81]		
			EXP	73.54 [61.77-85.31]	-0.05 [-0.1 to -0.02]		
	LMF _a	GSF	EXP	43.19 [35.84-50.09]	0.57 [0.33-0.76]		
			NULL	60.17 [49.34-71]			
			MM	91.59 [70.52-116.17]	3.81 [2.74-5.21]		
	Total leaf area		NULL	43.46 [34.77-52.15]			
			NULL	21.32 [17.06-25.71]			
			NULL	3.72 [3.02-4.51]			
	Stem height	R:FR+Superficial compaction	EXP	133.92 [120.53-147.31]	-1.16 [-1.41 to -0.94]		0.28 [0.24-0.31]
			NULL	144.51 [114.16-174.85]			
	SSL		NULL	846.69 [711.22-978.95]			
			NULL	26.07 [-33.34 to -18.03]	9.09 [7.82-10.55]		1.08 [0.86-1.3]
<i>Q. suber</i>	Total abov. biomass	Seed mass+GSF	LIN	-26.07 [-33.34 to -18.03]	9.09 [7.82-10.55]		1.08 [0.86-1.3]
			NULL	55.22 [41.97-68.48]			
	RGR _a	GSF	LIN	-497.41 [-657.91 to -332.9]	13.34 [9.31-17.42]		
			LIN	-648.48 [-809.52 to -481.76]	886.91 [662.75-1000]		
			NULL	5.52E-07 [0 - 164.35]			
	NAR _a		NULL	3.59 [1.98-5.18]			
	LAR _a		NULL	95.51 [86.91-104.11]			
	LMF _a	GSF	MM	91.66 [82.49-101.74]	8.4 [6.64-10.74]		
			NULL	60.32 [53.69-66.96]			
			NULL	-19.7 [-27.25 to -12.43]	7.49 [6.14-8.76]		1.06 [0.85-1.27]
	Total leaf area	Seed mass+GSF	LIN	51.69 [39.29-64.1]			
			NULL	6.28 [5.65-6.91]	0.023 [0.021-0.024]		
	N leaves	GSF	EXP	14.3 [12.87-15.73]			
			NULL	132.57 [117.99-145.83]	0.12 [0.10-0.13]		-0.79 [-1 to -0.6]
	Stem height	Seed mass+R:FR	EXP	170.06 [137.75-200.67]			
			NULL	2169.89 [2017.99-2304.79]	-108.24 [-130.97 to -87.21]		-916.82 [-1102.19 to -739.95]
	SSL	Seed mass+R:FR	LIN	1015.57 [822.61-1202.92]			
NULL			1015.57 [822.61-1202.92]				

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