

Ontogenetic conflicts and rank reversals in two Mediterranean oak species: implications for coexistence

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Summary

1. In heterogeneous environments, species segregate spatially in response to selective abiotic and biotic filters occurring throughout plant ontogeny. Ontogenetic conflicts in recruitment may lead to spatially discordant patterns of regeneration among microhabitats with different plant cover. In addition, species differing in seed size may be subjected to opposing ecological and evolutionary pressures throughout the life cycle of the plant.
2. We used a multi-stage demographic approach aimed at characterizing the main stage-specific probabilities of recruitment (seed survival, seed germination, seedling emergence and survival during the first 3 years of life) in two Mediterranean oak species coexisting at southern Spain. We calibrated linear and nonlinear likelihood models for each of these consecutive life history stages and calculated overall probabilities of recruitment along a wide range of plant cover and seed size variation.
3. Seed predation and seedling mortality over the dry season were the most limiting processes for the two studied oak species. However, species ranking diverged substantially through the life history stages considered in this study due to different ontogenetic trends among species.
4. At the intraspecific level, recruitment-driving processes during the seed and the seedling stages showed opposing tendencies along the explored range of plant cover and seed size. Thus, small-sized acorns and open areas were favoured for the seed stage, whereas large acorns and dense microhabitats did for the seedling stage.
5. The existence of opposing selective pressures on seed mass and their differential influence on the two studied oak species determined the occurrence of species-specific optimal seed sizes (small acorns for *Quercus canariensis* vs. acorns of large or intermediate size for *Quercus suber*).
6. The spatial patterns predicted by our overall-recruitment models provided some evidence of regeneration niche partitioning in the two coexisting oak species, supporting their current distribution patterns as saplings and adults at the study area.
7. *Synthesis.* We conclude that within- and among-species differences through plant ontogeny, arising from species differential response to microhabitat heterogeneity and seed size variation, could be of great importance for oak species niche segregation, driving stand dynamics and spatial pattern distribution along the landscape. The information provided by this study could be also applied to optimize management and restoration programmes since it has enabled us to identify the most favourable conditions and traits for recruitment in oak species that exhibit serious constraints for natural regeneration.

Key-words: Mediterranean forest, plant cover, *Quercus canariensis*, *Quercus suber*, regeneration niche, reproductive ecology, seed size, seed–seedling conflict

Introduction

In heterogeneous environments, such as Mediterranean-type forests, species segregate spatially in response to selective abiotic and biotic filters occurring throughout plant ontogeny (Grubb 1977; Nathan & Muller-Landau 2000). In most long-lived plant populations, these environmental sieves play an extensive role in determining species distribution during early life history stages (Ricklefs 1977; Kitajima & Fenner 2000). A common way of analysing the influence of environment heterogeneity on these younger demographic stages is to compare the suitability for the recruitment of different microhabitats with contrasting abiotic conditions (e.g. Battaglia, Foré & Sharitz 2000; Rey & Alcántara 2000; Gómez-Aparicio 2008). However, habitat filtering often occurs at very fine spatial scales, which demonstrates a need for the quantification of the most influential environmental factors operating at different sequential life history stages. Detailed studies explicitly measuring continuous gradients of microhabitat conditions are, therefore, essential to fully understand the optimal conditions where natural recruitment successfully occurs (concept of regeneration niche, *sensu* Grubb 1977) and thus to verify the existence of species habitat partitioning.

An accurate characterization of microhabitat-specific suitability for recruitment requires a 'linking-stages' approach, where plant recruitment is explored across consecutive demographic stages (seeds, seedlings, saplings) that are connected by transitional processes (dispersal, germination, emergence and survival) (Herrera *et al.* 1994; Clark *et al.* 1999). All these demographic processes are microhabitat-dependent (Schupp & Fuentes 1995; Hulme 1997), but they are not always influenced similarly by the same microhabitat conditions (Gómez-Aparicio 2008; Norden *et al.* 2009). This is particularly common in Mediterranean ecosystems, where recruitment-driving processes are frequently discordant due to different microhabitat associations through subsequent life history stages (Jordano & Herrera 1995; Rey & Alcántara 2000; Traveset *et al.* 2003). Discordant patterns of microhabitat suitability over the life cycle of the plant lead to ontogenetic conflicts since the most favourable sites for one stage may not be the most favourable for others (Schupp 1995). At the species level, a well-known demographic conflict involves the differential responses between seeds and seedlings (i.e. seed–seedling conflict), in which microhabitats with a high predation risk for seeds exhibit more favourable conditions for subsequent seedling establishment and vice versa (Houle 1992; Herrera *et al.* 1994; Schupp 1995; Rey & Alcántara 2000). At the community level, ontogenetic conflicts might also occur, involving changes in species' performance rankings across demographic stages (Baraloto, Goldberg & Bonal 2005a). In spite of their potential contribution as mechanisms of species coexistence, among-species rank reversals through ontogeny remain poorly understood (Clark & Clark 1992; Baraloto, Goldberg & Bonal 2005a), especially in Mediterranean-type ecosystems.

Recruitment-driving processes are not only influenced by microhabitat conditions but also by several intrinsic plant traits, such as seed size. Similarly to the above-discussed onto-

genetic conflicts across microhabitats, opposing selective pressures among demographic stages have been described in relation to seed size due to the compromise between increasing seedling performance and reducing attraction for predators, as well as favouring successful seed dispersal (Moegenburg 1996; Alcántara & Rey 2003; Gómez 2004). Although there may be a considerable intraspecific variability in seed size, theoretical models have predicted the evolution of an optimal propagule size based on the existence of a trade-off between offspring number and size (Smith & Fretwell 1974). However, the occurrence of ontogenetic conflicting pressures may hinder the identification of the seed size that maximizes the overall probability of recruitment (i.e. optimal seed size). This attribute may also contribute to interspecific performance differences and thus promotes the coexistence among species differing in seed size (Kneitel & Chase 2004; Baraloto, Forget & Goldberg 2005b). To gain an accurate view of the selective pressures acting on seed size and the extent to which interspecific differences in this trait favour that potentially competing species do coexist, it is advisable to consider the entire life cycle of the organisms (Moles & Westoby 2004). However, this has seldom been explored in long-lived perennial species due to the enormous costs for obtaining long-term data for different species across multiple life history stages (see Baraloto, Forget & Goldberg 2005b).

The present study comprises an array of information on the regeneration ecology of two dominant coexisting oak species – the deciduous *Quercus canariensis* Willd and the evergreen *Quercus suber* L. – that differ in several functional traits, such as seed size. In the study area, adults of both oak species segregate along environmental gradients of topography and soil moisture, forming forests with distinct canopy cover. *Quercus suber* tends to dominate in habitats with a lower availability of soil water and nutrients where the overstorey canopy is relatively sparse (Pérez-Ramos 2007), whereas *Q. canariensis* is more abundant in moister habitats with denser canopies (Urbieta, Zavala & Marañón 2008a). At regional scale, about 60–70% of inventoried forest plots with *Q. suber* and/or *Q. canariensis* lacked natural regeneration (Urbieta *et al.* 2011).

In this paper, we used a multi-stage demographic approach aimed at characterizing the main stage-specific probabilities of recruitment (seed survival, seed germination, seedling emergence and survival during the first 3 years of life) in the two coexisting oak species along a wide and continuous gradient of plant cover (used here as a surrogate of microhabitat conditions). In addition, we investigated the implications of seed size variation, using a broad range of seed mass for the two studied oak species. We calibrated linear and nonlinear likelihood models for each of these consecutive life history stages and calculated overall probabilities of recruitment along plant cover and seed mass variation. These models were further validated through comparisons with the natural distribution of saplings at the study area. Specifically, we aimed to answer the following questions: (i) Which are the most critical demographic processes for oak recruitment?; (ii) are there ontogenetic conflicts, both within- and among-species (i.e. species rank reversals),

along a continuous gradient of plant cover?; and (iii) are there opposing selective pressures on seed size among subsequent demographic stages?

By answering these questions, we seek to gain insights into the characterization of the regeneration niche of oak species with contrasting functional attributes, including seed size, and their relationships with distribution patterns of adults along the landscape. The identification of ontogenetic conflicts, both within- and among-species, will enable us to better understand the underlying mechanisms that promote species coexistence in Mediterranean mixed-oak forests. The information provided by this study will also contribute to develop ecologically based management and restoration strategies in Mediterranean forests.

Methods

STUDY AREA

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 Aljibe Mountains, near the Strait of Gibraltar, in southern Spain (see a detailed description of the experimental site in Quilchano *et al.* 2008 and Pérez-Ramos *et al.* 2008a). Climate is sub-humid Mediterranean-type, with mild and wet winters alternating with hot and dry summers. Annual mean temperature ranges from 14.6 to 18.4 °C (mean of 17 °C). Annual mean rainfall varies from 900 to 1800 (mean of 1265 mm), with the heaviest rainfall occurring in autumn, winter and spring, followed by dry summers. Bedrock is predominately Oligo-Miocene sandstone, which produces acidic, sandy and nutrient-poor soils, although frequently there are interspersed layers of marl sediments, yielding soils richer in clay. Vegetation is dominated by evergreen cork oak (*Q. suber*) forests, mixed with winter-deciduous oaks (*Q. canariensis*), which are more abundant near streams (Urbietta, Zavala & Marañón 2008a). The shrubby understorey is diverse and rich in endemic taxa (Ojeda, Marañón & Arroyo 2000). Most of the forested area was protected in 1989 as 'Los Alcornocales' (meaning 'cork oak forests') Natural Park, covering about 1680 km².

SAMPLING DESIGN AND DATA COLLECTION

Acorns of *Q. suber* and *Q. canariensis* were collected in the surroundings of the experimental site from several trees (at least 10 of each species) to encompass intraspecific variation. We selected healthy acorns, discarding those infected by moth or beetle larvae through flotation (Gribko & Jones 1995). Selected acorns were stored on a moist substrate at 2–4 °C until used in the experiments and individually weighed to the nearest 0.01 g. Mean \pm SD (standard deviation) acorn fresh weight was: 5.96 \pm 2.20 g for *Q. suber* (range of 2.31–17.27 g) and 2.57 \pm 1.03 g for *Q. canariensis* (range of 0.91–8.29 g). We used acorn fresh weight as a surrogate of dry seed mass, justified by their high correlation (Quero *et al.* 2007). Acorns of known weight were further distributed in experimental units (see subsections below on 'Seed survival' and 'Seedling monitoring') on the forest floor along a wide and continuous gradient of plant cover, from open spaces [up to 90% full sun and leaf area index (LAI) of 0.35] to shady microhabitats under shrubs and trees (down to 10% full sun, 4.00 LAI).

Plant cover was estimated by means of hemispherical photographs taken in the centre of each experimental unit, using a horizontally levelled digital camera with fish-eye lens of 180° field of view (Quil-

chano *et al.* 2008). Digital images were analysed with specific software (Hemiview Canopy Analysis; Delta-T Devices Ltd., 1999, v. 2.1). We selected plant cover (LAI) as the most representative variable of microhabitat conditions based on previous studies carried out at the same mixed-oak forests which aimed to identify the main abiotic factors affecting each stage-specific probability of recruitment (Gómez-Aparicio *et al.* 2008; Pérez-Ramos *et al.* 2008b; Urbietta *et al.* 2008b). In this study, we used a multi-stage demographic approach to explore the existence of within- and among-species differences during plant ontogeny along a broad range of microhabitats differing in plant cover. Specifically, we selected LAI because: (i) it was the environmental variable mostly affecting seed predation (Pérez-Ramos *et al.* 2008b); and (ii) it was significantly correlated with light and maximum soil water content, which are the most influential factors for seedling emergence and survival (Gómez-Aparicio *et al.* 2008; Urbietta *et al.* 2008b). Thus, plant cover was negatively correlated with the global site factor (GSF; $r = -0.91$, $P < 0.001$) as well as with the soil volumetric water content reached during the rainy season ($r = -0.39$, $P < 0.005$). Open areas tended to suffer events of sporadic soil waterlogging during the wet period due to less interception of rain by canopy and, in most cases, a higher proportion of clay (Urbietta *et al.* 2008b).

Seed survival

The probability of seed survival (i.e. non-removed acorns) was evaluated by individually monitoring a total of 576 acorns (including both species) randomly distributed across 144 experimental units. In each unit, four acorns of a single species were placed on the ground, in the corners of a 0.5-m² quadrat. Units were periodically visited and acorns individually monitored until there was no longer any evidence of seed removal (see Pérez-Ramos *et al.* 2008b for further details). This experiment was repeated during two consecutive reproductive cycles (2003/04 and 2004/05), which showed contrasting differences in seed production and, thereby, in food availability for seed consumers. Thus, the estimated seed production in *Q. canariensis* varied from 344 g m⁻² (2003/04 cycle) to 58 g m⁻² (2004/05 cycle) in the study area, whereas it remained low during both years (below 14 g m⁻²) in the case of *Q. suber* (Pérez-Ramos 2007).

Although it is likely that a small fraction of removed acorns escape consumption, in which case the animals responsible act as secondary seed dispersers (e.g. Pérez-Ramos *et al.* 2007; Pons & Pausas 2007; Purves *et al.* 2007; Gómez-Aparicio *et al.* 2008), a recent study on acorn dispersal in the study area has shown that most of them are completely eaten, mainly by rodents (I. M. Pérez-Ramos, J. R. Verdú, C. Numa & J. M. Lobo, unpublished data). Thus, from a quantitative perspective, we assumed that the seeds recorded in this study as 'removed' could be considered as 'losses' for recruitment. Therefore, 'seed removal' has been considered as a surrogate of 'seed predation' in this study.

Seedling monitoring

The processes of seed germination, seedling emergence and survival, and seedling growth were studied by conducting a seed sowing experiment at the same study site where seed removal was evaluated. In December 2003, a total of 600 acorns of each species were randomly placed across 60 experimental units distributed along the above-described gradient of plant cover. Ten acorns per species were sown in each unit at 1–3 cm depth, simulating biotic seed dispersal and burial by European jays (Kollmann & Schill 1996), rodents (Gómez, Puerta-Piñero & Schupp 2008) or dung beetles (Pérez-Ramos *et al.*

2007). All the experimental units were protected by wire cages (25 × 25 × 25 cm, 1.3 cm mesh size) to exclude seed predators. Seed germination was assessed after the first summer, unearthing non-emerged seeds and inspecting the presence of radicles. Seedling emergence and survival were monitored periodically from February 2004 to February 2007. Censuses were carried out bi-weekly during the first year and every 6 months (in late winter and after summer, coinciding with the peaks of maximum seedling mortality) during the two remaining years (see Urbietta *et al.* 2008b for further details).

For measurements of seedling growth, we selected one individual per species and available experimental unit. For each selected seedling, non-destructive measurements in stems and leaves were taken repeatedly during two consecutive growing seasons (2004 and 2005). Above-ground biomass for each year was estimated from these non-destructive measurements using linear regressions calculated in additional harvested seedlings (see details in Pérez-Ramos *et al.* 2010).

Abundance and natural distribution of saplings

To assess whether the natural sapling distribution of the two studied species mirrored the net results predicted by our models (i.e. model validation), a static survey of sapling abundance was conducted at the study area in autumn 2004. The number of saplings (i.e. individuals more than 2 years old) was counted in six randomly positioned transects (25 × 2 m), and the microhabitat in which they had established was also recorded. We categorized three types of microhabitats as a function of their predominant plant cover: dense shrub (inside shrub and tree overstorey, with LAI values ranging from 2 to 3.5), under tree (beneath tree canopy, without shrub understorey; LAI from 1.3 to 2) and open microsites (without the protection of shrub and tree canopy; LAI from 0.3 to 1.3). In addition, we estimated the natural availability of each microhabitat type at the study area by visually estimating the percentage covered by each of the three microhabitat types along the transects.

DATA ANALYSES

Among-species ontogenetic rank reversals

Interspecific differences for each of the stage-specific probabilities of recruitment were tested to explore the existence of among-species ontogenetic rank reversals. We used Generalized Linear Models assuming a logit relationship between the dependent (treated as a binomial variable) and the independent variable (the oak species). These analyses were carried out using STATISTICA (v. 6; StatSoft Inc., 2001).

Recruitment models along plant cover and seed mass variation

The stage-specific probability of recruitment was modelled independently for each of the life history stages considered in this study (seed survival, seed germination, seedling emergence and seedling survival during the first 3 years of life) as a function of plant cover and seed mass. The overall probability of recruitment was further calculated as the product of all these six stage-specific probabilities. In addition, we used the same modelling approach to fit models of seedling growth (particularly for 1- and 2-year-old seedling above-ground biomass) along the explored range of plant cover and seed mass. All models were fitted individually for each oak species, using maximum likelihood techniques (Edwards 1992) with simulated annealing (Goffe, Ferrier & Rogers 1994).

We tested five alternative functions (linear, exponential, Michaelis–Menten, logistic and power), which cover a wide range of possible responses. We first tested models for each predictor and function independently, and the best of the five models was then compared to the null model, which assumes no effect of any factor. Second, to test for interactions between both factors, we fitted bivariate models in which the second predictor (i.e. seed mass) was added either additively or multiplicatively. Competing models were compared with the Akaike's Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2002) as a measure of goodness of fit: the lower the AIC_c value, the better the model. The absolute magnitude of the differences in AIC_c (Δ AIC) between alternative models provided an objective measure of the strength of empirical support for each one of them (Akaike 1992). Models with Δ AIC between 0 and 2 were considered to have equivalent and substantial empirical support (Burnham & Anderson 2002).

For the seed stage, we combined maximum likelihood methods and survival time analysis to parameterize seed survival models as a function of plant cover and seed mass, considering not only the final 'fate' of each seed (i.e. survived or not) but also the time each seed remained non-removed (see Pérez-Ramos *et al.* 2008b for more details). The processes of seed germination, seedling emergence and survival were described by a binomial distribution, whereas seedling growth data were fitted to a normal distribution (see Urbietta *et al.* 2008b; and Pérez-Ramos *et al.* 2010 for more details). To test interspecific differences along the explored range of plant cover and seed mass, we calibrated a general model that was fitted to all the data (saturated model, without distinguishing between the species) for each of the life history stages considered in this study. The AIC_c of each saturated model was compared with the sum of AIC_c of their two corresponding species-specific models; only when Δ AIC_c > 2, differences between species were considered to be significant. Seed survival models were implemented in programs written in C (Borland C+; Borland International Inc., 1996, version 5.01). The remaining models were implemented using the *likelihood* package R.1.1, and software written specifically for this study in R.2.5.0 (R Development Core Team, 2006).

Abundance and natural distribution of saplings

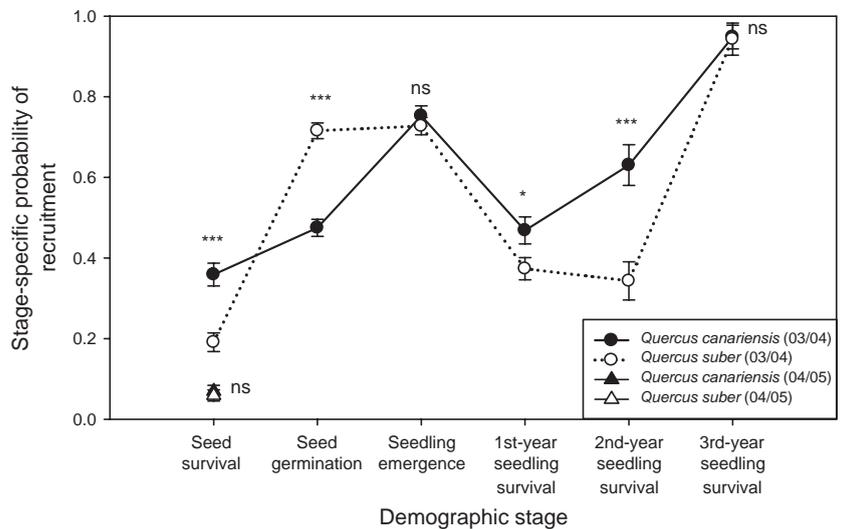
To assess whether natural saplings of both species were randomly distributed along the landscape and thus validate our overall-recruitment models, we conducted a Chi-square test to compare the observed frequencies of saplings among the three above-described types of microhabitats versus those expected by chance (i.e. the proportion of available microhabitats at the study site). This analysis was carried out using STATISTICA (v. 6; StatSoft Inc., 2001).

Results

CRITICAL DEMOGRAPHIC PROCESSES AND AMONG-SPECIES ONTOGENETIC RANK REVERSALS

We detected strong differences in the stage-specific probabilities of recruitment through ontogeny. In both oak species, the most critical demographic process occurred during the seed–seedling transition, with mean probabilities of seed survival below 0.4 (Fig. 1). The relative importance of this stage for overall recruitment was more marked in the 2004/05 cycle

Fig. 1. Stage-specific probabilities of recruitment from a dispersed seed to an established 3-year-old seedling, in the two studied oak species (*Quercus canariensis* is represented with black symbols and solid lines, whereas *Quercus suber* with white symbols and dotted lines). Seed survival was monitored during two consecutive reproductive cycles (2003/04 and 2004/05, represented with circles and triangles, respectively), with very contrasting initial seed supply. Significant interspecific differences for each of the life history stages considered in this study are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.



(with mean probabilities of seed survival close to zero; Fig. 1), where the estimated seed production – and consequently the natural resource availability for seed consumers – was substantially lower at the study site. During the seedling stage, the lowest stage-specific probabilities of recruitment were registered for seedling survival during the first 2 years (Fig. 1), seedling mortality being mainly caused by desiccation during the dry summer period. After 3 years, seedling survival rate increased strongly and mortality was negligible in both studied species (Fig. 1).

Species ranking diverged substantially between the life history stages considered in this study due to ontogenetic differences among species (Fig. 1). During the first reproductive cycle (2003/04), *Q. canariensis* showed higher probability of seed survival compared with the evergreen oak species ($\chi^2 = 20.58$; $P < 0.001$), although this difference disappeared during the low-production cycle (2004/05; $\chi^2 = 0.26$; $P = 0.6$). In contrast, the probability of seed germination was much higher in *Q. suber* than in *Q. canariensis* ($\chi^2 = 65.09$; $P < 0.001$). Finally, a new ontogenetic rank reversal was detected during the process of seedling survival, this time *Q. canariensis* outperformed its co-dominant oak species during the first 2 years of seedling growth ($\chi^2 = 5.84$, $P = 0.02$ and $\chi^2 = 14.78$, $P < 0.001$ for the first and the second year, respectively; Fig. 1).

WITHIN-SPECIES ONTOGENETIC CONFLICTS ALONG A PLANT COVER GRADIENT

We found strong evidence for within-species ontogenetic conflicts along the explored range of plant cover (LAI; Fig. 2). Seed survival decreased exponentially with LAI, whereas seed germination increased along the plant cover gradient in the two studied species (Fig. 2a,b; see Appendix S1 for model estimates). Seedling emergence was also correlated positively with LAI for *Q. suber*. Interestingly, a higher seed mass intensified the negative effects of LAI on seed survival (in *Q. canariensis*) and the positive effects of

LAI on germination and seedling emergence in *Q. suber*, as indicated by the strongest empirical support of the bivariate models including both predictors (Appendix S1). In addition, seedling survival during the third year decreased logistically with increasing plant cover, but only for *Q. suber* (Appendix S1 and Fig. 2b).

Regarding interspecific differences, *Q. canariensis* showed a higher probability of seed survival but a lower probability of seed germination compared with *Q. suber*, as indicated by the higher empirical support of the species-specific models in comparison with their respective saturated models ($\Delta AIC_c = 63.15$ and 55.72 for seed survival and seed germination, respectively).

CONFLICTING SELECTIVE PRESSURES ON SEED SIZE AMONG DEMOGRAPHIC STAGES

Opposite tendencies were found for *Q. suber* between the seed and the seedling stages along the explored range of seed mass. Thus, the processes of seed germination and seedling survival during the first year were correlated positively with seed mass, whereas seed survival was negatively correlated with this trait (Fig. 2d and Appendix S1). In *Q. canariensis*, seed survival also decreased linearly with increasing seed mass, but the rest of transitional processes were not significantly influenced by this trait (Fig. 2c and Appendix S1).

OVERALL-RECRUITMENT TRENDS

The results of this study provide some evidence of regeneration niche partitioning when comparing the overall-recruitment probabilities between the two studied oak species. The cumulative probabilities of recruitment were very low in both oak species (below 5%), especially during the low-production cycle (2004/05).

Although both species showed the lowest probabilities of recruitment at the high end of the LAI gradient (i.e. the most shaded microsites), they showed differences in recruitment at

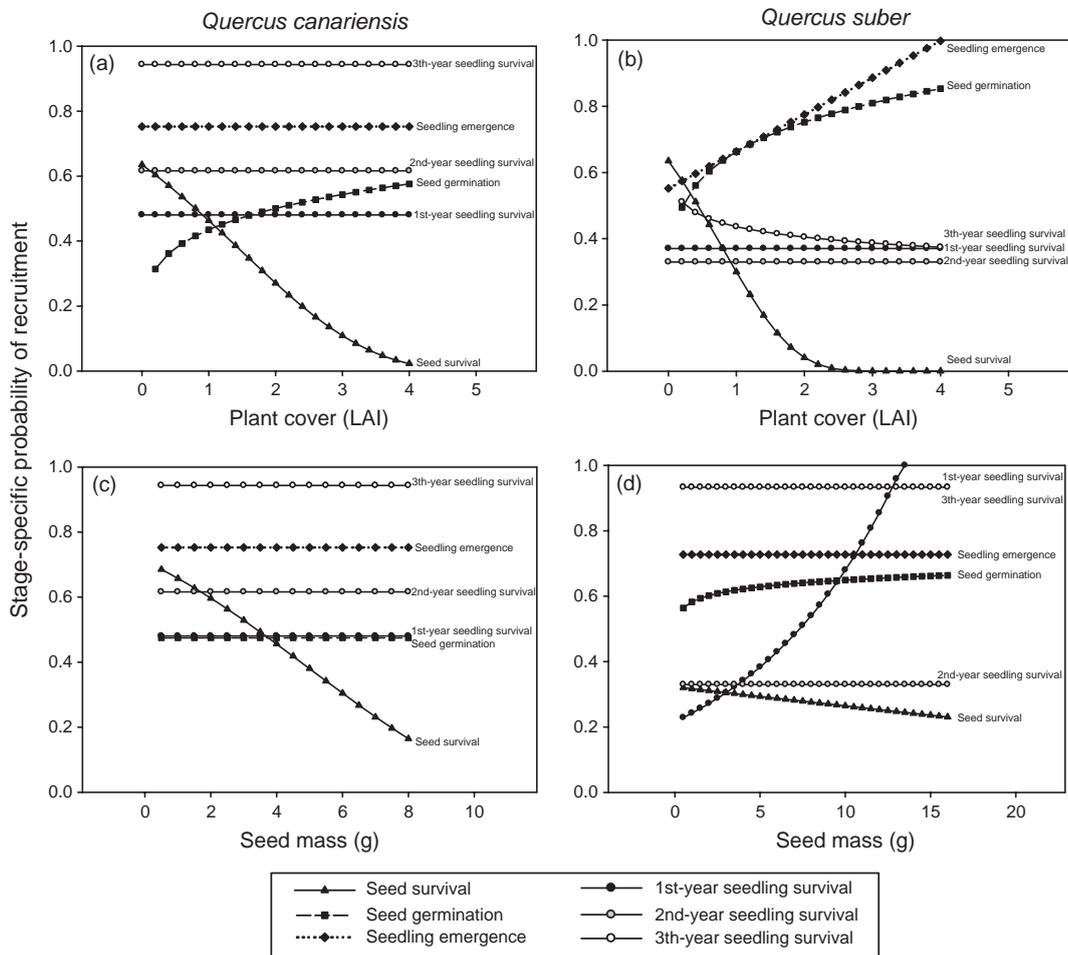


Fig. 2. Within-species ontogenetic conflicts along plant cover (a and b; LAI = leaf area index) and seed mass variation (c and d) for the two oak species. Seed survival data correspond to the 2003/04 reproductive cycle. Straight horizontal lines denote no effect of plant cover or seed mass on the stage-specific probabilities of recruitment, but they are included for comparative purposes.

low and intermediate LAI values. In *Q. canariensis*, the overall-recruitment probability slightly decreased as LAI approached zero, and peak recruitment appeared to occur in microhabitats with low-intermediate values of plant cover (LAI ~1; Fig. 3a). Interestingly, this recruitment peak was displaced towards the low end of the LAI gradient during the low-production cycle (2004/05; Fig. 3b). In comparison, *Q. suber* had the highest probabilities of cumulative recruitment in the most open microhabitats during the two sampling periods (Fig. 3a,b). *Quercus canariensis* outperformed its co-dominant oak species along most of the LAI gradient, but these interspecific differences disappeared in shady microhabitats (Fig. 3a,b).

Regarding seedling growth, the above-ground biomass (after two growing seasons) also decreased along the plant cover gradient in *Q. suber*, but no effect of LAI was detected for *Q. canariensis* (Appendix S1 and Fig. 3f).

The seed mass that maximized the overall probability of recruitment (i.e. optimal seed size) differed substantially between the two oak species, smaller seeds being favoured in *Q. canariensis*, whereas acorns of large (in 2003/04 cycle)

or intermediate size (in 2004/05 cycle) were favoured in *Q. suber* (Fig. 3c,d). First-year above-ground biomass increased with seed mass in both oak species (Appendix S1 and Fig. 3e), resulting in a trade-off for *Q. canariensis* when compared to the variation of its overall-recruitment probability.

ABUNDANCE AND NATURAL DISTRIBUTION OF SAPPLINGS

The natural distribution of *Q. canariensis* saplings in the three types of microhabitats was not random, compared with the availability of each of them in the study area ($\chi^2 = 49.52$; $P < 0.001$). The observed density of *Q. canariensis* saplings was lower than that expected by chance in the two extremes of the LAI gradient (i.e. both in open and dense microhabitats; Fig. 4). However, the observed distribution pattern of *Q. suber* saplings did not statistically differ from those expected by chance ($\chi^2 = 2.64$; $P = 0.27$), likely due to the low densities of saplings quantified at the study area for this species (Fig. 4).

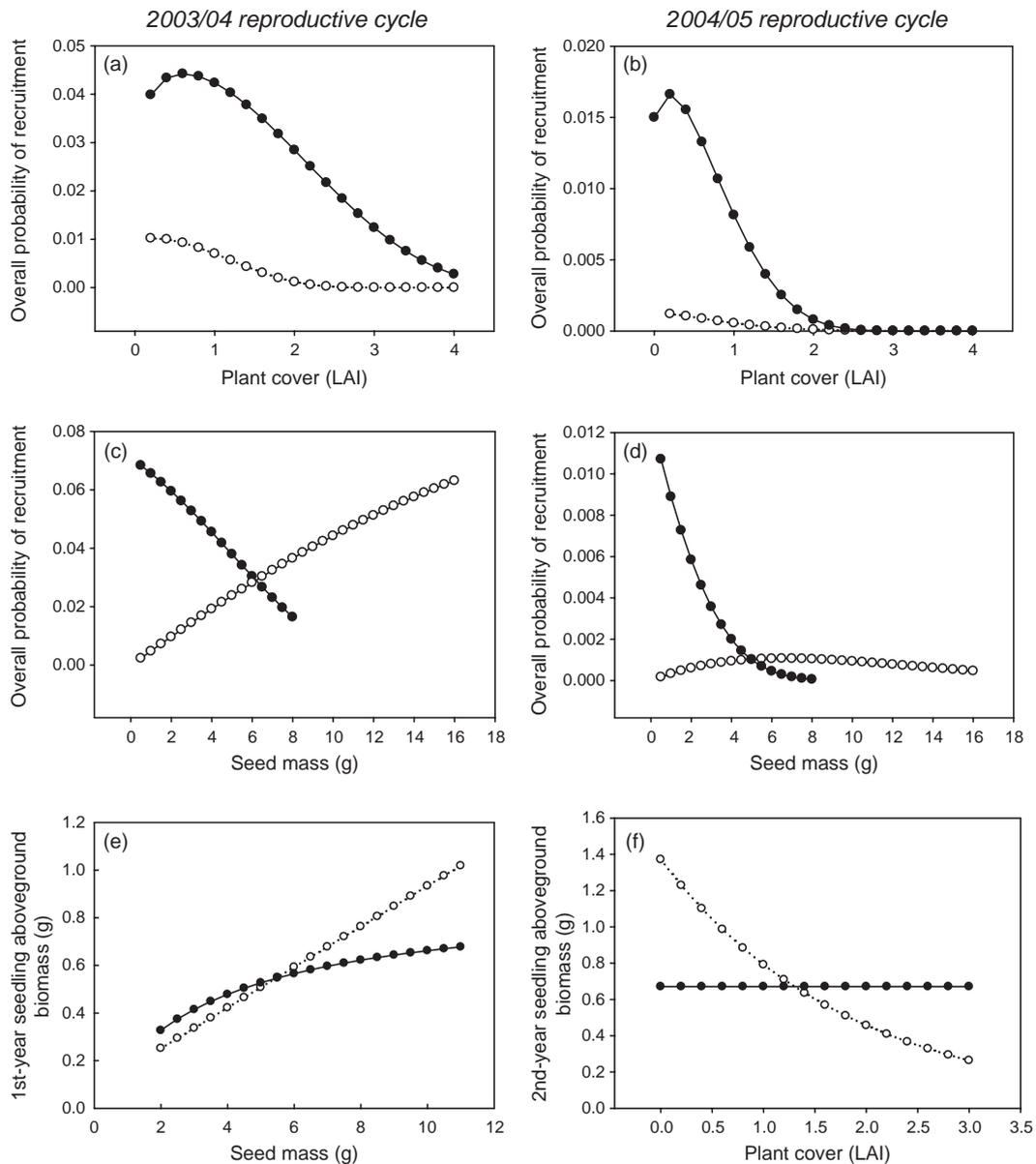


Fig. 3. Predicted variation in the overall probability of recruitment (a–d) and seedling above-ground biomass (e and f) along plant cover (LAI = leaf area index) and seed mass variation. The overall probability of recruitment was calculated as the product of all stage-specific probabilities from a dispersed seed to an established seedling of 3 years old. *Quercus canariensis* is represented with black symbols and solid lines, whereas *Quercus suber* with white symbols and dotted lines.

Discussion

CRITICAL DEMOGRAPHIC PROCESSES AND AMONG-SPECIES ONTOGENETIC RANK REVERSALS

The two studied oak species were strongly recruitment-limited in spite of their high co-dominance as adults in the forest canopy. Previous studies suggested that the regeneration process of these two species is more limited by safe sites than by seed availability (I. M. Pérez-Ramos & T. Marañón, unpublished data), a common feature in recruitment-limited species of Mediterranean forests (Gómez-Aparicio 2008; Mendoza *et al.* 2009). In contrast, a comparative study of two coexisting oak

species in NE Spain showed that predispersal predation and seed supply were the most critical processes, whereas no interspecific differences were observed either in post-dispersal predation or in seedling establishment (Espelta *et al.* 2009).

In our study, the most critical demographic process occurred during the seed–seedling transition, which has been identified as an important bottleneck in the regeneration of other Mediterranean oak species (Herrera 1995; Santos & Tellería 1997; Pulido & Díaz 2005; Pausas *et al.* 2009). Acorns are usually subjected to intensive predation pressure due to their large size and their high nutritional content, constituting an important part of the diet of many animals (e.g. Gómez, García & Zamora 2003; Pérez-Ramos & Marañón 2008).

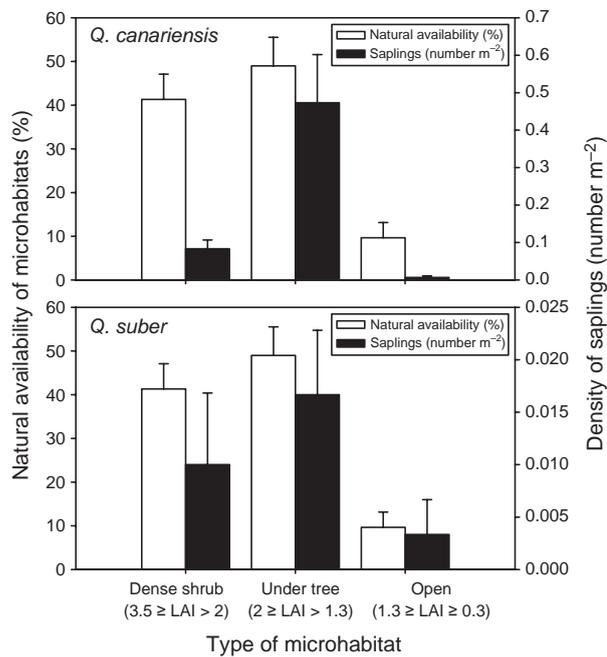


Fig. 4. Comparison between the natural availability of the three main types of microhabitats (dense shrub, under tree and open; LAI = leaf area index) and the density of saplings found in each of them at the study site for the two oak species (*Quercus canariensis* and *Quercus suber*). White bars represent the mean proportion cover of each microhabitat type. Vertical bars denote standard error values. Note that the represented scale of the right Y-axis is different for each of the two studied oak species.

As expected, the probability of seed survival substantially decreased in the reproductive cycle where the estimated seed production – and consequently the resource availability for seed consumers – was lower, supporting the predator-satiation hypothesis (Janzen 1970; Silvertown 1980).

Seedling survival during the first 2 years was the most limiting process at the seedling stage. Since most seedlings died during the dry summer season, the main cause of mortality may be attributable to the water stress experienced during this period, as has been reported by other studies in Mediterranean ecosystems (Lloret, Casanovas & Peñuelas 1999; Rey & Alcántara 2000; Castro *et al.* 2005; Pulido & Díaz 2005).

Species ranking diverged substantially through the life history stages considered in this study due to different ontogenetic trends among species. *Quercus canariensis* outperformed its coexisting oak species during the processes of seed and seedling survival, but this reversed during seed germination. These interspecific differences in seed germination seem to be an intrinsic characteristic of the two studied species, as demonstrated in a parallel study under controlled conditions (Pérez-Ramos & Marañón 2009). *Quercus canariensis* acorns were removed slowly and at lower proportion than those of *Q. suber*, likely due to its generally smaller seed size (Pérez-Ramos *et al.* 2008b). Afterwards, seedlings of the deciduous species emerged earlier, allowing them to benefit from growing season resources for a longer period of time (Urbieta *et al.* 2008b). A shortened time to emergence likely enabled seedlings to

develop more extensive root systems, thus enhancing their probability of survival during the dry period (Seiwa 2000; Verdú & Traveset 2005; Castro 2006). As a consequence of these among-species discordances, our overall-recruitment models predicted that *Q. suber* was more recruitment-limited than *Q. canariensis*, a fact that was supported by the lower density of saplings detected for this species at the study area. As predicted by theory (MacArthur & Levins 1964; Chesson 2000), shifts in species' performance rankings between different situations constitute a necessary, but not always sufficient, condition for species coexistence. Our findings suggest that among-species rank reversals through ontogeny could contribute to regeneration niche partitioning in the two co-occurring oak species, as will be discussed further on.

WITHIN-SPECIES ONTOGENETIC CONFLICTS ALONG A PLANT COVER GRADIENT

A highly significant contribution of this study is the demonstration of within-species ontogenetic conflicts along a wide and continuous gradient of plant cover. Recruitment-driving processes during the seed and the seedling stages showed opposing tendencies along the plant cover gradient. Seed survival severely decreased with increasing plant cover, which could be attributed to the higher foraging activity of rodents in more closed microhabitats where they find more protection against their own predators (Herrera 1995; Hulme & Hunt 1999; Gómez, García & Zamora 2003; Pons & Pausas 2007; Pérez-Ramos *et al.* 2008b). In contrast, seed germination and seedling emergence were reduced in more open microhabitats owing to the unfavourable environmental conditions generated by events of temporal waterlogging that are more frequent in this type of microsite that often have clayey soils (Urbieta *et al.* 2008b). The negative effects of waterlogging are related to the fact that seedlings may have experienced low oxygen concentration, potentially curtailing respiration and delaying root and shoot development before the onset of the dry period (Urbieta *et al.* 2008b). Similar uncouplings between seed and seedling stages have been previously documented in other studies that compared the suitability of different microhabitats with contrasting abiotic conditions (e.g. Houle 1994, 1998; Schupp 1995; Rey & Alcántara 2000). To our knowledge, the present study is the first that describes seed–seedling conflicts at very fine spatial scale across the exploration of a continuous gradient of microhabitat conditions.

Interestingly, another ontogenetic conflict was detected within the seedling stage in the case of *Q. suber*. Specifically, the higher success of shaded microhabitats for initial recruitment was reversed in 3-year-old seedlings. 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 (Pérez-Ramos *et al.* 2010). The absence of a negative response to light scarcity in the deciduous species supports previous studies identifying these species as highly shade-tolerant during early life history stages (Gómez-Aparicio, Valladares & Zamora 2006; Quero *et al.* 2006).

Most studies on ontogenetic niche shifts have only compared two life history stages (but see Jordano & Herrera 1995; Quero *et al.* 2008), such as seedlings and mature trees (Cavender-Bares & Bazzaz 2000) or juveniles of different ages (Espelta, Riba & Retana 1995). However, our multi-stage demographic approach has enabled us to identify several ontogenetic conflicts among subsequent demographic stages along a natural gradient of microhabitat conditions.

CONFLICTING SELECTIVE PRESSURES ON SEED SIZE AMONG DEMOGRAPHIC STAGES: IS THERE AN OPTIMAL SEED SIZE?

Conflicting selective pressures on seed mass through ontogeny have been found to be more complex than previously proposed (Eriksson & Jakobsson 1999) and can occur at different stages, from a dispersed seed to an established seedling. Larger seed size exercised a positive effect on different processes within the seedling stage, but reduced the probability to escape from predation during the seed stage, as reported for *Quercus ilex* in other Mediterranean forests (Gómez 2004). A possible advantage of larger seeds is that they could germinate above deeper leaf litter (Molofsky & Augspurger 1992). In addition, larger seeds produced larger seedlings, which are able to gain more access to limited resources with steep vertical gradients such as light or soil moisture (Leishman & Westoby 1994; Metcalfe & Grubb 1995). The advantages of large acorns on the seedling stage disappeared after the second year, consistent with previous studies demonstrating that effects of seed size decline over time (Castro 1999; Baraloto, Forget & Goldberg 2005b; Poorter & Rose 2005).

The consequences of seed size for population dynamics will depend on the probability of different microhabitats to receive seeds of larger or smaller size. It would be interesting to investigate how seed size modulates seed dispersal patterns by different animals and species-specific seed 'fate' through the mosaic of different microhabitats found in these forests (see example for a bird-dispersed plant in Alcántara *et al.* 2000).

The existence of opposing selective pressures on seed mass and their differential influence on the two studied oak species might support the occurrence of species-specific optimal seed sizes. In the case of *Q. canariensis*, our overall-recruitment models predicted that small-sized seeds were favoured against the larger ones due to their lower probability of predation as well as the absence of an effect of this trait on the subsequent life history stages. Nevertheless, the small fraction of large seeds escaping from predation produced larger seedlings, resulting in a trade-off among different fitness components (*sensu* Baraloto, Goldberg & Bonal 2005a). In *Q. suber*, however, the peak of maximum recruitment was predicted for seeds of large or intermediate size, depending on the natural resource availability for seed predators. Thus, in a low-production cycle, the positive effects of larger seeds on the seedling stage were partially altered by their opposite negative effects on seed survival, displacing the peak of maximum recruitment

towards intermediate values of seed size. The species-specific optimal seed sizes predicted by our modelling approach may explain why the natural phenotypic selection has favoured that *Q. canariensis* produces smaller-sized acorns compared with its co-occurring oak species at the studied forest sites.

REGENERATION NICHE AND OAK SPECIES COEXISTENCE

The exploration of a wide gradient of plant cover allowed us to determine a high variation among microhabitats in their specific suitability for overall recruitment, as a result of different selective forces operating at different stages of the regeneration cycle. In both oak species, the negative effects of denser plant cover on the seed stage were not counteracted by the positive effects exercised on the subsequent demographic processes occurring over the seedling stage. Since seed predation was the most limiting process, safe sites for recruitment could be defined as those where seeds showed a lower predation probability. As a consequence, the overall probability of recruitment strongly decreased as plant cover increased in both oak species. However, the less pronounced effect of this process on *Q. canariensis* acorns generated a peak of maximum recruitment at low-intermediate values of plant cover. Interestingly, this recruitment peak was displaced towards the lower end of the LAI gradient during a low-production cycle, where the lower abundance of resources decreased the probability of a seed to escape from predators and establish as a seedling (Kelly 1994; Kelly & Sork 2002; Pérez-Ramos & Marañón 2008). The spatial patterns predicted by our overall-recruitment models were validated with the static survey of sapling abundance conducted at the study area, which showed that microhabitats located under trees harboured the highest densities of saplings (particularly of *Q. canariensis*).

Overall, our modelling approach provides some evidence for regeneration niche partitioning between the two co-occurring oak species, in turn, influencing their distribution patterns as saplings and adults at the study area. These results are consistent with the tendencies reported by previous studies proposing deciduous species to be more frequent in habitats with denser canopy, where water and nutrient availabilities are usually higher (Aerts 1995; Maltez-Mouro, García & Freitas 2009). The differential species responses to microhabitat conditions detected in our study at early life stages support the role of regeneration niche partitioning as potential driver of species coexistence and tree community structure in Mediterranean forests (Grubb 1977; Silvertown 2004). Ontogenetic conflicts and among-species rank reversals in recruitment lead to spatially discordant patterns of regeneration among microhabitats with different plant cover as well as between coexisting species differing in seed size. We conclude that within- and among-species differences through plant ontogeny, arising from differential response patterns to microhabitat heterogeneity and seed size variation, could be of great importance for oak species niche segregation, driving stand dynamics and species spatial distribution in the landscape. The information provided

here about the most favourable conditions and traits for recruitment in the two oak species, with known regeneration impairments, could be applied to improve ecologically based management and restoration strategies in Mediterranean forests.

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Supporting Information

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

Appendix S1. Summary of the best-fitted models analyzing the variation of stage-specific probabilities of recruitment and seedling growth along the explored range of plant cover (LAI) and seed mass.

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Appendix 1. Summary of the best-fitted models analyzing the variation of stage-specific

probabilities of recruitment and seedling growth along the explored range of plant cover (LAI) and seed mass. The results of bivariate models in which seed mass was added either additively (+) or multiplicatively (*) are also shown. The signs of the relationships (positive or negative) between each dependent variable and the selected predictors are also indicated, separated by commas. Bold font denotes models with equivalent empirical support (i.e., $\Delta AIC < 2$). LIN, Linear model; EXP, Exponential model; MM, Michaelis-Menten model; LOG, Logistic model; POW, Power model; NULL, Null model.

	<i>Quercus canariensis</i>					<i>Quercus suber</i>					
	Factor	Best fit	Relation	AIC	Δi	Factor	Best fit	Relation	AIC	Δi	
Seed survival (2003/04 cycle)	LAI	LIN	(-)	357.931	0.00	Seed survival (2003/04 cycle)	LAI	EXP	(-)	255.92	0.00
		Null		376.71	18.78			Null			282.89
Seed survival (2004/05 cycle)	LAI* seed mass	EXP	(-, -)	139.87	0.00	Seed survival (2004/05 cycle)	LAI	LIN	(-)	128.28	0.00
	LAI	EXP	(-)	143.49	3.62		LAI	EXP	(-)	129.54	1.26
	LAI	LIN	(-)	144.25	4.38		Null			131.20	2.92
	LAI	LOG	(-)	144.56	4.69	Seed germination	LAI+ seed mass	LIN	(+, +)	621.07	0.00
	Seed mass	EXP	(-)	143.10	3.23		LAI	POW	(+)	626.56	5.49
	Seed mass	LOG	(-)	144.64	4.77		LAI	LIN	(+)	626.60	5.53
	Null		147.28	7.41	LAI		EXP	(+)	626.93	5.85	
Seed germination	LAI	POW	(+)	767.77	0.00	LAI	LOG	(+)	627.21	6.13	
	LAI	LOG	(+)	767.86	0.09	LAI	MM	(+)	628.38	7.30	
	LAI	LIN	(+)	767.99	0.23	Seed mass	EXP	(+)	629.77	8.70	
	LAI	EXP	(+)	768.34	0.57	Seed mass	POW	(+)	629.78	8.71	
	LAI	MM	(+)	768.70	0.93	Seed mass	LIN	(+)	629.81	8.74	
Seedling emergence		Null		279.02	0.00	Seed mass	LOG	(+)	629.84	8.77	
						Seed mass	MM	(+)	629.86	8.78	
1st-year seedling survival							Null		636.06	14.98	
		Null		284.51		Seedling emergence	LAI+ seed mass	LIN	(+, +)	699.62	0.00
2 nd -year seedling survival							LAI* seed mass	LOG	(+, +)	700.24	0.63
		Null		116.57			LAI* seed mass	MM	(+, +)	700.86	1.24
3 rd -year seedling survival							LAI	LIN	(+)	702.75	3.14
							LAI	POW	(+)	702.80	3.18
1st-year seedling aboveground biomass	Seed mass	LIN	(+)	110.40	0.00		LAI	LOG	(+)	703.94	4.32
		Null		108.32	2.08		LAI	MM	(+)	704.40	4.79
2 nd -year seedling aboveground biomass							LAI	EXP	(+)	704.53	4.91
		Null		364.42			Seed mass	MM	(+)	723.36	23.74
1st-year seedling survival							Seed mass	LOG	(+)	723.45	23.84
							Seed mass	POW	(+)	723.55	23.93
2 nd -year seedling survival							Seed mass	EXP	(+)	723.74	24.13
							Seed mass	LIN	(+)	723.78	24.17
1st-year seedling aboveground biomass							Null		728.73	29.12	
						Seed mass	LOG	(+)	357.77	0.00	
2 nd -year seedling aboveground biomass						Seed mass	MM	(+)	358.05	0.29	
						Seed mass	LIN	(+)	358.96	1.19	
1st-year seedling survival							Null		368.54	10.77	
							Null		117.42		
2 nd -year seedling survival						3 rd -year seedling survival	LAI	LOG	(-)	98.18	0.00
								Null		168.39	70.20
1st-year seedling aboveground biomass						1st-year seedling aboveground biomass	Seed mass	MM	(+)	501.44	0.00
							LIN	(+)	504.61	3.17	
							EXP	(+)	505.72	4.28	
							Null		508.31	6.87	
2 nd -year seedling aboveground biomass						LAI	EXP	(-)	294.58	0.00	
							LIN	(-)	295.87	1.29	
							Null		304.01	9.43	