



Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Population differences in juvenile survival under increasing drought are mediated by seed size in cork oak (*Quercus suber* L.)

J.A. Ramírez-Valiente ^a, F. Valladares ^{c,d}, L. Gil ^b, I. Aranda ^{a,*}

^a Instituto Nacional de Investigación Agraria y Tecnología Agroalimentaria, Centro de Investigación Forestal, Unidad Mixta INIA-UPM, Carretera Coruña Km 7.5, E-28040 Madrid, Spain

^b Unidad de Anatomía, Fisiología y Genética Forestal, Escuela Técnica Superior Ingenieros de Montes, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040 Madrid, Spain

^c Instituto de Recursos Naturales, Centro de Ciencias Medioambientales, CSIC, Serrano 115, E-28006 Madrid, Spain

^d Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/Tulipán s/n, E-28933 Móstoles, Spain

ARTICLE INFO

Article history:

Received 4 November 2008

Received in revised form 12 January 2009

Accepted 18 January 2009

Keywords:

Quercus suber

Acorn size

Populations

Climate change

Drought

ABSTRACT

Many studies have focused on the physiological and morphological responses of *Quercus suber* to high temperatures and summer drought. Nevertheless, our understanding of the potential of this species to cope with climate change is incomplete. An increase in severity, length and frequency of summer droughts is expected in the Iberian Peninsula over the 21st century. We investigated the potential of cork oak to adapt to climate change in a 4-year study comparing seedling survival from thirteen Spanish populations in a common garden. Acorn size was evaluated as a possible adaptive trait enhancing stress resistance during establishment. Populations originating from sites with the driest summers exhibited the highest survival rates under dry conditions. These populations were characterized by bigger acorns, suggesting selection for this trait across sites experiencing drought. Our findings reveal that northern populations are not well adapted to cope with increasing drought but suggest that they might cope well with the moderate drought increase expected for these zones. However, continental populations are intermediately adapted to dry conditions, while drastic and fast increases in summer droughts are expected to occur in these regions. This extensive and quick change will provide scant chances to adapt making the populations of cork oak in these regions particularly vulnerable to the future climatic conditions.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The Mediterranean basin is one of the European regions expected to be most affected by climate change, with temperatures expected to increase at least 2–4 °C, over the next century (Christensen et al., 2007). Precipitation is expected to decrease during summer and autumn, but to increase in winter (Déqué et al., 1998), with an overall decrease in water availability due to increased evapotranspiration, especially during the summer. If this change is as rapid as expected, forest climatic zone boundaries could move more rapidly than forest tree species can migrate (Davis and Zabinski, 1992; Higgins and Harte, 2006), so the survival of forest tree species will increasingly depend on evolutionary change (Davis and Shaw, 2001; Etterson and Shaw, 2001). In the short term, the potential of species to respond to these rapid changes will depend on their phenotypic

plasticity as much as intra-specific genetic variation for adaptive traits (Marchin et al., 2008).

Summer drought is the most important ecological filter to plant establishment in Mediterranean ecosystems and plants exhibit many morphological and physiological adaptations to cope with this environmental stress (Larcher, 2000). Seed size is one of the most important traits influencing the early stages of the life cycle of the plant. The importance of seed size in governing the fitness of progeny has been supported by extensive empirical evidence (Gómez, 2004); several studies have found that larger seeds help seedlings to endure drought (Leishman and Westoby, 1994; Seiwa, 2000), and promote germination (Milberg et al., 2000; Pearson et al., 2002), emergence (Castro, 1999), growth and survival (Seiwa, 2000; Baraloto et al., 2005). Species and population-level variation in this trait can be due to either maternal effects or local adaptation (Díaz-Fernández et al., 2004). Maternal effects can be caused by the maternal genotype, the maternal environment, or both (Schmitt et al., 1992). However, environmental maternal effects are generally stronger than genetic effects (Byers et al., 1997; Hunt and Simmons, 2002). Seed size can be affected by maternal environment, since it is influenced by resource

* Corresponding author. Tel.: +34 91 3476857; fax: +34 91 3572293.

E-mail addresses: valladares@ccma.csic.es (F. Valladares), aranda@inia.es (I. Aranda).

availability (Sultan, 1996; Krannitz et al., 1999; Wulff et al., 1999) and environmental stresses influencing the mother plant's conditions during seed formation (Wolfe, 1995; Sultan, 1996; Vaughton and Ramsey, 1998). Seed size has been observed to be an adaptive trait associated with environmental variables such as latitude (Yakimowski and Eckert, 2007), altitude (Yamada and Miyaura, 2005), temperature (Murray et al., 2004) and water availability (Parciak, 2002) but also with dispersal strategy and growth form (Moles and Westoby, 2004a). There are clearly two distinct time scales, the ecological and the evolutionary ones, but also to spatial scales, those corresponding to an individual tree vs. those corresponding to populations of trees under similar environmental conditions. Trends over populations provide information on evolution of seed size while individual responses to environmental conditions such as those by Quero et al. (2008) provide clues for mechanisms. Selection pressure on seed size acting through offspring fitness is widely accepted (Rees, 1997; Sakai et al., 1998; Leishman et al., 2000; Messina and Fox, 2001 and references therein). The importance of seed size lies in the influence that it exerts on seedling performance during establishment, especially under both competitive and resource-limiting conditions (Moles and Westoby, 2004b).

Cork oak (*Quercus suber* L.) is an evergreen tree species with a wide distribution in the western Mediterranean basin. It displays intermediate tolerance to drought and high temperatures, being considered a transitional species between the high drought-tolerant evergreen oaks such as *Quercus ilex* or *Quercus coccifera* (David et al., 2007) and the more mesic deciduous ones such as *Quercus faginea* or *Quercus pyrenaica* (Mediavilla and Escudero, 2003). In the Iberian Peninsula, the largest cork oak forests are located in Portugal and southwestern Spain, with other smaller forested regions in the north east of the Peninsula. Populations of cork oak become scarce and scattered going northward due to cold winters and eastward due to dry conditions and basic soils.

Models predicting suitable habitat for Iberian forest tree species under future climate change scenarios indicate that the range of *Q.*

suber could decrease drastically in southern and inland Spain although it should persist along the southwestern coasts (Benito Garzón et al., 2008). It could also extend its distribution northwards and to higher altitudes benefiting from a potential increase in winter temperatures (Benito Garzón et al., 2008). However, those models that predict species redistribution with climate change largely ignore within-species genetic variation (Hampe and Petit, 2005). Genetic variation at the population level may extend or curtail the predicted range of a species more than previously assumed (Higgins and Harte, 2006).

Our overall goal was to determine the capacity of *Q. suber* to cope with expected climate change by comparing population-level differences in survival in a common garden. Our specific objectives were (1) to quantify population-level variation in survival under dry conditions, (2) to estimate the influence of acorn size on the response of *Q. suber* to local climatic conditions and (3) to identify which populations would be the most susceptible to the climate change expected for the region.

Owing to large differences in environmental conditions among populations, we expected that *Q. suber* presents high inter-population variation in adaptive traits as a consequence of adaptation to the climate at the place of seed origin. These differences in adaptive traits should be reflected in the probability of survival under standardized conditions in a common garden. We also expected to find divergence among populations in acorn size. We anticipated that individuals from more stressed sites have the biggest acorns as an adaptation to more intensive droughts (e. g. Murray et al., 2004).

2. Materials and methods

2.1. Common garden

The study was performed in a common garden within the *La Sierra de Andújar* Natural Park (38°21'54"N, 3°51'40"W, 560 m,

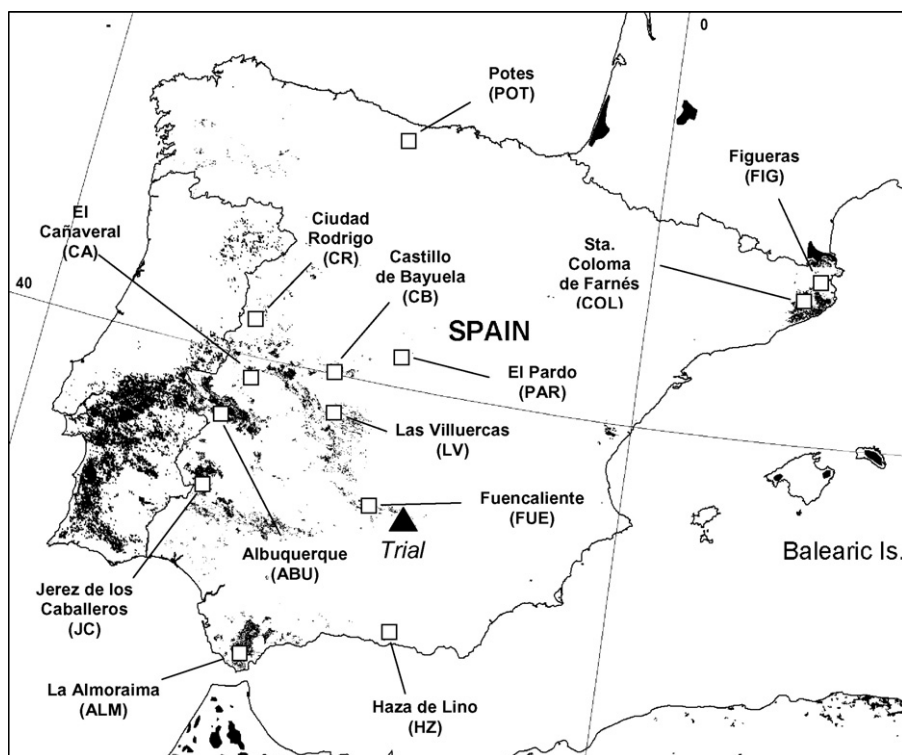


Fig. 1. Location of the sampled populations of *Quercus suber* and trial site (triangle) within the distribution area of the cork oak in the Iberian Peninsula. Map adapted from Aronson et al. (in press).

Table 1
Summary of mean weather conditions over a 20-year period (1987–2005) and during the years of study (1998–2001). Temperature values are in °C and precipitation values are in mm. Xerothermic index = $\sum(2TM - P)$ if $2TM > P$ or $Xi = 0$ if $2TM \leq P$, where TM is the monthly mean of the maximum and minimum temperatures (°C) and P is the monthly precipitation (mm) (Grossmann et al., 2002).

Year	Annual mean temperature	Summer mean maximum temperature	Hottest month mean maximum temperature	Annual precipitation	Four driest months precipitation	Summer precipitation	Xerothermic index
1998	13.1	32.7	34.5	415.3	46.2	25.2	132.4
1999	12.8	33.7	35.6	471.0	12.1	2.7	148.7
2000	13.7	32.6	34.0	658.7	27.4	10.1	149.5
2001	15.5	33.2	34.2	814.2	55.2	7.9	141.9
Period (1987–2005)	14.8	32.5	34.4	617.6	72.0	34.3	111.8

Table 2
Location and characterization of the parent populations, current and expected future climatic conditions. CGMC2 under A2 scenario was used to estimate the expected future climate. Annual mean temperature (°C), annual mean precipitation (mm) and xerothermic index (Xi)^a for the reference period and three future scenarios.

Pop	Latitude	Longitude	Annual mean temperature (°C)				Annual mean precipitation (mm)				Xerothermic index			
			Reference period	2011–2040	2041–2070	2071–2100	Reference period	2011–2040	2041–2070	2071–2100	Reference period	2011–2040	2041–2070	2071–2100
POT	43°09'N	4°37'W	13.2	14.4	15.6	17.1	736.4	701.1	674.5	597.2	21.0	41.0	67.6	78.9
FIG	42°24'N	2°48'E	15.7	16.9	18.1	19.5	648.3	677.3	611.7	571.1	43.2	57.4	76.2	100.5
COL	41°54'N	2°30'E	15.6	17.1	18.3	19.7	805.2	815.4	744.6	690.7	14.8	20.9	41.0	61.2
CR	40°35'N	6°26'W	13.2	14.7	16.1	17.9	524.5	500.6	436.3	360.4	62.4	104.4	138.3	182.3
PAR	40°31'N	3°45'W	13.5	15.1	16.5	18.4	474.2	468.3	420.6	274.6	90.6	117.6	142.5	226.5
CB	40°07'N	4°31'W	16.6	18.2	19.7	21.6	644.2	647.7	559.6	450.4	123.1	165.1	190.3	244.2
CA	39°22'N	6°22'W	16.8	18.5	20.0	21.9	701.5	586.6	527.6	426.0	123.1	200.3	222.7	279.3
LV	39°22'N	5°21'W	15.4	17.0	18.4	20.4	1008.3	981.4	864.2	705.8	87.1	135.1	164.2	194.9
ABU	39°13'N	7°13'W	15.4	16.9	18.2	20.0	643.2	623.5	550.9	432.5	112.9	164.7	186.2	233.5
FUE	38°24'N	4°16'W	14.8	16.6	18.0	20.0	435.8	412.1	343.3	257.5	123.6	162.7	207.7	271.7
JC	38°13'N	6°42'W	16.1	17.7	19.1	21.0	627.3	594.9	513.4	419.0	119.6	167.7	167.9	211.7
HZ	36°47'N	3°18'W	13.0	14.5	15.8	17.4	607.1	591.3	507.0	351.6	109.9	141.9	167.7	206.1
ALM	36°16'N	5°22'W	17.4	18.9	19.9	21.4	659.2	560.3	458.5	404.8	131.3	186.7	220.8	237.3

^a Xi = $\sum(2TM - P)$ if $2TM > P$ or $Xi = 0$ if $2TM \leq P$, where TM is the monthly mean of the maximum and minimum temperatures (°C) and P is the monthly precipitation (mm) (Grossmann et al., 2002).

Jaen) (Fig. 1). The climate there is continental Mediterranean with hot dry summers and cold winters. Average annual precipitation is 617 mm and average annual temperature is 14.7 °C. The minimum mean monthly temperature is 0.8 °C in January and the maximum mean monthly temperature in July is 34.4 °C (AEMET, Agencia Estatal de Meteorología, Table 1). The trial was laid out in a randomized complete block design and contained 13 populations, spanning the natural range of cork oak within Spain (Table 2). It included 30 blocks and four plants per population within each block (120 plants per population in total). Seedlings were planted with a spacing of 3 m × 3 m in a square plot.

2.2. Material and population characterization

Seed collection from native stands was made during the autumn–winter of 1996 from trees more than 100 m apart, to minimize the risk of sampling closely related individuals (see Skabo et al., 1998). Acorns were harvested from 20 to 30 trees per population. A sample of seeds (from 28 to 49 per population) was used to characterize the average acorn mass and size on a dry mass basis for each population (Table S1).

Acorns were carried to a nursery and sown early in 1997. Seedlings were grown for a year under optimum conditions prior to transplanting to the study site (spring 1998). Measurements of seedling height before planting were carried out on a sample of thirty individuals within each population (Table S1). A one-way ANOVA was performed to test for differences in seed mass and width and length among populations. Another one-way ANOVA was used to evaluate differences in seedling height. Spearman's correlation analysis was carried out to test for association between acorn mass and seedling height. The program STATISTICA v 6.0 (Statsoft, Tulsa, OK, USA) was used for statistical analyses.

2.3. Climate in the common garden and sites of origin

The study was carried out during the 4 years directly following planting in the common garden. Climatic data for this period were obtained from a meteorological station located 4 km from the trial site. Likewise, climate data for the site of each parent population were obtained from their nearest meteorological station (AEMET, Agencia Española de Meteorología) A xerothermic index (Xi) was calculated from the climatic data, following Grossmann et al. (2002), using the formula: $Xi = \sum(2TM - P)$ if $2TM > P$ or $Xi = 0$ if $2TM \leq P$, where TM is the monthly mean of the maximum and minimum temperatures and P is the monthly precipitation.

2.4. Survival

Survival was assessed every autumn for 4 years. We recorded “annual survival” each year and “final survival” in the last year of the study. “Annual survival” was defined as survival from year to year, ignoring those seedlings that had died at the time of the previous census. This produced an unbalanced design after the first year, but survival measurements were as independent as possible. Linear logistic models were constructed for final and annual survival data using proc GENMOD in the statistical package SAS 9.1 (SAS/STAT[®] Software; SAS Institute). A binomial distribution of the data was assumed and a logit function was used to link function and type 1 analysis.

The model equation is:

$$\log \left[\frac{Y_{ij}}{1 - Y_{ij}} \right] = \mu + P_i + B_j + \epsilon_{ij}$$

where μ is the general media, B_j represents the main effect of the j block; P_i represents the main effect of the i population; ϵ is the residual error for Y.

2.5. Survival, seed effects and increasing droughts

To test whether seed size was maternally affected or locally adapted non-parametric Spearman's correlations were performed between acorn traits and climate at the site of origin on the parent population. If subject to maternal effects, we expected that seed size was strongly influenced by the climate in 1996 (the year of ripening and collection) at the population-origin site, and if seed size was due to local adaptation we should find a stronger relationship between it and average climate.

To examine whether populations from drier sites responded better under dry conditions, we implemented non-parametric Spearman's correlations between final and annual survivals, the xerothermic index of the native stands and geographic data. Seedling height and average acorn size from each population were included in these analyses in order to examine whether these traits affect survival.

To help us consider how these populations might respond to climate change, we determined the expected future climate for the studied populations over the three time periods (2011–2040, 2041–2070 and 2071–2080) by extrapolation of numeric data calculated using the model CGMC2 developed by the Canadian Climate Modelling Centre (Flato et al., 2000). As anthropogenic emissions of CO₂ have increased more than those proposed by any recent model (Canadell et al., 2007), we estimated the expected future climate under the A2 scenario. This family of scenarios describes a global socio-economic situation that would cause the highest increases in the anthropogenic emissions of carbon dioxide and other greenhouse gases (IPCC, 2007). We calculated the expected future xerothermic indices for each period and population. To evaluate how fast the climate could change, we subtracted the xerothermic index value for one period from the value for the preceding period, to obtain the slope of the expected change. Likewise, to estimate the magnitude of the expected change, we calculated this difference in the xerothermic indexes between the first and the last of these periods.

3. Results

3.1. Climate in the common-garden site during the 4 years of study

In general, the climate during the study was characterized by very low rainfall and normal/high temperatures during summer (Table 1). The most severe conditions occurred in 1999, when low annual rainfall (471.0 mm, 76.3% of the average value) and a dry summer (2.7 mm, 7.9% between June–September) coincided with relatively hot temperatures (33.7 °C maximum temperatures in summer, Table 1). However, 2000 was also severe and at its peak summer drought was a little more intense than in 1999 (xerothermic index = 149.5 in 2000 versus 148.7 in 1999).

3.2. Characterization of populations according to seed mass

Seed mass, width and length varied highly significantly ($p < 0.0001$) among populations ($F_{12,499} = 47.953, 71.364$ and 24.866 , respectively) and were strongly correlated with each other ($r = 0.88, 0.88$ and 0.68 for mass vs. width, mass vs. length and width vs. length, Table 3). ALM population had the heaviest (7.74 ± 0.23 g) and the largest acorns (width = 17.30 ± 0.20 mm, length = 38.52 ± 0.46 mm) (Table S1). Seeds from FIG were the lightest (2.71 ± 0.19 g) and the shortest (22.42 ± 0.83 mm) and those from POT were the narrowest (13.96 ± 0.21 mm) (Table S1). Acorn mass was significantly negatively correlated with latitude, and average and 1996 summer precipitation (Figs. 2 and 3). Seedling size also differed among populations ($p < 0.0001$), ranging from 5.15 ± 0.44 cm for POT to 19.73 ± 1.47 cm for JC (Table S1). Acorn

parameters and seedling height were positively correlated (mass: $r = 0.81, p = 0.001$; width: $r = 0.82; p = 0.001$ and length: $r = 0.77, p = 0.002$, respectively, Table 3).

3.3. Survival

Final survival was highly significantly different among populations ($p < 0.0001$, Table 4). It ranged from $24.2 \pm 3.9\%$ for FIG to $60.8 \pm 4.5\%$ for the LV population (Fig. 4). Likewise, annual population survival rates also differed significantly in 1998 ($p < 0.0001$) and

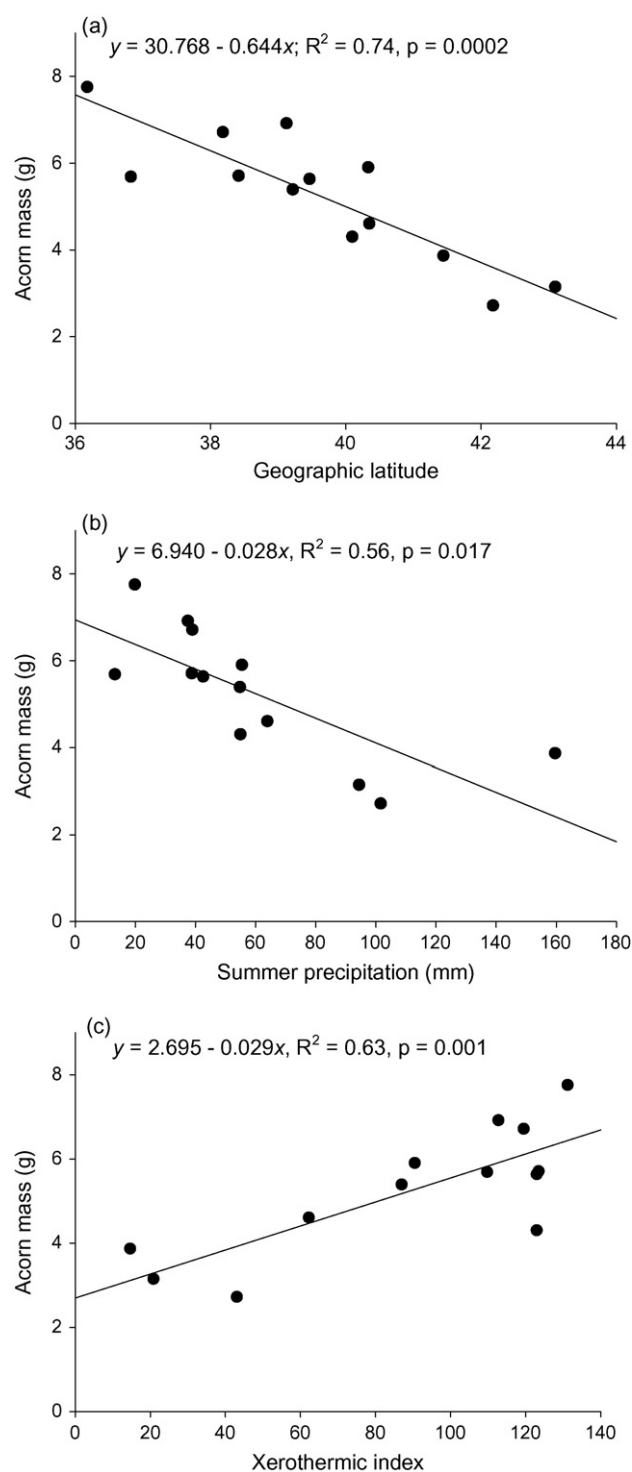


Fig. 2. Relationships between acorn mass and latitude of origin (a), summer precipitation (b) and xerothermic index (c) for 13 populations of *Quercus suber*.

Table 3
Spearman's coefficient correlation (*r*) among annual survivals (S1998–S2001), final survival (FS2001), geographic data, xerothermic index (Xi) at the place of origin, seedling height before planting and acorn size and mass.

	S1998	S1999	S2000	S2001	FS2001	Longitude	Latitude	Xi	Seedling height	Acorn width	Acorn length	Acorn mass
S1998	1.00	0.71**	0.64*	0.08	0.88***	-0.43	-0.67*	0.63*	0.75**	0.70**	0.66*	0.69**
S1999	0.71**	1.00	0.61*	0.03	0.91***	-0.45	-0.59*	0.51 ¹	0.73**	0.80**	0.73**	0.75**
S2000	0.64*	0.61*	1.00	0.33	0.82***	-0.60*	-0.32	0.38	0.42	0.58*	0.62*	0.57*
S2001	0.08	0.03	0.33	1.00	0.23	-0.65	-0.14	0.41	0.02	0.01	0.28	0.13
FS2001	0.88***	0.91***	0.82**	0.23	1.00	-0.57*	-0.60*	0.60*	0.73**	0.77**	0.76**	0.75**
Longitude	-0.43	-0.45	-0.60*	-0.65	-0.57*	1.00	0.47	-0.63*	-0.40	-0.57*	-0.73**	-0.65**
Latitude	-0.67*	-0.59*	-0.32	-0.14	-0.60*	0.47	1.00	-0.82**	-0.71**	-0.79**	-0.87***	-0.86***
Xi	0.63*	0.51 ^a	0.38	0.41	0.60*	-0.63*	-0.82**	1.00	0.71**	0.74**	0.84**	0.79**
Seedling height	0.75**	0.73**	0.42	0.02	0.73**	-0.40	-0.71**	0.71**	1.00	0.82**	0.77**	0.81**
Acorn width	0.70**	0.80**	0.58*	0.01	0.77**	-0.57*	-0.79**	0.74**	0.82**	1.00	0.90**	0.97***
Acorn length	0.66*	0.73**	0.62*	0.28	0.76**	-0.73**	-0.87***	0.84**	0.77**	0.90**	1.00	0.96***
Acorn mass	0.69**	0.75**	0.57*	0.13	0.75**	-0.65*	-0.86***	0.79**	0.81**	0.97***	0.96***	1.00

^a Marginally non-significant values ($p < 0.1$).
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

1999 ($p < 0.0001$). Also, there were marginally non-significant differences among populations in 2000 ($p = 0.083$) (Table 4). The lowest survival rates were from POT population in 1998 ($65.0 \pm 4.4\%$) and 1999 ($53.9 \pm 5.7\%$) and FIG in 2000 ($75.6 \pm 6.5\%$). LV in 1998 and 2000 (90.8 ± 2.6 , $92.9 \pm 2.8\%$, respectively) and ABU in 1999 ($79.7 \pm 4.0\%$) were the most successful populations.

3.4. Survival, environmental factors and maternal effects

Correlation analysis revealed a significant, positive relationship between final survival and initial seedling height ($r = 0.73$, $p = 0.004$, Table 3; Fig. 5a), and between final survival and acorn parameters (width: $r = 0.77$, $p = 0.002$; mass: $r = 0.76$, $p = 0.003$ and length: $r = 0.75$, $p = 0.003$, Table 3). A significant positive correlation

was present between final survival and the xerothermic index, meaning that seedlings from dry sites survived better ($r = 0.60$, $p = 0.032$, Table 3; Fig. 6b). Latitude and longitude were also negatively correlated with final survival ($r = -0.60$, $p = 0.029$ and $r = -0.57$, $p = 0.042$, respectively). Populations from southern and western sites had the highest survival. Survival in 1998 and 1999 was positively correlated with seedling height, acorn parameters and xerothermic index and negatively correlated with latitude (Table 3). Acorn mass and acorn size measurements were positively correlated with survival in 2000, and negatively correlated with longitude for both 2000 and 2001 (Table 3).

Future climate expectations for the original population sites are shown in Table 2. The climate is expected to become drier in all these sites. The largest increases in the intensity of summer drought (largest increases in xerothermic index) are expected in

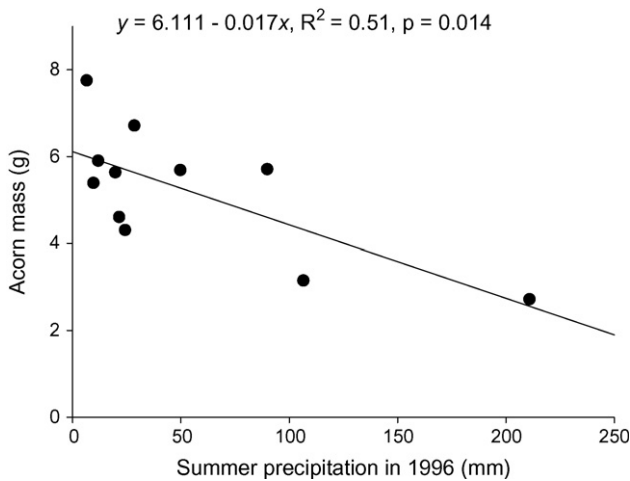


Fig. 3. Relationship between acorn mass and summer precipitation in 1996 (ripening and collection year) for 11 populations of *Quercus suber*. Sta. Coloma de Farnés (COL) and Albuquerque could not to be included in this analysis due to there was no available climatic data for these populations in 1996.

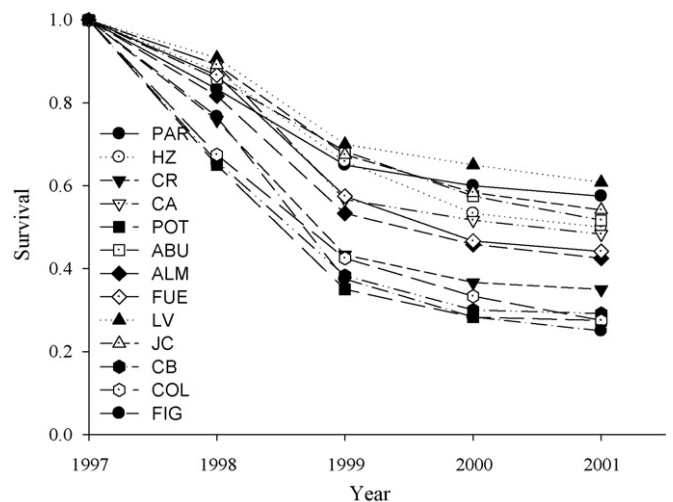


Fig. 4. Time course of survival in the common-garden trial during the 4 years of the experiment for 13 populations of *Quercus suber*.

Table 4
Chi-square and significance values from the Generalized Linear Models to determine the sources of variation for annual survivals (Syear) and final survival (FS2001).

Selladores trial	Chi-square					
	d.f.	S1998	S1999	S2000	S2001	FS2001
Population	12	77.299*** ($p < 0.001$)	52.842*** ($p < 0.001$)	19.243 ^{n.s.} ($p = 0.083$)	11.072 ^{n.s.} ($p = 0.523$)	93.44*** ($p < 0.001$)
Block	29	90.282*** ($p < 0.001$)	238.740*** ($p < 0.001$)	111.314*** ($p < 0.001$)	90.0770*** ($p < 0.001$)	361.02*** ($p < 0.001$)

Chi-square values with asterisks are significant (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

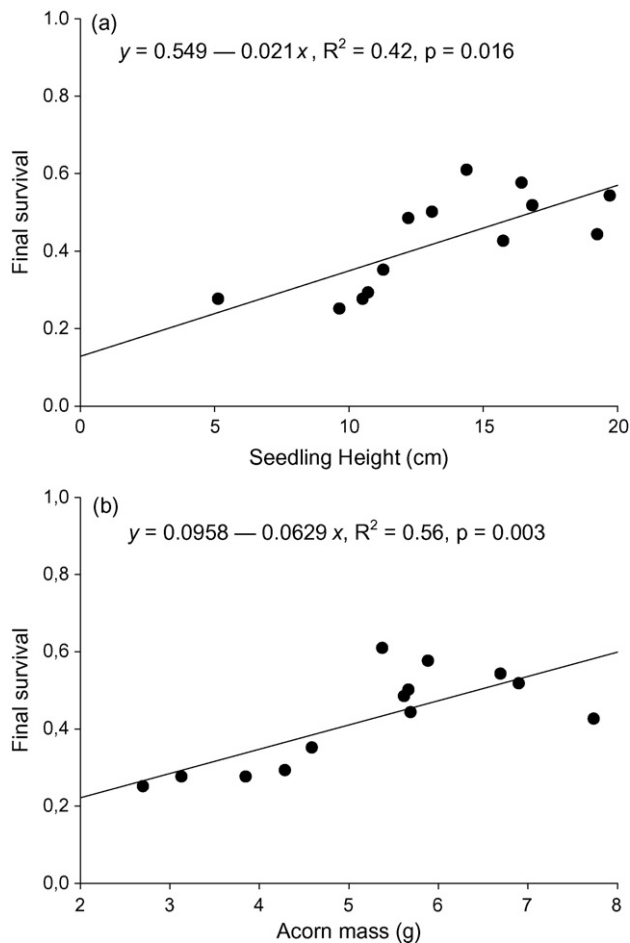


Fig. 5. Relationships between final survival in the common-garden trial and seedling height (a) and acorn mass (b) for 13 populations of *Quercus suber*.

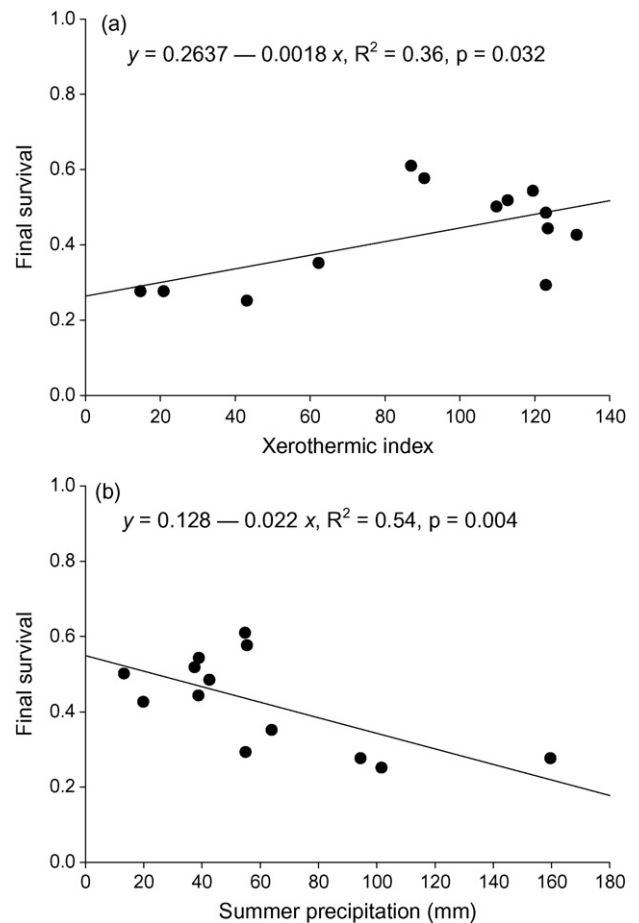


Fig. 6. Relationships between final survival in the common-garden trial and xerothermic index (a) and summer precipitation (b) for 13 populations of *Quercus suber*.

FUE (148.1), PAR (135.9) and CA (127.4), while COL (46.4), FIG (57.3) and POT (57.9) are expected to have the smallest increases in drought intensity (smallest increases of xerothermic index) (Table 2). At the end of the 21st century, COL (xerothermic index = 61.2), POT (78.9) and FIG (100.5) are expected to still be the wettest populations, while CA (279.3), CB (244.2) and ALM (237.3) are expected to become the driest sites. CA, ALM and ABU are expected to suffer the fastest change (xerothermic index is expected to increase by 77.2, 55.4 and 51.8 for the period of 2011–2040). The climate is expected to change least abruptly at northern sites (xerothermic index for the period 2011–2040 is expected to increase by 6.1, 14.2 and 20.0 in COL, FIG and POT, respectively).

4. Discussion

Q. suber seedlings in our common-garden trial exhibited variation in survival at the population level. Populations from the wettest sites had the smallest average seed size and the lowest final survival under the dry conditions at the trial site. During the 4-year experiment, conditions at the common-garden site were drier than those typically recorded over much of species current range (xerothermic index \approx 140). However, these values are still far milder than the expected conditions in the southern and central Iberian Peninsula (xerothermic index \approx 210) and are more extreme than those expected for the northern sites (xerothermic index \approx 80).

Our study makes three important findings. The first is that there is a geographical pattern in a phenotypic trait (seed size) related to

fitness in *Q. suber*. This contrasts with the low inter-population differentiation across the whole distribution range determined using isoenzymes markers ($F_{st} = 3.3\%$) (Jiménez et al., 1999). In general, neutral markers are weakly correlated with selected genetic diversity (McKay et al., 2001; Reed and Frankham, 2001; Frankham et al., 2002). *Q. suber* is an outcrossing, wind-pollinated species and is continuously distributed across most of its range. These characteristics are likely to enable high gene flow among populations via pollen, which would prevent genetic divergence via drift and may account for the lack of spatial genetic structure of neutral markers (O'Brian et al., 2007). However, if selection is strong enough, local adaptation may evolve even in presence of gene flow (Endler, 1977), thus representing a potential mechanism to explain the structured distribution of survival observed in the present study.

Our second finding is that *Q. suber* seedlings originating from sites characterized by more intensive droughts exhibited significantly higher survival rates than those from regions where drought is less severe (Fig. 6b). This pattern shows that populations differ in their tolerance to drought stress, and could be caused by differences in physiological and morphological traits as consequence of an adaptation to local environmental conditions. Nevertheless, (1) larger mean acorn size of seedlings sourced from sites with high summer drought and at southern latitudes, (2) the positive relationship between acorn traits and seedling height and (3) higher survival rates of larger seedlings during the first years of growth, suggest that selection favors bigger seeds at the harshest sites. Selection for other physiological or morphological

traits seems to be weak during the early years of seedling growth. In fact, only 2% of the variance in final survival explained by differences in xerothermic index was caused by factors other than acorn size.

Several studies have reported that bigger acorns lead to increased seedling growth (Buckley, 1982; Stock et al., 1990; Triphati and Khan, 1990; Osunkoja et al., 1994) and higher root/shoot ratios (Buckley, 1982; Lloret et al., 1999), which can improve the seedling performance by developing and maintaining deep and extensive root systems accessing water from deep within the soil profile (Dell and Havel, 1989). Selection for big acorns as a consequence of selection for tall seedlings is likely to be stronger in water-limiting environments, indeed, a positive relationship among acorn size, seedling height and summer survival has been reported for other Mediterranean oak species (Gómez, 2004).

Thus, local adaptation through natural selection can drive acorn size divergence. However, other mechanisms could also explain the distribution of seed size observed in the present study. One alternative explanation is a non-genetic effect of the climate and latitude on acorn size. Aizen and Woodcock (1992) found a positive relationship between acorn size and latitude in American *Quercus* species. In another study, Diaz-Fernandez et al. (2004) established that the percentage of biennial acorns produced and their ripening time differed with latitude across *Q. suber* populations. They suggested that a plastic response to shorter and (or) cooler growing season could explain these patterns. In our study, the conditions in 1996 were very similar to average climate and thus, there is a good correlation between acorn size and the two climatic data sets (see Figs. 2b and 3). This made it difficult to separate selection and environmental effects. However, acorn development in a Mediterranean climate is limited by high temperatures and summer drought, not by low temperatures, and in fact, humid and cooler summers could even favor acorn fattening. So, although environmental conditions probably affect acorn size, the effect of local adaptation is likely to be greater in our study.

Arguments for the adaptive value of seed size should also consider that although seed size promotes survival during early growth of progeny, its influence diminishes considerably with age (Schaal, 1984; Roach and Wulff, 1987; Lopez et al., 2003). In 2001, no correlation was observed between seedling height and survival indicating no effect of seed size during this year. Furthermore, height was assessed in a trial sub-sample in 2005 and neither acorn size nor initial height seedling effects were obtained (data not shown). However, accumulated survival in 2005 was still highly correlated to acorn size and initial seedling size (data not shown), indicating that although seed effects diminish rapidly with time, their imprint can remain for a long period of time in the populations.

The third major finding of this study is that not all populations are equally vulnerable to climate change. Under the ongoing climate change, all Iberian *Q. suber* populations are expected to incur more intensive drought periods, but Northern populations (FIG, POT, COL) are poorly adapted to dry conditions (low survival in the common garden and small acorn size). Theoretically, under a drier future climate these populations would not survive well. However, their xerothermic indexes are expected to remain low (low drought intensity) during the 21st Century. In fact, their xerothermic indexes for the immediate future are expected to be around half of that of the trial site during this study. Moreover, if the change in climate for these populations is slow and gradual (Table 2), they might be able to adapt to the drier environmental conditions. Southern populations (JC, HZ, ALM) are the best adapted to dry conditions (big acorns and high survival rates in the common garden). The climate change is expected to be fast for JC and ALM, and slow at the HZ population site. However, large increases of the intensity of summer droughts are not expected for

these populations (Table 2). Owing to their relatively good adaptation to dry conditions, and the moderate climate change expected in these areas, these populations are expected not to be seriously affected under the future climate scenarios. The outlook for inland, continental populations is not as bright as for northern and southern ones. These populations are intermediately adapted to dry conditions (moderate/high survival rates in the common garden and medium-sized acorns). However, drastic and fast increases in summer droughts are expected to occur in these regions (Table 3), so these central populations may not have much time to adapt to more arid conditions and could be substantially reduced.

The potential of the tree species to respond to the climate change will not only depend on the genetic variation in adaptive traits at among-population level, but also on the genetic variation at within-population level (Hamrick, 2004). Thus, intrapopulation divergence in adaptive traits should be analyzed in the future to better understand the potential of this species to cope with climate change.

In conclusion, our findings reveal important limitations in models assuming that all *Q. suber* populations in the Iberian Peninsula will respond similarly to climate change. *Q. suber* could disappear or become very scarce in most of inland Spain and Portugal due to the higher impact of the climate change in these areas combined with a moderate capacity of these populations to cope with arid conditions. Some new habitats may open up at the northern range limit, but overall the distribution of this species in Iberia is expected to be reduced.

Acknowledgements

We are grateful to Pedro Fernández, Laura Castro, Regina Chambel, José María Climent, Pilar Jiménez and all people from the Forestry School of Madrid that collaborated in the setting up of the cork oak field trials under the EU concerted action on cork oak, FAIR I CT 95 0202. We would like also to thank to Salustiano Iglesias and the DGB for the maintenance of the essays and partial financial support. We thank to AEMET (*Agencia estatal de Meteorología*) for providing the climatic data. We thank to Hervé Bohbot, Christelle Fontaine and James Aronson for providing the map of the distribution of cork oak. Finally, we would like to thank to Matthew Robson for reviewing the English version and his valuable suggestions. This work was funded by the Spanish Ministry of Science (PLASTOFOR, AGL-00536/FOR), Spanish Ministry of Environment and DGB (Convenio UPM-DGB). This study was also supported by a MEC-FPI fellowship (BES-2005-7573) to J.A.R.V.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2009.01.024.

References

- Aizen, M.A., Woodcock, H., 1992. Latitudinal trends in acorn size in eastern North American species of *Quercus*. *Can. J. Bot.* 70, 1218–1222.
- Aronson, J., Pereira, J.S., Pausas, J. Cork Oak Woodlands on the Edge: ecology, biogeography, and restoration of an Ancient Mediterranean Ecosystem, in press.
- Baraloto, C., Forget, P.M., Goldberg, D.E., 2005. Seed mass, seedling size and neotropical tree seedling establishment. *J. Ecol.* 53, 1156–1166.
- Benito Garzón, M., Sánchez de Dios, R., Sainz Ollero, H., 2008. Effects of climate change on the distributions of Iberian forests. *Appl. Veg. Sci.* 11, 169–178.
- Buckley, R.C., 1982. Seed size and seedling establishment in tropical arid dunecrest plants. *Biotropica* 14, 314–315.
- Byers, D.L., Plantenkamp, G.A.J., Shaw, R.G., 1997. Variation in seed characters in *Nemophila menziesii*: evidence of a genetic basis for maternal effect. *Evolution* 51, 1445–1456.
- Canadell, J.G., Le Quéré, C., Raupach, M.R., Field, C.B., Buitehuis, E.T., Ciais, P., Conway, T.J., Houghton, R.A., Marland, G., 2007. Contributions to accelerating

- atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18866–18870.
- Christensen, J.H., Hewitson, B., Busuioac, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Rueda, V.M., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Whetton, A.S.P., 2007. Regional climate projections. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), *Climate Change 2007: The Physical Science Basis*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 847–943.
- Castro, J., 1999. Seed mass versus seedling performance in Scots pine: a maternally dependent trait. *New Phytol.* 144, 153–161.
- David, T.S., Henriques, M.O., Kurz-Besson, C., Nunes, J., Valente, F., Vaz, M., Pereira, J.S., Siegwolf, R., Chaves, M.M., Gazarini, L.C., David, J.S., 2007. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiol.* 27, 793–803.
- Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. *Science* 292, 673–679.
- Davis, M.B., Zabinski, C., 1992. Changes in geographical range resulting from greenhouse warming effects on biodiversity in forests. In: Peters, R.L., Lovejoy, T.L. (Eds.), *Global Warming and Biological Diversity*. Yale University Press, New Haven, CT, pp. 298–308.
- Dell, B., Havel, J.J., 1989. The Jarrah forest, an introduction. In: Dell, B., Havel, J.J., Malajczuk, N. (Eds.), *The Jarrah Forest*. Kluwer Academic Publishers, Dordrecht, the Netherlands, pp. 1–10.
- Déqué, M., Marquet, P., Jones, R.G., 1998. Simulation of climate change over Europe using a global variable resolution general circulation model. *Clim. Dyn.* 14, 173–189.
- Díaz-Fernández, P.M., Climent, J., Gil, L., 2004. Biennial acorn maturation and its relationship with flowering phenology in Iberian populations of *Quercus suber*. *Trees* 18, 615–621.
- Endler, J.A., 1977. *Geographic Variation, Speciation and Clines*. Princeton Univ. Press, Princeton, NJ.
- Etterson, J.R., Shaw, R.G., 2001. Constraint to adaptive evolution in response to global warming. *Science* 294, 151–154.
- Flato, G.M., Boer, G.J., Lee, W.G., McFarlane, N.A., Ramsden, D., Reader, M.C., Weaver, A.J., 2000. The Canadian centre for climate modelling and analysis global coupled model and its climate. *Clim. Dynam.* 16, 451–467.
- Frankham, R., Ballou, J.D., Briscoe, D.A., 2002. *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge.
- Gómez, J.M., 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* 58, 71–80.
- Grossmann, A., Romane, F., Grandjanny, M., 2002. The Climate Environment of the 'CASCADE' Sites. II Report CNRS-CEFE for the EU Project EVK2-CT-1999-00006.
- Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecol. Lett.* 8, 461–467.
- Hamrick, J.L., 2004. Response of forest trees to global environmental changes. *Forest Ecol. Manag.* 197, 323–335.
- Higgins, P.A.T., Harte, J., 2006. Biophysical and biogeochemical responses to climate change depend on dispersal and migration. *Bioscience* 56, 407–417.
- Hunt, J., Simmons, L.W., 2002. The genetics of maternal care: direct and indirect genetic effects on phenotype in the dung beetle *Onthophagus taurus*. *Proc. Natl. Acad. Sci. U.S.A.* 99, 6828–6832.
- IPCC, 2007. *Climate change 2007: the physical basis*. Contribution of Working Group I to the Fourth Assessment of the Intergovernmental Panel on Climate Change. IPCC Secretariat, Geneva, Switzerland.
- Jiménez, P., Agundez, D., Alia, R., Gil, L., 1999. Genetic variation in central and marginal populations of *Quercus suber* L. *Silvae Gen.* 48, 278–284.
- Krannitz, P.G., Aarssen, L.W., Dow, J.M., 1999. The effect of genetically based differences in seed size on seedling survival in *Arabidopsis thaliana* (Brassicaceae). *Am. J. Bot.* 78, 446–450.
- Larcher, W., 2000. Temperature stress and survival ability of Mediterranean sclerophyllous plants. *Plant Biosyst.* 134, 279–295.
- Leishman, M.R., Westoby, M., 1994. The role of large seed size in shaded conditions: experimental evidence. *Funct. Ecol.* 8, 205–214.
- Leishman, M.R., Wright, I.J., Moles, A.T., Westoby, M., 2000. The evolutionary ecology of seed size. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. second ed. CAB International, Redwood Press, Melksham, pp. 31–57.
- Lloret, F.C., Casanovas, C., Peñuelas, J., 1999. Seedling survival of Mediterranean shrubland species in relation to root: shoot ration, seed size and water and nitrogen use. *Funct. Ecol.* 13, 210–216.
- Lopez, G.A., Potts, B.M., Vaillancourt, R.E., Apiolaza, L.A., 2003. Maternal carryover effects on early growth of *Eucalyptus globulus*. *Can. J. Forest Res.* 33, 2108–2115.
- Marchin, R., Emma, M., Sage, L., Ward, J.K., 2008. Population-level variation of *Fraxinus americana* (white ash) is influenced by precipitation differences across the native range. *Tree Physiol.* 28, 151–159.
- McKay, J.K., Bishop, J.G., Lin, J.-Z., Richards, J.H., Sala, A., Mitchell-Olds, T., 2001. Local adaptation across a climatic gradient despite small effective population size in the rare sapphire rockcress. *P. Roy. Soc. Lond. Bi. B* 268, 1715–1721.
- Mediavilla, S., Escudero, E., 2003. Stomatal responses to drought at a Mediterranean site: a comparative study of co-occurring woody species differing in leaf longevity. *Tree Physiol.* 23, 987–996.
- Messina, F.J., Fox, C.W., 2001. Offspring size and number. In: Fox, C.W., Roff, D.A., Fairbairn, D.J. (Eds.), *Evolutionary Ecology: Concepts and Case Studies*. Oxford Univ. Press, Oxford, UK, pp. 113–127.
- Milberg, P., Andersson, L., Thompson, K., 2000. Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Sci. Res.* 10, 99–104.
- Moles, A.T., Westoby, M., 2004a. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* 92, 372–383.
- Moles, A.T., Westoby, M., 2004b. What do seedlings die from and what are the implications for evolution of seed size? *Oikos* 106, 193–199.
- Murray, B.R., Brown, A.H.D., Dickman, C.R., Crowther, M.S., 2004. Geographical gradients in seed mass in relation to climate. *J. Biogeogr.* 31, 379–388.
- O'Brian, E.K., Mazanec, R.A., Krauss, S.L., 2007. Population variation of ecologically important traits of forest trees; implications for restoration. *J. Appl. Ecol.* 44, 583–593.
- Osunkojo, O.O., Ash, J.E., Hopkins, M.S., Graham, A.W., 1994. Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. *J. Ecol.* 82, 149–163.
- Parciak, W., 2002. Seed size, number, and habitat of a fleshy-fruited plant: consequences for seedling establishment. *Ecology* 83, 794–808.
- Pearson, T.R.H., Burslem, D.F.R.P., Dalling, J.W., Mullins, C.E., 2002. Interactions between environmental conditions and seed size on gap detection mechanisms in neotropical pioneer trees. *Ecology* 83, 2798–2807.
- Quero, J.L., Villar, R., Marañón, T., Zamora, R., Vega, D., Sack, L., 2008. Relating leaf photosynthetic rate to whole-plant growth: drought and shade effects on seedlings of four *Quercus* species. *Funct. Plant Biol.* 35, 725–737.
- Reed, D.H., Frankham, R., 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55, 1095–1103.
- Rees, M., 1997. Evolutionary ecology of seed dormancy and seed size. In: Silvertown, J., Franco, M., Harper, J.L. (Eds.), *Plant Life Histories: Ecology, Phylogeny and Evolution*. Cambridge Univ. Press, Cambridge, UK, pp. 121–142.
- Roach, D.A., Wulff, R.D., 1987. Maternal effects in plants. *Ann. Rev. Ecol. Syst.* 18, 209–235.
- Sakai, S., Kikuzawa, K., Umeki, K., 1998. Evolutionary stable resource allocation for production of wind-dispersed seeds. *Evol. Ecol.* 12, 477–485.
- Schaal, B.A., 1984. Life history variation, natural selection, and maternal effects in plant populations. In: Dirzo, R., Sarukhan, J. (Eds.), *Perspectives in Plant Population Ecology*. Sinauer, Sunderland, Massachusetts, USA, pp. 188–206.
- Schmitt, J., Niles, J., Wulff, R.D., 1992. Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *Am. Nat.* 139, 451–466.
- Seiwa, K., 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. *Oecologia* 123, 208–215.
- Skabo, S., Vaillancourt, R.E., Potts, B.M., 1998. Fine-scale genetic structure of a *Eucalyptus globulus* ssp. *globulus* forest revealed by RAPDs. *Aust. J. Bot.* 46, 583–594.
- Stock, W.D., Pate, J.S., Delfs, J., 1990. Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae. *J. Ecol.* 78, 1005–1020.
- Sultan, S.E., 1996. Phenotypic plasticity for offspring traits in *Polygonum persicaria*. *Ecology* 77, 1791–1807.
- Triphati, R.S., Khan, M.L., 1990. Seed mass and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* 57, 289–296.
- Vaughton, G., Ramsey, M., 1998. Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *J. Ecol.* 86, 563–573.
- Wolfe, L.W., 1995. The genetics and ecology of seed size variation in a biennial plant. *Hydrophyllum appendiculatum* (Hydrophyllaceae). *Oecologia* 101, 343–352.
- Wulff, R.D., Causin, H.F., Benitez, O., Bacalini, P.A., 1999. Intraspecific variability and maternal effects in the response to nutrient addition in *Chenopodium album*. *Can. J. Bot.* 77, 1150–1158.
- Yakimowski, S.B., Eckert, C.G., 2007. Threatened peripheral populations in context: geographical variation in population frequency and size and sexual reproduction in a clonal woody shrub. *Conserv. Biol.* 21, 811–822.
- Yamada, H., Miyaura, T., 2005. Geographic variation in nut size of *Castanopsis* species in Japan. *Ecol. Res.* 20, 3–9.