



Original article

Thriving at the limit: Differential reproductive performance in range-edge populations of a Mediterranean sclerophyll (*Olea europaea*)



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ABSTRACT

Peripheral populations are often lumped together on the assumption of thriving in marginal habitats where reproductive performance is compromised. We have tested this hypothesis in peripheral populations of wild olive tree (*Olea europaea* L.) presumably limited by different factors at the westernmost limit of the species range. Additionally, we hypothesized that differences in reproductive outcome among populations are better explained by site-specific environmental conditions (PAR, soil water, soil nutrients, air humidity and air temperature) than by differences in phenotypic traits (tree size and leaf traits). To test these hypotheses, we assessed the number of flowering trees, the flowering intensity, fruit set and seed viability in eight populations for three consecutive years. Our findings provided sufficient evidence to reject the first hypothesis. Peripheral populations that occur under oceanic conditions, resembling the Tertiary subtropical climate, consistently presented higher values for all components of reproductive performance than those at the thermal and rainfall tolerance limits. In support of our second hypothesis, the variation in reproductive performance among populations was primarily accounted for by local environmental conditions. Leaf traits, however, also explained reproductive variation but to a lesser extent. Finally, we found that small changes in tree size may cause large differences in reproductive performance. This close relationship between tree size and reproductive performance suggests that any impact on population size structure would likely jeopardize persistence and expansion at the range edge. Our results suggest that reproductive performance of wild olive trees was not shaped by the population geographic position within the species range, but by the interaction between local environment, as the main driver, and individual phenotypic traits.

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1. Introduction

Reproductive performance of peripheral populations is a key topic in the ecology and evolution of range limits (Sexton et al., 2009), climate change ecology (Hampe and Petit, 2005) and conservation of relict populations (Lesica and Allendorf, 1995). Peripheral populations are assumed to thrive in ecologically marginal habitats where abiotic or biotic stressful conditions compromise reproductive performance and survival (Vucetich and Waite, 2003; Kawecki, 2008). Stressful conditions can influence reproductive performance directly or indirectly. For example, nutrient deficiency may directly affect plant reproduction by preventing or arresting

the development of flowers, fruits and seeds (Ne'eman et al., 2006) or indirectly through alteration of floral rewards (Muñoz et al., 2005) or pollen quality and quantity (Lau and Stephenson, 1994). Moreover, in stressful environments, increased maintenance costs at the expense of vegetative growth reduce plant size, and individual size is strongly related to reproductive performance (e.g. Samson and Werk, 1986; Weiner et al., 2009; García-Verdugo, 2011); hence larger plants are expected to reproduce more often and have higher seed set than smaller plants (Kato and Hiura, 1999). Individuals of equivalent sizes, however, may show differential reproductive performance depending on habitat conditions (Parra-Tabla and Bullock, 2003; Méndez and Karlsson, 2004; Hampe, 2005). In addition to plant size, interactions among leaf phenotypic traits are expected to influence resource uptake and utilization, nutrient and biomass allocation, individual growth, and,

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ultimately, reproductive performance (Ackerly et al., 2000; Geber and Griffen, 2003). Thus, leaf traits are used as proxies of resource availability. For instance, plants experiencing stress conditions, such as drought and high irradiance levels, build smaller, thicker and steeper leaves than their counterparts growing under milder conditions (Gratani and Bombelli, 1999).

Although several studies have documented lower reproductive performance of peripheral populations, compared to central ones, some exceptions exist (Sagarin and Gaines, 2002; Sexton et al., 2009). We highlight three potential causes for these inconsistent results. First, peripheral populations can hardly be assigned to homogeneous comparison groups (Gaston, 1990; Hampe and Petit, 2005). For example, northern and southern range limits are expected to differ in relation to the importance of biotic and abiotic limiting factors (Gaston, 2009) and are expected to respond differently to environmental modifications (Hampe and Petit, 2005). Second, the assumption that all core populations share a common reproductive behaviour is also an unrealistic oversimplification, since they are usually spread throughout a large area and may occur under contrasted environmental conditions. Third, poor reproductive performance can result from reductions in one or several reproductive components, such as flowering frequency or intensity (Levin and Clay, 1984; Morin et al., 2007), fecundity (Dorken and Eckert, 2001; Angert and Schemske, 2005), seed viability or germination rates (García et al., 2000; Jump and Woodward, 2003; Sugiyama, 2003). These components, however, should not be considered in isolation. Final reproductive performance results from the combination of all these components and a decrease in one component may be mitigated by increases in another (Angert, 2006). Indeed, peripheral populations can also show particular adaptations to stressful conditions involving such reproductive compensations (Sexton et al., 2009).

The aim of the present study was to test whether peripheral populations share a reduced reproductive output. Peripheral populations of the Mediterranean wild olive tree (namely two subspecies of *Olea europaea* L.: *O.e. europaea* and *O.e. guanchica*) at the westernmost limit of its distribution provides an excellent scenario to investigate the reproductive performance of populations at the range edge occurring under contrasted environmental situations. First, some peripheral populations occur at the thermal tolerance limit imposed by minimal winter temperatures (Vargas and Kadereit, 2001; Rubio de Casas et al., 2002), while others occur at the lower rainfall limit of the species (Pansiot and Rebour, 1961). Second, the study subspecies of wild olive constitute a prominent element of the present day Mediterranean Flora. Phylogeographic

analyses suggest that these subspecies were differentiated within the *Olea* complex as a consequence of Tertiary climatic shifts and geographic isolation (Besnard et al., 2009). Strikingly, conditions similar to those of the ancestral environment prevail not at the core but at certain margins of the species range. Finally, interpretation of the reproductive patterns can be greatly aided by the detailed knowledge available on the genetic background and phenotypic variation within and among these populations (García-Verdugo et al., 2009a,b, 2010a,b,c; Granado-Yela et al., 2011; Rubio de Casas et al., 2011). In a representative sample of these populations, we have screened the major reproductive components, assessing the number of flowering trees, their flowering intensity, fruit set, and seed viability. We specifically addressed the following questions: 1) Do all peripheral populations of *O. europaea* present poor reproductive performance? 2) Which components of reproductive performance show greatest variation among populations? 3) To what extent are differences among populations related to site-specific environmental conditions and/or to divergence in phenotypic traits?

2. Materials and methods

2.1. Study species and populations

The genus *Olea* is andromonoecious, i.e. individual plants bear both male and hermaphroditic flowers. Flowers are grouped in axilar panicles and are wind pollinated. Fruits (single-seeded drupes) are dispersed by birds. Fruit production follows a supra-annual cycle of two or three years, depending on environmental conditions (Rey and Alcántara, 2000). Biogeographically, wild olives (*O. europaea* L.) are distributed throughout the Mediterranean region, although two out of six subspecies thrive in Central, South, Northeast Africa and South Asia (Rubio de Casas et al., 2006). The present study was conducted from 2007 to 2009 in eight populations located in the Iberian Peninsula and the Canary Islands (Fig. 1; Table 1). These populations were selected from a set of eleven populations genetically and phenotypically characterized in previous studies (García-Verdugo et al., 2009a,b, 2010a,b,c; Granado-Yela et al., 2011; Rubio de Casas et al., 2011). We chose populations at the westernmost limit of the species range where vegetation was dominated by *O. europaea*, regardless whether they belonged to the subspecies *europaea* L. (Iberian populations) or *guanchica* (Canarian populations). Among them, we only considered those in which introgression with cultivars do not obscure natural patterns of phenotypic and genetic variation (García-Verdugo et al., 2009a). Finally, we sampled two peripheral

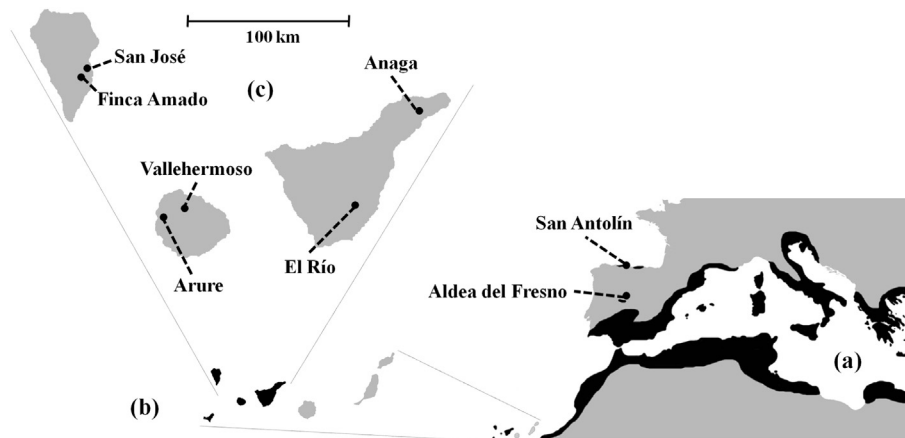


Fig. 1. Map of a) distribution of the wild olive (*Olea europaea* L.) in the western Mediterranean Basin and the Canary Islands (modified from Rubio de Casas et al., 2006), showing the two Iberian populations studied (San Antolín, Aldea del Fresno) b) distribution of the Canarian wild olive, c) populations on the islands of Tenerife (Anaga, El Río), La Gomera (Vallehermoso, Arure) and La Palma (Finca Amado, San José) (modified from García-Verdugo et al., 2010a).

Table 1

Coordinates, altitude and environmental variables for the eight studied populations of *Olea europaea*. Environmental variables were provided by the SIGA (Agricultural Geographic Information System from the Spanish 'Ministerio de Agricultura, Alimentación y Medio Ambiente; <http://sig.marm.es>). ETP: annual Thornthwaite Potential Evapotranspiration; R: accumulated Rainfall; T: mean Temperature; TM: average of the Maximum Temperatures; Tm: average of the minimum Temperatures.

Population	Coordinates	Altitude (m)	ETP (mm)	R (mm)	T (°C)	TM (°C)	Tm (°C)
Aldea del Fresno	40°20'N, 4°14'W	497	72	515	15.8	38.7	−1.4
Anaga	28°32'N, 16°10'W	420	75	363	19.4	30.9	11.8
Arure	28°08'N, 17°19'W	831	70	321	17.7	37.0	7.7
Finca Amado	28°38'N, 17°46'W	359	70	627	18.2	32.8	9.5
El Río	28°08'N, 16°32'W	415	85	112	21.3	35.0	12.0
San Antolín	43°26'N, 4°52'W	10	58	1152	13.2	25.9	0.5
San José	28°39'N, 17°46'W	88	80	324	20.4	28.8	12.6
Vallehermoso	28°11'N, 17°15'W	331	73	368	19.0	29.7	10.8

populations (Aldea del Fresno and San Antolín) at the thermal tolerance limit imposed by minimal winter temperatures (Rubio de Casas et al., 2002), two at the lower rainfall limit of the species at its westernmost edge (El Río and Arure; Pansiot and Rebour, 1961), and two populations on the island of La Palma (Finca Amado and San José), where Tertiary-like environmental conditions significantly depart from those prevailing in the present Mediterranean climate (particularly in terms of diffuse light and water availability; García-Verdugo et al., 2010a). Two additional populations were also sampled to improve robustness of the results (Anaga and Vallehermoso). In each population, we randomly chose 10 to 12 adult individuals. Population size was not notably different among populations.

2.2. Measurement of reproductive performance

We characterized the reproductive performance of each tree following the sequential production of flowers, fruits and seeds. Flowering trees (FT) were calculated as the ratio between reproductive trees and total sampled trees in each population ($n = 8$) and year ($n = 3$). We calculated flowering frequency (FF) as the proportion of years that each tree was found to be reproductive. Flowering intensity (FI) of each tree was assessed shortly before anthesis, in late May to early June, for years 2007–2009. We divided tree crowns into octants, i.e. geographic quadrants divided into an upper and a lower portion, in order to control for potential asymmetric flowering within the crown. We defined a categorical scale for scoring flowering intensity that was applied to a $1 \times 1 \text{ m}^2$ area superimposed over each octant: 0 = vegetative (no inflorescences); 1 = low (less than 12 inflorescences); 2 = medium (less than 120 inflorescences); and 3, high flowering intensity (more than 120 inflorescences). To account for missing octants in some trees, we weighted flowering intensity (FI) by calculating the ratio between the sum of the scores for each present octant and the maximum possible sum with the octants present.

We harvested 12 to 48 inflorescences per tree in years 2007 and 2008. In the laboratory, we counted and scored for gender the flowers within the inflorescences to calculate the ratio of hermaphroditic flowers (HF). We scored 32,410 flowers in 2007 and 18,883 flowers in 2008. In order to estimate Fruit Set (FS) we labelled 10 to 40 flowering twigs per tree and counted the number of inflorescences. We then counted the number of ripe fruits on the labelled twigs from late August to early September, before fruit dispersal (Rey and Alcántara, 2000). Fruit set (FS) per tree and year ($n = 2$) was calculated as the ratio between the number of ripe fruits and the estimated number of hermaphroditic flowers in the labelled twigs.

In October 2007, we collected approximately 20 ripe fruits from the entire crown in each reproductive tree. We then removed the pulp and stored the endocarps in a dark and dry place until analysis. Seeds were extracted from the endocarps and kept in water

overnight to facilitate extraction of the embryos. We assessed embryo viability by the tetrazolium test (Nachlas et al., 1960; Egle and Chandler, 1983). Viable seeds (VS) per tree were counted as the ratio between seeds bearing viable embryos and total sampled seeds in the tree. A seed was considered as viable when the embryo stained completely or when staining was observed in parts essential for germination (Leist and Krämer, 2003).

We estimated relative reproductive performance (RRP) for each individual using the following expression: $RRP = FF \times FI \times HF \times FS$ (modified from Méndez, 1997). In the equation, we implemented averaged values of all years sampled for each of the variables (i.e. three years for FF and FI, and two years for HF and FS). All components on the right side of the equation were calculated as ratios that ranged from 0 to 1, thus RRP also ranged from 0 to 1. In order to estimate absolute reproductive performance (ARP) for each individual, we weighted the relative reproductive performance by each tree size (see section 2.4). Thus, we substituted in the former equation FI for the flowering yield ($FY = FI \times \text{Size}$), which is an estimate of the absolute number of flowers per tree, giving $ARP = FF \times FY \times HF \times FS$.

2.3. Site-specific environmental conditions

To evaluate the effect of soil nutrients on reproductive performance, in November 2007 we collected approximately 500 ml of soil beneath each tree sampled in all eight populations ($n = 86$). Litter was removed and soil samples were taken to a depth of 10 cm. We estimated total nitrogen (N) and total phosphorus (P) concentrations, after extraction with hot KCl (Binkley and Vitousek, 1989), by Continuous Flow Analysis with a Skalar San⁺⁺ Analyzer (Skalar Analytical BV, Breda, the Netherlands).

In order to investigate site-specific environmental differences among the six populations on the Canary Islands, we placed, in each population, a U12 datalogger coupled with an S-LIA-M003 PAR sensor and an ECH₂O™ Sensor, and an RH/T H8 HOBO (Onset Computer Corp., MA, USA). Photosynthetically active radiation at open sky (PAR), soil water content at 50 cm depth (soil W), air relative humidity (air RH) and air temperature (air T) were recorded every 30 min from August 2006 to August 2007 (for further details see García-Verdugo et al., 2009b, 2010a).

2.4. Measurement of phenotypic traits (tree size and leaf traits)

To estimate plant size we measured the tree height (H) and the largest crown diameter (D) in all sampled trees ($n = 86$), following previous studies in *O. europaea* (García-Verdugo et al., 2009b; García-Verdugo, 2011). To calculate the flowering yield (see Section 2.2), we selected as the tree size estimate the largest crown diameter (D), rather than tree height (H), because crowns of the wild olive tend to be spherical, not cylindrical. Leaf sampling was performed in fully-expanded leaves during the summer of 2007.

We sought to examine resource-use strategies of the study populations through three key functional traits. First, we measured leaf angle to the horizontal (Ang) on 10 leaves per tree using a protractor. Then, we randomly took 30 leaves per tree and scanned them in the laboratory. Scanned leaves were analysed with Scion Image software (Scion Corp., MD, USA) to calculate leaf area (LA). Finally, these leaves were oven-dried (65 °C for 48 h) and weighed with a precision balance (Mettler Toledo, Greifensee, Switzerland) to estimate dry mass. Specific leaf area (SLA) was calculated as the ratio between LA and dry mass.

2.5. Data analyses

We performed three analyses at the population level. First, we investigated differences in the components of reproductive performance among the study populations. We included all eight populations for these analyses, although the likelihood of type II error (i.e. failing to find differences in reproductive components among populations when they actually exist) would increase since the Canarian populations are not truly independent. Second, we examined the contribution of each component to overall reproductive performance in each population. Finally, we investigated the effect of site-specific environmental conditions on reproductive performance across Canary Island populations. At the individual level, we analysed the relationship between reproductive performance and plant phenotypic traits (tree size and leaf traits) and between reproductive performance and soil properties.

2.5.1. Population level analyses

We tested for differences in FT among populations and years using a Friedman test. In addition, we tested for within-population differences in FT by means of G-tests (Sokal and Rohlf, 1995). Because not every tree produced flowers every year in some populations, a joint analysis was not feasible. Thus, we compared FI among populations in a given year using one-way ANOVA, after testing for normality with Shapiro–Wilks test, and homogeneity of variances with Levene's test. In addition, we performed a repeated-measures ANOVA with year as a within-subject factor for each population. Populations with a low number of flowering trees were excluded from the analysis (see Results). FI was rank-transformed to meet the assumptions of the analysis. We tested between-year variation in FS within each population using a *t*-test for paired samples, after confirming the normality in the distribution of fruit set values (Zar, 1999). Since average population for FS values were highly correlated between years across populations (see Results), and population Vallehermoso had only one flowering tree in 2008, we tested for significant differences in FS among populations only in 2007 by means of the Brown–Forsythe test. Differences among populations in FS were detected with the post-hoc Games–Howell test for multiple comparisons. We compared VS among populations using G-tests.

The influence of environmental variables on reproductive components in the Canarian populations was assessed by means of partial least squares regressions in SPSS 16.0 (SPSS Inc., IL, USA). We tested the influence of four site-specific environmental variables (PAR, soil W, T and air RH) on key phenological stages for the reproductive components during 2007. According to Sanz-Cortés et al. (2002), emergence/development of reproductive buds, inflorescence development and flowering occurs approximately from December to May, fruit development from May to October, and fruit ripening from September to December. Averages of each site-specific environmental variable for each time interval were used as predictors of FI, FS and VS, respectively.

The relative importance of each reproductive component contributing to ARP in each population was analysed following the

procedures detailed in Mott (1966). The variance of each component and the covariance between each pair of components were obtained on log-transformed data. Variances and covariances were standardised by expressing them as percentage of variance in log (ARP). The magnitude of standardised variance and covariance for each component estimates its contribution to between-plant variation in ARP in each population.

2.5.2. Individual level analyses

We used multiple ordinal regressions to test the effect of tree size, leaf traits and soil nutrients on FF. We created an ordinal variable with four categories (0–3) that summarized FF (i.e. flowering events in each tree along the three study years). Predictors variables included in the model were soil nutrients (N and P), crown features (*H*, *D* and Ang) and leaf traits (LA and SLA). A parallelism test was performed to test the null hypothesis of similar slope coefficients across response categories.

We studied the effect of tree size, leaf traits and soil nutrients on reproductive components by means of redundancy analysis in CANOCO 4.5 for Windows (ter Braak and Smilauer, 2002). Redundancy analysis is an ordination method which summarises overall variation in one set of variables (independent variables) in a few ordination axes which are linear combinations another set of variables (dependent variables). The dependent variables considered were FI, FS and VS of each year. The independent variables included were crown features (*H*, *D* and Ang), leaf traits (LA and SLA) and soil nutrients (N and P). The statistical significance of the resulting ordination was tested by means of a Monte Carlo permutation test with 9999 permutations.

We investigated the relationship between tree size and RRP by means of regression models in GraphPad Prism 5 (GraphPad Software, CA, USA). We applied an information-theoretic approach based on Akaike's information criteria (AIC; Burnham and Anderson, 2002) in order to check whether the relationship between tree size and RRP followed a linear or a nonlinear model. The nonlinear models included were exponential, quadratic and segmental linear with breakpoint.

3. Results

3.1. Variation in reproductive performance at the population level

We found significant differences in all components of the reproductive performance (except for the flowering intensity) among the eight study populations. The ratio of flowering trees (FT) ranged from 0.083 to 1 among populations and years (Table 2). FT significantly differed among populations ($\chi^2_7 = 14.474$, $p = 0.043$), but not among years ($\chi^2_2 = 2.154$, $p = 0.341$). The only population for which all monitored individuals consistently flowered throughout the three study years was Finca Amado, located on the island of La Palma. Populations San Antolín, at the thermal limit under oceanic conditions, and Finca Amado presented the highest ratios of FT, whereas populations El Río, at the rainfall limit, and Vallehermoso showed the lowest. Within populations, FT significantly differed between years in Anaga ($G_2 = 8.331$, $p = 0.008$), Aldea del Fresno ($G_2 = 5.841$, $p = 0.046$) and San José ($G_2 = 5.633$, $p = 0.043$).

Flowering intensity ranged from 0.250 to 0.933 (Table 2) and did not differ among populations or years. Within populations, FI varied significantly only in population San Jose ($F_{1, 3} = 16.667$, $p = 0.027$).

Fruit set (FS) ranged from 0 to 0.107 (Table 2). Average population FS values were highly correlated between years across populations ($r = 0.933$, $n = 8$, $p < 0.001$). The FS significantly differed among populations in 2007 (Brown–Forsythe statistics: 12.197, $df = 7$, 11.385, $p < 0.001$). One of the populations on La Palma (San

Table 2

Per-population values of flowering trees (FT), flowering intensity (FI), fruit set (FS) and viable seeds (VS) in the years studied (2007–2009). Standard deviations (\pm SD) are included when the values are averaged and sample size is given in brackets. In variable VS the first number in brackets indicates the number of trees and the second the total number of analysed seeds.

	Thermal limit		Rainfall limit		Tertiary-like conditions		Additional populations	
	Aldea del Fresno	San Antolín	El Río	Arure	San José	Finca Amado	Anaga	Vallehermoso
FT								
2007	1	0.8	0.273	0.364	0.917	1	0.9	0.583
2008	0.9	0.8	0.273	0.727	0.667	1	0.4	0.083
2009	0.4	0.9	0.583	0.643	0.917	1	0.909	0.273
FI								
2007	0.783 \pm 0.252 (10)	0.806 \pm 0.259 (8)	0.250 \pm 0.144 (3)	0.514 \pm 0.241 (4)	0.744 \pm 0.308 (11)	0.617 \pm 0.197 (10)	0.620 \pm 0.309 (9)	0.929 \pm 0.101 (7)
2008	0.630 \pm 0.232 (9)	0.667 \pm 0.318 (8)	0.750 \pm 0.220 (3)	0.566 \pm 0.289 (8)	0.483 \pm 0.406 (8)	0.825 \pm 0.169 (10)	0.750 \pm 0.215 (4)	0.500 \pm 0.000 (1)
2009	0.764 \pm 0.214 (4)	0.676 \pm 0.309 (9)	0.458 \pm 0.287 (6)	0.440 \pm 0.344 (6)	0.843 \pm 0.349 (11)	0.933 \pm 0.161 (10)	0.713 \pm 0.304 (9)	0.657 \pm 0.397 (3)
FS								
2007	0.060 \pm 0.031 (10)	0.041 \pm 0.027 (8)	0.004 \pm 0.004 (3)	0.005 \pm 0.006 (4)	0.107 \pm 0.044 (4)	0.020 \pm 0.023 (10)	0.013 \pm 0.010 (7)	0 (5)
2008	0.067 \pm 0.038 (8)	0.020 \pm 0.018 (7)	0 (3)	0.002 \pm 0.003 (4)	0.080 \pm 0.041 (3)	0.031 \pm 0.030 (7)	0 (4)	0 (1)
VS								
2007	0.235 \pm 0.115 (9/101)	0.367 \pm 0.261 (6/85)	0.045 \pm 0.064 (2/15)	0.643 \pm 0.171 (1/14)	0.355 \pm 0.107 (4/42)	0.597 \pm 0.199 (6/73)	0.518 \pm 0.383 (7/58)	0

José), under subtropical-like Mediterranean climate, showed the highest values of averaged FS, followed by both populations on the Iberian Peninsula (i.e. Aldea del Fresno and San Antolín), at the thermal limit. All four populations on the other islands, including those at the rainfall limit, presented average values of FS of zero or close to zero (Table 2). Within populations, no differences were found in FS between 2007 and 2008.

The ratio of viable seeds (VS) ranged from 0 to 0.643 (Table 2). There were significant differences in VS among populations that produced fruits ($G_6 = 58.932$, $p < 0.001$). Populations Anaga, Arure and Finca Amado exhibited the highest values of VS ($G_1 = 22.508$, $p < 0.001$), whereas populations Aldea del Fresno and El Río showed the lowest ones ($G_1 = 8.531$, $p = 0.008$).

FI was positively related to RH but negatively to PAR, FS was positively related to soil W and air T , and VS was positively related to PAR but negatively to air T (Table 3). The two significant variables in each analysis explained a high proportion of variance in FI, FS and VS (82.6%, 72.8% and 80.0%, respectively).

In all populations, most variation among plants in reproductive performance (ARP) resulted from differences in flowering yield, except one of the populations on La Palma (Finca Amado), where most of the variation was caused by differences in fruit set (Table 4). It is important to remark that most of the variability in flowering yield may result from within-population variability in tree size and that population Finca Amado exhibited the largest trees.

Table 3

Effect of site-specific environmental conditions [Photosynthetically active radiation at open sky (PAR), soil water content at 50 cm depth (soil W), air temperature (air T) and air relative humidity (air RH)] on flowering intensity (FI), fruit set (FS) and viable seeds (VS) of populations of *O. europaea* in the Canary Islands. w COMP 1: weights of each variable in the first regression component (weights whose squares are larger than 0.2 are shown in bold). R^2 : proportion of the variance in the response variable accounted for by the multiple regression analysis of the component of the regression.

	FI	FS	VS
	w	w	w
	COMP1	COMP1	COMP1
PAR	-0.524	0.161	0.619
Soil W	-0.166	0.731	0.276
Air T	0.348	0.656	-0.645
Air RH	0.759	-0.100	0.353
R^2	0.826	0.728	0.800
p	0.012	0.031	0.016

3.2. Variation in reproductive performance at the individual level

Flowering frequency of individual trees was positively related to N , D , LA and SLA (Table S1).

Variables D and N were positively related to all the reproductive components (FI, FS and VS; Fig. 2) and included within the first canonical axis ($F = 24.236$, $p < 0.001$) produced by the redundancy analysis ($F = 5.086$, $p < 0.001$). N and D explained 23.4% of the variance in FI, FS and VS. The second axis explained 2.4% of the variance and was related to LA, although it was not significant ($F = 0.903$, $p = 0.754$).

The relationship between tree size and reproductive performance (RRP) was positive but not linear (Fig. 3). The segmental-linear with breakpoint model was the best fitted model (AIC segmental-linear with break point: -446.59; AIC exponential: -442.55; AIC quadratic: -442.32; and AIC linear: -436.57).

4. Discussion

The present study is the first, to our knowledge, to investigate the whole reproductive process and performance of a plant species in several peripheral populations that occur under contrasting environmental conditions. In contrast to the general prediction that states that in all peripheral populations reproduction is compromised, we found large differences among peripheral populations of the Mediterranean wild olive tree (*O. europaea*) in the overall reproductive performance and in most phases of the reproductive process.

4.1. Reproductive performance of peripheral populations

Our findings illustrate that being peripheral in *O. europaea* does not necessarily mean to occur in ecologically marginal habitats where reproductive performance is compromised. We consistently found high reproductive performance in populations where differential exposure to oceanic influence (Finca Amado and San José; García-Verdugo et al., 2010a), results in environmental conditions that resemble the Tertiary subtropical climate to which *Olea* ancestors were well adapted (Terral et al., 2004). Strikingly, the wild olive, which survived glacial periods in riparian habitat refuges and withstood postglacial climate warming and variability (Terral et al., 2004), performs differentially better under the ancestral-like environmental conditions, both in terms of growth (García-Verdugo et al., 2010c) and reproduction (present study), than the other study populations occurring under more Mediterranean conditions.

Table 4

Percentage of variance in log absolute reproductive performance (ARP) explained by its different components in each population. Variance (in bold; on diagonal) and covariance (x^2 ; below diagonal) of log transformed data are shown. Frequency of flowering (FF), flowering yield (FY), ratio of hermaphroditic flowers (HF) and fruit set (FS).

	FF	FY	HF	FS
Aldea del Fresno				
FF	1.27			
FY	11.66	50.72		
HF	1.98	12.07	1.84	
FS	-2.39	12.14	0.46	10.25
Anaga				
FF	0.75			
FY	10.06	44.42		
HF	2.04	15.67	2.00	
FS	0.66	14.42	3.34	6.65
Arure				
FF	0.81			
FY	12.93	64.03		
HF	1.30	11.62	0.92	
FS	0.61	6.37	0.51	0.92
Finca Amado				
FF	0.00			
FY	0.00	8.39		
HF	0.00	0.30	0.05	
FS	0.00	21.32	0.57	69.37
El Río				
FF	0.80			
FY	14.61	67.16		
HF	1.15	9.62	0.86	
FS	0.46	4.07	0.85	0.42
San Antolín				
FF	0.66			
FY	10.97	51.99		
HF	0.99	8.19	0.60	
FS	2.26	12.02	3.19	9.12
San José				
FF	0.43			
FY	5.61	39.74		
HF	1.00	5.39	0.80	
FS	2.44	28.75	2.70	13.13
Vallehermoso				
FF	0.56			
FY	11.80	75.01		
HF	0.90	10.72	0.81	
FS	0.02	0.15	0.02	0.00

High reproductive performance was also observed in San Antolín, where oceanic influence enables thriving at the thermal limit as relict elements in coastal habitat refuges. We found in these three populations (Finca Amado, San José and San Antolín) values of over 70% in flowering probability (in most cases over 90%) and high values in flowering intensity, fruit set, and viable seeds in all years. Indeed, other studies conducted in populations in the core of the distribution on the Iberian Peninsula found similar values in the proportions of fruiting trees and fruit set (Jordano, 1987) as well as in the number of viable seeds (Rey and Alcántara, 2000) to those found in the present study in Finca Amado, San José and San Antolín.

This substantial investment in sexual reproduction in peripheral populations may partially account for the high values of genetic diversity found in these populations in previous studies (Rubio de Casas et al., 2006; García-Verdugo et al., 2009a, 2010b). Patterns of dispersal, however, considerably differ among populations on the island of La Palma and in the relict population in San Antolín. Whereas extensive gene flow mediated by seed dispersal results in moderate levels of differentiation among Canarian populations (García-Verdugo et al., 2010b), long-term reproductive isolation in

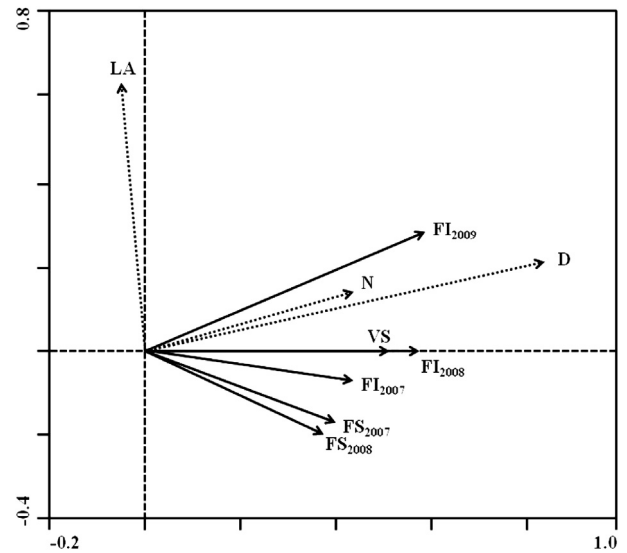


Fig. 2. Bidimensional plot summarizing the effect of tree size, leaf traits and soil nutrients on the reproductive components (FI: flowering intensity, FS: fruit set, and VS: viable seeds), according to the redundancy analysis. Data from all reproductive individuals in all 8 populations is included. Only three predictor variables (dotted lines) selected by a forward stepwise procedure are represented (*N*: total soil nitrogen, *D*: largest crown diameter, and *LA*: leaf area). Variables *D* and *N* were positively related to all the reproductive components and included within the first canonical axis. These two variables explained 23.4% of the variance in the reproductive components. The second axis explained 2.4% of the variance and was positively related to *LA*, although it was not significant.

the coastal habitat refuge has resulted in a marked genetic divergence from the nearest populations (Rubio de Casas et al., 2006).

4.2. Environmental influence on the components of reproductive performance

Among all study populations, site-specific environmental conditions accounted for most of the variation in reproductive performance, as shown by the partial least squares regressions. Under stressful environmental conditions, long-lived plants prioritize growth and maintenance over reproduction (Silvertown et al.,

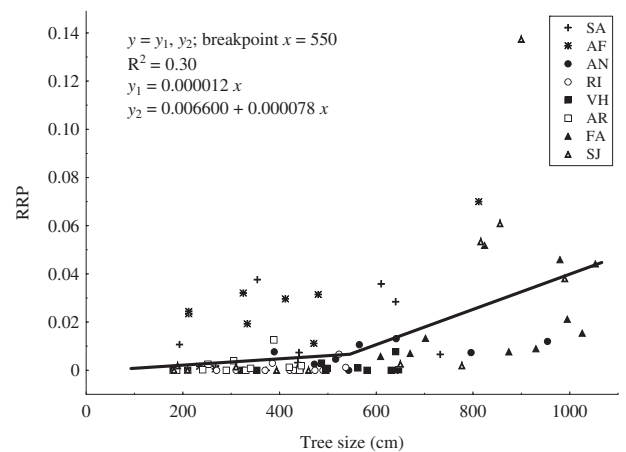


Fig. 3. Segmental linear relationship between tree size and relative reproductive performance. Tree size was calculated as largest crown diameter (cm). Relative reproductive-performance (RRP) was calculated using the following expression: $RRP = FF \times FI \times HF \times FS$ (FF: frequency of flowering; FI: flowering intensity; HF: ratio of hermaphroditic flowers; FS: fruit set). SA (San Antolín), AF (Aldea del Fresno), AN (Anaga), RI (El Río), VH (Vallehermoso), AR (Arure), FA (Finca Amado), SJ (San José).

1993). Large reproductive efforts should therefore be frequent in favourable environments and become more sporadic where maintenance expenses redound to the detriment of growth and reproduction (e.g. Waite and Hutchings, 1982; Lovett-Doust, 1989). In population El Río, at the rainfall limit, less than 30% of the small and scarcely fecund individuals were able to reproduce in most years. Under less stressful conditions, both at the thermal (Aldea del Fresno) and rainfall (Arure) limit, those years in which most individuals were reproductive alternated with a year in which only a few individuals were able to reproduce.

Besides, the extremely poor performance observed in Vallehermoso, one of the additional populations that were sampled to improve robustness of the results and, therefore, without any particular environmental limitation, indicates that stressful conditions are not privative of peripheral populations. In addition, this result suggests that the number of environmental factors that affect the reproductive performance is sufficiently large to hinder the timely identification of populations at the environmental limit of its range. In line with our main findings, this unexpected result emphasizes the distinction between geographic peripheral position and ecological marginality in plant populations. This distinction is particularly important in species distribution modelling, where it is too often assumed that geographic processes are dominant over environmental ones (Elith and Leathwick, 2009).

In this study local environmental fluctuations during reproductive stages (mainly during fruit formation) caused erratic patterns of reproductive performance. For example, the overall reproductive performance was jeopardized as a consequence of particularly extreme environmental conditions after anthesis (see FS values of zero, or nearly zero, in populations El Río, Vallehermoso and Arure all years, and in population Anaga in 2008). Our results indicate that low soil water availability during mid-summer was related to low fruit set, as suggested by other authors for the cultivated olive (e.g. Palese et al., 2010), and may play a key role at certain range limits. Local differences in soil nutrient availability also contributed to variation in reproductive performance among individuals. Soil nutrients are known to influence reproductive performance in many species (Nams et al., 1993). In the present case, the strong correlation between soil N and plant size did not allow to segregate the effect of nutrient availability on the reproductive performance from the effect of plant size. Finally, it is striking that the same environmental variables influenced different components of the reproductive performance in opposite directions (e.g. PAR was negatively related to the flowering intensity and positively related to viable seeds). All these findings provide a potential mechanism underlying cases of between-site discrepancies in vital rates and warn against the interpretation of population viability based on single reproductive components (Angert, 2006).

4.3. Relationship between phenotypic traits and reproductive performance

Within populations, our findings indicate that the reproductive performance of *O. europaea* was strongly influenced by tree size. In agreement with previous studies in woody species, plant size was related to frequency of reproduction (Thomas, 1996; Philipp and Nielsen, 2010), flowering intensity (Philipp and Nielsen, 2010) and fecundity (Abrahamson and Layne, 2002). Consequently, tree size was also related to relative and absolute reproductive performance. Nevertheless, the relationship between tree size and reproductive-performance was not strictly linear. Thus, small changes in size may cause large differences in reproductive performance. This size-related advantage could derive from more than linear gains in resource acquisition for larger sizes (Barot et al., 2005). Size advantage in the uptake of resources has long been

described in studies of competition for light among neighbouring plants: larger plants shade smaller plants and thus absorb much more light in relative and absolute terms (Weiner and Thomas, 1986; Weiner, 1990; Falster and Westoby, 2003). But size itself might be advantageous because large plants optimize the use of available resources to enhance resource foraging efficiency through active environmental screening, growth in favourable directions (Silvertown and Gordon, 1989; Bazzaz, 1991; Augspurger and Bartlett, 2003), or the exploitation of the different light-environments across tree crowns (Granado-Yela et al., 2011). Given the importance of size on reproductive performance, tree size class distribution at the population level appears to be a critical factor that links both natural and human disturbances to population viability at the species range edge.

The relationship between tree size and reproduction is likely modulated by small-scale factors such as resource patchiness and individual features (Parra-Tabla and Bullock, 2003; Hampe, 2005). Our findings show that *O. europaea* individuals with large leaves reproduce more frequently than individuals with small leaves. The relationship between these vegetative traits and individual fitness can be attributed either to the value of these traits as a proxy for favourable environmental conditions or to the expression of a more effective phenotype in the capture of light.

4.4. Peripheral populations of the wild olive in a scenario of climatic change

The Mediterranean wild olive at the western edge of its distribution faces contrasting situations, namely physiographic margins, where despite a high reproductive output, further expansion is prevented by the ocean barrier; historical margins, where population reproductive outcomes have been long confined in a habitat refuge, and ecological margins, where a poor reproductive performance reflects suboptimal environmental conditions. These scenarios, however, do not represent permanent or steady-state situations. On the contrary, population reproductive performance at these range margins largely determines the species ability to respond to changing environments (Hampe and Petit, 2005). In a scenario of climatic change, our data on reproductive performance suggest that these margins may either become expanding or rear edges. Based on regional climatic projections by 2011–2040 (Brunet et al., 2009), it is expected that those range limits set by the isotherm of the minimum mean temperature (Rubio de Casas et al., 2002) would become expanding edges. Our study populations at this thermal limit showed two contrasted scenarios: isolated genetically-divergent populations (San Antolín; Rubio de Casas et al., 2006) with a successful reproductive outcome, and less differentiated populations, such as Aldea del Fresno, with an uneven reproductive outcome but in the likely presence of a substantial interpopulation gene flow. On the contrary, the expected reduction in annual rainfall (cf. Brunet et al., 2009) will probably have severe effects on the Canarian populations currently growing at the rainfall limit. This limit will likely become a rear edge of the species range.

5. Conclusions

The present study shows that the biogeographical concept of range margin does not involve low reproductive performance. Among all study populations, site-specific environmental conditions accounted for most of the variation in reproductive performance: populations occurring under oceanic conditions exhibited high values in all components of the reproductive performance, whereas the rest of the studied peripheral populations showed low values. These results emphasize the relevance of the distinction

between geographic peripheral position and ecological marginality in plant populations. Due to the close relationship between plant size and fecundity, natural or human disturbances on population size structure will likely have major effects on the possibilities of persistence and expansion at the range edges. Our study helps to overcome simplistic assumptions of population performance across ranges. *Ad hoc* studies are needed to further understand the ecological and evolutionary consequences of differential reproductive performance of peripheral populations, and to support the management of plant populations under current global warming scenarios.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2013.07.002>.

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