Plant Ecology (2006) 183:329–336
DOI 10.1007/s11258-005-9043-x

Resistance of three co-occurring resprouter *Erica* species to highly frequent disturbance

Susana Paula[1,2] and Fernando Ojeda[1,*]
*[1]Departamento de Biología, CASEM, Universidad de Cádiz, Campus Río San Pedro, 11510 Puerto Real, Spain; [2]Fundación Centro de Estudios Ambientales del Mediterráneo (CEAM), c/ Charles R. Darwin, 14, 46980 Paterna, Spain; *Author for correspondence (e-mail: fernando.ojeda@uca.es; phone: +34 956 01 6766; fax: +34 956 01 60 19)*

Received 21 February 2005; accepted in revised form 10 August 2005

Key words: *Erica arborea*, *E. australis*, *E. scoparia*, Mediterranean heathlands, Resprouting vigour, Strait of Gibraltar

Abstract

The resistance to experimental, highly frequent disturbance has been analysed in three congeneric, strong-resprouter species (*Erica australis*, *E. scoparia* and *E. arborea*) that co-occur in heath-dominated communities of the northern side of the Strait of Gibraltar, southern Spain. To do so, mature individuals of the three species from a long undisturbed location were clipped at the ground level every sixth month during two years. The relationship between the resprouted biomass dry weight (as indicative of the resprouting vigour) and the upper surface area of the lignotuber along the experiment was established separately for each species at each clipping event by means of linear regressions analysis. The resprouting vigour of the three species was compared by means of independent one-way ANOVAs within each clipping event. Resprouting vigour decreased after recurrent clippings in the three species. Nevertheless, significant differences between species in this loss of resprouting vigour were detected, being *E. scoparia* the most resistant to the experimental, highly frequent clipping. It is concluded that experimental levels of recurrent disturbance may help to find out differences in resilience within similar (taxonomically, morfologically and/or ecologically), strong-resprouter plant species. Considering the history of forestry management in the nothern side of the Strait of Gibraltar, differences in this regard between the three *Erica* species may contribute to explain their somewhat segregated ecological distribution in this region.

Introduction

Competition and physiological specialisation are commonly invoked to explain patterns of distribution of species along ecological gradients (Austin 1985). Nevertheless, it is less frequent to consider differences in the response to unpredictable, severe disturbance events as the underlying factors explaining shifts in species relative abundance (but see Bond et al. 2001).

Traditionally, plants have been classified as either resprouter or non-sprouter based on their capacity to survive severe above-ground damage caused by unpredicted disturbance events, such as wildfires, hurricanes or strong herbivory (Bond and van Wilgen 1996; Vesk and Westoby 2004; Vesk et al. 2004). This simple, dichotomous classification characterizes, in a global manner, the response of plants to severe damage, and provides an adequate framework for ecological studies on functional traits in disturbance-prone ecosystems (e.g. Pausas et al. 2004). Nevertheless, within the reprouter group, post-disturbance survival is not alike for all species (e.g. see le Maitre et al. 1992; López-Soria and Castell 1992). In this sense, a dichotomous classification of resprouter plants in weak- and strong-resprouters provides a useful system for modelling the vegetation response to severe disturbance (Westman and O'Leary 1986; Vesk and Westoby 2004).

Furthermore, the response of a resprouter species, however weak or strong, is not a constant feature, but depends on the intensity (e.g. Moreno and Oechel 1991) and, more markedly, on the frequency of successive disturbance events (Zammit 1988; Riba 1998; Canadell and López-Soria 1998). Therefore, possible differences in the response to frequent, recurrent disturbance among co-occurring resprouter species will potentially drive drastic changes in species relative abundance and, ultimately, in species composition of presumably disturbance-resilient communities dominated by strong resprouter species, such as Mediterranean shrublands (Keeley 1986; Trabaud 1991; Clemente et al. 1996).

Mediterranean heathlands characterize the Strait of Gibraltar region, at the western end of the Mediterranean Basin, whose presence is determined by the existence of acid, nutrient-poor sandstone soils, and a relatively mild mediterranean climate (Ojeda et al. 1995, 1996a, 2001). While open heathlands cover exposed ridges and crests, on poorly developed sandstone soils, heath-dominated communities form the understorey of evergreen *Quercus suber* L. (cork oak), or semideciduous *Q. canariensis* Willd. woodlands (Ojeda et al. 1996a), on middle slopes and valley bottoms. Wildfire, forest thinning, scrub slashing, and browsing by free-range cattle and game (mainly red- and roe-deer) are the main disturbance agents on these heathlands (Ojeda et al. 1996a). Forest thinning and scrub slashing in this region are common management practices to optimize cork production, to facilitate cork harvesting, and to avoid forest wildfires (Ceballos and Martín-Bolaños 1930; Torres and Montero 2000), thus being particularly associated with *Q. suber* woodlands.

Three congeneric heath species, *Erica australis* L., *E. scoparia* L. and *E. arborea* L., are abundant in these Mediterranean heathlands. The habit and ecological requirements of these three species are rather similar: (1) they are multistemmed shrubs with small, 'ericoid' leaves; (2) they have a conspicuous lignotuber out of which they readily regenerate their above-ground biomass after slashing or burning (Riba 1997; Ojeda et al. 2000a; Cruz et al. 2003); and (3) they thrive on nutrient-poor, sandy soils and sunny exposures (de Benito 1948; Aubert 1978). Despite these similarities, the three species appear somewhat spatially segregated in the landscape of the Strait of Gibraltar (Ojeda et al. 2000a): *E. australis* is abundant only in open heathlands of ridges and crests, where it often co-occurs with *E. scoparia*. This second species becomes dominant on heath-communities of sandstone middle slopes, generally under sparse to moderate *Quercus suber* tree cover. Finally, *E. arborea* co-occurs with *E. scoparia* in heath understoreys under moderate to dense tree cover, becoming the only heath species present in denser forest communities. *Erica arborea* and *E. australis* very seldom co-occur. Tolerance to extreme conditions – high soil aluminium and dense tree cover – and interspecific competition have been previously invoked to explain this pattern of ecological distribution (Ojeda et al. 2000a).

Here, we present the results of a field experimental study aimed to ascertain the resprouting performance of these three *Erica* species after frequent, recurrent above-ground disturbance. Specifically, we tested whether, given their taxonomical proximity, their similar morphology, and their somewhat similar ecological requirements, they present a similar capability of withstanding frequent, successive clippings to the ground level. We finally discuss the implications of our results in helping to understand the ecological distribution of the three *Erica* species in Mediterranean heathlands of the Strait of Gibraltar.

Methods

Study area and field experiment

The field experiment was conducted in Monte Murta, within the Aljibe Mountains, at the northern side of the Strait of Gibraltar, South Spain (36°19′35″ N; 5°33′25″ W). For a concise environmental background of this region, see Ojeda et al. (2000b). Climate is mild Mediterranean, with a mean annual rainfall of *ca.* 1300 mm.

Altitude in Monte Murta ranges from 350 to 450 m asl. Soil is a mixture of sandstone and clay, except in ridges and upper slopes, where acid, nutrient-poor, sandstone soil emerges. Dominant vegetation is a medium to sparse *Quercus suber* (cork oak) woodland with a heath-scrub understorey. Open heathlands, with virtually no tree overstorey, cover sandstone crests and upper slopes.

Owing to the contrasted ecological optima between *E. arborea* and *E. australis* in this region (Ojeda et al. 2000a; see above), it was not possible to find the three *Erica* species co-occurring at the same location. Hence, two neighbouring sites (about 200–300 m apart) were initially chosen in this study. The first site was a heath-scrub understorey of a sparse cork oak woodland, where *E. arborea* and *E. scoparia* co-occurred with *Ulex borgiae* Rivas Mart. and *Cistus salvifolius* L. as the most abundant species. The second site was an open heathland on sandstone, where *E. scoparia* and *E. australis* were abundant, together with *Calluna vulgaris* (L.) Hull, *Stauracanthus boivinii* (Webb) Samp., and *Genista tridens* (Cav.) DC.

Sixteen adult plants of *E. arborea*, 26 of *E. scoparia* (10 plants from the first site plus 16 from the second), and 16 of *E. australis* were initially selected. They were chosen haphazardly, although care was taken that all plants had not undergone any major disturbance – by wildfire or slashing – at least within 10 years prior to this study.

The experiment started in February 1998, when all selected plants were clipped to the ground. Each plant was then clipped again every six months, until August 2000. In this way, all plants suffered six successive disturbance events. Clippings were conducted every February and August, just before the two seasonal growth flushes (spring and autumn respectively). After each clipping (except the first one) the resprouted biomass was harvested, oven-dried and weighed to the nearest 0.1 grams.

After the initial clipping, two main perpendicular diameters of the upper surface of the lignotuber were measured and their area estimated assuming elliptic shape. The upper surface area of the lignotuber was employed as a surrogate of the plant size (Canadell et al. 1991; Riba 1997; Moreno et al. 1999).

The plants were caged individually with 1 cm × 1 cm wire-mesh to exclude vertebrate herbivory. Unfortunately, several cages were broken and resprouts were browsed heavily by cattle and/or game. Those plants were removed from the experiment, thus changing the initial number of selected plants to 11, 23 and 16 plants of *E. arborea*, *E. scoparia* and *E. australis* respectively.

In a former study, Riba (1997) observed that the first phases of post-disturbance shoot growth in *E. arborea* are strongly dependent on soil water moisture. In order to determine the possible influence of water availability in plant regrowth during the field experiment, monthly rainfall records from 1998 to 2000 were obtained from the nearest available weather station (Jimena de la Frontera), 15 km to the north-east of the study site.

Statistical analysis

The resprouted biomass dry weight was used as indicative of the resprouting vigour, and it was the dependent variable in the statistical analyses aimed to detect differences among species.

In a simultaneous clipping experiment developed in the same two sites with several clipping frequencies, a two-way ANCOVA (the lignotuber upper-surface was included as a covariable) revealed a similar pattern of differential response of *E. scoparia* (the only species which appeared in the two sites) to the clipping frequency treatments between both sites (i.e. interaction of site and clipping frequency: *p*-value = 0.75; Paula and Ojeda, unpubl.). This allowed pooling the individuals of *E. scoparia* from the two sites, and proceed with the comparisons among species.

The existence of changes in the relationship between the resprouting vigour and the upper surface area of the lignotuber after the successive six-month clippings was explored separately for each species and clipping event by means of linear regression analyses. Both variables were log-transformed so as to meet normality and homoscedasticity requirements (Zar 1996).

The lignotuber upper-surface area (log-transformed) and the resprouting vigour (log-transformed) after each clipping event were compared between species by means of independent one-way ANOVAs. When necessary, *post-hoc* multiple comparisons were performed by means Scheffé's tests.

For the two ‘families’ of analyses (linear regression and one-way ANOVA) that we employed to test the same null hypothesis, we applied the *step-up false discovery rate* procedure (hereafter, step-up FDR) to establish the significance levels. This procedure allows adjusting for the probable inflation in Type I error under repeated testing (e.g. Rice 1989), without compromising heavily the Type II error (Benjamini and Hochberg 1995; García 2003).

Results

For the three species, resprouted biomass after the first clipping showed a significant positive relationship with surface area of the lignotuber (Table 1; Figure 1). This pattern was less marked, but still significant, in *E. scoparia* after the following five successive six-month clippings, whereas it disappeared in *E. arborea* and *E. australis* after the fourth and second clipping event, respectively (Table 1, Figure 1). This can be interpreted as a consequence of partial or total (i.e. death) exhaustion after recurrent disturbance (Figure 1).

Overall mortality throughout the experiment was 26%, out of which 12% corresponded to *E. australis*, 10% to *E. arborea*, and only 4% to *E. scoparia*. *Erica australis* was the species that first suffered mortality (August 1999; Table 1). The first deaths detected for *E. arborea* and *E. scoparia* were in February 2000, increasing notably in August 2000 for *E. arborea* (Table 1). Deaths were more prevalent in plants with large lignotubers, particularly in *E. australis* and, to a lesser extent, in *E. arborea* (Figure 1).

Average values of resprouting vigour (i.e. resprouted biomass dry weight) of each species after each successive clipping are summarized in Table 2. Due to the loss of linearity between resprouted biomass and upper surface area of the lignotuber after successive clippings in two of the three species (Table 1; Figure 1), lignotuber size could not be used as a covariate in the between-species comparisons of resprouting vigour within each clipping. Nevertheless, no significant differences were detected in the upper surface area of the lignotuber between the three species (see Table 2).

In general, there is a decrease in the resprouting vigour throughout the five successive clippings for the three species, although spring regrowths (harvested in the August clippings) were larger than autumn–winter ones (harvested in the February clippings). This seasonal trend, as well as the resprouting vigour decline, was similar in the three species until the last harvested regrowth, in August 2000, where resprouting vigour of both *E. australis* and *E. arborea* were significantly lower than that of *E. scoparia* (Table 2).

Cummulative rainfall in the six-month periods March–August and September–February increased steadily from 1998 to 2000 (Figure 2). Therefore, the decrease in resprouting vigour throughout the successive clippings cannot be attributed to a possible depletion in soil moisture levels.

Discussion

Resistance to highly frequent disturbance

In many fire and plant ecology contributions, obligate- (*sensu* Keeley 1986) or strong- (*sensu* Vesk et al. 2004) resprouter woody plants are assumed to be utmost resistant to recurrent disturbance such as wildfires (e.g. Keeley and Zedler 1978). However, short intervals between disturbance events have been reported to reduce

Table 1. Linear-regression results for the relationship between resprouting vigour (resprouted biomass dry weight, log-transformed) and upper surface area of the lignotuber (log-transformed) within each six-month regrowth in the three *Erica* species. Significant linear regressions (after step-up FDR) are shown in bold. Cumulative number of dead plants is shown in brackets.

	Erica arborea $n = 11$	*Erica scoparia* $n = 23$	*Erica australis* $n = 16$
August 1998	**$R^2 = 0.58$; $p = 0.006$**	**$R^2 = 0.66$; $p < 0.001$**	**$R^2 = 0.35$; $p = 0.015$**
February 1999	**$R^2 = 0.44$; $p = 0.026$**	**$R^2 = 0.30$; $p = 0.007$**	$R^2 = 0.14$; $p = 0.15$
August 1999	**$R^2 = 0.56$; $p = 0.009$**	**$R^2 = 0.45$; $p < 0.001$**	$R^2 = 0.14$; $p = 0.16$ (1)
February 2000	$R^2 = 0.20$; $p = 0.17$ (1)	**$R^2 = 0.28$; $p = 0.009$ (1)**	$R^2 = 0.01$; $p = 0.73$ (2)
August 2000	$R^2 = 0.01$; $p = 0.75$ (5)	**$R^2 = 0.24$; $p = 0.019$ (2)**	$R^2 = 0.03$; $p = 0.56$ (6)

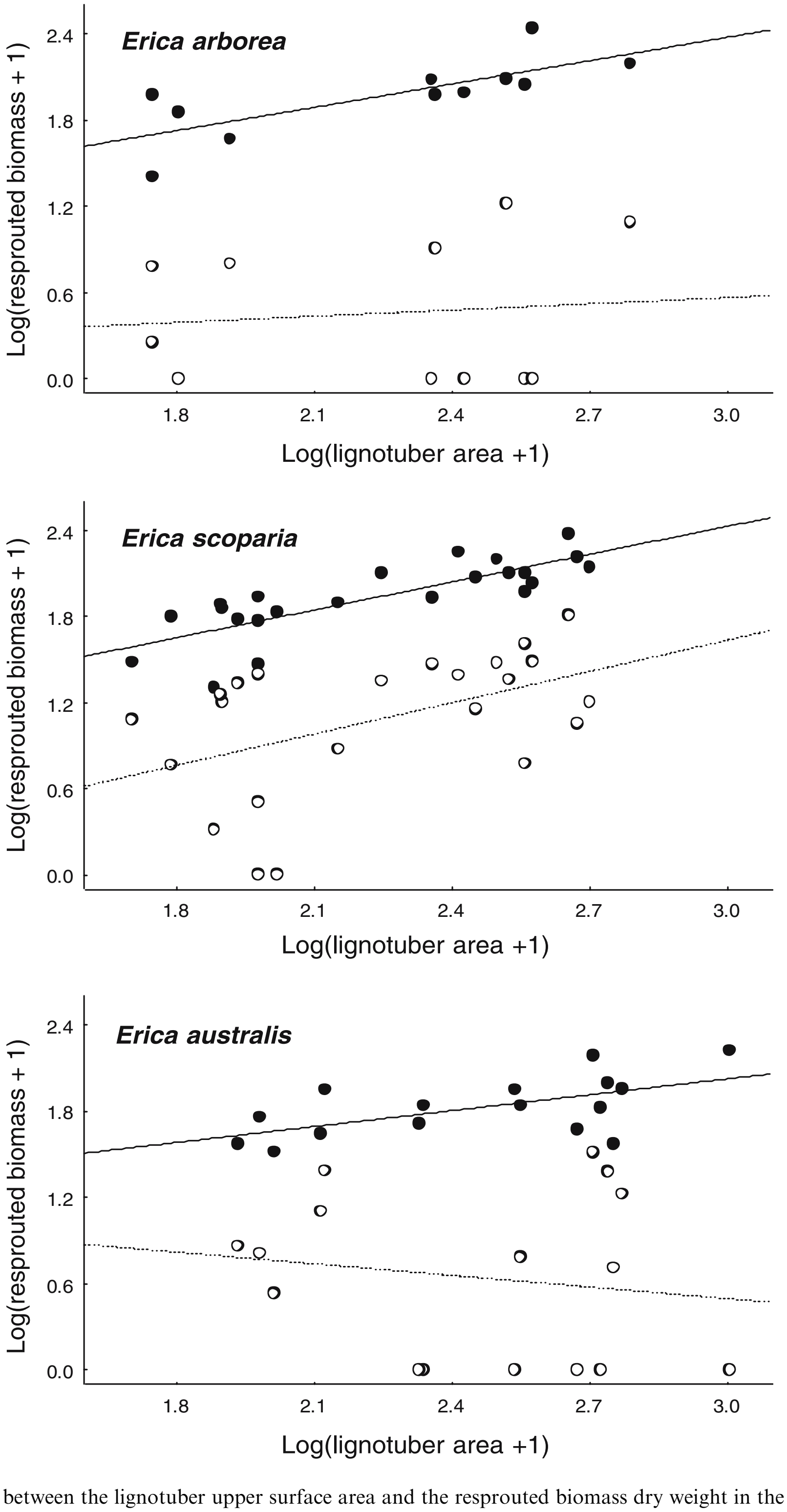

Figure 1. Relationship between the lignotuber upper surface area and the resprouted biomass dry weight in the three species of *Erica* after the first (solid circles and solid line) and the last clipping (open circles and dashed line).

Table 2. Mean values (± 1 SD) of lignotuber size (upper surface area; cm^2), measured at the begining of the experiment, and six-month-old resprouted biomass (dry weight; g) after each successive six-month clipping in *Erica arborea*, *E. scoparia* and *E. australis*. Results of the one-way ANOVAs for the comparisons among species are shown. The existence of significant differences (after step-up FDR for comparisons of the resprouted biomass) is shown in bold. Different letters indicate significant differences after *post-hoc* comparisons (Scheffé's test).

	E. arborea ($n = 11$)	*E. scoparia* ($n = 234$)	*E. australis* ($n = 16$)	ANOVA results
Lignotuber size (cm^2)	241.9 ± 175.3	220.5 ± 149.4	368.6 ± 255.6	$F_{2,47} = 2.1$; $p = 0.13$
Resputed biomass (g)				
August 1998	108.7 ± 64.7	99.0 ± 52.3	73.6 ± 39.2	$F_{2,47} = 1.4$; $p = 0.25$
February 1999	9.1 ± 9.0	13.0 ± 8.4	18.7 ± 20.1	$F_{2,47} = 2.4$; $p = 0.10$
August 1999	42.2 ± 40.8	51.8 ± 34.9	31.7 ± 24.9	$F_{2,47} = 1.7$; $p = 0.20$
February 2000	5.4 ± 4.9	8.6 ± 6.8	3.6 ± 4.2	$F_{2,47} = 4.1$; $p = 0.024$
August 2000	**4.1 ± 5.4 a**	**17.5 ± 14.8 b**	**8.0 ± 10.1 a**	$\mathbf{F_{2,47} = 6.4; p = 0.003}$

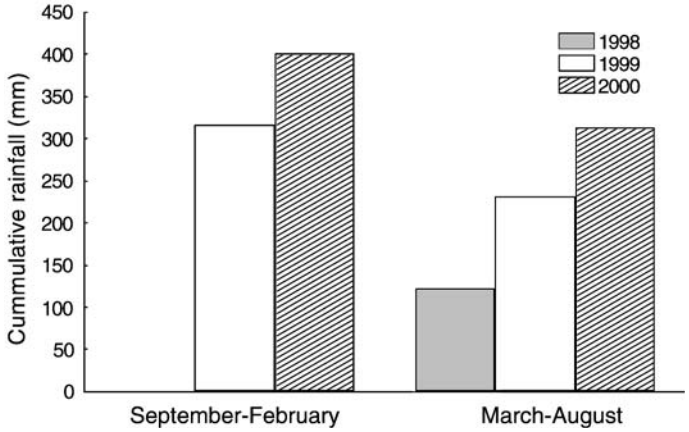

Figure 2. Overall rainfall in the six-month periods before each resprouted biomass harvesting throughout the field experiment.

the ability of strong resprouters to recover (Zedler et al. 1983; Canadell and López-Soria 1998; Bond et al. 2001), probably as a result of a progressive decrease in below-ground carbohydrate reserves (Trabaud 1991; Canadell and López-Soria 1998) and/or in the number of dormant buds (Bell and Pate 1996).

The three *Erica* species of the present study can be classified into the strong-resprouter class, since they recover vigorously after disturbance (Ojeda et al. 1996b; Riba 1997; Cruz et al. 2003; this study). Nevertheless, as Riba (1997) had already reported for *E. arborea*, the resprouting vigour of these strong resprouter species decreased after frequent clippings to the ground level. Spring regrowths (August harvests) were higher than autumn ones (February harvests) in the three species (see Table 2). Higher root starch reserves in early spring (Kays and Caham 1991; Cruz and Moreno 2001; Wildy and Pate 2002), and higher soil water levels (Riba 1997; Wildy and Pate 2002) have been proposed to account for this seasonal pattern. More remarkably, despite their taxonomic relatedness, similar morphology, and somewhat similar ecological requirements, the decrease in resprouting vigour was not equal in the three species, being *E. scoparia* the most resistant to the experimental, highly frequent clipping. However, it shall be stressed that such differences were not clearly detected until the fifth successive post-disturbance regrowth.

Resprouting ability in woody plants is frequently associated with fire as a selective pressure (e.g. Bond and Midgley 2001; Ojeda et al. 2005), and several studies have highlighted that resprouting vigour after burning could be lower than after clipping in *Erica* species (Lloret and López-Soria 1993; Cruz et al. 2003), as well as in other resprouter taxa (e.g. Vesk et al. 2004). However, although absolute values of resprouted biomass might thus be expected to be lower if plants of the three *Erica* species had been burnt successively instead of just been clipped, there is no reason to believe that the reported rank order of the three species in enduring repeated severe disturbance might change.

Ecological distribution of the three Erica species in the Strait of Gibraltar

The ecological distribution of these three species of *Erica* in the northern side of the Strait of Gibraltar was explained by Ojeda et al. (2000a) as a consequence of a high tolerance of *E. australis* and *E. arborea* to extreme environmental conditions (high soil aluminium and dense tree cover, respectively), and a higher performance of *E. scoparia* in intermediate conditions, such as those found in the understorey of *Quercus suber* (cork oak) sparse woodlands. However, the lower resistance of *E. australis* and *E. arborea* to frequent, recurrent disturbance reported in this study might account for the scarcity, or virtual absence (*E. australis*), of these species in most cork oak woodlands, since they have a long history of forest thinning and, particularly, frequent scrub slashing for optimising cork production, facilitating cork harvesting, and reducing the risk of fire (Ceballos and Martín-Bolaños 1930; Torres and Montero 2000). By contrast, the comparatively higher resistance to recurrent clipping would allow *E. scoparia* to withstand such management pressure, and would thus contribute to explain, together with its higher performance under relatively mesic conditions (Ojeda et al. 2000a), its predominance in most Mediterranean heathlands of the northern side of the Strait of Gibraltar. This study supports the idea that land use and management should be definitely taken into account to understand current ecological patterns in the Mediterranean vegetation (Pausas 1999).

However, the dominance of *E. arborea* in most woody plant communities of the southern (Moroccan) side of the Strait of Gibraltar, subjected to a higher slashing pressure (Ojeda *et al.* 2000a), do not seem to be explained by the results reported in this study. We propose two, non-mutually exclusive, testable explanations so as to account for this overall abundance of *E. arborea* in northern Morocco. First, the Strait of Gibraltar might have acted as a biogeographical barrier for this circummediterranean species, being the genetic distance between *E. arborea* populations across the Strait higher than expected by their geographic distance. Hence, we hypothesise that there might be differences in enduring frequent disturbance between *E. arborea* populations from both sides of the Strait of Gibraltar. Second, considering the broader edaphic requirements of *E. arborea* (Aubert 1977, 1978; Ojeda et al. 2000a), this species would be comparatively less affected by the more fragmented arrangement of sandstone patches in the Moroccan side of the Strait of Gibraltar (Ojeda et al. 1996a), thus being less prone to local extinction.

Acknowledgements

This study was financed by DGES (APC98–0085), FEDER-CICYT (1FD97-0743-CO3-03), TRAGSA-UCA (OT190–99) funds. It was also supported by a research grant attached to a “Ramón y Cajal” contract (MCYT-UCA) to FO, and by a FPI-UCA scholarship (OT190–99) to SP. Felipe Oliveros, director of Los Alcornocales Natural Park provided facilities for field work. Manu Victoria, M. Ángeles Muñoz, Redouan Ajbilou, Teodoro Marañón and Juan Arroyo helped with fieldwork. Juan Arroyo, Miguel Verdú, and John Pannell made valuable comments on a previous version of the manuscript.

References

Aubert G. 1977. Essai d’interprétation écologique de la répartition des Ericacées en Provence (région du Sud-est de la France). Ecologia Mediterranea 3: 113–123.

Aubert G. 1978. Relations entre le sol et cinq espèces d’ericacées dans le sud-est de la France. Oecol. Planta. 13: 253–269.

Austin M.P. 1985. Continuum concept, ordination methods and niche theory. Ann. Rev. Ecol. Syst. 16: 39–61.

Bell T.L. and Pate J.S. 1996. Growth and fire response of selected Epacridaceae of south-western Australia. Aust. J. Bot. 44: 509–526.

Benjamini Y. and Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. Roy. Stat. Soc., Series B 57: 289–300.

Bond W.J. and Midgley J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16: 45–51.

Bond W.J. and van Wilgen B.W. 1996. Fire and Plants. Chapman and Halls, London.

Bond W.J., Smythe K.A. and Balfour D.A. 2001. *Acacia* species turnover in space and time in an African savannah. J. Biogeogr. 28: 117–128.

Canadell J., Lloret F. and López-Soria L. 1991. Resprouting vigour of two Mediterranean shrub species after experimental fire treatments. Vegetatio 95: 119–126.

Canadell J. and López-Soria L. 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Funct. Ecol. 12: 31–38.

Ceballos L. and Martín-Bolaños M. 1930. Estudio sobre la vegetación forestal de la provincia de Cádiz. Instituto Forestal de Investigaciones y Experiencias, Madrid.

Clemente A.S., Rego F.C. and Correia O.A. 1996. Demographic patterns and productivity of post-fire regeneration in portuguese Mediterranean maquis. Int. J. Wildland Fire 6: 5–12.

Cruz A. and Moreno J.M. 2001. Seasonal course of total nonstructural carbohydrates in the lignotuberous mediterranean-type shrub *Erica australis*. Oecologia 128: 343–350.

Cruz A., Pérez B. and Moreno J.M. 2003. Resprouting of the Mediterranean-type srhub *Erica australis* with modified lignotuber carbohydrate content. J. Ecol. 91: 348–356.

de Benito N. 1948. Brezales y brezos. Instituto Forestal de Investigaciones y Experiencias, Madrid.

Garcia L.V. 2003. Controlling the false discovery rate in ecological research. Trends Ecol. Evol. 18: 553–554.

Kays J.S. and Canham C.D. 1991. Effects of time and frequency of cutting on hardwood root reserves and sprout growth. Forest Sci. 37: 524–539.

Keeley J.E. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B., Hopkins A.J.M. and Lamont B.B. (eds) Resilience in Mediterranean-Type Ecosystems. Dr. W. Junk Publishers, Dordrecht, pp. 95–112.

Keeley J.E. and Zedler P.H. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. Am. Midland Nat. 99: 142–161.

le Maitre D.C., Jones C.A. and Forsyth G.G. 1992. Survival of eight woody sproutiing species following an autumn fire in Swartboskloof, Cape Province, South Africa. S. Afr. J. Bot. 58: 405–413.

López-Soria L. and Castell C. 1992. Comparative genet survival after fire in woody Mediterranean species. Oecologia 91: 493–499.

Lloret F. and López-Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. J. Veg. Sci. 4: 367–374.

Moreno J.M., Cruz A. and Oechel W.C. 1999. Allometric relationshipin two lignotuberous species from mediterranean-type climate areas of Spain and California. J. Mediterr. Ecol. 1: 49–60.

Moreno J.M. and Oechel W.C. 1991. Fire intensity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern California chaparral. Oecologia 85: 429–433.

Ojeda F., Arroyo J. and Marañón T. 1995. Biodiversity components and conservation of Mediterranean heathlands in Southern Spain. Biol. Conserv. 72: 61–72.

Ojeda F., Arroyo J. and Marañón T. 2000a. Ecological distribution of four co-occurring Mediterranean heath species. Ecography 23: 148–159.

Ojeda F., Brun F.G. and Vergara J.J. 2005. Fire, rain, and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. New Phytologist 168: 155–165.

Ojeda F., Marañón T. and Arroyo J. 1996a. Patterns of ecological, chorological and taxonomic diversity at both sides of the Strait of Gibraltar. J. Veg. Sci. 7: 63–72.

Ojeda F., Marañón T. and Arroyo J. 1996b. Postfire regeneration of a mediterranean heathland in southern Spain. Int. J. Wildland Fire 6: 191–198.

Ojeda F., Marañón T. and Arroyo J. 2000b. Plant biodiversity in the Aljibe Mountains (S. Spain): a comprehensive account. Biodiversity and Conservation 9: 1323–1343.

Ojeda F., Simmons M.T., Arroyo J., Marañón T. and Cowling R.M. 2001. Biodiversity patterns in South African fynbos and Mediterranean heathland. J. Veg. Sci. 12: 867–874.

Pausas J.G. 1999. Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecol. 140: 27–39.

Pausas J.G., Bradstock R.A., Keith D.A., Keeley J.E. and GCTE Fire Network. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85: 1085–1100.

Riba M. 1997. Effects of cutting and rainfall pattern on resprouting vigour and growth of *Erica arborea* L. J. Veg. Sci. 8: 401–404.

Riba M. 1998. Effects of intensity and frequency of crown damage on resprouting of *Erica arborea* L. (Ericaceae). Acta Oecol. 19: 9–16.

Torres E. and Montero G. 2000. Los alcornocales del Aljibe y sierras del Campo de Gibraltar. Miniterio de Agricultura, Pesca y Alimentación, Madrid.

Trabaud L. 1991. Fires regimes and phytomass growth dynamics in a *Quercus coccifera* garrigue. J. Veg. Sci. 2: 307–314.

Vesk P.A. and Westoby M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. J. Ecol. 92: 310–320.

Vesk P.A., Warton D.I. and Westoby M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. Oikos 107: 72–89.

Westman W.E. and O'Leary J.F. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio 65: 179–189.

Wildy D.T. and Pate J.S. 2002. Quantifing above- and bellow-ground growth responses of the western Australian oil mallee, *Eucalyptus kochii* subsp. *plenissima*, to contrasting decapitation regimes. Ann. Bot. 90: 185–197.

Zammit C. 1988. Dynamics of resprouting in the lignotuberous shrub *Banksia oblongifolia.* Aust. J. Ecol. 13: 311–320.

Zedler P.H., Gautier C.R. and McMaster G.S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64: 809–818.

Zar J.H. 1996. Biostatistical Analysis, 2nd ed. Prentice-Hall, Englewood Cliffs.