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Leaf traits and resprouting ability in the Mediterranean basin

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Summary

1. Resprouting is a primary persistence mechanism in fire- and drought-prone ecosystems. Plants with this mechanism (resprouters) tend to exhibit deeper root-system and higher stem and leaf water potential. We test the extent to which non-resprouters counteract their lower root allocation by means of leaf traits that confer higher drought resistance.

2. Leaf mass per area (LMA), leaf dry matter content (LDMC), area-based leaf nitrogen content (LNC_a) and integrated water-use efficiency ($\delta^{13}C$) were measured for 33 woody species in the eastern Iberian Peninsula. Phylogeny and biogeographical history (Tertiary *vs* Quaternary) were considered in all comparisons.

3. Non-resprouters showed higher LMA, LNC_a and $\delta^{13}C$ when considering either all species, or Quaternary species only. Tertiary and Quaternary resprouters differed exclusively in $\delta^{13}C$, which was higher for Tertiary species.

4. These results suggest that, at leaf level, non-resprouters have higher potential for structural resistance to drought and higher water-use efficiency than resprouters. We propose that the existence of a physiological trade-off at leaf level between drought resistance and carbon gain should explain the leaf-trait values exhibited by resprouters.

Key-words: drought, fire, leaf mass per area (LMA), leaf nitrogen, water-use efficiency (WUE)

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Introduction

One of the more relevant characteristics of Mediterranean ecosystems is the simultaneity of the driest and the hottest part of the year (Di Castri, Goodall & Specht 1981). Moreover, the low summer moisture increases plant flammability and fire risk (Gill, Trollope & Macarthur 1978). As a consequence, drought and fire are the two main disturbances faced by plants in Mediterranean ecosystems. Resprouting permits recovery from these and other disturbances by means of dormant buds that consume below-ground reserves even when all above-ground biomass has been removed (Bond & Midgley 2001).

Resprouters tend to be deep-rooted species, whereas non-resprouters are usually shallow-rooted (Keeley 1986; Bell 2001; Silva, Rego & Martins-Loução 2002). It has been proposed that such differences could be explained by the higher allocation to roots of resprouters to sustain plant regrowth (Pate *et al*. 1990; Bell, Pate & Dixon 1996; Davis *et al*. 1999; Verdaguer & Ojeda 2002; Schwilk & Ackerly 2005). Because deep-rooted species achieve most favourable water status (Filella & Peñuelas 2003), water potential during summer is usually higher for resprouters than for non-resprouters (Davis *et al*. 1999; Ackerly 2004; Gratani & Varone 2004; Clemente, Rego & Correia 2005), so it has been suggested that resprouters have higher resistance to drought (Bell *et al*. 1996; Davis *et al*. 1999; Enright & Goldblum 1999). Nevertheless, resprouters and non-resprouters coexist in fire-prone ecosystems (Pausas *et al*. 2004) and, at landscape level, non-resprouters are often even more abundant than resprouters on drier sites in different Mediterranean ecosystems (Keeley 1986; Ojeda 1998; Pausas *et al*. 1999; Clarke & Knox 2002). Thus non-resprouter above-ground organs must have other physiological, chemical and/or structural features that counteract their lower allocation to roots to confer drought resistance.

Leaf attributes reflect resource-uptake and use-efficiency strategies in plants, and variations in leaf traits are strongly correlated with whole-plant and ecosystem properties (Reich *et al*. 1999). One of the distinctive features of Mediterranean plants is sclerophylly: thick, tough leaves with thick cuticles and small, thick-walled cells (Schimper 1903; Read & Sanson 2003). In ecosystems with seasonal drought, such as Mediterranean

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ecosystems, sclerophylly has been interpreted as an adaptive response to low water availability during summer (Schimper 1903; Cunningham, Summerhayes & Westoby 1999; Niinemets 2001; Lamont, Groom & Cowling 2002; see Wright, Reich & Westoby 2001 for comparative analysis of the role of nutrients and drought in relation to sclerophylly). Sclerophylly may confer resistance to wilting by reducing leaf transpiration, avoiding tissue compression and favouring leaf recovery after drought-induced cavitation (Salleo, Nardini & Lo Gullo 1997 and references therein). Leaf mass per area ratio (LMA) has been widely used as a sclerophylly index (Groom & Lamont 1997; Salleo *et al.* 1997; Lamont *et al.* 2002; Filella & Peñuelas 2003; Read & Sanson 2003), and higher LMA values have often been reported in drier sites (Wright *et al.* 2004 and references therein). Similar patterns have also been found with LMA components such as leaf thickness and density (Garnier & Laurent 1994; Niinemets 1999; Wright & Cannon 2001; Lamont *et al.* 2002). Leaf dry matter content (LDMC) has been used as a surrogate of leaf density (Garnier & Laurent 1994; Niinemets 1999; Wright & Cannon 2001; Vile *et al.* 2005).

Plants growing in drier sites also show higher nitrogen content per unit area (LNC_a; Cunningham *et al.* 1999; Niinemets 1999; Reich *et al.* 1999; Wright *et al.* 2001; Lamont *et al.* 2002; Wright *et al.* 2005), which has been related to high irradiance (Cunningham *et al.* 1999). Nevertheless, Wright *et al.* (2001) argued that leaves with high LNC_a probably make greater investments in the photosynthetic machinery, thus permitting a given photosynthetic rate to be reached at lower stomatal conductance and enhancing water conservation during photosynthesis. In fact, plants from drier sites also show higher values of integrated water-use efficiency (WUE_i; Schulze *et al.* 1998; Lamont *et al.* 2002; Llorens *et al.* 2004), which has been estimated through the relative abundance of ^{13}C *vs* ^{12}C in plant tissues ($\delta^{13}C$; Farquhar, Ehleringer & Hubick 1989; Groom & Lamont 1997; Lamont *et al.* 2002; Filella & Peñuelas 2003).

The aim of this study was to test whether resprouters and non-resprouters differ in leaf traits related to drought resistance. For this purpose, we analysed easily measured ('soft') traits that can be considered surrogates for physiological measures, thus acquiring similar information for a wide range of species (Weiher *et al.* 1999). Based on the review above, we predict that non-resprouters should have higher LMA, LDMC, LNC_a and $\delta^{13}C$ than resprouters. Because most Mediterranean basin resprouters evolved under tropical conditions (Tertiary lineages) and most non-resprouters under Quaternary Mediterranean climate (Herrera 1992; Verdú *et al.* 2003; Pausas & Verdú 2005), leaf trait differences could be masked by lineage history. Therefore age of lineage was also considered when comparing Mediterranean basin resprouter and non-resprouter leaf traits.

Materials and methods

STUDY AREA AND SPECIES

The study was conducted in Serra de la Murta (39°4′ N, 0°12′ W), located in the eastern Iberian Peninsula (Valencia, Spain). Altitude ranges between 400 and 480 m a.s.l. The climate is sub-dry meso-Mediterranean (Thornwaite 1948). Mean annual temperature at the nearest weather station (6–12 km north of the study site) is 17·4 °C and annual rainfall is 633 mm, with the summer precipitation being less than the 8% of total annual rainfall (Pérez 1994; 1960–91). The dominant vegetation is a typical, mature, well preserved Mediterranean *maquia*. One of the species, *Juniperus phoenicea*, was sampled in Cerro Simon (Requena, 39°15′ N, 0°35′ W) in an open *Pinus halepensis* forest separated ≈70 km from the main sampling site.

We selected 33 common woody species in the study region: four trees, 17 shrubs, three climbers and nine dwarf shrubs. All persist after fire (by means of resprouting or propagule persistence, cf. Pausas *et al.* 2004), except *J. phoenicea* (Fig. 1). Both the scientific literature and personal observations were used to assign a resprouting ability to each species. The selected species represent the range of persistent types in the Mediterranean basin, thus the number of non-resprouters is low and phylogenetically aggregated (Pausas & Verdú 2005). Most of the species are evergreen, a few are drought semi-deciduous (like the non-resprouters *Cistus* spp. or the resprouter *Calicotome spinosa*), and only *Crataegus monogyna* is winter deciduous. The age of the lineage (Tertiary *vs* Quaternary lineages) was assigned following Herrera (1992) and Verdú *et al.* (2003); taxa were considered Tertiary if there are fossil records before the Pliocene.

SAMPLING AND MEASUREMENTS

Sampling was carried out in July and August 2004, in 10 individuals per species. All plants sampled were located in areas unburned for more than 10 years, although the real age of resprouting species was unknown. We followed Garnier *et al.* (2001) for LMA and saturated LDMC measurements. During the morning, we selected twigs with young, fully expanded, well lit, non-damaged leaves. The leaves were completely rehydrated by re-cutting the base of the twigs inside water and maintaining them in deionized water at 4 °C for 24 h in darkness. Petioles or rachis were discarded. One to several leaves were taken from each individual to obtain, at least, a one-side area of ≈2 cm^2. For *J. phoenicea*, with scaly leaves adpressed to the branches, we selected the youngest green branches as a functional analogue of the leaves. Leaves were weighed to obtain saturated fresh mass, and afterwards the one-side area was digitalized with a flatbed scanner and measured with image analyser

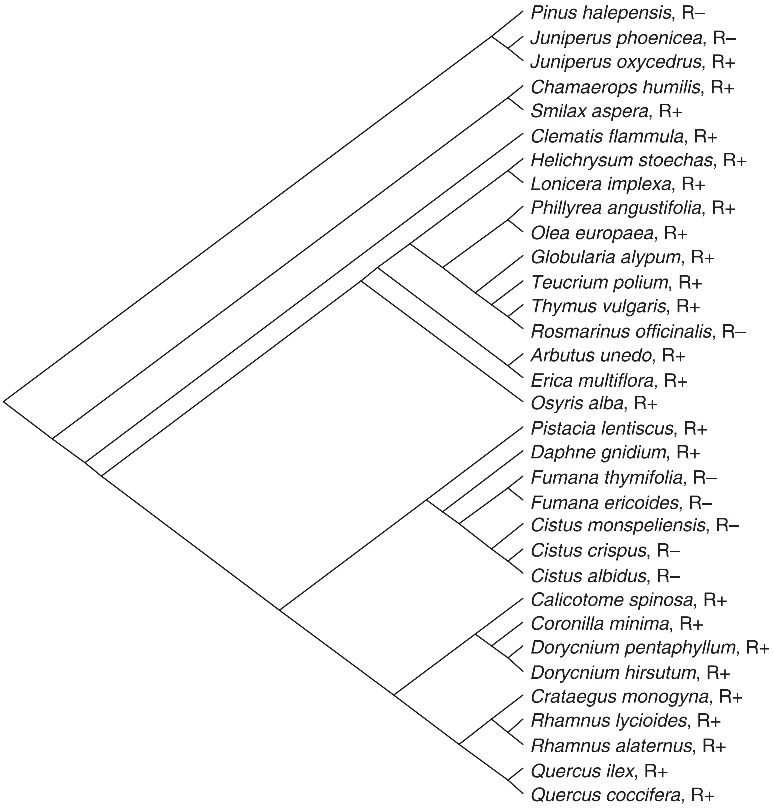

Fig. 1. Phylogenetic tree of sampled species. Resprouting ability is indicated as *R*+ for resprouters, and *R*– for non-resprouters. Nomenclature follows Mateo & Crespo (1990).

software (MATROX INSPECTOR 4·1, Matrox Electronic Systems Ltd, Dorval, Canada). Samples were oven-dried at 60 °C for at least 48 h, and weighed. The LMA was calculated by dividing the leaf dry weight by the one-side projected area. Although the LMA of needles (and of green branches for the adpressed scaly leaves) can be calculated on the basis of total surface area (e.g. Niinemets 1999), we preferred to use the same LMA definition for all the species because: (1) it permits interspecific comparisons when different leaf shapes are included; and (2) photosynthesis parameters are better correlated with one-side projected area than with total surface area (Lusk, Wright & Reich 2003). Saturated LDMC was calculated as the quotient between dry leaf mass and saturated leaf mass.

Dry leaves of each individual were pooled and their N content determined by means of a Carlo Erba NA 2100 PROTEIN elemental analyser (Carlo Erba Instruments, Milan, Italy). Aliquot samples of all individuals were pooled to one sample for each species to determine $\delta^{13}C$. Analyses were carried out with a Flash 1112 elemental analyser (ThermoQuest, Milan, Italy) coupled to a Delta C isotope ratio mass spectrometer by means of a Conflo III interface (Thermo-Finnigan MAT, Bremen, Germany). Calibrations were performed using atropine for elemental analyses and isotopic standards of carbon for isotopic ratio determinations (IAEA-CH3, CH6 and CH7, Vienna, Austria). More negative values of $\delta^{13}C$ indicate higher WUE_i (Farquhar *et al.* 1989).

STATISTICAL ANALYSIS

In all comparisons, we considered phylogenetic relatedness to interpret the current leaf-trait patterns, because both resprouting ability and lineage age are phylogenetically structured in the study area (Herrera 1992; Pausas & Verdú 2005). For this purpose we applied a Generalized Estimating Equation (GEE) procedure that uses a GLM approach incorporating the phylogenetic relatedness among species as a correlation matrix in the model (see Paradis & Claude 2002 for a detailed description and evaluation of the method). One of the advantages of using GEE rather than other comparative methods such as phylogenetic independent contrast (PIC; Felsenstein 1985) is that GEE permits the use of qualitative variables such as resprouting abilities.

A phylogenetic tree was assembled for this data set by pruning the Soltis *et al.* (2000) tree to family level, and subsequently grafting on the species used in this study (Fig. 1). Infrafamily phylogenetic relations were obtained from Doyle *et al.* (1997), Allan & Porter (2000) (Fabaceae), Guzmán & Vargas 2005 (*Cistus*), and the Angiosperm Phylogeny Website (ver. 6, May 2005; http://www.mobot.org/MOBOT/research/APweb) (Lamiaceae). In this way, we obtained a fully resolved phylogenetic tree in which the unit branch lengths were assumed.

First, we carried out a two-way comparison considering resprouting ability and lineage age; the

Table 1. Trait means (± SD) for different resprouting abilities and lineage ages

Species	n	LMA (g m^{-2})	LDMC (mg g^{-1})	LNC$_a$ (g m^{-2})	δ^{13}C
All species					
Resprouters	25	135·8 ± 37·3	412·3 ± 71·7	2·02 ± 0·56	–27·69 ± 1·65
Non-resprouters	8	191·5 ± 75·7	415·9 ± 31·1	2·26 ± 0·86	–27·16 ± 2·01
Tertiary	17	160·6 ± 59·6	441·3 ± 57·4	2·30 ± 0·76	–26·75 ± 1·71
Quaternary	16	137·3 ± 45·5	383·2 ± 57·5	1·85 ± 0·37	–28·43 ± 1·29
Tertiary species					
Resprouters	15	145·0 ± 32·5	442·7 ± 58·3	2·16 ± 0·62	–27·00 ± 1·40
Non-resprouters	2	277·3 ± 105·4	431·4 ± 70·0	3·34 ± 1·14	–24·83 ± 3·28
Quaternary species					
Resprouters	10	122·0 ± 41·4	366·7 ± 67·6	1·82 ± 0·39	–28·73 ± 1·48
Non-resprouters	6	162·9 ± 43·3	410·8 ± 15·8	1·90 ± 0·37	–27·94 ± 0·78

interaction was not included due to the low number of Tertiary non-resprouter species (Table 1). Because almost two-thirds of the resprouters were Tertiary (Table 1), we also analysed the differences between resprouting abilities for Quaternary species only, and between lineage ages for resprouters only, by means of two independent one-way comparisons. These analyses should allow us to ascertain whether the lineage age affected the results of the former comparisons.

To provide a more powerful test, we account for individual variability in leaf traits (except for δ^{13}C) by performing all statistical analyses for the mean values ($n = 10$) of each species as well as for 100 randomly generated values following a normal distribution with the mean and SD values of each variable for each species. Thus the results are expressed as both the significance of the mean and the percentage of significant cases ($P < 0·05$), assuming the individual variability found. For δ^{13}C, only the significance of the mean at species level was analysed, because samples of different individuals were pooled together before analysis (see above).

Finally, we determined the correlation between LMA, LNC$_a$ and δ^{13}C for all the species sampled. We performed both cross-species and PIC correlations (Felsenstein 1985). All phylogenetically informed analyses (GEE and PIC) were performed with APE software (ANALYSES OF PHYLOGENETICS AND EVOLUTION; Paradis, Claude & Strimmer 2004). In all the analyses, LMA and LNC$_a$ were log(10)-transformed to meet normality and homoscedasticity requirements, although mean and SD values reported in the text and tables are untransformed.

Results

Non-resprouters showed significantly higher LMA, LNC$_a$ and δ^{13}C than resprouters (Tables 1 and 2). Although we found marginal differences between resprouters and non-resprouters for LDMC, the magnitude of these differences was very small (Table 1) and only 21% of the comparisons performed with simulated data produced significant differences (Table 2). Differences between resprouters and non-resprouters were maintained when we considered only Quaternary species. Note also that this latter comparison does not include the two conifers (which are Tertiary non-resprouters) and therefore removes the possible effect of the way leaf area was computed for the two needle- and scale-leaved species. Quaternary resprouters showed higher LDMC than non-resprouters (Table 1), although the differences were only marginally significant and were maintained for a relatively small percentage (23%) of the analyses performed with simulated data (Table 2).

Table 2. P values of mean leaf-trait comparisons between resprouting abilities and lineage ages, and (in brackets) proportions of analyses that were significant when using randomly generated data

Species	LMA	LDMC	LNC$_a$	δ^{13}C
All species				
Resprouting ability	0·001 (100)	0·098 (21)	0·004 (95)	0·025
Lineage age	ns (0)	0·052 (30)	ns (10)	0·013
Quaternary species				
Resprouting ability	0·013 (100)	0·091 (23)	0·025 (67)	0·056
Resprouting species				
Lineage age	ns (0)	0·027 (73)	ns (1)	0·035

P values are shown when <0·1 (ns otherwise). When P values are significant, leaf trait values were higher for non-resprouters (in resprouting-ability comparisons) and for Tertiary lineages (in lineage-age comparisons).

Regarding comparisons between lineages, Tertiary species showed higher LDMC and δ^{13}C than Quaternary species, but did not differ in LMA and LNC$_a$, either for all species or for resprouters alone.

We found a significant positive correlation between LMA and LNC$_a$ for both cross-species analyses ($r = 0·63$, $P < 0·001$) and PIC ($r = 0·74$, $P < 0·001$; Fig. 2). Likewise, δ^{13}C was positively correlated with LMA for both cross-species and PIC ($r = 0·56$, $P < 0·001$ and $r = 0·52$, $P = 0·002$, respectively; data not shown). Nevertheless, we found only a marginally significant correlation between δ^{13}C and LNC$_a$ for interspecific analysis ($r = 0·34$, $P = 0·055$; data not shown) and no significant correlation when we considered the phylogenetic relatedness.

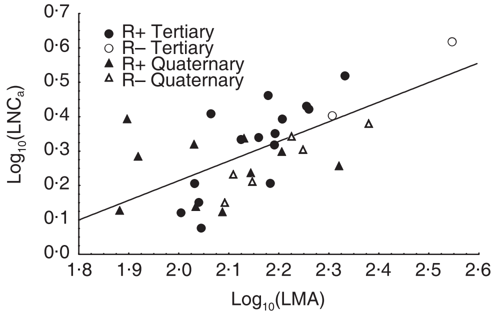

Fig. 2. Relationship between leaf mass area ratio (LMA) and area-based leaf nitrogen content (LNC_a) for resprouters (*R*+) and non-resprouters (*R*–). Correlation coefficients for both cross-species analyses ($r = 0{\cdot}63$) and PIC ($r = 0{\cdot}74$) were highly significant ($P < 0{\cdot}001$).

Discussion

As predicted, non-resprouters showed higher LMA (Table 2) than resprouters, independently of lineage age and phylogenetic relationships (Tables 1 and 2); thus non-resprouter leaves showed a higher potential structural resistance to water deficit. Ackerly (2003) found a similar pattern for *Ceanothus* in Californian chaparral: non-resprouters (subgenus *Cerastes*) had high LMA, shallow roots and high drought resistance, while resprouters (most species of the subgenus *Ceanothus*) showed low LMA, deep roots and moderate drought resistance. Similar results were also observed in a congeneric comparison between resprouting and non-resprouting woody species in eastern Australia, except for the genus *Acacia* (Knox & Clarke 2005).

Tertiary resprouter species of the Mediterranean basin are traditionally used as example of sclerophyllous species (Herrera 1992; Verdú *et al.* 2003). Nevertheless, they showed lower LMA than non-resprouters (Table 1). The thick cuticle or outer wall of the epidermis confers higher leaf stiffness, which is the qualitative leaf trait that many botanists use to assign sclerophylly (Read & Sanson 2003), despite there being other properties that also confer high LMA values (Wright & Cannon 2001; Read & Sanson 2003). The use of stiffness as the only leaf trait for attributing the degree of sclerophylly might contribute to explaining the disagreement between our results and the sclerophylly values assumed for Tertiary species. Detailed anatomical studies on leaves would help to explain the differences in LMA between both resprouting abilities and biogeographical histories.

Non-resprouters showed higher LNC_a than resprouters, independent of their lineage age. Increases in LNC_a might be expected to arise from increased photosynthetic tissues per unit area, that is, higher LMA. In fact, they are often correlated (Fig. 2; Cunningham *et al.* 1999; Wright *et al.* 2001). Nevertheless, LNC_a and LMA may not necessarily be correlated, as in the case where high LNC_a is the consequence of high chloroplast density (Cunningham *et al.* 1999). It has been suggested that higher values of LNC_a have significant benefits in terms of enhancing water conservation during photosynthesis, because high LNC_a facilitates carbon gain at lower stomatal conductance by increasing carboxylation (Wright *et al.* 2001). Nevertheless, we found that LMA, not LNC_a, contributes to explaining the variability of $\delta^{13}C$ and therefore of WUE_i (see similar results in Hoffmann *et al.* 2005). High leaf density and/or thickness (i.e. high LMA) are likely to reduce internal CO_2 conductance and/or increase carbon demand, thus a lower internal CO_2 is achieved for a constant stomatal conductance, and increasing $\delta^{13}C$ (Parkhurst 1994; Lamont *et al.* 2002).

We found that resprouters have lower $\delta^{13}C$ and thus lower WUE_i, although many resprouters are Tertiary species and show higher $\delta^{13}C$ than Quaternary species. Differences between resprouting abilities are maintained when considering exclusively Quaternary species (Tables 1 and 2). Differences between biogeographical histories for resprouters in $\delta^{13}C$ have been explained in terms of differences in rooting depth (Filella & Peñuelas 2003).

In conclusion, all these results suggest that non-resprouters have higher drought resistance at leaf level because: (1) they have higher WUE_i, probably because higher LMA and/or higher LNC_a draw down internal CO_2 for a constant stomatal conductance (see above); and (2) they have high LMA, which should confer on them high structural resistance to low leaf water content. However, in resprouters the increase in drought susceptibility through low LMA would enhance their physiological performance with respect to carbon assimilation by deploying a larger light-capture area per mass (Reich *et al.* 1999; Wright *et al.* 2001) and shorter diffusion paths from stomata to chloroplasts (Parkhurst 1994). Furthermore, lower N levels should decrease carbon costs in both dark respiration rate and N acquisition (Wright *et al.* 2001; Wright, Reich & Westoby 2003). We can expect that the leaf performance of resprouters should permit enough carbon assimilation to meet the high metabolic demands of resprouting (Bloom, Chapin & Mooney 1985; Pate *et al.* 1990; Iwasa & Kubo 1997). It has been suggested that the size and metabolic activity of sinks alter photosynthetic rate and capacity (Marcelis 1996). Thus we propose the existence of a physiological trade-off at leaf level between drought resistance and carbon gain to meet resprouting costs. Nevertheless, we should take into account that: (1) total carbon input depends not only on the net photosynthetic rate, but also on the plant weight fraction allocated to leaves (Poorter 1989); and (2) drought resistance suggests anatomical, metabolic and physiological features that involve the whole plant (Ackerly 2004). Therefore further physiological studies at the whole-plant level are recommended to fully understand the relationship between drought and fire-persistence strategies.

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