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Leaf physiological traits in relation to resprouter ability in the Mediterranean Basin

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Abstract In Mediterranean ecosystems, fire is a strong selective agent among plants, and the different post-fire regeneration strategies (e.g. resprouting and non-resprouting) have implications for other plant traits. Because young plants of non-resprouters need to grow quickly and mature well before the next fire, we predict that they should possess leaf traits related to increased efficiency in growth and resource acquisition compared with resprouter species. To test this hypothesis, we measured specific leaf area, leaf nitrogen and carbon concentrations and leaf physiological traits, including gas exchange parameters and chlorophyll fluorescence, in 19 Mediterranean species cultivated in a common garden. Both cross-species and phylogenetically informed analyses suggest that non-resprouters have better physiological performance at the leaf level (i.e. higher photosynthetic capacity) than resprouters. All these results suggest that non-resprouter species are able to take greater advantage for vegetative growth and carbon fixation than resprouters during periods when water is readily available. The contrasted physiological differences between resprouters and non-resprouters reinforce the idea that these two syndromes are functionally different (i.e. they are functional types).

Keywords Functional traits · Leaf nitrogen and carbon · Non-resprouters · Photosynthetic capacity · PSII photochemical efficiency · Resprouters · Specific leaf area

Introduction

Fire is an ancient ecological process characteristic of many terrestrial ecosystems (Pausas and Keeley 2009). In Mediterranean-climate regions, dry and warm summers increase plant flammability, favouring the recurrent fire regimes (Piñol et al. 1998; Pausas 2004). Recurrent fires determine many aspects of the ecology and evolution of Mediterranean-type ecosystems (Naveh 1975; Verdú and Pausas 2007; Keeley et al. 2011). Most plant communities from Mediterranean-type ecosystems are highly resilient to recurrent fires, since they recover their structure and composition relatively quickly. This recovery capacity

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has been related to the evolutionary history of disturbances in the Mediterranean Basin (Pausas and Verdú 2005).

Resprouter and non-resprouter species coexist in fire-prone ecosystems and represent the two main types of post-fire regeneration strategies (Bond and van Wilgen 1996; Pausas et al. 2004). The differential survival and growth exhibited by seedlings and resprouts after fire determine the composition of the post-fire mature vegetation (Keeley 1986; Bond and Midgley 2001; Pausas et al. 2004). After a fire, resprouter species do not die and regenerate their above-ground tissues from protected buds using stored carbohydrates (Bowen and Pate 1993; Schutz et al. 2009). However, non-resprouters are killed by fire and the regeneration of their populations depends on seed traits and seedling performance (Paula and Pausas 2008; Moreira et al. 2010). Specifically, young plants of non-resprouters need to grow fast and mature early to ensure offspring before the next fire (Pausas et al. 2004). Our general hypothesis is that seedlings and saplings of non-resprouter woody species, compared to resprouters, will have leaf traits related to high carbon gain and efficient photosynthetic activity.

Leaf traits play an important role in carbon gain and water relations of plants, and consequently affect plant performance (Paula and Pausas 2006; Hernández et al. 2009, 2010). Specific leaf area (SLA), net photosynthetic rates and water use efficiency are all considered as the key variables in the overall efficiency of species at the leaf level (Jacobsen et al. 2008; Hernández et al. 2010; Medrano et al. 2009). Indeed, the study of leaf functional traits can help to predict changes in vegetation composition under future scenarios (Valladares 2008; Medrano et al. 2009).

Leaf area per unit leaf mass (SLA), is a fundamental measure of allocation strategy and reflects the light-capture area deployed per unit of carbon invested in leaves (Wright and Westoby 2001). In addition, as a major component of chlorophyll, leaf nitrogen content is related to photosynthetic performance (Meziane and Shipley 2001; Gulías et al. 2003).

Photosynthetic activity and photochemical efficiency of PSII are closely coordinated across species (Valladares and Sánchez-Gómez 2006; Galmés et al. 2007). Quantum yield of PSII (Φ_{PSII}) is a measure of the rate of linear electron transport and thus is an indicator of overall photosynthesis (Maxwell and Johnson 2000). Therefore, analyses of chlorophyll fluorescence together with gas exchange parameters are an important means of evaluating the internal apparatus driving the photosynthetic process (Maxwell and Johnson 2000).

We hypothesized that functional leaf characteristics are related to post-fire reprouting ability. Specifically, because young plants and saplings of non-resprouters need to grow fast and mature early before the next fire (Pausas et al. 2004), we predict that they should have leaf traits related to high efficiency in light capture and carbon fixation, compared with resprouters. To test this hypothesis, we performed a common garden experiment with resprouter and non-resprouter species that normally coexist in Mediterranean ecosystems and measured their structural and physiological leaf traits.

Materials and methods

Plant species

We selected 19 common species that co-occur in fire-prone ecosystems of the western Mediterranean Basin, including species with and without the ability to resprout after disturbance, and from a wide range of families (Fig. 1). Resprouting ability of each species was assigned from the BROT database (Paula et al. 2009) and personal observations. The selected 19 species represent the range of persistent types in the Mediterranean Basin, with the number of non-resprouter species being lower than the number of resprouter species (Pausas et al. 2004).

Seeds of these species were collected from wild populations in south-eastern Spain (Valencia region) and germinated under nursery conditions. After their first year of growth, in February 2007, seedlings were individually transplanted into 3.5 l pots containing a mixture of peat and coconut peat (1:1 v/v) and fertilized with 1 g of a slow-release fertilizer (N:P:K, 14:8:14) per litre of substrate. Seedlings were grown in the Santa Faz forest nursery (38°23′N; 0°26′W; 80 m above sea level; mean annual rainfall 353 mm and mean annual temperature 18°C) and watered to saturation twice a week. In January 2008, seedlings were placed in a greenhouse (30.3°C day/15°C night mean temperature, under natural photoperiod, with a mid-day radiation intensity of 800–900 μmol m^{-2} s^{-1}) and kept well-watered. On 23rd

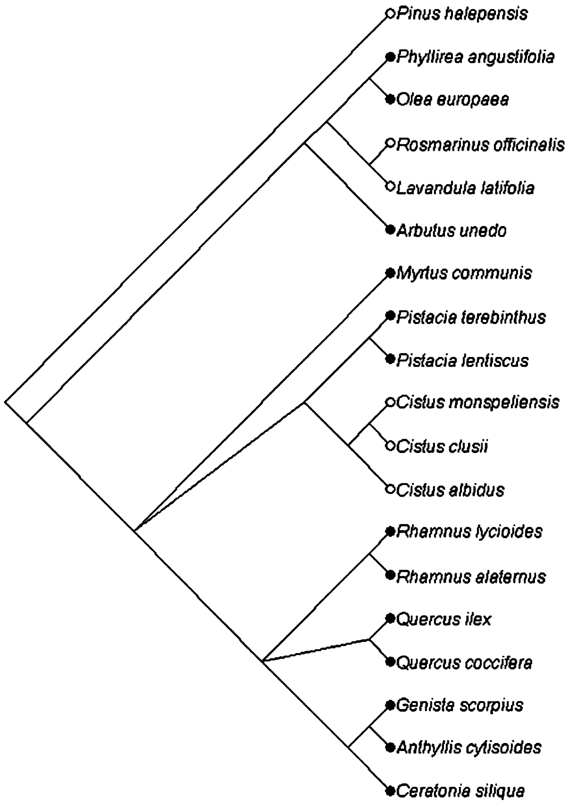

Fig. 1 Phylogenetic relations of the 19 species considered in this study, with an indication of species with the ability to resprout after fire (*filled circles*) and those that lack this ability (*open circles*)

April 2008, four similar-sized plants of each species were selected for measurements.

Measurements

Leaf gas exchange rates and chlorophyll fluorescence measurements were performed between 08 and 11 h00. All plants were watered to field capacity the night before the measurements. Leaf gas exchange measurements were performed with a portable infrared gas analyzer (Li-6400, Li-Cor Inc., Lincoln, NE, USA), in a chamber set at 55 ± 5% relative humidity, saturating light intensity (1500 μmol photon m^{-2} s^{-1}), 25.6 ± 0.5°C mean temperature and 400 μmol mol^{-1} CO_2 concentration. One undamaged mature leaf per plant was chosen to measure the leaf gas exchange response. For each seedling, we measured maximum CO_2 assimilation rate, stomatal conductance and transpiration (E) scaled on the basis of leaf area (Assimilation rates per area (Aa), Stomatal conductance (g_s) and E, respectively). Intrinsic water use efficiency (WUEi) was estimated as the Aa/g_s ratio (Larcher 1995). We measured chlorophyll fluorescence using a PAM-2100 portable fluorometer (Walz, Effeltrich, Germany). Maximal photochemical PSII efficiency (Fv/Fm) measurements were performed after dark adaptation and before sunrise. Maximum quantum yield of photosystem II photochemistry (Φ_{PSII}) was measured on light-adapted leaves. After measurements, individual leaves were removed from each plant. Leaf area was measured by scanning each individual leaf and analysing the images with specific software (WinRhizo, Régent Instruments Inc., Quebec Canada). These leaves were then oven-dried at 65°C until they reached constant weight to obtain dry leaf mass.

Specific leaf area, leaf nitrogen and carbon concentrations were determined on the same leaf samples that were used for physiological measurements. SLA was calculated as leaf area per dry leaf mass (mm^2 mg^{-1}). Leaf nitrogen and carbon concentrations were measured by means of an elemental analyzer (Model NA 1500, Carlo Erba, Milan, Italy). Nitrogen and carbon contents were calculated both per leaf area (Na and Ca) and per leaf mass (Nm, Cm).

Data analysis

For each of the measured variables, the difference between regeneration responses was tested by analysis of variance, using species as a random factor nested in regeneration response (cross-species analysis). All leaf traits were log-transformed for normality and homoscedasticity prior to statistical analysis. The phylogenetic relatedness among species was tested for each of the measured variables by means of a generalized estimating equations (GEE) procedure. GEE uses a generalized linear model approach incorporating the phylogenetic relatedness among species as a correlation matrix in the model (Paradis and Claude 2002). Phylogenetic relatedness was obtained by assembling a phylogenetic tree with the help of the Phylomatic database implemented in Phylocom 3.41 (Webb et al. 2008) and additional information from Guzmán and Vargas (2009).

The relationships between the studied variables were determined by both cross-species analysis (Pearson's correlation) and phylogenetically independent contrasts (PICs; Felsenstein 1985). All cross-species statistical analyses were performed with SPSS 15.0 (SPSS, Inc., Chicago, USA) software package while phylogenetically informed analyses were performed using the APE package (Paradis et al. 2004).

Results

Resprouters showed significantly higher SLA and leaf nitrogen content per mass (Nm), while leaf nitrogen content scaled per leaf area (Na) was higher for non-resprouters (Table 1). Non-resprouter species also showed significantly greater leaf carbon content per area (Ca); however, when leaf carbon content was scaled per mass unit (Cm) the differences between the two regeneration strategies were not statistically significant (Table 1).

*A*a ranged from 5.7 to 19.0 μmol CO_2 m^{-2} s^{-1} across species, and were significantly higher in non-resprouter species (Table 1). g_s and *E* also showed significant differences between regeneration responses, with higher values in non-resprouters (about 2 and 1.5×, respectively). WUEi was higher in resprouter species. Differences in the chlorophyll fluorescence parameters measured were significant between regeneration strategies, with non-resprouters showing higher predawn maximal photochemical PSII efficiency (Fv/Fm_{pd}) and Φ_{PSII} than resprouters (Table 1).

In general, significant pair-wise correlations were found between the leaf traits measured (Supplementary material). Across all species, diverse correlation patterns were found between the different leaf traits evaluated. SLA showed a significant positive correlation with Nm but a significant negative correlation with both Na and Ca. SLA also showed significant correlations with physiological leaf traits, so that it was negatively correlated with *A*a, g_s, Fv/Fm_{pd}, Φ_{PSII} (Fig. 2) and positively correlated with WUEi. Leaf nitrogen content was associated with gas exchange variables and photochemical efficiency variables. Decreased Nm was correlated with increased *A*a, g_s, Fv/Fm_{pd} and Φ_{PSII} for cross-species correlations. *A*a showed positive significant associations with Na, Cm and Ca when the phylogenetic relationships among species were considered.

Discussion

Our results show that resprouter and non-resprouter Mediterranean species differ in their leaf functional traits. This is in agreement with the differences observed in many other traits (Bond and van Wilgen

Table 1 Mean ± SD of leaf structural and functional traits for the different resprouting abilities (resprouters and non-resprouters)

Traits	Code (units)	Resprouters	Non-resprouters	*P* values (cross-species)	*P* values (phylogenetic relatedness)
Specific leaf area	SLA (mm^2 mg^{-1})	8.02 ± 0.65	5.25 ± 0.17	**0.026**	**0.017**
Leaf nitrogen content/area	Na (g m^{-2})	1.61 ± 0.32	2.10 ± 0.29	0.089	**0.038**
Leaf nitrogen content/mass	Nm (mg g^{-1})	12.18 ± 0.68	9.20 ± 0.51	**0.015**	**0.050**
Leaf carbon content/area	Ca (g m^{-2})	63.9 ± 2.5	90.9 ± 3.7	**0.007**	**0.008**
Leaf carbon content/mass	Cm (mg g^{-1})	452.1 ± 1.3	461.2 ± 1.9	0.322	0.565
Assimilation/area	A_a (μmol CO_2 m^{-2} s^{-1})	8.45 ± 0.65	15.13 ± 0.69	**<0.001**	**0.002**
Stomatal conductance	g_s (mol H_2O m^{-2} s^{-1})	0.11 ± 0.01	0.25 ± 0.01	**<0.001**	**0.008**
Transpiration	*E* (mol H_2O m^{-2} s^{-1})	2.09 ± 0.24	3.51 ± 0.44	**0.003**	**0.019**
Intrinsic water use efficiency	WUEi (μmol mol^{-1})	84.97 ± 3.92	64.59 ± 4.32	0.065	**0.044**
Predawn maximal photochemical PSII efficiency	Fv/Fm_{pd} (no units)	0.71 ± 0.01	0.74 ± 0.01	**0.005**	**0.038**
Maximum quantum yield of photosystem II	Φ_{PSII} (no units)	0.25 ± 0.02	0.42 ± 0.03	**<0.001**	**0.019**

The *P* values of the statistical comparison according to cross-species analyses and phylogenetically controlled tests. Values in bold indicate significant differences

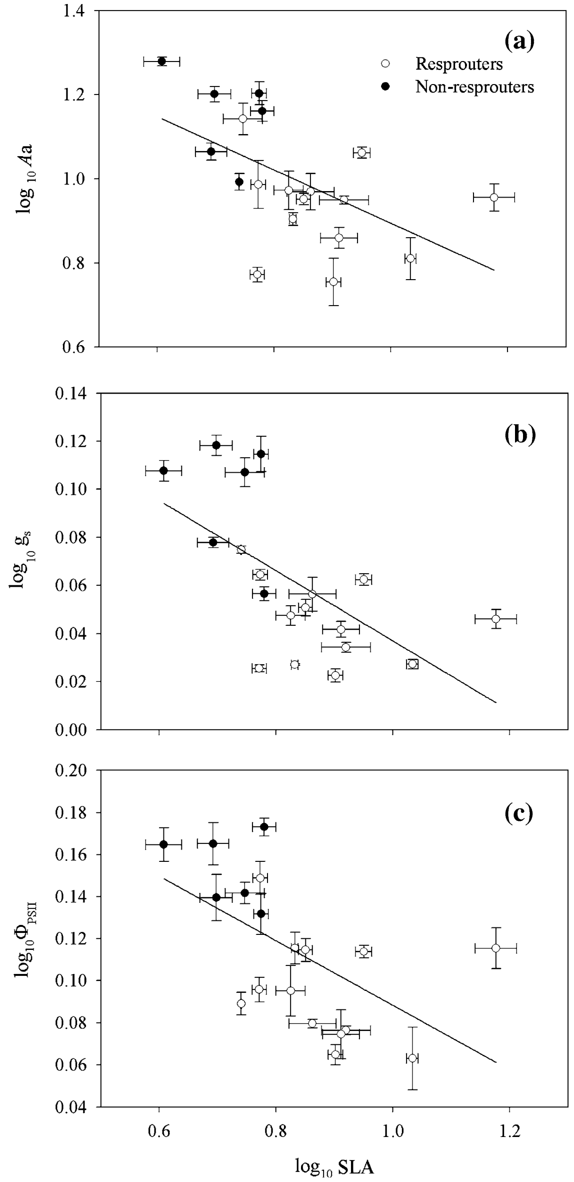

Fig. 2 Specific leaf area ($\log_{10}$ SLA) versus **a** maximum assimilation rate per area ($\log_{10}$ *A*a), **b** maximum stomatal conductance ($\log_{10}$ g_s) and **c** maximum quantum yield of photosystem II ($\log_{10}$ Φ_{PSII}) for resprouter and non-resprouter species. Correlation coefficients and PIC are: **a** $r = -0.56$*, PIC = −0.51*; **b** $r = -0.61$*, PIC = −0.36, **c** $r = -0.56$*, PIC = −0.42. *Significant at $P < 0.05$

1996; Pausas 1999; Lamont and Wiens 2003; Pausas and Verdú 2005; Pratt et al. 2007, 2009; Paula and Pausas 2008), suggesting that these two groups of species represent two distinct syndromes with different ways of functioning. The higher sclerophylly (i.e. lower SLA) of non-resprouters is observed not only in adult plants under field conditions (Paula and Pausas 2006), but also in seedlings and saplings growing under the same experimental conditions.

Leaf gas exchange together with chlorophyll fluorescence provided valuable information on the performance of the photosynthetic apparatus. When water was not limiting, non-resprouter species showed a better performance of leaf gas exchange traits than resprouters, since *A*a, g_s and *E* were much higher in non-resprouters. Variables related to photochemical efficiency and electron movements at PSII level (Fv/Fm and Φ_{PSII}) were also higher in non-resprouters. The high efficiency of leaf photosynthetic processes present in non-resprouters indicate that non-resprouter seedlings and saplings put more into above-ground vegetative growth than resprouters (Montès et al. 2004). First, because recruitment success is more limiting for the former and, second, because allocation to root systems is lower in non-resprouters than resprouter species (Ackerly 2004; Pugnaire et al. 2006; Paula and Pausas 2011). The higher photosynthetic rates in non-resprouters should also provide a higher photochemical sink for electrons, protecting the photosynthetic apparatus against the accumulation of excessive excitation energy under high irradiance conditions (Valladares et al. 2002; Galmés et al. 2007).

Specific leaf area was positively correlated with nitrogen content per mass according to previous studies performed over a large range of species and biomes (Wright et al. 2001; Lamont et al. 2002; Gulías et al. 2003). In contrast, Na and Aa were significant and negatively correlated with SLA as found in global analyses (Wright et al. 2004), suggesting a higher allocation of leaf nitrogen to the photosynthetic apparatus in non-resprouter species. Higher Na is related to higher rates of photosynthesis and high Rubisco specific activity (Poorter and Evans 1998; Wright and Westoby 2001; Wright et al. 2001), indicating that non-resprouters have traits associated with more efficient carbon gain which could be related with the higher growth rates developed by this strategy. Indeed, there is previous evidence of higher growth rates in non-resprouter than in resprouter species from Mediterranean-type ecosystems (Pate et al. 1990; Pausas et al. 2004). These differences should reflect different strategies in relation to the availability and use of nutrients in both functional groups of species (Reich et al. 1995, 1999; Ackerly 2004).

Plants living in water-limited environments have evolved strategies in which stomatal behaviour is regulated to maximize the efficiency of water use (Levitt 1980; Meziane and Shipley 2001; Lamont et al. 2002; Ackerly 2004; Schwilk and Ackerly 2005; Vilagrosa et al. 2010). While non-resprouters show higher integrated WUE (δ^{13}C) than resprouters under field conditions (Paula and Pausas 2006), instantaneous WUE in non-resprouter seedlings is lower when water is available. That is, although Mediterranean plants are traditionally considered to be conservative in their use of water (Larcher 1995; Vilagrosa et al. 2003; Hernández et al. 2010), the high rates of gas exchange observed in young plants of non-resprouter species under high water availability conditions might indicate a facultative water spender strategy (Levitt 1980). These species would be able to extract water from soil more efficiently and transport it to leaves quicker than co-occurring resprouters. These functional characteristics would also suggest differences in plant hydraulic properties between resprouting abilities that allow non-resprouters to take fuller advantage of moist periods. These differences that were previously reported for Californian Rhamnaceae species (Pratt et al. 2009) seem to be general in Mediterranean ecosystems.

In conclusion, resprouters and non-resprouters differ in their leaf physiological traits. Despite having different evolutionary histories (Verdú 2000; Pausas and Verdú 2005), the differences are not related to their phylogenetic affiliation, but to ecological processes driven by their differential regeneration niche. Non-resprouter species show higher leaf gas exchange rates than resprouters, which is indicative of a higher efficiency in resource capture, and thus, a better capacity to take advantage of water when it is freely available. In contrast, resprouters showed a water conservative strategy taking advantage of their greater water use efficiency and moderating the consumption of water from the soil. These physiological differences together with previously observed differences in other traits highlight the importance of these two syndromes and contribute to explaining species coexistence in Mediterranean climate ecosystems.

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