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## Implications of opposite phyllotaxis for light interception efficiency of Mediterranean woody plants

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**Abstract** Opposite leaves lead to a greater leaf overlapping than leaves spirally arranged along a shoot, decreasing light interception efficiency ( $E_a$ , fraction of the light reaching the plant actually intercepted by the leaves) of the crown. However,  $E_a$  results from a whole suite of morphological traits. The interplay between phyllotaxis, crown architecture, leaf morphology and  $E_a$  was explored in 12 woody species from Mediterranean-type ecosystems, where the abundance of woody species with opposite phyllotaxis is unusually high. The three-dimensional model Y-plant was used to estimate  $E_a$  in unbranched, vertical shoots of each species encompassing the natural morphological variation found from moderate shade to open light environments.  $E_a$  exhibited significant interspecific differences, ranging from 0.25 in *Daphne gnidium* to 0.75 in *Cistus ladanifer*, *Olea europaea* and *Salvia officinalis*, decreasing with leaf inclination angle and leaf area ratio (LAR), and increasing with internode-to-leaf-length ratio and supporting biomass. Species with spiral vs. opposite phyllotaxis did not differ in their mean  $E_a$ . However, the former had higher  $E_a$  than the latter at short internode lengths. The natural range of variation in internode length had a larger effect on  $E_a$  than the natural range of leaf elevation angle. Principal component analysis segregated species with opposite phyllotaxis from those with spiral leaves because of their greater self-shading for high sun elevation angles ( $>45^\circ$ ); they were in turn distributed in two groups, one with high  $E_a$ , large investment in supporting biomass and long internodes, and another with low  $E_a$  and large LAR. Species with spiral phyllotaxis all had intermediate or low  $E_a$  and steep leaf elevation angles. Species with opposite phyllotaxis can compensate their less efficient leaf arrangement by decreasing leaf elevation angle and increasing internode length, but they may expe-

rience a real phylogenetic constraint for light interception when biomass allocation to supporting tissues (internodes and petioles) becomes very costly. This constraint could be involved in the shade intolerance of woody Mediterranean species exhibiting opposite phyllotaxis.

**Keywords** Phyllotactic patterns · Light interception efficiency · Crown architecture · Mediterranean woody plants · 3-D model

### Introduction

Leaves can be arranged in space in many different manners giving way to the diversity of crown architectures exhibited by plants (Guerreiro and Rothen 1995; Valladares 1999). All these different leaf arrangements can lead to a different light capture efficiency and photosynthetic performance of plants coexisting in a given habitat (Falster and Westoby 2003), or, on the contrary, they can be functionally equivalent, as shown by the convergence in light capture efficiency of understory plants with contrasting architectures (Valladares et al. 2002). While extensive attention has been devoted to the influence on light capture of architectural features such as leaf area ratio, leaf clustering and leaf inclination angle (Herbert 1996; Reich et al. 2003; Valladares 1999), other aspects such as phyllotaxis (i.e. the geometric arrangement of leaf primordia around stems during plant growth) have been far less explored (Niklas 1998; Sekimura 1995). Phyllotactic patterns have attracted the attention of both botanists and mathematicians for many centuries, who were fascinated by the beauty of their symmetry, the intriguing frequency of the golden divergence angle among successive leaves and the strong predominance of the Fibonacci sequences in these angles (Adler et al. 1997; Douady and Couder 1992). The few studies exploring the influence of phyllotaxis on light interception efficiency report lower efficiencies of opposite (decussate) leaves than spirally arranged leaves, but they also suggest that other architectural features such as leaf angle or internode length can compensate

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for these inefficiencies (Niklas 1988, 1998; Sekimura 1995). However, most of these studies relied on computer simulations that did not take into account interception of diffuse light (only direct sunbeam) or the whole suite of morphological traits that real plants exhibit in combination with a given phyllotaxis (Valladares and Brittes 2004).

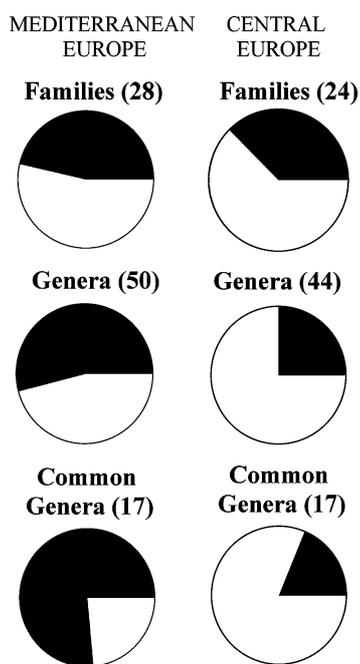
Species with opposite phyllotaxis are unusually abundant in the Mediterranean woody flora. In fact, an analysis of the Mediterranean and non-Mediterranean woody taxa of Europe revealed a significantly higher proportion of species with opposite leaves in the Mediterranean dendroflora (Fig. 1). This overrepresentation of opposite phyllotaxis in Mediterranean woody taxa is mainly due to the families Labiatae, Cistaceae and Oleaceae, which contain some of the most characteristic and common genera of Mediterranean woody flora. Approximately 75% of these genera contain species with opposite phyllotaxis, while this proportion is only 20% in Central Europe. In this study we wanted to determine the implications for light interception efficiency of the opposite phyllotaxis in 12 woody plant species from Mediterranean-type ecosystems, where this phyllotaxis is so abundant. The implications were studied including the whole suite of morphological attributes (leaf size and shape, internode length, leaf elevation angle, leaf area ratio) that are associated with the phyllotactic pattern of a given species using the computer model Y-plant (Percy and Yang 1996). Y-plant has been successfully used in a number of studies of light capture and utilization efficiency by plant crowns (Falster and Westoby 2003; Muraoka et al. 2003; Percy et al. 2004; Valladares and Pugnaire 1999) and its estimations for light interception

by individual leaves within a complex foliage have been validated using photon flux density microsensors attached to real plants in the field (Valladares and Percy 1998). We hypothesised that opposite phyllotaxis is part of a suite of interrelated morphological features that affect light interception efficiency by plant crowns. To test this hypothesis we first explored the influence of phyllotaxis, internode length, leaf elevation angle, leaf area ratio and investment in supporting biomass (petioles plus stems) on light interception efficiency, and then segregated the study species in a multidimensional space resulting from all these features to determine whether species with opposite and spiral phyllotaxis are distinctive morpho-functional groups.

## Materials and methods

Twelve species of evergreen woody plants representative of Mediterranean-type ecosystems were studied (Table 1). Species were selected for exhibiting contrasting phyllotactic patterns and for covering a range of variation in structural features such as size and shape of the leaves, length of the internodes and leaf elevation angles. For the sake of simplicity, opposite phyllotaxis is used in the text instead of opposite-decussate, which is the real phyllotaxis exhibited by the plants studied (see Bell (1993) for descriptions). All plants studied for a given species were growing in a gradient from moderately shaded to totally open sites (i.e. receiving 30–100% sunlight). Thus, the range of variation considered for each species was a combination of differences between individual plants and sun-shade differentiation. We avoided deep shade environments because they are not well represented in Mediterranean habitats and can lead to unusual crown and leaf morphologies. Morphological measurements obtained from natural populations in the field or from planted semi-natural formations in botanical gardens were used to reconstruct ideal, unbranched, vertical shoots with the three-dimensional computer model Y-plant to examine light harvesting consequences of the structural features of the shoot (Percy and Yang 1996). The usage of vertical shoots in this study is done for the sake of simplicity; the study is still realistic because vertical shoots with scant lateral branches are characteristics in plants from Mediterranean-type ecosystems (Valladares and Percy 1998).

The geometrical information required by Y-plant was obtained from measurements in a minimum of 20 shoots from each of 5 individuals of each species. For each shoot, the angles and azimuths of the stem, of the petiole and surface of any leaf originating from a node were recorded with a compass-protractor. In addition, the azimuth of the midrib, the lengths of internodes, petioles and leaves, and the diameters of the petioles and internodes were recorded. Nodes were numbered proceeding from the base to the top of the plant and along each branch. By recording the mother node (the node from which a subsequent node arises) for each node, the proper topology of the shoot could be reconstructed by Y-plant. Leaf shape was established from x, y coordinates of the leaf margins, and up to 20 leaf shapes



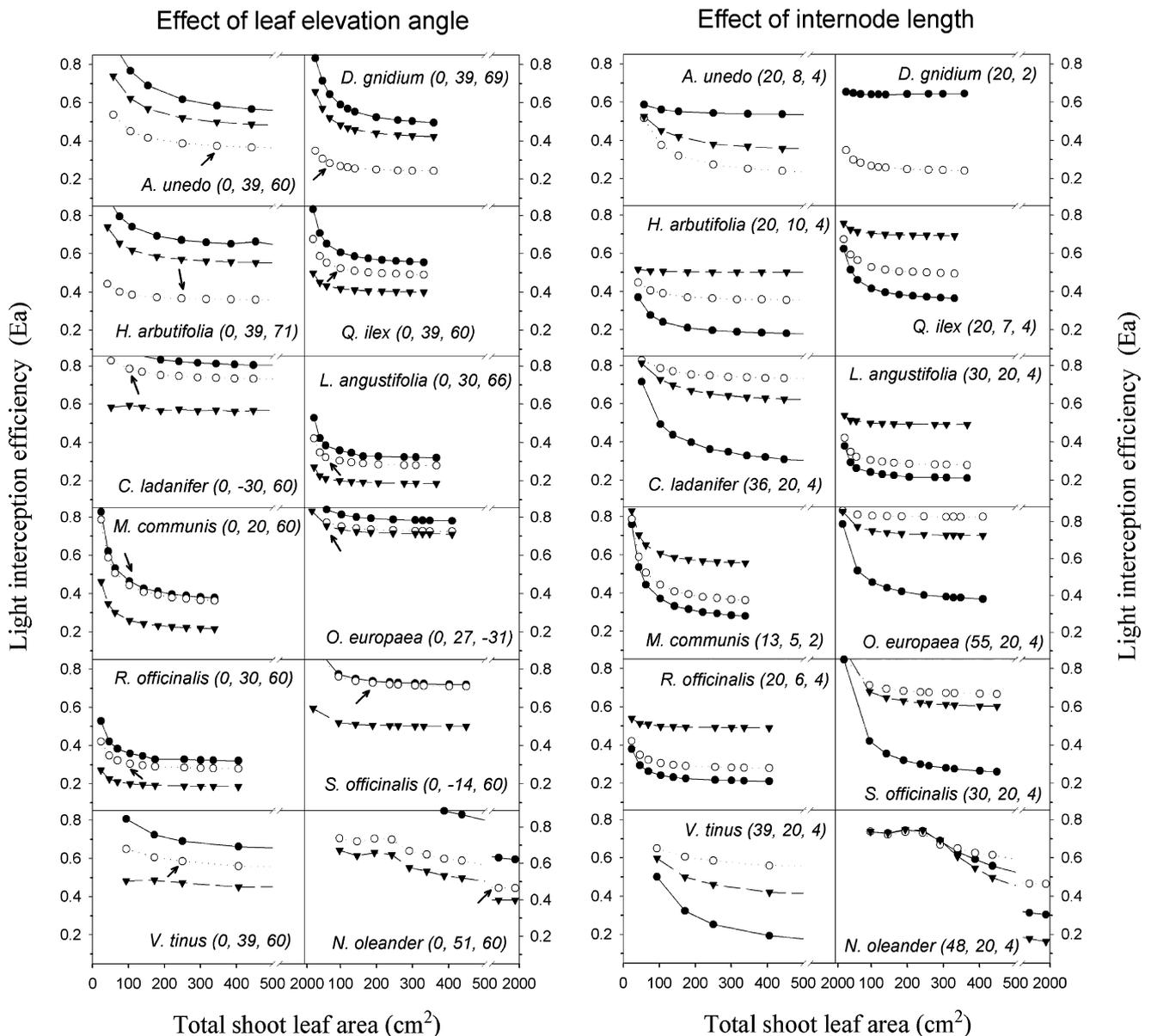
**Fig. 1** Proportion of families, genera and common genera of woody plants with opposite phyllotaxis (*black*) vs. spiral phyllotaxis (*white*) in Mediterranean vs. Central Europe flora. Numbers within brackets indicate the total number of taxa considered in each case. Data from Tutin et al. (2001)

**Table 1** Phyllotaxis, origin of material, and mean plus range of variation (within parentheses) of leaf elevation angle, internode length, leaf length and area of 12 woody species from Mediterranean-type ecosystems

Species	Origin of material	Phyllotaxis	Leaf elevation angle	Internode length (mm)	Leaf length (mm)	Leaf Area (cm <sup>2</sup> )
<i>Arbutus unedo</i> L	Cenicientos, Madrid, Spain (40°17' N 4° 18'W)	Spiral	60 (0–65)	7.6 (4–20)	58 (50–70)	9.6 (9.2–10.3)
<i>Daphne gnidium</i> L	Sierra de Cazorla, Jaén, Spain (38°00' N 2° 54'W)	Spiral	69 (0–70)	2.1 (2–23)	35 (31–42)	1.7 (1.5–2.3)
<i>Heteromeles arbutifolia</i> L	Cold Canyon, Davis, California, USA (39°15' N 121° 18'W)	Spiral	71 (0–75)	10.1 (4–20)	55 (49–93)	6.9 (4.5–12.3)
<i>Quercus ilex</i> L	El Pardo, Madrid, Spain (40°30' N 3° 43' W)	Spiral	39 (0–60)	7.0 (4–25)	29 (21–63)	3.8 (2.1–7.1)
<i>Cistus ladanifer</i> L	El Pardo, Madrid, Spain (40°30' N 3° 43' W)	Opposite decussate	32 (0–62)	36.5 (4–40)	79 (65–90)	8.6 (6.0–10.1)
<i>Lavandula angustifolia</i> Miller	Botanical Garden, Madrid, Spain (40°24' N 3° 42'W)	Opposite decussate	66 (0–72)	8.0 (4–21)	39 (30–47)	1.6 (1.4–2.3)
<i>Myrtus communis</i> L	Matas Nacionais, Valados Frades Portugal (39°35' N 9° 03'W)	Opposite decussate	20 (0–61)	5.5 (3–13)	37 (29–45)	3.9 (3.0–5.2)
<i>Olea europaea</i> L	Matas Nacionais, Valados Frades Portugal (39°35' N 9° 03'W)	Opposite decussate	28 (0–58)	19.3 (4–55)	56 (43–67)	3.4 (2.8–4.5)
<i>Rosmarinus officinalis</i> L	El Pardo, Madrid, Spain (40°30' N 3° 43' W)	Opposite decussate	30 (0–63)	6.2 (4–20)	39 (31–47)	0.6 (0.5–1.4)
<i>Salvia officinalis</i> L	Botanical Garden, Madrid, Spain (40°24' N 3° 42'W)	Opposite decussate	14.2 (0–64)	29.9 (20–35)	34 (26–44)	2.0 (1.3–2.8)
<i>Viburnum tinus</i> L	Botanical Garden, Madrid, Spain (40°24' N 3° 42'W)	Opposite decussate	39 (0–55)	39.3 (4–40)	58 (43–67)	16.0 (13–19)
<i>Nerium oleander</i> L	Botanical Garden, Madrid, Spain (40°24' N 3° 42'W)	Whorled	51 (0–61)	48 (4–50)	157 (135–177)	48.5 (35–68)

were considered for each species. Leaf size was then scaled from the measured leaf length. Values used for the different variables were mean values for all the shoots studied of each species. The influence of these variables on light interception was explored by modifying their values within the natural range of variation found in real plants (Table 1). Following reconstruction of the three-dimensional shoot image, Y-plant was then used to determine the interception of diffuse photosynthetic photon flux density (PPFD) from 160 sky sectors covering the entire hemisphere assuming standard overcast conditions, and direct PPFD from specific angles and azimuths corresponding to the solar track of a given day. In our case, calculations were run for the summer solstice (June 21st) and at 42° N of latitude. Standard equations were used to simulate the radiation reaching the shoot on a completely clear day (Pearcy 1989). The simulated interception of PPFD by the shoot was then determined with a simple ray tracing technique (Pearcy and Yang 1996). Summation over all sectors gave the total diffuse PPFD intercepted. A similar approach was used for direct PPFD. The outputs of Y-plant used in this study were the intercepted PPFD (mol m<sup>-2</sup> day<sup>-1</sup>) and measures of the efficiency of the shoot for light interception. These efficiency measures were the projection efficiency (foliage area projected towards a given sky direction divided by the

total foliage area [Ep]), the display efficiency (the fraction of foliage that is not self-shaded and is projected towards a given sky region [Ed]), and the efficiency of light interception (mean PPFD per unit leaf area intercepted by the shoot divided by PPFD incident on a horizontal surface right above the shoot [Ea]). Mutual shading among leaves within a shoot (referred here as self-shading) was calculated as the difference between Ep and Ed. Self-shading was calculated for sun elevation angles greater and smaller than 45° separately. Since shoot size influence negatively light interception efficiency due to increasing mutual shading among leaves, the relationship between shoot size and light interception was investigated in each species by running Y-plant with shoots of increasing size till a plateau was reached (Fig. 2). Petioles were considered to be 1 mm long in all species except in the two species with well-developed petioles (*Salvia officinalis* and *Nerium oleander*) for which real, mean values of petiole length were used. Species differences in PPFD absorbance by the leaf were not considered in this study in order to isolate the influence of shoot geometry (internode length, leaf elevation angle, phyllotaxis and morphology) on light capture. For this reason, Ea is here taken as light interception efficiency and not as light absorption efficiency as done elsewhere (e.g. Valladares et al. 2002).



**Fig. 2** Influence of leaf elevation angle (left-hand panels) and internode length (right-hand panels) on the relationship between light intercepting efficiency by vertical shoots ( $E_a$ ) and total leaf area of the shoot in 12 woody plant species from Mediterranean-type ecosystems. The different values of leaf elevation angle ( $^{\circ}$ ) and of internode length (mm) used in each graph and for each line are indicated within

parentheses in top-down order. Values corresponding to mean elevation angle or internode length are indicated by open symbols and dotted lines. Note that phyllotaxis is spiral in the first four species, opposite in the next seven species, and whorled in the last one (*Nerium oleander*). Small arrows in left-hand panel indicate the smallest shoot at which  $E_a$  approached the asymptote for each species

The geometric information of each shoot needed for  $Y_{\text{plant}}$  was also used to estimate aboveground biomass and total leaf area of each shoot combining this information with data on density of stems and petioles and leaf mass per unit area from previous studies (Table 2). With these estimations, the fraction of aboveground biomass invested in support (petioles plus stems vs. total biomass) and the aboveground leaf area ratio ( $LAR_a$ ) were calculated for each shoot.

One-way analysis of variance (ANOVA, SIGMASTAT 2.1 Windows version, Jandel Scientific, San Diego, USA) was used to test for differences among species with differ-

ent phyllotactic patterns in leaf elevation angle,  $E_a$ ,  $LAR_a$ , internode-to-leaf length ratio, and supporting biomass. In all cases, the data met the assumptions of normality and homocedasticity. Linear regression was used to explore relationships between  $E_a$  and the different shoot geometry and architecture variables studied. Finally, principal component analysis (SYSTAT 6.0 Windows version 1996, SPSS, Chicago, Illinois, USA) was used to explore the ordination of species considering eight independent variables spanning from leaf elevation angle to self-shading, and to explore the loading of each variable in this ordination.

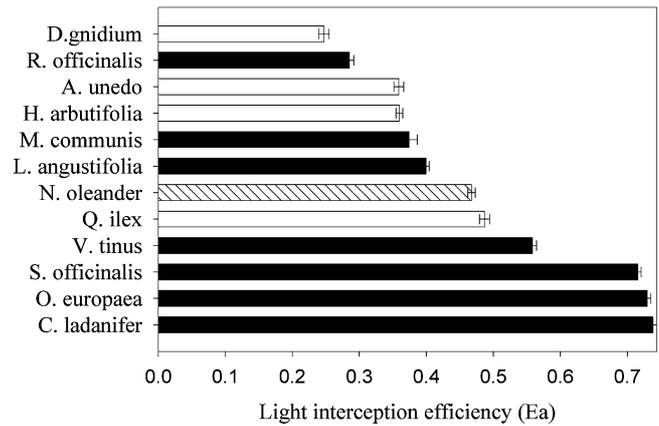
**Table 2** Stem density and leaf mass per unit area (LMA) used in the calculations of above ground biomass of the shoots of each of the 12 species studied. Data elaborated from (Cornelissen et al. 1996; Valladares and Pearcy 1998; Villar-Salvador 2000)

Species	Density ( $\text{g cm}^{-3}$ )	LMA ( $\text{g m}^{-2}$ )
<i>Arbutus unedo</i>	0.63	171.9
<i>Daphne gnidium</i>	0.40	110.5
<i>Heteromeles arbutifolia</i>	0.63	231.8
<i>Quercus ilex</i>	0.71	177.7
<i>Cistus ladanifer</i>	0.73	173.1
<i>Lavandula angustifolia</i>	0.72	48.0
<i>Myrtus communis</i>	0.72	170.0
<i>Olea europaea</i>	0.73	250.6
<i>Rosmarinus officinalis</i>	0.72	156.8
<i>Salvia officinalis</i>	0.72	95.0
<i>Viburnum tinus</i>	0.67	131.9
<i>Nerium oleander</i>	0.72	170.5

## Results

Light interception efficiency (Ea) of vertical shoots decreased towards an asymptote with increasing leaf area of the shoot, but the curve was different for each species (Fig. 2). The relationship between Ea and total leaf area of the shoot was affected by leaf elevation angle and internode length, the former decreasing and the latter increasing Ea with increasing leaf area (Fig. 2). The natural range of variation of internode length found in different shoots and individuals of the different species studied had a larger effect on Ea than the natural range of leaf angle elevation. These two parameters were set at the mean values for each species to obtain an Ea characteristic for vertical shoots of each species. This Ea characteristic for each species was taken at the asymptote (see Fig. 2 for details). Differences in this characteristic Ea among species were highly significant (ANOVA,  $p < 0.001$ ), and ranged from 0.25 in *Daphne gnidium* to 0.75 in species like *Cistus ladanifer*, *Olea europaea* and *Salvia officinalis* (Fig. 3). While the highest values of Ea were found for four species with opposite phyllotaxis, differences between species pooled according to phyllotaxis were not significant (Kruskal-Wallis non-parametric test,  $p = 0.1$ ) due to the large within group variance. The same lack of significant differences between the two groups of species was obtained for self-shading (data not shown). However, when comparisons among species were carried out with shoots set at the minimum internode length (4 mm) and with the mean leaf elevation angle of each species, species with spiral phyllotaxis were more efficient in capturing light than species with opposite leaves (ANOVA,  $p = 0.05$ ).

The different shoot and leaf morphologies of each species determined that mean Ea of vertical shoots was achieved at different shoot sizes in each case. Total leaf area of the shoot at which Ea reached the asymptote ranged from 130  $\text{cm}^2$



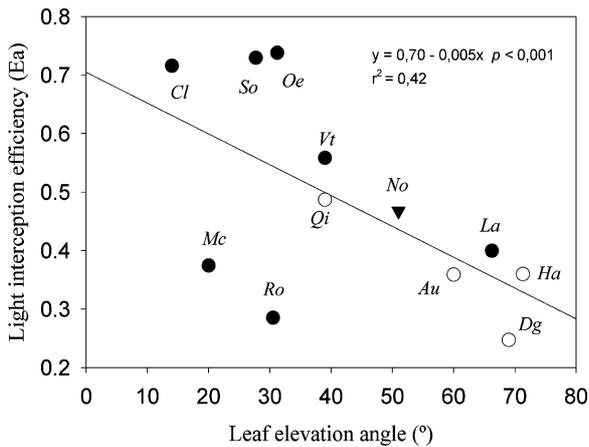
**Fig. 3** Light interception efficiency of vertical shoots (Ea) in 12 woody species from Mediterranean-type ecosystems. Ea values were taken for vertical shoots approaching the asymptote for each species (see Fig. 2). Shoots used for calculations had the mean leaf elevation angle and internode length observed for each species. White bars indicate spiral, black bars opposite, and hatched bars whorled phyllotaxis. Error bars represent SD;  $n = 4-7$  plants

in *Lavandula angustifolia* to 1455  $\text{cm}^2$  in *Nerium oleander*, and shoot height at which Ea reached the asymptote ranged from 15 cm in *Myrtus communis* to 55 cm in *Nerium oleander* (Table 3).

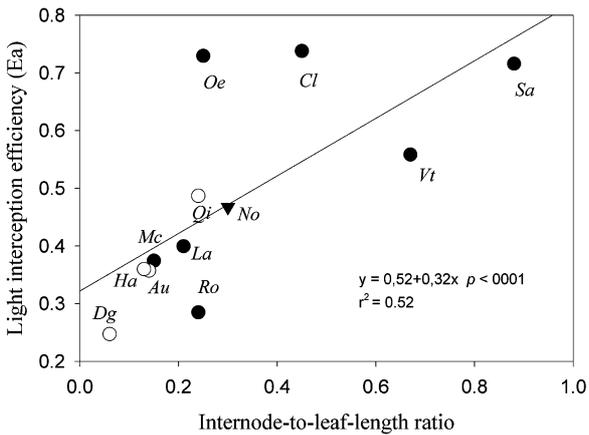
Ea exhibited significant correlations with most of the architectural variables studied. Ea decreased with leaf elevation angles (Fig. 4), increased with internode-to-leaf-length ratio (Fig. 5), increased with supporting biomass (Fig. 6), and decreased with above ground leaf area ratio ( $\text{LAR}_a$   $\text{cm}^2 \text{g}^{-1}$ ) (Fig. 7). Species with opposite phyllotaxis exhibited more horizontal leaves, had longer internode-to-leaf-length ratios, and exhibited larger investments in supporting biomass than species with spiral phyllotaxis (ANOVA  $p < 0.05$ ). The different suite of traits of species with different phyllotaxis was reflected in a principal component analysis (Fig. 8). The first two factors of the principal component analysis, which explained 72.4% of the variance,

**Table 3** Shoot height and total leaf area of the smallest shoot at which light interception efficiency (Ea) approached the asymptote in the 12 species studied (see Fig. 1). Species are ordered according to height and those with spiral phyllotaxis are in bold face

Species	Height (cm)	Total leaf area ( $\text{cm}^2$ )
<i>Myrtus communis</i>	15	181
<b><i>Daphne gnidium</i></b>	<b>19</b>	<b>139</b>
<i>Rosmarinus officinalis</i>	21	174
<i>Lavandula angustifolia</i>	26	130
<i>Viburnum tinus</i>	33	250
<b><i>Quercus ilex</i></b>	<b>34</b>	<b>177</b>
<b><i>Arbutus unedo</i></b>	<b>37</b>	<b>442</b>
<i>Cistus ladanifer</i>	42	143
<i>Olea europaea</i>	44	189
<b><i>Heteromeles arbutifolia</i></b>	<b>48</b>	<b>316</b>
<i>Salvia officinalis</i>	50	190
<i>Nerium oleander</i>	55	1455

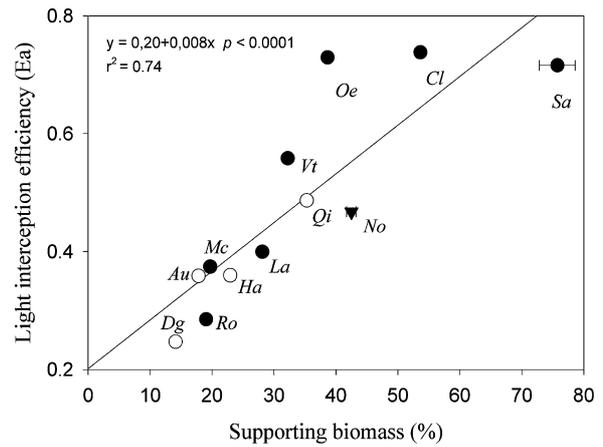


**Fig. 4** Light interception efficiency of vertical shoots ( $E_a$ , calculated for shoots approaching the asymptote for each species) versus mean leaf elevation angle in 12 woody species from Mediterranean-type ecosystems. Line represents linear regression best fit to all data points. The whorled species *Nerium oleander* is represented by a black triangle. Abbreviations of the species correspond to the first letter of the genus plus the first letter of the specific epithet

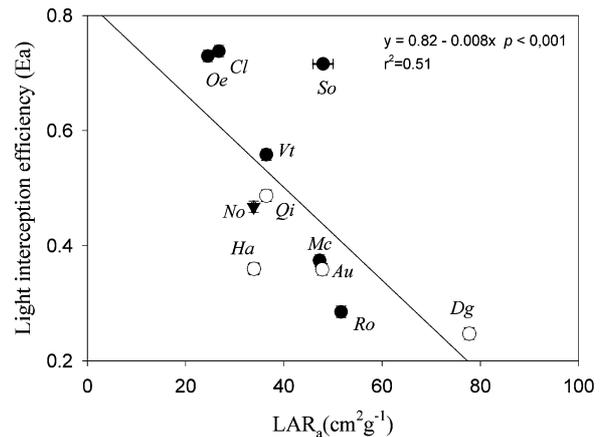


**Fig. 5** Light interception efficiency of vertical shoots ( $E_a$ , calculated for shoots approaching the asymptote for each species) versus mean internode-to-leaf-lengths ratio in 12 woody species from Mediterranean-type ecosystems. Line represents linear regression best fit to all data points. The whorled species *Nerium oleander* is represented by a black triangle. Abbreviations of the species correspond to the first letter of the genus plus the first letter of the specific epithet

segregated species with opposite phyllotaxis from species with spiral phyllotaxis primarily because of their greater self-shading for high sun elevation angles ( $>45^\circ$ ). The former species were in turn distributed in two groups, one formed by *O. europaea*, *C. ladanifer*, *V. tinus* and *S. officinalis* sharing long internodes, high supporting biomass, low  $LAR_a$ , low leaf elevation angle and high  $E_a$ , and another one formed by *M. communis*, *R. officinalis* and *L. angustifolia* with low  $E_a$  and large LAR. Species with spiral phyllotaxis constituted a relatively homogeneous group and all had intermediate or low  $E_a$  and steep leaf elevation angles. *Nerium oleander* was clearly segregated from the other species primarily by its large leaf size and long internode length (Fig. 8).



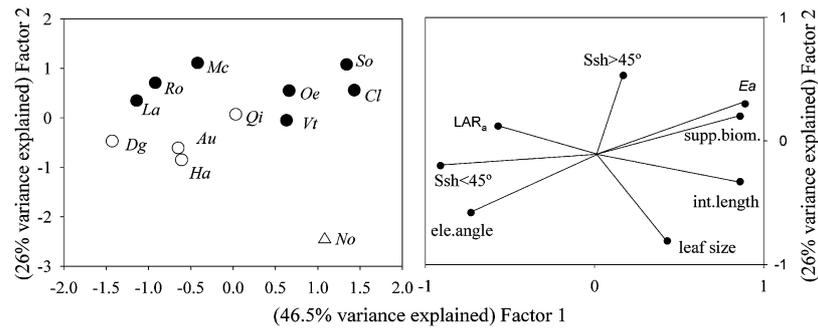
**Fig. 6** Light interception efficiency of vertical shoots ( $E_a$ , calculated for shoots approaching the asymptote for each species) versus mean supporting biomass (percentage of above ground biomass invested in stem and petioles) in 12 woody species from Mediterranean-type ecosystems. Line represents linear regression best fit to all data points. The whorled species *Nerium oleander* is represented by a black triangle. Abbreviations of the species correspond to the first letter of the genus plus the first letter of the specific epithet



**Fig. 7** Light interception efficiency of vertical shoots ( $E_a$ , calculated for shoots approaching the asymptote for each species) versus mean above ground leaf area ratio ( $LAR_a$ ) in 12 woody species from Mediterranean-type ecosystems. Line represents linear regression best fit to all data points. The whorled species *Nerium oleander* is represented by a black triangle. Abbreviations of the species correspond to the first letter of the genus plus the first letter of the specific epithet. *Lavandula angustifolia* was omitted in the analysis after checking for outliers

## Discussion

When shoots of the Mediterranean woody plants studied here had the same (short) internode length, spiral phyllotaxis rendered higher light interception efficiency ( $E_a$ ) than opposite phyllotaxis. This finding confirms suggestions from a previous study where 3-D shoots of woody species with spiral phyllotaxis were modified to exhibit opposite leaves (Valladares and Brittes 2004). However, when  $E_a$  was estimated in plants exhibiting their mean species-specific architectural features, there were no significant differences in  $E_a$  between species with opposite and



**Fig. 8** Principal components analysis of 12 woody species from Mediterranean-type ecosystems for eight morphological and light interception variables. The graph on the left represents the relative position of each species for the first two factors. The graph on the right represent variable loadings. Abbreviations of the species correspond to the first letter of the genus plus the first letter of the specific epithet. Abbreviations for the variables are:  $LAR_a$ , above ground leaf area ratio;  $Ssh > 45^\circ$ ,  $Ssh < 45^\circ$ , fraction of total leaf

area self-shaded for sun elevation angles  $>$  and  $<$   $45^\circ$  respectively;  $Ea$ , light interception efficiency;  $supp.biom.$ , fraction of the above ground biomass invested in supporting structures (stem and petioles);  $int.length.$ , internode length;  $ele.angle$ , elevation angle of the leaves. White circles represent species with spiral phyllotaxis, black circles represent species with opposite phyllotaxis and the white triangle represents whorled phyllotaxis

spiral phyllotaxis. This result agrees with previous theoretical works examining adaptive walks based on the ability of phenotypes to harvest light in a morphospace for leaf arrangement, which have shown that light harvesting of less efficient phyllotactic patterns can be compensated by the effects of other structural features such as the elongation of internodes and changes in leaf shape and orientation (Niklas 1986 1998). The results from these theoretical simulations indicated that despite their rigid genetic determination, phyllotactic patterns do not constitute a constraint in plant performance at least from a photobiology perspective (Niklas 1988 1998). The significant regressions found here between a number of architectural traits (supporting biomass, internode-to-leaf length ratio, leaf elevation angle, leaf area ratio) and  $Ea$  provides further support to the notion that light capture is the result of a suite of interrelated traits, as has been shown in previous studies (Niklas 1992a; Planchais and Sinoquet 1998; Valladares and Pearcy 1999). Another evidence for the capacity of plants to counterbalance the inefficient leaf display of opposite phyllotaxis was provided by a study of a tropical shrub that exhibited a leaf reorientation in deep understory shade. The reorientation resulted from bending of the petioles of lower leaves that were potentially self-shaded by the upper leaves, and led to a rotation of the lamina around the stem's orthotropic axis so that self-shading was reduced and potential photosynthetic carbon gain increased (Galvez and Pearcy 2001). This rotation was mediated by phytochrome responses to low red-far red ratios (R:FR) and seems to be an alternative to stem elongation, a much more common plant response to low R:FR (Smith 1995), since the species did not exhibit elongation under low light and reduced R:FR. Leaf twisting and re-positioning by means of petiole bending is common in most plants (Bell 1993) and it can significantly counterbalance an inefficient phyllotactic pattern. Elongation of petioles is another effective way for avoiding heavy mutual shading among neighbour leaves, but in this case there is a cost in term of biomass that can be relatively high in shaded environments (Pearcy and Yang 1998).

However, the ordination of the woody Mediterranean plants in multivariate space using several crown morphology and light interception variables segregated the species according to their phyllotaxis. Thus, leaf phyllotaxis of woody Mediterranean plants was associated with a suite of architectural traits in a way that contrasting leaf phyllotaxis could lead to similar  $Ea$ . We argue that even though an inefficient leaf phyllotaxis can be compensated by plastic adjustments in other traits as maintained by Niklas (1988), there is an indirect phylogenetic and developmental constraint on  $Ea$  due to phyllotaxis when  $Ea$  confers enhanced performance, since the possible values for these other traits exhibit their own internal and external restrictions and achieving these values can be costly. In low light conditions, species with opposite phyllotaxis can compensate their less efficient leaf arrangement by increasing their internode and petiole lengths, but they experience a real constraint in light interception because biomass allocation to supporting tissues comes at the cost of a reduced leaf area (Pearcy and Valladares 1999; Pearcy and Yang 1998). And the same applies to compensations via horizontal (plagiotropic) shoots, since these shoots require an increased biomass investment for a given unit length to make them biomechanically stable (Niklas 1992b). Our results suggest that these indirect constraints imposed by leaf phyllotaxis could be involved in the shade intolerance of many woody Mediterranean species exhibiting opposite phyllotaxis.

The species studied exhibited significant differences in their characteristic  $Ea$  ranging from 0.25 in *Daphne gnidium* to 0.75 in species like *Cistus ladanifer*, *Olea europaea* and *Salvia officinalis*. This is in contrast to the remarkable convergence in  $Ea$  found in a comparison of 24 species of contrasting architectures coexisting in the understory of a tropical moist forest (Valladares et al. 2002). These opposing results can be reconciled by considering the different ecological advantage of an enhanced  $Ea$  in each habitat, which is large in dark tropical forest understories but low or negligible in Mediterranean moderately shaded or open habitats, respectively.

The natural range of variation of internode length found in different shoots and individuals of each species studied had a larger effect on Ea than the natural range of leaf angle elevation. Leaf elevation angle has been shown to influence significantly light capture in a number of species and environmental conditions (McMillen and McClendon 1979; Niinemets and Fleck 2002; Oliveira and Peñuelas 2002; Valladares and Pearcy 1998), but this influence has been compared with that of other architectural traits only occasionally (Herbert 1996; Pearcy and Valladares 1999). In a comparative survey of the crown architecture of 38 perennial species of Australia, Falster and Westoby (2003) found that self-shading, rather than leaf angle, explained most of the variance between species in Ea, which was in turn primarily determined by leaf size. Although not explicitly studied here, leaf size also had an impact on the characteristic Ea of each species. For example, *Nerium oleander*, the species with the largest leaves, was clearly segregated from the other species in the principal component analysis. In a comparison of three Mediterranean shrubs of the genera *Salvia* and *Cistus*, transpiration was found not enough to overcome heat loads during the summer, and morphological features such as small and folded leaves were crucial to cope with heat stress (Szwarcbaum 1982). Similarly, steep leaf angles were found important in Mediterranean plants for avoidance of photoinhibition (Oliveira and Peñuelas 2002; Valladares and Pearcy 1997; Werner et al. 1999) and for a more efficient distribution of light among all the foliage units due to enhanced light penetration to lower leaves (Valladares and Pearcy 1998). Species with spiral leaves were found to have steeper leaves than species with opposite phyllotaxis in our study, so we conclude that spiral phyllotaxis has potential ecological advantages not only in low light, since it allows for high Ea for a given investment in supporting biomass, but also in high light, since it allows for a more uniform illumination of the foliage units, as both prevent photoinhibition of upper leaves and maximizes whole crown photosynthesis.

Mediterranean climate was initiated in the Mediterranean basin in the Pliocene, followed by an increased aridity, frequency of human-induced fires and intensity of grazing during the Holocene (di Pasquale et al. 2004). These circumstances led to an increased importance of high light conditions in Mediterranean ecosystems, with the concomitant impacts on plant recruitment and performance. The true Mediterranean taxa established during this environmental transition coexisted with old, pre-Mediterranean taxa, remnants of the tropical conditions predominant during the Tertiary (Palamarev 1989). Leaf phyllotaxis, a phylogenetically determined trait, had little ecological relevance, if any, under the high light conditions that were common during the Pliocene and Holocene. This agrees with the general view that traits found among the Mediterranean dendroflora at present must not be seen only as the result of adaptive processes. Phylogenetic constraints, historical effects and sorting processes, all have had an important effect in determining the functional traits of the present Mediterranean woody flora (Herrera 1992). Thus, the abundance of plants with opposite leaves in the current

Mediterranean dendroflora (Fig. 1) is the likely result of evolution under no selective pressure for light interception efficiency, particularly since light is commonly excessive and potentially harmful in Mediterranean-type ecosystems (Valladares 2003). An analogous case of evolution under no selection for light capture enhancement is that of divaricate shrubs, a habit that involves heavy self-shading and that is intriguingly abundant in New Zealand (Lusk 2002). However, environmental conditions are rapidly changing in the Mediterranean basin. Global dimming (Stanhill and Cohen 2001) coupled with land abandonment in many areas of Southern Europe (Scarascia-Mugnozza et al. 2000) is gradually increasing the ecological relevance of low light and shaded conditions, under which opposite leaves render poorer results than spirally arranged leaves. Our study, then, opens the question of whether the decreased light interception efficiency of woody plants with opposite leaves and the associated costs in biomass investment required to equal the efficiency of their counterparts with spiral phyllotaxis could be involved in future changes in the relative species abundance of the Mediterranean dendroflora in a global change scenario.

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