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## The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub

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**Abstract** The functional roles of the contrasting morphologies of sun and shade shoots of the evergreen shrub *Heteromeles arbutifolia* were investigated in chaparral and understory habitats by applying a three-dimensional plant architecture simulation model, YPLANT. The simulations were shown to accurately predict the measured frequency distribution of photosynthetic photon flux density (PFD) on both the leaves and a horizontal surface in the open, and gave reasonably good agreement for the more complex light environment in the shade. The sun shoot architecture was orthotropic and characterized by steeply inclined (mean = 71°) leaves in a spiral phyllotaxy with short internodes. This architecture resulted in relatively low light absorption efficiencies ( $E_A$ ) for both diffuse and direct PFD, especially during the summer when solar elevation angles were high. Shade shoots were more plagiotropic with longer internodes and a pseudo-distichous phyllotaxis caused by bending of the petioles that positioned the leaves in a nearly horizontal plane (mean = 5°). This shade-shoot architecture resulted in higher  $E_A$  values for both direct and diffuse PFD as compared to those of the sun shoots. Differences in  $E_A$  between sun and shade shoots and between summer and winter were related to differences in projection efficiencies as determined by leaf and solar angles, and by differences in self shading resulting from leaf overlap. The leaves exhibited photosynthetic acclimation to the sun and the shade, with the sun leaves having higher photosynthetic capacities per unit area, higher leaf mass per unit area and lower respiration rates per unit area than shade leaves. Despite having 7 times greater available

PFD, sun shoots absorbed only 3 times more and had daily carbon gains only double of those of shade shoots. Simulations showed that sun and shade plants performed similarly in the open light environment, but that shade shoots substantially outperformed sun shoots in the shade light environment. The shoot architecture observed in sun plants appears to achieve an efficient compromise between maximizing carbon gain while minimizing the time that the leaf surfaces are exposed to PFDs in excess of those required for light saturation of photosynthesis and therefore potentially photo-inhibitory.

**Key words** Functional plant architecture · *Heteromeles arbutifolia* · Light harvesting · Phenotypic plasticity · Photosynthesis

### Introduction

Both very high and very low photon flux density (PFD, photosynthetic photon flux density,  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ ) conditions can be limiting factors for photosynthetic carbon gain. In full sunlight, photoinhibition can occur, leading to a reduction in photosynthetic carbon gain, especially when other stresses are also present (Ögren and Sjöström 1990; Long et al. 1994). In the shade, photosynthesis is limited directly by the available PFD. Thus it is not surprising to observe that plants occupying a range of microenvironments from sunlit to shaded exhibit a highly plastic series of compromises that function to minimize the potential for photoinhibition when exposed to high PFD but maximize light capture when the plant is in the shade. This plasticity, which at the leaf-physiological level takes the form of photosynthetic sun/shade acclimation and photoprotection via energy dissipation, has been extensively studied (see reviews by Demmig-Adams and Adams 1992; Pearcy and Sims 1994). Widely recognized but less well studied are the crown morphological characteristics that function to increase or decrease light interception capacity. The

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consequences of leaf angle, including diurnal movements, have indeed been well documented (Ehleringer and Forseth 1980; Gamon and Pearcy 1989; Poulson and DeLucia 1993) but much less attention has been paid to the more complex problem of leaf display on a shoot that results in an intricate pattern of changing self-shading.

Understanding the ecological significance of above-ground structural patterns requires an integrated view of morphological, architectural and physiological attributes of plants, but such integrated analyses are extremely few, especially for woody plants (Küppers 1989). It is generally accepted that it is the light environment that primarily limits potential benefits and that demands specific canopy shapes (Horn 1971). Optimal canopy architectures have been described for low and high light environments, but real plants usually deviate from these patterns due to the existence of other factors such as crown competition for space and light, and constraints due to biomechanical cost of support, which also affect canopy architecture.

In this study we examined the functional implications of the shoot architecture and of the physiological acclimation to the light environment in the evergreen chaparral shrub *Heteromeles arbutifolia* M. Roem. This shrub is common in the chaparral and woodland communities of California. In the chaparral, shoots in the upper part of the crown are exposed to full sunlight combined with high air temperatures during the dry season. In woodland communities, *H. arbutifolia* occurs both in open sites and in the understory. In a previous study, we found a remarkable tolerance of *H. arbutifolia* to the co-occurring summer stresses of high light, high temperature and water deficit (Valladares and Pearcy 1997). We also pointed out in that work that leaf angle was an apparently plastic character that could affect dramatically the patterns of light interception, potentially playing an important role in avoidance of radiation loads and leaf temperatures above the physiological limits of tolerance of this plant. One central objective of this study was to explore the trade-offs between structural photoprotection (avoidance of interception of excessive radiation by individual leaves) and potential carbon gain in shoots of natural sun populations of *H. arbutifolia*. These trade-offs were compared with those exhibited by natural shade populations of this plant, which in turn allowed for a better understanding of the ecological importance of phenotypic plasticity in shrubs from semi-arid places.

## Materials and methods

### Field site

The plants of *H. arbutifolia* studied were located in the G.L. Stebbins Cold Canyon Reserve of the University of California Natural Land and Water Reserve System (38°30'N, 122°06'W). The vegetation consisted of a mixture of evergreen chaparral averaging 2–3 m in height interspersed in a woodland. The overstory

trees in this woodland were primarily *Quercus douglasii* and *Q. wislizenii*. For this study, plants in two areas, one consisting of a small patch of chaparral and the other the understory in the adjacent oak woodland (sun and shade sites respectively), were selected. This region has a strong Mediterranean climate with clear, hot, dry summers but cool, wet winters. The mean elevation of the study sites is 150 m. Minimum and maximum air temperatures are –1°C and 21°C in winter and 21°C and 41°C in summer, respectively, while the mean annual precipitation is 540 mm (University of California, Division of Agriculture and Natural Resources, weather database information for the last 30 years for the station Winters C).

### Structural parameters of leaves and shoots

Shoots of ten sun and ten shade plants were transported to the laboratory in black plastic bags containing wet filter paper, and processed within 45 min after collection. Leaf surface area was estimated by point-counting on a transparent sheet (Ascaso and Valladares 1994). Leaf specific mass and leaf area ratio (for the shoots only) was calculated from dry weight measurements (80 °C for 3 days). Measurements of leaf blade thickness (midway between the margins and the midrib) were made by overlapping the image and a ruler with the camera lucida under a Carl Zeiss (Oberkochen, Germany) light microscope.

### Chlorophyll and nitrogen contents

The chlorophyll content of the leaves was measured at three different times during spring and summer 1994 and the total average calculated. In each extraction, two mature leaves of each of ten sun and ten shade plants were used. Chlorophylls were extracted in 80% acetone 20% HEPES buffer and concentrations were measured spectrophotometrically (Porra et al. 1989). Leaf nitrogen concentration was measured in five to seven leaves from each of five sun and five shade plants. The leaves were oven dried at 60°C and then ground in a Wiley mill to a fine powder prior to analysis for total nitrogen in a Carlo Erba CHN analyzer in the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California, Davis.

### Leaf gas exchange and absorptance

The diurnal course of leaf gas exchange in five sun and five shade plants was measured during several clear days in the spring, 1994 with a portable closed-system gas-exchange apparatus (Li-Cor 6200, Li-Cor, USA). Maximum rates of net photosynthesis and dark respiration were obtained from these measurements. Ten leaves of each plant were collected and transported to the laboratory, where the light dependence of O<sub>2</sub> evolution was determined with a leaf-disk oxygen electrode (Hansatech, Norfolk, UK). Photosynthetic quantum yield and the curvature factor (determined by the nature of the transition from light limited to light saturated photosynthesis) were calculated from these light response curves. Leaf absorptance (400–700 nm) was measured in an Ullbricht sphere with a Li-Cor photometer.

### Light measurements and model calculations of canopy light interception and photosynthesis

The incident PFD on leaf surfaces of selected shoots was measured with GaAsP photosensors (Hanamatsu model G1118) mounted on the leaf surface and connected to a portable datalogger (Campbell Scientific Model CR21X). A total of eight sensors mounted either on the abaxial or adaxial surface of leaves at different position in the shoot were logged at 1- to 5-min intervals, depending on the

particular experiment. The light measurements were carried out over the full photoperiod so that the daily PFD as well as the distribution of irradiances at the leaf surface for specific parts of the day could be determined.

The three-dimensional computer model YPLANT (Pearcy and Yang 1996) was used to simulate the shoot architecture, and thence, the light interception and carbon gain for whole shoots of selected sun and shade plants. Briefly, the architectural structure of the shoots was characterized by measurements of shoot geometry. From a node, the azimuth, angle from horizontal, and the distance to the next node were used to describe a vector in three-dimensional space to the next node. The vector for a petiole was determined in a similar fashion. Leaves were connected at the distal end of the petiole with their position in space determined by the angle and azimuth of the normal to the surface, and the azimuth of the longitudinal axis corresponding to the midrib. Sun and shade leaves had different shapes as specified by a series of coordinates describing the leaf edge, but within each shoot all leaves were considered to have the same shape, which was then scaled to the proper size according to the leaf length. The edge coordinates were obtained by tracing the outline of a representative leaf onto graph paper. Measurements of azimuths and angles were made with a compass and a simple angle finder constructed from a level and a protractor, respectively. Full details of the measurement procedure and the model are given in Pearcy and Yang (1996). The measurements were then used in YPLANT to reconstruct a three dimensional image of the shoot. By rotating this image to specific vectors corresponding to a direction of incident PFD, YPLANT calculated the fraction of PFD from this direction that would be absorbed. Simulations of direct PFD absorption were based on the interception of light from the angle and azimuth of the solar disk at specified intervals over the day. Hemispherical (fisheye) photographs taken over the plants were used to quantify the gap fraction distribution over the hemisphere above the shoot and hence the directional distribution of diffuse PFD in the understory. Photographs were analyzed with the microcomputer program CANOPY (Rich 1989). Simulations of diffuse PFD absorption were based on vectors for 160 different sky sectors (8 azimuth and 20 angle classes). YPLANT assumed that 10% of the incident radiation at the site was sky radiation. The occurrence of gaps along the solar track as recorded by the fisheye photograph were used to indicate in YPLANT whether direct PFD actually reached the plant.

Quantification of the relative performance of the shoot architectures was made on the basis of several different measures of efficiency. The efficiency of light absorption ( $E_A$ , mol absorbed  $\text{mol}^{-1}$  incident) was calculated as the ratio of the mean PFD absorbed by the leaves to the PFD incident on a horizontal plane. This measure of efficiency includes both the effects of leaf angle and self shading. The effective leaf area ratio ( $\text{LAR}_e$ , light absorption efficiency per unit of biomass,  $\text{cm}^2 \text{g}^{-1}$ ) is the product of the leaf area ratio ( $\text{LAR}$ ,  $\text{cm}^2 \text{g}^{-1}$ ) of the shoot and  $E_A$ . This measure of efficiency, which is equivalent to the ratio of the PFD absorbed per gram shoot to the PFD incident on a horizontal surface, provides an index of how efficiently the biomass is invested for light capture in different shoots. Two additional measures focus specifically on the architectural arrangement of foliage. The projected leaf area normal to a direction of incident PFD is the actual leaf area reduced by the cosine of incidence, and the projection efficiency ( $E_p$ ) is the ratio of the potential projected leaf area to the actual leaf area. It expresses the angular effects on light interception in the absence of leaf overlap (self shading) in this direction. The displayed area is projected area as reduced by leaf overlap. The display efficiency ( $E_D$ ) is the ratio of the displayed area to the actual leaf area.

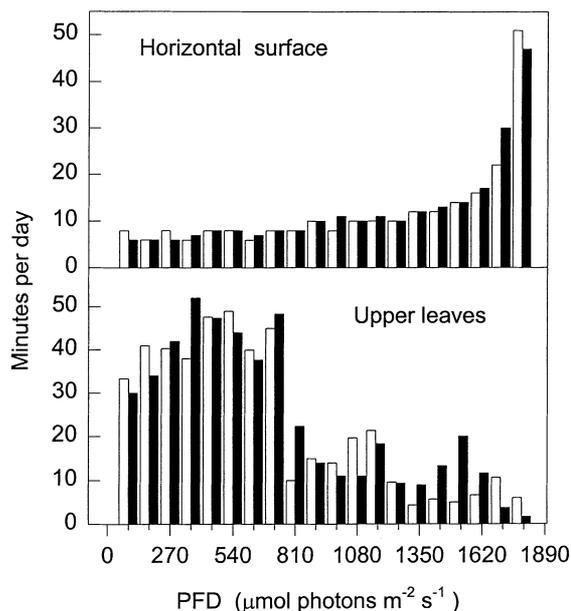
Carbon gain was calculated by YPLANT using the values of light interception by the three-dimensional plant crown together with mean values of net photosynthesis, dark respiration, photosynthetic quantum yield, curvature factor of the light response curve and light absorptance measured in single leaves. The assimilation rate of each leaf type (up to 20 types of leaves with different physiological properties can be entered in the model) was modeled using the rectangular hyperbolic response to PFD (Thornley 1976).

YPLANT calculated net assimilation for the shaded and unshaded portions of the leaf separately.

## Results

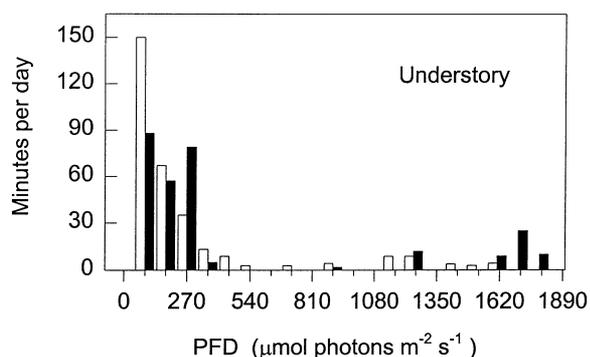
To test the ability of YPLANT to predict the distribution of PFD on the leaf surfaces, we compared the frequency distribution of PFD values measured with sensors mounted on the surface of leaves to those predicted for these leaves by YPLANT (Figs. 1 and 2). Excellent agreement was achieved between the predicted and measured distributions for a horizontal surface both in the open and in the understory ( $\chi^2 = 7.5$  and 12.5 respectively,  $df = 19$ ) and for real leaves of the upper parts of sun shoots with their actual angles and orientations ( $\chi^2 = 8.9$ ,  $df = 19$ ). Thus, YPLANT accurately predicted the PFD distribution, taking into account both leaf angle effects and self shading within the shoot. For shade shoots, the overstory canopy created a complex pattern of sun and shade, including penumbral effects. YPLANT does not account for penumbral effects so simulated sunflecks have a higher PFD but occur for a shorter duration than do real sunflecks. Nevertheless, there was still reasonably good agreement between the measured and predicted frequency distributions for PFD on a horizontal surface placed in the understory (Fig. 2).

Large differences in the light environment between the sun and shade habitats were evident, with plants in the open receiving on average 7 times more daily PFD



**Fig. 1** Frequency distribution of photosynthetic photon flux density (PFD) intercepted by a horizontal surface (*upper graph*) and by upper leaves of a sun plant shoot of *Heteromeles arbutifolia* (*lower graph*) in the open for a clear spring day (14 April 1994) measured with light sensors (*open bars*) and simulated with YPLANT (*filled bars*). The light sensors were placed on the same eight leaves selected in YPLANT for calculations. Values are the average of 8 data points

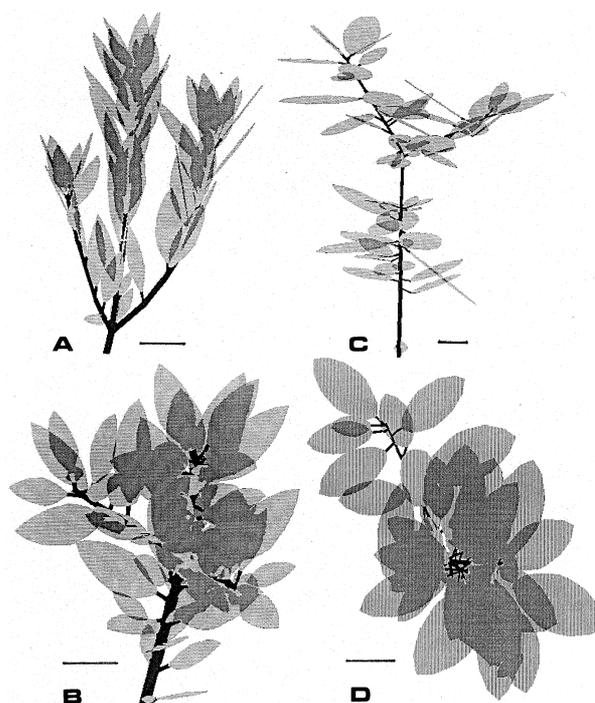
than those in the shade site (e.g., 54.3 versus 7.7 mol m<sup>-2</sup> day<sup>-1</sup> in a clear day of July). Although the absolute values varied with the seasons, the ratio of total daily PFD incident on the sun and shade plants was relatively constant throughout the year. A consequence of this large difference in PFD was the development of dramatically different shoot architectures and structural characteristics in the sun and in the shade (Fig. 3). Sun plants consisted of orthotropic shoots, with essentially radial symmetry, spiral, alternate phyllotaxis and short internodes. The leaves on sun shoots were smaller and much steeper than those of shade plants (Table 1). Shade plant shoots tended to be more plagiotropic, with pseudo-distichous phyllotaxis, longer internodes and larger leaf area ratios (Table 1). Leaves of sun plants were thicker and heavier, and exhibited larger photosynthetic capacity, dark respiration, and chlorophyll and nitrogen contents on an area basis than leaves of shade plants (Table 1). No differences between the two groups of leaves were found in the above physiological parameters when they were expressed on a mass basis, except



**Fig. 2** Frequency distribution of PFD intercepted by a horizontal surface in the understory of a *Quercus* spp. forest for a clear spring day (14 April 1994) measured with light sensors (*open bars*) and simulated with YPLANT (*filled bars*) using the report file of the fisheye photograph analysis obtained with the program CANOPY

for the chlorophyll content, which was larger in shade than in sun plant leaves.

The contrasting architectures of the sun and shade shoots resulted in each having very different efficiencies of light capture (Table 2). For direct PFD, values of  $E_A$  and  $LAR_e$  were higher in shade than sun shoots, and for both measures of efficiency, the values for sun shoots were higher in winter than summer. Seasonal changes were the result of the interplay of leaf and changing solar angles and their consequences for leaf projected areas



**Fig. 3** Computer images of stems of **A, B** sun and **C, D** shade plants of *H. arbutifolia* as viewed from the sunpath (YPLANT three-dimensional model). **A** and **C** are early morning views, **B** and **D** are midday views. Bars = 4 cm

**Table 1** Structural and physiological parameters of sun and shade plants of *Heteromeles arbutifolia*. Standard deviation is given in parentheses. Significant differences are given after an ANOVA

	Sun	Shade	<i>P</i>
Internode distance (cm)	1.08 (0.06)	1.65 (0.02)	< 0.05
Leaf angle	71.3 (16.3)	5.3 (4.3)	< 0.01
Leaf surface area (cm <sup>2</sup> )	10.1 (0.3)	21.4 (0.8)	< 0.01
Leaf blade thickness (μm)	462.5 (10.9)	292.4 (9.5)	< 0.01
Leaf mass per unit area (g m <sup>-2</sup> )	231.8 (9.3)	155.4 (10.1)	< 0.01
Shoot leaf area ratio (cm <sup>-2</sup> g <sup>-1</sup> )	25.5 (1.3)	37.2 (2.4)	< 0.01
Leaf absorptance	0.83 (0.03)	0.79 (0.02)	n.s.
Photosynthetic capacity, area basis (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	14.1 (2.0)	9.0 (1.7)	< 0.01
Photosynthetic capacity, mass basis (μmol CO <sub>2</sub> kg <sup>-1</sup> s <sup>-1</sup> )	60.8 (10.1)	58.1 (11.2)	n.s.
Dark respiration, area basis (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	0.7 (0.1)	0.5 (0.05)	< 0.05
Dark respiration, mass basis (μmol CO <sub>2</sub> kg <sup>-1</sup> s <sup>-1</sup> )	3.0 (0.3)	3.2 (0.4)	n.s.
Quantum yield ( <i>A</i> -PFD curve)	0.040 (0.005)	0.036 (0.006)	n.s.
Curvature factor ( <i>A</i> -PFD curve)	0.85 (0.08)	0.96 (0.07)	n.s.
Chlorophyll content, area basis (mg m <sup>-2</sup> )	280.5 (15.3)	226.7 (14.0)	< 0.01
Chlorophyll content, mass basis (mg g <sup>-1</sup> )	1.23 (0.04)	1.49 (0.03)	< 0.05
Chlorophyll <i>a/b</i> ratio	3.2 (0.10)	3.1 (0.11)	n.s.
Leaf nitrogen content, area basis (g m <sup>-2</sup> )	1.97 (0.25)	1.71 (0.21)	< 0.05
Leaf nitrogen content, mass basis (% dry weight)	0.91 (0.31)	0.96 (0.30)	n.s.

**Table 2** Light absorption efficiency ( $E_A$ ) for diffuse and direct PFD, effective leaf area ratio ( $LAR_e$ ), projection efficiency ( $E_P$ ), display efficiency ( $E_D$ ) and fractional leaf area shaded by other leaves during the central hours of the day (1100–1500 hours) of shoots of sun and shade plants of *Heteromeles arbutifolia* in summer and winter in their respective light environments.  $E_D$  for shade plants was calculated from sunflecks occurring during this period of the day. Each value is the average of five plants and the letter codes indicate groups that differed significantly (ANOVA,  $P < 0.05$ )

	Sun plants		Shade plants	
	Summer	Winter	Summer	Winter
$E_{A, \text{ direct PFD}}$	0.28 <sup>a</sup>	0.44 <sup>b</sup>	0.55 <sup>c</sup>	0.53 <sup>c</sup>
$E_{A, \text{ diffuse PFD}}$	0.22 <sup>a</sup>	0.22 <sup>a</sup>	0.35 <sup>b</sup>	0.35 <sup>b</sup>
$LAR_e$ (cm <sup>2</sup> g <sup>-1</sup> )	7.1 <sup>a</sup>	11.7 <sup>b</sup>	20.5 <sup>c</sup>	19.7 <sup>c</sup>
$E_P$	0.55 <sup>a</sup>	0.80 <sup>b</sup>	0.88 <sup>b</sup>	0.54 <sup>a</sup>
$E_D$	0.33 <sup>a</sup>	0.38 <sup>a, b</sup>	0.41 <sup>b</sup>	0.43 <sup>b</sup>
Fraction self-shaded	0.22 <sup>a</sup>	0.42 <sup>b</sup>	0.47 <sup>b</sup>	0.11 <sup>a</sup>

normal to the solar beam and self shading. This can be seen in the seasonal changes in  $E_P$ , which was higher in sun shoots but lower in shade shoots in the winter as compared to the summer (Table 2). The fractional leaf area shaded by other leaves within the shoot, which is given by the difference between  $E_P$  and  $E_D$ , was highest in winter in sun shoots but highest in summer for shade shoots.

These differences in sun/shade shoot architecture, coupled to differences in the physiological responses of the leaves, had a direct effect on the simulated daily carbon gain for each shoot type. Despite having 7 times more PFD available, sun shoots only intercepted 4 times more PFD per unit leaf area in their open environment than did the shade shoots in their understory environment (Table 3). Moreover, the predicted daily carbon gain for sun shoots was only double of that of shade plant shoots because for much of the time in the open environment the PFD was above light saturation. Simulations for sun and shade shoots under the open light environment revealed that both intercepted roughly the same total daily PFD, and that despite the sun shoots having a higher maximum rate of net photosynthesis ( $A_{\text{max}}$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) their simulated carbon gain per unit leaf area was only slightly larger than that found

for shade shoots (Table 3). On a leaf dry mass basis, there were no differences in the simulated daily carbon gain for sun and shade shoots in the open environment. In the shaded environment, however, the shade shoot architecture conferred a substantial advantage in terms of daily carbon gain largely because their  $E_A$  was greater for diffuse PFD than that of sun shoots.

Since leaf angle was the most plastic character in the response of *H. arbutifolia* shoots to the light environment, we focused on the effect of different leaf angles on light harvesting and carbon gain at the whole shoot level. The inclination angle of individual leaves was modified in the computer files of real sun shoots in order to obtain three different foliage arrangements: foliage with vertical, horizontal and downwards (leaf angles changed to the inverse of their actual leaf angle so that they pointed down rather than up) leaves. Shoots with vertical leaves would absorb 20–30% less PFD, depending on the season, and would have 30% lower daily carbon gain than normal shoots (Fig. 4). In April to July, the peak period for growth, the simulations showed that shoots with horizontal leaves would absorb 30–45% more PFD but would gain only about 10% more carbon than normal sun shoots due to the fact that most of the additional PFD absorbed would be above light saturation. A shoot with downwards leaves would result in 5–15% less PFD absorbed but also in a 25% reduction in shoot carbon gain as compared to normal shoots (Fig. 4).

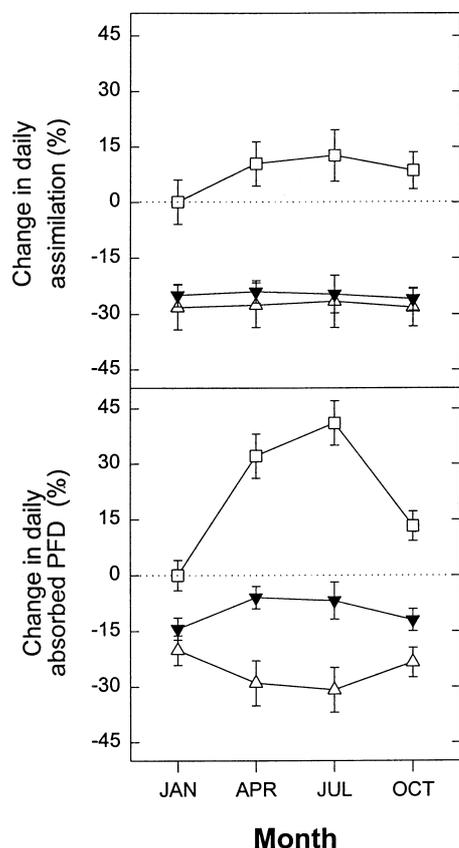
In addition to influencing carbon gain directly through light interception, shoot architecture can also play a role in preventing absorption of excessive PFD. Ideally, in terms of minimizing excessive radiation load while maximizing assimilation, a leaf should be oriented so that the PFD on the leaf surface is just below saturation. For a shoot such as those of *H. arbutifolia* with fixed leaf orientations in the short term (days), most leaves could be expected to be either above or below this optimum for a significant part of the day because of changes in solar elevation and azimuth. We examined the consequences of leaf angle on the amount of time leaves were above or below light saturation in the sun shoots in the open light environment by changing the leaf angles within YPLANT and then determining the frequency distributions of PFD on the leaf surface

**Table 3** Total daily PFD absorbed,  $\text{CO}_2$  assimilation ( $A$ ) and photosynthetic nitrogen use efficiency (NUE, daily assimilation divided by the total leaf nitrogen content) of shoots of sun and shade plants of *Heteromeles arbutifolia*. PFD absorption and  $A$  were simulated with YPLANT for plants either in their respective

and in their opposite light environments and the ratio ( $R = \text{sun plants/shade plants}$ ) is given in each case. Each value is the average of five plants and of the different seasons of the year. The letter codes indicate groups that differed significantly (ANOVA,  $P < 0.05$ )

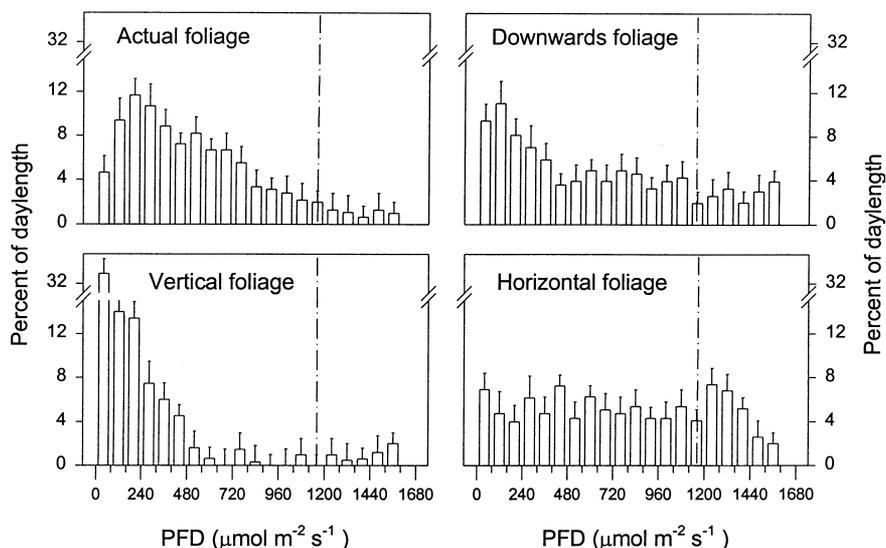
	Sun environment			Shade environment		
	Sun plants	Shade plants	$R$	Sun plants	Shade plants	$R$
PFD (mol photon m <sup>-2</sup> day <sup>-1</sup> )	14.5 <sup>a</sup>	17.4 <sup>a</sup>	0.8	3.2 <sup>b</sup>	4.3 <sup>b</sup>	0.7
$A$ , mass basis (mol CO <sub>2</sub> kg <sup>-1</sup> day <sup>-1</sup> )	76.2 <sup>a</sup>	89.1 <sup>a</sup>	0.8	26.3 <sup>b</sup>	52.6 <sup>c</sup>	0.5
$A$ , area basis (mmol CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )	297.8 <sup>a</sup>	235.2 <sup>b</sup>	1.3	107.2 <sup>c</sup>	140.8 <sup>d</sup>	0.8
NUE (mmol CO <sub>2</sub> g <sup>-1</sup> N day <sup>-1</sup> )	151.2 <sup>a</sup>	137.5 <sup>a</sup>	1.1	54.4 <sup>b</sup>	82.3 <sup>c</sup>	0.6

(Fig. 5). We did the calculations for a clear summer day (1 July, daylength = 14 h 12 min), when photoinhibition is potentially more relevant due to co-occurring



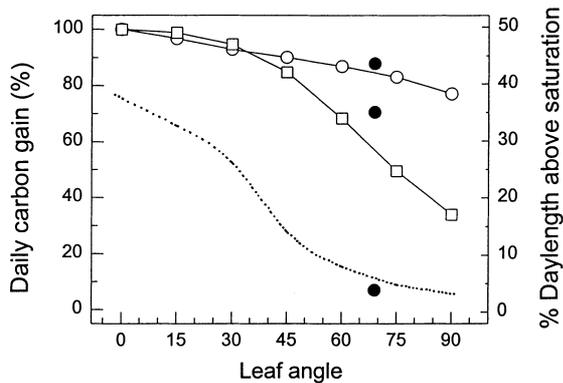
**Fig. 4** Simulation of the whole-day absorbed PFD and CO<sub>2</sub> assimilation of shoots of sun plants of *H. arbutifolia* with vertical (*open triangles*), horizontal (*open squares*) and downwards (inverse angle of real leaves, *closed triangles*) foliage. The values are expressed as a percent change from the values of the actual sun plant shoots. The simulations were performed for a clear day of each season of the year. Each point is the average of five plants. The *bars* give  $\pm 1$  SD

**Fig. 5** Frequency distribution of PFD absorbed by an average upper leaf of a sun plant of *H. arbutifolia* in the open. Simulations were carried out with real, vertical (upwards), horizontal and downwards (inverse angle of real leaves) foliages for a clear summer day (1 July, daylength = 14 h 12 min). The *dashed vertical line* indicates the average PFD for light saturation of CO<sub>2</sub> assimilation rate. Values are the mean of simulations for 100 leaves (shoots from 5 different plants, 20 leaves per shoot). Bars indicate  $\pm 1$  SE



water stress and high temperatures. For the observed leaf angles (normal shoots), leaves of sun shoots were above saturation for  $1.7 \pm 0.2$  h day<sup>-1</sup> and at lowest PFDs ( $4\text{--}80 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) for only  $0.7 \pm 0.2$  h day<sup>-1</sup>. This translated in a cumulative PFD above saturation of  $1.7 \text{ mol m}^{-2} \text{ day}^{-1}$ . A shift in the leaf angles to vertical would reduce the time the shoot would be at or above saturation ( $1.1 \pm 0.2$  h) and the cumulative PFD above saturation ( $1.1 \text{ mol m}^{-2} \text{ day}^{-1}$ ) but would also greatly increase the time per day the leaves were at the lowest PFDs ( $4.7 \pm 0.5$  h). If leaf angles were changed to horizontal, the PFD received would be above saturation for  $5.4 \pm 0.8$  h per day and the cumulative PFD above saturation would be  $2.9 \text{ mol m}^{-2} \text{ day}^{-1}$ . If leaf angles were changed to the inverse of their actual leaf angle (pointing down instead of up) then the leaves would be above saturation for  $3.5 \pm 0.4$  h day<sup>-1</sup> and the cumulative PFD above saturation would be  $2.7 \text{ mol day}^{-1}$  (Fig. 5).

To further examine the effects of leaf angle on shoot light capture and carbon gain, we varied leaf angles between 0 and 90° to simulate the daily carbon gain and determine the percentage of the day that PFD was above the saturation point (Fig. 6). Leaf angle influenced the interception of both direct and diffuse PFD but had only a small effect on assimilation due to the absorption of direct PFD since direct PFD was above saturation for much of the day. However, leaf angles above 45° caused a substantial decrease in assimilation that was due to absorption of diffuse PFD (Fig. 6). Diffuse PFD represented, on average, only 5% of the total light absorbed by the leaves of *H. arbutifolia* sun plants but it alone could be responsible for more than 20% of the total carbon gain per day. For this reason, structural features affecting diffuse PFD harvesting (mainly leaf angle, but also internode length, phyllotaxis, branching pattern) had a direct and relatively large impact on potential CO<sub>2</sub> assimilation of *H. arbutifolia* plants even in the open light environment. The fraction of the day that leaves



**Fig. 6** Simulated daily carbon gain (*open symbols*) and time absorbing light above the saturation point for photosynthesis (*dashed line*) as a function of leaf angle for shoots of sun plants of *H. arbutifolia* in a clear summer day (1 July). Carbon gain due to the absorption of diffuse PFD alone (*squares*) is plotted independently from that due to absorption of direct PFD (*circles*). *Closed circles* represent the values for carbon gain in direct PFD, in diffuse PFD and time above saturation obtained in simulations with shoots with real leaf angles

were above light saturation decreased markedly from leaf angles of 0 to 45° and then decreased more gradually at steeper leaf angles. Overall, the shoot architecture observed in sun plants of *H. arbutifolia* appears to achieve an efficient compromise between maximizing carbon gain while minimizing the time that the leaf surfaces are exposed to supra-optimal PFDs.

## Discussion

The consequences of plant architecture for light interception and photosynthetic efficiency created by various branching patterns and phyllotaxis has been traditionally assessed in terms of reduction of leaf overlapping (Horn 1971; Honda and Fisher 1978; Niklas 1988). Plagiotropic versus orthotropic shoots and distichous versus spiral phyllotaxis were related to low and well-lit habitats respectively on the basis of this concept (Hallé et al. 1978; Givnish 1995). These studies were basically two-dimensional (overlapping of leaf silhouettes as viewed from the sun) and missed the vertical component of plant architecture that has a strong impact on the diffuse light penetration and distribution. Ackerly and Bazzaz (1995) found that the orientation of the crown of some seedlings in the vicinities of forest gaps responded to diffuse light rather than direct light, and Clearwater and Gould (1996) also observed an important effect of diffuse light on leaf orientation of tree seedlings in a partially shaded forest environment. The plants studied here shifted to plagiotropic shoots and semi-distichous phyllotaxis in the shade but the resulting overlapping of leaf surface area as viewed from the sun was little affected by these changes (as indicated by a difference of 5–8% in  $E_D$ , Table 2), while diffuse light interception at the whole-shoot level increased significantly in the shade plants (as indicated by a difference of 13% in

$E_{A,diffuse\ light}$ , Table 2). Simulations with YPLANT indicated that diffuse rather than direct light (sunflecks) was determinant for daily carbon gain in *H. arbutifolia* in the shaded site. Sunflecks contributed 40–60% of the total daily PFD intercepted by the shade shoots, but their utilization accounted for only 20–40% of the simulated total daily  $CO_2$  assimilation of these shoots. If induction and stomatal limitations (Percy 1994; Valladares et al. 1997), which were not included in the simple light response model, were added then sunflecks would be likely to contribute even less to assimilation. The relatively low efficiency of direct PFD absorption (for an average sunfleck during the central hours of the day, almost half of the leaf surface area was shaded by neighboring leaves, Table 2) emphasized the importance of diffuse light interception for the shade shoots of this chaparral shrub.

Diffuse light capture was also important for maximal whole shoot photosynthesis of *H. arbutifolia* growing in sunny environments. The direct PFD was generally well above saturation for the leaves of these plants while the reverse was true for the diffuse light. Most of the differences in the PFD distribution and in the daily carbon gain obtained in the YPLANT simulations of sun shoots with different leaf angles (Figs. 4–6) were due to changes in the diffuse light absorption at the whole-shoot level. The shoot architecture of the sun plants (orthotropic shoots and steep foliage) favoured diffuse PFD penetration from the vertical axis, so that even leaf blades well within the shoot still received substantial diffuse PFD.

Variation in leaf nitrogen content has been widely identified as a determinant of net photosynthetic capacity. Plants growing in the shade usually exhibit lower photosynthetic capacity per unit of nitrogen because they partition relatively more nitrogen into the thylakoids (Evans 1989). As expected, nitrogen content on a leaf surface area basis of sun-acclimated plants of *H. arbutifolia* was larger than that of shade-acclimated plants (Table 1). Instantaneous nitrogen use efficiency ( $A_{max}/\text{nitrogen content}$ ) was also larger in leaves from sun plants ( $7.2 \mu\text{mol } CO_2 \text{ g}^{-1} \text{ N s}^{-1}$ ) than in leaves from shade plants ( $5.3 \mu\text{mol } CO_2 \text{ g}^{-1} \text{ N s}^{-1}$ ). However, when the photosynthetic nitrogen use efficiency was calculated on a per day basis and the light harvesting limitations imposed by each crown architecture were taken into account, these differences disappeared in simulations of sun and shade shoots in the open light environment, and exhibited the reverse pattern (shade > sun) in simulations in the shade (Table 3). Thus, shade plants of *H. arbutifolia* successfully counterbalanced their reduced photosynthetic capacity at the leaf level, both on a surface area and on a nitrogen bases, with the enhanced light harvesting provided by their shoot architecture at the whole-plant level.

The shoot architecture of *H. arbutifolia* expressed in the sun environment has been shown in this study to have important consequences for whole-shoot photosynthesis and avoidance of excessive PFD. Herbert

(1996) has shown that a simple model plant consisting of a few vertical leaves exhibits a complex functional relationship between total plant photosynthetic rate and inclination angle of each of the leaves. For a given plant, there can be many different sets of leaf inclination angle which can result in similar maximum total plant photosynthetic rates (Herbert 1992). However, not all are equally efficient in terms of protection against excessive PFD. Our comparison between simulations with the real shoot architecture of the sun plants and simulations with different leaf angles showed that the observed leaf angles, including the within shoot variation, provided the best solution among those assessed to the opposing problems of minimizing excess radiation absorption while maximizing shoot photosynthesis. Minimization of excess radiation absorption is important in protection against photoinhibition (Powles 1984; Long et al. 1994) and in the leaf energy balance and consequently leaf temperature and transpiration. In a previous study where leaf angles of seedlings of *H. arbutifolia* were manipulated with wires we concluded that leaf angle played a crucial role in prevention of leaf temperatures above the tolerance limits (Valladares and Pearcy 1997). In two tussock grasses of the semi-arid regions of the central Rocky Mountains (United States) steeply oriented leaves resulted in higher whole-plant daily net photosynthesis and lower risk of photoinhibition than horizontal leaves (Ryel and Beyschlag 1995). Contrary to dark forest understories, where light harvesting is enhanced by horizontal leaves with little overlapping, in high light environments a dense foliage made up by steep leaves seems to be a general solution towards enhanced whole-plant photosynthesis and reduced overheating and photoinhibition of individual leaves.

The compromise between minimizing excess radiation and maximizing shoot photosynthesis in *H. arbutifolia* was brought about both by the leaf angles and orientations and by the resulting self-shading due to the shoot architecture. For instance, most of the reduction in displayed area during midday for south-facing leaves was due to self-shading and not to the steep leaf angles (F. Valladares and R.W. Pearcy, unpublished work). For relatively simple canopies, leaf angle and orientation may be the main structural photoprotective features (Werk and Ehleringer 1984; Smith and Ullberg 1989) whereas in more complex, multilayered canopies self-shading by both leaves and stems may assume an important role (Roberts and Miller 1977; Caldwell et al. 1986). Much less attention has been given to self-shading than to leaf orientation probably because of the complexity it presents. Even though the fraction of the total leaf surface area of the sun-acclimated shoots of *H. arbutifolia* displayed during the central hours of the day was rather constant throughout the year, the fraction that was self-shaded varied from 0.22 in summer, when the main factor reducing leaf display was leaf angle and orientation, to 0.42 in winter. The consideration of self-shading effects in modern canopy models allow for rather unexpected conclusions such as those obtained by

Beyschlag et al. (1994) that shedding of older needles does not necessarily reduce primary production of Norway spruce, and by Ryel and Beyschlag (1995) that net transpirational losses were not affected by leaf angle in two tussock grasses in a semi-arid environment.

Single-leaf measurements of light interception and carbon gain may not truly reflect the behavior of whole plants, and canopy models can provide the required link between single-leaf and whole plant responses (Kim and Verma 1991; Ryel et al. 1993; Ryel and Beyschlag 1995). Since much of the present work is based upon simulations with a canopy model (YPLANT), model performance is vital. Validations of certain aspects of this model have been made in the original description (Percy and Yang 1996). In this work, the rather good correspondence between the measured PFD in different leaves of sun and shade plants and the calculated PFD from the model (Figs. 1, 2) provides further validation of YPLANT. Two main categories of canopy models for assessment of light capture can be found in the literature: geometrically-based deterministic models using ray tracing techniques (e.g., YPLANT, and the models in Niklas 1988; Dickmann et al. 1990; Takenaka 1994), and statistical models in which the probability of light penetration to a particular canopy layer or spatial cylinder is calculated (e.g., the models of Caldwell et al. 1986, and of Ryel et al. 1993). Statistical models assume the existence of a series of homogeneous layers within the canopy for each of which average values for parameters such as leaf angle are entered as inputs for the calculations. Statistical models are suited for complex and very large canopies in which measurements of all individual leaves and stems would be difficult. YPLANT is more suited for simulating small to medium-size individual canopies (up to 1000 leaves) where the ray tracing method gives a more accurate estimate of light interception.

Light interception, carbon gain and PFD above saturation shown in Figs. 4–6 in foliages with different leaf angles were derived by setting all leaves to the identical leaf angle. The real shoot architecture of sun-acclimated plants of *H. arbutifolia*, for which leaf angles varied around the mean value of 71° (Table 1), yielded higher values of carbon gain in direct and especially in diffuse PFD, and lower percentage of the day above light saturation than the simulations in which all leaves had the same angle. Thus it appears that local variations in angles within a shoot achieved mostly by bending and twisting of the petiole could serve to enhance carbon gain. It seems unlikely that a statistical canopy model would be able to address with enough detail questions related to the local light environment at the level of individual leaves such as the one mentioned above. Detailed exploration of the heterogeneity of the local light environment within the shoot of sun plants of *H. arbutifolia* and the plastic response of each of the two sides of the dorsiventral leaves of this species are the topics of another paper (F. Valladares and R.W. Pearcy, unpublished work).

To our knowledge, only two geometrically based canopy models previous to YPLANT (Dickmann et al. 1990; Wang and Jarvis 1990) have been specifically linked to a photosynthetic model in order to assess the carbon gain implications of a particular canopy architecture. Despite the relative simplicity of the photosynthetic model used in YPLANT, just by taking into account the non-linear nature of the photosynthetic response to irradiance interesting questions on the potential fate of absorbed photons and on the avoidance of excessive radiation can be addressed. Such analyses seem especially appropriate in the study of plants from arid and Mediterranean-type environments, where light is frequently saturating.

*H. arbutifolia* exhibited a very plastic response to the light environment, both in the structural parameters studied here and in the physiological features studied previously (Valladares and Pearcy 1997). This plasticity is especially noteworthy in this species since *H. arbutifolia* can be considered a stress tolerator and a mediocre competitor (Morrow and Mooney 1974; Davis and Mooney 1986), and a reduced plasticity is usually expected for this type of plants (Grime and Campbell 1991). However, avoidance of excessive stress seems to be more important for survival and growth of *H. arbutifolia* than phenotypic plasticity in itself. Crown architecture of sun-acclimated plants of *H. arbutifolia* avoided absorbance of an important fraction of the available PFD, sacrificing potential carbon gain under conditions of light and temperature well below the physiological limits of tolerance. Actually, high light triggered down regulation of stomata and of photochemical efficiency and increased resistance to high leaf temperature before any water or high temperature stress occurred in seedlings of this chaparral shrub (Valladares and Pearcy 1997). The ecological success of *H. arbutifolia* seems to be based, at least in part, on structural avoidance of the risks associated with high light. However, structural and physiological plasticity enables this plant to cope with a moderate limitation in light availability, such as that occurring in the relatively shady understory of chaparral *Quercus* spp.

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