F. Valladares · R.W. Pearcy

The geometry of light interception by shoots of *Heteromeles arbutifolia*: morphological and physiological consequences for individual leaves

Abstract The influence of leaf orientation and position within shoots on individual leaf light environments, carbon gain, and susceptibility to photoinhibition was studied in the California chaparral shrub *Heteromeles arbutifolia* with measurements of gas exchange and chlorophyll fluorescence, and by application of a three-dimensional canopy architecture model. Simulations of light absorption and photosynthesis revealed a complex pattern of leaf light environments and resulting leaf carbon gain within the shoots. Upper, south-facing leaves were potentially the most productive because they intercepted greater daily photon flux density (PFD) than leaves of any other orientation. North-facing leaves intercepted less PFD but of this, more was received on the abaxial surface because of the steep leaf angles. Leaves differed in their response to abaxial versus adaxial illumination depending on their orientation. While most had lower photosynthetic rates when illuminated on their abaxial as compared to adaxial surface, the photosynthetic rates of north-facing leaves were independent of the surface of illumination. Because of the increasing self-shading, there were strong decreases in absorbed PFD and daily carbon gain in the basipetal direction. Leaf nitrogen per unit mass also decreased in the basipetal direction but on a per unit area basis was nearly constant along the shoot. The decrease in leaf N per unit mass was accounted for by an increase in leaf mass per unit area (LMA) rather than by movement of N from older to younger leaves during shoot growth. The increased LMA of older lower leaves may have contributed directly to their lower photosynthetic capacities by increasing the limitations to diffusion of CO_2 within the leaf to the sites of carboxylation. There was no evidence for sun/shade acclimation along the shoot. Upper leaves and especially south-facing upper leaves had a potential risk for photoinhibition as demonstrated by the high PFDs received and the diurnal decreases in the fluorescence ratio F_v/F_m. Predawn F_v/F_m ratios remained high (> 0.8) indicating that when in their normal orientations leaves sustained no photoinhibition. Reorientation of the leaves to horizontal induced a strong sustained decrease in F_v/F_m and CO_2 exchange that slowly recovered over the next 10–15 days. If leaves were also inverted so that the abaxial surface received the increased PFDs, then the reduction in F_v/F_m and CO_2 assimilation was much greater with no evidence for recovery. The heterogeneity of responses was due to a combination of differences between leaves of different orientation, differences between responses on their abaxial versus adaxial surfaces, and differences along the shoot due to leaf age and self-shading effects.

Key words Light interception · *Heteromeles arbutifolia* · Photoinhibition · Light acclimation · Water use efficiency

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Introduction

An adaptive feature of the growth of woody plants is the architectural arrangement of the biomass in space. The arrangement of leaves within a plant canopy affect the radiation, heat, atmospheric water vapor and CO_2 concentration experienced by individual leaves, which in turn influence whole-plant photosynthesis and transpiration (Valladares 1999). In a cost-benefit analysis of plant photosynthesis, Harper (1989) pointed out that the cost of producing a leaf is the investment of resources, e.g., carbon, and nitrogen, while the benefit is the carbon fixed by the leaf in photosynthesis. Costs of leaf construction and maintenance have been calculated for several wild plant species, and have proven to change

with leaf age (Merino et al. 1982). Leaf photosynthetic properties also vary with age and shading by neighboring leaves, two factors that are very difficult to separate because older leaves are generally located in lower positions in the canopy and are consequently also shaded (Oren et al. 1986; Hikosaka et al. 1993). Canopy photosynthesis has been studied intensively, but realistic estimations of whole-plant carbon gain have always been very difficult due to the heterogeneity of the light environment within the canopy and the variation in physiological response among leaves (Hollinger 1992). Several computer models have been developed (see references in Caldwell et al. 1986; Pearcy and Yang 1996; Beyschlag and Ryel 1999). In many species, within-canopy variation in leaf photosynthetic properties is related to differences in leaf nitrogen concentration (Evans 1989a, b), which tends to be distributed so that leaves receiving the highest photosynthetic photon flux density (PFD) have the highest nitrogen content and hence photosynthetic capacity (Field 1983; Hirose and Werger 1987). Canopy gas exchange is not only a function of the local leaf microenvironments within the canopy, but also of the degree to which leaves exhibit a physiologically plastic response to these microenvironments (Caldwell et al. 1986).

Full sunlight is usually saturating for photosynthesis and is likely to cause photoinhibition under certain environmental conditions (Long et al. 1994; Valladares and Pearcy 1997), while plants growing in the shade often experience irradiances close to their light compensation point. The opposing problems of coping with high or low light are faced not only by plants in sunny versus shady locations but also by leaves of different situations within a canopy, and even by different cells within a leaf. The highest PFD is intercepted in most leaves by the adaxial side, and these leaves typically exhibit a sun/shade differentiation between the two sides (Terashima 1989; Delucia et al. 1991).

In this study, we have assessed the consequences of the shoot architecture of *Heteromeles arbutifolia* M. Roem., and the heterogeneity in the light environments it creates, on the morphology and physiology of individual leaves within the crown. This sclerophyll shrub is common in the chaparral communities of California, in regions characterized by cool, wet winters and warm summers with virtually no precipititation. In previous studies (Valladares and Pearcy 1997, 1998), we have shown that interactions between drought, high temperatures and light are important in determining photoinhibition and photosynthetic carbon gain, and that this species possesses a plastic shoot architecture in response to sun and shade environments that manages the compromise between maximizing carbon gain while minimizing the potential for photoinhibition. Here, we have examined the consequences of shoot architecture for leaf-level performance. The three-dimensional canopy architecture model, Y-plant (Pearcy and Yang 1996), was used in combination with standard gas exchange techniques to calculate light interception, carbon gain, and transpiration by individual leaves and whole shoots of *H. arbutifolia*. We also used chlorophyll fluorescence techniques to characterize photoinhibition in response to the heterogeneous light environments within the shoot.

Materials and methods

The plants of *H. arbutifolia* M. Roem. studied were located in a small patch of chaparral vegetation 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). More detailed information on the vegetation and climate of the site can be found in Valladares and Pearcy (1998). The architecture of two shoots on each of five different plants was characterized following the procedure of Pearcy and Yang (1996). Details of the measurement procedures for the necessary architectural and physiological parameters can be found in this reference. The shoots utilized here were the same as those used by Valladares and Pearcy (1998) in the open environment. The three-dimensional canopy model, Y-plant, modified from the original version reported by Pearcy and Yang (1996) was used to simulate light interception, carbon gain, and transpiration by these shoots. Y-plant was shown to predict accurately the measured frequency distribution of PFD on the leaves of the simulated shoots (Valladares and Pearcy 1998). The modifications to the original version were inclusion of a leaf energy budget simulation, which then allowed prediction of transpiration rates, increasing the capability for output of individual leaf behavior. Stomatal conductance was predicted from its empirical relationship with photosynthesis (Ball et al. 1986), as influenced by humidity and CO_2 concentration. Leaf boundary layer conductances were predicted from wind speed and the characteristic leaf dimension normal to it using standard equations for flat plates. Thermal radiation fluxes were predicted by assuming that the sky radiated at a temperature 20°C cooler than the air temperature and that the ground and surrounding vegetation were at air temperature.

In this study, we focused on properties of the architecture of individual shoots rather than whole crowns. Since shading of adjacent shoots could have an important influence on the PFD incident on lower leaves of the target shoot, we used a multiple-shoot simulation to add the effects of this additional shading to that created by the studied shoot itself. To accomplish this, we created four replicates of the studied shoot within the input file for Y-plant and attached them with additional "branches" at the base so that they surrounded the studied shoot in a manner similar to the observed branching in *H. arbutifolia* shrubs. Y-plant was then run to obtain output for selected individual leaves from the central studied shoot.

To study microvariations in PFD on leaf surfaces, a small (20 mm^2), square "leaf" was simulated to be just above or below the studied leaf so that it intercepted the PFD normally received at this spot on the adaxial or abaxial surface of the studied leaf. The model was run multiple times with the position of the sampling leaf varied by varying its petiole length so that ultimately both the entire abaxial and adaxial surfaces were sampled.

To study the heterogeneity within the crown, both in a radial pattern around the shoot and along the shoot, individual leaves were classified according to the orientation of their adaxial surface (north- south- east-, and west-facing leaves) and the distance to the apical meristem of the shoot (A < 10 cm, B 10–30 cm, C 30–50, and D > 50 cm). The estimated average age of each leaf class was: A < 1 year, B 1–2 years, C 2–3 years, and D > 3 years.

To examine the variation in photosynthetic properties, leaves were sampled from different positions in nearby shoots that were similar to those used for the shoot architecture measurements. The leaves were enclosed in a black plastic bag with a wet paper towel and transported immediately to the laboratory for measurements of the light dependence of photosynthesis in a Clark-type oxygen electrode (Hansatech, Norfolk, UK). The measurements commenced within 45 min of collection. Separate measurements were made on two leaf discs from each leaf, with one being inverted in

the chamber for measurements when the PFD was received on the abaxial side. The other disc was placed in the chamber so that the PFD was incident on the adaxial side. All measurements were made at 25°C. The PFD was varied with neutral-density filters.

The leaves on which O_2 evolution rates were determined were also used for characterization of variation in leaf anatomical properties and leaf nitrogen contents. Transverse 12-μm-thick sections of the leaves were cut with a Minitome Cryostat (International Equipment Company, USA) and examined under a Carl Zeiss (Oberkochen, Germany) light microscope equipped with a camera lucida. Leaf and tissue thickness (midway between the margins and the midrib) were measured by overlapping the image and a ruler with the camera lucida. The proportion of the leaf volume occupied by the cells of each tissue was estimated by point counting on a grid overlapped on the image with a camera lucida (as discussed in Ascaso and Valladares 1994). Leaf nitrogen concentration was measured in five to seven leaves from each of five plants. The leaves were oven dried at 60°C and then ground in a Wiley mill to a fine powder prior to analysis of total nitrogen content with a Carlo Erba CHN analyzer in the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California, Davis.

The relationship between absorbed PFD and photochemical efficiency of photosystem II (PSII) was studied in leaves of different orientations and positions in the field during the relatively cool summer of 1997. Five to six leaves of each orientation and position within shoots were selected for detailed PFD and chlorophyll fluorescence measurements on each side of the leaf. Spots were marked on the leaf surface and the diurnal course of F_v/F_m was determined at these spots with a pulse-modulated fluorimeter (Walz, Germany; model PAM 2000). The head of the fluorimeter was shielded with black plastic so that when in place, the leaf was darkened for 60 s and then given a far-red pulse. Fluorescence before and in an 800-ms saturating light pulse was recorded 60 s after clipping the head onto the leaf. The 60-s dark period and far-red pulse was chosen to allow fluorescence quenching due to the proton gradient across the thylakoids to dissipate (Walters and Horton 1991). The value of F_v/F_m recorded therefore reflected only the more slowly relaxing quenching due to photoinhibitory down-regulation of PSII and any sustained photoinhibition due to damage. Diurnal courses of incident PFD at the same spots were recorded on the following day. This was done by mounting small (1.2 mm^2) GasP photosensors (Hanamatsu model G1118; Gutschick et al. 1985) directly on the leaf surfaces. These sensors were connected to a portable datalogger (Campbell Scientific Model 21X) with the outputs logged at 1-s intervals. The days for which the measurements are presented were cloudless; therefore, the PFDs recorded should reflect the light environments experienced at the spots on the previous day when fluorescence was determined.

We utilized the PFD measurements to calculate a weighted PFD dose according to the procedure of Ögren and Sjöström (1990). Briefly, the PFD measurements for the previous 6 h were multiplied by a weighting factor that linearly varied from 1 for the current measurement to 0 for the measurement 6 h earlier. These weighted PFD values were then integrated for the 6-h period. Ögren and Sjöström (1990) demonstrated that this measure was a good predictor of photoinhibition in willow leaves.

Differences in the responsiveness of the two leaf surfaces to changes in PFD were investigated in a field experiment carried out during spring 1994. The skies were clear at this time resulting in high PFDs but temperatures were moderate and significant drought stress (as assessed with Scholander pressure chamber measurements) had not yet developed. Four healthy, approximately 1-year-old leaves from the upper part of each shoot were reoriented to horizontal and restrained there with thin, flexible wire loops. Only east- and west-facing leaves were manipulated in this manner because they were the most abundant and can be considered the most representative of an average leaf. Special care was taken not to damage any part of the plant in contact with the wire, and to avoid possible shading by neighboring foliage. Half of the leaves were restrained with the adaxial surface facing up (so called horizontal leaves), and half with the abaxial surface facing up (so

called inverted leaves). Diurnal courses of leaf gas exchange were determined with the LI-COR 6200 portable photosynthesis system just prior to altering the leaf position and 1, 2, 7, 10 and 15 days later. In addition, predawn F_v/F_m was measured with the PAM-2000 fluorimeter on both the abaxial and adaxial surfaces of these leaves.

Results

Interactions between leaf orientation and position resulted in a complex mosaic of light environments within shoots of *H. arbutifolia*. Along the shoot axis, successively older leaves were increasingly self-shaded by the younger, upper leaves. From the position of bud scars, leaves were determined to survive 3–4 years at most and by that time were overtopped by 50–90 younger leaves. As a result, the fraction of leaf area displayed during midday (1100–1300 hours) and the absorbed PFD per day decreased exponentially with increasing distance from the shoot apex (Fig. 1). The effect of orientation on light capture by leaves was more evident in those near the shoot apex, where self-shading effects were less important. Leaves at the shoot top were exposed to PFDs differing by an order of magnitude depending on the orientation of each particular leaf surface (Table 1). The adaxial side of south-facing leaves intercepted more daily PFD and was exposed to higher midday PFDs than the adaxial side of leaves of any other orientation, while the reverse was true for the abaxial side of these leaves (Table 1). Adaxial surfaces intercepted most of the PFD,
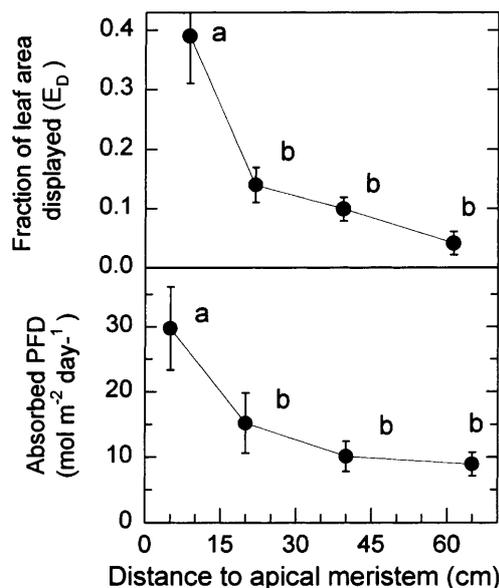
Fig. 1 Simulated daily photon flux density (PFD) absorbed and the fraction of leaf area displayed during the central hours of the day (1100–1300 hours) by leaves at different positions along *Heteromeles arbutifolia* shoots. The simulations were for a clear spring day (15 May, day length 14 h 4 min). Values are the mean ± 1 SD for 100 leaves from each of five shoots from five different plants. Significant differences (ANOVA, Tukey test $P < 0.05$) among points are indicated by different letters

but for some leaf orientations, abaxial surfaces intercepted significant direct-beam solar irradiance because of the steep leaf angles (mean = 71.3°). This was especially so for north-facing leaves in the winter, which intercepted higher daily maximum and integral PFDs on the abaxial than on the adaxial side (Table 1). Petiole twisting displaced leaves away from positions defined by the phyllotaxy so that there were significantly fewer north- and south-facing leaves than east- and west-facing leaves (data not shown). While shading by adjacent shoots was negligible for upper (A-type) leaves, it was as important as within-shoot shading for lower (D-type) leaves. When adjacent shoots were removed in the simulations, the daily integral PFD absorbed by D-type leaves increased by a factor of 2 over the values shown in Fig. 1.

We examined whether the large differences in PFD experienced by the different leaf orientations resulted in morphological and physiological acclimation to local, leaf-scale light microenvironment. The anatomy of leaves of different orientations differed significantly (Table 2). Lower epidermis and cuticle were significantly thicker in north-facing leaves than in exposed leaves with other orientations. Similar responses to local light environment were observed in the relative volumetric importance of the two chlorenchyma layers. Spongy cells contributed the largest and palisade cells the smallest proportion to the mesophyll in north-facing leaves whereas the reverse was true in south-facing leaves (Table 2). West- and east-facing leaves were intermediate in this respect. Stomatal densities did not differ with leaf orientation. Furthermore, when illuminated from the adaxial side, there were no significant differences in light-saturated O_2 evolution rates among leaves of different orientations but, depending on orientation, leaves responded differently to adaxial versus abaxial illumination (Table 3). South-facing leaves which receive most of their PFD on the adaxial surface had 50% lower photosynthetic rates when illuminated on the abaxial compared to the adaxial side. In contrast, north-facing leaves, which received similar PFDs on the two surfaces, exhibited no significant dependence of photosynthetic rate on the surface that was illuminated. The differences in responses of the abaxial and adaxial surfaces of differently oriented leaves were consistent with the acclimation of the different surfaces to the contrasting light regimes they experience.

Table 1 Simulated maximum and average photon flux densities (PFDs; $\mu mol\ m^{-2}\ s^{-1}$) intercepted by the abaxial (*Ab*) and adaxial (*Ad*) surfaces of *Heteromeles arbutifolia* leaves during the middle of the day (1100–1300 hours local time), and the simulated daily total PFDs (mol $m^{-2}\ day^{-1}$) received by these surfaces for a clear day in summer (15 July) and in winter (15 January). The values shown are the results of simulations for five leaves of each of three orientation categories (*N* north, *S* south and *W-E* west-east) selected from the upper part of each of five independent shoots. Interactions between leaf orientation and side of the leaf were significant in all cases (two-way ANOVA $P < 0.01$). Significant differences among means (Tukey test) are shown for the adaxial and abaxial side independently

	N		S		W-E		Adaxial	Abaxial
	Ad	Ab	Ad	Ab	Ad	Ab		
Maximum PFD								
Summer	1905	1552	2100	400	2004	1150	n.s.	N = W-E > S
Winter	430	956	1978	106	1397	957	S > W-E = N	N = W-E > S
Average PFD								
Summer	802	156	1546	84	523	187	S > N = W-E	N = W-E > S
Winter	166	579	631	22	296	114	S > N = W-E	N = W-E > S
Daily total PFD								
Summer	27	6	32	5	18	10	S = N > W-E	S = N = W-E
Winter	12	19	21	4	12	8	S > N = W-E	N > W-E = S

Table 2 Anatomical and structural properties of leaves of different orientations and positions within shoots of *H. arbutifolia*. Each value is the average of 10–15 leaves. Letter codes indicate groups that differed significantly (ANOVA, $P < 0.05$)

	Upper leaves				Lower leaves
	North	South	West	East	
Blade thickness (μm)	473.2[a]	462.2[a]	470.2[a]	445.2[a]	383.1[b]
Upper cuticle thickness (μm)	15.3[a]	15.2[a]	17.0[a]	14.0[a]	13.9[a]
Upper dermis thickness (μm)	43.9[a]	49.3[a]	48.3[a]	47.6[a]	21.1[b]
Palisade parenchyma					
Thickness (μm)	122.5[a]	148.0[b]	141.4[b]	139.2[b]	126.6[a]
Percent of leaf volume	27.8[a]	35.2[b]	34.2[b]	32.7[b]	31.4[b]
Spongy parenchyma					
Thickness (μm)	258.5[a]	211.0[b]	222.7[b]	211.7[b]	185.0[c]
Percent of leaf volume	34.5[a]	25.4[b]	28.2[c]	29.7[c]	28.8[c]
Lower epidermis thickness (μm)	28.7[a]	22.7[b]	18.0[b]	20.5[b]	20.8[b]
Lower cuticle thickness (μm)	12.2[a]	9.7[b]	10.5[b]	9.8[b]	8.1[c]
Stomata density (mm^{-2})	220.3[a]	203.9[a]	238.1[a]	246.9[a]	219.1[a]

Table 3 Maximum photosynthetic O_2 evolution rates under saturating CO_2 and light and the saturation (PFD at which 90% of maximum photosynthetic rate was observed) of the adaxial and abaxial leaf surfaces of leaves of different orientations from the upper parts of the shoots of sun plants of *H. arbutifolia*. Each value is the average of five plants and the letter codes indicate groups that differed significantly (ANOVA, $P < 0.05$)

	North		South		West-east	
	Adaxial	Abaxial	Adaxial	Abaxial	Adaxial	Abaxial
Photosynthetic capacity (μmol O_2 m^{-2} s^{-1})	25.6[a]	22.8[a,b]	26.3[a]	12.5[c]	25.3[a]	20.1[b]
Saturation PFD (μmol m^{-2} s^{-1})	1203[a]	1105[a]	1320[a]	610[b]	1237[a]	1152[a]

In parallel with the gradients in leaf age and PFD along the shoot, gradients in gas exchange properties, nitrogen content, and leaf mass were also evident. Upper leaves had considerably greater photosynthetic capacities than lower leaves both on a dry weight and on a surface area basis (Fig. 2). Leaf nitrogen contents per unit dry mass (N_{leaf}) decreased in a basipetal direction but, when expressed on an area basis, the N contents exhibited no change with position along the shoot. Leaf mass per unit area (LMA) increased, due to an increase in leaf density, with age since the blade was thinner in lower leaves (Table 2). The instantaneous nitrogen use efficiency (assimilation rate per unit N_{leaf}) decreased markedly along the shoot (Fig. 2). PFD required to

Fig. 2 Leaf mass per unit area, nitrogen content (dry weight and surface area bases), maximum net photosynthetic rates (at saturating PFD and ambient CO_2, on dry weight and surface area bases), dark respiration, PFD for 90% A_{max}, and nitrogen use efficiency of leaves at different positions along *H. arbutifolia* shoots. Values are the means ± 1 SD for 40 leaves of each of five shoots from five different plants. Significant differences (ANOVA, $P < 0.05$) among points are indicated by the letter code

reach 90% A_{max} also decreased basipetally. However, dark respiration exhibited no differences among leaves of different positions along the shoot.

Photochemical efficiency in the field as measured by the fluorescence ratio, F_v/F_m, varied diurnally according to both the PFD intercepted and the photosynthetic characteristics of each side of each particular leaf (Fig. 3). The adaxial side of east-facing leaves exhibited a morning reduction in F_v/F_m, whereas for west-facing leaves, this reduction was observed in the afternoon. Self-shading effects translated into a relatively constant and high F_v/F_m on the adaxial side of lower leaves. However, the abaxial side of lower leaves exhibited

significant diurnal changes in F_v/F_m depending on leaf orientation (Fig. 3). Even though the abaxial surfaces of south-facing leaves received the lowest PFDs (Table 1), they exhibited very large diurnal decreases in F_v/F_m (Fig. 3). Large diurnal changes in F_v/F_m did not, however, lead to any sustained photoinhibition since there was in all cases overnight recovery to values of 0.80–0.82 that are indicative of maximum PSII photochemical efficiencies.

The diurnal courses of F_v/F_m and the PFD measurements taken the following day at the same spots on the leaf were used to examine the relationship between light dosage and reduction in PSII photochemical effi-

Fig. 3 Diurnal course of F_v/F_m measured in September 1997 on the abaxial and adaxial surfaces of upper and lower leaves on shoots of *H. arbutifolia*. Symbols for the orientation of the adaxial side of each leaf are: *circle* east, *square* west, *up triangle* north, *down triangle* south. Values are means ± 1 SD for five to six leaves
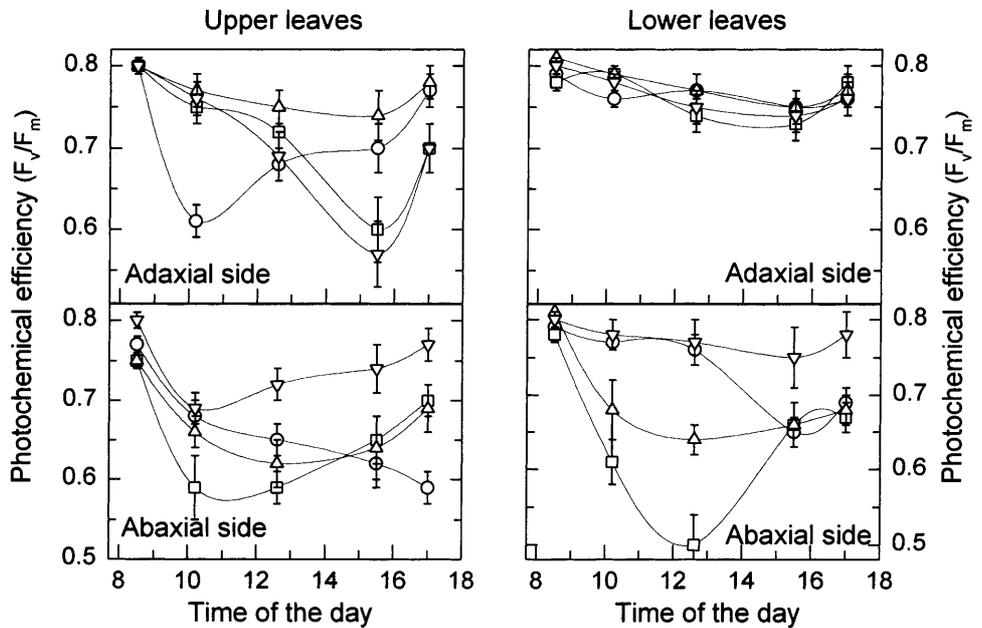
Fig. 4 Relationships between weighted PFD dose and the inhibition of photochemical efficiency from predawn values for upper and lower *H. arbutifolia* leaves. For each, the relationship is shown for independent measurements on the adaxial and abaxial surface. R^2 was > 0.65 in all cases except for the adaxial side of lower leaves where no significant regression was obtained. Single fit of all data points in each graph rendered higher R^2 than fit of each category of data point independently. The data were obtained from measurements during clear days in early September 1997. Symbols for the orientation of the adaxial side of each leaf are: *circle* east, *square* west, *up triangle* north, *down triangle* south. Values are the mean ± 1 SD for five to six leaves
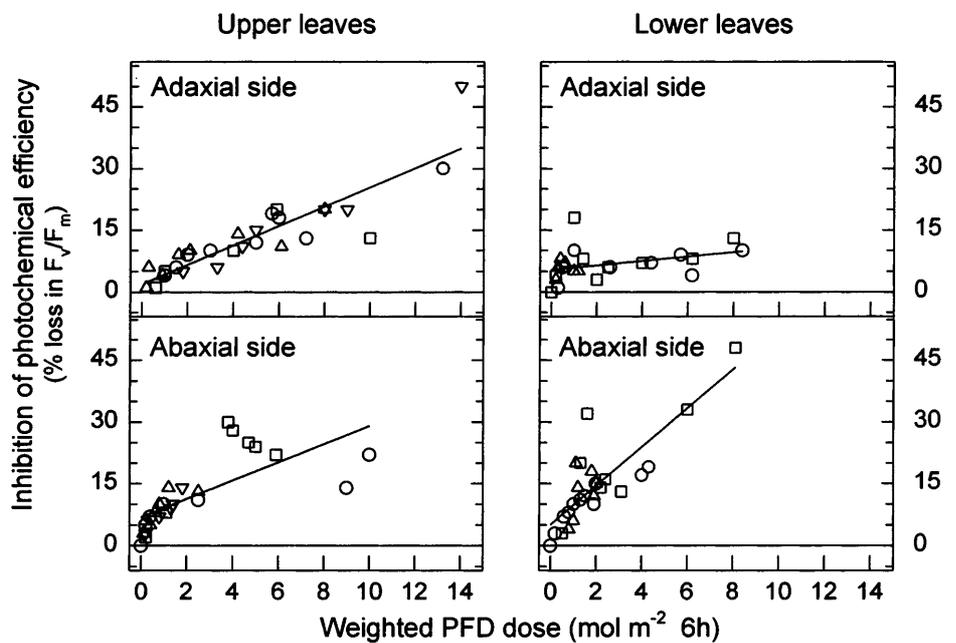
ciency. Significant correlations between the linearly weighted PFD dose of the 6-h period preceding the measurement and the reduction in F_v/F_m were found for all surfaces except the adaxial side of lower leaves (Fig. 4). Thus weighted light dose as determined by surface orientation was in general a good predictor of photoinhibition of PSII. No significant differences were found in the weighted PFD dose predicted for south-facing versus east- and west-facing leaves, but north-facing leaves received a somewhat lower weighted PFD dose than the others (Fig. 5).

Another measure of photoinhibitory potential is the duration that the PFD exceeds the photosynthetic light saturation point for the leaves. For comparative purposes, this duration was normalized to the duration that would be experienced by a horizontal leaf with the same photosynthetic properties. Relative to predictions for an unshaded, horizontal leaf, north- and south-facing leaves exceeded light saturating PFDs for only 7% and 25% as much time, respectively (Fig. 5). Thus, shoot architecture effectively reduced the potential time that its leaves would spend above light saturation, but much more so for north- as compared to south-facing leaves. Along the shoot, the time above saturation and weighted PFD dose received by leaves decreased in a basipetal direction with most of the decrease occurring in the first 15 cm (Fig. 6).

We examined whether an increase in PFD would lead to more photoinhibition by reorienting leaves to the horizontal using thin wire loops to hold them in place. When the adaxial side was in its normal position (facing up), reorientation of the leaf to horizontal caused an initial inhibition of A_{max} on day 2, followed by a gradual recovery that was complete by day 10 (Fig. 7). A strong decrease in predawn F_v/F_m on both surfaces also occurred, and also gradually recovered over the following days. Thus, even though the abaxial surface received less incident PFD incident following reorientation, a strong reduction in F_v/F_m occurred, presumably due to the increased PFD on the adaxial surface. Partial recovery was evident for the adaxial surface whereas complete recovery was evident by day 15 for the abaxial surface. These results reveal that increasing the PFD causes a sustained photoinhibition but also an acclimation response that allows at least partial recovery. If leaves were also inverted so that the abaxial surface, which normally receives less PFD, faced up, they were unable to acclimate, as indicated by a significant and lasting inhibition of A_{max} and a dramatic decrease in F_v/F_m measured on the abaxial surface (Fig. 7). For the adaxial surface, which normally receives more PFD but received much less after inversion, a small increase in F_v/F_m was evident.

South-facing leaves exhibited higher simulated daily transpiration and midday leaf temperatures than leaves of other orientations (Fig. 5). However, water use efficiency did not vary significantly with leaf orientation because the higher transpiration of south-facing leaves was accompanied by a higher carbon gain. Lower leaves were predicted to have lower daily transpiration but also
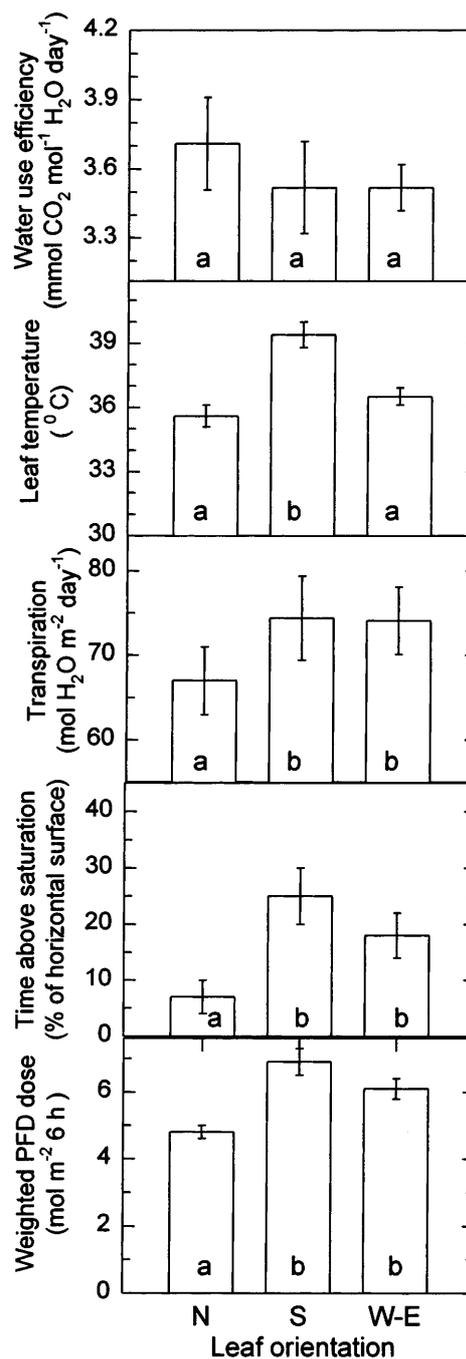
Fig. 5 Leaf water use efficiency, transpiration rate, leaf temperature, weighted PFD dose, and the time that the leaf was above saturation (relative to a horizontal leaf) for upper leaves of different orientations on *H. arbutifolia* shoots. The simulations were for a clear spring day (15 May) with maximum air temperature = 35°C, minimum relative humidity = 20%, wind speed = 0.1 m s^{-1} and ambient CO$_2$ = 370 ppm. The weighted PFD dose for a horizontal surface with no shading effects and under the conditions of the simulations was 27.2 mol m^{-2}. Values are the mean ± SD (100 leaves from five shoots of five different plants). Significant differences (ANOVA, $P < 0.05$) among orientations are indicated by the letter code

lower water use efficiencies than upper leaves (Fig. 6). The predicted leaf temperatures did not vary with leaf position along the shoot since greater latent heat loss
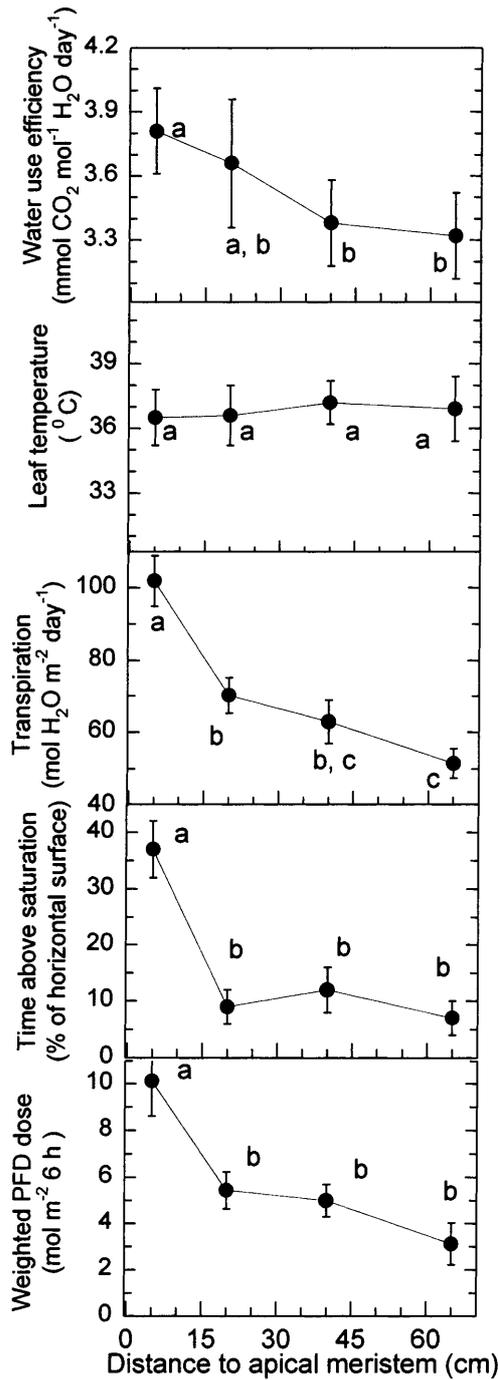
Fig. 6 Leaf water use efficiency, transpiration rate, leaf temperature, weighted PFD dose, and the time that the leaf was above saturation (relative to a horizontal leaf) for leaves at different positions along *H. arbutifolia* shoots. See the legend to Fig. 5 for the conditions of the simulation. Values are means ± 1 SD for 100 leaves from five shoots of five different plants). Significant differences (ANOVA, $P < 0.05$) among positions are indicated by the letter code

Fig. 7 Changes in maximal photosynthetic rate and predawn photochemical efficiency of PSII (F_v/F_m) of sun leaves of *H. arbutifolia* following the restraint into horizontal (*open triangles*) and inverted (horizontal but with the abaxial side upwards, *closed circles*) positions. F_v/F_m is given for the two sides of the leaf independently. Each point is the mean of five leaves ±1 SD. In all graphs, the differences between the last two points of the curves were significant (ANOVA, $P < 0.05$)

compensated increased irradiance absorption in upper leaves.

Functional implications of the observed within-shoot heterogeneity in the light environment and leaf physio-logical properties of the leaves were explored by ana-lyzing the relative contribution of each leaf type to whole-shoot carbon gain. Due to the combined effect of the greater PFD interception and their greater A_{max}, leaves at the top of the shoot were contributed signifi-cantly more to whole-shoot photosynthesis than did lower leaves. Leaves within the first 10 cm represented 30% of the total leaf area but contributed more than half of the predicted potential daily assimilation of the shoot (Table 4). West- and east-facing leaves were the most abundant on the shoot at any distance from the apical meristem. Thus, they were the ones contributing most to whole-shoot carbon gain in absolute terms.

Table 4 Potential net assimilation of leaves and whole shoots of *H. arbutifolia* simulated for a clear day during the peak growth period (15 May, day length 14 h 4 min). Data are presented for leaves at increasing distances from the apical meristem (leaves A–D; see Materials and methods) and with different orientations (*N* north, *S* south, and *W-E* west-east). Percentage of foliage represented by each leaf type is given together with the relative contribution to whole-shoot net assimilation by each leaf type. Mean whole-shoot net assimilation was 293.5 mmol CO_2 m^{-2} day^{-1}. Values for the whole shoot are the mean ± SD of five shoots from five different plants. Values for each leaf type are means of 100 leaves, 20 from each shoot

Leaf type	Percentage of foliage represented	Net assimilation (mmol CO_2 m^{-2} day^{-1})	Relative contribution to whole-shoot assimilation (%)
A, N	5	413 ± 15	9
A, S	6	497 ± 18	13
A, W-E	19	348 ± 16	29
Whole A	30	389 ± 17	51
B, N	7	343 ± 44	8
B, S	7	234 ± 47	6
B, W-E	17	231 ± 33	14
Whole B	31	257 ± 39	28
C, N	6	271 ± 23	4
C, S	5	136 ± 24	2
C, W-E	14	218 ± 18	7
Whole C	25	213 ± 21	13
D, N	3	196 ± 12	2
D, S	3	111 ± 13	1
D, W-E	8	185 ± 13	5
Whole D	14	171 ± 13	8

Their relative contribution to whole-shoot carbon gain (on a per area basis) was smaller than that of either south- or north-facing leaves in the two most apical zones (A and B), but the reverse was true in the two lower zones (C and D) due to increasing shading of south- and north-facing leaves (Table 4). South-facing leaves were potentially the most productive leaves in the upper parts of the shoot but north-facing leaves had the highest water use efficiency in these simulations (Fig. 5). North-facing leaves were the most productive in the lower parts due to increased self-shading of south-facing leaves (Table 4).

Discussion

The individual leaf light environments within the shoot of *H. arbutifolia* are highly heterogeneous, changing both around and along the shoot axis because of leaf orientation and self-shading. Although photosynthetic capacity was largely independent of orientation near the shoot apex, it decreased strongly on either a leaf mass or area basis basipetally along the shoot axis. Since this corresponds to the expected gradient for either shade acclimation or leaf aging effects, either phenomenon could be responsible for the decreased photosynthetic capacities. Separation of leaf aging and acclimation effects in canopies is difficult because older leaves become overtopped and shaded as new leaves develop, con-

founding changes in light and age. In elegant experiments with *Ipomea tricolor*, Hikosaka et al. (1993) showed, by manipulating the light environments of young and old leaves, that both aging and sun/shade acclimation were important but, overall, acclimation had a more dominant role in the gradients of photosynthetic capacity and leaf N along the shoot. Sun/shade acclimation of photosynthetic capacity in plant canopies is generally thought to function to allow more efficient use of N via movement of N from lower to newly developing upper leaves where the associated increase in photosynthetic capacity would have the greatest carbon gain benefit for the canopy as a whole (Field 1983; Hirose and Werger 1987; Evans 1989a, b). It also increases canopy carbon gain because lower, shade-acclimated leaves are net contributors rather than net parasites, as would be the case without acclimation (Meister et al. 1987). It should be noted that the carbon gain benefit has generally been found to be greater for dense canopies with high photosynthetic capacities (Hirose and Werger 1987) than for the more open canopies of trees or shrubs like *H. arbutifolia* with low total N and low photosynthetic capacities (Field 1983; Leuning et al. 1991). In addition, the reallocation of N within the chloroplast can increase the efficiency of N use.

For *H. arbutifolia* shoots, no net reallocation of N from older to younger leaves along the shoot appeared to be occurring. We found no differences in N per unit leaf area, and while N per unit mass decreased in the expected pattern this could be entirely accounted for by the increase in LMA in older leaves (Fig. 2). Leaf N may be withdrawn just before abcission but this would not generate the N and photosynthetic capacity gradients following the light gradient that are necessary for optimal canopy N use. Thus, changes in total leaf N normally associated with sun/shade acclimation are not occurring and we conclude that the decreasing photosynthetic capacities along the shoot axis are not the result of acclimation-related N redistribution among leaves.

If sun/shade acclimation were occurring along *H. arbutifolia* shoots, then other components of the sun/shade syndrome should also show characteristic changes. Decreased respiration rates would be expected in shade- versus sun-acclimated leaves but no significant differences in respiration rates were evident between upper and lower leaves along the shoots. Similarly, shade-acclimated leaves would be expected to have lower chlorophyll (Chl) a/b ratios. Although chlorophyll contents were not measured along these shoots, comparisons between shoots of plants growing in the sun and shade, an even greater gradient in light availability, revealed no significant differences (Valladares and Pearcy 1998), so none should be expected along the shoot. A decrease in Chl a/b can be associated with greater allocation of N to light-harvesting Chl-protein complexes at the expense of investment in Rubisco (Dale and Causton 1992; Evans 1989a, b). The lack of changes

in Chl a/b suggests that acclimation-based changes in N partitioning within the chloroplasts are not occurring in *H. arbutifolia*.

An explanation for the decreased photosynthetic capacities may lie in the higher LMA of older, lower leaves. Calkin and Pearcy (1984) previously noted an increase in the apoplast versus symplast volume in second- versus first-year *H. arbutifolia* leaves which they attributed to an apparent thickening of the cell walls. The slight decrease in overall leaf thickness with the increase in LMA from younger to older leaves indicates an increased dry mass density of the leaf, consistent with the addition of cell wall material. Thicker cell walls and reduced intercellular airspace would lower internal conductances to CO_2, resulting in lower CO_2 pressure at the site of Rubisco, thereby limiting the photosynthetic rate (Evans and Von Caemmerer 1996). Parkhurst and Mott (1990) have shown that the thick leaves of sclerophylls may pose a significant limitation for internal CO_2 diffusion in the intercellular airspace. Moreover, Syvertsen et al. (1995) found that cell wall conductance to CO_2 in thick, sclerophyllous leaves can be an even larger constraint on CO_2 diffusion to the chloroplast than diffusion in the intercellular air spaces. The additional cell wall material in *H. arbutifolia* may therefore impose a direct constraint on photosynthetic rate that increases with leaf age.

The basipetal increase in LMA in *H. arbutifolia* contrasts with the usual pattern noted in canopies of decreasing LMA with increasing shading (Givnish 1988). However, most studies have been of deciduous tree or herbaceous canopies (Ellsworth and Reich 1993) and have not generally distinguished between leaves that developed at the canopy top and those that developed in the shade. All the leaves of *H. arbutifolia* that were studied had developed in high light and were then shaded as they were overtopped. Increases in LMA with needle age have been reported for *Picea abies* and other conifers (Oren et al. 1986; Niinemets 1997). When *H. arbutifolia* leaves develop in the shade they also have much lower LMAs than sun leaves (Valladares and Pearcy 1998) as commonly observed in virtually all species. The function, if any, of the increase in LMA is unclear. Since it involves decreased symplastic volume, it may improve water relations by decreasing the osmotica required for osmotic adjustment (Calkin and Pearcy 1984). It may also be involved in increased mechanical resistance to damage or herbivores. Whatever its function, the consequences for photosynthetic carbon gain of the associated decrease in photosynthetic capacity are small. Lower internal conductances for CO_2 would primarily impact light-saturated photosynthetic rates but, because of leaf angles and self-shading, the lower leaves are mostly at PFDs well below saturation.

Plants like *H. arbutifolia* that grow in hot, arid, high-light environments must have leaf displays that maximize carbon gain and at the same time minimize potential stresses due to photoinhibition or high leaf temperatures. Indeed, high temperatures strongly exacerbate photoinhibition (Gamon and Pearcy 1990; Mulkey and Pearcy 1992). Previous experiments (Valladares and Pearcy 1997) in which leaf angles of *H. arbutifolia* were manipulated on droughted plants in the summer induced strong and lasting photoinhibition as well as spots of leaf necrosis that were probably due to high-temperature damage. The experiments reported here were done in the spring so temperatures were much less severe, probably allowing for faster recovery. Simulations with Y-plant in which leaf angles were varied revealed that shallower angles greatly increase the PFD received, the total time the leaves are above light saturation PFDs, and the maximum leaf temperatures of the sunlit leaf area (Pearcy and Valladares, in press). On the other hand, steeper angles resulted in strong reductions in carbon gain and much lower water use efficiencies. Thus, the shoot architecture of *H. arbutifolia* appears to achieve a very efficient compromise between maximizing carbon gain and minimizing conditions that could lead to photoinhibiton through the effect of leaf angles and patterns of self-shading. This type of structural photoprotection seems to be a characteristic of many arid-zone plants (Beyschlag and Ryel 1999; Valladares and Pugnaire 1999; Valladares and Pearcy, in press).

With the steep leaf angles of *H. arbutifolia*, both the adaxial and abaxial surfaces receive high PFDs, depending on leaf orientation and time of day. The dorsiventral structure of leaves like those of *H. arbutifolia* is usually associated with functional asymmetry and different photosynthetic properties for each surface (e.g., Syvertsen and Cunningham 1979). Poulson and DeLucia (1993) correlated differences in photosynthetic response between leaf surfaces with a dorsiventral structure with differences in the light environment. The response of *H. arbutifolia* was similar, with functional symmetry in terms of photosynthetic capacity more evident for leaves with orientations which resulted in a more equal distribution of PFD on both surfaces. Adaxial and abaxial surfaces behave independently depending on the direction of the PFD. We found that the adaxial surfaces, which are usually exposed to higher PFD, exhibited a greater capacity to acclimate when reoriented so that they received increased PFD. In contrast, leaves that were inverted so that their abaxial surface received high PFD not only did not acclimate, but showed sustained photoinhibition measured both as a reduction in F_v/F_m and in maximum rates of CO_2 assimilation (Fig. 7). Studies with other species have demonstrated full acclimation of either leaf surface following inversion (Terashima 1986) and an independence of this capacity from anatomical symmetry or asymmetry (Ögren and Evans 1993). These studies were done in growth chambers where the maximum PFDs were much lower than full sun, whereas those reported here were done in the field. Thus, the much higher PFDs in our study may have interfered with the acclimation of the abaxial surface in *H. arbutifolia*.

Although the architecture of sun shoots of *H. arbutifolia* provides structural photoprotection against the

sustained photoinhibition observed when leaf angles are manipulated (Fig. 7), photoinhibition may still cause a loss in potential carbon gain. Ögren and Sjöström (1990) found that photoinhibition in willow canopies reduced carbon gain by about 10%. In *H. arbutifolia*, strong reductions in F_v/F_m occurred with a diurnal pattern that depended on leaf surface orientation (Fig. 3). Diurnal changes in F_v/F_m have been shown to be due to increased thermal dissipation of excess energy via operation of the xanthophyll cycle (Demmig-Adams and Adams 1996). This cycle has been postulated to provide additional photoprotection against sustained photoinhibition. These diurnal reductions in F_v/F_m were correlated with the weighted PFD dose. Because of the dynamic nature of photoinhibition, weighted PFD dose rather than the current PFD is a better predictor of F_v/F_m (Ögren and Sjöström 1990). Temporal patterns of sun and shade resulting from self-shading are important because partial recovery most likely occurs in the shade periods.

The fluorescence ratio, F_v/F_m, is an indicator of PSII efficiency, which primarily influences photosynthetic rates at low PFD but usually not at saturating PFDs unless the photoinhibition is especially severe and lasting. Nevertheless, it can have a significant impact on carbon gain in the curvilinear part of the light response between light limitation and saturation (Ögren and Sjöström 1990). Therefore, the potential impact of photoinhibition on carbon gain will depend on the proportion of carbon gain that occurs at PFDs in this range and below following conditions that lead to photoinhibitory reductions in PSII efficiency. Because of the leaf angles and self-shading, upper leaves of *H. arbutifolia* are at PFDs just at or below saturation for more than 90% of the day (Valladares and Pearcy 1998). This value is based on the light saturation characteristics for leaves in the spring and therefore may be an overestimate for mid summer conditions when water stress and low humidities are likely to restrict photosynthetic rates over midday, resulting in a lower light saturation PFD. However, it is still likely that conditions that would strongly exacerbate photoinhibition occur relatively infrequently because of the structural photoprotection afforded by the shoot architecture. On the other hand, to the extent that photoinhibition does occur, conditions where it could impact carbon gain are relatively frequent. These conclusions must be tempered by the fact that very little is known about how the temporal pattern of self-shading created by the shoot architecture influences photoinhibition. Recovery during the shade periods would be expected to lessen the impacts of photoinhibition. Lower leaves are, on average, likely to be protected from photoinhibition because of the self-shading that reduces both the weighted PFD dose received and the time that the leaf is above light-saturating PFDs (Fig. 6).

The conclusions from this research must be qualified somewhat because Y-plant uses a simple light response model to predict photosynthesis. Thus, the values reflect the potential carbon gain and not the lower photosynthetic rates and carbon gain likely to occur under summer drought and temperature conditions. Moreover, predictions of daily carbon gain from Y-plant do not reflect any losses actually due to photoinhibition. The available evidence suggests that the losses due to photoinhibition will be small. In periodic measurements of leaves in their natural orientations throughout the spring and summer, we have found no evidence of sustained photoinhibition (F. Valladares and R.W. Pearcy, unpublished observations). Although assimilation decreased strongly due to stomatal closure in mid and late summer, predawn F_v/F_m values remained high. It is possible that more severe conditions would generate significant sustained photoinhibition. Periods of very high air temperature lasting 4–10 days occur in central California during the summer, their frequency varying from year to year. These high-temperature periods were shown to correspond to reductions in F_v/F_m and photosynthesis in wild grape leaves (Gamon and Pearcy 1989). The fluorescence studies reported here were carried out in a relatively mild year. More severe years or future years with global warming may raise the photoinhibitory losses.

Many studies have examined the role of leaf angles and orientations in light interception, leaf energy balance, and photoprotection, (see references in Valladares 1999). These studies have, however, typically focused on the expected pattern of irradiance interception without considering the effects of self-shading by other leaves on the shoot. Assessment of the role of self-shading resulting from the architectural arrangement of leaves has been made difficult by the complex pattern of sun and shade that is generated (Valladares and Pearcy, in press). A three-dimensional architecture model such as Y-plant provides insights into how shoot and crown structure influence the intricate patterns of self-shading and hence also the leaf-level interception of solar radiation (Pearcy and Valladares, in press). We have shown here that the result, in terms of carbon gain, of the interactions between leaf orientation, leaf position, leaf age, and physiological acclimation to the heterogeneous PFD environment observed within a shoot, is not obvious. This finding should be considered in scaling exercises since simulations that do not consider the complexity and heterogeneity of both the light environment and the leaf physiology within a shoot may bias estimates of canopy photosynthesis and transpiration.

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