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Petiole twisting in the crowns of *Psychotria limonensis:* implications for light interception and daily carbon gain

Abstract We used Y-plant, a computer-based model of crown architecture, to examine the implications of leaf reorientation resulting from petiole bending in *Psychotria limonensis* (Rubiaceae) seedlings. During this reorientation process, bending of the petioles of lower leaves that are potentially self-shaded by the upper leaves rotates the lamina around the stem's orthotropic axis so that self-shading is reduced. Simulations of daily light capture and assimilation revealed a 66% increase in daily C gain due to reorientation of the leaves as compared to simulations where the leaves remained in their characteristic opposite decussate pattern set by the phyllotaxy. This was due to enhanced carbon (C) gain of the lower leaves because of the reduction of shading by upper developing leaves in the same vertical plane. The light signal for this movement was experimentally examined by placing leaf-shaped filters above already fully expanded leaves and following the resulting shade-avoiding movements. The filters were either neutral density shade cloth that reduced the photon flux density (PFD) but did not alter the red to far red ratio (R:FR) or a film that reduced the PFD equivalently but also reduced the R:FR. Leaf reorientation was much more rapid and complete under the low R:FR as compared to the high R:FR indicating involvement of a phytochrome photosensory system that detected the presence of a shading leaf. Plants in gaps were found to lack a reorientation response indicating that the reorientation is specific to the shaded understory environment.

Keywords Crown architecture · Petiole twisting · Self-shading · Light capture · Carbon dioxide assimilation

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Introduction

The capture of light energy by a plant is governed by a combination of leaf physiology and the display of those leaves within the crown as set by the crown architecture. For individual leaves, the orientation (azimuth and angle of the surface) is a critical determinant of light capture and leaf energy balance. At the plant crown level the pattern of self-shading as determined by the spatial arrangement of the leaves is an additional determinant of light capture and photosynthesis. Diurnal solar tracking and solar avoidance movements have been reported for a large number of species in open habitats (Ehleringer and Forseth 1980; Forseth and Ehleringer 1983; Kao and Forseth 1992; Koller 1990). These studies have focused on individual leaves with little consideration of the impact of these reorientations on the performance of whole plant crowns. There has also been little attention given to understory plants. The spatial arrangement of leaves within a crown depends on many factors including shoot phyllotaxy (Niklas 1988; Takenaka 1994), branching angles and frequencies (Fisher 1986; Waller and Steingraeber 1986), lengths of petioles and internodes (Takenaka 1994; Pearcy and Yang 1998; Yamada et al. 2000; Takenaka et al. 2001), and leaf size and orientation. Most research on crown architecture has focused on branching patterns (Halle et al. 1978; Pickett and Kempf 1980; Honda et al. 1997; Hatta et al. 1999), leaf display (Chazdon 1985; Ackerly and Bazzaz 1995) or phyllotaxy (Niklas 1988; Takenaka 1994) and their effects on light capture. Only a few studies (Pearcy and Yang 1998; Valladares and Pearcy 1998) have evaluated the effects of architecture on photosynthetic carbon (C) gain or other physiological attributes. While photosynthesis will be related to light capture, especially in low light environments, the curvilinear response of photosynthesis to light causes the relationship to depend on the interaction between leaf physiological properties and light interception. Since the main function of leaf display is photosynthesis rather than light interception (Pearcy and Valladares 1999; Valladares 1999) the consequences of

a particular architectural arrangement of leaves is best evaluated by considering its impact on photosynthetic C gain.

Monoaxial-stemmed plants present perhaps the simplest architectural leaf arrangement and consequently have been more extensively investigated in terms of their light capture and biomechanical properties than more complex branched architectures (Givnish 1995; Niklas 1988; Takenaka 1994). Monoaxial plants with a few large leaves are relatively common in tropical forest understories. Those few leaves must be able to maximize light absorption for CO_2 assimilation in order to maximize the whole plant C gain necessary for growth in these extremely shaded microenvironments (Pearcy 1999). Simulations with model plants of defined architecture have shown that phyllotaxy, leaf size, internode length and petiole length interact in complex ways so that the effect of any one character is not readily apparent without considering it in the context of the other character states (Niklas 1988, Takenaka 1994).

Psychotria limonensis. Krause (Rubiaceae), is an evergreen, broad-leaved understory shrub common on Barro Colorado Island in Panama. It is locally abundant in deeply shaded understory but also is found in treefall gaps. Croat (1978) lists it as common in understories of moist to wet forest from southern Mexico to northern Colombia. Usually, it has a monoaxial crown, or rarely branches. Stems on mature plants often lodge and root adventitiously at nodes, which then can give rise to new shoots. The resulting shoots are mostly orthotropic, bearing large (200–300 mm long) broadly elliptic leaves arranged in an opposite decussate phyllotaxy. The leaves can persist for up to 4 years. Petioles are typically 40–80 mm long. The opposite decussate leaf insertion pattern potentially causes considerable self-shading in the vertical projection since alternate leaf pairs overlap completely. Since the small gaps inherent in otherwise closed overstory canopies are much more frequent overhead than to the side, this phyllotactic pattern is potentially costly in terms of C gain. We observed, however, that leaves on understory plants were often displaced from their true phyllotactic angle, giving rise to a leaf display superficially resembling that of a spiral rosette, which we have termed a pseudo rosette. The leaf displacement, which was due to petiole twisting, appeared to occur in response to their shading by newly produced upper leaves. This reorientation only occurred in understory plants; those in gaps exhibited no displacement of their leaf orientation from that created by an opposite decussate phyllotaxy.

We used Y-plant, a three-dimensional computer based model that reconstructs plant crown geometry and simulates its light capture and C gain (Pearcy and Yang 1996), in order to characterize the dynamics of the leaf reorientation and to determine its functional role in whole-plant light capture and daily C gain. We also examined the nature of the signals promoting reorientation with experimental manipulations of light quality and quantity using specially constructed light filters mimicking leaves. We show that reorientation of lower leaves of *P. limonensis* strongly enhances C gain in the understory and that a phytochrome response to light quality [red to far red ratio (R:FR)] is involved.

Materials and methods

Field site and plant material

All experiments were conducted in an area of secondary tropical forest on Buena Vista Peninsula (BVP) that has been largely undisturbed for at least 50 years in the Barro Colorado Natural Monument, Panama (9°10'N, 79°51'W). BVP is located across the Panama Canal (approximately 1 km) from the Smithsonian Tropical Research Institute, Barro Colorado Island, Field Station (BCI). BCI receives 2,650 mm precipitation per year and has a strong, well-defined dry season typically lasting from December to April.

Seedlings were grown from locally collected seed in 4-l pots in a partially shaded growing house. The shade-cloth screened roof resulted in a reduction in the daily photon flux density (PFD) to approximately 12% of the total daily PFD in the open on BCI with no change in the R:FR (R:FR=1.1). After germination, the plants were thinned to a single plant per pot. After 2 months, 12 plants were transferred to a fenced 7×7-m exclosure in the forest understory and another 12 plants to a similar exclosure located in an approximately 75-m² tree fall gap that had been cleared of debris and vegetation. Both exclosures were located nearby on BVP. The plants at this time were approximately 20 cm tall and had three of four leaf pairs. The older one or two leaf pairs on each plant were removed so that only the upper two leaf pairs remained. Since these two leaf pairs would not yet have exhibited any reorientation (i.e., the successive leaf pairs were at a 90° rotation to one another and therefore not self-shaded), their reorientation could be followed from the beginning as new leaves were produced above them. The older leaves that were removed were small and shaded by the upper leaves and, from simulations, make virtually no contribution to the whole-plant C gain.

Simulation of light capture and C gain for understory plants

After removal of the lower leaves, those remaining on a plant were carefully marked and the length, the azimuth and angle of the normal to the surface, the azimuth of the midrib axis, and the azimuth and angle of the petioles and internodes were recorded. These initial data provided information on the orientation of leaves prior to the development of new leaves above them. After 7 months, two to three new leaf pairs had developed and the above measurements were again made on both the original and the new leaves. Hemispherical photographs were taken over each plant and at a range of other understory sites with a Nikon model FM 35 mm single lens reflex camera and Nikkor 8 mm fisheye lens. The photos were analyzed with the program HemiView (version 2.1, Delta-T Instruments, Cambridge) to determine the angular and azimuthal distribution of gap fraction in the overstory canopy above each plant, and the gap distribution along solar tracks for specific dates as required for Y-plant. Leaf physiological parameters that are also required to parameterize Y-plant were determined from light response curves measured on other *P. limonensis* plants growing nearby. The light response curves were constructed with a Li-Cor 6400 (Li-Cor, Lincoln, NE) photosynthesis system. Measurements were made on the most recently fully expanded leaves of three plants and values of light-saturated CO_2 assimilation rates, the apparent quantum yield and the dark respiration rate were determined by least squares curve fitting to a rectangular hyperbola light-response model (see Pearcy and Yang 1996). The mean values from the three curve fits were then used as input into Y-plant. After

leaf expansion, the photosynthetic capacity of understory *Psychotria* spp. leaves in the BCI understory has been shown to decline only slowly until senescence (K. Kitajima, personal communication).

After parameterization, Y-plant was used to reconstruct the 3-dimensional architecture of each plant and then to calculate the absorbed PFD and photosynthetic rate of each leaf, and by summation over all leaves, the whole plant light absorption and photosynthesis. Simulations in which the leaf laminas were returned to their original position prior to reorientation were used to study the effect of petiole reorientation on light capture and C gain. This adjustment of the azimuths of the petioles and leaf midribs input into Y-plant thus created the opposite decussate leaf arrangement that would have occurred if it were not for petiole reorientation. Comparisons of Y-plant simulations for the pseudo rosette and the reconstructed opposite decussate architectures were made under five different understory light regimes as simulated from hemispherical photographs taken at different microsites in the understory.

Simulation of light capture and C gain of gap-grown plants

In order to examine the potential consequences of petiole reorientation for plants in the gap light environments with higher PFD levels, we manipulated both the leaf arrangement and the internode length in Y-plant simulations. We measured the morphometric parameters required for Y-plant on six opposite decussate 1-year-old *P. limonensis* plants growing in a gap garden. Leaf photosynthetic parameters were from measurements on similar plants in the gap gardens following the same protocols as used for the understory plants. We ran Y-plant simulations for opposite decussate or pseudo-rosette leaf insertion patterns and for architectures in which the internode lengths were varied from 15 to 200 mm. Y-plant simulations utilized a hemispherical photo taken in the middle of the garden (daily integral PFD=7.30 mol m^{-2} day^{-1}).

Light quality effects on leaf reorientation

We utilized a shade cloth enclosure in the BCI growing house and transferred into it twenty, 10-month old *P. limonensis* plants that had initially been grown under the same conditions as those transferred to the field exclosures. The shade cloth used reduced the PFD at plant height in the enclosure to 80–130 μmol m^{-2} s^{-1} at midday on clear days (approximately 5% of full sun, see Valladares et al. 2000). At the time of transfer, the plants exhibited a typical decussate leaf insertion pattern. After 14 days in the new light environment, we randomly selected a fully expanded mature leaf located below the terminal leaf pair on each plant, and above it we placed a leaf-shaped wire frame supporting either a selective filter (Energy Film; Gold Point ST7 STL-60, Panama) or a neutral density filter (ND) constructed of shade cloth. The selective filter will be identified as the LEAF filter since it mimicked the shading by a leaf. It had a low transmission from 400 to 690 nm wavelengths but cut on to a higher transmission in the near IR. Thus, the transmitted PFD was reduced and the R:FR decreased to values similar to those found in forest understories (Chazdon et al. 1996, Lee 1987). It had transmission characteristics in terms of PFD and R:FR that were similar to those of a *P. limonensis* leaf (Fig. 1). The ND filter, which had no effect on the R:FR, was adjusted by altering the shade cloth combinations until one was found that gave nearly the same reduction in PFD as the LEAF filter. The PFD transmission and the R:FR under each filter were determined using a quantum sensor (Li-189; Li-Cor) and a R:FR sensor (SKR 110; Skye instruments, Powys, UK), respectively. Following installation of the leaf filters, we recorded the midrib azimuth of each leaf that was shaded by a filter with a compass every 2 days for 27 days.
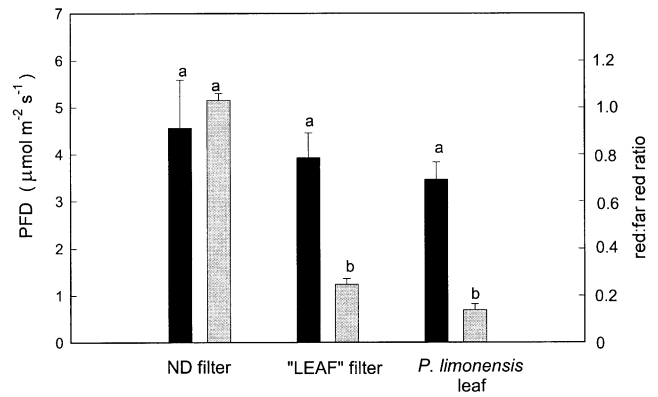

Fig. 1 Photon flux density (PFD) (*black bars*) and the red:far red ratio (R:FR) (*gray bars*) light transmitted by the neutral density (*ND*) filter, the energy film (*LEAF*) filter and a *Psychotria limonensis* leaf. *Each bar* gives the mean and SE for five measurements and *bars with different letters* are not significantly different at the *P*=0.05 level

Results

After 7 months in forest understory, all plants had naturally reoriented their lower leaves in order to avoid the shadows cast by the newly expanded upper leaves. This reorientation occurred in two different ways. In the first, petioles of shaded leaves bent so as to rotate each leaf blade around the axis in the same radial direction (Fig. 2A). This created a new axis of symmetry offset 45° from those of the upper leaf pairs. Development of a new leaf pair resulted in a similar rotation of a lower leaf pair to occupy the remaining non-shaded space (Fig. 2B). At this time, a rosette-like appearance (a pseudo rosette) of leaf display was evident when the plants were viewed from above. In the second mode of leaf reorientation, which was less commonly observed, the two lower leaves shaded by developing upper leaves rotated in opposite radial directions around the axis (Fig. 2C). This initially formed a non-symmetrical crown which could be later returned to symmetry with an opposite rotation of other leaf pairs.

Y-plant simulations with decussate versus pseudo-rosette architectures in the understory showed that the latter had a significant advantage in terms of light capture and C gain. Simulations were done for five different light environments representing a range of daily PFDs characteristic of different microsites in the understory (Fig. 3) using the leaf photosynthetic properties shown in Table 1. Across all environments, daily C gain depended strongly on the daily PFD (r^2=0.942 and 0.975 for the decussate and pseudo-rosette plants, respectively) but plants with the observed pseudo-rosette crowns had a significant C gain advantage in comparison with simulated decussate plants (ANOVA, P <0.005). Variations about the regression lines in Fig. 3 were due to the effects of the local directionality of the light environments. The apparent whole-plant light compensation point was much lower in the pseudo-rosette as compared to the decussate plants
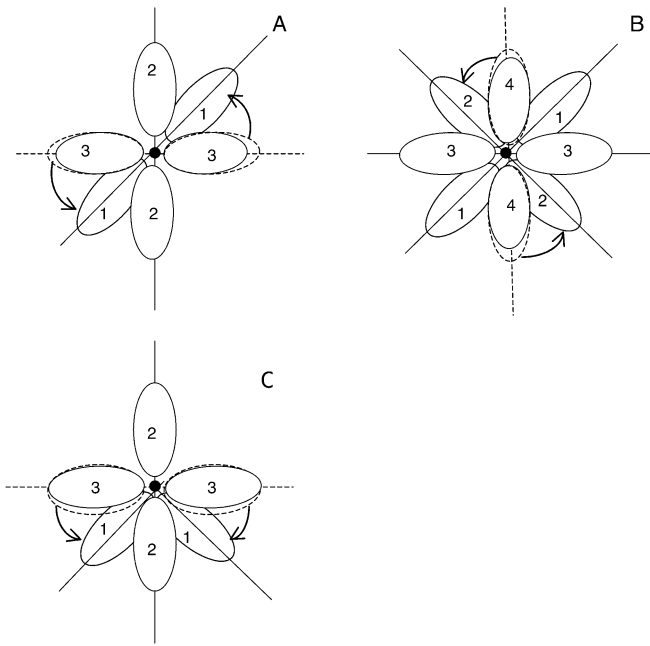
Fig. 3 Simulations of the daily CO_2 assimilation in five different understory light environments differing in daily PFD of the naturally occurring pseudo-rosette crowns (○) and of the simulated opposite decussate crowns (●) of *P. limonensis*. Each data point gives the mean and SD for six plants

Fig. 2A–C Schematic diagrams illustrating the departures from decussate phyllotaxis resulting from petiole twisting in *P. limonensis*. Leaf pairs are numbered in the sequence of development. The original position of a leaf prior to rotation is shown by the *dashed outline*. **A** Twisting of the petioles of lower leaves (*1*) displaces the leaf blades outside the shadow of the newly expanded leaves (*3*) forming a new axis of symmetry at 45° to the original axis. **B** With the expansion of the next leaf pair (*4*), the leaves below them (*2*) are displaced forming another axis of symmetry and completing the change from a decussate to the pseudo-rosette crown arrangement. **C** Less commonly, the shaded leaves (*1*) were displaced in opposite directions after new leaves (*3*) expanded, forming a non-symmetrical crown. Later rotations of leaf pairs in the opposite direction could then return the crown to symmetry

(0.33 versus 0.66 mol m^{-2} day^{-1}, respectively). In the highest PFD microsite (1.2 mol m^{-2} day^{-1}), the pseudo-rosette architecture exhibited a daily C gain nearly double that of the decussate architecture. This difference was clearly due to the increased C gain of the lower, reoriented leaves (Fig. 4) as compared to those of the simulated decussate leaf arrangement where the C gains of the lower leaves were negative. As expected, upper
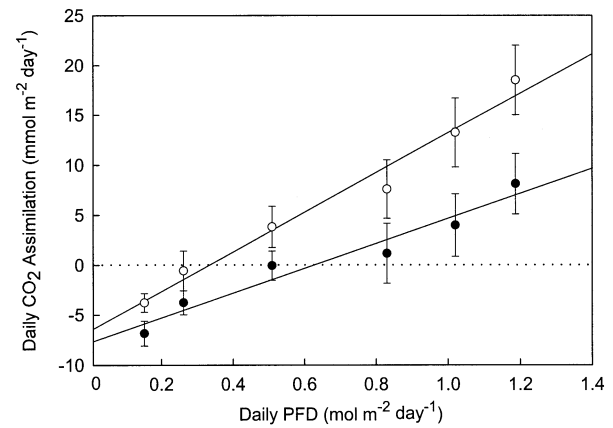
leaves had identical daily assimilation in both architectures.

P. limonensis plants in tree fall gaps did not exhibit the reorientation characteristic of understory plants and instead maintained a decussate leaf arrangement. These plants, however, had much longer internodes than did the understory plants, potentially allowing greater lateral light penetration to lower leaves. We examined the interactions between leaf arrangement and internode length in the gap environments with Y-plant simulations to estimate daily assimilation and water loss. Measurements of leaf photosynthesis revealed substantial acclimation to the higher PFDs of the gap environment as compared to the understory (Table 1). Therefore we used the photosynthetic parameters derived from measurements on the gap plants in these simulations. Since young seedlings produced much shorter internodes (10–40 mm) than older plants (160–210 mm), we varied internode length as well as leaf arrangement (decussate versus pseudo-rosette). Simulations of daily assimilation revealed that pseudo-rosette plants maintained a 20% C gain advantage (two factor ANOVA, $P<0.0001$) over those with a decussate leaf

Table 1 Photosynthetic characteristics[a] of *Psychotria limonensis* leaves from understory and gap light environments on Buena Vista Peninsula

	A_{max}	Quantum yield	Curvature	Dark respiration
	(μmol m^{-2} s^{-1})	(mol CO_2 mol^{-1} photons)	(Dimensionless)	(μmol m^{-2} s^{-1})
Understory	3.28±0.11	0.063±0.006	0.769±0.041	−0.206±0.032
Gap	10.44±0.59	0.068±0.004	0.559±0.204	−0.471±0.151

[a]The values shown are from a least squares fitting of the rectangular hyperbolic model:

$$A(I) = R_d + \frac{\phi I \sqrt{(\phi I + A_{max})^2 - 4\phi\theta I A_{max}}}{2\theta}$$

to photosynthetic light dependence responses where $A(I)$ is the photosynthetic rate at a PFD of I, R_d is the dark respiration rate, A_{max} is the light saturated photosynthetic rate, is the quanturm yield for CO_2 uptake and is the curvature factor. Each is the mean and SE derived from the fits to the light-response curves for three leaves
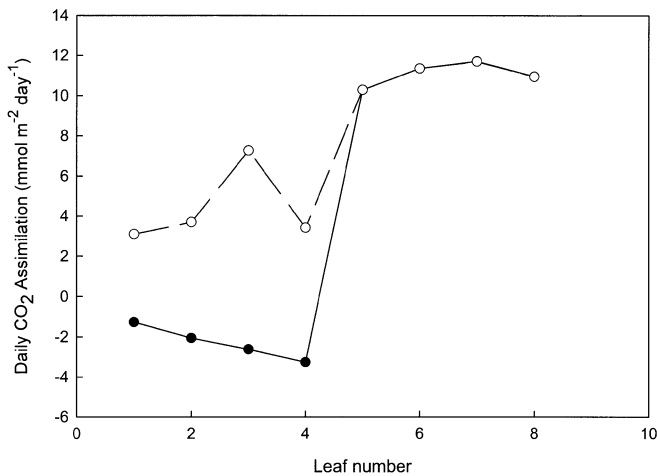
Fig. 4 Simulated daily CO_2 assimilation for individual leaves within the crown of pseudo-rosette plant (○) of *P. limonensis,* and the reconstructed decussate plant (●) derived from it. Leaf position is the node number from the lowest to the highest leaf pair
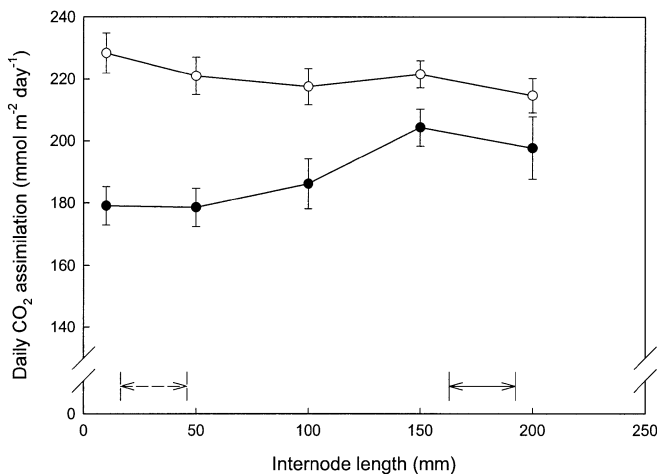

Fig. 5 Differences in daily CO_2 assimilation of simulated plants with decussate (●) and pseudo-rosette (○) leaf insertion patterns on complete open gap light conditions. The *horizontal dotted and solid lines* show the range of typical internode lengths during seedling and mature plant stages, respectively. Each data point represents the mean and SD for simulations for six plants

Table 2 Simulated absorbed photon flux density (*PFD*), assimilation and transpiration at midday under open sky conditions for upper and lower leaves on *P. limonensis* plants with either opposite decussate or pseudo-rosette architectures. Pseudo-rosette architectures were created from measured plants with decussate architectures by modifying the petiole and leaf orientations. Seedlings had 10-mm internode lengths and increasing leaf sizes from the base to apex whereas the mature plants were simulated as having constant leaf sizes and 200-mm internodes. Values for the upper leaves were means for the two upper leaf pairs while values for the lower leaves are for the six lowest leaf pairs

	Decussate		Pseudo-rosette	
	Upper	Lower	Upper	Lower
Absorbed PFD at midday (μmol m^{-2} s^{-1})				
Seedling	1,775	163	1,844	1,170
Mature	1,825	675	1,811	1,020
Photosynthetic rate (μmol m^{-2} s^{-1})				
Seedling	9.6	2.8	9.7	7.5
Mature	9.7	6.1	9.7	7.4
Transpiration rate (mmol m^{-2} s^{-1})				
Seedling	0.060	0.024	0.061	0.045
Mature	0.061	0.053	0.061	0.051

of the PFD still originated near the zenith reducing any impact of longer internodes. Examination of the simulated daily assimilation of upper and lower leaves revealed the expected pattern from the whole plant results, with the lower self-shaded leaves on decussate plants having a lower C gain than the comparable leaves on the pseudo-rosette plants and with the difference being largest for seedlings (Table 2). This difference in assimilation was accompanied by a 50% lower transpiration rate of the lower leaves on seedlings.

We explored the role of light quality effects, specifically the R:FR, in the leaf reorientation by shading leaves with either the ND or LEAF filters. Escape from the shadows cast by the upper leaves should be maximized when the leaf reaches a midpoint between the two perpendicular symmetry axes of the outlines of the upper leaves (see Fig. 2). This corresponds to a displacement angle of 45°, which we define as the maximum escape angle. Indeed, shading with the LEAF filter, which transmitted more FR, resulted in much more rapid and complete movement towards this maximum escape angle than observed with shading with a ND filter. A two-factor repeated measures ANOVA revealed that the extent, the rate of movement and the interaction term were all highly significant ($P<0.0001$). During the first 6 days after installation of the filters, leaf laminas under the LEAF filter displaced 29°, which is 65% of the maximum escape angle (Fig. 6). In contrast, leaves under the ND filter rotated only 6° or 13% of the maximum escape angle. After 19 days reorientation was complete (Fig. 6), with the leaves under the LEAF filter reaching their maximum displacement from their true phyllotaxy (44±3°), which was not significantly different from the maximum escape angle. In contrast, by 19 days leaves under ND leaf filters had rotated only 34±4° and exhibited no further reorien-

insertion pattern (Fig. 5) but internode length and the interaction between internode length and phyllotaxy had no significant effect (P=0.33 and *P*=0.06, respectively). Thus, the advantage in daily assimilation was maintained over the full range of internode lengths found in gap plants.

The lack of reorientation observed in gap plants is present in spite of an apparent C gain advantage for reorientation. Internode length interacts with phyllotactic pattern and in open environments where there is significant lateral light, simulations have shown that longer internodes can mitigate the impact of phyllotaxies that result in self-shading by allowing more lateral light interception (Niklas 1988; Takenaka 1994). However, in the medium gaps for which this simulation was run, most
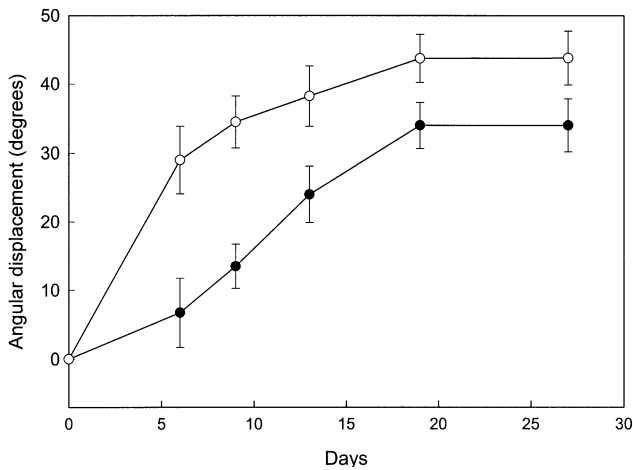
Fig. 6 Displacement of leaf blades from the initial angle established by the shoot phyllotaxis following shading with either the LEAF filter (○, low R:FR) or the ND filter (●, high R:FR). Each data point gives the mean and SD for a leaf on each of five plants. For abbreviations, see Fig. 1

tation. Thus, while leaves rotated under both types of shading, the rate of rotation was much faster and more complete under decreased R:FR. We observed that no reorientation occurred in the absence of shading by either a newly developing upper leaf or the artificial leaves. If a developing leaf on an understory plant was removed then the lower leaf that would have been shaded by it did not reorient. However, the opposite lower leaf, which was shaded by the newly developing opposite leaf, did reorient as expected.

Discussion

The positioning of leaves around a shoot axis is a function of phyllotaxy, the angle and length of the petioles, and any reorientation of the lamina due to either diurnal movements or petiole or internode bending and twisting. The latter are thought to be irreversible in the long term but are clearly an important dynamic component that can maximize the efficiency of light capture. Previous studies of the role of petioles in leaf display have focused on the effects of petiole lengths and angles (Pearcy and Yang 1998; Takenaka 1994; Takenaka et al.2001; Yamada et al. 2000) and petiole deflection due to biomechanical load (Niinemets 1998; Niklas 1992). To our knowledge, this study is the first to quantify the effects of petiole twisting for the C gain of plants and to identify signals involved in the response. Previous studies of photomorphogenetic responses (e.g., Marcuvitz and Turkington 2000) of petioles have focused on reorientation and petiole extension during development of new leaves rather than movements of already expanded leaves as occurs in *P. limonensis*.

Niklas (1988) and Takanaka (1994) studied the central role of phyllotaxy in efficient light capture and its interaction with other morphological traits. Opposite leaf

arrangements have an advantage in that leaf area is distributed on both sides of the node, minimizing the support costs as compared to an equivalent leaf area located on only one side. However, a disadvantage of the opposite decussate architecture is that leaves on alternate nodes are positioned directly above each other. Longer internodes can reduce self-shading created by inefficient phyllotaxies, especially when there is significant sidelight. However, investment in additional internode length is costly in terms of C that must be allocated to stems rather than leaves. Since the understory vegetation is sparse in forests where *P. limonensis* occurs, there is no particular competitive advantage of elongating internodes as has been demonstrated in denser herbaceous understories in temperate forests (Givnish 1982). Moreover, most of the PFD available in understories originates from canopy gaps near the zenith with little originating from the side, minimizing the light capture advantages gained with longer internodes. Alternate leaf arrangements in spiral phyllotaxies with divergence angles approaching 137.5° are potentially more efficient because they maximize the distance between leaves that overlap in the vertical projection (Bell 1991; Niklas 1988). Most plants with spiral phyllotaxies exhibit divergence angles approaching this value, which maximizes light capture efficiencies. Reorientation of *P. limonensis* leaves mimics a spiral architecture. That such a reorientation is significant in terms of C gain is clearly shown by the 66% increase in C gain at the normal range of PFDs found in the understory habitat. This enhancement of whole-plant C gain is likely to be crucial for survival of *P. limonensis* plants in much darker microsites than would be possible without reorientation.

Photomorphogenetic responses of plants are known to be regulated by both blue and R:FR light photoreceptor systems. Phototropic responses of stems have generally been attributed to directional receipt of blue light via the phototropin photoreceptor system (Casal 2000; Liscum and Stowe-Evans 2000). However, R and FR light acting through phytochrome have been shown to enhance the response to blue light, causing phototropic curvature to be more rapid (Liscum and Stowe-Evans 2000). Directional light cues may be provided by blue light with FR reception by phytochromes functioning to modulate the magnitude of the curvature. It is also possible that phytochrome alone can be a significant phototropic receptor, especially in closed canopies, since significant R:FR gradients can occur across tissues (Ballare 1994; Ballare et al. 1991; Iino 1990). Due to the lack of suitable filters we were unable explore the involvement of blue light in leaf reorientation of *P. limonensis*. However, our results showing greater and more rapid movements in response to FR-enriched shading clearly support the involvement of a phytochrome-mediated response as at least part of the sensory transduction mechanism. Since leaves are strong absorbers of R wavelengths but transmit and reflect much more FR radiation, the R:FR serves as a good indicator of shading by other leaves (Ballare 1999; Smith 1995). Reorientation occurred in both neutral or FR-enriched shade but was more rapid and greater in the

latter. This response is consistent with morphogenetic responses to neutral and FR shade where for example stem elongation occurs in response to both but is greater in the latter (Lotscher and Nosberger 1997).

Although one of the classic responses to reduced R:FR is stem elongation (Smith 1995), we saw no evidence of stem elongation responses in *P. limonensis* in the shade. Thus, the leaf reorientation response seems to be rather specific and not a general simulation of phytochrome-mediated morphogenetic responses. Indeed, understory plants have been shown to have much reduced stem elongation responses to low R:FR as compared to high-light species (Morgan and Smith 1979), presumably because stem elongation is a costly allocation pattern in these light- and hence C-limited environments. R:FR is already 0.2–0.3 in the understory giving a phytochrome photoequilibrium strongly shifted to the Pr form. While transmission through an additional leaf will lower it further the scope for change is small. The reorientation response in *P. limonensis* must therefore be quite sensitive to small changes in R:FR.

Phytochrome is known to be localized both in leaves and stems (Morgan et al. 1980). In our experiments only the leaf lamina and not the petioles or stems were shaded by the filters, suggesting that the leaf is the site of perception of the R:FR signal involved in leaf reorientation. Thompson (1995) found that the petiole tip was the site of photoreception for FR in red clover leaves. It is likely that our filters also influence the light environment of the petiole tip so we cannot rule out involvement of this site as a photoreceptor. But clearly the R:FR received by the leaf lamina was much more altered by the filter than was the R:FR at the petiole tip. Moreover, phototropic bending responses occur in response to light gradients across the organ; it seems unlikely that a significant lateral light gradient could be generated at the petiole tip.

Leaf development involves both lamina expansion and petiole extension. The lamina of leaves that reoriented were fully expanded at the time of development of the upper shading leaf but it is possible that petioles may not reach full extension until sometime later. Petiole elongation continued for a mean of 91 days in the tropical tree species *Macaranga gigantea* even though lamina expansion required only 21 days (Yamada et al. 2000). This example may be more extreme than the case for the much shorter petioles of *P. limonensis* but it is possible that some potential for extension remained at the time of reorientation. Except for diurnal leaf movements, which involve a reversible swelling or shrinking of a pulvinus (Koller 1990), other phototropic responses occur in growing organs. Blue light-mediated phototropic bending of stems is caused by an inhibition of growth on the shaded compared to the illuminated side, with little or no net effect on overall growth, leading to a bending towards the light source. If lamina are the site of perception of shading by an upper developing leaf then transport of a signal to the petioles is required. Greater shading on one leaf side than the other could generate a differential signal. Translocation

of this signal via the pattern of venation could then carry it differentially to one side of the petiole.

Although simulations of plants in medium gaps showed that reorientation to the pseudo-rosette leaf arrangement would yield a C gain advantage, no such reorientation was actually observed. Plants in gaps maintained the opposite decussate leaf arrangement set by the phyllotaxy of *P. limonensis.* This lack of reorientation contrasts with findings of Ackerly and Bazzaz (1995) for pioneer tree species seedlings, which oriented their leaves in the direction of the prevailing diffuse light in gaps. The reasons for no movement in *P. limonensis* are not known but several possible factors could be involved. First, in the high light of the gap environment, the signal transduction mechanisms may have been saturated and rendered inoperable. It is clear that in order for the mechanisms to work in the shade environment they must be very sensitive to very low photon fluences, which may then limit their function in high light. The pioneer tree species Ackerly and Bazzaz (1995) studied are adapted to much higher light environments and the leaves appear to orient during development rather than after full expansion. It may also be that a different signal transduction mechanism, such as a blue light response acting alone, is responsible for the leaf orientation during development. Second, in this high light environment, C gain is unlikely to be limiting, especially in a species principally adapted for growth in understories. Therefore, a mechanism that increases C gain may have little selective advantage. Finally, simulations of transpiration of the lower leaves show that it is higher in seedlings with a pseudo rosette as compared to an opposite decussate leaf arrangement. This may be an important cost of reorientation in gap environments, especially in the long dry season characteristic of central Panama.

In conclusion, this study has shown that reorientation of lower leaves of *P. limonensis* via petiole twisting significantly enhances whole-plant C gain in deeply shaded tropical forest understories. This reorientation involves at least in part perception of shading by an upper developing leaf through shifts in the R:FR of the light received by the lower leaf. The lack of reorientation in gap environments suggests that the response is specific to shaded conditions where the advantage is greatest. Our field observations indicate that leaf reorientation due to petiole twisting is common in many species in both shaded understories where it could function to enhance C gain as we have shown with *P. limonensis* and in high light environments where it may minimize receipt of excess radiation, reducing stresses (Pearcy and Valladares 1999; Valladares and Pearcy 1998). Further studies are warranted of both the mechanisms underlying these responses and their consequences for light capture, C gain and stress avoidance.

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