

Research review

Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model

Author for correspondence:
Robert W. Pearcy
Tel: +1 530 752 1288
Fax: +1 530 752 1449
Email: rwpearcy@ucdavis.edu

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Robert W. Pearcy¹, Hiroyuki Muraoka² and Fernando Valladares³

¹Section of Evolution and Ecology, University of California, Davis, CA 95616, USA; ²Institute for Basin Ecosystem Studies, Gifu University, 1-1 Yanagido, Gifu, 501-1193, Japan; ³Centro de Ciencias Medioambientales, C.S.I.C., Serrano 115 dpdo. 28006 Madrid, Spain

Summary

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Sun and shade environments place markedly different constraints on the photosynthetic performance of plants. Leaf-level photosynthetic responses to sun and shade have been extensively investigated, whereas there has been much less research on the functional role of crown architecture in these environments. This paper focuses on the role of architecture in maximizing light capture and photosynthesis in shaded understories and in minimizing exposure to excess radiation in open high light environments. Understanding these contrasting roles of architecture is facilitated by application of a three-dimensional structural–functional model, Y-plant. Surveys of understory plants reveal a diversity of architectures but a strong convergence at only modest light-capture efficiencies because of significant self-shading. Simulations with *Psychotria* species revealed that increasing internode lengths would increase light-capture efficiencies and whole plant carbon gain. However, the costs of the additional required biomechanical support was high, which, in terms of relative growth rates, would override the advantage provided by higher light-capture efficiencies. In high light environments, leaf angles and self-shading provide structural photoprotection, minimizing potential damage from photoinhibition. Simulations reveal that without these structural protections photoinhibition of photosynthesis is likely to be much greater with daily carbon gain significantly reduced.

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Introduction

The arrangement of leaves within the crown of a plant is one of the most basic parameters affecting its light capture and photosynthetic carbon (C) gain. Ideally, leaves in shaded understory environments would be horizontally arranged

with minimum overlap in the horizontal plane, thereby minimizing self-shading for light from above, where it mostly originates in a forest. The reality is usually far from this ideal, with most crowns even in understory plants having significant self-shading and unequal light distribution among leaves. In high light environments, avoidance of excessive radiation

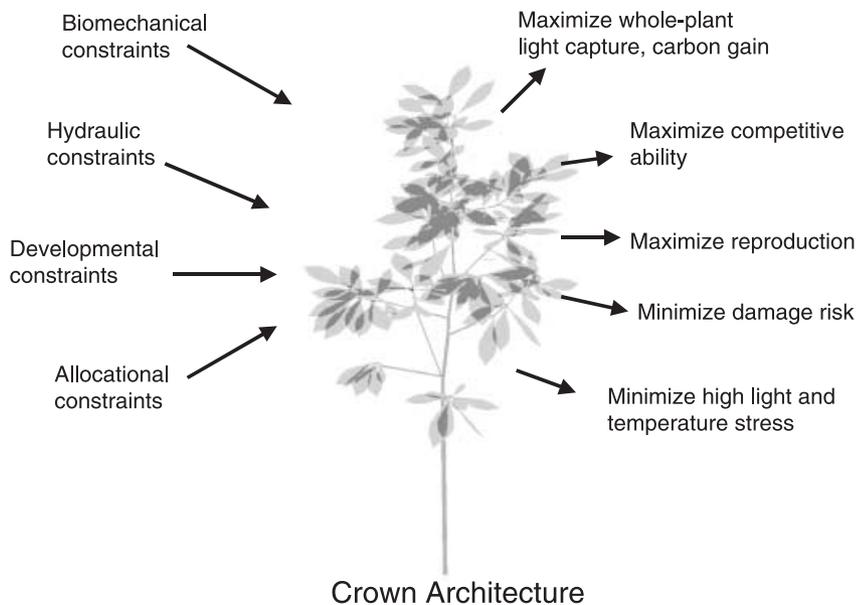


Fig. 1 The multiple constraints and functions that are important in crown design and its evolutionary optimization.

through structural features such as leaf angle and the packing of foliage that increases self-shading are major factors in the architectural design of crowns. In both sun and shade, the resulting highly heterogeneous light environment within the crowns strongly influences integrated crown functions such as photosynthesis, transpiration and water flow.

Until recently, studies of plant architecture focused almost exclusively on light capture by crowns with its potential effect on photosynthesis (Horn, 1971; Honda & Fisher, 1978; Waller & Steingraeber, 1986). Indeed, it is easy to think first about light capture but also important to remember that crowns have multiple functions and constraints that influence their design (Fig. 1). Some of these functions such as light capture, biomechanical support and hydraulics have been investigated individually to a considerable extent, but their interactions have been much less studied. Others such as resistance to damage from falling debris in forests are not well understood. Investment in sufficient biomechanical support and hydraulic sufficiency of the stems is costly and the result is less leaf area and less light capture. Positioning of reproductive structures may also be significant selective pressures influencing the evolution of crown architecture but have been little investigated. Developmental constraints such as the particular phyllotaxy constrain the way that resources can be allocated within the crown. Indeed, it is not surprising that a diversity of architectures appear to coexist, given the many constraints and functions. Simulations of adaptive walks of crown design in fitness landscapes for simple forms mimicking primitive plants revealed that as additional functions were added, more phenotypes representing local optima emerged (Niklas, 1994). However, conflicts in design principles caused the apparent fitness value of phenotypes representing the best compromises between multiple functions to be lower than that of phenotypes for which fewer functions were considered.

The challenge with real canopies is how to evaluate the role of these competing functions and constraints (Farnsworth & Niklas, 1995).

Here we address the relationships between crown structure and function in sun and shade environments. We focus especially on our work utilizing the structural–functional model Y-plant and address the multiple trade-offs involved in crown design.

Modelling crown architecture

Plant architecture models useful for structure–function studies fall into two main categories: statistical models based on a turbid medium analogy and geometric models that position specific architectural elements such as leaves or stems in space within the crown dimensions. Statistical models were originally developed for modeling horizontally uniform crop canopies but have been applied successfully to individual plants by dividing the crowns into different layers or cells, each with its own leaf area density and angle distribution (Cescatti, 1997; Werner *et al.*, 2001). Statistical models are scalable to large crowns, but because the foliage distributions are treated as an abstraction, they are less suited than geometric models for exploring the function of specific architectural traits. Geometric models rely on information specifying the spatial positioning of crown elements and the connections between them to reconstruct a crown in computer space. The necessary geometric information can be obtained either from direct measurements of plant crowns *in situ* or by application of morphological or developmental rules to construct a plant crown. Those that rely on developmental rules such as the L-systems models (Prusinkiewicz *et al.*, 1994; Room *et al.*, 1996) can simulate the growth of a crown and can incorporate developmental responses to, for example, light quality. The

realism with which a crown and its pattern of growth can be reconstructed is quite remarkable. Although there is no inherent limitation to doing so, developmental-rule-based models have not been used much to evaluate the functional role of crown architecture in the physiological or ecological performance of plants.

The alternative approach for geometric models is to simulate the crown from field measurements on actual plants of the orientations and dimensions of the component parts (Percy & Yang, 1996; Takenaka *et al.*, 1998). Tools for this can be as simple as a compass, angle finder, ruler and callipers, or it can be a three-dimensional digitizing system (Falster & Westoby, 2003). This reconstruction gives the architecture at a point in time, reflecting the effects of both past and present environments on the architecture. The structural–functional model Y-plant (Percy & Yang, 1996) is of this type and was developed specifically to assess the role of crown architecture in plant function. Hemispherical photographs taken above the plant are used along with standard equations for solar and diffuse radiation (Gates, 1980) to simulate the quantity and geometry of the light incident on the crown. Diurnal courses of air temperature and relative humidity are simulated from simple sine wave functions. From these inputs, light absorption, CO₂ assimilation, leaf temperature and transpiration from a leaf energy balance simulation are computed for the sunlit and shaded parts of each leaf, given their unique environments, and then summed over the crown to give whole-crown performance estimates. Y-plant has been shown to accurately predict the frequency distributions of photon flux density (PFD) on the leaf surfaces of shoots based on comparisons of model outputs and measurements with leaf-mounted sensors (Valladares & Percy, 1998).

In the most current version of Y-plant, a Farquhar–von Cammerer–Berry leaf photosynthesis model updated to take into account temperature dependence of photosynthesis is used (Medlyn *et al.*, 2002). It is coupled to the Ball–Woodrow–Berry stomatal submodel and a leaf energy balance submodel (Baldocchi, 1994) to simulate responses to light, temperature, vapor pressure deficit and CO₂ pressure. Parameterization of the leaf photosynthesis and stomatal models came from gas exchange measurements of assimilation vs light and intercellular CO₂ and water vapor pressure deficit (VPD) response curves of stomatal conductance as determined with a LI-6400 photosynthesis system (LI-COR, Lincoln, NE, USA). Reductions in assimilation due to dynamic photoinhibition are simulated with the models of Ögren and Sjöström (1990) as implemented by Werner *et al.* (2001). Stem water fluxes and water potential gradients are simulated using the approach of Tyree *et al.* (1991). A map based on allometric equations relating stem hydraulic conductivities to diameters and lengths is used along with the predicted transpiration rates to compute stem water fluxes and water potential drops. Finally, harvests of nearby plants are used to generate allometric relationships between linear dimensions and mass of stems and petioles,

and to determine the specific leaf areas. These relationships can then be used to calculate the mass of the component parts and therefore the biomechanical load at any point in the crown. By combining detailed physiological models at the leaf and stem level with a realistic architectural model, a rich understanding of whole crown performance and of the contribution of both architectural and physiological parameters to it can be obtained.

The functional biology of crown architecture in shaded understories: constraints on maximizing light capture

Shaded tropical and temperate forest understories typically receive no more than 0.5–2% of the daily PFD incident at the top of the forest. Thus, the expectation is that selection should maximize light capture through increases in efficiency of investment of resources and arrangement of the foliage. Given the wide diversity of crown architectures of understory plants, either there is substantial variation in efficiency possibly related to different functional constraints, or trade-offs between characters result in architectures with essentially equivalent light-capture efficiencies. This possibility was explored with a survey in a Panamanian tropical forest understory in which Y-plant was used to estimate light absorption efficiencies (E_a : mol photons absorbed per m² leaf area/mol photons incident per m² horizontal surface; Valladares *et al.*, 2002). Because the PFD is low in the understory and on the linear part of the light response curve of photosynthesis, the E_a value and the daily net assimilation of the leaves are highly correlated (Percy *et al.*, 2004). Despite wide variation in growth form, taxonomic affinity and patterns of resource allocation as shown by investment in supporting structures and leaf area ratio (LAR), a strong convergence in E_a values was evident (Fig. 2). This supports the idea that there are multiple ways to arrive at functionally equivalent architectures depending on trade-offs between different characters and functional constraints. In the simulations, the maximum attainable E_a value is equal to the leaf absorptance, which ranged from 0.82 for very thin leaved species to 0.92, which is well above the actual E_a values. Those with the highest E_a values were mostly herbs with relatively simple architectures with minimal self-shading, whereas those with low E_a values were woody species with more complex branched architectures or species with steep leaf angles. Indeed, many of the species with high E_a values had architectures that constrained their height or were simply the seedling stage of much taller plants. A second survey focusing on 11 shrub species of the genus *Psychotria* that mostly have complex branched architectures found E_a values ranging from 0.43 to 0.64, at the low end of the range of plants in the understory (Percy *et al.*, 2004). The architecture of these *Psychotria* species differ in many of the details such as leaf size, leaf longevity and branching frequency and bifurcation, yet a strong convergence in E_a was again

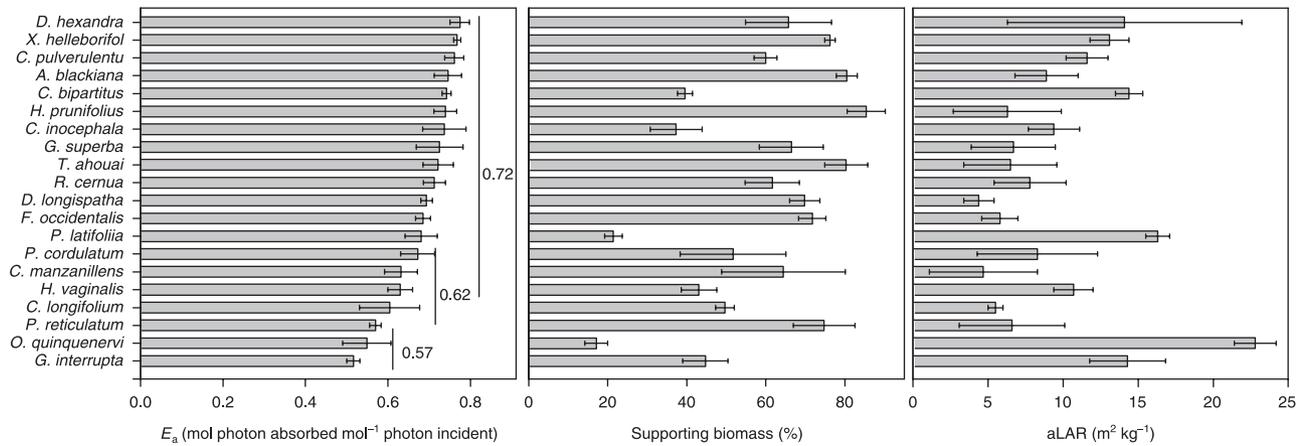


Fig. 2 Variation in the efficiency of light absorption (E_a), investment in supporting biomass and above-ground leaf area ratio (aLAR) among understory plants in a tropical forest in Panama. Shown are the means and SD for three individuals of each species. The vertical line marks groups of species that are not significantly different from each other (Tukey test, $P < 0.01$). The mean for each group is given on the right-hand side of the vertical lines. Adapted from Valladares *et al.* (2002).

apparent. Species that are dependent on gaps with higher available light had on average only slightly lower E_a values than those classified as shade-tolerant species, but the two groups overlapped. The low E_a values of the shade-tolerant species are surprising, given that *Psychotria* species are the most abundant species in this Panamanian forest understory.

We hypothesized that other crown functions could constrain E_a to seemingly rather low values in the *Psychotria* species. We chose to examine the interactions between light capture, hydraulics and biomechanics as three of the main crown functions that interact to determine crown design. Farnsworth and Van Gardingen (1995) have shown that Sitka spruce branches appear to conform more closely to biomechanical design considerations than to hydraulic design. However, they raised the possibility that the shoot design could instead follow rules for efficient light capture, which they did not characterize. Because internodes are the primary support structure minimizing leaf overlap and because their size influences both stem hydraulics and biomechanics, we chose to simulate the effect of internode length on these crown functions. This is similar to the approach used by Pearcy and Yang (1998) that demonstrated an optimal partitioning between leaves and petioles, maximizing light capture and C gain in the redwood forest understory rosette plant, *Adenocaulon bicolor*. It also is similar to the approach of Takenaka *et al.* (2001), who found that allocation to petioles in an understory palm *Licuala arbuscula* was optimal for light capture. Because changing internode size changes their biomass cost, we varied leaf size concurrently so that the total leaf plus internode biomass was constant.

Stems exhibit a deflection that depends on the loads at the end, their length and their flexural stiffness. The flexural stiffness is in turn a function of the modulus of elasticity and the second moment of area. Combining these terms, for a round stem the deflection δ is given by

$$\delta = \frac{4PL^3}{3E\pi R^4}, \quad (\text{Eqn 1})$$

where P is the load on the distal end of the segment, E is the modulus of elasticity, L is the length and R is the radius. E is measured for a branch segment by supporting the branch at one end and then adding small weights to the other free end and measuring the deflection (Niklas, 1992). Morgan and Cannell (1988) have shown that a branch can be treated as a series of cantilevered beams with a point load on the end equal to the mass of leaves and branches distal to it. Their results show that this applies reasonably well up to a branch angle of 60° but they did not test it for greater angles. While it probably does not strictly apply to more vertical stems, similar rules must apply because these stems are subject to lateral stresses from wind and other loadings, and also must be self-supporting. Eqn 1 can be used to calculate the additional increment (or decrement) in radius required to maintain the same deflection as length is varied. The result is that with increased internode length, leaves are more spread out, reducing self-shading, but their position relative to overall crown shape would be maintained. Because this entails a change in the load, an iterative procedure was employed to compute the proper partitioning between leaves and internodes, starting at the distal end of the branch and proceeding basipetally. Hence, as internode length was increased or decreased, leaf size would decrease or increase, respectively. This computation was applied to leaves and their supporting internode, because it is the developmental unit where internode length and leaf size are determined. For stem sections where leaves had been shed, we simply calculated the necessary increment in diameter to maintain the same deflection, based on the load distal to it.

Fig. 3 shows the results of simulations in which internode length was varied either without changing internode diameter

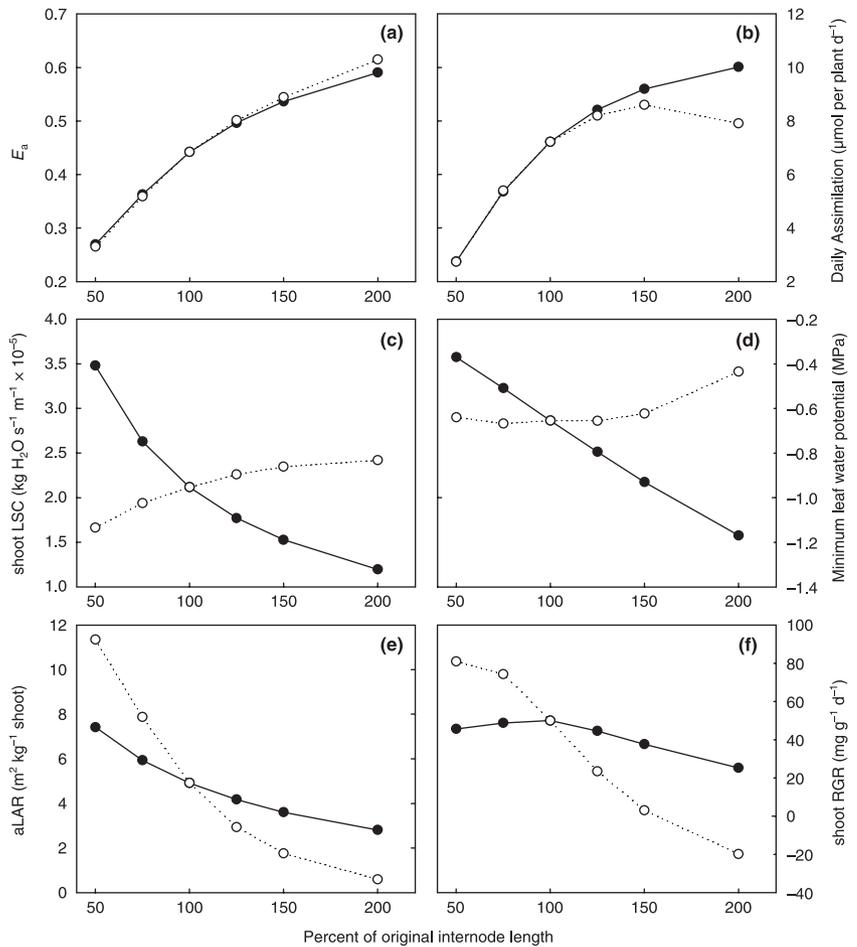


Fig. 3 The effect of increasing internode length on (a) light absorption efficiencies (E_a); (b) daily assimilation; (c) leaf specific hydraulic conductance (LSC); (d) minimum leaf water potential; (e) above-ground leaf area ratio (aLAR); and (f) relative growth rate (RGR). Closed circles, simulations in which internode length was increased with no change in diameter (no compensation for biomechanical load); open circles, simulations where diameter was adjusted to maintain biomechanical support. Simulations are with the *Psychotria marginata* plant shown in Fig. 1; results with two other *P. marginata* and three *P. brachiata* plants exhibited similar optima and trends.

so that the changes in biomechanical support requirements were not compensated for, or with changes in internode diameter and therefore the investment in biomechanical support that would be required to maintain overall crown shape. When internode lengths were varied without compensating for biomechanical support, no optimum internode length was observed with respect to E_a , and daily C gain increased up to the longest internode lengths tested. However, if the diameter was also changed to maintain sufficient biomechanical support then an optimum internode length was observed, but this length was considerably longer than the naturally observed lengths. In terms of light capture and assimilation, the crowns were operating well below their optimum allocation between internodes and leaves. We then asked whether they could be operating at this point because of hydraulic constraints. Increases in internode length without changes in diameter caused a significant decrease in the leaf area specific hydraulic conductance (LSC) of the shoot and the minimum leaf water potential. However, when the diameter was also increased to maintain biomechanical support, LSC and minimum leaf water potentials generally increased as internodes were lengthened. Therefore, the increase in diameter required to maintain sufficient biomechanical support was more than

sufficient to maintain hydraulics. Biomechanics rather than hydraulics appears to constrain architectural design, at least with respect to light capture and assimilation in these species.

The cost of maintaining biomechanical support is clearly high, as shown by the large decrease in LAR as internode length is increased. Because the relative growth rate (RGR) of a plant is product of the unit leaf rate and the LAR, the apparent shoot RGR (ignoring the roots) can be calculated from the output of the simulations. As shown in Fig. 3, the original internode lengths (100%) maximize shoot RGR in the absence of diameter compensation for changes in biomechanical load. However, inclusion of diameter compensation causes the shoot RGR to be maximal at much shorter internodes because much more of the biomass in the simulation is allocated to leaves. Thus, in terms of RGR alone and including compensation for biomechanics, the simulations show that the optimum architecture would be one with short internodes and large leaves with substantial self-shading. This would probably reduce competitiveness and possibly interfere with reproduction. This is consistent with the findings of Givnish (1986) that the strategy that maximizes growth in the absence of competitors may lead to poor performance in the presence of competitors.

The results of these simulations illustrate how difficult it may be to identify optimal character combinations because of the multiple design constraints that operate on crown architecture. While the simulations show that crowns of *P. marginata* are not optimal with respect to the design objective of light capture, it does not mean that they are not optimal if the compromises necessary for the multiple design objectives in Fig. 2 had been considered. However, identifying this multiobjective optimum is clearly a much more complicated problem than when only a single design objective is considered. Farnsworth and Niklas (1995) outline some possible approaches to multiobjective optimization studies, but to date these have not been applied in the analysis of plant architectural performance.

The functional biology of crown architecture in sunny environments: the problem of excessive radiation

High light environments, particularly those with other stresses such as drought and high temperatures, impose very different demands on architecture than those imposed in the understory. Under full sunlight conditions, there is strong evidence for the fundamental role that architecture plays as the first line of defense against temperature extremes and photoinhibition through avoidance of excessive radiation loads on the leaf surfaces (Ryel & Beyschlag, 1995; Valladares & Pearcy, 1998). Except for plants with very high photosynthetic capacities, full sunlight presents excessive radiation that must be dissipated in some manner. Biochemical mechanisms involving the xanthophyll cycle and reactive oxygen scavenging pathways serve to dissipate this excess energy and protect against damage (Demmig-Adams & Adams, 1996), whereas structural avoidance mechanisms minimize excessive

radiation in the first place. In the absence of these structural and biochemical mechanisms, photoinhibitory damage is likely, leading to long-term reductions in photosynthesis. This damage may be exacerbated by combinations of stresses such as high temperature or drought with high light (Valladares & Pearcy, 1997). However, the biochemical dissipating mechanisms that serve to protect against photodamage are a form of photoinhibition themselves, because they reduce the quantum yield of photosynthesis and therefore potentially also cause lost C gain. This type of photoinhibition has been termed dynamic photoinhibition, compared with the chronic photoinhibition associated with damage (Osmond, 1994). Structural mechanisms, especially steep leaf angles and shoot structures that promote self-shading and reduce receipt of excess light may therefore allow for less investment in biochemical-dissipating mechanisms and at the same time minimize chronic photoinhibitory losses. While much is known about these basic mechanisms, the costs of photoinhibition in terms of lost C gain or the role of structural mechanisms in ameliorating these losses has been little investigated.

The consequences of shoot architecture for light interception in high light environments are evident in comparisons of two Californian evergreen shrub to small-tree species (Fig. 4). Both species have a spiral phyllotaxy, but *Arbutus menziesii* has its relatively few large horizontal leaves clustered near the branch tips whereas *Heteromeles arbutifolia* has its smaller, steeply angled leaves (mean = 72°) distributed along a longer stem section. Both species had nearly 50% of their leaf area self-shaded at midday. Except in the early morning and late afternoon, *Arbutus* projects and displays more of its leaf area towards the sun than does *Heteromeles*. *Arbutus* had a distinct midday maximum in projection and display efficiencies, whereas *Heteromeles* exhibited if anything a slight reduction in midday due to its steep leaf angles. Consequently, the E_a value

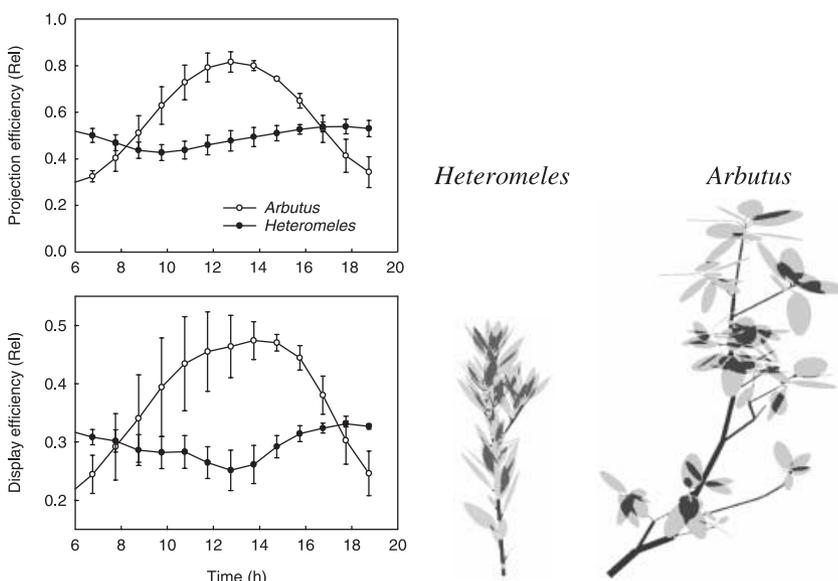


Fig. 4 Projection and display efficiencies for branches of *Heteromeles arbutifolia* and *Arbutus menziesii*. Projection and display efficiencies are the projected and displayed leaf area, respectively, in the direction of the sun, expressed relative to the total leaf area.

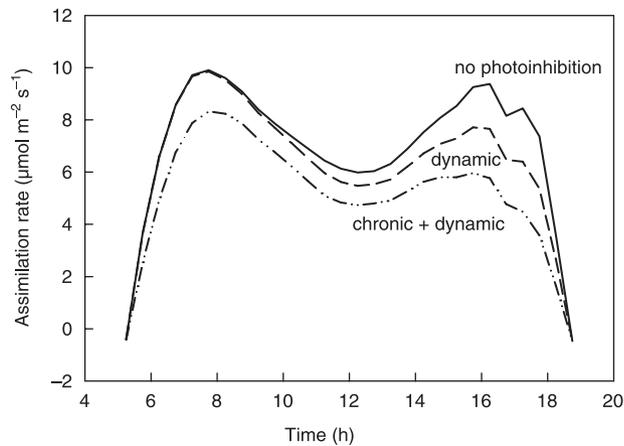


Fig. 5 The simulated diurnal course of assimilation of a *Quercus crispula* seedling growing in the open with no photoinhibition (solid line), with dynamic photoinhibition (dashed line) or with dynamic + chronic photoinhibition (dot-dashed line).

in midday (1000–1500 h) was only 0.24 for *Heteromeles*, whereas for *Arbutus* it was 0.42. Moreover, in *Heteromeles*, the PFD on the sunlit portions of the leaves was only about $628 \mu\text{mol m}^{-2} \text{s}^{-1}$, whereas in *Arbutus* it was $1275 \mu\text{mol m}^{-2} \text{s}^{-1}$. Because under well-watered conditions both species exhibited light saturation of assimilation rate by about $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, *Heteromeles* needs to dissipate far less energy at midday than *Arbutus*. Also, because of energy balance considerations, leaf temperatures under identical climatic conditions were 2–3°C higher in *Arbutus* due to its larger leaf size. This may be an important factor restricting its occurrence to cooler, more coastal and mountainous regions of California as compared with the more interior and lower-elevation distribution of *Heteromeles*.

Measurements with leaves have shown that the diurnal course of dynamic photoinhibition is related to a cumulative light dose rather than the current PFD. We simulated the consequences of photoinhibitory down-regulation of photosystem II (dynamic photoinhibition) by first computing a weighted photon flux density on the leaf surface over the previous 6 h, which is a strong predictor of the fluorescence ratio F_V/F_M (Ögren & Sjöström, 1990; Valladares & Pearcy, 1999; Werner *et al.*, 2001). Following the approach of Werner *et al.* (2001), we then reduced the quantum yield and the curvature factor for the light response of photosynthesis in proportion to the reduction in F_V/F_M . Chronic photoinhibition was simulated as an additional long-term reduction in F_V/F_M from 0.8 to 0.6 in the morning. With no photoinhibition, a midday depression of the cool-temperate tree seedling *Quercus crispula* is apparent principally because of temperature effects on photosynthesis and VPD effects on stomatal conductance (Fig. 5). Recovery of assimilation rates occurred in the late afternoon as temperatures cooled and relative humidities increased. Dynamic photoinhibition, which accumulated over the day, had little effect on assimilation in the morning

but limited it in the afternoon. Chronic photoinhibition caused a reduction in the morning as well as the afternoon. Photoinhibition affects light-limited assimilation, and assimilation in the transition from light limitation to saturation. Consequently the shaded fraction exhibited a much greater reduction (20% for dynamic; 50% for dynamic + chronic) in assimilation due to photoinhibition than the sunlit fraction (7.4% for dynamic; 21.8% for dynamic + chronic). Because the sunlit leaf area fraction contributes much more to the total daily C gain, the reductions due to dynamic and dynamic + chronic photoinhibition were 9% and 26%, respectively. This simulation shows that the consequences of photoinhibition and conversely of the structural photoprotection depend very much on the interactions between leaf physiology and the distribution of PFD as influenced by self-shading and leaf angles.

The consequences of photoinhibition for C gain for *Q. crispula* agrees closely with estimates of 10% for *Salix* spp. in Sweden (Ögren & Sjöström, 1990). However, for many species, particularly drought-tolerant evergreens, simulations suggest even lower losses on the order of 2–6% due to efficient structural photoprotection (Valladares *et al.*, 2005).

To elucidate further the role of leaf angles and self-shading in providing structural photoprotection, we ran simulations in which leaf angles of *Heteromeles* were varied, both for whole shoots and for individual leaves. The latter were at the same mean leaf angle as those attached to the shoot but had no shading. Both reducing leaf angles and eliminating self-shading had a marked effect on F_V/F_M (Fig. 6). Comparisons of simulations with and without dynamic photoinhibition revealed only a modest 6–8% reduction in C gain. Surprisingly, the C gain of the photoinhibited shoots actually increased slightly as leaf angles were decreased; low leaf angles enhanced the ability to utilize lateral light in the morning and evening, which offset the greater dynamic photoinhibition.

The plasticity of shoot architecture: responses of individuals to sun and shade

One of the most striking aspects of architecture is its plasticity in response to sun and shade growing conditions. This plasticity includes responses such as a shift from orthotropic to more plagiotropic shoot orientations, increased internode and petiole lengths, and increased leaf size but decreased leaf mass per unit area in shade vs sun shoots. Petioles clearly play an important role in the plasticity both by elongation responses reported in herbaceous species and through bending and twisting responses. A dramatic example of the role of petiole twisting was found in *Psychotria limonensis*, which has orthotropic shoots and a decussate phyllotaxy that potentially places a leaf pair directly above a lower pair. However, as a new leaf pair develops, causing self-shading, the lower shaded pair rotates in the horizontal plane to a position where self-shading is minimized. This rotation is driven in part by changes in the red to far-red ratio of the transmitted light. Y-plant

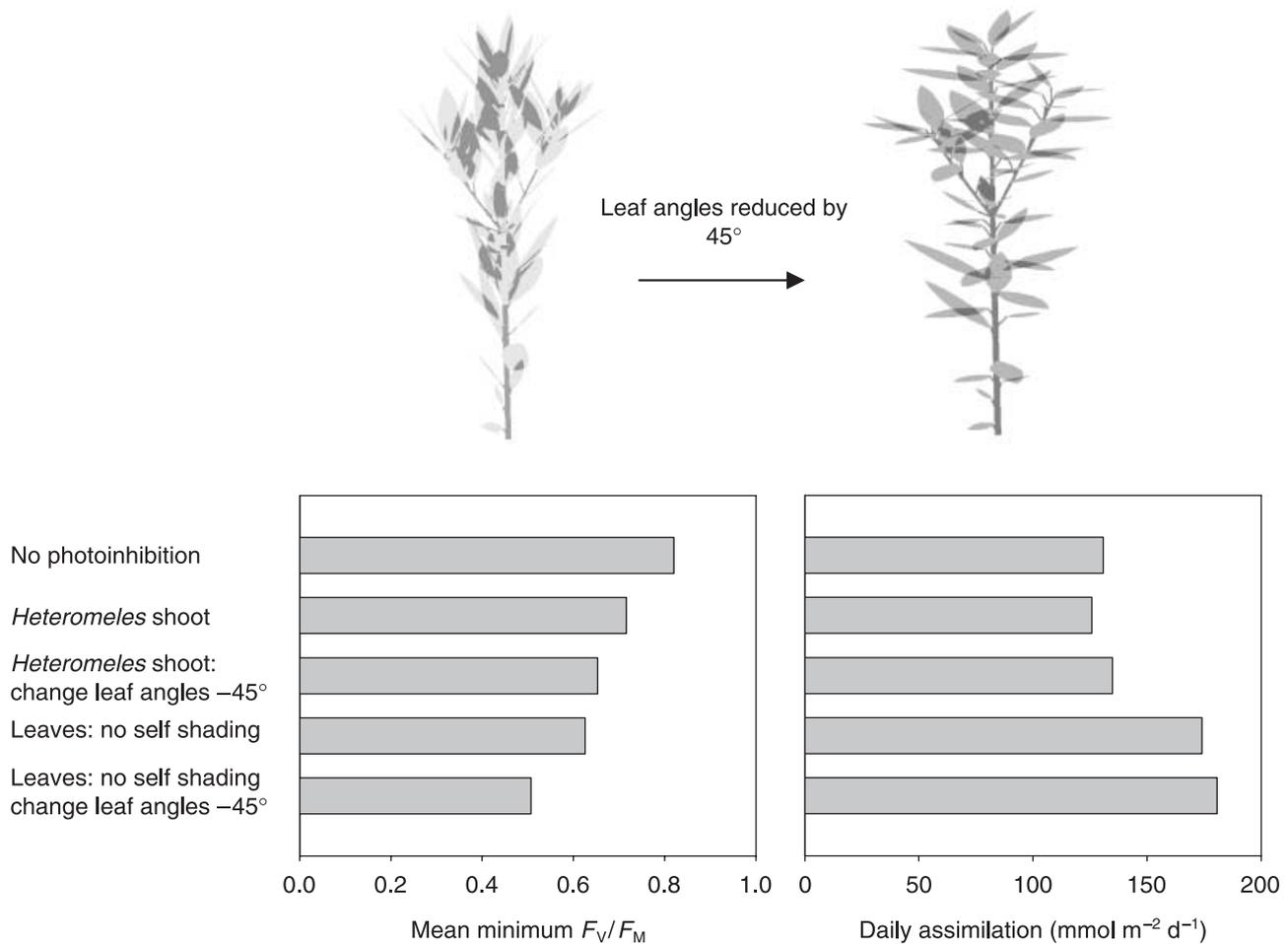


Fig. 6 The effect of changing leaf angle on the minimum F_V/F_M (left-hand panel) and daily assimilation (right-hand panel) for a *Heteromeles arbutifolia* shoot. The bars for leaves with no self-shading are for simulations for individual leaves so that no self-shading was present which were then averaged. Shown above as an example of the changes are the shoot with normal leaf angles and leaf angles reduced by 45° .

simulations with a strictly decussate architecture as compared to the resulting 'pseudo-rosette' architecture after leaf reorientation showed that the latter would be able to maintain a positive C balance at much shadier microsites in the understory. Reorientation of leaf lamina into more favorable light environments is quite common. Muraoka *et al.* (2003) found that leaves of tree seedlings in an understory of a cool-temperate deciduous forest in Japan were preferentially oriented to maximize photosynthesis in direct (sunfleck) light rather than to diffuse light. Interestingly, leaf orientations were fine-tuned to the extent that they did not face in a way that maximized direct light interception itself, but rather the lamina directions were such that a compromise was reached between maximizing photosynthesis and minimizing receipt of excessive PFDs. Congruence of maximum light interception and maximum assimilation is not necessary because photosynthesis in these shade leaves saturates at relatively low PFDs. In contrast to these results, Ackerly and Bazzaz (1995) found

that leaves of tropical pioneer tree species in treefall gaps were preferentially oriented to increase interception of diffuse rather than direct light. Differences in the amounts of available light and the predictability of diffuse vs direct light may account for the differences.

Structural acclimation of shoot architecture has been shown to have strong effects on shoot performance in sun and shade environments. Valladares and Pearcy (1998) found that the PFD above understory plants of *Heteromeles* was only 14% of that in the open, but shoots on these plants had a daily assimilation that was 68% of that of sun shoots on open-grown plants. Although sun-shade acclimation of leaf photosynthesis was a contributor, the higher E_a for diffuse light of the shade as compared with the sun shoots was a major factor, causing the convergence of whole-shoot C gain in spite of the large differences in available light. Similar results were found by Planchais and Sinoquet (1998) for sun and shade branches of *Fagus sylvatica*.

Concluding remarks

Plant crowns are complex three-dimensional structures that must perform many simultaneous tasks. These tasks often compete for resources with the consequence that the efficiency of investment with respect to any given task such as light capture may be reduced to below optimal levels. Thus, the competition between providing sufficient biomechanical support vs maximizing light capture can explain the relatively low light-capture efficiencies of understory *Psychotria* species. On the other hand, biomechanical support and hydraulic conductances are correlated with respect to the effect of changes in stem diameter, so deciding which is more limiting depends on how each scales. In *Psychotria*, scaling the diameter to maintain biomechanical support is more than sufficient to maintain hydraulic conductance, suggesting that the former is the more limiting design constraint. The trade-offs are dependent on the environment, and different results are likely in high light habitats where the structural photoprotection afforded by shoot architecture may be an important crown design consideration and where transpiration may be greater.

The complexity of both crown structure and function has inhibited research directed towards understanding the role of plant architecture in the ecological success of species and of the trade-offs involved in crown design. The development of three-dimensional structural–functional models like Y-plant provides a tool for unraveling this complexity. A current limitation, however, is that models like Y-plant are static, addressing only the crown in its current environment and not the developmental processes underlying crown formation. Thus, they should be linked to developmental-rule based models like L-systems in order to understand better the developmental plasticity that is so evident in plant crowns.

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