

Evaluating shrub architectural performance in sun and shade environments with the 3-D model Y-plant: are there optimal strategies?

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Functional structural models combining architecturally detailed geometric models of plant crowns with sub-models of leaf and crown physiological functions can play important roles in ecology, forestry and agriculture. First, they can provide insight into how variation in crown architecture influences leaf microenvironments, especially light environments and energy balance, and therefore photosynthesis and transpiration of individual leaves and whole crowns. Second, they can provide insight into the constraints on crown architecture imposed by other crown functions such as biomechanics or hydraulics. Models of this type can also provide an important linkage between leaf level physiological performance and ecosystem or community level models in evaluating issues such as global change.

We have utilized a functional structural model, Y-plant (Pearcy and Yang, 1996), to explore the relationship between leaf physiological performance and crown architecture in deeply shaded forest tropical forest understories in Panama where light capture could be expected to be a priority and in open chaparral communities where stress avoidance associated with excessive light is a priority. The basic strategy utilized in Y-plant is shown in figure 1.

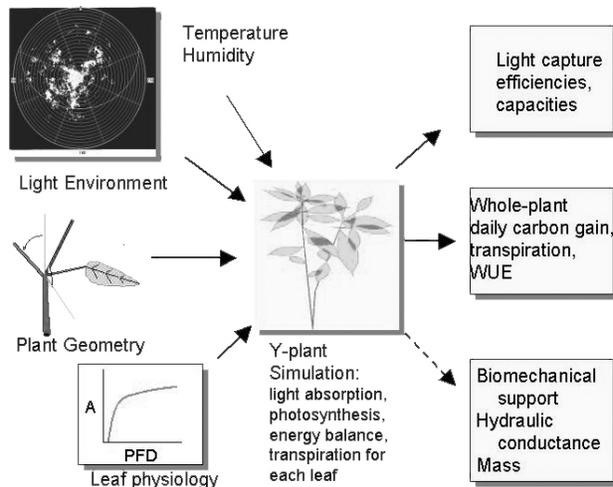


Figure 1. The modeling strategy in Y-plant. Light geometry and quantity is simulated from fisheye photos and standard equations for solar radiation. Inputs of measured leaf physiological parameters allow for leaf-by-leaf simulation of physiological performance, which is then summed to give crown performance. A hydraulic map routine simulates stem water fluxes and water potential gradients.

Studies in a Panamanian tropical forest understory involved a survey of a wide range of species and life forms designed to reveal the variation in light capture efficiencies and a more detailed study of eleven species in the genus *Psychotria* native to the high (tree fall gap) and low (understory) ends of the light availability gradient. The survey revealed that

in spite of contrasting architectures and life forms there was a strong convergence of light capture efficiencies (E_a : moles photons absorbed per m^{-2} leaf area/ moles photons incident per m^2 horizontal surface) on values around 0.7 (range 0.30-0.84; Valladares et al., 2002). No individual species significantly exceeded 0.7 while about 30 % of the species sampled had significantly lower values. Path analyses revealed that leaf angles, and to a lesser extent, leaf mass per unit area, biomass allocation to supporting biomass (stems and petioles) and the internode length/leaf length ratio were the primary factors contributing to the variation in the efficiency of leaf area display for light capture. The *Psychotria* study was undertaken to explore in more detail variation in light capture efficiency. These species were all shrubs with an opposite decussate phyllotaxy, but they differed remarkably in the details, with a five-fold range of leaf longevity, a thirty-fold range in leaf size as well differences in branching frequency and bifurcation. As a group, species classified as shade tolerant had higher E_a 's than species classified as tree fall gap dependent (Percy et al., 2004). Significant species differences were evident only in the gap dependent group. Overall, E_a values were surprisingly low (0.43 to 0.64); especially since several of the shade tolerant species are among the most abundant species in the understory. Self-shading was a major contributor to the low E_a values.

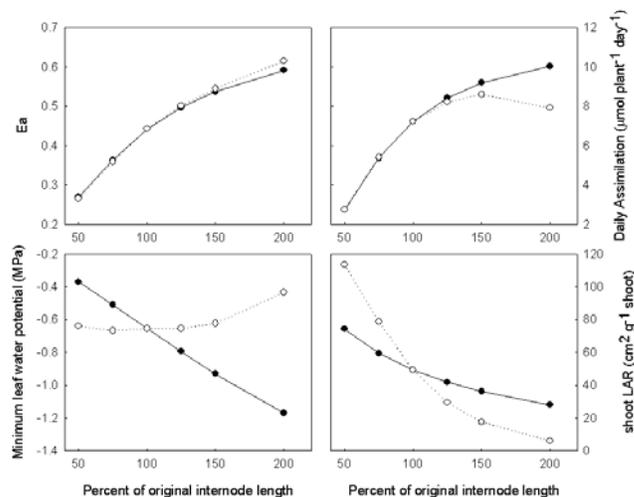


Figure 2. Effect of increasing internode length on E_a , daily assimilation, minimum leaf water potential and shoot leaf area ratio (LAR). Closed circles are for increasing internode length alone; open circles are for also increasing diameter to maintain biomechanical support. Simulations are with a *P. marginata* plant; results with other plants were similar.

Since light capture is but one of the multiple functions of plant crowns we asked whether other functions might be constraining E_a to seemingly rather low values. Reduction of self-shading would require a spreading of the crowns through, for example, longer internodes to give less leaf overlap. However, this spreading would entail significant biomechanical and hydraulic efficiency costs. For two contrasting species, *Psychotria marginata*, a widely distributed, shade tolerant species, and *P. brachiata*, a gap dependent species occurring in moist sites, we simulated a change in biomass partitioning between internodes and leaves such that as internodes length (mass) increased leaf size (mass) decreased. We also computed the increase in internode diameter and therefore the mass required to maintain constant branch deflection. We then also simulated the drop in water potential due to the change in hydraulic conductivity as diameters, lengths and leaf areas (hence transpiration) varied. Increasing internode length decreased self-shading and increased E_a and CO_2 assimilation but also caused stem water potential gradients to be significantly greater. When internode diameter was

increased to maintain constant biomechanics an optimum internode length in terms of CO₂ assimilation was apparent but this optimum was at 150 to 200% of the observed lengths. If diameter was increased sufficiently for maintenance of biomechanical support, then water potential gradients actually decreased below those of the natural plants. Thus, biomechanical support and not hydraulics appeared to be the primary constraint. Increasing biomechanical support as internode length increased was found to be very costly and significantly constrained growth rate. We conclude that the high costs of biomechanical support are a significant constraint on E_a in these plants.

In Mediterranean-climate environments in California, the problem is not too little solar radiation but excessive radiation coupled with high temperatures and water stress. In these environments, selection could be expected to favor architectures that minimize stresses through reduction in solar radiation absorbed. We have studied the role of architecture of two contrasting species *Heteromeles arbutifolia* and *Arbutus menziesii*. Both are shrubs to typically multi-stemmed small trees. Although their ranges overlap, leading to co-occurrence, *Heteromeles* is more common in warmer, more arid interior sites supporting chaparral communities whereas *Arbutus* principally occurs in cooler, higher elevation and more coastal sites supporting broad-leafed evergreen forests. Measurements were made on branch units as a more convenient scale than whole shrubs since it was shown that shading within branches is more important in *Heteromeles* crowns than shading between branches (Valladares and Percy, 1999). Both species have a spiral phyllotaxy but in *Arbutus* the relatively few large horizontal leaves are clustered near the branch tips whereas in *Heteromeles* the smaller leaves have steeper leaf angles and occur along a longer stem section. 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* exhibits if anything a slight reduction in midday due to its steep leaf angles

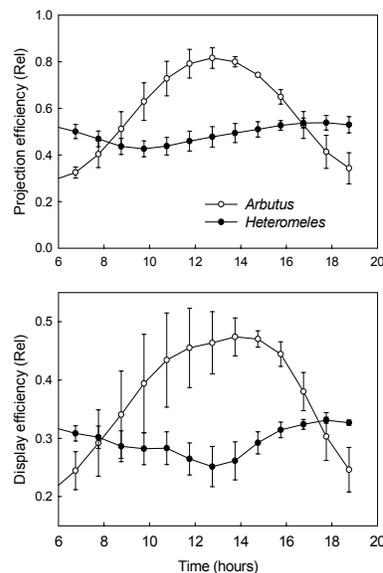


Figure 3 (left) Projection and display efficiencies for *Heteromeles* and *Arbutus* shoots. (below) Y-plant images of *Heteromeles* and *Arbutus* shoots displayed to relative scale. The dark areas indicate self-shading from the viewpoint.

Heteromeles arbutifolia



Arbutus menziesii



We examined the roles of leaf angle and self-shading in mitigating stresses by simulating the diurnal course of CO₂ assimilation and the potential photoinhibition from downregulation of photosystem II that could result from excessive light interception. Simulations for both species exhibited a typical mid-morning maximum of CO₂ assimilation and a midday depression due to supra-optimal temperatures and stomatal closure because of high vapor pressure deficits (Fig. 4). We simulated the consequences of photoinhibitory down regulation of photosystem II by first computing a weighted photon flux density on the leaf surface over the previous 6 hours, which is a strong predictor of the fluorescence ratio Fv/Fm (Ögren and Sjöström 1990; Valladares and Pearcy, 1999). We then reduced the quantum yield and the curvature factor for the light response of photosynthesis in proportion to the reduction in Fv/Fm in order to simulate the effect of photoinhibitory down regulation of PSII. The simulations revealed a strong reduction in Fv/Fm in *Heteromeles* and a somewhat lesser reduction in *Arbutus*; those in *Heteromeles* agreed well with diurnal measurements (Valladares and Pearcy, 1999). Since the reduced quantum yield and curvature primarily affected photosynthesis in the shaded portions of the crown (Fig. 4), the simulated shoot carbon gain was reduced by only about 2-3 %. As compared to *Heteromeles*, leaf temperatures in midday were 2-3 °C warmer in *Arbutus* because of its larger, more horizontal leaves.

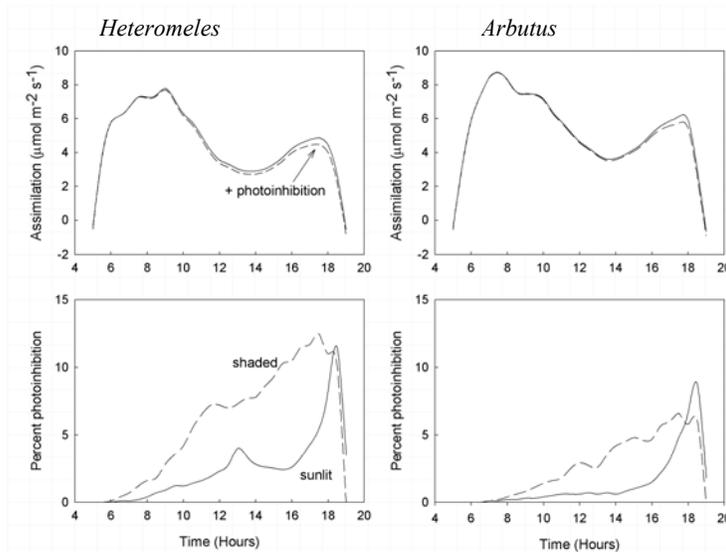


Figure 4. Top: Simulated diurnal courses of CO₂ assimilation with (dashed lines) and without photoinhibition (solid line). Bottom: Percentage reduction in assimilation for the sunlit (solid line) and shaded (dashed line) parts of the leaves

The role of leaf angles and self shading in the structural photoprotection of *Heteromeles* shoots were investigated by changing leaf angles in the simulated shoots and by comparing leaves simulated in isolation (no self-shading) to intact shoots (Fig. 5). These simulations revealed that the self-shading afforded by the shoot architecture provide structural photoprotection by minimizing the cumulative light dose on the leaf surface. Additionally, the steep leaf angles provided further structural photoprotection.

In conclusion, Psychotrias in the understory did not achieve an optimal canopy architecture for light capture because of the constraints imposed by biomechanical support requirements. This is in contrast to findings with an understory herb where

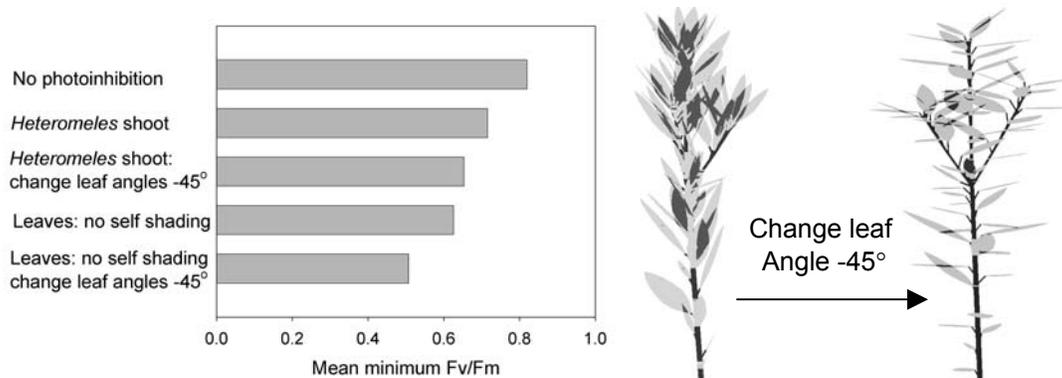


Figure 5. The mean Minimum Fv/Fm ratios in diurnal simulations either with a *Heteromeles* shoot or with individual leaves, resulting in no self shading. The values for individual leaves are the means of four leaves at N, E, W, and S azimuth orientations at the mean leaf angle (58°) or with the leaf angle reduced by 45°

observed petiole lengths were apparently optimal for maximizing light capture and carbon gain (Percy and Yang, 1988). An optimal architecture taking into account the multiple functions and objectives in crown design may well exist in the Psychotrias, but identifying it will require new optimization techniques (Farnsworth and Niklas, 1995). For *Heteromeles* in arid environments shoot architecture appears to function to provide structural photoprotection and to minimize other stresses such as leaf over temperatures during hot weather. Despite its essentially horizontal leaf display, *Arbutus* appeared to be well protected from photoinhibition but may be limited by higher leaf over temperatures.

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