

The Adaptive Geometry of Trees Revisited

Thomas J. Givnish*

Department of Botany, University of Wisconsin–Madison, Madison, Wisconsin 53706

Submitted September 10, 2019; Accepted December 10, 2019; Electronically published April 7, 2020

ABSTRACT: *The Adaptive Geometry of Trees* had an important conceptual influence on plant ecology and helped inspire many new approaches to understanding succession, plant adaptation, and plant competition. Its central model provided an elegant potential explanation for how optimal canopy form should shift with ecological conditions, change those conditions through time, and thus help drive succession and be a consequence of it. Yet on close examination, this deeply inspirational model does not lead to the predictions for which it is widely known. Here I show that the Horn model actually favors monolayer canopies over multilayers under all light conditions if relative growth rate (growth per unit investment) is maximized. Horn's conclusion that multilayers would be favored over monolayers in brighter sites is an artifact. I propose that self-shading multilayers might gain an advantage in brightly lit sites by reducing water loss, reducing the costs of branch construction and maintenance, reducing photoinhibition, increasing light capture in sidelight microsites, and increasing water and nutrient supplies (or leaf longevity) when combined with one or more of the previous potential advantages. I conclude with a brief discussion connecting Horn's model to other conceptual frameworks in plant ecology and outlining possible future extensions.

Keywords: adaptation, monolayer, multilayer, growth maximization, optimality theory.

The greatest homage that can be paid to an empirical theory is the constructive criticism that makes it obsolete at an early age. (Horn 1971, *The Adaptive Geometry of Trees*)

Nearly half a century ago, Horn (1971) used two simple principles—the nonlinear response of photosynthesis to photon flux and the filtering of sunlight within tree canopies—to explain why early-successional trees in temperate deciduous forests often scattered their leaves in multiple layers (e.g., birch, aspen) while late-successional species often packed their leaves in a single, densely packed layer (e.g., beech, hemlock; fig. 1). He argued that these differ-

ences in canopy geometry maximized carbon acquisition under sunny versus shady conditions, that as a result multilayers would have a growth advantage early in succession and monolayers an advantage later, and that the density of shade cast by forests would perforce increase through time after canopy closure. *The Adaptive Geometry of Trees* was a seminal and highly creative contribution to plant ecology, explaining how optimal plant form should shift with ecological conditions, change those conditions through time, and thus both help drive succession and be a consequence of it.

Horn's slender book had an outsized influence on thinking about optimality theory, plant competition, and succession, racking up 1,224 citations (Google Scholar, April 2019), including many by influential publications (e.g., Grime 1979; Givnish 1982, 1988; Tilman 1987, 1994; Canham et al. 1990, 1994; Pacala et al. 1996; Weiher et al. 1998; Westoby et al. 2002 [all cited >275 times each]). For those of us reading it at the time, *The Adaptive Geometry of Trees* was highly stimulating because it showed how simple principles might lead to quantitative predictions of how competitively optimal plant form should vary with environmental conditions, providing potential explanations for species distributions in time and space, trait-environment correlations, and temporal and spatial patterns in plant community composition and structure—themes that all of the authors just cited explored in depth.

Yet Horn's model is, in terms of its original formulation, flawed, and it does not yield the predictions for which it is widely recognized. This fact has escaped all notice, and it removes the only explanation we had for the early dominance of multilayers and the later dominance of monolayers in temperate forest succession. Here I briefly lay out the problem and outline a number of other factors that may instead drive the multilayer-monolayer shift.

Horn's (1971) model assumes horizontal leaves, a stationary sun directly overhead, no wind or clouds, a non-reflective forest floor, and a closely packed forest canopy that eliminates sidelighting. There are two central assumptions. The first is that net photosynthesis P shows a Michaelis-Menten response to incident photon flux density

* Email: givnish@wisc.edu.

ORCID: Givnish, <https://orcid.org/0000-0003-3166-4566>.

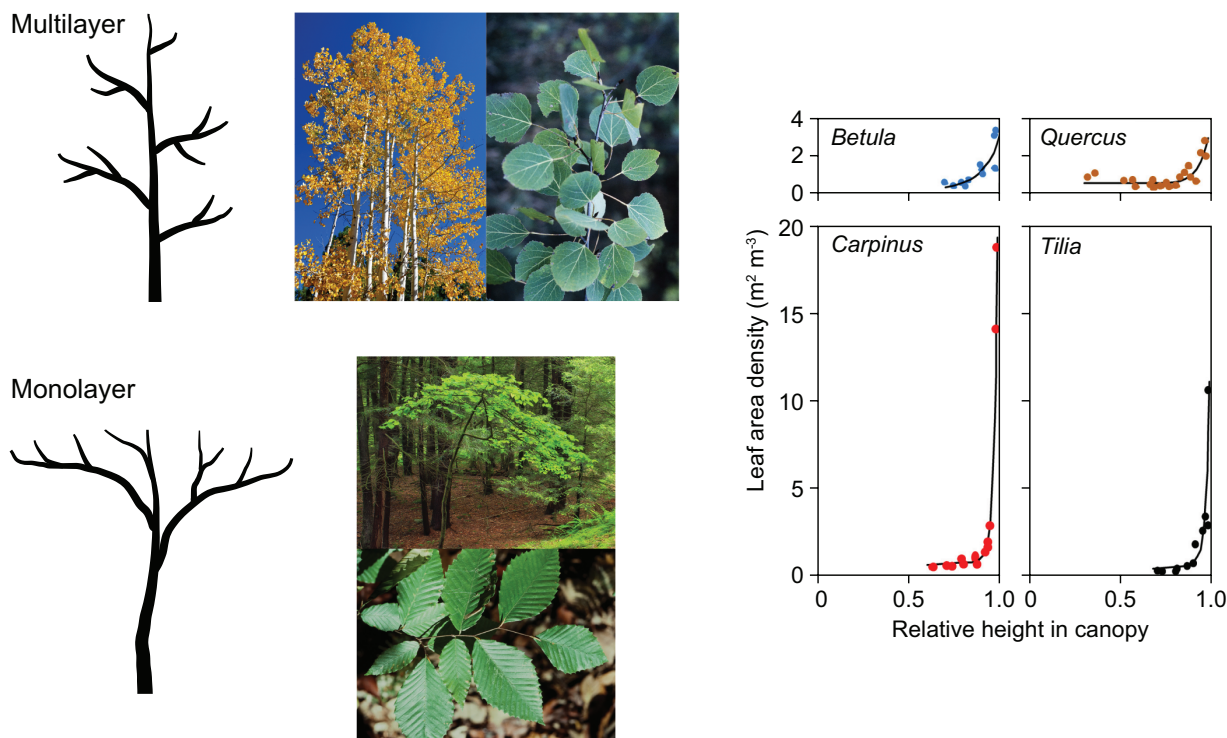


Figure 1: Multilayer and monolayer phenotypes. *Left to right:* Drawings of typical differences in branching pattern, with several vertically overlapping branches in multilayers and a shell of branches in monolayers; multilayered canopy of early-successional, sun-adapted quaking aspen (*Populus tremuloides*) from Colorado versus monolayered canopy of late-successional, shade-adapted witch hazel (*Hamamelis virginiana*), an understory tree in a Pennsylvania forest; orthotropic shoot (with erect axis and leaves scattered in loose spirals) of quaking aspen (orthotropy is characteristic of many multilayered trees and is adapted for energy capture and canopy growth in sunny environments [Givnish 1995]) versus plagiotropic shoot (with horizontal axis and leaves packed tightly in two horizontal ranks) in American beech (*Fagus grandifolia*; plagiotropy is characteristic of many monolayers and is adapted for energy capture and canopy growth in shady environments [Givnish 1995]); and plots of leaf area density as a function of relative height in the canopies of four tree species in temperate German forests (Hagemeier and Leuschner 2019). Shade-tolerant, late-successional *Carpinus betulus* and *Tilia cordata* strongly concentrate their foliage in a single layer, while shade-intolerant, early-successional *Betula pendula* and *Quercus petraea* scatter their foliage more evenly across several layers. Note, however, that all species shown hold their leaves in multiple layers and that the total leaf area index (m^2 leaves m^{-2} ground area occupied) is slightly lower in the multilayers, contrary to the Horn model. The photograph of quaking aspen was taken by Brady Smith, USDA Forest Service, Coconino National Forest, and the photograph of witch hazel was taken by Nicholas A. Tonelli; both images are available for reproduction via Wikimedia Commons (CC BY-2.0). The photographs of shoots of quaking aspen and American beech were taken by the author.

I (PFD; μmol photosynthetically active radiation $\text{m}^{-2} \text{s}^{-1}$) with half-saturation at $I = k$, dark respiration R , and asymptotic approach to $P_{\max} - R$:

$$P = \frac{P_{\max} I}{(I + k) - R}. \quad (1)$$

The second is that the PFD penetrating the canopy to a given depth obeys Beer's law:

$$I = I_0 \exp\left(-\int F(h) dh\right), \quad (2)$$

where I_0 is the PFD at the top of the canopy, $F(h)$ is the fraction of ground covered by leaves at height h , and the

integral is taken from the top of the canopy to the desired depth. All parameters used in this article are listed in table 1.

Given these constraints, Horn (1971) asks which of two trees occupying a given ground area A —a monolayer, with leaves packed in a single shell, or a multilayer, with leaves scattered over several layers—will have the highest total carbon gain $G = \int AP(h)F(h) dh$, integrated from the top to the bottom of the canopy. The best monolayer under these conditions involves complete coverage of a single layer and has a total return of

$$G = A \left(\frac{P_{\max} I_0}{(I_0 + k) - R} \right). \quad (3)$$

**Typesetter error
see final page
for correct form
used in
calculations**

**Typesetter error
see final page
for correct form
used in
calculations**

Table 1: Parameters used in this article

Parameter	Description
P	Net photosynthetic rate per unit leaf area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
P_{\max}	Maximum gross photosynthetic rate per unit leaf area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
k	Photon flux density that results in half-saturation of net photosynthesis in the Michaelis-Menten model ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)
R	Respiration rate per unit leaf area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
C	Instantaneous light compensation point ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)
I	Photon flux density in the photosynthetically active spectrum ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)
I_0	Photon flux density at the top of a plant's canopy ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
$P(h)$	Net photosynthetic rate as a function of leaf height ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
$P(I)$	Net photosynthetic rate as a function of photon flux density ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
$F(h)$	Fraction of ground area occupied by horizontal leaves at height h (unitless)
A	Ground area occupied by a plant canopy (m^2)
G	Total instantaneous carbon gain for a plant canopy ($\mu\text{mol CO}_2 \text{ s}^{-1}$)
LAI	Leaf area index (m^2 leaf area m^{-2} ground area)
L	Total leaf area (and mass) of a canopy (m^2 leaf area or g leaf mass)
α	Cost of leaf construction (g $\text{CO}_2 \text{ m}^{-2}$ leaf)
Ω	Net photosynthetic return per unit investment per unit time (s^{-1})
LMA	Leaf mass per unit area (g leaf tissue m^{-2} leaf tissue)
SLA	Specific leaf area = $1/\text{LMA}$ (m^2 leaf tissue g^{-1} leaf tissue)
B	Annual cost of branch construction for a monolayered canopy
B'	Annual cost of branch construction for a multilayered canopy
Λ	Branch length = canopy radius (m)
b	Allometric exponent relating branch construction cost to branch length
m	Number of leaf layers in a multilayered tree canopy

According to Horn's model, the optimal multilayer under the same conditions will add leaves to the bottom of the canopy until the return P goes to zero at the instantaneous leaf compensation point $C = Rk/(P_{\max} - R)$, resulting in a total return of

$$G = A \left(P_{\max} \ln \left(\frac{I_0 + k}{C + k} \right) - R \ln \left(\frac{I_0}{C} \right) \right). \quad (4)$$

When G per unit ground area is plotted against incident PFD for a monolayer and multilayer for plants with the same photosynthetic parameters, the curves cross, with the optimal monolayer having an energetic advantage at low I_0 and the optimal multilayer having an advantage at high I_0 (fig. 2). Furthermore, the optimal multilayer will hold a greater leaf area index (LAI; ratio of leaf area to ground area occupied) the greater the amount of light at the top of the canopy. Given Beer's law, $I_0 \exp(-\text{LAI}) = C$, where C is the instantaneous leaf compensation point (see above). Consequently, according to Horn's model, the optimal LAI (leaf area per unit ground area, $\text{m}^2 \text{ m}^{-2}$ [unitless]) for an individual tree crown would be

$$\text{LAI} = -\ln \left(\frac{C}{I_0} \right) = \ln I_0 - \ln C, \quad (5)$$

implying that optimal LAI should increase with the logarithm of light availability.

Canopy geometries that return more energy under a given set of conditions are assumed to yield a competitive advantage under those conditions. According to Horn (1971), monolayers have an advantage in low light because they exhibit no self-shading, which would decrease or negate photosynthesis under shady conditions (eq. [1]); multilayers have an advantage under brighter conditions because they can maintain several layers of leaves ($\int F(h) dh > 1$) at full or at least nonnegative rates of net photosynthesis. Horn (1971) uses this model to predict that multilayers will dominate early succession, soon after a disturbance removes the canopy and creates sunny conditions, but that as those plants grow and shade the ground they favor saplings below them with fewer and fewer layers, more and more densely packed, so that canopy geometry tends increasingly toward monolayers and understory shade increases through succession.

The fundamental but previously unrecognized problem with this model—in both its mathematical and verbal form—is that it involves a comparison between big plants (multilayers) with lots of leaf tissue and small plants (monolayers) with much less. If we instead ask whether a monolayer or a multilayer will yield a greater photosynthetic return for a given total investment in leaf mass (assumed proportional to leaf area), then we have to divide G in equations (3) and (4) by total leaf mass. If, for simplicity,

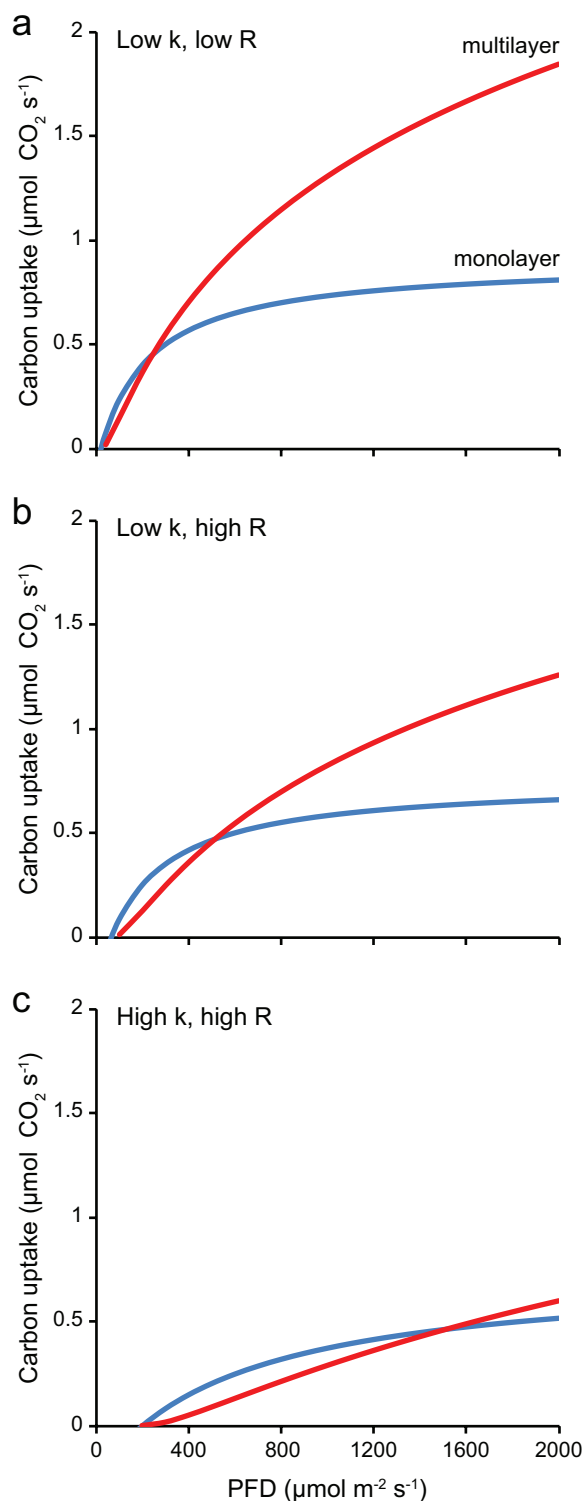


Figure 2: Sample calculations of photosynthetic returns per unit area for optimal monolayers (red) and multilayers (blue) as a function of photon flux density (PFD), based on the Horn (1971) model. All assume that $P_{\max} = 1$; for A, $k = 200$, $R = 0.1$; for B, $k = 200$, $R = 0.25$; and for C, $k = 600$, $R = 0.25$. Note the crossover in the

we choose our units so that $A = 1$ and leaf mass per unit area = 1, then an optimal monolayer will have a total leaf area (and mass) $L = 1$, while the optimal multilayer will have total leaf area (and mass) defined by $C = I_0 \exp(-L)$ (eq. [1] and Horn's optimality criterion of $P = 0$ at the bottom of a multilayer). Dividing G by L to get the photosynthetic return on a given investment ($\text{g CO}_2 \text{ g}^{-1} \text{ leaf day}^{-1}$)—a key determinant of whole-plant relative growth rate ($\text{g g}^{-1} \text{ plant day}^{-1}$; e.g., see Kruger and Volin 2006)—we invariably find that monolayers outperform multilayers at all light levels (fig. 3). There is no crossover; monolayers always win.

Cutting through all the equations, it is easy to see why. If we assume a Michaelis-Menten photosynthetic response to light (eq. [1]) and self-shading within a multilayer's canopy, each unit area (or mass) of leaf can do no better than a leaf at the top of a monolayer's canopy and will often do substantially worse. Consequently, monolayers always win, often by a proportionally very large amount (fig. 3). Generally, the bigger k is and the greater R is relative to P_{\max} , the bigger the advantage of monolayers when the costs of leaf construction are ignored; large values of k and R increase the negative effect of self-shading on the return on investment of the lower leaves. However, when leaf construction costs are included, monolayers are favored over multilayers regardless of the relative magnitude of k and R . If α is the cost of leaf construction ($\text{g CO}_2 \text{ m}^{-2} \text{ leaf}$), then G/L is proportional to $G/(\alpha L)$, the ratio of return rate to initial cost (which we used above as a growth metric), and is linearly related to net energetic return per investment per unit time: $\Omega = (G - \alpha L/T)/\alpha L = G/\alpha L - 1/T$, where T is leaf longevity and $\alpha L/T$ is the cost of constructing a unit area of leaf, amortized over its lifetime but not taking into account opportunity costs (see Givnish 1984; Givnish et al. 2004).

This approach to assessing optimal canopy geometry, based on optimizing the returns on a given energetic investment, is similar to the one I used to reanalyze the classic data of Björkman et al. (1972) on photosynthetic adaptation of individual leaves to high, intermediate, and low PFDs (fig. 4; Givnish 1988). Björkman et al. (1972) used measurements of photosynthesis per unit leaf area as a function of PFD— $P(I)$ —for leaves of *Atriplex triangularis* grown at $I = 920, 290$, and $92 \mu\text{mol m}^{-2} \text{ s}^{-1}$ to show that those response curves crossed and to make the paradigmatic argument that, as a result, the differences in acclimation shown were adaptive, with plants grown at low light having an energetic advantage at low light levels, those grown at intermediate light having an advantage

curves, with monolayers having an advantage at low PFD and multilayers having an advantage at high PFD, with the crossover point increasing with k and R .

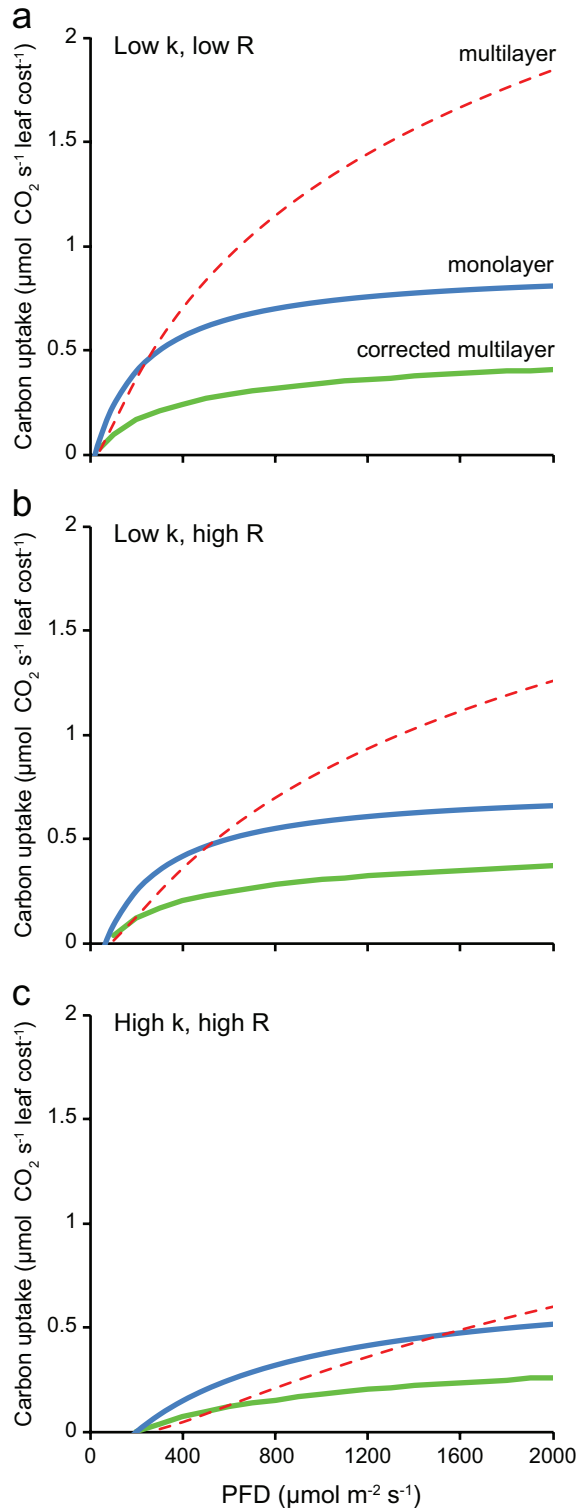


Figure 3: Sample calculations of photosynthetic returns per unit leaf investment (assumed to be 1 per unit area here) for optimal monolayers (green) and multilayers (blue) as a function of photon flux density, based on the model presented in this article. Multilayer photosynthesis per unit area (dashed red line) based on the

at intermediate light levels, and those grown at high light having an advantage at high light levels. The problem is that Björkman et al. (1972) blurred the distinction between what they defined as “Low,” “Intermediate,” and “High” light—the specific PFDs at which the plants were grown and supposedly adapted—and low, intermediate, and high light ranges in general. Givnish (1988) showed that there was no evidence for leaves acclimated to low or intermediate light levels having higher photosynthetic rates at those specific levels. However, there is no reason why photosynthesis per unit leaf area should yield an energetic or growth advantage per unit investment, given that area per se has little or no cost and that leaves acclimated to higher light levels have greater mass per unit area (LMA ; g m^{-2}) and higher N concentration ($\text{mg N g}^{-1} \text{ leaf}$). Only when photosynthesis is expressed per unit leaf mass or per unit soluble protein (main component of leaf N) do we see clear evidence for an energetic advantage of different kinds of leaves at the light levels at which they were developed (fig. 3).

In the case of *Atriplex* leaf acclimation, there are superficial parallels to Horn’s ideas regarding the advantages of multilayers and monolayers, given that the leaves acclimated to brighter light are thicker (although this trend may be general only in temperate deciduous plants, given that shade tolerance should often increase with leaf longevity [Givnish 1988, 2002] and some highly shade-tolerant tropical understory plants have long-lived, thick, tough leaves [Coley 1983; Santiago and Wright 2007]). But greater leaf thickness—and greater mass per unit area and number of layers of chlorophyllous cells—in *Atriplex* leaves from brighter conditions are also coupled to greater leaf soluble protein content per unit mass and greater stomatal conductance. The data presented by Givnish and Montgomery (2014) on photosynthetic light responses of Hawaiian lobeliads—arguably the strongest case to date for interspecific leaf-level adaptation to different light levels, with crossover in mass-based light response curves—show instead an increase and then a decrease in leaf mass per unit area with native PFD among the species with the highest photosynthetic rates at increasing PFDs.

Generally, among plants in sunny environments, leaf mass per unit area decreases with leaf nitrogen concentration and increases with leaf longevity (Reich et al. 1998; Wright et al. 2004); often, quite thick and long-lived leaves are seen in evergreen C_3 treelets found in the densely shaded understories of tropical rain forests (Bruy et al. 2018). Greater leaf longevity can increase shade tolerance—and make the long-term returns from even cells deep within a densely shaded leaf positive—by amortizing

Horn model is shown for comparison. The same parameter values for P_{max} , k , and R were used as in figure 1. Note that return on investment is always greater for monolayers.

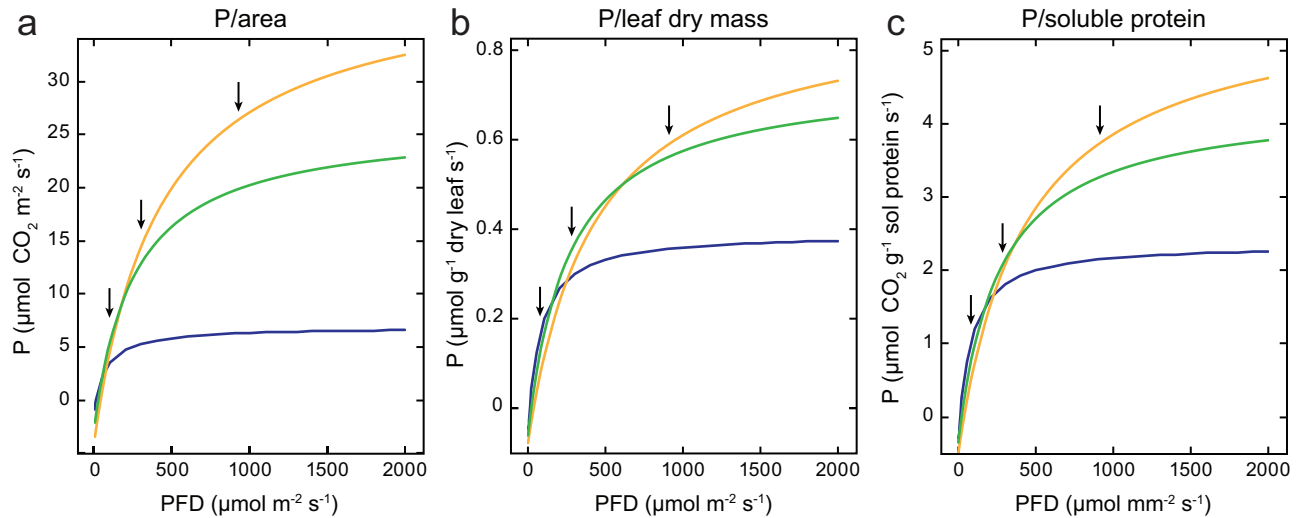


Figure 4: Photosynthesis as a function of photon flux density (PFD) in *Atriplex triangularis*, expressed as daily carbon balance per unit leaf area (a), mass (b), and soluble protein content (c; based on calculations of Givnish 1988). Within each graph, arrows indicate the specific high, intermediate, and low PFDs to which leaves were acclimated (920 , 290 , and $92 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). In each graph, leaves acclimated to high PFD have the greatest photosynthetic rates at high irradiance levels, those acclimated to intermediate PFD have intermediate rates, and those acclimated to low PFD have the lowest rates. However, leaves acclimated to a given irradiance have the greatest photosynthetic rate at that irradiance in all cases only if photosynthesis is expressed per unit investment in mass or soluble protein (Givnish 1988).

construction costs over long periods (Givnish 2002). Leaf thickness often increases toward drier environments among evergreen species (Orians and Solbrig 1977; Givnish et al. 2014), but deciduous species in such environments can have quite thin leaves (Grubb 1992). Thus, a simple one-to-one mapping of PFD to leaf mass per unit area (and, often, leaf thickness) does not exist and cannot be used to support Horn's original model by analogy.

We are left with a paradox: Horn's model, when corrected, predicts that monolayers should have an advantage across all stages of succession, from open to fully closed sites, yet multilayered birches, poplars, and willows do dominate early succession. While Horn's original model is flawed, his method for quantifying the number of leaf layers within tree crowns at different stages of succession remains solid, but it should be complemented with measures of total LAI. We are left, however, with the central question: What factors might give multilayers an advantage, and why would they do so under brightly lit conditions especially?

Several factors might yield a energetic advantage for multilayered canopies: (1) reductions in water loss and the associated costs of root and xylem investment or photosynthesis foregone, (2) savings in the costs of constructing and maintaining branches, (3) reduced photoinhibition in lower leaf layers, (4) adaptation to sidelit microsites, and (5) greater supplies of water and/or soil nutrients (or greater leaf longevity) when combined with one or more

of the previous potential advantages. All of these could provide an advantage to multilayers, even when their LAI is the same (or even less) than that of co-occurring monolayers—a circumstance that can arise as a result of sparse coverage within individual layers of multilayers (see fig. 1) and that would be fatal to the original Horn model.

Factor 1: Reduced Water Loss

The shaded leaves lower in multilayered canopies in sunlit sites will be exposed to a far lower heat load than leaves at the top of the canopy as well as cooler air temperatures, greater humidity, and lower wind speeds, all caused partly by the leaves higher in the canopy. As a result, transpiration should be greatly curtailed lower in a multilayered canopy while photosynthesis will be less affected, given the saturating response of carbon uptake to PFD (eq. [1]). Reductions in water loss could yield substantial energetic savings and increase whole-plant growth compared with a monolayer having identical physiological characteristics, by reducing the costs of root and xylem construction or by increasing leaf water potential at a given root and xylem allocation and thereby increasing photosynthesis via effects on stomatal conductance or mesophyll photosynthetic capacity (Givnish 1979, 1986; Tang et al. 2002; Brodribb and Holbrook 2003; Tezara et al. 2003; Lawlor and Tezara 2009; Scoffoni et al. 2018). Several of the models mentioned use the concept of "transpirational costs" or the "cost of water

loss”—in terms of the required allocation to roots, depression of cellular photosynthetic capacity, or a limited daily total of transpiration—introduced by Givnish and Vermeij (1976) and Cowan and Farquhar (1977) to account for global patterns in leaf size and stomatal conductance; transpirational costs should also be considered in evaluating the impact of canopy geometry on plant growth.

Horn (1971) himself recognized that multilayers would have lower water requirements than monolayers but viewed that as an additional benefit of a multilayered canopy, not the principal driver favoring such a canopy. Forty-nine years ago, Horn did not understand how water shortage could be made commensurate with carbon gain and reduce whole-plant growth, nor did he see the fundamental problem for his light-centered theory created by the fact that multilayers would have lower energetic returns on investment than monolayers at all light levels. I suggest that water economy may instead be one of a few prime drivers favoring multilayered canopies. Their apparent disadvantage in photosynthesis (fig. 3) may be offset, in terms of effects on whole-plant growth, by savings in root and xylem costs or by greater realized carbon uptake due to higher stomatal conductance and/or mesophyll photosynthetic capacity as a result of operating at higher leaf water potentials. Brighter conditions would favor plants with greater LAI both by creating greater heat loads and evaporative demands, thus increasing the benefits of self-shading, and by reducing the photosynthetic disadvantage of some lower, partly shaded leaves. Givnish (1984) made a directly related argument for why leaf bases of butterflyweed (*Asclepias tuberosa*) shift from being heart- to wedge-shaped in moving from sunny/dry sites to shadier/rainier sites along transects from Missouri to Pennsylvania and Virginia (Wyatt and Antonovics 1981). All leaf-base shapes have roughly equal widths and, thus, similar convective and water loss properties, but leaf arrangement along erect stems leads to greater self-shading and lower water loss if the leaf bases are heart-shaped and to less self-shading and greater water loss if they are narrowly wedge-shaped (Givnish 1984). The canopy near the stem has effectively more layers with cordate leaves, and such multilayered canopies occur in sunnier or drier habitats, as argued above for tree canopies.

To the extent that windier conditions or hotter temperatures increase transpiration of leaves in the upper canopy, we might expect them to favor greater numbers of leaf layers. Wider leaves also tend to increase transpiration under sunlit conditions, favoring more leaf layers, but this must be set against the shadows cast deeper into the canopy by such leaves, favoring fewer layers (see Horn 1971).

In either woody and herbaceous plants, after we take into account the benefits of water savings of multilayers for whole-plant growth, we might still apply Horn's optimality criterion of adding leaves to the lower part of the

canopy until no net return comes from them. However, the compensation point C —traditionally calculated only on the basis of instantaneous rates of net photosynthesis (see eqq. [1], [5])—must be adjusted to take into account nighttime leaf respiration, the costs of leaf construction amortized over leaf life span, and the costs of stem and root construction associated with new leaves amortized over a similar period (Givnish 1984, 1988, 2002). These costs increase the effective value of R and decrease the optimal LAI of multilayers. Such adjustments favor changes in the opposite direction to those expected on the basis of water savings mentioned in the previous paragraph, with greater root costs and lower maximum rates of photosynthesis per unit leaf elevating the ecological compensation point (Givnish et al. 2004) that incorporates all of the costs mentioned. The balance of these two effects should favor increased LAI with increased moisture, nutrient, or CO_2 supply under constant light conditions and decrease LAI in taller plants at sites of a given level of productivity. These patterns reflect the expected impact on optimal LAI of declines in the amortized cost of roots per unit leaf mass, increases in maximum photosynthetic rate, or increases in the amortized cost of stem tissue per unit leaf mass, respectively.

Globally, LAI of whole communities does tend to increase with precipitation (Specht and Specht 1989; Ellis and Hatton 2008; Donohue et al. 2013; Jin and Goulden 2014; Berner and Law 2015; Berner et al. 2017) and with the ratio of precipitation to potential evapotranspiration (Iio et al. 2014). Across a rainfall gradient in Oregon, LAI also increases with leaf N concentration (Pierce et al. 1994). Increased PFD at a given moisture supply should favor higher LAI if the resulting benefits of reduced water loss outweigh the downsides of maintaining shaded leaves low in the canopy under such conditions. We do not yet have a quantitative model to weigh those two factors against each other. However, the recent elegant analysis of Yang et al. (2018) might be modified to apply to individual plants rather than communities and to maximize the rate of carbon uptake per area per leaf investment per area—that is, the rate of carbon uptake per leaf investment—rather than simply the rate of carbon uptake per area. Yang et al. (2018) weigh the advantages of increasing LAI versus stomatal conductance (and, hence, photosynthesis) of individual leaves against each other, taking the cost of transpiration into account, and predict that LAI should (as observed) increase with the ratio of precipitation to potential evapotranspiration and with increasing CO_2 levels.

Factor 2: Reduced Branch Costs

Given that branch mass increases with the third to fourth power of branch length (King 1981), multilayers might

have an advantage in whole-plant growth in mass because they can support the same total leaf mass as a monolayer in a narrower crown with shorter branches that are individually—and, potentially, in aggregate—cheaper than those of the monolayer. If the yearly cost of an increment to a branch of length Λ is $\kappa\Lambda^b$ and a monolayer requires n such radial branches to support a total area $A = \pi\Lambda^2$ of closely packed leaves, its annual cost of branch construction would be $B = n\kappa\Lambda^b = n\kappa(A/\pi)^{b/2}$. By comparison, consider a multilayer with leaves that cover only half of each layer but bears the same aggregate leaf area A in m layers ($m > 2$), each having a total leaf area of A/m and involving a canopy area of $A/2m$. Its annual branch cost would then be $B' = mn\kappa(A/2m\pi)^{b/2} = 2^{-b/2}m^{1-b/2}B$. If $b/(2-b) < 2 \ln m / \ln 2$, a multilayer will have an annual cost of branch construction less than a comparable monolayer; this is true for all reasonable values of b and m and involves a relative savings of 50%–90% (fig. 5). Given that trees allocate roughly 35% of their annual biomass growth to branches and twigs (Givnish 1995), this savings should be a substantial fraction of whole-plant carbon uptake; savings in branch costs might thus also be a key factor favoring multilayered canopies.

In addition to an advantage in energy capture, a multilayered canopy that sheds lower branches while they are still short and redirects energy to the leader can have a big advantage in height growth (Horn 1971; Givnish 1988, 1995). Conversely, broader crowns and an emphasis on

horizontal spread can give monolayers an advantage in the shade well below a forest canopy but reduce the rate of height growth and the cost of replacing old, shaded branches (Givnish 1988, 1995).

Iwasa et al. (1984) formulated a game-theoretic model for the height distribution of foliage within tree crowns based on shading and its impact on photosynthesis as well as on the costs of vertical and horizontal branches for trees with a given total amount of foliage. They concluded that for stands of identical individuals, the evolutionarily stable strategy involved vertically tapering gradients of leaf area density for isolated trees and taller crowns with progressively more of the foliage held higher in the canopy at increasing tree density. The predicted canopies were thus all multilayers, not monolayers, and the cost of branches was a major driver. This model is a step in another useful direction and shows how the Horn model might also be modified to produce predictions favoring multilayers over monolayers under at least some conditions. However, ambiguities exist in the Iwasa et al. (1984) model regarding the relationship of total leaf area density to height above the ground and the crown diameter at that height, and excluding the substantial costs of transpiration and branch construction, the possibility of varying the total amount of leaf tissue per unit area, the calculation of rates of return per unit leaf and branch mass, and the opportunity costs associated with holding foliage low versus high in the canopy all leave openings for a great deal of interesting

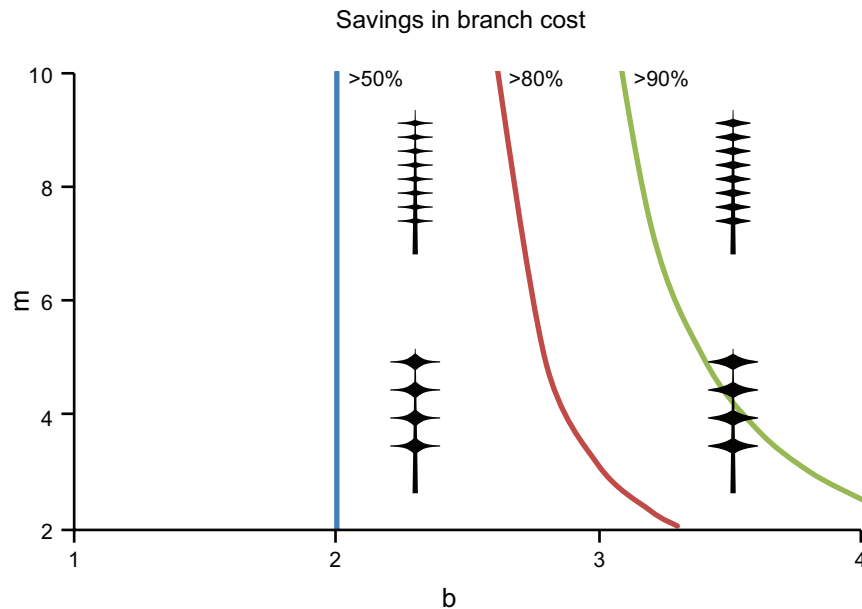


Figure 5: Percent savings of modeled branch costs as a function of the allometric branch exponent b and the number of branch layers m (see main text). Blue indicates savings of 50%, red indicates savings of 80%, and green indicates savings of 90%. As indicated by the tree diagrams, branch cost savings in multilayers increase as crown width declines, the number of branch layers increases, and (especially) as the power-law exponent relating branch cost to branch cost increases.

theoretical work to adapt the original Horn model and incorporate the impact of canopy geometry on water loss and the costs of roots and branching. One of the big questions is how the existence of such opportunity costs could ever permit plants to hold shaded leaves; the high inefficiency of nutrient retranslocation (only ~50% for N and P; see Zhang et al. 2018) and the complete abandonment of cellulose in shed leaves and twigs would almost surely be important.

Factor 3: Reduced Photoinhibition

Photoinhibition is a reduction in photosynthetic capacity caused by exposure to bright light and is especially likely and pronounced when temperature, nutrient availability, water shortage, or salinity limit carbon uptake and interrupt the ongoing process of photosystem II repair (Murata et al. 2007; Nishiyama and Murata 2014). Plants employ a variety of morphological and physiological mechanisms to protect against photoinhibition, including reduction of incoming radiation via steeply inclined or highly reflective leaves, leaf movement, chloroplast movement, and non-photosynthetic chlorophyll fluorescence quenching involving the zeaxanthin-violaxanthin cycle (Powles and Björkman 1982; Powles 1984; Demmig-Adams and Adams 1992; Osmond and Grace 1995; Ruban 2009, 2016). The possibility that a multilayer could benefit by protecting some of its lower leaves via self-shading is an intriguing possibility that appears never to have been recognized, let alone explored, theoretically or empirically. The potential benefits of multilayers would be greatest in sunny, open sites that are short on water or nutrients or are exposed to especially high or low temperatures. It is possible that photoinhibition might be important only at particular times of year; in this case, an important question becomes whether a greater or lesser number of leaf layers is favored by fluctuating conditions.

Factor 4: Adaptation to Sidelighting

Horn's model ignores the possibility of sidelighting because it assumes a stationary sun directly overhead and closely packed neighboring trees. However, Horn (1971) also noted that the low angle of the sun at high latitudes might favor steeply sided conical canopies in conifers in the boreal zone; sidelighting would, in other words, directly illuminate a canopy perpendicular to the sun's rays. Such a steeply conical canopy would be multilayered in the sense of having multiple branches that are superimposed vertically, but it would also effectively approach a monolayer oriented toward the sun. I would add that if vertically overlapping branches are sufficiently far apart, as louvers, sidelighting can illuminate leaves held in the interior of the

crown. Conical canopies and flexible limbs in conifers at high altitudes and latitudes also help shed snow (Horn 1971).

Kuuluvainen (1992) provided calculations demonstrating that—as long suspected (Horn 1971; Brünig 1976; Ashton 1978; Terborgh 1985)—broad, flat canopies intercept more light at lower latitudes and narrow, conical, and cylindrical canopies intercept more at higher latitudes. However, Oker-Blom and Kellomäki (1982), Kuuluvainen (1992), Vermeulen (2014), and Lindh et al. (2017) also realized that at high latitudes, lateral shading of trees due to low solar angles is important in dense stands. Vermeulen (2014) argued that as a result, the evolutionarily stable strategy for crown shape in the boreal zone should actually be umbrella-like in crowded stands and conical only in open, less well-stocked stands. Sidelighting might be important in favoring multilayered or pagoda-like canopies in tropical forests as well. In a Peruvian tropical lowland forest, Terborgh and Mathews (1999) compared two understory trees: *Rinorea viridiflora*, with whorls of vertically superimposed branches, and *Neea chlorantha*, with more vertically oriented branches. *Rinorea* was more common in microsites lit from low zenith angles, and their multilayered, pagoda-like canopies with superimposed branches were more efficient in intercepting light from lateral sources; *Neea* was more common in microsites lit from high zenith angles, and their canopies were more efficient in intercepting light from above.

Factor 5: Effect of Greater Moisture or Nutrient Supplies and Greater Leaf Longevity

As argued above, greater supplies of soil moisture and nutrients should favor greater LAI in early-successional trees exposed to full sunlight, partly by reducing the ecological compensation point of individual leaves. Increased leaf longevity should do the same thing by allowing leaf construction costs to be amortized over longer periods of time, thus reducing their costs per unit time (Givnish 1984, 1988, 2002). In temperate forests, evergreen foliage may be positively associated with shade tolerance in moist and/or relatively fertile sites (e.g., in *Abies*, *Ilex*, *Taxus*, and *Tsuga*), where substantial leaf longevity decreases the ecological compensation point, and negatively associated with shade tolerance on dry, infertile sites (e.g., in *Pinus*), where long-lived leaves are favored by resource shortage and almost surely associated with high root costs and a high ecological compensation point for individual leaves (Givnish 2002). Considerations of how a leaf's ecological compensation point should increase with soil moisture and fertility and decrease with plant height also naturally leads to predictions regarding how maximum tree height should increase along gradients of increasing moisture

supply versus demand, of increasing soil nutrients, and of decreasing disturbance rate (Givnish 1984, 1988; Givnish et al. 2014).

Moister or more fertile conditions (or greater leaf longevity) might also help favor greater LAI in early-successional or canopy trees because greater illumination would reduce the proportional disadvantage of self-shading (fig. 3). For this reason, greater PFD should favor greater LAI whenever any of the four other factors discussed above give multilayers an advantage.

Broader Issues

Horn's (1971) model for optimal canopy geometry helped shape thinking by a generation of plant ecologists. Like all ecological models, Horn's analysis obtained clarity and interpretability at the cost of reduced realism; there are many relevant factors that simply were not included in the monolayer-multilayer model. Specifically, that model did not include within-crown variation in leaf inclination and orientation, temperature, and photosynthetic capacity and photosynthetic light response; movement of the sun across the sky; shading by adjacent competitors; shading by a tree's own trunk and branches; costs of building and maintaining leaf, stem, and root tissue; and eddy transport of carbon dioxide through the canopy (Givnish 1988). Some of these are likely to have important effects and should be included in more sophisticated models; the preceding discussion shows how inclusion of tissue construction costs, solar angle, and crowding might affect predictions. Leaf inclination would, almost surely, greatly increase optimal LAI. With a stationary sun, leaves at the top of a sunlit canopy could be inclined so as to hold much more leaf area per unit ground area and—at least potentially—maintain full photosynthetic capacity while reducing transpirational costs per unit leaf area; this effect might be an important driver of observed patterns in community LAI, together with ecohydrological integration (see Yang et al. 2018).

King (1981) used the calculus of variations to answer a question that Horn (1971) articulated but was unable to tackle: How should trees allocate energy between the canopy and the supporting branches and trunk in order to maximize the rate of height growth? Quaking aspen (*Populus tremuloides*) operates very close to the optimal canopy-to-bole ratio (King 1981). Perhaps not surprisingly, the crown width-to-height ratio associated with maximum rates of height growth is similar to the mean ratio seen across crowded forest stands around the world, suggesting that maximization of height growth and associated tree allometry is a driver of the self-thinning law (Givnish 1986). Field (1983) analyzed how shifts in leaf photosynthetic properties—and especially leaf N content, which helps set those properties—with shading and leaf age should de-

termine the optimal pattern of N retranslocation within growing canopy and its implication for optimal leaf life span. This important idea has received extensive study (e.g., Kitajima et al. 1997, 2002, 2005; Anten and Ackerly 2001; Mediavilla and Escudero 2003; Wright et al. 2006), with the most recent definitive study by Reich et al. (2009) pointing to positive, instantaneous leaf-level carbon balances at the end of a leaf life spans—and thus the need to integrate nonleaf costs in predicting optimal leaf longevity, as argued by Givnish (1984, 1987, 2002).

Horn's observation that mid- and late-successional trees with few branch layers replace pioneers with larger numbers of branch layers may apply best only to temperate forests. Low-density stands (e.g., savannas, woodlands, partially open wetlands), in which only a small fraction of the ground is covered by tree canopies, would perforce increase sidelighting. Other things being equal, such low-density stands should favor more leaf layers within individual tree crowns. As noted earlier, trees (especially conifers) at high altitudes and latitudes often have conical canopies and flexible limbs to help shed snow; these inevitably tend to hold their leaves in multiple layers. Finally, in tropical forest succession, pioneers such as *Cecropia*, *Ochroma*, and *Macaranga* tend to have monolayered canopies with gigantic leaves held at low angles, while later-successional species often have multilayered canopies (at least in the sun) with smaller leaves held at higher angles (Bazzaz and Pickett 1980). The sun crowns of temperate pioneers *Betula* and *Quercus* hold their leaves at high angles, while those of later-successional *Carpinus* and *Tilia* hold their leaves at low angles (Hagemeier and Leuschner 2019). The possible advantage of gigantic simple or compound leaves as “throwaway branches” in sparsely branched, shade-intolerant pioneers (see Givnish 1979) is likely to be greatest in tropical forests that permit long periods of continuous development, are sheltered from seasonal frosts that might kill the one or few buds on which sparsely branched palms and treelets depend, and have high enough rainfalls and humidity to allow large, often very broad leaves to function. Large leaves cast massive shadows and perforce are likely to be arranged in monolayered crowns.

Reich et al. (1992) proposed that higher leaf N concentrations and specific leaf area (SLA; g m^{-2} leaf) lead to higher photosynthetic rates per unit leaf mass and, thus, to higher rates of overtopping, resulting in shorter optimal leaf life spans and the leaf economic spectrum of covariance in leaf N content, SLA, mass-based photosynthetic rate, and leaf life span, a generality of great ecological importance (Reich et al. 1997; Wright et al. 2004; Shipley et al. 2006; Santiago 2007; Donovan et al. 2011; Sack et al. 2013; Asner et al. 2016; Anderegg et al. 2018). The observed tie of leaf photosynthetic capacity per unit

area with vein density and leaf hydraulic conductance (Brodribb et al. 2007; Sack and Scoffoni 2013; Scoffoni et al. 2015, 2016)—driven by the inevitable coupling of water loss with CO₂ uptake—has led in turn to the recognition of a three- to fourfold increase in angiosperm photosynthetic capacity between 140 and 100 million years ago, based on observed shifts in vein density in fossil leaves (Boyce et al. 2009; Brodribb and Feild 2010). This shift is likely to have increased global rainfall due to increased rates of plant transpiration (Boyce et al. 2009) and to have helped trigger massive species diversification in the angiosperms well after their origin, based on selection for chemically diverse but cheap qualitative defenses (toxins) to defend leaves with high photosynthetic capacity (Givnish 2010).

Horn (1971) has thus, directly and indirectly, had a profound influence on our understanding of plant ecology and evolution. Even this article—representing a major reworking of Horn's model and a proposal of alternative explanations for the patterns in tree canopy geometry that Horn rightly recognized but incorrectly explained—would not have been possible without his original, lucid, inspirational analyses. Inspiration is often overlooked as one of the most important contributions that a scientist can make. For those who came of age in the 1950s, 1960s, and 1970s, few works inspired as many of us to pursue careers in plant ecology and evolutionary biology as Corner's (1949, 1953, 1954a, 1954b, 1966) durian theory, Horn's (1971) adaptive geometry of trees, and Stebbins's (1974) broad schema of angiosperm evolution above the species level. Each of these proved to be flawed, to a greater or lesser extent, factually and/or conceptually, yet they each added great excitement to their fields and drove many subsequent discoveries and new insights. This article is, accordingly, dedicated to the fond memory of Henry S. Horn—a great source of inspiration to me and many of my colleagues as well as to the field of plant ecology as a whole. Henry died in March 2019, actively engaged in scientific research to nearly his last breath.

Acknowledgments

This research was supported by National Science Foundation grant IOS-1557509 to T.J.G., Katherine McCulloh, Mark Adams, and Thomas Buckley. I would like to thank Jill Anderson, Robert Holt, Simon Levin, Chris Muir, Donald Waller, and an anonymous reviewer for their helpful comments. Sarah Friedrich polished the figures.

Literature Cited

- Anderegg, L. D. L., L. T. Berner, G. Badgley, M. L. Sethi, B. E. Law, and J. HilleRisLambers. 2018. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters* 21:734–744.
- Anten, N. P. R., and D. D. Ackerly. 2001. Canopy-level photosynthetic compensation after defoliation in a tropical understory palm. *Functional Ecology* 15:252–262.
- Ashton, P. S. 1978. Crown characteristics of tropical trees. Pages 591–615 in P. B. Tomlinson and M. H. Zimmermann, eds. *Tropical trees as living systems*. Cambridge University Press, Cambridge.
- Asner, G. P., D. E. Knapp, C. B. Anderson, R. E. Martin, and N. Vaughn. 2016. Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences of the USA* 113:E4043–E4051.
- Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11:287–310.
- Berner, L. T., and B. E. Law. 2015. Water limitations on forest carbon cycling and conifer traits along a steep climatic gradient in the Cascade Mountains, Oregon. *Biogeosciences* 12:6617–6635.
- Berner, L. T., B. E. Law, and T. W. Hudiburg. 2017. Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences* 14:365–378.
- Björkman, O., N. K. Boardman, J. M. Anderson, S. W. Thorne, D. J. Goodchild, and N. A. Pyliotis. 1972. Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Institute of Washington Year Book* 71:115–135.
- Boyce, G. K., T. J. Brodribb, T. S. Feild, and M. A. Zwienieki. 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society B* 276:1771–1776.
- Brodribb, T. J., and T. S. Field. 2010. Leaf hydraulic conductance led a surge in leaf photosynthetic capacity during early angiosperm evolution. *Ecology Letters* 13:175–183.
- Brodribb, T. J., T. S. Field, and G. Jordan. 2007. Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology* 144:1890–1898.
- Brodribb, T. J., and N. M. Holbrook. 2003. Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiology* 132:2166–2173.
- Brüning, F. T. 1976. Tree forms in relation to environmental conditions: an ecological viewpoint. Pages 139–156 in F. B. Golley, ed. *Tree physiology and yield improvement*. Academic Press, London.
- Bruy, D., T. Hattermann, L. Barrabe, A. Mouly, D. Barthelemy, and S. Isnard. 2018. Evolution of plant architecture, functional diversification and divergent evolution in the genus *Atractocarpus* (Rubiaceae) for New Caledonia. *Frontiers in Plant Science* 9:1775.
- Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20:620–631.
- Canham, C. D., A. C. Finzi, S. W. Pacala, and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests—interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24:337–349.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–234.
- Corner, E. J. H. 1949. The Durian theory or the origin of the modern tree. *Annals of Botany* 13:367–414.

Anderegg, L. D. L., L. T. Berner, G. Badgley, M. L. Sethi, B. E. Law, and J. HilleRisLambers. 2018. Within-species patterns challenge

- . 1953. The Durian theory extended—I. Phytomorphology 3:465–476.
- . 1954a. The Durian theory extended—II. The arillate fruit and the compound leaf. Phytomorphology 4:152–165.
- . 1954b. The Durian theory extended—III. Pachycauly and megaspermy—conclusion. Phytomorphology 4:263–274.
- . 1966. The life of plants. Weidenfeld & Nicholson, London.
- Cowan, I., and G. D. Farquhar. 1977. Stomatal function in relation to leaf metabolism an environment. Pages 471–505 in D. H. Jennings, ed. Integration of activity in the higher plants. Symposium of the Society of Experimental Biology. Cambridge University Press, Cambridge.
- Demmig-Adams, B., and W. W. Adams. 1992. Photoprotection and other responses of plants to high light stress. Annual Review of Plant Physiology and Plant Molecular Biology 43:599–626.
- Donohue, R. J., M. L. Roderick, T. R. McVicar, and G. D. Farquhar. 2013. Impact of CO₂ fertilization on maximum foliage cover across the globe's warm, arid environments. Geophysical Research Letters 40:3031–3035.
- Donovan, L. A., H. Maherali, C. M. Caruso, H. Huber, and H. de Kroon. 2011. The evolution of the worldwide leaf economics spectrum. Trends in Ecology and Evolution 26:88–95.
- Ellis, T. W., and T. J. Hatton. 2008. Relating leaf area index of natural eucalypt vegetation to climate variables in southern Australia. Agricultural Water Management 95:743–747.
- Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia 56:341–347.
- Givnish, T. J. 1979. On the adaptive significance of leaf form. Pages 375–407 in O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, eds. Topics in plant population biology. Columbia University Press, New York.
- . 1982. On the adaptive significance of leaf height in forest herbs. American Naturalist 120:353–381.
- . 1984. Leaf and canopy adaptations in tropical forests. Pages 51–84 in E. Medina, H. A. Mooney, and C. Vásquez-Yanes, eds. Physiological ecology of plants of the wet tropics. Dr. Junk, The Hague.
- . 1986. Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. Pages 171–213 in T. J. Givnish, ed. On the economy of plant form and function. Cambridge University Press, Cambridge.
- . 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytologist 106(suppl.):131–160.
- . 1988. Adaptation to sun vs. shade: a whole-plant perspective. Australian Journal of Plant Physiology 15:63–92.
- . 1995. Plant stems: biomechanical adaptations for energy capture and influence on species distributions. Pages 3–49 in B. L. Gartner, ed. Plant stems: physiology and functional morphology. Chapman & Hall, New York.
- . 2002. On the adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. Silva Fennica 36:703–743.
- . 2010. Ecology of plant speciation. Taxon 59:1326–1366.
- Givnish, T. J., and R. A. Montgomery. 2014. Common-garden studies on adaptive radiation of photosynthetic physiology among Hawaiian lobeliads. Proceedings of the Royal Society B 281:20132944.
- Givnish, T. J., R. A. Montgomery, and G. Goldstein. 2004. Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: light regimes, static light responses, and whole-plant compensation points. American Journal of Botany 91:228–246.
- Givnish, T. J., and G. J. Vermeij. 1976. Sizes and shapes of liane leaves. American Naturalist 110:743–778.
- Givnish, T. J., S. C. Wong, H. Stuart-Williams, M. Holloway-Phillips, and G. D. Farquhar. 2014. Determinants of maximum tree height of *Eucalyptus* along a rainfall gradient in Victoria, Australia. Ecology 95:2991–3007.
- Grime, J. P. 1979. Plant strategies, vegetation processes, and ecosystem properties. Wiley, Chichester.
- Grubb, P. J. 1992. A positive distrust in simplicity—lessons from competitions among plants and among animals. Journal of Ecology 80:585–610.
- Hagemeyer, M., and C. Leuschner. 2019. Functional crown architecture of five temperate broadleaf tree species: vertical gradients in leaf morphology, leaf angle, and leaf area density. Forests 10:265.
- Horn, H. S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, NJ.
- Iio, A., K. Hikosaka, N. P. R. Anten, Y. Nakagawa, and A. Ito. 2014. Global dependence of field-observed leaf area index in woody species on climate: a systematic review. Global Ecology and Biogeography 23:274–285.
- Iwasu, Y., D. Cohen, and J. A. Leon. 1984. Tree height and crown shape, as results of competitive games. Journal of Theoretical Biology 112:279–297.
- Jin, Y., and M. L. Goulden. 2014. Ecological consequences of variation in precipitation: separating short- versus long-term effects using satellite data. Global Ecology and Biogeography 23:358–370.
- King, D. 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia 51:351–356.
- Kitajima, K., S. S. Mulkey, M. Samaniego, and S. J. Wright. 2002. Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. American Journal of Botany 89:1925–1932.
- Kitajima, K., S. S. Mulkey, and S. J. Wright. 1997. Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. American Journal of Botany 84:702–708.
- . 2005. Variation in crown light utilization characteristics among tropical canopy trees. Annals of Botany 95:535–547.
- Kruger, E. L., and J. C. Volin. 2006. Reexamining the empirical relation between plant growth and leaf photosynthesis. Plant Functional Biology 33:421–429.
- Kuuluvainen, T. 1992. Tree architectures adapted to efficient light utilization: is there a basis for latitudinal gradients? Oikos 65:275–284.
- Lawlor, D. W., and W. Tezara. 2009. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. Annals of Botany 103:561–579.
- Lindh, M., D. S. Falster, L. Zhang, U. Dieckmann, and Å. Brännström. 2017. Latitudinal effects on crown shape evolution. Ecology and Evolution 8:8149–8158.
- Mediavilla, S., and A. Escudero. 2003. Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. New Phytologist 159:203–211.
- Murata, N., S. Takahashi, Y. Nishiyama, and S. I. Allakhverdiev. 2007. Photoinhibition of photosystem II under environmental stress. Biochimica et Biophysica Acta Bioenergetics 1767:414–421.
- Nishiyama, Y., and N. Murata. 2014. Revised scheme for the mechanisms of photoinhibition and its application to enhance the abiotic stress tolerance of the photosynthetic machinery. Applied Microbiology and Biotechnology 98:8777–8796.

- Oker-Blom, P., and S. Kellomäki. 1982. Theoretical computations on the role of crown shape in the absorption of light by forest trees. *Mathematical Biosciences* 59:291–311.
- Orians, G. H., and O. T. Solbrig. 1977. Convergent evolution in warm deserts: an examination of strategies and patterns in deserts of Argentina and the United States. Dowden, Hutchinson, & Ross, Stroudsburg, PA.
- Osmond, C. B., and S. C. Grace. 1995. Perspectives on photo-inhibition and photorespiration in the field: quintessential inefficiencies of the light and dark reactions of photosynthesis? *Journal of Experimental Botany* 46:1351–1362.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* 66:1–43.
- Pierce, L. L., S. W. Running, and J. Walker. 1994. Regional-scale relationships of leaf area index to specific leaf area and leaf nitrogen content. *Ecological Applications* 4:313–321.
- Powles, S. B. 1984. Photoinhibition of photosynthesis induced by visible light. *Annual Review of Plant Physiology* 35:15–44.
- Powles, S. B., and O. Björkman. 1982. Photoinhibition of photosynthesis—effect on chlorophyll fluorescence at 77 in intact leaves and in chloroplast membranes of *Nerium oleander*. *Planta* 156:97–107.
- Reich, P. B., D. S. Falster, D. S. Ellsworth, I. J. Wright, M. Westoby, J. Oleksyn, and T. D. Lee. 2009. Controls on declining carbon balance with leaf age among 10 woody species in Australian woodland: do leaves have zero daily net carbon balances when they die? *New Phytologist* 183:153–166.
- Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf lifespan in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* 62:365–392.
- . 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA* 94:13730–13734.
- . 1998. Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* 12:948–958.
- Rubán, A. V. 2009. Plants in light. *Communicative and Integrative Biology* 2:50–55.
- . 2016. Nonphotochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants from photo-damage. *Plant Physiology* 170:1903–1916.
- Sack, L., and C. Scoffoni. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* 198:983–1000.
- Sack, L., C. Scoffoni, G. P. John, H. Poorter, C. M. Mason, R. Mendez-Alonzo, and L. A. Donovan. 2013. How do leaf veins influence the worldwide leaf economic spectrum? review and synthesis. *Journal of Experimental Botany* 64:4053–4080.
- Santiago, L. S. 2007. Extending the leaf economics spectrum to decomposition: evidence from a tropical forest. *Ecology* 88:1126–1131.
- Santiago, L. S., and S. J. Wright. 2007. Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology* 21:19–27.
- Scoffoni, C., C. Albuquerque, H. Cochard, T. N. Buckley, L. R. Fletcher, M. A. Caringella, M. Bartlett, et al. 2018. The causes of hydraulic vulnerability and its influence on gas exchange in *Arabidopsis thaliana*. *Plant Physiology* 178:1584–1601.
- Scoffoni, C., D. S. Chatelet, J. Pasquet-kok, M. Rawls, M. J. Donoghue, E. J. Edwards, and L. Sack. 2016. Hydraulic basis for the evolution of photosynthetic productivity. *Nature Plants* 2:16072.
- Scoffoni, C., J. Kunkle, J. Pasquet-kok, C. Vuong, A. J. Amish, R. A. Montgomery, T. J. Givnish, and L. Sack. 2015. Light-induced plasticity in leaf hydraulics, venation, anatomy, and gas exchange in ecologically diverse Hawaiian lobeliads. *New Phytologist* 207:43–58.
- Shipley, B., M. J. Lechowicz, I. Wright, and P. B. Reich. 2006. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* 87:535–541.
- Specht, R. L., and A. Specht. 1989. Canopy structure in *Eucalyptus*-dominated communities in Australia along climatic gradients. *Acta Oecologica* 10:191–213.
- Stebbins, G. L. 1974. Flowering plants: evolution above the species level. Belknap, Cambridge, MA.
- Tang, A. C., Y. Kawamitsu, M. Kanechi, and J. S. Boyer. 2002. Photosynthetic oxygen evolution at low water potential in leaf discs lacking an epidermis. *Annals of Botany* 89:861–870.
- Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *American Naturalist* 126:760–776.
- Terborgh, J., and J. Mathews. 1999. Partitioning of the understory light environment by two Amazonian treelets. *Journal of Tropical Ecology* 15:751–763.
- Tezara, W., D. Martínez, E. Rengifo, and A. Herrera. 2003. Photosynthetic responses of the tropical spiny shrub *Lycium nodosum* (Solanaceae) to drought, soil salinity and saline spray. *Annals of Botany* 92:757–765.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57:189–214.
- . 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Vermeulen, P. J. 2014. Crown depth as a result of evolutionary games: decreasing solar angle should lead to shallower, not deeper crowns. *New Phytologist* 202:1249–1256.
- Weihner, E., G. D. P. Clarke, and P. A. Keddy. 1998. Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 31:125–159.
- Wright, I. J., M. R. Leishman, C. Read, and M. Westoby. 2006. Gradients of light availability and leaf traits with leaf age and canopy position in 28 Australian shrubs and trees. *Functional Plant Biology* 33:407–419.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. The world-wide leaf economics spectrum. *Nature* 428:821–827.
- Wyatt, R., and J. Antonovics. 1981. Butterflyweed re-revisited: spatial and temporal patterns of leaf shape variation in *Asclepias tuberosa*. *Evolution* 35:529–542.
- Yang, J., B. E. Medlyn, M. G. De Kauwe, and R. A. Duursma. 2018. Applying the concept of ecohydrological equilibrium to predict steady state leaf area index. *Journal of Advances in Modeling Earth Systems* 10:1740–1758.
- Zhang, H. Y., X. T. Lü, H. Hartmann, A. Keller, X. G. Han, S. Trumbore, and R. P. Phillips. 2018. Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Global Ecology and Biogeography* 27:875–885.

Erratum

In “*The Adaptive Geometry of Trees Revisited*” (*The American Naturalist* 195:935–947), there are errors in equations (1) and (3), which appear on page 936. The correct equations appear here:

$$P = \frac{P_{\max}I}{I + k} - R \quad (1)$$

and

$$G = A \left(\frac{P_{\max}I_0}{I_0 + k} - R \right). \quad (3)$$

The publisher regrets the error.

THOMAS J. GIVNISH

Department of Botany, University of Wisconsin–Madison, Madison,
Wisconsin 53706

Submitted June 29, 2021; Electronically published July 13, 2021
