

Adaptation to Sun and Shade: A Whole-plant Perspective

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Abstract

Whole-plant energy capture depends not only on the photosynthetic response of individual leaves, but also on their integration into an effective canopy, and on the costs of producing and maintaining their photosynthetic capacity. This paper explores adaptation to irradiance level in this context, focusing on traits whose significance would be elusive if considered in terms of their impact at the leaf level alone. I review traditional approaches used to demonstrate or suggest adaptation to irradiance level, and outline three energetic tradeoffs likely to shape such adaptation, involving the economics of gas exchange, support, and biotic interactions. Recent models using these tradeoffs to account for trends in leaf nitrogen content, stomatal conductance, phyllotaxis, and defensive allocations in sun v. shade are evaluated.

A re-evaluation of the classic study of acclimation of the photosynthetic light response in *Atriplex*, crucial to interpreting adaptation to irradiance in many traits, shows that it does not completely support the central dogma of adaptation to sun v. shade unless the results are analysed in terms of whole-plant energy capture. Calculations for *Liriodendron* show that the traditional light compensation point has little meaning for net carbon gain, and that the effective compensation point is profoundly influenced by the costs of night leaf respiration, leaf construction, and the construction of associated support and root tissue. The costs of support tissue are especially important, raising the effective compensation point by $140 \mu\text{mol m}^{-2} \text{s}^{-1}$ in trees 1 m tall, and by nearly $1350 \mu\text{mol m}^{-2} \text{s}^{-1}$ in trees 30 m tall. Effective compensation points give maximum tree heights as a function of irradiance, and shade tolerance as a function of tree height; calculations of maximum permissible height in *Liriodendron* correspond roughly with the height of the tallest known individual. Finally, new models for the evolution of canopy width/height ratio in response to irradiance and coverage within a tree stratum, and for the evolution of mottled leaves as a defensive measure in understory herbs, are outlined.

Introduction

A central objective of plant ecology is to understand the causes of patterns in the distribution and abundance of species. Physiological ecologists advance this goal by studying how various morphological and physiological properties permit a plant to survive and compete successfully in certain environments but not in others. Physiological ecology thus provides an important window on the proximal mechanisms that underlie species differences in distribution and habitat-specific competitive ability.

Photosynthetic energy capture provides green plants with almost all of their chemical energy, and is central to their ability to compete and reproduce. Photosynthesis, in turn, is directly and dramatically influenced by the amount of light striking a plant's leaves. Many investigators have therefore studied how different levels of irradiance by photosynthetically active radiation affect photosynthesis, and how the leaf traits that develop under different levels of irradiance influence a plant's photosynthetic response to light level. Comparative studies of the photosynthetic response and leaf characteristics of plants grown under high and low levels of irradiance have provided crucial

insights into the significance of several leaf-level traits seen in plants adapted to sunny v. shady conditions (see reviews by Boardman 1977 and Björkman 1981). The key to most of these insights, in turn, has been the study of the photosynthetic light response of individual leaves and the impact that various leaf traits have on it. Species, ecotypes, or acclimated forms with higher rates of leaf photosynthesis under specific light levels have, by and large, been inferred to have an edge in energy capture and competitive ability under those conditions.

Yet, whole-plant growth and competitive ability depend not only on the photosynthetic rate of individual leaves, but also on the geometry and dynamics of a plant's canopy, and the pattern of energy allocation among all organs. Insofar as many traits characteristic of sun- v. shade-adapted plants entail energetic costs involving non-photosynthetic organs, or influence the physical environment experienced by other leaves, the significance of such traits may prove difficult to understand if energy capture is considered at the leaf level alone. In this paper, I outline three basic energetic tradeoffs at the whole-plant level likely to shape the evolution of adaptations for energy capture in sun v. shade, and illustrate each with leaf- or canopy-level traits whose significance would be elusive, or simply not evident, if considered at the leaf level alone. I begin by briefly examining the central question of how differences between sun- and shade-grown plants can be inferred to be adaptations to irradiance level. Throughout I assume that natural selection favours plants whose form and physiology tend to maximise their net rate of energy capture, because such plants often have the greatest resources with which to reproduce and compete for additional space (Horn 1971; Oriens and Solbrig 1977; Givnish 1982, 1986a; Cowan 1986).

Sun/Shade Differences as Adaptations

Several features of plant form, physiology, and resource allocation vary with the level of irradiance to which plants are acclimated and/or ecologically restricted (Table 1). Traditionally, three approaches have been used to identify variations in such features as *adaptations* to a specific level of irradiance, based on (1) convergence, (2) correlation with photosynthetic impact, and (3) detailed cost-benefit analysis. Convergence among species from different families or orders in the expression of a given trait in plants restricted to, or grown under, a specific level of irradiance is usually taken as *prima facie* evidence that such behaviour is a result of natural selection. This approach can be applied to either fixed or developmentally plastic traits; in the latter case, convergence in the pattern of response to different irradiance levels would identify the pattern of acclimation—presumably itself genetically determined—as adaptive. Arguments based solely on convergence are, however, limited because they cannot identify how or why variation in a given trait contributes to competitive ability.

A second, more mechanistic approach to identifying traits as adaptations to irradiance level is based on a detailed study of the photosynthetic light response of leaves acclimated to different light levels, together with an analysis of how various features of their morphology and physiology contribute to photosynthetic performance under those levels (e.g. Björkman 1968a, 1981; Björkman *et al.* 1972a, 1972b; Boardman *et al.* 1972; Nobel 1976; Björkman and Powles 1984; Ludlow and Björkman 1984). This approach generally involves two tacit assumptions: (i) that the photosynthetic rates of leaves acclimated (or ecologically restricted) to a specific irradiance level are greater *at that level* than the photosynthetic rates of leaves grown under other irradiance levels; and (ii) that if variation in a given trait enhances leaf photosynthesis—expressed almost invariably per unit area—at a specific irradiance level, then it is an adaptation to that level.

The first of these assumptions seems valid, at least in extreme cases: leaves of plants grown under, or ecologically restricted to, high irradiance levels generally have higher

photosynthetic rates per unit area at those levels than do leaves of plants restricted or acclimated to low irradiance levels, and vice versa (Björkman *et al.* 1972*a*, 1972*b*; Jurik *et al.* 1979; Björkman 1981; but see analysis to contrary below). The second assumption seems more questionable. For example, Björkman (1981) argues that because leaves with higher concentrations of Rubisco (RuP₂ carboxylase-oxygenase) have higher photosynthetic rates at high irradiance levels—where carboxylation is likely to limit photosynthesis—the high levels of Rubisco in sun-adapted leaves are adaptive. Con-

Table 1. Characteristic differences between plants adapted or acclimated to sunny v. shady extremes in irradiance level

Derived from Boardman (1977), Björkman (1981), Bazzaz *et al.* (1987) and Givnish (1987)

Trait	Sun	Shade
<i>Leaf-level</i>		
Photosynthetic light response		
Light-saturated rate	High	Low
Compensation irradiance	High	Low
Saturation irradiance	High	Low
Biochemistry		
N, Rubisco, and soluble protein content/mass	High	Slightly lower
Chlorophyll <i>a</i> /chlorophyll <i>b</i> ratio	High	Low
Chlorophyll/soluble protein ratio	Low	High
Anatomy and ultrastructure		
Chloroplast size	Small	Large
Thylakoid/grana ratio	Low	High
Morphology		
Leaf mass/area	High	Low
Leaf thickness	High	Low
Stomatal size	Small	Large
Stomatal density	High	Low
Palisade/spongy mesophyll ratio	High	Low
Mesophyll cell surface/leaf area ratio	High	Low
Leaf orientation	Erect	Horizontal
Iridescence, lens-shaped epidermal cells	None	Rare
Reddish leaf undersides	Very rare	Infrequent
<i>Canopy-level</i>		
Leaf area index	High to low	Low
Phyllotaxis	Spiral	Distichous
Twig orientation	Erect	± Horizontal
Asymmetric leaf bases	Very rare	Infrequent
<i>Plant-level</i>		
Fractional allocation to leaves	Low	High
Fractional allocation to roots	High	Low
Reproductive effort	High	Low

versely, he argues that low Rubisco levels are adaptive under shady conditions because Rubisco content is correlated with rates of dark respiration, and hence inversely correlated with net photosynthesis at low irradiance levels. However, the problem with such

analyses is that, although they are based firmly on the functional impact of particular traits on leaf photosynthesis, they do not explain why a specific expression of any given trait (e.g. Rubisco content) is adaptive. What factors favour a specific, finite level of Rubisco in leaves? What sets the upper limit on the Rubisco content that would enhance photosynthesis at high irradiance levels, or the lower limit on what would be adaptive at low irradiance levels?

One means of addressing such questions is cost-benefit analysis, the third common approach to identifying adaptations to irradiance level. Cost-benefit analysis involves the assessment of the net effect of a variant of a trait on energy capture, balancing the variant's impact on energy gain against the energetic costs incurred by the plant in producing it, and then analysing which variant would maximise the net rate of energy capture. For example, higher levels of Rubisco may enhance photosynthesis under sunny conditions, but entail increased energetic costs of nutrient capture and enzyme synthesis (Mooney and Gulmon 1979); the resulting increase in leaf N content may also increase exposure to damage by herbivores, resulting in increased rates of leaf loss and/or increased allocation to anti-herbivore defences (Mooney and Gulmon 1982; Givnish 1986*b*). The 'optimal' level of Rubisco under those conditions would maximise the differences between these benefits and costs; other things being equal, plants with this Rubisco level should have an edge in competition under those conditions.

The validity of the assumption that underlies cost-benefit analysis—namely, that competition in a given environment favours plants whose form and physiology maximise their net rate of carbon gain there—has been discussed at length by Horn (1971, 1979) and Givnish (1982, 1986*a*). However, the specific application of cost-benefit analysis to adaptations to irradiance level requires three comments. First, such analyses simply carry mechanistic studies of the impact of various traits on photosynthesis to their logical conclusion, explicitly detailing and (at least potentially) quantifying costs and benefits that would otherwise be discussed in vague or qualitative terms. The specific costs and benefits included in any particular analysis may be disputed on conceptual or empirical grounds, but their stark exposure in a model affords the clearest test of the assumptions that underlie them.

Second, many cost-benefit analyses focus on a trait's impact on leaf photosynthesis, not whole-plant energy capture. Yet, this approach ignores any effect a trait has on whole-plant carbon gain through its impact on canopy geometry and dynamics, on the microenvironments experienced by other leaves, or on energy allocation between photosynthetic and non-photosynthetic tissue. However, analysis at the leaf level alone can be justified if it asks how a fixed amount of energy should be allocated between two or more leaf compounds (e.g. Rubisco *v.* chlorophyll or carbonic anhydrase, chlorophyll *a* *v.* chlorophyll *b*), tissues (spongy mesophyll *v.* palisade), or organelles (plastid thylakoids *v.* grana) (see Björkman 1968*a*, 1981; Cowan 1986; Parkhurst 1986). Focusing on the *ratio* of investment in different leaf subunits is a valid means of circumscribing the problem of optimal allocation, and should yield sensible results within the limits specified. This approach, however, cannot solve the broader problem of what determines the optimal *total* investment in different leaf subunits, or the *absolute* energy invested in each. Absolute levels of investment in leaf traits, by virtue of their association with costs involving non-photosynthetic organs, almost inevitably involve energetic tradeoffs at the whole-plant level.

Finally, many traits that vary in response to irradiance level are also known to respond to other environmental factors, many of which are themselves correlated with irradiance level. Clough *et al.* (1979) observe that this raises a profound problem for all approaches to the study of adaptation to irradiance level, namely: Are the traits seen in sun (or shade) plants adaptations specifically to irradiance level, to factors correlated with irradiance level, or to the synergistic effects of both? Cost-benefit models can contribute to resolving this difficult question by analysing how plants should respond

if only irradiance level, or relative humidity, or some other environmental parameter were to vary, and then comparing the magnitudes of the resultant responses with each other, and with the responses expected if such parameters were to vary in concert. Analyses incorporating the interactive effects of irradiance and other environmental factors (e.g. Osmond 1983; Ludlow and Björkman 1984) are in their infancy.

Energetic Tradeoffs at the Whole-plant Level

In analysing the net contribution of a trait to the whole-plant rate of net carbon gain, three basic kinds of energetic tradeoffs are likely to arise and influence the evolution of that trait and the distribution of species bearing it. These involve the economics of gas exchange, the economics of support, and the economics of biotic interactions:

(1) The economics of gas exchange (Givnish 1986c) arise from the unavoidable link between carbon gain and water loss: any passive structure that permits the passage of large, slow-moving CO₂ molecules will also allow the diffusion of smaller, faster molecules of water vapour. As a result, the photosynthetic benefit of any trait that increases the rate at which CO₂ can diffuse into a leaf must be weighed against the energetic costs associated with increased water loss. Such transpirational costs might include a reduction in mesophyll photosynthetic capacity caused by a decrease in leaf water potential, an increased allocation of energy to unproductive roots or xylem, and/or a shortened period of photosynthetic activity (Givnish and Vermeij 1976; Orians and Solbrig 1977; Givnish 1979, 1984). A complementary tradeoff results from the inevitable conflict between leaf photosynthetic capacity and the energetic costs of constructing and maintaining tissue capable of high photosynthetic rates (Mooney and Gulmon 1979; Gulmon and Chu 1981). Highly productive leaves require large inputs of nitrogen, phosphorus, and other mineral nutrients to create the pools of enzymes and pigments needed to sustain high rates of CO₂ uptake (Field and Mooney 1986).

Tradeoffs involving the economics of gas exchange have been implicated in the evolution of several traits that differ between sun- and shade-adapted plants and that influence both photosynthesis and transpiration. Such traits include effective leaf size (Givnish and Vermeij 1976; Givnish 1987), stomatal conductance (Cowan 1977, 1986; Cowan and Farquhar 1977; Givnish 1986d), leaf absorptance (Ehleringer and Mooney 1978), leaf orientation (Ehleringer and Forseth 1980; Ehleringer and Werk 1986; Nobel 1986), leaf nitrogen content and mesophyll photosynthetic capacity (Mooney and Gulmon 1979; Gulmon and Chu 1981; Field 1983), chlorophyll/protein and chlorophyll/Rubisco ratios (Björkman *et al.* 1972b; Björkman 1981; Cowan 1986), chlorophyll *a*/chlorophyll *b* ratio (Björkman *et al.* 1972b; Björkman 1981), internal leaf architecture (Parkhurst 1986) and leaf area index (Horn 1971).

(2) The economics of support arise because, among the leaf and crown forms that have equivalent effects on photosynthesis and transpiration, many differ in the efficiency with which the leaves can be mechanically supported (Givnish 1986e). Such differences imply tradeoffs between photosynthetic benefits and mechanical costs. Such tradeoffs, in turn, have been implicated in the evolution of several aspects of leaf shape and arrangement that are likely to affect whole-plant energy capture in sun v. shade. These include leaf shape (Givnish 1979, 1984), stem branching angles (Honda and Fisher 1978, 1979; Borchert and Tomlinson 1984; Givnish 1986f), compound v. simple leaves (Givnish 1979, 1984), and asymmetric leaf bases, anisophylly, and opposite v. alternate leaf arrangements (Givnish 1984). Both the economics of support and of gas exchange appear to be involved in the evolution of spiral v. distichous phyllotaxes (Givnish 1984).

(3) The economics of biotic interactions arise because many traits that enhance a plant's potential rate of growth—such as high leaf nitrogen content, heavy allocation to foliage, low allocation to defensive compounds or mutualists, or an erect growth habit—may also increase its potential attractiveness to herbivores, implying a tradeoff

between photosynthetic benefits and biotic costs (Janzen 1974; Chew and Rodman 1979; Mooney and Gulmon 1982; Givnish 1986*b*; Gulmon and Mooney 1986). Such tradeoffs, together with those associated with gas exchange and support, may underlie visual mimicry or divergence in leaf form (Gilbert 1975; Barlow and Wiens 1977; Rausher 1978, 1980; Givnish 1984; Ehleringer *et al.* 1986), allocation to defensive compounds (Janzen 1974; McKey *et al.* 1978; Chew and Rodman 1979; Mooney and Gulmon 1982; Bazzaz *et al.* 1987), and leaf flushing (Coley 1983), and may also influence the evolution of such leaf traits as toughness, pubescence, and nitrogen content (Lincoln *et al.* 1982; Coley 1983). Similar tradeoffs may also be involved in the evolution of carnivory and mutualisms with ants or nitrogen-fixing symbionts (Givnish *et al.* 1984; Givnish 1988*a*).

Several leaf and canopy traits that vary with irradiance level can be understood only in terms of their impact on whole-plant carbon gain, not leaf-level photosynthesis. The following three sections address the significance of a few key such traits in terms of their impact on the economics of gas exchange, the economics of support, and the economics of biotic interactions.

Economics of Gas Exchange

Leaf nitrogen content, stomatal conductance and photosynthetic light response show characteristic responses to irradiance level, and are thought to exert a profound influence on plant carbon gain under different light regimes (Björkman 1981; Gulmon and Chu 1981; Schulze and Hall 1982). Models to account for trends in the first two traits are briefly reviewed below.

Variation in photosynthetic light response with irradiance level has been used to support the most tightly held dogma of adaptation to sun v. shade: namely, that leaves acclimated to a given light level photosynthesise more rapidly at that level than do those acclimated to other levels (e.g. Björkman and Holmgren 1963; Boardman 1977; Björkman 1981). This dogma has been crucial to interpreting the responses of several traits to irradiance as adaptive. Yet, a critical analysis of the classic study of acclimation to irradiance level (Björkman *et al.* 1972*b*) reveals that the data, as originally analysed, do not completely support the dogma that they had almost universally been seen to support. This analysis, presented in the final portion of this section, shows that support for the dogma re-emerges when the costs of leaf construction are incorporated.

Optimal Leaf Nitrogen Content

Leaves of plants acclimated or adapted to high irradiance levels generally have higher maximum rates of photosynthesis, expressed per unit area, than leaves acclimated or adapted to lower irradiance levels (Björkman *et al.* 1972*b*; Boardman 1977; Björkman 1981). To help identify the mechanistic bases for this fundamental difference between sun and shade leaves, Björkman (1981) analysed the correlations between peak photosynthetic rate and several aspects of leaf biochemistry, physiology and morphology. He found that, across species, light-saturated rates of photosynthesis showed little relation to factors that determine the efficiency of light absorption (such as chlorophyll content) but a strong relation to factors likely to limit the rate of dark reactions (such as Rubisco or total soluble protein content). Wong *et al.* (1979, 1985*a*, 1985*b*) and Schulze and Hall (1982) also found that, within species, stomatal conductance varies in direct proportion to photosynthesis as either short-term irradiance or conditioning irradiance during leaf ontogeny varies. Analyses by Björkman *et al.* (1972*b*), Björkman (1981), and Farquhar and Sharkey (1982) indicated that the higher photosynthetic rates of sun leaves are a result of both higher stomatal conductance, and higher intrinsic photosynthetic capacity of the mesophyll at a given conductance. Presumably, the higher mesophyll capacity of sun leaves reflects, at least in part, their higher concen-

tration of Rubisco and other photosynthetic enzymes. Indeed, maximum photosynthetic rate tends to increase linearly with leaf nitrogen concentration across species adapted to different levels of irradiance or soil fertility (Mooney *et al.* 1978; Field and Mooney 1986).

If mesophyll photosynthetic capacity and maximum photosynthetic rate increase with total leaf nitrogen or soluble protein, why don't shade leaves also have high levels of nitrogen or soluble protein? Mooney and Gulmon (1979) presented a conceptual model to answer this and related questions, based on the impact of leaf nitrogen content on whole-plant growth. They argued that as leaf nitrogen content increases, so does leaf photosynthetic rate, but so also do the root costs the plant must pay in order to obtain that nitrogen. The extent to which additional nitrogen—in the form of various dark reaction enzymes, including Rubisco—can enhance photosynthesis is likely to be greater in sunny than in shady environments, because carboxylation is more likely to limit photosynthesis at high irradiance. Specifically, Mooney and Gulmon (1979) argued that the leaf nitrogen level at which photosynthesis begins to plateau should be higher in sunny than in shady environments. Thus, the optimal leaf nitrogen content—at which the difference between photosynthesis and the energetic investment in roots needed to obtain a given amount of nitrogen is maximised—should be higher in sun than in shade. Based on the higher returns expected from a given investment in nitrogen if water availability does not limit photosynthesis, and on the lower costs of obtaining a given amount of nitrogen on more fertile soils, Mooney and Gulmon (1979) concluded that optimal leaf nitrogen content should also be higher on moister or more fertile sites.

Gulmon and Chu (1981) present data supporting one assumption of this model as it applies to sun v. shade adaptation: photosynthesis does increase more rapidly with leaf nitrogen (g N m^{-2}), and saturate at higher levels of leaf nitrogen, at higher levels of irradiance in *Diplacus aurantiacus*. Provided that root costs increase with nitrogen uptake, optimal leaf nitrogen content should thus increase with irradiance. However, although the Mooney–Gulmon model is consistent with this finding, and accords qualitatively with trends seen in leaf nitrogen content in plants exposed to different levels of light, moisture, and soil fertility, the model has five important shortcomings:

(1) Quantifying the root costs associated with nutrient uptake has remained difficult, presumably because roots have other functions (e.g. water uptake) and because nutrient uptake involves active transport, necessitating measurements of both root construction and maintenance costs. This has prevented any quantitative test of the model to date.

(2) The model as originally advanced does not incorporate the fact that, at least across leaves acclimated or adapted to different irradiance levels, maximum rates of photosynthesis are strongly correlated with rates of dark respiration (Fig. 1). Dark respiration averages about 7% of peak photosynthesis, so that every increase in the latter of $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ decreases photosynthesis at low irradiance levels by $0.07 \mu\text{mol m}^{-2} \text{s}^{-1}$, and increases the instantaneous leaf compensation point by $1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, given the average quantum yield of $0.05 \text{ mol CO}_2 \text{ mol}^{-1}$ absorbed quanta in C_3 plants (Ehleringer and Björkman 1977). This raises the possibility that low irradiance may favour low leaf nitrogen contents and peak photosynthetic rates mainly because they maximise net leaf-level photosynthesis under shady conditions, irrespective of the costs of obtaining a given amount of nitrogen. The impact of leaf nitrogen content on photosynthesis at low and intermediate irradiance levels via its effect on dark respiration should be incorporated in any updated analysis. Note, however, that dark respiration is not tightly coupled to leaf nitrogen content in plants exposed to the same light environment, but differing in soil nitrogen supply (Gulmon and Chu 1981) or intrinsic leaf nitrogen content (Armond and Mooney 1978).

(3) Variation in leaf nitrogen content reflects variation in both leaf mass per unit area and nitrogen concentration per unit mass; at least in certain cases (e.g. Gulmon and Chu 1981), most of the difference between sun and shade leaves in nitrogen content per

unit area reflects a change in leaf density, not nitrogen concentration. Applying the Mooney–Gulmon model to such cases is inappropriate, insofar as the observed variation in leaf nitrogen content per unit area involves no difference in the total nitrogen costs associated with a given investment in leaf tissue. Analysis should instead focus on the significance of packaging a given amount of leaf tissue in an extensive photosynthetic surface of relatively thin leaves with a low mass/area ratio, or in a less extensive surface

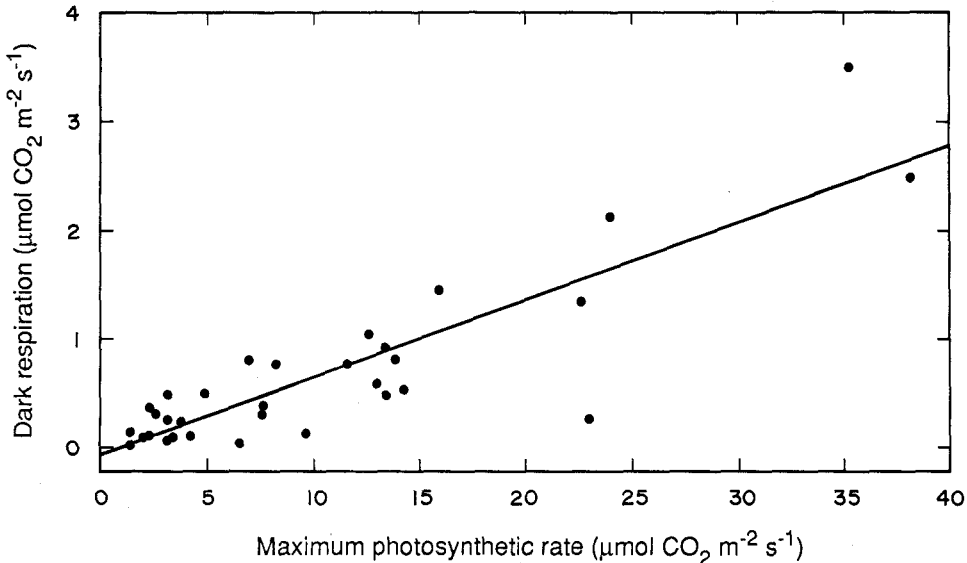


Fig. 1. Dark respiration rate as a function of maximum photosynthetic rate, for sun- and shade-adapted species and individual species acclimated to different irradiance levels. The line is $y = 0.071x - 0.065$, $r^2 = 0.755$, $P < 0.001$ for 31 d.f. The outlier is *Mimulus cardinalis*; excluding it yields $y = 0.078x - 0.088$ ($r^2 = 0.855$, $P < 0.001$ for 30 d.f.). Sources of data: Björkman 1968b (*Adenocaulon bicolor*, *Aralia californica*, *Echinodorus berteroi*, *Mimulus cardinalis*, *Plantago lanceolata*, *Trillium ovatum*); Björkman *et al.* 1972b (*Atriplex triangularis*); Boardman *et al.* 1972 (*Alocasia macrorrhiza*, *Cordyline rubra*); Bunce *et al.* 1977 (*Glycine max*); Clough *et al.* 1979 (*Solanum dulcamara*); Ehleringer and Björkman 1978 (*Encelia californica*); Ludlow and Wilson 1971 (*Phaseolus atropurpureus*); Patterson *et al.* 1978 (*Abutilon theophrasti*, *Gossypium hirsutum*); Wallace and Dunn 1980 (*Acer rubrum*, *Cornus florida*, *Liriodendron tulipifera*); Wilmot and Moore 1973 (*Silene alba*, *S. dioica*).

of thicker leaves with a higher mass/area ratio. Such an analysis, incorporating the effects of leaf thickness on internal self-shading, competition among chloroplasts for CO_2 , total evaporative surface, and root costs associated with transpiration, has been provided in qualitative form by Givnish (1979). Any comprehensive model must include these effects, those modelled by Mooney and Gulmon (1979), and the impact of leaf mass per unit area on dark respiration and net photosynthesis at low and intermediate irradiance levels.

(4) The Mooney–Gulmon model does not incorporate the effects of stomatal conductance explicitly. Stomatal conductance also affects transpiration and associated root costs, and helps determine the photosynthetic benefit associated with a given investment in leaf nitrogen (Givnish 1986d). Thus, a comprehensive model for optimal leaf nitrogen content must also include selection on stomatal conductance and incorporate the costs associated with transpiration.

(5) Finally, the Mooney–Gulmon model analyses costs and benefits only at the level of individual leaves, and does not analyse their integration into an effective canopy. Field (1983) predicts that leaf nitrogen content at different points within a canopy should be adjusted so that the marginal rate of return per unit investment in nitrogen (i.e. the

increment in photosynthesis for a given increment in nitrogen content) is equal for all microsites within the canopy. Canopies satisfying this criterion would have the maximum photosynthetic return for a given total investment in nitrogen. Field (1983) presents data for the chaparral shrub *Lepechinia calyculata*, showing that the reduction in nitrogen content and photosynthetic capacity of leaves as they age is consistent with maximising canopy carbon gain, given the increased shading experienced by older leaves. Hirose and Werger (1987) present a similar analysis for *Solidago altissima*, and conclude that nitrogen retranslocation is particularly important in plants with dense canopies.

The predictions produced by these canopy-level models should diverge from those of leaf-level models, because the presence of less shaded microsites within a canopy creates an opportunity cost of maintaining nitrogen in shaded leaves. Yet, an assessment of the precise extent to which the predictions of leaf- and canopy-level models diverge must await a quantification of the root costs associated with obtaining a given amount of nitrogen. Measurement of these costs is also needed to demonstrate that the *absolute* levels of nitrogen observed by Field (1983) and Hirose and Werger (1987) actually maximise whole-plant carbon gain.

Optimal Stomatal Conductance

Stomata are the principal conduits through which CO_2 diffuses into the leaf and water vapour diffuses out. Consequently, potential increases in photosynthesis resulting from greater stomatal conductance must be weighed against the costs associated with increased transpiration, such as increased root allocation, decreased mesophyll photosynthetic capacity, and/or shortened season of photosynthetic activity (Givnish and Vermeij 1976; Givnish 1986d). In recent years, two different groups of models have been advanced to address this fundamental tradeoff and account for variation in stomatal conductance. Cowan and Farquhar (1977) and Cowan (1977, 1986) analysed how stomatal conductance $g(t)$ should vary diurnally in response to changing environmental conditions, based on maximising total daily photosynthesis $\int A(g,t).dt$ for a given daily total amount of transpiration $\int E(g,t).dt$. They derived the necessary criterion

$$\partial E(g,t) / \partial g(t) = \lambda \cdot \partial A(g,t) / \partial g(t) \quad (1)$$

or

$$\lambda = \frac{\partial E}{\partial A} = \frac{\partial A(g,t) / \partial g(t)}{\partial E(g,t) / \partial g(t)}, \quad (2)$$

where λ is an unspecified constant Lagrangian multiplier. Several studies have now shown that, within a given species, $\partial E / \partial A$ remains roughly constant as stomatal conductance varies in response to shifts in irradiance, relative humidity, water stress, soil fertility, and ambient CO_2 concentration (Farquhar 1979; Wong *et al.* 1979, 1985a, 1985b, 1985c; Farquhar *et al.* 1980a; Hall and Schulze 1980; Field *et al.* 1982; Meinzer 1982; Schulze and Hall 1982; Mooney *et al.* 1983; Ball and Farquhar 1984a, 1984b). These results are consistent with the Cowan-Farquhar criterion, and hence maximise total photosynthesis for a given total amount of transpiration; the question is whether the total amounts of transpiration corresponding to the observed values of λ —and hence, $g(\lambda,t)$ —maximise whole-plant growth. Cowan (1986) addresses this crucial question with a model for λ based on optimal allocation of energy to roots. This model analyses how root allocation affects whole-plant growth via its effects on (i) a plant's proportion of productive tissue, (ii) its chance of exhausting its water supply between rainfalls in a stochastic climate, and thus (iii) the probable length of its period of photosynthetic activity. At present, however, there are no independently derived data to enable this model to predict a specific value of λ —and hence, a specific time course of stomatal conductance $g(\lambda,t)$ —for any set of environmental conditions. Furthermore, Cowan's model clearly cannot predict a finite stomatal conductance for plants with essentially constant access to soil moisture, such as waterlilies or mangroves.

Givnish (1986*d*) analysed the question of optimal stomatal conductance and allocation to roots from a different perspective. He asked how variations in stomatal conductance and root v. leaf allocation would affect whole-plant growth in a *constant* environment, through their effects on (i) a plant's proportion of productive tissue, (ii) its leaf water potential, and thus (iii) its photosynthetic rate per unit leaf mass. This formulation leads to an independent derivation of a constant value of $\partial E/\partial A$, and a direct means of calculating the value of $\partial E/\partial A$ that maximises whole-plant carbon gain. Observed values of root hydraulic conductivity per unit mass, and of the sensitivity of mesophyll photosynthetic capacity to leaf water potential, permitted the quantitative prediction of both stomatal conductance and root v. leaf allocation in *Phaseolus vulgaris* as a function of several environmental and physiological parameters. For the single set of conditions for which data on actual stomatal conductance and root allocation were available, predicted values accord with those observed.

Both the Cowan-Farquhar and Givnish models predict that stomatal conductance should increase with irradiance unless water availability is limited, reflecting the greater potential for carbon gain at a given conductance (i.e. mesophyll photosynthetic capacity) and associated level of transpirational costs. Both predict that other factors that increase mesophyll photosynthetic capacity (e.g. nutrient supply), or decrease transpiration (e.g. relative humidity) or the costs associated with a given amount of transpiration (e.g. root hydraulic conductivity), should favour higher conductances. Both predict a linear relationship between photosynthesis and conductance as mesophyll photosynthetic capacity varies, and a curvilinear relationship as factors affecting the costs of transpiration vary. However, the benefits they assign to increased root allocation differ, involving increased length of the period of photosynthetic activity in the Cowan-Farquhar model, and increased leaf water potential and photosynthetic capacity in the Givnish model. These benefits are likely to apply in pure form only at either end of a xeric-mesic gradient of environmental conditions, with the Cowan-Farquhar model capturing the most important tradeoffs for plants growing in xeric sites whose photosynthesis can be cut short by excessive transpiration or inadequate roots, and the Givnish model capturing the most important tradeoffs for plants growing in mesic sites with essentially continuous access to soil water (Givnish 1986*d*). A comprehensive model for stomatal conductance must incorporate both sets of tradeoffs. Further work on optimal conductance must also resolve the fundamental problem of separating the root costs of water uptake from those of nutrient absorption, and take the benefits of each into account. This suggests the need for an integrated approach to the study of optimal stomatal conductance, leaf nitrogen content, leaf thickness, and root allocation (see previous section).

Photosynthetic Light Response

The photosynthetic response of individual leaves to irradiance level has been studied extensively and is fundamental to our understanding of adaptation to sun and shade (Björkman 1981). The paradigmatic study of Björkman *et al.* (1972*b*) on acclimation of the photosynthetic light response to irradiance in *Atriplex triangularis* (then known as *A. patula*) provides perhaps the best illustration of the characteristic differences in response seen in leaves grown under sunny v. shady conditions, and has been widely used to support the view that such differences (and related morphological and physiological traits) are adaptive. Yet, an unnoticed aspect of this classic study seems to undercut its support for adaptive variation in photosynthetic response; as shown below, this support re-emerges if the data are reanalysed in terms of energetic tradeoffs at the whole-plant level.

Björkman *et al.* (1972*b*) grew seedlings of *Atriplex triangularis* in growth chambers under a 16 h photoperiod at one of three different irradiance levels: high (920 μmol

$\text{m}^{-2} \text{s}^{-1}$), intermediate ($290 \mu\text{mol m}^{-2} \text{s}^{-1}$), and low $92 \mu\text{mol m}^{-2} \text{s}^{-1}$). They then measured the net photosynthetic rate per unit area of leaves acclimated to these conditions as a function of irradiance ranging from 0 to $2500 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Björkman *et al.* (1972*b*) regarded the photosynthetic responses of leaves acclimated to different irradiance levels to be adaptive to those levels for three reasons. First, leaves grown at high irradiance had a higher maximum photosynthetic rate, and higher rate at high irradiances ($>c. 450 \mu\text{mol m}^{-2} \text{s}^{-1}$), than leaves grown at intermediate or low irradiance. Second, leaves grown at low irradiance had lower respiration rates than those acclimated to other irradiance levels. Given that all leaves showed the same initial slope (quantum yield) relating photosynthesis to irradiance, the lower respiration rate of leaves acclimated to low irradiance resulted in their having a lower light compensation point (i.e. the irradiance at which the instantaneous leaf rates of gross photosynthesis and respiration just balance). Consequently, at the lowest irradiances leaves grown at low irradiance had the highest net photosynthetic rate. Finally, leaves grown at intermediate irradiance had a higher respiration rate and light compensation point, and their photosynthesis saturated at higher irradiance, than did those grown at low irradiance; leaves grown at high irradiance had the highest respiration rate and light compensation point, and their photosynthesis saturated at the highest irradiance. These findings suggested that leaves acclimated to each irradiance level are those best adapted to that level, insofar as they appear to have the highest rate of leaf photosynthesis under those conditions.

Close examination of the photosynthetic curves published by Björkman *et al.* (1972*b*) reveals that at the low irradiance of $92 \mu\text{mol m}^{-2} \text{s}^{-1}$, leaves acclimated to that irradiance appear to have a net photosynthetic rate similar to those acclimated to intermediate irradiance. At the intermediate irradiance of $290 \mu\text{mol m}^{-2} \text{s}^{-1}$, leaves acclimated to that irradiance also appear to have a rate similar to those acclimated to high irradiance. Thus, in two of three instances, there is no clear indication that leaves acclimated to a given irradiance level have the highest photosynthetic rate under those conditions. This paradox cuts to the very heart of previous interpretations of adaptation to irradiance level.

Part of the problem is that comparisons based on leaf photosynthesis per unit area fail to include the energetic costs associated with night leaf respiration and leaf construction. Such costs must be considered in calculating the net benefit to the plant of different kinds of leaves, even in the absence of other differences (e.g. leaf orientation, canopy architecture, root allocation) that could override sun/shade differences in the photosynthetic rate of individual leaves.

For plants grown in growth chambers with an on/off light regime (like those studied by Björkman *et al.* 1972*b*), night leaf respiration can be incorporated by calculating leaf carbon balance based on a 24 h cycle. Leaf construction costs are more difficult to quantify because they entail not only the cost, in terms of fixed carbon, of synthesising various leaf compounds, but also the cost of constructing and maintaining roots and stems needed to obtain the nutrients required to synthesise such leaf compounds (Mooney and Gulmon 1979). These construction costs (C) must be set against 24 h leaf carbon balance (P) and expected leaf lifetime (T) to yield the net energetic return ($PT - C$) expected from a leaf, exclusive of other associated root and stem costs and the effects of intracanalopy shading. The net *rate* of return per unit investment in leaf tissue is an important determinant of the overall rate of plant growth, and is given by $(PT - C)/(TC) = P/C - 1/T$. Leaf lifetime T is not independent of the ratio P/C , because more rapidly growing plants with higher ratios of leaf photosynthetic rate to construction costs will more rapidly shade their lower leaves, favouring their senescence (Field 1983) at a more rapid rate than in less rapidly growing plants. The ratio P/C may therefore be a useful index of the rate of energetic return per unit investment in leaves.

Thus, from an economic point of view, it might prove more illuminating to express photosynthesis not per unit leaf area, but per unit leaf mass (or, perhaps, per unit leaf nitrogen content). Leaf construction costs per unit area should scale like leaf biomass per unit area, provided the leaves in question do not vary much in composition (Osmond *et al.* 1980); if the latter were true, P/C would be directly proportional to photosynthesis per unit leaf mass. However, leaf composition does vary with irradiance, notably in the fraction devoted to soluble protein (Björkman 1981) and nitrogen (Field and Mooney 1986). In the limiting case in which the costs of acquiring nitrogen for protein are very large compared with the cost of synthesising other leaf compounds, photosynthesis per unit leaf nitrogen (or protein) might be a better measure of P/C .

Based on these considerations, I re-analysed the data of Björkman *et al.* (1972b) to determine whether the paradox that emerges if photosynthesis is measured per unit area disappears if it is instead measured per unit leaf mass or per unit leaf protein, as more appropriate measures of net contribution to whole-plant carbon gain. In the absence of additional data that would permit the use of more sophisticated photosynthetic models (e.g. Farquhar *et al.* 1980b), daytime photosynthesis P_d was approximated using the standard Michaelis-Menten model:

$$P_d = P_{\max} I / (I + k) - R, \quad (3)$$

where I is irradiance, k is the Michaelis-Menten constant, R is the dark respiration rate, and $P_{\max} - R$ is the maximum photosynthetic rate. Published data were fitted to the model by substituting the reported respiration rate for R , and replacing k with the reported irradiance required to achieve half the maximum photosynthetic rate. The value of P_{\max} was then adjusted to yield the reported maximum photosynthetic rate at $2500 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is the irradiance at which the maximum rate was measured for leaves acclimated to high and intermediate irradiance; the light-saturated level of leaves acclimated to low irradiance was measured at a somewhat lower irradiance in order to avoid the effects of photoinhibition. The values of P_{\max} , k , and R used in the calculations presented below are given in Table 2. Leaf carbon balance over a 24 h period was calculated using the formula $P = (16P_d - 8R)/24$, based on the 16 h on/off photoperiod. The average values reported by Björkman *et al.* (1972b) for total dry mass and soluble protein content per unit area for leaves acclimated to each irradiance level were used to convert carbon balance per unit area to carbon balance per unit mass and per unit soluble protein, respectively.

Table 2. Parameters used to fit data of Björkman *et al.* (1972b) on photosynthetic light response of *Atriplex triangularis* grown at high ($920 \mu\text{mol m}^{-2} \text{s}^{-1}$), intermediate ($290 \mu\text{mol m}^{-2} \text{s}^{-1}$), or low ($92 \mu\text{mol m}^{-2} \text{s}^{-1}$) irradiance

Conditioning irradiance	P_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	R ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	k ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
High	43.72	3.48	429
Intermediate	28.32	2.12	264
Low	7.73	0.83	77

Calculated leaf carbon balance per unit leaf area, mass, and soluble protein are plotted as a function of incident and conditioning irradiance in Fig. 2. The daily carbon balance per unit area of leaves acclimated to low irradiance is 29% lower at low irradiance than that of leaves acclimated to intermediate irradiance (Fig. 2a). Similarly, carbon balance per unit area of leaves acclimated to intermediate irradiance is 6% lower at intermediate irradiance than that of leaves acclimated to high irradiance. Thus, when carbon balance is expressed per unit area, leaves acclimated to a specific irradiance do less well than those acclimated to another irradiance in two of three cases.

However, if carbon balance is expressed per unit leaf mass, or per unit soluble leaf protein, a different picture appears (Figs 2*b* and 2*c*). In both cases, leaves acclimated to low irradiance do better at low irradiance than those acclimated to other irradiances; leaves acclimated to intermediate irradiance do better than others at intermediate irradiance; and leaves acclimated to high irradiance do better than others at high irradiance.

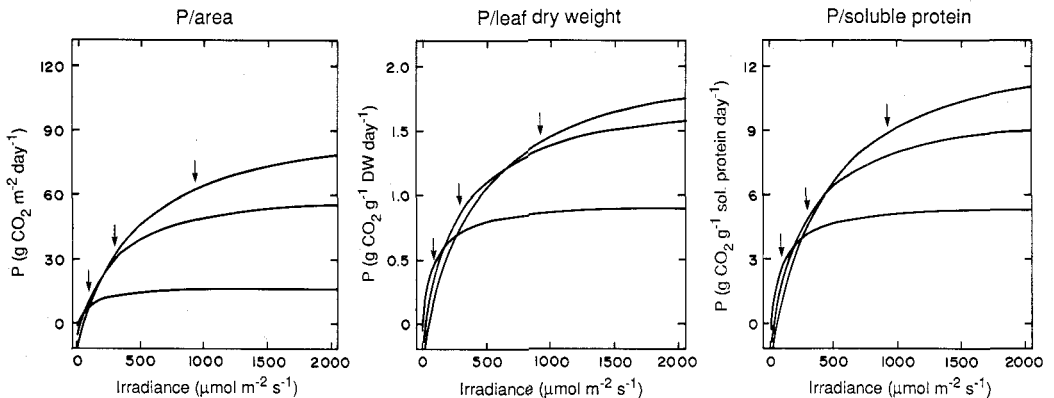


Fig. 2. Photosynthesis as a function of irradiance in *Atriplex triangularis*, expressed as daily carbon balance per unit leaf area (*a*), mass (*b*), and soluble protein content (*c*) (see text). Within each graph, arrows indicate the high, intermediate, and low irradiance levels to which leaves were acclimated. In each graph, leaves acclimated to high irradiance have the greatest photosynthetic rates at high irradiance levels; those acclimated to intermediate irradiance have intermediate rates; and those acclimated to low irradiance 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.

This suggests that expressing photosynthesis and respiration as a function of leaf mass or protein content, and thereby indirectly incorporating leaf construction costs, may be more useful in assessing adaptation to light level than expressing them as a function of leaf area. Reporting photosynthesis per unit area affords ease of analysis for such traits as quantum yield, but may bias one's perspective by ignoring the effect of leaf construction costs on whole-plant energy capture. The reason for differences in the results based on leaf area v. leaf mass or soluble protein is clear: leaves acclimated to low irradiance levels have low photosynthetic rates per unit area at those levels, but also have a much lower biomass and soluble protein content per unit area than leaves acclimated to higher irradiance levels. When photosynthesis is expressed per unit investment in either leaf mass or soluble protein, the higher rates of return at low irradiances of leaves acclimated to those conditions become apparent.

Four points should be made in connection with the preceding analysis. First, it does not incorporate differences between plants acclimated to different irradiances in root or stem costs, leaf orientation, or total leaf area. Although data do not exist to quantify root costs (*sensu* Givnish 1986*d*), they seem unlikely to affect this particular analysis, given that calculated transpiration rates per unit leaf mass at different irradiances differ little between leaves acclimated to those irradiances.

Second, the Michaelis-Menten equations used in the preceding calculations (equation 3, Table 2) provide a reasonable but inexact fit to the data of Björkman *et al.* (1972*b*). Consequently, the conclusions drawn should be viewed as tentative until confirmed using more sophisticated modelling techniques. Third, although a comparative analysis of photosynthesis of sun- and shade-acclimated leaves under *constant* low irradiance may be warranted for plants grown in growth chambers, such as *Atriplex triangularis*

in the case considered above, such an approach would greatly oversimplify the factors affecting relative gas exchange under the dynamic, highly variable light regimes prevailing in natural shaded habitats. Research by Pearcy and his colleagues (Percy *et al.* 1985; Chazdon and Pearcy 1986a, 1986b; Chazdon 1986) on trees growing in tropical forest understories has elegantly demonstrated the importance of photosynthetic induction and non-steady-state behaviour in sunflecks for gas exchange under 'shady' conditions.

Finally, Osmond *et al.* (1980) presented an analysis similar to that given here, but reached different conclusions based on two inappropriate assumptions. They found that leaves acclimated to a given irradiance have a greater 24 h carbon balance at that irradiance than leaves acclimated to another irradiance, regardless of whether photosynthesis is expressed per unit area or per unit mass. However, they assumed a sinusoidal variation in irradiance during the photoperiod, rather than the on/off switch to which the leaves were actually acclimated. A sinusoidal variation introduces a daytime period during which leaves acclimated to high irradiance would be below their compensation point in chambers at 'low' irradiance, and artificially inflates the advantage of leaves acclimated to low irradiance under such conditions. More importantly, comparisons were made only between leaves acclimated to low and high irradiances, at only those two irradiance levels. Thus, Osmond *et al.* (1980) did not recognise the crucial complications introduced by leaves acclimated to intermediate irradiance which—when carbon balance is expressed per unit leaf area—do better than leaves acclimated to low irradiance at that irradiance, and worse than leaves acclimated to high irradiance at intermediate irradiance (Fig. 2a).

Economics of Support

This section addresses three aspects of leaf arrangement likely to be shaped by tradeoffs involving the economics of support: leaf area index, relative crown width, and spiral *v.* distichous phyllotaxis. All three traits involve the integration of individual leaves into an effective photosynthetic canopy. Analysis of optimal variation in the first trait requires a whole-plant perspective on how to measure light compensation point and photosynthetic light response, and bears on the issue of maximum plant height at a given irradiance. The second trait entails allocation to leaves *v.* support tissue in dynamic canopies. The third involves a key trait at the twig, rather than the canopy, level. Additional constraints on the evolution of phyllotaxis are reviewed by Givnish (1979, 1984).

Leaf Area Index, Effective Compensation Point and Maximum Plant Height

Leaf area index (LAI) is the ratio of a plant's total leaf area to the horizontal area covered by its canopy. In other words, LAI is the average number of leaf layers over each point occupied by a canopy. Horn (1971) presented an early, highly simplified model for evaluating the relative photosynthetic outputs at a given irradiance from canopies that differ in their number of leaf layers (see also Blackman and Black 1959). This model does not incorporate many traits and processes that help determine whole-canopy photosynthesis and whole-plant carbon gain, including: within-crown variation in leaf orientation, distribution, temperature, and photosynthetic capacity; movement of the sun across the sky; shading by adjacent competitors; shading by a plant's own trunk and branches; costs of building and maintaining support tissue; and eddy transfer of CO₂ through canopy. Nevertheless, Horn's model has the notable advantage of exposing and analysing in the clearest possible terms one tradeoff central to adaptive variation of LAI, involving the balance between number of leaf layers and photosynthesis per layer. Canopies with more leaf layers have a greater potential for carbon gain because they contain more photosynthetic tissue, but they also entail more self-shading,

reducing the rate of photosynthesis in some of the lower layers and raising the possibility that some leaves may not yield a net energetic return.

Horn (1971) concluded that optimal LAI depends on irradiance and the photosynthetic light response of individual leaves. To maximise the net rate of instantaneous canopy photosynthesis, a plant should add leaf layers until the net return from the bottom, most heavily shaded layer is zero. That is, leaf area index should be adjusted until the irradiance impinging on the most heavily shaded leaves equals their compensation point, at which their instantaneous rates of photosynthesis and respiration just balance. If LAI were any smaller than this optimal value, enough light would penetrate the plant's canopy that adding more leaves would be profitable; if LAI were any larger, too little light would penetrate to the lowest leaves to permit positive net photosynthesis, and shedding some leaves would be profitable. Higher levels of ambient irradiance increase the irradiance that penetrates through a given number of leaf layers, so that optimal LAI should increase with ambient irradiance. Sunlit plants should thus arrange their leaves diffusely in several layers, shaded plants should arrange their leaves in fewer layers, and in extreme shade plants should pack their leaves tightly into a single layer with no overlap.

This model helps explain why tree species with multilayered canopies grow rapidly in sunlit conditions and thus compete successfully in open habitats and early in succession, and why trees with more nearly monolayered canopies grow rapidly relative to competitors in denser shade later in succession and in forest understories. Horn (1971) also showed how this model can help account for successional trends in species composition and diversity. Although the model could be made more precise by incorporating some of the traits and processes listed earlier, it already serves to explain, at least in qualitative terms, many of the ecologically salient features regarding the canopy form, successional status, and diversity of temperate tree species adapted to different irradiance levels.

Yet, there are two assumptions inherent to this simplest model, involving leaf compensation point and photosynthetic light response, that must be modified if the model is to apply—even on its own terms—to whole plants. The first assumption—that all leaves in a given canopy share the same photosynthetic light response—can be easily relaxed to take into account acclimation of leaves to different irradiance regimes within the canopy. All that is needed is to replace the photosynthetic light response of a leaf acclimated and adapted to a single irradiance regime, with photosynthesis as a function of the irradiance to which a leaf is acclimated (i.e. photosynthesis at the irradiance to which a leaf is acclimated, measured over a series of leaves acclimated to different irradiances).

The second assumption—that the irradiance required for an energetic 'break-even' for a leaf is given by its light compensation point—is clearly inaccurate. Such a view does not take into account several costs—such as night leaf respiration and leaf construction—that must be balanced against leaf photosynthesis to determine a leaf's net return to the plant (Givnish 1984). Insofar as a leaf's energetic break-even point determines not only how many layers of leaves a plant should hold, but also whether it can survive in a given irradiance regime (cf. Björkman *et al.* 1972a, 1972b; Björkman 1981), it is natural to ask if these additional costs would significantly affect the break-even irradiance, and if these costs would swamp the effect of observed variation in instantaneous leaf light compensation points.

To answer these questions, let us consider some model calculations using photosynthetic data gathered by Wallace and Dunn (1980) on the relatively shade-intolerant *Liriodendron tulipifera* (Magnoliaceae), a multilayered tree native to forests in the eastern United States (Table 2). Instantaneous net leaf photosynthesis P_{net} ($\text{g CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$) can be roughly modelled using Michaelis-Menten kinetics as:

$$P_{\text{net}} = P_{\text{max}} I / (I + k) - R_{\text{inst}}, \quad (4)$$

where R_{inst} is the instantaneous rate of leaf respiration ($\text{g CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$), $P_{\text{max}} - R$ is the maximum net rate of photosynthesis ($\text{g CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1}$), P_{max}/k is the initial slope ($\text{g CO}_2 \text{ g}^{-1} \text{ leaf s}^{-1} \mu\text{mol}^{-1} \text{ photons m}^2 \text{ s}$) of the photosynthetic light response curve, and I is irradiance ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). For *Liriodendron* leaves grown at 10% of full solar irradiance in a lathhouse in Georgia, U.S.A., $R_{\text{inst}} = 8.27 \times 10^{-8} \text{ g g}^{-1} \text{ s}^{-1}$, $P_{\text{max}} = 1.63 \times 10^{-6} \text{ g g}^{-1} \text{ s}^{-1}$, and $k = 236 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Wallace and Dunn 1980). Leaves grown in full sunlight show no significant differences from shade-grown leaves in P_{max} , P_{max}/k or R_{inst} .

The instantaneous leaf light compensation point I_{cp} , usually viewed as *the* light compensation point, is defined by $P_{\text{net}} = 0$. Equation (4) implies that $I_{\text{cp}} = R_{\text{inst}} k / (P_{\text{max}} - R_{\text{inst}})$. For *Liriodendron* leaves grown at 10% sunlight, I_{cp} is thus roughly $13 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Fig. 3). To calculate the effective energetic break-even irradiance for a leaf—its *ecological compensation point*—at which total leaf benefits and costs just balance, R_{inst} must be augmented by six additional costs (Givnish 1984). These include (i) night leaf respiration; (ii) effective daily cost of leaf construction, amortised over the

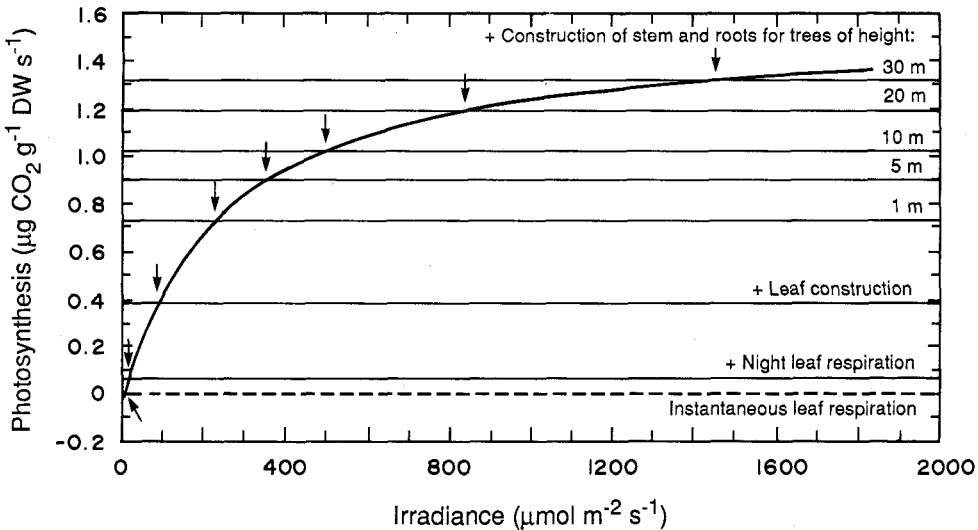


Fig. 3. Effective leaf compensation point in *Liriodendron tulipifera* as a function of the inclusion of various respiratory costs. The curve is the instantaneous rate of net leaf photosynthesis, plotted as a function of irradiance; the dashed line is the instantaneous rate of leaf respiration; the arrow at their intersection marks the traditional compensation point. The solid lines represent the cumulative respiration rates associated with night leaf respiration, leaf construction, and construction of support and root tissue (see text); the corresponding arrows mark the effective compensation points associated with including each additional source of respiration.

life of a leaf; (iii) marginal costs of roots, xylem, and phloem needed to supply an additional leaf; (iv) marginal mechanical cost of supporting an additional leaf in a given position; and (v) expected loss of productivity due to herbivory or disease. The ecological compensation point must be further increased to account for the fact that, although a leaf may be operating above its compensation point as determined by the preceding five costs, its net photosynthesis may be so low that it would pay the plant to extract nutrients from the leaf and place them in a new, well-lit leaf (Field 1983). This sixth energetic decrement in leaf productivity might best be considered an opportunity cost; Field (1988) provides an innovative approach to incorporating this cost in the calculation of optimal LAI.

The five remaining costs are incorporated in the following, highly simplified calculation of an ecological compensation point for *Liriodendron* leaves, assuming constant irradiance during the photoperiod and constant temperature. Data for shade-grown leaves are used in order to estimate compensation points as conservatively as possible, and to produce estimates applicable to the lowermost, shaded leaves of a multilayered canopy and, thus, to Horn's (1971) model. Compensation points calculated for sun-grown leaves are slightly higher than those reported for shade-grown leaves, but the underlying differences between them in photosynthetic parameters are not significant (see above).

Night leaf respiration

If the dark period is a fraction α of the photoperiod, the instantaneous rate of leaf respiration should be multiplied by a factor $1 + \alpha$ to correct for nocturnal respiration. This results in an augmented instantaneous respiration rate R_{inst} which can be balanced against the instantaneous daytime rate of gross photosynthesis to yield P_{net} . Our model yields $I'_{\text{cp}} = R(1 + \alpha)k / (P_{\text{max}} - R(1 + \alpha))$. For a dark period which fluctuates from about 66 to 100% of the length of the photoperiod during the growing season in Georgia, an average of $\alpha = 0.83$ may be substituted, yielding $I'_{\text{cp}} = 24 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3).

Leaf construction

The instantaneous daytime respiration rate equivalent to the amortised cost of leaf construction may be approximated as the initial cost of leaf construction β ($\text{g CO}_2 \text{g}^{-1}$ leaf), divided by the lifetime T (s) of the leaf during the daylight hours. This approximation is nearly exact when leaf production is continuous during the growing season, and there is little growth in total leaf mass. Estimates of β differ somewhat: Mooney (1972) estimates that the uptake of 1 g CO_2 yields 0.68 g glucose, which in turn yields 0.28 g leaf; the conversion efficiencies cited by Raven (1986) suggest instead that 1 g CO_2 yields 0.48 g leaf. Averaging these values yields $\beta = 2.63 \text{ g CO}_2 \text{g}^{-1}$ leaf; estimating T as roughly $8.5 \times 10^6 \text{ s}$ ($= 6 \text{ months} \times 30 \text{ photoperiods per month} \times 13.1 \text{ h per photoperiod} \times 3600 \text{ s h}^{-1}$), we thus obtain $R_{\text{const}} = 3.10 \times 10^{-7} \text{ g}^{-1} \text{s}^{-1}$. This additional respiration adds $69 \mu\text{mol m}^{-2} \text{s}^{-1}$ to the compensation point, yielding $I''_{\text{cp}} = 93 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3).

Allocation to stem and root tissue

The fraction of production allocated to stem tissue increases with plant height, reflecting the disproportionate increase in support tissue required to maintain mechanical stability (Givnish 1982). Whittaker and Woodwell (1968) present allometric equations relating plant height and annual production of trunk, branch, bark, twig and leaf tissue to basal diameter in woody species spanning a height range from short shrubs to trees roughly 30 m tall, including *Liriodendron*. These equations can be used to calculate the fraction of biomass production allocated to leaves as a function of height in woody plants (Fig. 4). As can be seen, the fractional allocation to leaves declines roughly linearly with the logarithm of plant height, from 46.9% in plants 1 m tall to 24.8% in plants 30 m tall. For purposes of comparison, data on fractional allocation of shoot biomass to leaves in forest herbs from Givnish (1982) are also plotted in Fig. 4; although these data are not completely comparable to those for woody plants because they do not include net annual root production, that omission should not have a large effect. Note that herbs seem mechanically more efficient than woody plants at canopy heights less than about 0.5 m, allocating less of their annual production to support tissue and more to leaves, but are less efficient at greater heights (Fig. 4). This is because herbs have less durable, less costly support structures than woody plants at any given

canopy height, but must produce their entire support structure each year, whereas woody plants merely add small increments to their existing structure. The greater mechanical efficiency of woody plants taller than 0.5 m is probably an important reason why there are so few species of forest herbs much greater than that height, together with the inability of taller herbs to exceed their ecological compensation points and achieve positive carbon balance in deep shade (see Givnish 1984; Raven 1986; and analysis below).

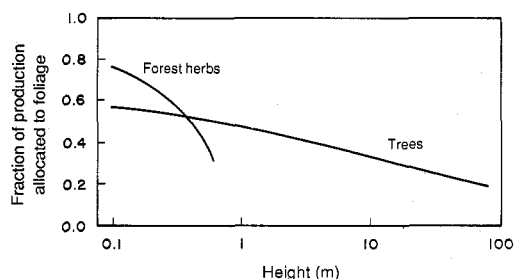


Fig. 4. Proportion of annual biomass production allocated to foliage as a function of plant height. The curve for trees is based on allometric regressions given by Whittaker and Woodwell (1968), root production estimated as 20% of stem production, and a 71% allocation to leaves in the leaf-twig fraction of *Liriodendron* (Whittaker *et al.* 1963). The curve for forest herbs is based on data of Givnish (1982), but excludes root production.

If we assume energy allocation parallels biomass allocation, then if γ is the fraction of biomass allocated to leaves, the energy allocated to non-leaf tissue should be $(1 - \gamma) / \gamma \cdot R_{\text{const}}$. Given the biomass allocation patterns shown in Fig. 4, the additional respiratory cost associated with stem and root production range from $1.13R_{\text{const}}$ in woody plants 1 m tall, to $3.03R_{\text{const}}$ in trees 30 m tall. Adding this cost to those associated with night leaf respiration and leaf construction, we find that the ecological compensation point (I_{ecp}) of a *Liriodendron* leaf increases from roughly $233 \mu\text{mol m}^{-2} \text{s}^{-1}$ in plants 1 m tall, to $355 \mu\text{mol m}^{-2} \text{s}^{-1}$ in plants 5 m tall, to $1438 \mu\text{mol m}^{-2} \text{s}^{-1}$ in plants 30 m tall (Fig. 3). In other words, even though *Liriodendron* has an instantaneous leaf compensation point of $13 \mu\text{mol m}^{-2} \text{s}^{-1}$, its saplings must receive at least $233 \mu\text{mol m}^{-2} \text{s}^{-1}$ to survive to 1 m, and at least $355 \mu\text{mol m}^{-2} \text{s}^{-1}$ to survive to 5 m; even very short seedlings must receive at least $24 \mu\text{mol m}^{-2} \text{s}^{-1}$ (see calculation of I'_{cp} above).

The steeply non-linear rise in I_{ecp} with tree height results from the precise nature of the plateauing of the photosynthetic light response given by Michaelis-Menten kinetics; if the actual response were to saturate more sharply, I_{ecp} would not rise as rapidly. Even so, given *Liriodendron*'s maximum photosynthetic rate, costs of leaf respiration and construction, and scaling of support and root costs with height, *Liriodendron* exposed to light-saturating irradiance should grow no taller than 50 m. Reduced allocation to root production on unusually moist or fertile sites could raise this to an absolute maximum height of 77 m. (Although these conclusions are based on the values of P_{max} and R_{inst} for individual shade-grown leaves, in *Liriodendron* they should apply to entire crowns, given that P_{max} and R_{inst} do not vary significantly between sun- and shade-grown leaves. *Liriodendron* was chosen for analysis based on this latter fact, which obviates many potential complications arising from differences in irradiance and acclimation at different levels within a crown.) These estimates compare with a height of 60 m for the tallest *Liriodendron* individual known (Preston 1976), found growing in Great Smoky Mountains National Park, tending to confirm Whittaker and Woodwell's (1968) hypothesis that the height-dependent scaling of support costs may determine maximum plant height. Note that both estimates underestimate stem and root costs by ignoring respiration by these organs.

Herbivory

Insects consume roughly 7% of annual leaf production in broad-leaved temperate forests in North America (Whittaker and Woodwell 1968). If we assume that such consumption occurs, on average, midway through the growing season, the average instantaneous rate of net photosynthesis must be discounted by roughly 3.5%. Except when other costs raise the ecological compensation point to irradiances near saturation, herbivory should thus have a relatively small effect on I_{ecp} .

Conclusions

For *Liriodendron* the inclusion of the costs of night leaf respiration, leaf construction, and associated stem and root tissue results in a staggering 7- to 110-fold increase in the compensation point over that expected based on instantaneous leaf respiration alone. The increase from 12 to 1438 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in compensation point due to such factors is huge compared to the range of instantaneous leaf compensation points seen among vascular plants, and suggests that certain of these factors—notably the construction costs of leaves, stems, and roots—may have an overwhelming effect on a plant's ecological compensation point. Of what significance is an instantaneous leaf compensation point of 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, or 0.001 $\mu\text{mol m}^{-2} \text{s}^{-1}$, if tissue construction costs raise the ecological compensation point by 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$?

The foregoing analysis suggests the prime importance of support costs and, by inference, plant height in determining a plant's ability to persist in deep shade. The costs of leaf and root production may be reduced in shade-adapted leaves because they possess lower enzyme levels and transpire at lower rates. However, the support costs outlined above are essentially fixed as a function of plant height, no matter what are the mass and gas-exchange properties of the leaves. These support costs are likely to insure that the ecological compensation points of tall trees are usually greater than those of herbs, regardless of differences in leaf photosynthetic light response (Givnish 1982, 1984; Raven 1986). The fact that these costs are minimal in very short plants suggests that such plants may develop the lowest leaf respiration rates in shaded environments. This is because the photosynthetic light response of individual leaves would be most important as a determinant of shade tolerance in plants of the shortest stature. As shown quantitatively above, the height-dependent scaling of support costs may also limit maximum plant height, perhaps in concert with the effects of other height-dependent factors, such as reduced leaf water potential and/or increased susceptibility to drought.

A whole-plant perspective also suggests that plants in moister or more fertile sites may generally have lower ecological compensation points, based on reduced root costs (Givnish 1984), achieve higher maximum height and LAI at a given irradiance, and tolerate lower irradiance levels at a given height. Indeed, along gradients of increasing rainfall, forests generally increase in stature and LAI (e.g. Grier and Running 1977; Waring *et al.* 1978). The quantitative predominance of support and root costs in setting the ecological compensation point of *Liriodendron* strongly suggests that the investigation of shade adaptation requires a synthesis of studies aimed at roots, stems and leaves, and should incorporate the effects of water and nutrient supplies in determining the ability of a plant to persist at a given irradiance level.

Relative Crown Width

In addition to LAI, an important aspect of canopy geometry determining whole-plant carbon gain is mechanical efficiency, the fraction of energy allocated to foliage *v.* unproductive support tissue. Yet, because a plant's canopy is both an organ of energy capture and a direct instrument of competitive interference, analyses based purely on mechanical efficiency are inadequate. Among canopies having an adaptive LAI, the most mechanically efficient are extremely short and narrow, with horizontal and vertical lever arms

of vanishingly small length and cost (Givnish 1982). Yet short plants are readily overtopped, and narrow canopies can incorporate little leaf area. A more important question, at least for woody plants of indeterminate growth, is which canopy geometries allow the greatest rate of height growth.

King (1981) addressed an important aspect of this question and presented a quantitative model for energy allocation between a tree's canopy (leaves and branches) and trunk that would maximise its overall rate of height growth. The fundamental tradeoff involved can be summarised as follows. If a tree allocates almost all of the photosynthetic return from its canopy into the trunk, it will produce little new foliage to fuel further height growth. As fractional allocation to the canopy increases, so does foliage area and canopy output, but with two costs. First, fractional allocation to the trunk is reduced; second, the more massive the leaf canopy, the more massive and costly the branches that must be replaced as the tree grows upward. At very high canopy allocations, these costs would reduce height growth to zero. Thus, an intermediate allocation to canopy v. trunk produces optimal height growth.

King (1981) tested this model using allometric data on branch and trunk mass in aspen (*Populus tremuloides*) growing in crowded stands undergoing self-thinning. The observed allocation between canopy and trunk was close to that predicted, and resulted in a calculated rate of growth nearly equal to the maximum possible rate. Perhaps not coincidentally, the ratio of canopy diameter to tree height observed in these optimally designed aspens (0.17) is very nearly the same as that seen across 19 single-species stands undergoing self-thinning, and across 79 mixed-species forest stands (Givnish 1986g). This suggests that selection, at least in crowded stands, does favour canopies with a geometry that maximises height growth; Givnish (1986g) used this canopy diameter/height ratio, in combination with constraints on LAI and the biomechanical properties of wood, to explain the slope and intercept of the $-3/2$ power law of self-thinning (White 1981).

How should the optimal width/height ratio of a tree's canopy vary with irradiance? In King's model, terms involving photosynthetic rate per unit canopy mass cancel, and the optimal allocation between trunk and canopy should not vary with irradiance. However, reductions in irradiance reduce the optimal density of leaves per unit area of ground occupied by the canopy (i.e. LAI), tending to reduce the mass of leaves and branches associated with a given canopy diameter. Thus, given that canopy mass should increase monotonically with canopy diameter, shady conditions should favour broader canopies.

There is another, more subtle reason why this should be true. On moist, relatively fertile sites, the canopies of understory shrubs or trees are likely to cover a lower proportion of the ground than are trees in the forest canopy: there are simply fewer microsites where ambient irradiance exceeds the ecological compensation point of such plants. Consequently, subcanopy plants will often find themselves surrounded by empty space. In the limiting case in which an understory tree—incapable of reaching the canopy—has *no* neighbours, growing upwards and slightly outwards in accordance with the canopy diameter/width ratio predicted by King's model will not increase energy capture as much as simply growing outwards. This is because vertical growth yields no benefit (at least in terms of light capture), whereas horizontal growth expands the area over which light can be captured. Thus, extremely uncrowded understory conditions should favour very broad, low canopies that maximise a plant's net rate of energy capture in the absence of competitors. Completely crowded conditions, on the other hand, place height growth at a premium, and narrower canopies that maximise height growth are favoured. At intermediate levels of subcanopy coverage, selection should favour trees with diameter/height ratios which are intermediate between these extremes, and which maximise net energy capture in the *presence* of competitors.

The evolutionarily stable diameter/height ratio for understory trees, which results in

a net rate of energy capture that cannot be bettered by competitors with another ratio, must depend on subcanopy coverage and the resulting probability of a tree being adjacent to, and shaded by, a competitor. At very low subcanopy coverage, very broad canopies that maximise energy gain in the absence of competitors also maximise energy gain in the presence of competitors. At very high subcanopy coverage, narrow canopies with a diameter/height ratio in accord with King's (1981) model are the only ones not surely overtopped, and again maximise energy gain in the presence of competitors. Canopies that expand at an intermediate diameter/height ratio should maximise energy gain realised in subcanopies of intermediate coverage, reflecting a balance between the energetic costs of outgrowing all possible neighbours, the chance of encountering a neighbour, and the energetic benefits of a broad canopy. To the extent that stratal coverage is lower in shade than in sun, and lower in the subcanopy than the forest canopy, the diameter/height ratio of individual trees should be greater in subcanopy trees and shade-adapted canopy species.

Data to test these ideas were culled from the register of 'champion trees' for North America (Hunt 1986). Unusually large individuals of each species qualify as 'champions' based on a combination of their girth, height and canopy spread. Undoubtedly, most grow on sites that are, or have been, more open than is typical for their species; in that sense, the use of such individuals may reduce somewhat the effects of systematic differences between shade-tolerant and shade-intolerant species in the environmental conditions experienced during ontogeny. Canopy diameter/height ratios were calculated for all tree species occurring in eastern North America that could unequivocally be assigned to one of three classes: obligate subcanopy species, shade-tolerant canopy species, and shade-intolerant canopy species (Table 3). The expectation was that obligate subcanopy species, experiencing shady conditions throughout their lives, would have the greatest diameter/height ratios; that shade-tolerant species that achieve the canopy would have somewhat lower ratios; and that shade-intolerant canopy species would have the lowest ratios. This is exactly what is seen (Table 3): the mean diameter/height ratio for subcanopy species is 1.09 ± 0.47 ($n=8$); for shade-tolerant canopy

Table 3. Ratio of canopy diameter to height in selected 'champion' trees of eastern North America (see text)

Subcanopy species		Shade-tolerant canopy species		Shade-intolerant canopy species	
<i>Acer pensylvanicum</i>	0.49	<i>Acer saccharinum</i>	1.07	<i>Betula papyrifera</i>	0.70
<i>Acer spicatum</i>	0.55	<i>Acer saccharum</i>	0.87	<i>Liriodendron tulipifera</i>	0.98
<i>Amelanchier arborea</i>	1.30	<i>Betula allegheniensis</i>	1.20	<i>Nyssa sylvatica</i>	0.59
<i>Carpinus caroliniana</i>	1.55	<i>Fagus grandifolia</i>	0.58	<i>Platanus occidentalis</i>	0.81
<i>Cercis canadensis</i>	1.83	<i>Tilia americana</i>	0.66	<i>Populus grandidentata</i>	0.63
<i>Cornus alternifolia</i>	1.67			<i>Populus tremuloides</i>	0.43
<i>Hamamelis virginica</i>	0.86			<i>Prunus pensylvanica</i>	0.35
<i>Lindera benzoin</i>	0.96			<i>Robinia pseudoacacia</i>	0.96
<i>Ostrya virginica</i>	1.21			<i>Sassafras albidum</i>	0.49
				<i>Sorbus americana</i>	0.65

species, 0.88 ± 0.26 ($n=5$); and for shade-intolerant canopy species, 0.66 ± 0.21 ($n=10$). The distributions of the ratios for each group of species differs significantly in the direction expected ($P < 0.05$, Wilcoxon paired-rank test). These results confirm the trend predicted, and should be followed by further tests and a quantitative version of the model. It should be noted that the coverage-dependent argument for canopy diameter/height ratio in trees of indeterminate growth is, in many ways, analagous to the game-theory model for the evolution of leaf height in forest herbs of determinate growth, advanced and quantitatively tested by Givnish (1982, 1986f).

Orthotropy v. Plagiotropy

At a smaller scale of canopy geometry than overall canopy width and leaf area index, two modes of leaf arrangement, or phyllotaxis, are especially common. These involve the packing of leaves in spirals or whorls about erect twigs (spiral phyllotaxis on orthotropic axes), or in planar arrays along more or less horizontal axes (distichous phyllotaxis on plagiotropic axes) (Hallé *et al.* 1978). Spiral phyllotaxis on erect axes is common in sun plants, and distichous phyllotaxis on horizontal axes is common in shade plants (Leigh 1972, 1975; Hallé *et al.* 1978). Why should this be the case?

Givnish (1984) provides a qualitative explanation for this pattern, assessing the impact of phyllotaxis on twigs as organs of energy capture and as direct instruments of competitive interference. As organs of energy capture, orthotropic axes with a spiral phyllotaxis have an advantage in sunny environments because (i) erect lever arms can support more leaf mass per unit twig mass; (ii) greater self-shading relative to distichy would have a relatively small effect on carbon gain at irradiance levels near photosynthetic saturation; and (iii) such self-shading would substantially decrease heat load and transpirational costs in a high-radiation environment. Plagiotropic axes with a distichous phyllotaxis should be favoured in shady environments in spite of their mechanical inefficiency, because (i) their low degree of self-shading would have a large impact on net carbon gain at irradiance levels near the photosynthetic compensation point; and (ii) the additional transpirational costs imposed by direct exposure in a low-radiation environment would almost be nil. As organs of growth, orthotropic axes should be favoured in sun-adapted plants whose total carbon gain would be most strongly enhanced by vertical growth and attainment of the forest canopy, whereas plagiotropic axes should be favoured in shade-adapted plants whose total input would be most strongly enhanced by horizontal spread and an increase in canopy area.

Economics of Biotic Interactions

Irradiance level, by influencing the potential photosynthetic return from leaf tissue and the optimal allocation of energy to various photosynthetic compounds, affects the likely benefits and opportunity costs associated with different kinds and amounts of defensive measures aimed against folivores (Mooney and Gulmon 1982; Coley 1983; Coley *et al.* 1985; Givnish 1986*b*; Gulmon and Mooney 1986; Bazzaz *et al.* 1987). This section briefly reviews a general model for defensive allocation in sun and shade, and then discusses the possible significance of leaf mottling, an unusual feature of certain shade-adapted species, as an anti-herbivore defence.

Amounts and Kinds of Defensive Compounds as a Function of Irradiance

Angiosperms display an extraordinary range in the kind and amount of chemical, physical, and biological defences they deploy against folivores (Janzen 1966, 1983; Gilbert 1975, 1980; Feeny 1976; Barlow and Wiens 1977; Rausher 1978; Price *et al.* 1980; Berenbaum 1981; Schultz and Baldwin 1982; Denno and McClure 1983; Strong *et al.* 1984). Recently, attention has focused on attempts to predict the nature of such defences as a function of the ecological characteristics of the plants bearing them. Two classes of models have been developed, based on either (i) the effects of a plant species' abundance and/or longevity on the effectiveness of different defences (Feeny 1976; Rhoades and Cates 1976; Rhoades 1979); or (ii) the impact of different defences on a plant's net rate of energy capture as a function of environmental context (Janzen 1974; Mooney and Gulmon 1982; Coley 1983; Coley *et al.* 1985; Gulmon and Mooney 1986; Bazzaz *et al.* 1987). The latter set of cost-benefit models bears directly on the question of how irradiance level should influence the kind and amount of defences deployed against herbivores.

Coley (1983) predicted that shade-adapted species should allocate more to defence than sun-adapted species, because the effective cost of replacing a given amount of leaf tissue is larger in slow-growing shade plants, and because the opportunity cost associated with a given amount of defence is larger in fast-growing sun plants. That is, given the low photosynthetic rates characteristic of shaded leaves, it would take plants of a given size longer to replace an eaten leaf than it would under more productive sunny conditions. Similarly, given the high photosynthetic rates characteristic of sunlit leaves, a given allocation to defence instead of photosynthetic tissue would more greatly reduce a plant's potential growth than it would under less productive shady conditions. This analysis can be seen as a logical extension of Janzen's (1974) argument that the costs of replacing leaves eaten by herbivores would be greater in nutrient-poor habitats than in more fertile sites, given the longer time required to recoup the costs of leaf construction.

Coley *et al.* (1985) generalise the preceding arguments to conclude that, at least between species, defensive allocations should be greater in plants growing on less productive sites, regardless of the particular factor responsible for reduced productivity. In addition, they suggest that sunny conditions should favour carbon-based defensive compounds (e.g. tannins, phenols), whereas shady conditions should favour nitrogen-based defences (e.g. alkaloids). This is because nitrogen is more likely to limit photosynthesis under sunny conditions (Mooney and Gulmon 1979; Gulmon and Chu 1981), and because fixed carbon is likely to be in less abundant supply under shaded conditions. Finally, Coley *et al.* (1985), Bazzaz *et al.* (1987), and Coley (1987) suggest that 'quantitative' defences (e.g. tannins, phenols)—which reduce feeding or digestive efficiency, are effective only at relatively high concentrations, but are effective against almost all herbivores (Feeny 1976)—should be favoured in shade-adapted plants, and that 'qualitative' defences (e.g. alkaloids, cardiac glycosides)—which are toxins effective at low concentrations against most species, but which are ineffective against certain specialist herbivores—should be found in sun-adapted plants. They argue that the costs of construction are higher for quantitative defences, but have low continuing costs once deployed, so that they should be most cost-effective in long-lived leaves, typical of slow-growing plants (see Field 1983). Qualitative defences are effective at lower doses and thus have lower construction costs, but often turn over at high rates (Mooney and Gulmon 1982), implying that they might have substantial continuing costs and be cost-effective only in short-lived leaves, typical of faster-growing plants.

The predictions that result from the preceding arguments are in accord with many of the known facts regarding the nature and kind of chemical defences seen in sun- v. shade-adapted plants (Coley 1987), and the arguments might also apply to certain kinds of physical defences (e.g. thick cell walls, silica inclusions) and biological defences (e.g. extrafloral nectaries to attract ant bodyguards).

However, assessing the costs associated with visual biological defences—such as mimicry, aposematic coloration, or cryptic coloration (Gilbert 1975; Barlow and Wiens 1977; Rausher 1978)—can be more difficult. Ehleringer *et al.* (1986) provide a model for rigorously testing theories regarding visual defences, in their work on the degree of mimicry of host leaf shape in poorly defended mistletoes with high v. low levels of leaf nitrogen. Smith (1986) presents a hypothesis that mottled or variegated leaves may constitute an irradiance-dependent visual defence against leaf miners, in that they may (i) serve to mimic miner damage and thereby deter actual oviposition by leaf miners; (ii) reduce leaf temperature and transpiration in sunny, hot, and/or dry sites; but (iii) reduce light interception and photosynthesis, particularly in shady sites, given the masking or absence of chlorophyll over the mottled areas of the leaf. Consequently, mottled leaves should be favoured in sunny but not shady microsites.

Smith (1986) supports this conclusion with data on the distribution, growth, and damage by leaf miners of mottled and unmottled morphs of *Byttneria aculeata* Jacq.

(Sterculiaceae), a weedy tropical subcanopy vine growing in Panama. As predicted, mottled individuals are relatively more frequent in clearings than under closed canopies. In addition, leaf production by transplants in the absence of herbivory increases with the average amount of variegation per leaf in open habitats, and decreases with the average amount of variegation in shaded sites. Finally, mottled leaves are indeed less heavily attacked than unmottled leaves where they occur at similar frequencies. These results appear to provide the first experimental evidence for the adaptive significance of leaf variegation in sunny *v.* shady environments. Yet their applicability may be limited; Givnish (1988*b*) presents data showing that, at least in the flora of the north-eastern U.S.A., mottled leaves are far more common in herbs of shaded forest understories than in any other growth form, and are essentially absent in trees, shrubs, herbs or vines of sunny sites. He presents an alternative hypothesis that mottling serves to camouflage the foliage of certain, particularly vulnerable phenological groups of species (e.g. evergreens, spring ephemerals), by disrupting their outline as perceived by colour-blind vertebrate herbivores in sun-dappled understories. As Neger (1913) noted, the puzzling and oft-overlooked phenomenon of leaf mottling remains a rich field for further physiological and ecological studies.

Conclusions

This paper has illustrated the value of a whole-plant perspective in generating and testing hypotheses regarding adaptation to irradiance level, and in resolving certain paradoxes regarding the adaptive value of specific leaf and canopy traits. Three general conclusions emerge:

(1) To understand the adaptive significance of variations in leaf form, physiology, and arrangement, we must consider the functional integration of leaves with other plant parts, particularly roots and mechanical tissue. Many leaf and canopy traits that enhance whole-plant carbon gain have associated costs involving the uptake of water and nutrients, mechanical support and interactions with herbivores. The balance between these costs and associated energetic benefits create tradeoffs that underlie the economics of gas exchange, support and biotic interactions. Analysis of these tradeoffs is the key to understanding the response to irradiance of such key traits as photosynthetic light response, leaf nitrogen content, stomatal conductance, leaf area index, relative canopy width, whole-plant compensation point and allocation to antiherbivore defences.

(2) Two major themes of research on adaptations to irradiance level are likely to emerge over the next few years. First, approaches to the study of leaf, canopy and root adaptations are likely to merge, given that any completely quantitative theory for a trait influencing photosynthesis must incorporate the associated costs of transpiration and root function. Physiological ecologists—who heretofore have mainly been leaf physiologists—must collaborate more closely with root biologists if we are to achieve continued advances in our understanding of photosynthetic adaptations.

Second, the integration of support costs offers many opportunities for further study. This paper has shown that these costs profoundly affect the effective light compensation point of individual leaves as canopy height varies. Consequently, canopy height affects optimal leaf area index and the whole-plant compensation point. Irradiance level sets a limit on maximum canopy height, and canopy height defines the minimum irradiance level required for survival. In the case of the tree *Liriodendron tulipifera*, the maximum height observed accords fairly closely with the limits calculated from support costs. These results exemplify the kinds of conclusions that might be drawn by meshing traditional approaches to physiological ecology with biomechanical considerations, with the aim of determining whether particular growth forms confer a context-specific competitive advantage. The opportunities for such research—focusing on the significance of various aspects of canopy geometry, branching pattern and leaf arrangement—are,

in many ways, as exciting as those facing physiological ecology in the 1960's and 1970's.

(3) Analysing the impact of a trait on whole-plant carbon gain is an important, if not essential, step toward understanding its adaptive value, but such studies alone are inadequate to demonstrate that such a value exists and is biologically relevant. Only appropriately controlled studies of competition between plants with different expressions of a trait, conducted under natural conditions, can demonstrate that such variants have adaptive significance. Natural within-population variation in traits that affect adaptation to irradiance level has been little studied, and the implications of such variation for whole-plant carbon gain under different conditions have been largely ignored. Ultimately, to demonstrate adaptation to irradiance level more rigorously, we must relate within-population variation to differences in whole-plant carbon gain, growth and reproductive success under different irradiance levels.

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