

Leaf Form and Photosynthesis

Do leaf structure and orientation interact to regulate internal light and carbon dioxide?

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Morphological and anatomical features of plant leaves are commonly associated with metabolic type (e.g., Kranz anatomy of C_4 species), amount of sun exposure (e.g., sun and shade leaves), or water stress (e.g., xeromorphism). However, although the primary function of the leaf is to absorb and process sunlight and carbon dioxide for photosynthesis, few structural features of leaves have been related mechanistically to these tasks. For example, it has been known for over a century that the internal anatomy of leaves is characterized by different cell layers (e.g., the palisade and spongy mesophyll) and that stomatal pores can be located on one or both sides of a leaf. Yet, only recently has any functional relationship between leaf form and photosynthetic performance been suggested.

A variety of ecological studies have correlated numerous leaf structural parameters with photosynthetic performance (e.g., Abrams and Kubiske 1990, 1994, Hinckley et al. 1989,

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Terrestrial plants responded to the amount of sunlight and stress in a given habitat by evolving leaf structural properties in concert with leaf orientational capabilities

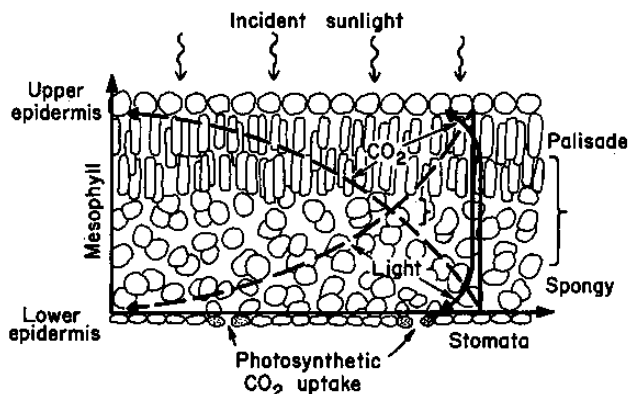
Koike 1988, Reich et al. 1991, Walter 1973), but mechanistic evidence pointing to a complex influence of leaf structure on photosynthesis has been obtained only recently (Terashima and Hikosaka 1995, Vogelmann et al. 1996a). A comprehensive synthesis of the functional significance of leaf structure, as related to photosynthesis, has yet to be proposed. In addition, no studies have associated leaf structural characteristics with differences in leaf orientation relative to the Sun, despite the recognition that both structure and orientation can have dominant influences on whole-leaf photosynthesis.

In this article, we present a synthesis of current findings in ecology, physiology, and biochemistry that points to a fundamental relationship between the evolution of leaf form (structure and orientation) and pho-

tosynthetic performance. This relationship includes a strong coupling between leaf structure and orientation that is not documented in the literature and that has not been attributed to photosynthetic function. We describe field observations of correlations among leaf structural symmetry, leaf orientation, and the resulting amount of incident sunlight on both leaf surfaces. We also summarize physiological and biophysical evidence of the impact of this structural symmetry on the capture and processing of sunlight and carbon dioxide for photosynthesis. We propose that the evolution of leaf structural symmetry is based on leaf orientation and the regulation of incident sunlight and is driven by a common functional theme—maximizing photosynthesis per unit leaf biomass by regulating light and carbon dioxide gradients inside the leaf. Although differences in chloroplast abundance, physiology, and behavior at different locations across the mesophyll are also important to this central theme (e.g., Evans 1996, Terashima 1992, Terashima and Hikosaka 1995), these topics are not emphasized.

For a typical plant leaf, sunlight is incident on the upward-facing (adaxial) side, whereas carbon dioxide uptake occurs predominately at the lower (abaxial) side, where most, if not all, of the leaf stomatal pores are found (Figure 1; Meidner and Mansfield 1986). Thus, whereas chloroplasts just beneath the upper epidermis of this leaf should experience the highest light regimes, the

Figure 1. A cross-section of a typical leaf showing the opposing gradients of internal light and carbon dioxide when sunlight is incident on the upper leaf surface and stomata are present predominantly on the lower surface. Two pairs of hypothetical curves are drawn: one pair (dashed lines) shows strong gradients that generate a narrow zone of overlap (indicated by small bracket) between high light and carbon dioxide, and another pair (solid lines) shows smaller gradients that generate a broader zone of overlap (large bracket) between high light and carbon dioxide. A broader zone of overlap would generate greater photosynthesis per unit leaf biomass, which may be a fundamental driving force in the evolution of leaf form (i.e., structure and orientation).



carbon dioxide concentration is highest on the opposite side of the leaf, next to the lower epidermis. Steep, opposing gradients in light and in carbon dioxide would not seem to be optimal for maximizing photosynthetic efficiency across the entire thickness of the leaf (Figure 1). It seems logical that leaf form would have evolved so as to maximize photosynthesis per unit leaf biomass in the face of these opposing internal gradients of light and carbon dioxide.

Does leaf structure regulate internal light?

Considerable evidence indicates that the structural properties of leaves (apart from changes in chloroplasts) may influence photosynthetic performance. Most of this evidence comes from observations (Terashima and Hikosaka 1995) that the shape of the light-response curve of photosynthesis (i.e., the amount of carbon fixed per amount of light) can be altered by changing the angle of incidence of direct-beam light, the directional composition of the incident light (i.e., whether the beam is diffuse or direct), and the type of leaf structure (i.e., whether it is asymmetric or symmetric). Experimentally disrupting the parallel rays of direct-beam light by using a light diffuser caused substantial alterations in the light response of photosynthesis (DeLucia et al. 1991, Terashima 1989). Similar alterations in photosynthesis have been observed

when structurally asymmetric leaves, which naturally intercept direct sunlight only on one surface, are illuminated on the opposite side instead (e.g., Evans et al. 1993, Kirschbaum 1987, Poulson and DeLucia 1993, Terashima 1989).

Increasing evidence implicates the leaf surface and all of the major cell types within a leaf (i.e., epidermis, palisade, and spongy mesophyll) as influencing the capture and internal processing of absorbed sunlight (Vogelmann et al. 1996a). Moreover, orientational and corresponding structural effects may have strong influences on photosynthetic properties. Chloroplast acclimation to altered light regimes appears unable to compensate entirely for alterations in natural light regimes or normal leaf optical properties.

Upper epidermis. Leaf surface structures, such as epicuticular waxes and epidermal hairs, have been reported to affect whole-leaf photosynthesis due to alterations in absorbed sunlight. For example, high solar reflectance from pubescent leaves of desert broad-leaf species results in optimal leaf temperatures, reduced transpiration, and enhanced photosynthesis (Ehleringer and Werk 1986, Johnson 1975, Smith 1978). Also, the hydrophobic nature of leaf pubescence found in numerous species may prevent a water film from forming during dew and rainfall, a potentially large barrier to photosynthetic carbon dioxide exchange (Brewer and

Smith 1994, 1997, Smith and McClean 1989). However, this same water repulsion may also create a monolayer of small water droplets over the entire leaf surface. Because of the lensing effects of these water droplets, a highly variable sunlight pattern develops over the leaf surface, ranging from full shade to over 20 times full sun at focal points beneath individual droplets (Brewer et al. 1991). In most species tested, a layer of leaf trichomes holds the dew droplets above the leaf surface, well beyond their focal distances, greatly reducing the potential damage of this focused sunlight to the photosynthetic system.

Another common feature of the leaf epidermis is their lens-like cells, which were originally thought to be involved in orienting the leaf toward the sun (Haberlandt 1914). More recently, however, it has become clear that these lens-like epidermal cells both collect and focus incident light into the leaf interior, possibly to enhance photosynthesis (Bone et al. 1985, Lee 1986, Poulson and DeLucia 1993, Poulson and Vogelmann 1990). These findings also show that the geometry of individual epidermal cells may vary according to sunlight exposure. Spherical epidermal cells may be more beneficial in shaded environments, adding a much greater absorbing area, not only for the predominant levels of less intense diffuse light, but also for the direct sunlight (sunflecks) that penetrate the canopy at low angles of incidence (Smith et al. 1989). In addition, spherical epidermal cells would focus light to the shallow depths that are necessary for these typically thinner shade leaves. In sunnier habitats, more elliptical epidermal cells would generate deeper focal points for a more even distribution of internal light throughout thicker leaves (Vogelmann et al. 1996a). Moreover, any bending of incident, direct-beam sunlight by epidermal cells is important for lengthening photon path lengths inside the leaf and, thus, increasing the probability for absorption by chloroplasts (Vogelmann et al. 1996b).

Mesophyll. The optical properties of cell layers inside leaves (i.e., the palisade and spongy mesophyll) also appear to regulate the internal distri-

bution of sunlight for enhanced photosynthesis (Vogelmann 1993, Vogelmann et al. 1996a). For example, the more columnar palisade cells typical of thick sun leaves act as light conduits that propagate light deeper into the mesophyll (Figure 1), thus distributing light more evenly throughout the leaf (Terashima 1989, Vogelmann and Martin 1993). In addition, the cell walls of the spherical spongy mesophyll cells and the large fraction of air space in the leaf interior generate large quantities of scattered light, increasing light absorption by chloroplasts within the mesophyll (DeLucia et al. 1996). Overall, internal light scattering within leaves generates photon fluence levels three to four times greater than sunlight incident on the leaf surface, enhancing the absorption of weakly absorbed wavelengths in particular (Vogelmann 1993).

Lower epidermis. Another fundamental influence of epidermal structure on photosynthesis may result from leaf bicoloration, in which the leaf side that faces away from the sun is lighter in color than the leaf surface facing toward the sun. Bicoloration is especially common in species that occupy more shaded habitats (Smith 1981). Bicoloration could enhance "light-trapping" in the spongy mesophyll by providing a reflective surface on the internal side of the lower epidermis (Lin and Ehleringer 1983, Smith 1981, Woolley 1971). In these studies, removal of the lower epidermis of a bicolored leaf resulted in large increases in light transmittance. The reflective properties of the spongy mesophyll and of the inside of the lower epidermis are also important for increased light retention and absorption in bicolored leaves (DeLucia and Nelson 1993, DeLucia et al. 1996).

Light and carbon dioxide gradients in leaves

It is reasonable to expect leaf orientation and structure to interact so that high light areas inside a leaf are matched with high carbon dioxide concentrations. Otherwise, full photosynthetic potential will not be achieved (Figure 1). Although sub-

stantial gradients in light do appear to form across the leaf mesophyll (Vogelmann et al. 1996a), with corresponding effects on whole-leaf photosynthesis, carbon dioxide levels inside leaves have not been measured directly, and much less is known about their characteristics (Parkhurst 1994). However, relatively large gradients of carbon dioxide across the mesophyll thickness have been estimated (Parkhurst 1978) using indirect methods that measure carbon dioxide exchange in whole leaves that are exposed to carrier gases infused from different sides of the leaf (Parkhurst and Mott 1990). Estimates of up to a 16 Pa pressure difference in internal carbon dioxide between opposite leaf sides have been reported for leaves with large, experimental differences in ambient carbon dioxide concentrations between the two leaf surfaces and nearly equal numbers of stomata on both sides of the leaf (Parkhurst et al. 1988). Actual gradients of carbon dioxide inside natural leaves may be less, although the common occurrence of stomata on only one side of the leaf would enhance steeper gradients that would be in opposition to the light gradient (Figure 1). Parkhurst (1994) concluded that intercellular gaseous diffusion is a substantial limitation to photosynthetic carbon dioxide assimilation in the large number of species that have thick leaves and stomata on the lower leaf surface only. To date, measurements of both light and carbon dioxide gradients within the same leaf are not available for any plant species.

Although carbon dioxide gradients have not been measured directly inside leaves, experiments using pulse dosages of labeled carbon dioxide, with subsequent paradermal sectioning and autoradiography, have shown variation in the location of carboxylation activity inside leaves (Nishio et al. 1993). Initial studies indicated that the internal light gradients of sun and shade leaves of spinach did not correspond to the carbon fixation gradient (Nishio et al. 1993). However, a subsequent study reported that light absorption profiles predicted from chlorophyll concentration gradients did match carbon dioxide fixation profiles measured within spinach leaves (Evans 1996),

although this study did not measure internal light and carbon dioxide.

Logically, photosynthesis could be maximized if chloroplasts were situated at locations within the mesophyll at which both light levels and carbon dioxide availability were optimized by the appropriate combination of leaf orientation and structure. The observation that mesophyll cell surface area, chlorophyll concentration, and photosynthetic activity per unit leaf thickness are not uniform across the leaf thickness indicates that certain strata of the leaf may experience an optimum overlap of the opposing light (from above) and carbon dioxide (from below) gradients (Terashima and Hikosaka 1995). Evaluation of the relationship among leaf thickness, stomatal distribution, and whole-leaf photosynthesis could provide ecophysiological evidence for the importance of the overlap of light and carbon dioxide gradients inside the leaf.

The interaction of leaf orientation and structure

If leaf orientation and structure do interact to regulate sunlight absorption and distribution inside the leaf, then the structural asymmetry identified above (e.g., epidermal lens cells and palisade cells beneath the upper leaf surface of horizontal leaves) should correspond to the quantity and type of sunlight incident on each leaf surface. The focusing capabilities of epidermal lens cells require direct-beam sunlight (diffuse light is poorly focused by any lens), whereas palisade cells, if they function to propagate light deeper into the leaf, should occur beneath the leaf surface with greatest incident light. If carbon dioxide is to be supplied adequately to the increased mesophyll cell area in sun leaves, then the corresponding increase in leaf thickness should be accompanied by a more equal distribution of stomata on both leaf sides. However, few ecological studies have related the occurrence of these structural differences in leaf symmetry, thickness, and stomatal distribution with differences in incident light between the two leaf surfaces under natural field conditions.

One might also expect to find changes in leaf structure that would

diminish light absorption when a plant is experiencing other sources of stress—that is, when light is not limiting but temperature, water, or nutrients may be. Numerous studies have documented the detrimental impact of high light on photosynthetic performance, especially when a plant is under stress from other environmental factors (Baker and Bowyer 1994). For example, one rarely observes leaves of any species oriented perpendicular to full sunlight, unless leaf temperatures are low and transpirational water is abundant (Smith 1978). High incident sunlight will result in leaf wilt (midday wilt) even for plants whose roots are in water-saturated soil (Young and Smith 1980).

One of the best-documented observations of ecological patterns in leaf structure, already mentioned above, is the ability of most species to develop sun leaves under high sunlight exposure (e.g., Boardman 1977, Hansen 1917). In general, sun leaves are smaller in dimension (at least width, if not also length) but greater in thickness (e.g., De Soyza and Kinkaid 1991, Johnson 1978, Nobel 1991, Smith 1978). This reduced leaf dimension in sun leaves generates a significant increase in convective heat dissipation, an important factor for plant survival in drier, high-sun habitats, where overheating and high transpiration rates are detrimental (Gates 1980).

The greater leaf thickness characteristic of sun leaves results in a substantial increase in mesophyll cell surface area for carbon dioxide absorption, providing a structural mechanism for the observed increases in photosynthesis per unit leaf area, even though photosynthesis per unit leaf biomass may remain unchanged (Nobel 1980). A greater mesophyll cell area also generates greater water-use efficiency because of the substantially greater impact on carbon dioxide uptake than transpirational water loss. For species native to the most sun exposed, stressful habitats (e.g., desert shrubs, subalpine and boreal conifer trees), smaller, thicker leaves become almost cylindrical, with a more inclined leaf orientation. Similarly, photosynthetic stems commonly replace true leaves in evergreen shrubs of hot deserts, and

the frequent appearance of species with leaf and stem succulence (e.g., cacti and euphorbs) are further examples of the occurrence of cylindrical geometry in highly stressful habitats. (We address the functional significance of a cylindrical leaf form in terms of light and carbon dioxide processing for photosynthesis in the next section.)

Most terrestrial plant species with thin, laminar leaves have many more stomata on the lower side of the leaf than on the upper side (i.e., they are hypostomatous), although a significant fraction (including most grasses) have almost equal numbers of stomata on both leaf surfaces (i.e., they are amphistomatous; Meidner and Mansfield 1986). Only a few species with thin, laminar leaves have stomata exclusively on the upper leaf side (e.g., lily pads; Brewer and Smith 1995). Increased leaf thickness has been associated with a more equal number of stomata on both leaf surfaces for numerous species and taxa (Parkhurst 1978). Mott and Michaelson (1991) reported that increased incident light generated an increase in both leaf thickness and the number of stomata on the upper leaf surface in *Ambrosia cordifolia*. Having stomata on both sides of a thicker sun leaf may increase the supply of carbon dioxide to the mesophyll cells (Mott et al. 1982, Parkhurst 1994, Parkhurst and Mott 1990). These studies provide evidence that the presence of stomata on both leaf surfaces greatly enhances carbon dioxide supply to the greater mesophyll cell area found in thicker sun leaves, both of which may be necessary to support the greater photosynthetic rates per unit leaf surface area. Thus, both stomatal distribution and mesophyll cell area contribute to the higher rates of photosynthesis in sun leaves.

In a recent study, leaf structural and orientational data were collected for numerous evergreen species from five communities in Western Australia to evaluate possible associations between leaf structure and orientation (Smith et al. in press). These communities occur along opposing gradients in annual rainfall and daily incident sunlight due to an increase in understory species in the more mesic communities. At the time of

sampling, the five communities were composed of a high diversity of evergreen species only, whose leaves must endure seasonal drought (Beard 1990, Pate and McComb 1982). Such stress “tolerators” may be particularly indicative of adaptive relationships between leaf form and function (Fahn and Cutler 1992, Levitt 1980).

For the five Australian communities, strong positive correlations occurred between total daily sunlight and the proportion of species in a given community with thicker leaves, more cylindrical leaves, an inclined leaf orientation, palisade cell layers on both leaf sides, and stomata on both leaf sides (Smith et al. in press). Also, the presence of palisade cell layers on both leaf sides was correlated more strongly with a lower ratio (top-to-bottom) of incident sunlight than with the total amount of sunlight incident on the upper leaf surface only. By contrast, the number of species with distinctly bicolored leaves (with the top side darker than the bottom side) was greater in the more mesic, shaded communities. Because these understory species also had typical shade leaf structure, leaf bicolored leaves was strongly correlated with the thin, laminar leaf structure and horizontal leaf display. Similarly, leaf bicolored leaves was nearly ubiquitous in understory plants of the subalpine zone of the Rocky Mountains (Smith 1981).

Corresponding changes in leaf orientation and structure in response to seasonal changes in stress is another example of the strong interaction between leaf structure and orientation. For example, the numerous drought-deciduous species in the deserts of the southwestern United States develop large, ephemeral leaves with horizontal orientation soon after rainfall (Beatley 1974). As the soil dries, these initial leaves are replaced by smaller, more inclined leaves. With increasing soil dryness, numerous species shed these leaves and only green stems remain, generating a more inclined arrangement of curved photosynthetic surfaces within the crown. Smith and Nobel (1977, 1978) also reported that high incident light had the greatest effect on leaf morphology (e.g., size, thickness, pubescence) and

Table 1. Influence of incident sunlight and stress level of the habitat on leaf orientational and structural characteristics and on photosynthetic potential in 234 species (86 families) of native plants (sampled predominantly from five Western Australia communities). Modified slightly from Smith et al. 1997.

Leaf form	Environmental conditions			
	High sun, ^a low stress ^b	High sun, high stress ^b	Low sun, ^a low stress	Low sun, high stress
Orientation	Horizontal; tracks the sun	Vertical or cylindrical; avoids the sun	Horizontal	Horizontal
Top-to-bottom ratio of incident light	>3.5 ^c	<2.0	<3.5	2.5–3.5
Thickness (mm)	>600	400–600	<400	<300
Thickness-to-width ratio	<0.1	>0.1	<0.1	>0.1
Morphology	Large laminar broad-leaf	Small and cylindrical	Large laminar broad-leaf	Small linear or laminar broad-leaf
	Hypostomatous and amphistomatous ^d	Amphistomatous	Hypostomatous	Hypostomatous
	Structures to protect abaxial stomata; no bicoloration	No bicoloration	Bicoloration	Weak bicoloration
Anatomy	Upper palisade layers	Upper and lower palisade layers	Single or no palisade layer	No palisade layer
Maximum photo- synthetic potential ^e	1	2	3	4

^aDaily incident sunlight values computed over a 12-hour day were considered “high” if photosynthetically active radiation (PAR) was over 40 mol · m⁻² · d⁻¹ (as measured by a horizontal sensor) and “low” if PAR was less than 10 mol · m⁻² · d⁻¹.

^bStress was considered “high” if annual precipitation was less than 7 cm and “low” if it was greater than 10 cm.

^cAll values indicated for each category are rounded off to the nearest significant figure (e.g., to the nearest 100 for leaf thickness).

^dLeaves were classified as hypostomatous if more than 70% of the total leaf stomata were on the leaf underside; otherwise, they were classified as amphistomatous.

^eRelative ranking: 1 is greatest and 4 is least.

anatomy (mesophyll cell surface area and palisade development) in several drought-deciduous shrubs. However, high light and temperature combined with low water stress generated the thickest leaves. Thus, sunlight exposure and the level of water stress all interacted to significantly influence leaf structure. Körner et al. (1989) came to similar conclusions about the effects of temperature and light on leaf structure in high-elevation plants of the Central Alps.

Table 1 and Figure 2 present a synthesis, based on four generalized permutations of sunlight exposure and stress level in a habitat, that associates leaf orientational and structural characteristics with photosynthetic potential. Plant species that have leaves with the greatest photosynthetic capacity occur in high-light, low-stress situations and have corresponding orientational and structural features that generate high photosynthetic rates—that is, horizontal, thicker leaves with multiple palisade layers on the leaf side facing the sun, and a more equal number of stomata on both leaf sides. As sunlight and stress increase, leaf orientation becomes more inclined, with re-

duced sunlight interception, whereas leaf structure becomes more symmetrical (e.g., palisade cells occur on both top and bottom of mesophyll). With excessive sunlight exposure and stress, leaves become cylindrical, and the resulting radial diffusion eliminates the need for asymmetry in internal anatomy. For species adapted to low-light regimes (i.e., that have horizontal, thin leaves with no palisade cells, and stomata only on the leaf underside), photosynthetic potential is low (Table 1 and Figure 2). These differences in leaf structure and photosynthetic potential can change within the same plant or among plants of a given habitat, according to seasonal changes in sunlight exposure or stress.

Evolutionary perspective

The simplest explanation for the patterns in leaf structure and orientation discussed above is that during their evolution, terrestrial plants responded to the amount of sunlight and stress in a given habitat by evolving leaf structural properties in concert with leaf orientational capabilities (Table 1 and Figure 2). This interactive evolution between leaf

orientation and structure probably began in heavily shaded, humid microsites that were close to the ground (Thomas and Spicer 1987). The evolution of thin, laminar, horizontal leaves led to the most efficient interception of sunlight.

The restriction of stomata to the underside of shade leaves may have been necessary to prevent photo-oxidative damage to the chlorophyll-containing guard cells in the epidermis (Baker and Bowyer 1994). Even today, only extreme shade plants have been reported to have abundant chloroplasts in the upper epidermis (Lee 1986), and most species with stomata on the upper leaf surface that are exposed to direct sunlight have guard cells sunken in pits and covered by epidermal projections, such as highly reflective pubescence (Uphof and Hummel 1962). Moreover, stomata on the underside of horizontal leaves in wind-sheltered microsites experience much higher humidity, due to the buoyancy effects on water vapor; thus, transpiration is substantially lower for the same degree of stomatal opening and photosynthetic carbon dioxide gain (Foster and Smith 1986).

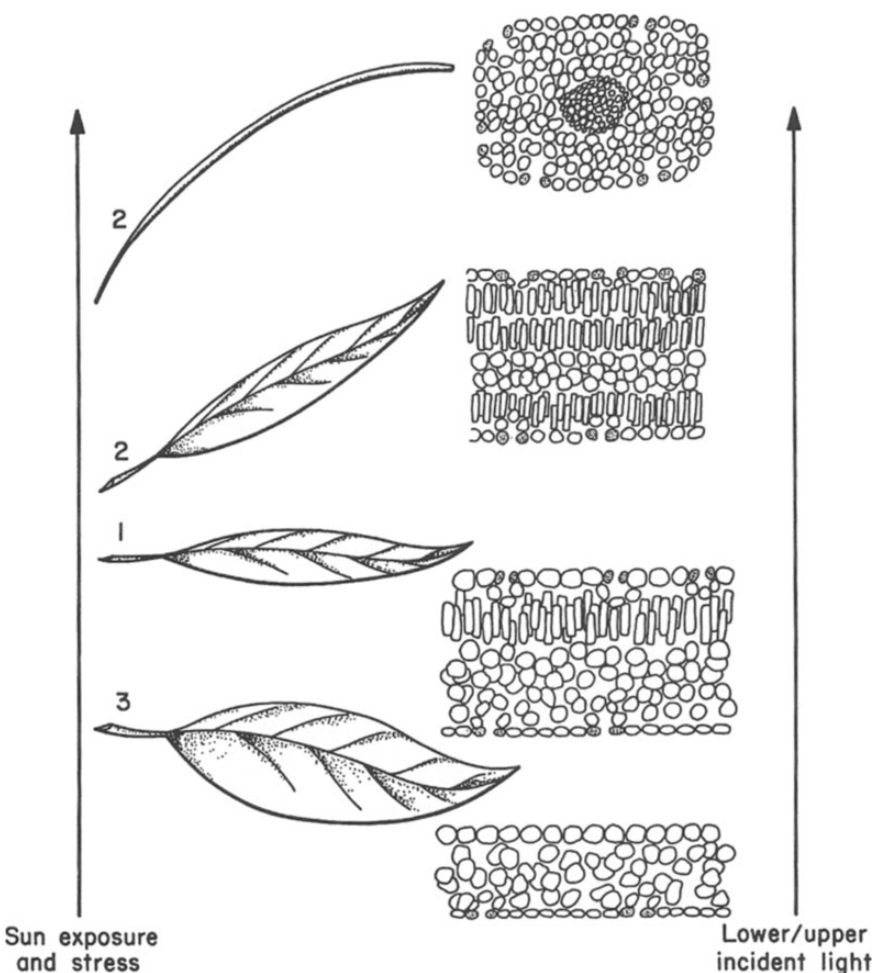


Figure 2. The interaction between leaf structure and orientation, and the amount of sunlight incident on the top and bottom of the leaf, according to the environmental conditions listed in Table 1. Numbers correspond to the rankings that are given for photosynthetic potential in Table 1, and the cross-sections show the corresponding structural and orientational features of each type of leaf.

Shade species would also benefit by evolving leaves with more spherical epidermal cells in the upper epidermis for enhanced light gathering and more shallow focal points (i.e., a thin leaf), as well as from a bicolored leaf with an internally reflective lower epidermis for greater light trapping (Table 1 and Figure 2). There is also evidence that stomatal opening and closing in hypostomatous shade leaves occur in response to the much greater amount of sunlight that is incident on the upper leaf surface (over 20-fold greater) and propagates to the lower epidermis, where the stomata are present (Smith 1981). This scenario implies that the guard cells of these abaxial stomata respond to the light incident on the upper, opposite leaf surface, where few, if any, stomata are present. This stomatal response to light absorbed

from the upper leaf surface would have enabled a better coupling between available light for photosynthesis (predominantly from above) and carbon dioxide supply from the lower leaf surface.

An internally reflective lower epidermis (leaf bicolored) would ensure that this propagated light would not escape the leaf interior. More spherical epidermal cells and bicolored leaves would act to enhance light collection in a light-limited habitat and retention of absorbed light within the leaf, respectively. Thus, in low-light environments, the evolution of thin, horizontal, bicolored laminar leaves with stomata limited to the leaf underside was probably the result of selective pressure for maximizing light capture, avoiding the harmful effects of exposing stomata (with their chlorophyll-containing

guard cells) to direct sunlight, and minimizing transpirational water loss. Internal distribution of absorbed light and carbon dioxide was probably not a problem for such thin leaves. This scenario may be representative of the first vascular plants, which successfully exploited atmospheric carbon dioxide in low-light, humid environments that were contiguous with aquatic habitats (Thomas and Spicer 1987, Ziegler 1987).

As land plants evolved to tolerate and use higher levels of incident sunlight, leaf structure evolved toward the so-called sun leaf (Esau 1977). Although it was an advantage to present a smaller leaf dimension to the wind to enhance convective cooling (e.g., De Soyza and Kinkaid 1991), sun leaves also became thicker, with the addition of palisade cell layers on the upper surface. By increasing the absorbing area for carbon dioxide in the mesophyll and allowing for more efficient light propagation deeper into a thicker leaf, these palisade cell layers enabled increased photosynthesis per unit leaf area. However, the evolution of thicker leaves in high-sun microhabitats may have presented a new problem—how to efficiently use absorbed light coming from the upper leaf surface, while carbon dioxide is diffusing from the opposite surface.

Maximizing photosynthesis per unit leaf biomass requires that both carbon dioxide and light be distributed efficiently within the leaf. Although in thick-leaved species, stomata are more frequent on the upper side of the leaf than they are in thin-leaved species, in concert with the greater photosynthetic capabilities and carbon dioxide demand of thicker leaves, guard cells of thick leaves still may require protection from full sun by the cuticle or such epidermal features as pubescence and sunken pits (Fahn and Cutler 1992, Uphof and Hummel 1962). Another strategy to avoid damage from excessive sunlight is a more inclined leaf display, which probably occurred early in the evolution of sun leaves (Gamon and Pearcy 1989). In addition, as leaves became more inclined (with lower and more equal amounts of daily sunlight incident on both leaf surfaces), the addition of epider-

mal lens cells and palisade cell layers to both sides of the leaf was necessary for more effective capture, propagation, and distribution of light throughout the mesophyll. As described previously, stomata on the upper leaf surface appear to be most common when leaves are thicker and leaf orientation is inclined, so that incident light on the chlorophyll-containing guard cells is reduced. It remains to be determined whether epidermal cell shape and focusing properties can also adjust to incident light level.

In environments with the greatest sun exposure, especially those with concurrent stresses, such as water limitation, the ultimate evolution of leaf form appears to be toward a more cylindrical instead of laminar leaf (Table 1 and Figure 2). The reduction in leaf width enhanced convective heat dissipation, and the surface curvature reduced incident sunlight; together, these lowered leaf temperatures and transpiration and may have led to the evolution of the more radial, cross-sectional geometry of cylindrical leaves. Incident light on a cylindrical leaf is substantially reduced over the leaf surface, regardless of leaf orientation, because of the increased angle of incidence (i.e., the cosine law) generated by the curved leaf surface (Jordan and Smith 1993, Smith and Brewer 1994). However, with even a slight inclination away from the sun, a leaf with a curved surface experiences a compound reduction in incident sunlight. In addition, leaves with a higher volume-to-surface area ratio desiccate more slowly and have greater mechanical strength to withstand associated factors such as high wind and herbivory (e.g., spiny leaves).

The cylindrical shape and radial geometry of leaves of high-light species in high-stress habitats may also create advantages that are related directly to the distribution of light and carbon dioxide inside the leaf. Extant species with cylindrical leaves (e.g., conifers) tend to have a more even distribution of stomata over the entire leaf surface, possibly as a result of the reductions in incident light described above. Stomatal guard cells (with chloroplasts) will receive less intense light on a curved surface. The radial diffusion characteristic of

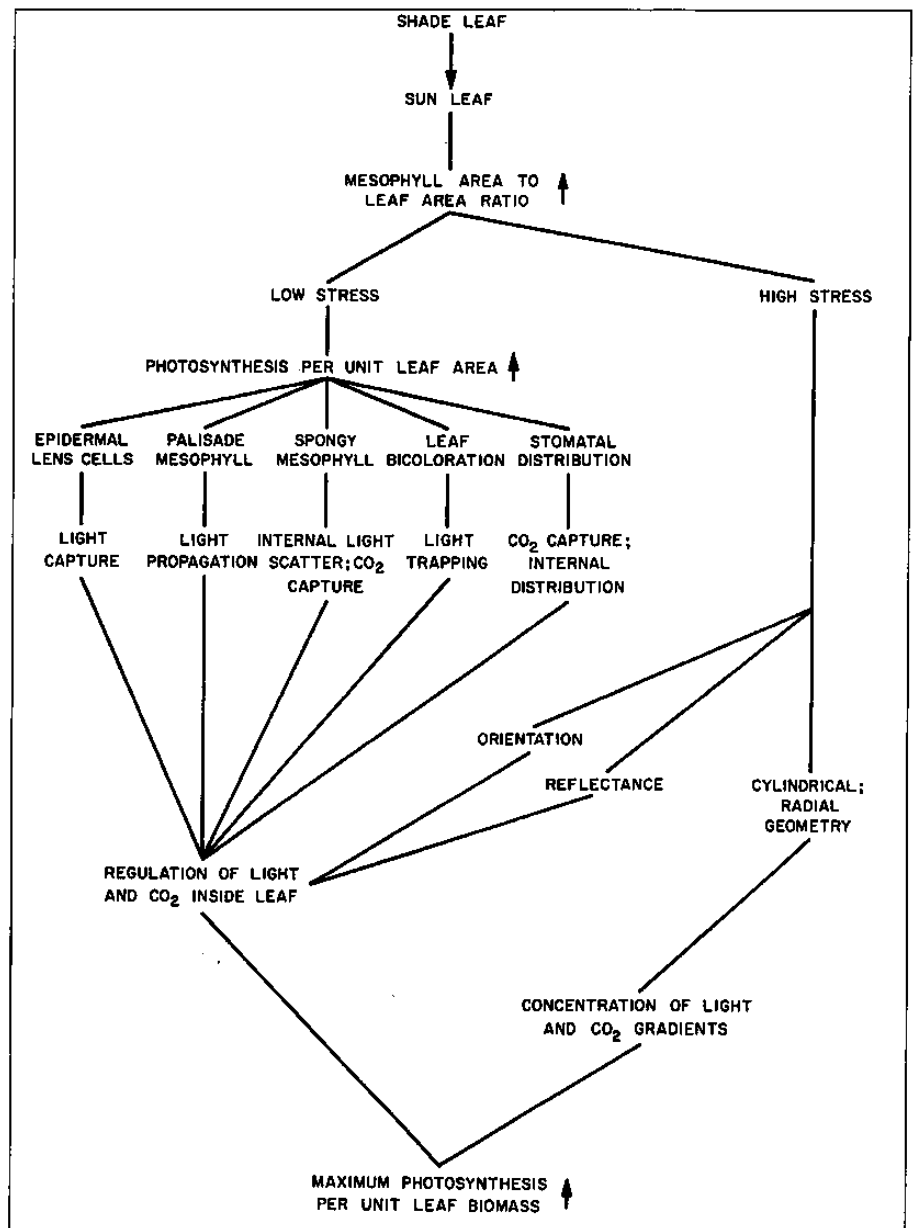


Figure 3. Leaf structural components involved in the evolution of sun leaf photosynthesis. The interaction of leaf structural characteristics influences photosynthetic light and carbon dioxide capture and processing, photosynthetic rate per unit leaf area, and, ultimately, photosynthesis per unit leaf biomass. During the evolution of shade to sun leaves, the development of a thicker leaf with greater mesophyll area and carbon dioxide assimilation capabilities led to greater photosynthesis per unit leaf area. However, this change must have been accompanied by the evolution of numerous other structural features (e.g., epidermal lens cells, palisade and spongy mesophyll cell layers, leaf bicoloration, and stomatal distribution patterns) that contributed to the regulation of internal light and carbon dioxide gradients for maximum photosynthesis per unit leaf biomass. Leaf orientation away from the sun, leaf reflectance of incident sunlight, and the evolution of more cylindrical leaves with radial diffusion properties probably reflect the extent to which plants leaves have evolved to cope with excessive sunlight and stress. See text for a more detailed explanation.

cylinders dictates that both absorbed light and carbon dioxide should become more concentrated with greater distance from the epidermis (Nobel 1991). Thus, light propagation and

carbon dioxide diffusion to greater depths in a thicker leaf should be considerably less of a problem in a cylindrical leaf than a laminar one. Accordingly, leaf bicoloration, pali-

sade cell layers, and such epidermal features as pubescence may be unnecessary and, thus, are rare for species with cylindrical leaves (Table 1).

Conclusions

As Figure 3 indicates, numerous leaf structural parameters appear to influence whole-leaf photosynthesis through effects on light capture at the leaf surface, as well as via its propagation and attenuation within the leaf. These structural adaptations are strongly linked to leaf orientation and to the total sunlight incident on both leaf surfaces (Table 1 and Figure 2). The evolution of greater leaf thickness in sun leaves and corresponding structural asymmetry according to leaf inclination is strong evidence that both leaf orientation and structure influence light and carbon dioxide processing at the whole-leaf level. In the case of a characteristically thin shade leaf, for which light, and not carbon dioxide supply, is the primary limitation to photosynthesis, this optimum zone of light and carbon dioxide overlap may be broader and closer to the center of the leaf (Figure 1). Moreover, shade-type plants grow in locations (e.g., forest understories) that are sheltered from wind (as well as sun) and in which carbon dioxide therefore commonly accumulates to above-normal levels, lessening the problem of carbon dioxide supply.

As a leaf becomes thicker with higher sun exposure, and stomata and palisade cell layers become common on both leaf sides (broadening the zone of light and carbon dioxide overlap inside the leaf), photosynthesis per unit leaf area increases and, therefore, so does light-use efficiency (the amount of sunlight absorbed per carbon dioxide that is assimilated for photosynthesis; Figures 1 and 2). The presence of epidermal lens cells and palisade cell layers generates a more efficient distribution of internal light and a greater photosynthetic rate per unit leaf biomass, or photosynthetic efficiency.

As sunlight and stress become excessive, leaf orientation becomes more inclined relative to the sun, with a concomitant increase in leaf symmetry (e.g., palisade on both leaf sides). In the most sun exposed, high

stress habitats (or at the most stressful times of year), leaves become more cylindrical and more inclined in orientation, reducing the negative impact of high sun exposure and eliminating the need for palisade cells due to the concentrating effects of radial diffusion on internal light and carbon dioxide (Figures 2 and 3).

Future studies that attempt to explain the relationships between leaf form and function, as related to photosynthetic performance, should be directed toward identifying the mechanisms that control light and carbon dioxide gradients inside leaves, as well as the corresponding effects of these mechanisms on whole-leaf photosynthesis (Figure 3). The relationship between leaf form and light and carbon dioxide capture and processing that we have described in this article provides an important perspective for evaluating the impact of future global climate change scenarios (e.g., elevated atmospheric carbon dioxide) on the survival of species with different leaf forms. For example, the proliferation of species with leaves whose photosynthesis appears to be limited by carbon dioxide capture and processing (i.e., in which stomatal distribution and leaf thickness are constraints) may be favored in a high-carbon dioxide atmosphere.

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