

Progress in Coupling Plant Form and Photosynthetic Function

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ABSTRACT Photosynthetic adaptation in terrestrial vascular plants involves a complex interaction of components that extend across a broad structural and spatial hierarchy, often functioning in concert with one another at multiple scales. Thus, understanding the evolutionary mechanisms leading to these adaptations requires evaluation across the entire spectrum of plant form from the chloroplast to the landscape. Adaptive traits across this structural/spatial hierarchy can emerge at any level and then feed-back or feed-forward to cause adaptive changes at adjacent levels. Today's sophisticated instruments enable direct measurement of photosynthesis at most of these hierarchical levels and across phylogenetic boundaries. As a result, identification of functional properties in plant form (architectural and spatial), independent of physiological processes, is becoming a reality. In this review we focus on one apparent theme across this hierarchy of organizational complexity—the impact of plant form on the distribution of incident sunlight to photosynthetic surfaces, and the transfer and processing of mass nutrients (e.g. CO₂ and water). The trade-offs and net effects of these exchange processes drive photosynthetic adaptation, and appear to be related to economic efficiencies rather than simply magnitude.

INTRODUCTION In recent reviews of photosynthetic adaptation in vascular plants, structural traits have become recognized as a more common venue for adaptation than changes in the highly conserved biochemical pathways of photosynthesis (Smith et al. 2004). Despite this recognition, considerably less attention has been given to the functional impacts of plant “form” on photosynthetic performance compared to the biochemistry of the photosynthetic pathways. For the current review, plant form is defined broadly to include size, shape, orientation, and spatial arrangement of photosynthetic units that occur at any particular structural/spatial level (e.g. chloroplasts inside a leaf, leaves inside a canopy, or individual plants across the landscape; Figure 1). It is important to note that, although the leaf is most often the photosynthetic unit of interaction with the environment, the individual plant (within the context of the population) is the functional evolutionary unit. Thus, any level of the organizational hierarchy can have strong impacts on

a functional character such as photosynthetic performance and, thus, the fitness of a species and, ultimately, accompanying ecosystem processes (Figure 1).

When scaling upward from the organism level through the population, community, and landscape levels of plant form, it is important to recognize that both plant architecture and spacing can influence important environmental factors (e.g. sunlight incidence, temperature, moisture), as well as a host of other microclimatic factors that influence photosynthesis less directly. For example, germination and establishment of seedlings according to microsite preference can dictate spatial relationships for future adults at the population, community, and landscape levels (Germino and Smith 2000, Smith et al. 2003). Older plants can then feed back to seedling germination and survival by creating additional microsites for subsequent generations of seedlings (e.g. nurse plant and facilitation effects). The purpose of the present review is to highlight and summarize progress being made concerning the relationship between plant form and photosynthetic function across the full spectrum of the structural

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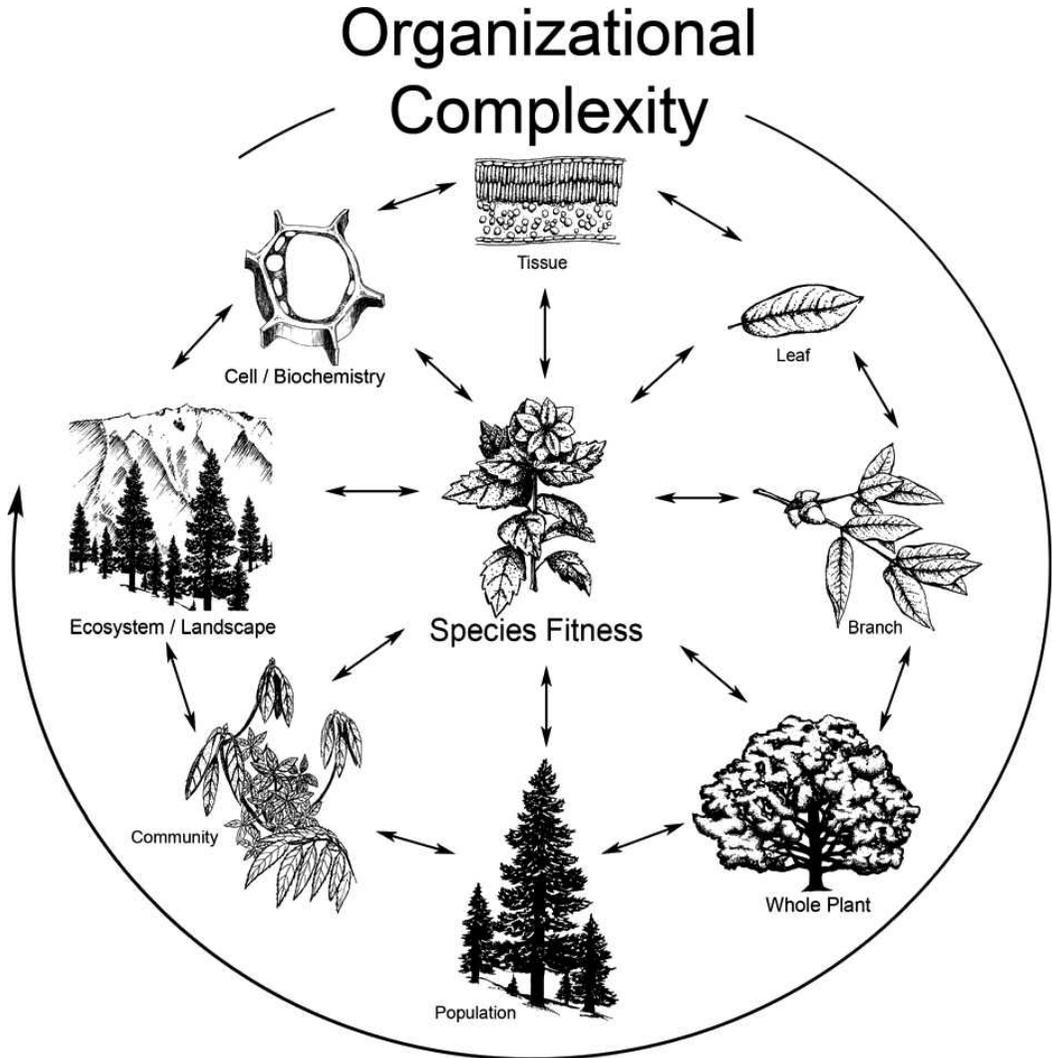


Figure 1. Organizational hierarchy of feed-back and feed-forward relationships involved in photosynthetic adaptation across the full spectrum of plant form from the cellular to the landscape and ecosystem levels.

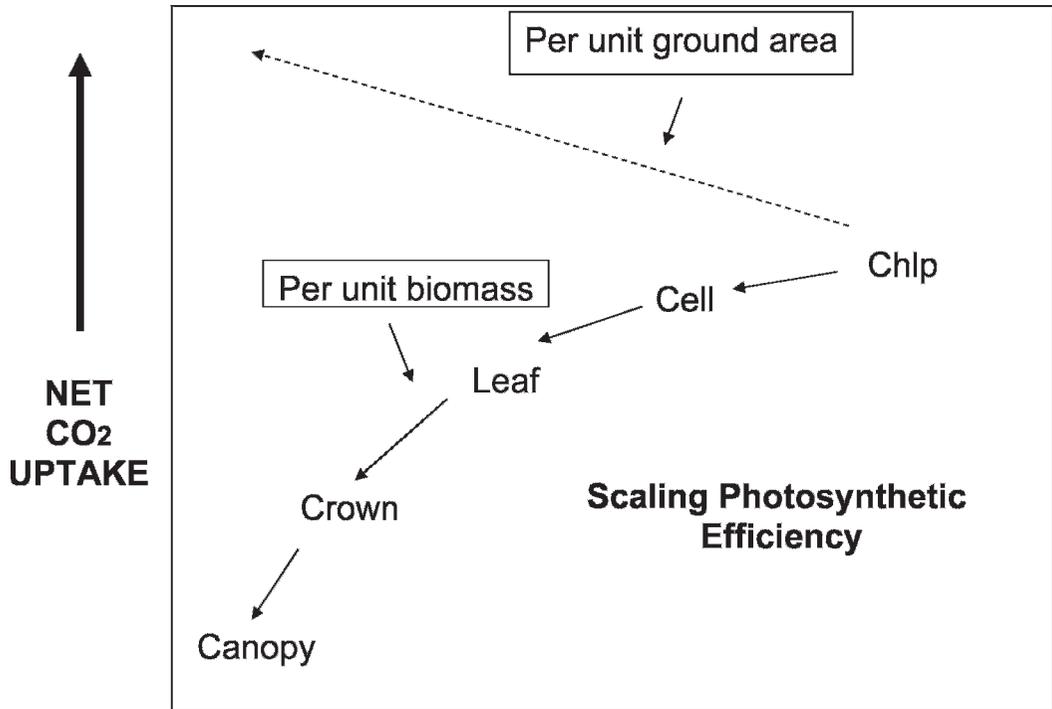
and spatial hierarchy found in terrestrial vascular plants (similar to the approach in Smith et al. 2004). In general, the challenge of increasing photosynthetic carbon gain for a species, despite decreases in photosynthesis per unit leaf area or biomass upscale in the architectural hierarchy, is the conceptual basis of evaluating photosynthetic adaptation at higher levels of organizational complexity (Figures 1–3).

The economics of investment versus gain

Fundamental to the evolution of plant functional traits at any spatial scale is the benefit of that trait (usually in terms of photosynthetic carbon gain) relative to the metabolic

costs involved in its development, display, and/or maintenance. Cost-benefit analyses are typically computed over the lifetime of a photosynthetic unit, keeping in mind that both may vary with habitat and/or location within the canopy (e.g. Küppers 1989, Wright et al. 2004). Furthermore, net costs and benefits must be viewed within the context of several spatial scales, not simply at the leaf-level alone. This concept is commonly overlooked in studies on architectural adaptation, which is understandable given the complexity introduced by multiple scales.

The energy and biomass invested in producing photosynthetic tissue can be estimated from calorimetric analyses where total bio-



Plant Hierarchy of Organizational Complexity

Figure 2. Photosynthetic efficiency expressed on a unit area or mass basis declines as structural/spatial complexity increases across the organizational hierarchy of plant form. Mutual shading among leaves and stems results in a corresponding decline in STAR (silhouette to total area ratio) that can account for much of this decline in efficiency. Moreover, greater plant size and/or spacing constraints result in the need for greater stem biomass for efficient leaf display to incident sunlight. Possible advantages due to aerodynamic, boundary air layer effects, e.g. leaf warming and the trapping of water vapor or CO₂, are also possible, except less studied. However, the exact shape of these curves is known for only a few comparisons over only a portion of this scale. The evolution of plant form at all structural/spatial levels moves toward a flattening of the per-unit-biomass curve and an increase in the slope of the per-unit-ground area curve.

mass is converted into total energy units of heat production, or calculated from a biochemical analysis of synthetic pathways and corresponding energetic requirements for the synthesis of the organic compounds involved. However, such instantaneous, and usually leaf-level, approaches overlook the indirect costs rendered by scales above and below those directly measured, e.g. self-shading, increased costs of support, and competitive interactions. Some of these problems may be circumvented by using experimental approaches which consolidate factors taken from multiple scales. For example, the ratio of total leaf-to-stem biomass can be used to estimate an index of leaf display efficiency on a whole-plant basis, although the amount of leaf biomass actually exposed to sunlight would be a better estimate of display efficien-

cy (Fournier et al. 1996). For increasingly complex levels of organization, the amount of leaf area per unit ground area (leaf area index, LAI) of a particular plant, plant population, or community, can be used to estimate the relative potential for photosynthetic carbon gain (net primary production, see Running et al. 2004), plus the corresponding amount of water and nutrient used per unit ground area across a landscape (e.g. water and nutrient use efficiencies at the community level, Figure 2).

Categorizing form and function

In addition to evaluating plant economics by comparing metabolic costs versus photosynthetic contributions, the specific traits involved can provide a basis for classifying plants into functional groups that associate



Figure 3. Moving from the leaf to shoot level in a conifer tree (e.g. *Abies lasiocarpa*) demonstrates the emergent dominance of the shoot-level (left: shade shoot, right: sun shoot) for determining such important factors as sunlight incidence and temperature effects on individual needles (see text).

carbon gain efficiency, plant form, and specific habitat type (Chapin et al. 1993, Reich et al. 1998b, Ackerly et al. 2002, Berry and Roderick 2002, Wright et al. 2004, Domingues et al. 2007, Moles et al. 2008). For some time now, carbon exchange has been measured and evaluated on a higher level of plant form than the leaf, all the way to the stand/community, landscape and ecosystem levels (e.g. carbon flux per unit ground area). It is hoped that these relatively new instruments and methodologies will enable identification of structural/functional relationships in plant form, and the identification and quantification of the terrestrial carbon sinks, sources, and storage (sequestration) components of the Earth (Wright et al. 2006, Pugnaire and Valladares 2007). A recent example of this application is the identification of functional groupings for invasive versus native species— invasive species tend to exhibit an increased capacity for capturing high sunlight levels, and exhibit high photosynthetic rates accordingly, relative to native species (Moles et al. 2008). However, some recent attempts at identifying functional plant groups have fallen short of expectations (Wright et al. 2006), probably due to the lack of information about specific, mechanistic associations between plant form and ecophysiological function, especially photosyn-

thetic performance. Ultimately, important ecophysiological functions will be linked to easily recognizable and measurable characteristics of plant form, along with corresponding global distribution patterns among different species (Reich et al. 1999). Otherwise, the very expensive and labor-intensive ecophysiological techniques currently employed on a world scale (e.g. eddy co-variance towers for measuring CO₂ exchange at higher architectural levels) will continue to be required before a complete closure of the Earth's carbon budget is possible. The following sections will address the functional significance of plant form separately according to each architectural level, while recognizing the important connectivity between the entire organizational hierarchy that defines the plant kingdom (Figures 1 and 2).

THE LEAF The leaf is the primary functional unit of photosynthesis for most terrestrial, vascular plants, justifying the traditional focus on this level of the plant architectural hierarchy (see Gutshick 1999 for review). However, traditional methods for estimating plant carbon gain based on leaf-level measurements alone overlook several important factors regarding plant form, e.g. variations in sunlight incidence on leaves throughout the crown or canopy due to mutual-shading

and variable leaf orientation. Such variations can easily lead to miscalculations in whole plant carbon gain, especially considering that many measurements of photosynthetic carbon gain for individual leaves are derived from standard gas exchange instruments with light sources oriented directly perpendicular to individual leaves (e.g. LED-fitted leaf cuvettes). Perhaps the only situations in which such protocols would be appropriate would be for species that are solar trackers, plants with no self-shading, or plants in diffuse (e.g. shade) light environments. However, there are several strategies for circumventing this problem. For example, one may first reference leaf angles to horizontal or vertical, and then the angle and corresponding intensity of incidence of the sun's rays can be estimated (via Cosine Law) from measurements of sunlight incidence on a horizontal or perpendicular planar sensor. These values can then be used to calculate photosynthesis accordingly using measured light-response curves of photosynthesis. This strategy is effective for calculating photosynthesis for individual leaves, or for whole plants or canopies by estimating sunlight incidence on leaves of different orientations. However, even this approach does not include the directional quality (e.g. direct versus diffuse sunlight), which can also strongly affect light absorption by individual leaves (Brodersen and Vogelmann 2007).

In addition to effects on sunlight incidence, leaf exposure and orientation to the upper sky hemisphere is also important because the long-wave thermal radiation from a cold night sky can significantly influence minimum leaf temperatures and seasonal frost occurrence (e.g. Jordan and Smith 1993; Germino and Smith 2000, 2001). Besides direct effects on leaf temperature, night-time cooling (clear skies) can significantly reduce photosynthesis the following day via low-temperature photoinhibition of photosynthesis, photo-oxidative damage, and stomatal closure (Germino and Smith 2000). Smaller leaf size (related traditionally to sunlight exposure) has also been associated with nighttime sky exposure, and correspondingly, can lead to warmer leaf temperatures at night (Jordan and Smith 1995). Thus, exposure to both the sun and night sky can have significant impacts on photosynthetic performance, although the latter has received

comparatively little attention. As such, truly accurate estimates of carbon gain must factor in the negative effects of increased sky exposure on carbon gain as well as the positive. Many studies over-estimate seasonal carbon gain by basing models on sunlight regimes alone—estimating photosynthesis from light-response curves measured on warm (i.e. highest performing) days. A more accurate model would include a temperature component as well, referencing multiple curves derived following a range of night-time temperatures. In this regard, the interesting 'sleep response' (nyctinasty, leaf drooping and folding at night) of a large number of leguminous species deserves additional study (Ueda and Nakamura 2006).

Measuring the amount and nature of sunlight driving photosynthesis: a critical parameter

For the common laminar leaf form, estimation of light-interception can be estimated simply on a traditional, total leaf area (TLA) basis, especially if light distribution is homogeneous across the leaf's surface. However, for complex structures, i.e. non-laminar leaves, a shoot, crown, or canopy, the complexity of estimating quantitatively the incident sunlight levels over the total leaf surfaces becomes more complicated, constraining an accurate, quantitative comparison of functional characteristics like area-specific photosynthesis (Smith et al. 1991). For example, using TLA for a single conifer needle-like leaf, or for computing photosynthetic leaf areas at higher architectural scales (e.g. summing the leaf areas of individual needles), will usually lead to a large over-estimation of the actual sunlight levels striking individual leaves (as mutual shading effects are overlooked), as well as over-estimations of cosine and reflectance effects. For this reason, alternative measurement techniques such as projected leaf area (PLA) and silhouette leaf area (SILA) should be employed for more complex structures and spatial scales. PLA is the shadow area projected when both the leaf and the projection surface are perpendicular to the sun's rays, while SILA represents the area of the shadow cast on a perpendicular surface positioned behind a leaf (or other structure, such as a branch or canopy) in its natural orientation to the light source. Because PLA represents maximum light interception, and SILA represents actual light

interception, ratios of SILA to TLA ratio (or STAR—silhouette to total leaf area ratio) can be useful for evaluating the effective absorption and intensity of incident sunlight (e.g. Carter and Smith 1985). Maximum STAR values for broadleaves approach 0.5, and for more cylindrical, needle-like leaves, about 0.3. These values can decrease significantly at higher structural scales (e.g. shoot, crown, and canopy) due to orientation and mutual shading effects. One should note, however, that when using cast shadows for SILA measurements, care must be taken so as not to project fuzzy edges on the cast shadow due to penumbra effects (Smith et al. 1989, Stenberg 1995, Cesscati and Niinemets 2004).

Estimates of sunlight capture measured either on a TLA, PLA, and SILA basis can yield significantly different photosynthesis values for complex leaf arrangements. For example, using total leaf area for conifer needle shoots can often lead to low estimates of the photosynthetic potential, because the leaves in the measurement chamber (assuming natural needle orientations) are not all exposed directly to incident light, but rather, differ greatly in orientation and exposure (Smith et al. 1991, Stenberg 1998). Use of PLA for needles detached from the measured stem length may result in a large overestimate of sunlit leaf area, ignoring natural needle orientation differences. Likewise, SILA of the measured shoot length may not account for mutual shading among needles in highly packed sun-shoots. Even simulated light levels over the entire surfaces of individual leaves with different geometries resulted in large differences in predicted photosynthesis based on photosynthetic light response curves (Jordan and Smith 1993). Therefore, ultimate comparisons of photosynthetic capabilities among different leaves and species require an accurate determination of the distribution of irradiance values over the entire leaf surface, and then integration (Jordan and Smith 1993). Photosynthetic estimations for leaves other than planar require all three measurements (TLA, PLA, and SILA) for a better evaluation of photosynthetic performance using standard CO₂ exchange methods (Smith et al. 1991). Until more studies incorporate all three of these leaf area measurements, a greater precision in characterizing species and plant form according to photosynthetic potential (e.g. conifer

shoots versus broadleaves) will not be possible at any structural or spatial scale.

Expressing photosynthesis: area, weight, or volume?

Meaningful comparisons of photosynthetic performance among species and habitats require uniformity in expressing photosynthesis, i.e. on a leaf area or weight (mass) basis. At the leaf level, photosynthesis is dependent on the leaf area exposed to sunlight (photon capture), but also the amount of biomass involved in the capture of sunlight and CO₂ for processing. For many decades, the amount of leaf surface area per unit leaf weight (specific leaf area, SLA) has been employed to characterize sunlight capture efficiencies and, thus, photosynthetic potential (e.g. Niinemets 2001). A simple example of this is the sun versus shade leaf, with shade leaves investing more biomass in display (leaf area available for photon capture) versus processing (cells and biochemistry available for processing) relative to sun leaves—hence a higher SLA. The reciprocal of SLA (the leaf weight to unit area ratio, or specific leaf weight, SLW) has been used to evaluate the photosynthetic potential per mass investment by a particular leaf (Ellsworth and Reich 1993). Whether one expresses photosynthetic performance in terms of SLA or SLW is simply a matter of emphasis—with SLA emphasizing photon capture potential, and SLW emphasizing investment. SLW is functionally important for quantifying efficiency of photon and CO₂ processing, and has been shown to be directly proportional to absorption of both by chloroplasts inside the leaf (Vogelmann et al. 1996, Smith et al. 1998). Even more precise estimates of biomass investment per unit leaf surface area are possible if non-photosynthetic tissues (e.g. cuticles, epidermal tissues, water storage cells) are eliminated from the leaf biomass measurement (Niinemets 2001). For example, more xeric sclerophyllous-leaved species have higher SLW due to more cell wall biomass per leaf biomass, not just tissue involved in photosynthesis (Read and Sanson 2003, Aranda et al. 2004). Beyond measurements of area and mass, leaf weight (mass) per unit volume (LWV) is useful for defining the photosynthetic potency of a leaf in terms of its density, thereby normalizing leaf thickness (Niinemets 2001).

SLA, SLW, and LWV may also be used to characterize photosynthetic efficiency at structural scales both above and below the leaf level. For example, by calculating SLA for an entire plant, one may quantify photon capture efficiency at the whole-plant, species level, which may be useful for classifying functional groups (Witkowski and Lamont 1991, Reich et al. 1998a and b). However, comparisons of SLA versus SLW seem to be a more meaningful, functional evaluation of species fitness when used on a whole-plant basis rather than on an individual leaf level. Scaling upwards, one must begin to account for factors beyond the leaf level that also directly affect carbon gain, such as the indirect costs involved in maintenance and display of an individual leaf (e.g. stem biomass required for appropriate leaf display). Total leaf mass or area per unit canopy volume can be useful in this regard, and may be used to quantitatively compare shoots, branches, crowns, and canopies in terms of not only light capture properties, but aerodynamic characteristics as well. Denser crowns and canopies (higher leaf mass per unit volume) will be less coupled to air temperature due to greater restriction of intra-canopy air flow.

Recent studies of the relative photosynthetic capabilities at the leaf level have also expressed photosynthesis on a unit area of chloroplast surface area appressed to the anticlinal walls of the mesophyll cells. This approach scales downward to the organelle, intracellular level to understand possible advantages for creating the shortest path for cytosol diffusion and, possibly, the greatest exposed surface area for photon interception, given the largely diffuse nature of absorbed sunlight within the mesophyll (see Evans et al. 2004a, 2004b for reviews).

Anatomical effects on CO₂ and photon capture
Considerable attention over the past century has been focused on the similarities in internal anatomy of sun and shade leaves for a diverse number of species across a broad phylogenetic spectrum. Typically, sun leaves are a smaller size but have thicker mesophyll compared to the larger, thinner leaves found in the shade, as well as distinct structures to maximize light and CO₂ absorption across a thicker lamina (i.e. palisade and spongy mesophyll cells, respectively). Higher photo-

synthetic rates for thicker sun leaves relative to shade leaves have also been documented for numerous species. These similarities in anatomical and photosynthetic adaptation across phylogenetic boundaries implicate a strong functional connection between leaf anatomy and photosynthesis. Furthermore, these differences in anatomical structure are now being integrated within such parameters as SLA, SLW, and leaf density, in order to increase accuracy of photosynthetic estimations at an even finer scale. An accumulating data set on leaf structural parameters such as these is now being used to predict ecosystem processes, although with limited success (Wright et al. 2006).

One of the first findings of a direct effect of internal leaf structure on photosynthesis in C₃ species was the relationship between internal mesophyll cell area (A_{mes}) and photosynthetic CO₂ uptake expressed on a leaf area basis (Nobel et al. 1975). This seminal finding attributed the high photosynthesis values found for thicker sun leaves purely to internal leaf structure, or the amount of mesophyll cell surface area beneath a unit area of leaf surface, implicating the increased surface area for absorption of CO₂ as the cause of the substantial increase measured in photosynthesis expressed per unit leaf area. Apparently, no changes in cellular biochemistry were necessary to accomplish the high photosynthesis characteristic of sun-type leaves. By adding more of the same cells, it was possible to increase leaf photosynthesis to the high levels measured in sun leaves of numerous species and habitats. In some cases, the amount of mesophyll area per unit of leaf area may also be increased simply by having smaller and more packed cells that can result in little change in mesophyll thickness (e.g. the desert shrub, *Encelia farinosa* A. Gray ex Torr). Regardless, photosynthesis expressed on a leaf area basis has been linearly correlated with this increased internal cell surface versus leaf surface area for thicker leaves. Biochemical changes of individual mesophyll cells may also contribute to differences in photosynthesis expressed on a leaf area basis, which can be revealed by expressing photosynthesis on a leaf mass or volume basis (Björkman 1981, Tatenno and Taneda 2007).

At a lower structural scale, mesophyll cells might also place chloroplasts nearer the cell

walls (decreasing liquid phase diffusion of CO₂ and reducing chloroplast shading) and thus accomplish greater photosynthetic potential without changes in mesophyll anatomy or photosynthetic biochemistry of individual cells (Brugnoli and Björkman 1992, Terashima and Hikosaka 1995; see Evans et al. 2004a for review). Though very little is known about the possible positioning and movements of individual chloroplasts in individual mesophyll cells, both have been observed to some degree (see Evans et al. 2004a). Chloroplasts do appear to adhere closely to mesophyll cell walls, thus shortening the diffusion pathway for CO₂, and may also reposition in order to either reduce or maximize mutual chloroplast shading (Brugnoli and Björkman 1992, Terashima and Hikosaka 1995). Although specific effects of chloroplast movements on whole-leaf photosynthesis have not been found (Gorton et al. 2003), evidence for photosynthetic protection against excessive photons and the prevention of photoinhibition has been reported (Kasahara et al. 2002). This approach is just one example of how scaling from one structural level to another can integrate function between levels.

In addition to the above, there now appear to be other anatomical factors associated with enhancing photosynthesis capabilities in sun-type leaves and their typical dorso-ventral asymmetry in structure where sunlight absorption is adaxial but CO₂ uptake abaxial (Smith et al. 1997). Internal leaf structure could involve the positioning and shaping of chloroplasts for better light capture and CO₂ uptake, while external morphology could involve the placement of stomata for improved CO₂ supply to the leaf interior, or the occurrence of leaf surface structures that alter sunlight absorption. First, thicker leaves are also associated with an increase in the degree of amphistomy (more equal number of stomata on both leaf sides) and, thus, a more uniform, isolateral supply of CO₂ to the leaf interior and greater whole-leaf photosynthesis (Mott and Michaelson 1991, Syvertsen et al. 1995). In fact, there now appears to be a control system reported for maize (C₄ species) that may tightly couple the incidence of sunlight on one leaf side with the stomata opening on the opposite leaf side, as well as an asymmetric CO₂ uptake capability on the sunlit leaf side with open stomata (Smith 2008, Soares et al. 2008).

Second, the more even distribution of absorbed sunlight throughout a thicker mesophyll requires greater photon propagation deeper into leaves that receive incident sunlight primarily on the upper, adaxial leaf surface. Currently, there is evidence that the classical anatomy of sun-type leaves, i.e. one or more palisade cell layers, functions to propagate absorbed photons more deeply and, thus, more evenly throughout the mesophyll (Vogelmann et al. 1996, Vogelmann and Han 2000, Vogelmann and Evans 2002). There is also the possibility that adaxial epidermal cells (which are generally clear) could act to focus and, thus, propagate light deeper into the mesophyll, and the spongy mesophyll is also particularly effective at scattering absorbed photons, increasing the probability of absorption by chloroplasts of mesophyll cells before escape through the leaf underside (Evans 1999). However, Brodersen and Vogelmann (2007) found no evidence for such focusing. During drought stress epidermal lens cells might also change shape, influencing their focal points and, thus, propagation of photons to different depths inside the leaf. There is also evidence that the lower epidermis of the lighter leaf underside is highly reflective, and effectively acts to prevent loss of photons through the lower epidermis (Woolley 1971, Lin and Ehleringer 1983, DeLucia et al. 1996). In total, these structural attributes for increasing photon absorption account for the light trapping and high level of brightness measured inside leaves with fiber-optic microprobes (Vogelmann et al. 1996) and microscopic fluorescence techniques for observing photosynthetic potential across the mesophyll (Vogelmann and Evans 2002). These functional possibilities, as well as the others mentioned above, need to be tested by experiments and further documentation.

Leaf form: structure and orientation

While leaf anatomy appears to have a strong influence on the internal processing of absorbed sunlight and CO₂ for photosynthesis, leaf orientation and corresponding light incidence on different leaf sides may function in concert with, if not dictate, both leaf anatomy and morphology influencing photosynthetic performance (Smith et al. 1997, 1998). Morphological differences typically include a lighter abaxial surface, resulting in an almost

ubiquitous leaf bi-coloration in terrestrial vascular plants that may act to reduce absorption of photons by the more photosensitive abaxial surface (Sun and Nishio 2001), as well as trap photons in the spongy cell layer (Smith et al. 1998). Red pigmentation is also commonly observed in abaxial surfaces of high light species, and is similarly suspected to protect sensitive abaxial surfaces from potentially damaging irradiance (Hughes and Smith 2007). Abaxial red coloration in understory species may also function in photoprotection, and some evidence exists that these pigments buffer internal light levels during potentially damaging, high-intensity sun-patches (Gould et al. 1995, Hughes et al. 2008). In contrast to horizontal shade leaves, more vertically-oriented leaves, especially at more sunlit, apical locations, tend not to show such strong red coloration or bi-coloration between the two leaf surfaces (Smith et al. 1997, 1998).

Leaf structure and orientation seem to have evolved in parallel within the overall framework of leaf form and the selective pressure for improved photosynthetic function (Smith et al. 1997, Werner 2002, Falster and Westoby 2003). The temporal- and intensity-related dynamism of incident sunlight striking a horizontal, laminar leaf is quite different over a day or year compared to the same leaf inclined away from horizontal, regardless of latitude (King 1998, Werner et al. 2001). Some of the photosynthetic adaptations related to orientation appear to be purely structural (e.g. palisade mesophyll in both abaxial and adaxial sides of vertically-oriented leaves), and reflect functional differences in internal leaf anatomy and symmetry that must have evolved in parallel. However, few studies have documented the association between leaf structure and orientation, and the asymmetric differences in sunlight incidence on both leaf surfaces under field conditions (e.g. Smith et al. 1998, James and Bell 2000). This asymmetry in leaf form and light incidence can lead to very interesting effects on leaf-level photosynthesis (e.g. Long et al. 1989, Soares et al. 2008). Typically, when sunlight strikes the underside of a normally horizontal leaf, photosynthesis is reduced due to both stomatal and non-stomatal effects related to internal light processing (Smith et al. 1997, 1998).

In contrast to the majority of angiosperms with laminar leaves, there are many species

that have relatively thick, more cylindrical leaves with a more radial geometry in cross-section (e.g. the needle-like conifer leaf) (Figure 4). These leaves also tend to be more circular in cross section, have a more inclined leaf orientation from horizontal, and less structural differentiation between the adaxial and abaxial leaf sides, both externally and internally. An interesting evolutionary perspective is that many conifer species also have more flattened leaves on shade branches, as well as corresponding changes in internal anatomy. Thus, the evolution of the needle-like leaf geometry appears to have been in concert with the phylogenetic expansion of conifer tree species during glacial periods of cooler temperatures, sunnier conditions, and lower atmospheric CO₂ (Blyakharchuk et al. 2004, Johnson et al. 2005). The requirement that laminar leaves capture and process sunlight adaxially, but CO₂ abaxially, seems to have been solved structurally with more radial geometry in cross section (e.g. needle-like leaves of conifers). Radial propagation of absorbed photons of light or CO₂ diffusion acts to concentrate both further into the leaf. In this regard, little is known regarding the coupling of adaxial and abaxial stomata in more cylindrical leaves such as found in many conifer species.

Too much sunlight: orientation and non-photosynthetic pigments

It is now well-documented that a more inclined orientation for a laminar leaf, in particular, under exposure to excessive sunlight, avoids overheating and prevents the now well-known negative impacts of photo-inhibition of photosynthesis (Smith et al. 1997, Valladares and Pugnaire 1999, Werner 2002). Leaves of most species wilt in response to midday sunlight exposure, especially in understory environments where sunlight patches are at full sunlight levels and wind speed is substantially reduced (Young and Smith 1980, Knapp and Smith 1987). Many species also show extensive leaf rolling in response to desiccation, yet little is known about photosynthetic impacts, although a recent study reported an interesting coupling of adaxial and abaxial stomatal responses in rolled leaves of a C₄ grass species (Smith 2008, Soares et al. 2008). Upon rolling, the newly-shaded adaxial stomata closed, corresponding with the cessation of photosynthesis by



Figure 4. Scaling plant form and function. The conifer needle is remarkably different than a typical laminar leaf in terms of both morphology and anatomy, reducing the potential problem of excessive sunlight absorption and the need for differentiated mesophyll cells and photo-protective pigments (Jordan and Smith 1993, Johnson et al. 2005). At the shoot level (Figure 3), this needle-like leaf structure also enables a tight packing of individual leaves on a sun shoot (top right), resulting in significant leaf warming that outweighs relatively small losses in photosynthesis due to self-shading (Smith and Carter 1988). The crown level (lower left) also generates an emerging property that is critical for survival in the alpine treeline ecotone. Formation of the bush-like krummholz mat by the conifer tree species acts to trap snow and insure snow burial of all leaves but the apical leaders at the wind-exposed locations on the outside of the mat. At the stand or community level, the formation of larger mats and tree islands (lower right) leads to the first appearance of forest-like tree structures that escape vertically from krummholz mats and tree islands due to a mutual protection from blowing snow and other growth-limiting factors of microclimate. The ultimate reduction in spacing between tree islands due to greater tree colonization leads to a greater uncoupling from macroclimate and the ultimate formation of new subalpine forest with a corresponding new treeline and timberline (Smith et al. 2003, Holtmeier and Broll 2007).

the adjacent mesophyll cells. Oppositely, the abaxial surface generated greater photosynthesis in response to the increased sunlight incidence (Soares et al. 2008).

In addition to orientational means of avoiding excess sunlight, transient or permanent production of red non-photosynthetic pigments (e.g. anthocyanins and betalains)

inside the leaf can also enhance photosynthetic carbon gain by diminishing light intensity during periods of high-light stress (Gould 2004). In contrast to photosynthetic pigments of the chloroplast (i.e. chlorophylls and carotenoids), non-photosynthetic pigments are located in parts of the cell not directly associated with photosynthesis, most

commonly the vacuole (e.g. anthocyanins and betalains) but also chromoplasts (rhodoxanthin) and cell walls (riccionidin). Because these pigments are spatially separated from the site of electron transport, light-energy absorbed by non-photosynthetic pigments is not used for photosynthesis, but is rather dissipated as heat. The remaining, unabsorbed wavelengths (i.e. those reflected or transmitted) will continue to be transmitted through leaf cells, where they may or may not be absorbed by photosynthetic pigments (Gould 2004). The optical properties of non-photosynthetic pigments are therefore of functional importance, as they directly influence the wavelengths and intensity of light available to be used for photosynthesis within a leaf.

Because red pigments have absorbance peaks in blue-green wavelengths, the generalized effect of red pigmentation in photosynthetic tissues is a reduction in transmittance of blue-green light through the leaf. Pietrini and Messacci (1998) estimated that anthocyanins in *Zea mays* could intercept up to 43% incoming photosynthetically active radiation (PAR), primarily between 400–600 nm, which reduced apparent quantum yield of CO₂ fixation and non-cyclic electron transport of PSII proportionately. Considering that blue-green light contains the most highly-abundant, high-energy wavelengths of the solar spectrum, that blue-green light deeply penetrates leaf tissues (Cui et al. 1991), and that wavelengths responsible for photoinhibition and photo-bleaching are primarily between 520 and 680 nm (Merzlyak and Chivkunova 2000), the value of blue-green light absorbing pigments during high sunlight exposure becomes increasingly apparent. The down-regulation of internal light for photoprotection has thus become a popular explanation for the widespread occurrence of non-photosynthetic pigments in leaves and other photosynthetic tissues, especially in high-light habitats, though evidence also exists on the contrary (e.g. Burger and Edwards 1996, Dodd et al. 1998, Lee et al. 2003, Kyprisiss et al. 2007). Red non-photosynthetic pigments which have been implicated as photoprotectant molecules include anthocyanin (for reviews see Chalker-Scott 1999, Steyn et al. 2002, Gould 2004), rhodoxanthin (Weger et al. 1993, Han et al. 2003, Hormaetxe et al. 2004, Merzlyak et al. 2005) and betalains

(Wang and Liu 2007). *In vivo*, red tissues have been observed to be less photoinhibited under blue and green light than green tissues of the same species, but equally photoinhibited under red light, which is poorly absorbed by red pigments (Smillie and Hetherington 1999, Feild et al. 2001, Hughes et al. 2005).

Perhaps one of the most significant differences between reducing light absorbance via non-photosynthetic pigments rather than leaf structural changes (e.g. pubescence, epicuticular waxes, internal anatomy), is that non-photosynthetic pigments can be synthesized and degraded relatively quickly, rendering them a relatively plastic and dynamic strategy for modifying light absorbance by the leaf. Visible reddening due to anthocyanin accumulation, for example, has been observed within a few hours of exposure to high light stress in fully mature leaves of *Zea mays* (Janda et al. 1996). In contrast, alterations in leaf structure once a leaf has reached maturity may take much longer, if they are even possible. For this reason, synthesis of non-photosynthetic pigments during moderate to long-term periods of high-light stress may be more physiologically feasible than less plastic, developmental controls in leaf structure. Examples of cases where internal light adjustments are needed temporarily include light-sensitive ontogenetic stages (e.g. development and senescence), periods of water or nutrient deficiencies, or seasons characterized by increased susceptibility to photoinhibition (e.g. winter). As might be expected, non-photosynthetic pigments have been observed in leaves experiencing all of these conditions (Chalker-Scott 1999, Steyn et al. 2002, Gould 2004). However, the effects of non-photosynthetic pigments on photosynthetic performance have yet to be compared to the benefits of many other structural traits related to photosynthetic function, or to ultimate impacts on species fitness.

Unresolved questions involving whole-leaf form
Evidence suggests that sun leaves are both structurally and functionally dorso-ventral and strongly dependent on receiving sunlight on the adaxial surface for maximum photosynthetic performance (Delucia et al. 1991, Sun and Nishio 2001). Dynamic processes at the organelle-level inside the leaf, which might maximize light capture and CO₂ diffusion, are also poorly understood. These

processes include the positioning and movements of individual chloroplasts within mesophyll cells, which is thought to maximize efficiency of light capture and curtail photo-inhibition of photosynthesis (Brugnoli and Björkman 1992, Terashima and Hikosaka 1995, Kasahara et al. 2002). In this way, chloroplasts may be behaving similarly to leaves that orient to sunlight, though on a more rapid time scale of minutes, if not seconds. Although specific effects of chloroplast movements on whole-leaf photosynthesis have yet to be found (Gorton et al. 2003), the idea that the re-fixation of CO₂ released intracellularly from respiration and photorespiration might be enhanced by purely structural means (e.g. positioning of chloroplasts relative to mitochondria) also remains an interesting question yet to be fully explored (Sharkey et al. 2004). Investigations of bulk organelle movements (e.g. cytosolic streaming) may reveal some important impacts on the liquid-phase, bulk transport of CO₂ that could offset diffusional limitations inside the cell, as well as the importance of internal sources of CO₂ (e.g. mitochondria and peroxisomes; Wada and Suetsugu 2004). There is also recent evidence that the diffusion and assimilation of CO₂ in mesophyll cells is facilitated by the occurrence of aquaporins-hydrophobic proteins that act to channel water across cell membranes in both plants and animals (Preston et al. 1992, Terashima and Ono 2002, Uehlein et al. 2003). This venue for adaptation is one of the few identified as an important CO₂ uptake feature of cells that is entirely structural, and one that might result in rather dramatic changes in the liquid-phase conductance to CO₂ and, thus, photosynthetic performance.

There are also studies that show a strong impact of leaf surface wetness on CO₂ uptake capabilities due to the very slow diffusion of CO₂ across even a thin water film (e.g. Smith and McClean 1989, Lefts and Mulligan 2005.). An almost ubiquitous occurrence of hydrophobic leaf surfaces occur in the plant kingdom, occurring only on leaf sides with abundant stomata (Smith and McClean 1989, Brewer et al. 1991, Brewer and Smith 1997, Brewer and Nunez 2007). This effective water repulsion from the leaf surface (bead formation) during a variety of common wetting events (e.g. rain, dew, fog, cloud-immersion) prevents the formation of a

continuous water film on the leaf surface and severe restrictions to CO₂ uptake (mass diffusion is ~10,000× slower in water than air). Structurally, trichomes and pubescence layers on the leaf surface can contribute significantly to the high degree of leaf hydrophobicity found in many species, in addition to the important effects of leaf pubescence for reflecting sunlight in desert environments (Ehleringer et al. 1976, Smith 1978, Smith and Nobel 1978). Different types of trichomes on the same leaf have been reported (e.g. *Verbascum* spp.) that interact to both repel water (bead formation) and retain droplets, minimizing transpirational water loss from open stomata (saturated boundary air layer) and maximizing water use efficiency (Brewer et al. 1991). However, water droplets also act as ball lenses that can focus sunlight onto the leaf epidermis at just over 4× full sunlight. Thus, the specific height of the trichome layer above the leaf surface may function to elevate droplets at a distance above the surface that prevents the focal point from striking the leaf surface. In still other species, especially in water-limited habitats, trichomes may function to absorb water (e.g. Pridgeon 1981). These structural, functional relationships between leaf photosynthesis and leaf water repellency and absorption need further study.

THE SHOOT/BRANCH It is often difficult to separate and compare quantitatively shoot-, branch-, crown-, and canopy-level effects on photosynthesis for an individual species (see **HIERARCHICAL STUDIES** below). For example, a tight packing of individual leaves on a shoot can alter the microclimate of a single leaf, but so can an aggregation of branches that make up a crown, or the spacing of plants to form a stand or community canopy with different degrees of openness (Figures 3, 4). Both the radiation and aerodynamic regimes of individual leaves can be influenced significantly by any level of the organizational hierarchy. As a result, the arrangement of leaves on a shoot, or shoots on a branch, can have large impacts on photosynthetic carbon gain when expressed per unit leaf area, stem length, total plant biomass, or per unit ground area (Cescatti 1998). However, in species with very open crowns, or spreading branch habits, the leaf/shoot/branch levels may independently

dominate the functional impacts of plant architecture (see review by Cescatti and Niinemets 2004).

Regardless of the amount or efficiency of leaf-level photosynthesis, CO₂ gain per individual plant can be altered dramatically at the shoot level due to mutual shading among leaves (Cescatti and Niinemets 2004). Greater leaf packing along stems can result in greater mutual shading among leaves (lower STAR value), but also substantial effects on convective properties of individual leaves due to an increased still-air boundary layer generated at the shoot/branch level (Smith 1980, Nobel 2005). In some conifer tree species, the beneficial warming effect of a thicker boundary air layer on photosynthesis may compensate for slight losses in photosynthesis due to mutual shading in the cold environments of high-elevation forests. Furthermore, leaf warming can also benefit photosynthesis by reducing vulnerability to low-temperature photoinhibition (Smith and Carter 1988, Smith and Brewer 1994). Finally, despite mutual shading effects, leaf packing in conifer species does not appear to significantly reduce sunlight incidence, because of the needle-like leaf structure and the upright orientation of individual needles (low STAR values; Figure 3). In addition, foliage clumping and mutual shading have greater impacts on incident light levels and photosynthesis in leaf canopies than changes in leaf inclination properties (Stenberg 1998, Farque et al. 2001). Apart from these reports, few studies have compared the effects of different arrangements of leaves on stems on the thermal versus light capture influences on photosynthesis.

In general, SILA and PLA both decline for a shoot compared to a single leaf for nearly all species. However, there are exceptions in species that show relatively small up-scale (e.g. leaf to shoot to crown) declines in these parameters, including most vine-like species that form a linear arrangement of asexual ramets (e.g. *Arnica* spp. and *Hydrocotyle* spp.). One extreme exception is the relatively unique architecture found in the desert shrub (*Dicoria canescens* A. Gray), a relatively large, hemispherical shrub (>1.0 m height) with well over a hundred leaves at full maturity (Pavlik 1980). Leaves of this species track the sun during the day, yet also have a mean shoot STAR of near 0.41 ± 0.3 for any stem

segment over the entire day, compared to a value only slightly higher for individual leaves (mean = 0.46 ± 0.3) (W.K. Smith unpublished data). By an unknown mechanism, this particular species appears capable of developing new leaf buds at locations in the crown that will not result in shading by older leaves, even on opposite sides of the crown. In this case, there appears to be very little impact of a higher structural scaling, retaining the importance of individual leaf properties.

Regarding the arrangement of individual leaves on a stem (e.g. alternate versus opposite), less is known regarding the details of leaf arrangement for individual stems or branches of different species within a crown. A particularly relevant example of the influence of leaf arrangement on stem-level photosynthesis occurs in conifer tree species, where needle-like leaves are arranged in a variety of configurations around the stem according to species and sunlight exposure (Niinemets et al. 2001). Leaves lower in the crown are often thinner and flatter in cross-section and more horizontal in orientation. Also, as previously mentioned, a much tighter packing of needles per unit stem length on sun-exposed shoots resulted in a greater temperature benefit to photosynthesis (Figure 3; Smith and Carter 1988, Cescatti and Zorer 2003). A recent study has shown an interesting application of natural isotope studies which verifies that needle packing in conifers acts to warm leaves above ambient, providing a form of structural form of homeothermy in plants across a wide latitudinal gradient (Helliiker and Richter 2008). Apart from this work on conifers, the importance of shoot/branch architecture to photosynthetic performance, versus the whole-plant (crown) level of organization, has yet to be comprehensively addressed.

THE WHOLE-PLANT CROWN Changes in whole-plant form in response to environmental change are well documented in the literature (see Valladares et al. 2002 and Rambal et al. 2003 for reviews). Shoot and branch number can differ according to compass direction, resulting in increased aggregation at different locations in the crown. Branch aggregation can also result in different numbers of leaves and stems with differing sizes, shapes, and physiologies (i.e. sun/shade) at particular locations the crown

(Rubio de Casas et al. 2007). The central question is—how much photosynthetic carbon gain is altered by crown-level architecture, relative to photosynthesis measured at the leaf, shoot, and branch level (Figure 2)? Comparison of leaf or shoot STAR values versus whole-plant (crown) values provides a quantitative estimate of leaf, shoot, and whole-crown display efficiencies. If a maximum value of 0.5 is possible for a laminar leaf oriented perpendicularly to the sun's rays, then a whole-plant STAR value approaching 0.5 might also indicate a plant which has an abundance of self shading, or shading of leaf area by woody stems. Particularly low values of STAR might also indicate a plant which has an abundance of self shading and, thus, protection from excessive sunlight, temperature, and water stress. As mentioned above, the high display efficiency for individual leaves (0.44 ± 0.2) and, especially for the crowns of whole plants (0.41 ± 0.06) during an entire day in *Dicoria canescens* (W.K. Smith, unpubl. data), may be remarkable among terrestrial vascular plants. However, comparisons of STAR values for individual leaves, shoots, and crowns for different species, or within the same species according to habitat or population, are rare in the literature. Thus, comparisons of sunlight interception efficiencies according to scale are not currently possible for many species or habitat types. Moreover, conversions of sunlight interception to actual photosynthetic estimates are rare in the literature, and often based on poorly defined photosynthesis and light-response relationships. Only rarely are the effects of different directional forms of sunlight (e.g. direct, diffuse, penumbra, scattered) included in an analysis of crown sunlight interception, and thus crown photosynthesis (e.g. Stenberg 1998).

Measurement of STAR values for multiple structural scales would give some quantitative indication of structural/spatial scale on sunlight interception, especially in conjunction with LAI measurements. It can be anticipated that both STAR and photosynthesis measured at the leaf level will be greater than the shoot level, followed by the branch and crown levels due to mutual shading and orientation effects. It is generally rare to find a species whereby STAR values at the crown level do not show a significant decrease compared to the shoot and branch levels (however, re-

member the *D. canescens* example above). In general, a greater display efficiency is required at each level upscale, unless leaf physiological characteristics (e.g. shade acclimation) can offset the potential shading effects of an increasingly more complex architecture (Falster and Westoby 2003, Cescatti and Niinemets 2004). Commonly, a steeper leaf inclination for leaves at the top of a tree crown will insure greater sunlight penetration to leaves deeper in the canopy. This greater penetration of sunlight will also be of a more diffuse nature due to strong penumbral effects (Smith et al. 1989). Albeit, studies comparing the relative levels of photosynthetic light saturation of all leaves in a naturally sunlit crown (whole-plant) are rare.

Typically, increased drought conditions result in greater leaf inclination or rolling, a reduction in leaf size, and a decline in crown leaf density in a host of desert species, and other species from water-limited habitats (Cescatti and Niinemets 2004). These changes in crown structure result in a diminution in the dominance of crown form on sunlight interception in favor of leaf form. In such a case, leaf form becomes more important for determining the microenvironment and accompanying mass and thermal exchange processes than crown configuration, similar to the discussion of leaf aggregation on shoot/branch form and function. A greater porosity to sunlight and wind (due to a lower leaf density) are the primary driving factors for this transition (see also **The Stand/Community Canopy** section below). In addition, these changes are typically associated with higher photosynthetic production per leaf, lower photosynthesis on a per plant basis or per unit projected ground area beneath an individual plant. In these situations, estimates of whole plant productivity based on individual leaf-level measurements (independent of STAR and SLA) are probably justified.

There are scattered references to mutual shading advantages, light interception benefits (layered branch arrangements in conifer trees), thermal heating advantages, and even humidity trapping qualities that could increase photosynthesis and even water use efficiency at the whole plant level (e.g. Neufeld et al. 1988, Rasmuson et al. 1994, Rambal et al. 2003). There are also rare reports of crown-level adaptation not related to sunlight capture at the crown level. Despite

these reports, the adaptive nature of crown architecture has been somewhat neglected compared to single leaf and even canopy studies (see Cescatti and Niinemets 2004, Williams et al. 2004 for reviews). Even the common basal rosette form characteristic of a variety of plant species has received only limited study (e.g. Geller and Smith 1982).

THE STAND/COMMUNITY CANOPY

Similar to the architecture of the individual plant crown, canopy architecture of single or multiple species can directly influence a variety of microclimate features, which feedback to influence photosynthetic performance of a species (Cescatti and Niinemets 2004, Williams et al. 2004). In contrast to crown-level effects, canopies made up of multiple layers tend to alter microclimate even more due to a greater disruption of airflow throughout the entire height of the forest. Similar to a very compact leaf crown (e.g. mosses, cushion plants), the penetration of sunlight and the supply of CO₂ from the ambient atmosphere and soil (plus re-fixation of respired and photo-respired canopy CO₂) into a leaf canopy can influence photosynthesis directly, as well as indirectly via additional microclimate alterations. For example, temperature and humidity gradients generated by canopy structure can play a strong indirect role in dictating canopy photosynthesis (Cavieres et al. 2006). Wind profiles (including turbulence characteristics) are critical to mass concentration gradients within canopies, and typically play an even greater role in altering microclimate than individual crowns. More open canopies in forest and shrub communities may generate substantial sunlight penetration, and similarly, though not necessarily, a matching penetration of wind. Hypothetically, higher sunlight levels with reduced wind flow can result in a canopy that is especially "uncoupled" from ambient air temperatures (see Williams et al. 2004 for review), which may result in leaf temperatures elevated well above air temperature, and with substantially lower CO₂ but higher water vapor concentrations relative to ambient. Such uncoupling from atmospheric conditions would increase deeper in the canopy, and be greatest in the understory community. Indeed, in the understory of more open forests with good sunlight penetration but low wind penetration, maximum leaf temperatures were nearly 20°C

above air temperature in sun patches (Foster and Smith 1986). The corresponding effects on photosynthesis of any uncoupling with ambient air may then elicit a complex interaction between both non-stomatal and stomatal responses. Therefore, a key functional feature of the architectural configuration of a canopy would be the relative penetration of sunlight and wind into the leaf canopy, both of which could be dictated, not only by crown structure, but by plant spacing characteristics determined at the seed germination and seedling life stages.

Specific architectural features can contribute to the degree of canopy-atmosphere coupling and the functional significance of canopy architecture to photosynthetic performance. Similar to individual plant crowns, sunlit leaf areas and canopy porosity can have major effects on any uncoupling with the atmosphere and, thus, photosynthetic carbon gain per unit leaf area and biomass, per total plant biomass, or per ground area. Canopy porosity to both light and wind can be estimated in terms of leaf density (number of leaves per unit volume), although leaf size, orientation, and arrangement can have independent effects on intra-canopy sunlight penetration and wind flow (Cescatti and Niinemets 2004, Williams et al. 2004). As a general example, canopies of desert plants are typically wind-coupled, due to both wide plant spacing and porous plant crowns, while tropical rain forests typically have tightly-woven canopies that prevent both sunlight and wind penetration, similar to their individual crowns. However, even in these dense forests, tree fall and gap generation can create a complex combination of wind versus sunlight penetration, resulting in varying degrees of coupling between the atmosphere and canopy. Uncoupled canopies during clear days may be characterized by warmer leaf temperatures, higher humidity, and lower CO₂ levels, but higher CO₂ levels at night due to respiratory activities of the canopy and soil. If a canopy has relatively good sunlight penetration (i.e. gapiness), but poor wind penetration (tall but spaced trees), then both canopy CO₂ and water vapor levels, as well as leaf temperatures, could increase even further than for uncoupled canopies without good sunlight penetration. During the night, greater sky exposure (cold sky radiation sink) combined with poor wind penetration could

also lead to colder plant and air temperatures. Of course, feed-back effects from such factors as air humidity could also influence any equilibrium conditions in microclimate and leaf gas exchange. The photosynthetic consequence of these interactive variables has not been dealt with comprehensively for any forest stand or plant community.

In addition to the above, very little is known regarding the spatial and temporal occurrence, and subsequent influence, of diffuse, scattered, and internally reflected sunlight within canopies (Gu et al. 2003). Compared to direct (collimated) sunlight penetration, diffuse sunlight appears to penetrate deeper and more uniformly into leaf canopies than direct sunlight, but at much lower maximum and higher minimum irradiance levels deeper in the canopy (e.g. Young and Smith 1980). In this regard, diffuse light has also been associated with higher photosynthetic rates at much lower costs in transpirational water lost in understory species (Young and Smith 1979) as well as forest canopies (Gu et al. 2002, 2003; Williams et al. 2004).

At both the population and community stand level, canopy microclimate can vary according to species, age, and successional stage, as well as habitat type and topography. Overall, this level of complexity in spatial and architectural relationships rarely has been studied comprehensively for any given species or community type. Even variations in LAI according to these canopy variables are relatively unknown except for some forest species that are important commercially. In particular, the combination of LAI and, for example, STAR values for a given canopy type could be used to identify important architectural features that might also reflect physiological function. The idea that both competitive and facilitative interactions among species could also lead to benefits in carbon dynamics across the landscape has not been evaluated in any detail. It is plausible that individual species have evolved adaptations, for example at the germination level, that could lead to a particular plant spacing pattern and the resulting canopy architecture of a stand (monospecific), or a community. Moreover, a particular canopy structure derived from the original spacing patterns of seedlings, could feed-back to the seedling level to select for a particular seed

and seedling traits that would be adaptive for growth in the understory of a particular canopy type (Figure 2). In general, very little is known about the relative adaptive significance of canopy-level in photosynthetic performance across the structural/spatial hierarchy found in the plant kingdom. Some important structural characteristics have been identified (e.g. leaf size and orientation, foliage clumping, and directional light quality effects), but the actual effects on photosynthesis and differences among species and community types are just beginning to be addressed (see Smith et al. 2004 for edited review).

THE LANDSCAPE It is not difficult to conceptualize how plants might evolve traits at the organismal level that would scale to the leaf, shoot, branch, crown and canopy levels for the capture and processing of sunlight and CO₂. Could there be similar adaptations at the organism level that would feed-forward to landscape- and ecosystem-levels, and then feed-back to the organism and population levels and be selected for within the evolutionary process? Topographic and micro-topographic variations (which generate corresponding variations in microclimates) form the basis of landscape patterns independently of stand or community levels of organization. Both sunlight incidence and wind flow patterns can be strongly influenced by macro-, meso-, and micro-topographic features (e.g. mountain ranges, ridge tops and valleys, gullies and debris on the soil surface, respectively) and, each of these can be affected strongly by vegetation pattern. One example might be the effects canopy structure of prevailing winds. As discussed above for crowns, canopy porosity is directly proportional to wind penetration, which can have significant effects on seedling germination and growth characteristics (which feed-forward to further affect plant spacing and canopy type). The existence of extensive aerodynamic fetch, or a smooth, homogeneous surface structure (e.g. microsite facilitation on the leeward side of larger plants), might also insure greater snow capture, and corresponding increases in soil moisture during the spring. Not only would the direct benefits of increased water and nutrients be realized, but other species benefiting might bring additional biotic advantages to the

dominant species driving the aerodynamic characteristics of the landscape (Smith et al. 2003).

A specific example of landscape-level adaptation, plus feed-back and feed-forward interactions, is the remarkable growth form of krummholz mats by conifers in the alpine treeline ecotone (Figure 4). This dramatic alteration in tree form generates a distinct snow deposition pattern that generates a unique plant community on the leeside of each mat. The question here is whether or not this wind-driven landscape pattern benefits the species generating this pattern. In fact, there does appear to be directional movement of these krummholz mats in the downwind direction across the landscape, gradually occupying the former position of the leeside plant communities generated by the mats themselves (Seastedt and Adams 2001). However, the dependence of the movement of the mat on the pre-existence of a leeside community has yet to be directly tested, and the role the plant community plays in facilitation of the krummholz mat is also unclear. The transient nature of sand dunes created by wind and tidal forces is another example of the dynamic coupling of substrate and vegetation in a feed-back and feed-forward relationship.

These sorts of ecosystem-landscape questions about adaptive evolution are difficult to establish experimentally, but are still credible conceptually. Eliminating the krummholz tree form from the landscape would alter the biotic and abiotic community dramatically, as well as the associated ecosystem processes such as soil water and nutrient relations. In this case, it is the landscape-driven level of plant form that impacts not only the landscape vegetation pattern, but ecosystem processes as well. Of all the levels of the hierarchy in plant structure-form, this has received the least attention, probably because it is also the most complex and difficult to study (Smith et al. 2004).

HIERARCHICAL STUDIES Only a few studies have provided specific comparisons of photosynthetic effects of plant form across multiple levels of the structural hierarchy for any particular species. For example, a recent study investigating a fir tree species (*Abies amabilis* Douglas ex J. Forbes) evaluated the importance of leaf, shoot, branch, and crown

architecture to survival in the understory of late successional forests (Mori et al. 2008). Investment in stem over leaf biomass, as well as greater leaf and stem longevity, compared to plants in more sun-exposed locations, enabled the formation of a bush-like, low-spreading crown in response to sunlight limitation. This phenotypic acclimation in carbon allocation was also accompanied by greater longevity of more flattened leaves, stems, and even branches and the ultimate growth to a forest-stature tree when sunlight became more abundant.

The understory saplings of *Abies lasiocarpa* (Hook.) Nutt. in the Rocky Mountains, United States, have a similar structural acclimation to low understory light regimes, and have also been observed to initiate vertical growth (and root formation) at the tip of lateral branches that begin to grow vertically after encountering a higher-light microsite (W.K. Smith, unpubl. data). Sunlight levels of greater than $\sim 450 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (photosynthetically-active wavelengths) measured at mid-day appear to stimulate this abrupt conversion from a ground-spreading to vertical-growth pattern. Thus, interaction across multiple structural scales enables the capture of adequate sunlight required for a shift to sun-exposed architecture, the initiation of main trunk formation, and greater vertical growth potential. Similar changes in growth form in response to incident sunlight intensity have been documented for numerous species that exhibit etiolation of stem growth (with achlorophyllous leaves and stems) until a higher-light microsite is intercepted.

Emerging properties in plant form at the leaf, shoot, branch, and crown level also appear fundamental to the survival of evergreen trees at high elevations and latitudes (Figure 4). At the leaf level, the more cylindrical shape of the conifer needle is not only mechanically strong in an environment with strong mechanical forces (e.g. snow loading), but also acts to avoid high sunlight levels and photoinhibition of photosynthesis while enhancing CO_2 supply to the leaf interior (due to a more circular cross-sectional geometry that generates a radial diffusion regime; Johnson et al. 2005). A needle-like leaf shape also enables greater needle-packing on shoots and a resulting warming with relatively minor mutual shading effects (Smith and Carter 1988). At the shoot, branch, and crown

level, a dense clustering of shoots also enables an efficient snow collection (Figure 4, Hadley and Smith 1987). Thus, structural acclimation at the leaf, branch, and crown levels interact with the impacts of blowing ice crystal abrasion to generate a dense leaf crown ($LAI > 20$) that greatly enhances snow capture and early burial beneath a protective snowpack early in winter. Evergreen tree species occurring in particularly harsh environments typically cannot afford to extend shoots beyond the snow surface during winter, and only species with the capability for forming extensive lateral shoots will be capable of forming the bush-like, *krummholz* mat (Figures 4c and d). During summer, this growth form also has a substantially warmer temperature, allowing greater photosynthesis in an environment where photosynthesis may be retarded by low temperatures.

Despite these rather dramatic examples of adaptations in plant form, very little is known regarding the photosynthetic advantages of differences in plant form at all structural/spatial levels except the leaf, diminishing rapidly at the higher levels of the organizational plant hierarchy. An interactive feedback and feed-forward system of structural/spatial traits acts to couple every hierarchical level of plant organization and complexity within an overall adaptive framework, often involving both direct and indirect effects on photosynthetic carbon gain or processing.

INDIRECT EFFECTS OF PLANT FORM ON PHOTOSYNTHESIS

At all structural levels, the acquisition of light and CO_2 for photosynthesis are considered source limitations. Other limitations involving the processing of assimilated carbon (sink limitation) can also have strong, negative feed-back effects on photosynthetic carbon fixation. The build up of starch is well known to inhibit photosynthesis, a process that involves cellular and tissue storage, the transport of soluble carbohydrates in the phloem, and the 'sink' areas that are actively growing (cell division and expansion) such as new shoot and root tips (Arp 1991). Similarly, increases in the bulk leaf elastic modulus (ϵ) in response to soil drying can result in improved water relations and, thus, greater photosynthetic capabilities under drought stress (e.g. Niinemets 2001). However, a trade-off between improved water relations and photosynthesis also appears to

occur, resulting in lower photosynthesis with increasing leaf density and ϵ . The commonly observed differences in leaf venation patterns may also have important influences on water supply and phloem loading/unloading to prevent localized water stress or feedback from carbon processing to the CO_2 supply processes (e.g. stomatal behavior) (Evans et al. 2004a). For tall trees, sun exposure was more closely associated with shoot and leaf traits than the height on the tree, indicating a greater importance of light rather than hydraulic limitations for influencing crown architecture (Osada et al. 2004).

Another rather extreme example of the potential adaptive nature of the crown level of plant form is the noteworthy "*krummholz*" (twisted wood) tree form found at high altitudes in alpine treeline ecotones discussed in the previous section (Figure 3, Hadley and Smith 1987). For decades these often stunted, dwarfed and disfigured tree forms were interpreted as simply the stress effects of an extreme environment involving very cold air temperatures, high wind and blowing snow, dry air, high sunlight, and extended seasonal snow cover. Dead needles were often observed on new shoot leaders that grew during the previous summer, but desiccated and died after the first winter due to exposure to blowing ice crystals and cuticle erosion. However, the adaptive structural features of these crowns was not fully understood or recognized until recently. In short, the conifer tree species commonly found at treeline (e.g. spruce and fir species) have one common feature that seems to be highly adaptive for survival in this extreme habitat type. This adaptation is the capability to respond to damaged stem vertical shoots by forming abundant lateral buds and shoots (similar to the "bonsai tree" effect), a characteristic feature not shared by other treeline species such as pine species. As a result, a LAI value of greater than 20 and a $STAR$ of less than 0.1 can occur—some of the most extreme values measured for trees and shrubs. As the more wind-exposed, vertical leaders from the previous summer are damaged, the increase in lateral shoots results in a tightly compacted crown and, importantly, a crown structure that enhances the collection and retention of snow (Figure 3; Hadley and Smith 1983). This structural facilitation of snow cover serves to protect all older shoots, but not the younger,

more exposed vertical leaders at the top of the crown. Thus forms the familiar, wind-swept crown that tapers into the prevailing wind direction during winter. Moreover, these species are found at the upper limits of the treeline ecotone only when facilitated microclimatically by other structures, both animate and inanimate (Smith et al. 2003). Moreover, the benefits of facilitation appeared to outweigh the accompanying costs of such detriments as increased soil water competition with neighboring plants (Germino et al. 2002).

FUTURE CHALLENGES Much of what has been proposed for the form-function relationships discussed here, especially at hierarchy levels above and below the whole-leaf level, still remains incompletely documented and mostly unresolved. For example, relatively little information exists concerning the positioning dynamics of chloroplasts within individual cells, or among different mesophyll cells, in response to incident sunlight. The role of non-photosynthetic pigments to the photosynthetic process is also still poorly understood, especially on an ecological basis, despite the common occurrence of pigments such as anthocyanin; indeed, the realization that too much sunlight can be an important environmental constraint to photosynthesis is a relatively new idea compared to the much more established findings concerning low sunlight constraints. Regarding the thermal effects of sunlight, the trade-offs between thermal versus photosynthetic advantages have not been addressed comprehensively across the entire spectrum of structural/spatial complexity. For example, the idea that large, broad leaves are typically less thermally coupled to air temperature (often well above and below air temperature) than smaller leaves has not been compared with the corresponding temperature responses of photosynthesis. It could be hypothesized that larger, uncoupled leaves also have broader temperature response curves of photosynthesis. Of course, scaling to higher levels of the architectural hierarchy, this same coupling process needs further study to evaluate the adaptive importance of the crown and canopy compared to the leaf level. This perspective concerning the degree of environmental coupling and uncoupling, especially at higher scales of plant form, may provide a more

unified approach for characterizing functional plant groups according to ecophysiological function. Tradeoffs between advantages and disadvantages of plant form to photosynthetic function, for virtually all life stages, have been recognized previously as a challenging research question of the future (Gutschick 1999).

Another characteristic of plant form not completely understood in terms of photosynthetic function is the considerable variation in dorso-ventrality observed in leaf structure (both internal and external) of many species. Related to this asymmetry in leaf structure is the important omission of field measurements detailing the amount and nature of incident sunlight on both leaf surfaces and corresponding photosynthetic effects. For example, the functional importance to photosynthesis of the typical conifer needle leaf (Johnson et al. 2005) or the characteristic C_4 "Kranz" anatomy found for a host of species remain only partially explained (Soares et al. 2008, Smith 2008). And finally, a host of questions still remain about the photosynthetic influence of structural differences at higher structural scales such as the crown and canopy, including the effects of these structures on sunlight and CO_2 capture and processing (various chapters in Smith et al. 2004). As one example, the effects of plant form on the absorption of different directional forms of sunlight (i.e. direct beam, diffuse, scattered, reflected) and corresponding effects on the photosynthetic process remains an open question of considerable ecophysiological importance (e.g. cloud forests, air pollution, cloudy versus clear-sky habitats, etc.), especially within the framework of current scenarios of global change impacts on temperature, atmospheric CO_2 level, and moisture/cloud regimes.

Probably the most promising approach for understanding of indirect architectural effects on photosynthesis will come from studies on the coupling of carbon gain (source) with processing (sink) in plants (Arp 1991, Paul and Driscoll 1997). This coupling involves the balance between carbon supply (photosynthesis) and demand (respiration, tissue repair and growth). Central to this coupling is the effective transport of water and carbon compounds throughout the plant by the non-photosynthetic tissues (e.g. leaf, stem, and root conducting tissue) (Ryan et al. 2006).

Evolutionarily, all effects of plant form on nutrient capture, transport within the plant, and ultimate processing (e.g. sunlight, CO₂, soil water and accompanying nutrients, as well as temperature regulation), will need to be evaluated across the entire hierarchy of organization and complexity that must compensate for the familiar organ systems of animals, as well as for their highly advanced mobility for avoiding environmental stress.

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