
Structural determinants of leaf light-harvesting capacity and photosynthetic potentials

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1 Introduction

The traits characterizing plant functioning include simple dimensions such as leaf area, leaf thickness (T), display angle, and ratios of simple traits [e.g., leaf dry mass per unit area (M_A)] as well as normalized rates [e.g., net maximum photosynthetic rate per unit mass (A_{mass}) or per unit area (A_{area})], contents [e.g., N per unit dry mass (N_{mass})], and “efficiencies” [gain/cost; e.g., photosynthetic N-use efficiency ($\text{PNUE} = A_{\text{mass}}/N_{\text{mass}}$)]. Current plant science research mostly emphasizes the role of physiological traits in altering plant competitive ability, but the determinants of leaf light-harvesting capacity and foliar photosynthetic potentials also include numerous structural traits. In fact, while chloroplastic metabolism has remained remarkably conserved throughout phylogeny, plant evolution has led to a large diversity in foliar anatomy, morphology and shape that may tremendously modify the resource capture efficiency of leaves with essentially the same metabolic constitution (Smith et al. 2004).

Apart from evolutionary adaptations, all traits have an enormous spatial and temporal variability. The evolutionary, developmental and environmental variations in traits, and the large number of potentially important traits and trait combinations, complicate predictions of relevant plant functions from the collections of traits. However, many traits that alter the same plant function co-vary along environmental gradients and among species. Understanding such coordinated variations among trait assemblages may significantly simplify projections of plant functioning in changing environmental conditions. Analyses of the trait co-variations have identified a series of general correlations among relevant plant structural and functional traits. For instance, across large species sets, A_{mass} correlates positively with N_{mass} and negatively with M_A and leaf life-span (Reich et al. 1997, 1999; Niinemets 2001; Wright et al. 2004b).

We review recent work on inter-coordinated structural traits relevant to the capture and utilization of irradiance and carbon, mainly focusing on leaf tissue and whole-leaf scales. We demonstrate major structural controls on light-harvesting efficiency that result from constraints on leaf size, shape and support investments, and emphasize the important role of leaf venation architecture and internal leaf structure in the supply of water to the leaves and the internal diffusion limitations of photosynthesis. Because in natural environments, N is generally found in concentrations limiting leaf development and photosynthesis, we further examine the coordinated variations in leaf carbon gain potentials with foliar N content. As the cost/benefit ratios of specific leaf constitutions depend on leaf life-span, we also consider the relationships with leaf aging and longevity as part of the fundamental trade-offs.

2 Structural limitations of leaf light-harvesting efficiency

A variety of structural characteristics operative at different hierarchical scales affect light interception per unit leaf area. At a tissue scale, structural modifications alter the amount of light intercepted per unit chlorophyll, while at a leaf scale, structural changes modify the exposure of single leaves. Finally, leaf arrangement and aggregation on the shoot further significantly alter the average irradiance on the leaf surface (Fig. 1).

Although the theoretical light interception efficiencies of specific leaf architectures may be very high, in evaluating the adaptive adjustments, it is

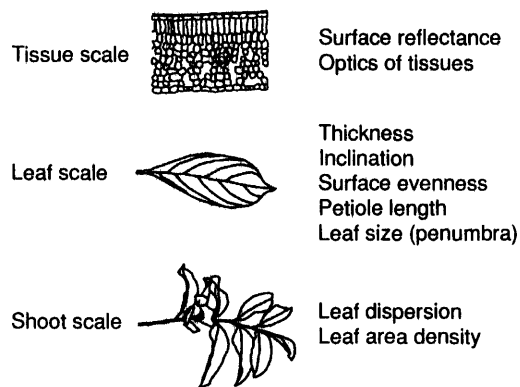


Fig. 1. Summary of the structural determinants of leaf light-interception efficiency at various hierarchical levels. At the tissue scale, the structural characteristics primarily modify the distribution of light within the leaf and the amount of light intercepted per unit chlorophyll. At the leaf and shoot scales, foliage structural characteristics alter the average irradiance and the distribution of light on the leaf surface

necessary to consider that enhanced light interception may be costly. In addition to large N investments in chlorophyll and associated pigment-binding proteins, structural modifications of light interception at every hierarchical level involve costs as well. These may be direct costs such as the biomass required for the construction of extra structures or indirect costs such as the reduction of leaf photosynthetic activity due to enhanced diffusion limitations. Due to large structural costs, the light-harvesting efficiencies of various leaf displays are always lower than the maximum efficiencies even in most light-limited environments (Valladares et al. 2002).

2.1 Tissue-Scale Limitations of Light Interception

The organization of structural elements within the leaf plays a major role in light capture. Because chlorophyll absorbs light very efficiently, most irradiance is often absorbed near the top layers of the leaf (Buckley and Farquhar 2004). To increase the uniformity of the illumination field within the leaves, and the total amount of light intercepted per unit chlorophyll, many plant species possess lens-like epidermal cells that focus the light in the leaf interior (Poulson and Vogelmann 1990; Smith et al. 1997). Leaf transversing bundle-sheath extensions in heterobaric leaves also transfer light into deeper layers (Nikopoulos et al. 2002), implying a potentially important linkage between leaf venation architecture and leaf light interception capacity. In many Mediterranean sclerophylls that possess a sclereid network anchored to the inner surface of epidermis, sclereids appear also to function as optical fibers guiding light into the inner leaf layers (Karabourniotis et al. 1994; Karabourniotis 1998). However, enhancement of light-harvesting capacity by these specific adjustments involves specific trade-offs with leaf photosynthetic capacity. Bundle sheath extensions cover up to 50% of the leaf surface area (McClendon 1992; Nikopoulos et al. 2002), thereby significantly reducing leaf photosynthetic capacity per unit area. Furthermore, bundle sheath extensions also effectively avoid the lateral diffusion among neighboring compartments surrounded by bundle sheath extensions (areoles; Terashima 1992), potentially reducing leaf photosynthesis when stomata are non-uniformly open.

A further important factor modifying leaf light interception efficiency, is the differentiation of leaf mesophyll into palisade and spongy layers. The cells in palisade parenchyma are elongated and parallel to the direction of direct light, facilitating light channeling into the leaf (Vogelmann and Martin 1993). The spongy mesophyll cells are less regularly arranged, leading to greater effective light pathlength and light scattering (Terashima 1989;

DeLucia et al. 1996; Evans et al. 2004). Consequently, the amount of light intercepted per unit chlorophyll is greater in spongy than in palisade mesophyll (Terashima 1989; DeLucia et al. 1996). This implies that the efficiency of leaves with given chlorophyll content and mesophyll thickness varies according to the distribution of mesophyll between palisade and spongy layers and the relative distribution of incident light between direct and diffuse components. Furthermore, due to different light interception efficiencies of palisade and spongy mesophyll as well as differences in distribution of photosynthetic enzymes along the leaf, leaf photosynthesis rates are different for an adaxial and abaxial illumination (Sun and Nishio 2001; Evans and Vogelmann 2003; Buckley and Farquhar 2004).

In many species in stressful environments with potentially high fractions of excess light energy, the leaf surface is covered by trichomes that reduce penetration of visible and UV light (Karabourniotis and Bornman 1999; Karabourniotis et al. 1999). Leaf pubescence is a very effective means of reducing light interception [see Cescatti and Niinemets (2004) for a review], but the overall cost to the plant may be large. Few data of the cost of pubescence are available, but in the tropical evergreen broadleaf species *Metrosideros polymorpha*, at high elevations up to 15% (34 g m^{-2}) of foliar biomass may be invested in trichomes (total $M_A=229 \text{ g m}^{-2}$; Geeske et al. 1994).

2.2 Thickness (I) and Inclination Effects on Light Harvesting

Thicker leaves have a greater number of mesophyll cell layers, and a higher light absorption per unit area. However, light capture will not increase linearly with T , as fewer photons penetrate to additional mesophyll layers (Vogelmann and Evans 2002), and the amount of light intercepted per unit chlorophyll invested decreases as more chlorophyll is stacked within the leaf. Due to multiple scattering within the leaves, at a common chlorophyll content, the light interception capacity is larger for thicker leaves (Evans and Poorter 2001). For a series of forest species, it has been demonstrated that an increasing fraction of chloroplasts functions below light saturation with increasing T (Green and Kruger 2001), further demonstrating the trade-offs between high investment of structural and photosynthetic compounds per unit leaf area and efficiency of light interception. Thus, for maximization of whole plant light interception with a certain amount of N and C available for the construction of foliage, plants should optimize leaf chlorophyll content and T simultaneously with total leaf area (Cescatti and Niinemets 2004).

Apart from the internal architecture, thickness and chlorophyll content, the leaf light interception capacity depends on the inclination. Numerous studies have explored the efficiency of light harvesting of leaves with different inclinations [see Valladares (2003) for a review], leading to a general consensus that more horizontal leaves intercept light more efficiently, especially in understory environments where most of the light penetrates at low zenith angles (Valladares 2003; Cescatti and Niinemets 2004). Yet, the adaptive significance of specific leaf inclinations must be assessed within the context of other leaf and shoot structural characteristics. For densely leafed shoots, where the leaf angle is kept constant, foliar light interception efficiency is significantly enhanced by increasing the length of petioles, because this minimizes the self-shading between neighboring leaves (Takenaka 1994; Pearcy and Yang 1998). However, the biomass of the petiole necessary to keep the leaf at a certain angle increases with the cube of petiole length (Niklas 1999), implying that the maintenance of horizontal angles becomes increasingly costly with increasing petiole length.

Overall, there is a strong general relationship between foliar biomass investment in petiole and petiole length (Fig. 2A), further underscoring these biomechanical limitations. As part of this relationship, the fractional biomass investment in the leaf rachis in compound-leaved species increases with the number of leaflets per leaf (Fig. 2B). The latter relationship illustrates the trade-off between the support costs, which are minimized when

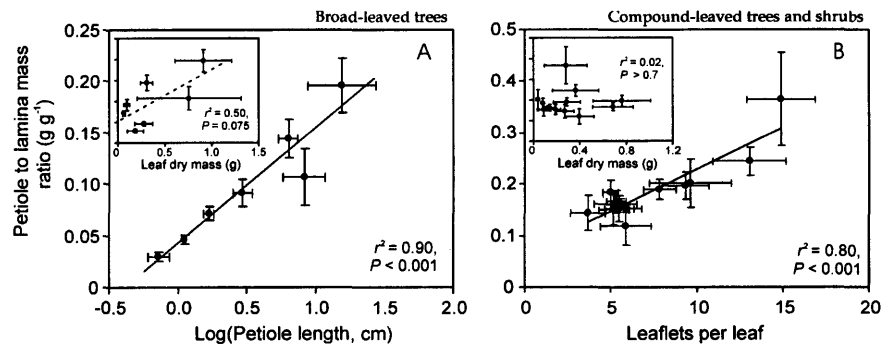


Fig. 2. Petiole dry mass (M_p) to leaf lamina dry mass (M_l) ratio in relation to (A) petiole length in seven temperate broadleaved deciduous trees, and (B) the number of leaflets in 16 compound-leaved temperate deciduous trees and shrubs. Insets demonstrate the relationships between M_p/M_l and total leaf dry mass. Error bars indicate \pm SD. The data in A ($n=18-156$ for each species) were derived from Niinemets and Kull (1999; *Betula pendula*, *Fraxinus excelsior*, *Populus tremula*, *Tilia cordata*) and Niinemets and Fleck (2002b: *Liriodendron tulipifera*, 2002a: *Fagus orientalis*, *F. sylvatica*). The data in B are modified from Niinemets (1998). Data are fitted by linear regressions

the mass is located closer to the axis of rotation, and the light interception efficiency, which is maximized when there is no overlap between neighboring leaves. Thus, for a maximum light interception efficiency, foliar mass should be located farther away from the axis of rotation as more leaflets are added to the leaf rachis.

These relationships collectively demonstrate that effective light interception via maintenance of favorable leaf inclination angles may have a significant cost for the plant. Although the petioles contain chlorophyll and Rubisco, the concentrations of these photosynthetic compounds are four- to ten-fold less than in the leaf lamina (Niinemets 1999a), and the surface area to mass ratio is also several-fold lower, so the photosynthetic activity of petioles is minor compared to that of the leaf lamina (Hibberd and Quick 2001). These data suggest that, depending on the fractional investment of foliar biomass in petiole and rachis, plants investing a constant fraction of biomass in leaves, and with the same M_A of leaf laminae, may have widely differing photosynthetic activities per unit total foliage dry mass.

2.3 Light Capture Dependence on the Flatness of the Leaf Lamina

The inclination of leaf lamina with respect to the horizontal is commonly measured as the angle between the lamina tip and bottom, but leaf laminae are rarely completely flat. More frequently, leaf laminae are curled, folded or rolled to a varying extent, whereas the degree of leaf rolling increases with leaf exposure in the canopy (Fig. 3). Due to complexities in formal analysis

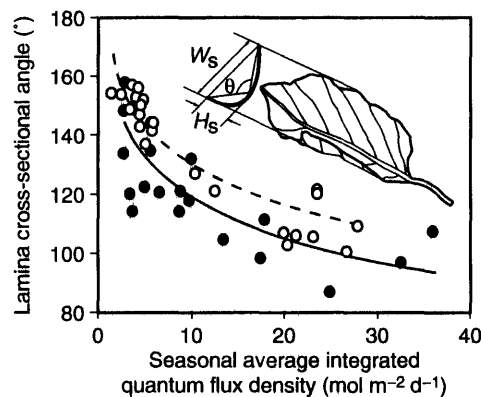


Fig. 3. Lamina cross-sectional angle (θ) in relation to average integrated leaf irradiance in a dominant (filled symbols, $r^2=0.64$) and a sub-dominant (open symbols, $r^2=0.77$, $P<0.001$ for both) *Fagus sylvatica* tree [modified from Fleck et al. (2003)]. θ as defined in the inset. In addition to θ , the degree of leaf rolling can also be characterized by the width (W_s) and height (H_s) of the leaf space.

of uneven lamina light interception efficiency, the influence of such three-dimensional lamina architecture on leaf light harvesting has been characterized in only very few instances (Sassenrath-Cole 1995; Sinoquet et al. 1998; Farque et al. 2001; Fleck et al. 2003). Overall, these studies demonstrate a strong reduction of leaf light-harvesting efficiency in rolled leaves and also shifting contributions of upper and lower leaf surfaces to total leaf light interception (Fleck et al. 2003).

Although the increases in the degree of leaf rolling and lamina total to projected area ratio decrease leaf light-harvesting efficiency, they also increase the photosynthesis per unit projected lamina area due to stacking of photosynthetic biomass. Because enhanced foliage stacking at higher light increases light penetration to deeper canopy layers, such a fundamental trade-off between C gain potential and light-harvesting efficiency may maximize the light interception and C gain of dense canopies at a common biomass investment in leaves.

2.4 Modification of Light Harvesting by Leaf Size

Geometrical models considering the sun as a point light source predict that leaf size per se and leaf lobing do not directly alter leaf light-interception efficiency (Niklas 1989). These models, however, suggest that decreases in leaf size and increases in leaf lobing may increase the occurrence of light-flecks in deeper canopy layers (Niklas 1989). Given that in deeply shaded canopy layers more than half of the total irradiance can penetrate as short-duration lightflecks (Chazdon and Pearcy 1991), the variation in leaf size may modify whole-canopy C gain to a significant extent.

Apart from the modification of the sunlit and shaded leaf area fractions, leaf size can also affect the intensity of direct solar radiation on the leaf surface. This is because, in reality, the solar disk as viewed from the earth has a finite radius of about 0.27 degrees. While in full sun the entire solar disk is visible, and no sun is visible in a complete shade, in intermediate situations that are called penumbra, the solar disk is only partly shaded by phytoelements. Because penumbra makes the light environment more uniform compared with the existence of only sunlit and shaded areas, a large degree of penumbral canopy leaf area increases the whole canopy photosynthetic potential (Cescatti and Niinemets 2004). It is generally thought that the significance of penumbra increases with decreasing leaf size, but the relevant parameter characterizing the role of penumbra is actually leaf size to canopy height ratio rather than leaf size alone (Cescatti and Niinemets 2004). Thus, at a common leaf size, penumbra plays a more prominent role in taller canopies.

Leaf size may further significantly alter the light interception by modifying shoot architecture. In particular, smaller leaves can be more densely packed on the shoot, thereby maximizing the shoot light interception when the irradiance is high (King and Maindonald 1999; Bragg and Westoby 2002, Fig. 1). However, denser leaf packing inevitably results in larger self-shading within the shoot (Valladares and Pearcy 1999), and reduces the average irradiance on the leaf surface (Niinemets et al. 2004b). Thus, less densely leafed shoots become more efficient with decreasing irradiance (Valladares and Pearcy 1999; Niinemets et al. 2004b). As larger leaves require less woody branches to support a common leaf area, and can also be arranged in space relatively independently of stem axes due to lamina translation around the petiole, and changing leaf and petiole curvatures and petiole length, an increase in leaf size may be favored by decreases in light availability.

3 How Structure Determines Leaf Photosynthetic Capacity

Efficient light harvesting must be matched by CO_2 assimilation potentials to ensure optimal conversion of light to chemical energy and finally to growth. A plethora of varying leaf anatomical structures exists across different plant functional types, strongly modifying the photosynthetic efficiency of unit foliar area and mass. Photosynthetic organs differ in the volume fraction of different tissues as well as in the size and packing of cells in specific tissues, and in the thickness and chemical composition of cell walls. To characterize this vast heterogeneity, a general and easily measurable leaf variable, M_A , is employed in studies describing the effect of leaf structure on leaf photosynthesis. However, the relationships between photosynthesis and M_A are often variable. Such variability is partly because M_A is a product of thickness (T) and density (D) that may vary independently, and that affect leaf photosynthetic capacity differently (Witkowski and Lamont 1991; Niinemets 1999b).

3.1 Photosynthetic Capacity in Relation to Leaf Tissue Types and Thickness

The assimilation of CO_2 depends on the diffusion into the leaf intercellular spaces, and absorption by exposed mesophyll cells. The exposed mesophyll surface area per unit lamina area (S_m) ranges from 5 to 50 $\text{m}^2 \text{m}^{-2}$ among broadleaved species (Hanba et al. 1999, 2001, 2002), and strongly increases with increasing T (Hanba et al. 1999). Because most of the chloroplasts adhere to the inner surface of exposed mesophyll cell walls, scaling of S_m

with T implies also a positive relationship between T and exposed chloroplast to total lamina surface area ratio, directly enhancing the internal diffusion conductance (Syvertsen et al. 1995; Hanba et al. 1999, 2002).

Overall, these data demonstrate a larger surface area for diffusion in thicker leaves (Terashima et al. 2001) such that the increase in T does not necessarily imply enhanced within-leaf diffusion limitations. However, it is further relevant that thicker leaves which contain additional layers of mesophyll also have higher total contents of Rubisco and leaf N per unit area (Nobel 1977; Koike 1988; Niinemets 1999b; Roderick et al. 1999). Therefore, A_{area} increases with increasing T due to stacking of photosynthesis-limiting proteins per unit leaf area (Niinemets 1999b).

Superimposed by these general trends, species- and functional type-specific leaf anatomical characteristics may further modify leaf photosynthetic potentials for any particular T . The correlation between A_{area} and T assumes that changes in thickness are primarily due to changes in mesophyll within the leaves. However, leaf mesophyll is embedded within cuticle and epidermal layers, which contribute differently to total T among species, implying a significant variation in leaf photosynthetic potentials. In addition, plants from high altitudes generally possess a pronounced hypodermis, significantly reducing the fraction of mesophyll in the leaf lamina for a common T (Grubb 1977). Furthermore, at a common T , cells with differing size and shape result in widely varying values of S_{m} . For instance, more elongated palisade cells relative to spongy mesophyll cells (Nobel 1977; Slaton et al. 2001) or smaller cells with a given geometry (Wilson and Cooper 1970) provide a larger exchange surface area.

3.2 Does the Efficiency of Intraleaf Diffusion Vary for Leaves of Differing Structure? Role of D and M_A

It has been suggested that woody species with inherently larger M_A and D have lower internal diffusion conductances per unit area (g_{area}) than the herbaceous species with less tightly packed mesophyll and thinner cell walls (Lloyd et al. 1992; Epron et al. 1995; Syvertsen et al. 1995). Because the values of g_{area} scale positively with A_{area} , this conclusion of structural determinants of g_{area} has been recently challenged (Evans and Loreto 2000). Evans and Loreto (2000) suggested that because of the coordination of g_{area} with A_{area} , the overall drawdown in the CO_2 mole fraction between sub-stomatal cavities (C_i) and chloroplasts (C_c) due to internal conductance ($C_c = C_i - A_{\text{area}}/g_{\text{area}}$) is similar among species with differing leaf structure. Indeed, data demonstrating variations in the C_c/C_i ratio in leaves of varying g_{area} are essentially lacking. However, conceptually it is

further important that for three-dimensional structures such as leaf laminae the C_c/C_i ratio is a volume-weighted average estimate, and should accordingly scale with g_{mass} (g_{area}/M_A) and A_{mass} (A_{area}/M_A) and not necessarily with the area-based estimates.

We compiled the published data for g_{area} and A_{area} , and g_{mass} and A_{mass} for 22 species, and calculated the C_c/C_i ratios for all measurements (Fig. 4). These data demonstrate a strong coordination between both g_{area} and A_{area} (Fig. 4A) and g_{mass} and A_{mass} (Fig. 4B), but also that the relationships tended

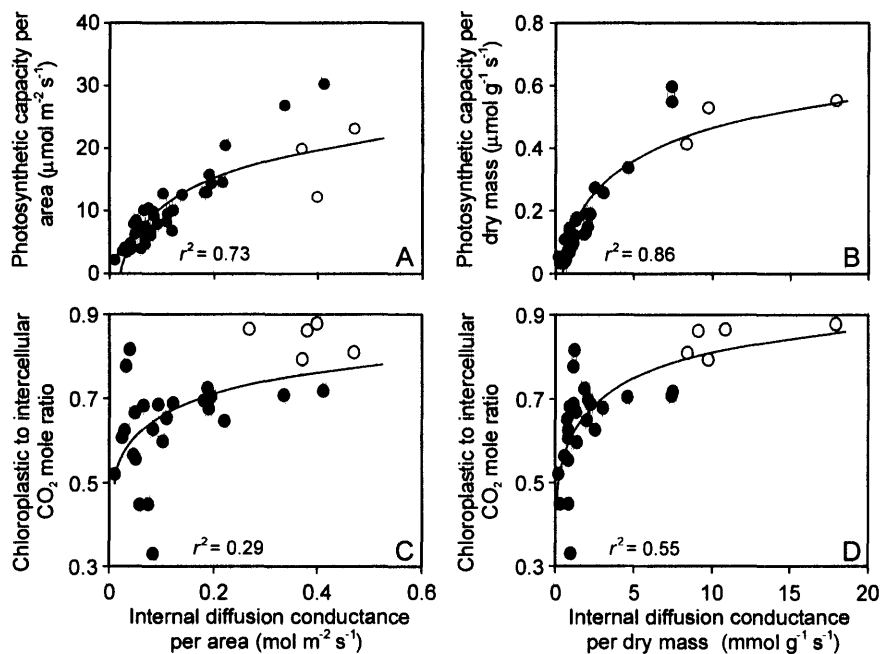


Fig. 4. Co-variations of leaf photosynthetic capacity per unit area (A_{area}) (A) and dry mass (A_{mass}) (B) with internal diffusion conductance per unit area (g_{area}), and dry mass (g_{mass}), and the relationships between the ratio of chloroplastic to intercellular CO_2 mole ratio and g_{area} (C) and g_{mass} (D) for a wide range of mature leaves of broad-leaved shrubs and trees (filled symbols) and herbs (open symbols). Data were fitted by non-linear regressions in the form of $y = \log(ax) + b$ and are all significant at $P < 0.001$ ($n = 42$). The data were derived from studies of the following species: *Acer mono*, *Alnus japonica* and *Populus maximowiczii* (Hanba et al. 2001); *Juglans regia* and *J. nigra* × *regia* (Piel et al. 2002), *Acer mono*, *A. palmatum* and *A. rufinerve* (Hanba et al. 2002); *Citrus limon*, *C. paradisi*, *Macadamia integrifolia* and *Prunus persica* (Lloyd et al. 1992; Syvertsen et al. 1995); *Camellia japonica*, *Castanopsis sieboldii*, *Cinnamomum camphora*, *Ligustrum lucidum*, *Quercus glauca*, and *Q. phillyraeoides* (Hanba et al. 1999); *Polygonum cuspidatum* (Kogami et al. 2001); *Phaseolus vulgaris*, *Metrosideros umbellata* and *Weinmannia racemosa* (DeLucia et al. 2003); and *Nicotiana tabacum* (Evans et al. 1994)

to saturate at higher internal conductance (Fig. 4A,B). The C_c/C_i ratios increased with increasing both g_{area} (Fig. 4C) and g_{mass} (Fig. 4D), indicating that the leaves of differing structural characteristics do have varying internal diffusion limitations of photosynthesis. The latter relationship was less scattered with g_{mass} , suggesting that g_{mass} is the true determinant of the volume-weighted average chloroplastic CO_2 concentration.

To further test for the anatomical limitations of diffusion, we examined the dependencies of g_{area} and g_{mass} on M_A for a species set with limited variation in leaf photosynthetic capacity (Fig. 5). In this set of data, g_{area} did not correlate with M_A , but g_{mass} significantly decreased with increasing M_A , conclusively demonstrating the dependence of internal diffusion limitations on leaf structure.

M_A is an integral measure, and it is pertinent to explore which specific structural characteristics are responsible for the variations in internal diffusion conductance and A_{mass} . Differences in cell wall thickness and chemical composition can exert a major control over leaf photosynthetic capacity.

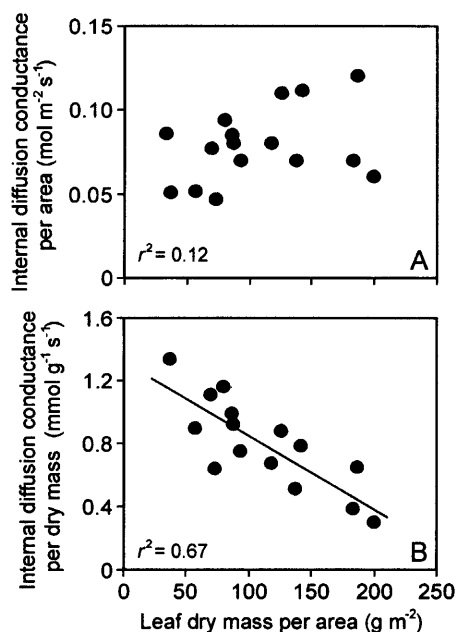


Fig. 5. Internal diffusion conductance per unit area (A) and dry mass (B) in relation to leaf dry mass per unit area (M_A) for a constrained range of leaf photosynthetic capacities ($10 \mu\text{mol m}^{-2} \text{s}^{-1} \leq A_{\text{area}} \leq 5 \mu\text{mol m}^{-2} \text{s}^{-1}$, subset of data in Fig. 4). Because of a strong scaling of mesophyll diffusion conductance with leaf photosynthetic capacity, the relationships between leaf structural variables and diffusion conductance can only be tested conclusively if foliar photosynthetic potentials are kept essentially constant

In particular, thicker and less porous cell walls can strongly impede liquid-phase CO_2 diffusion from the outer surface of cell walls to carboxylation sites in the chloroplasts (Kogami et al. 2001; Terashima et al. 2001; Miyazawa et al. 2003). Thicker and denser cell walls contribute to an overall greater bulk D , and thus, greater volume fraction of non-photosynthetic cell walls and larger liquid-phase diffusion resistance may provide an explanation for the interspecific strong negative relationships between A_{mass} and D (Niinemets 1999b) and A_{mass} and M_A (Wright et al. 2004b).

Increases in D are also associated with decreases in the volume fraction of internal air space within the leaves (Niinemets 1999b; Sack et al. 2003a). A decrease in the air volume fraction is expected to reduce the gas-phase component of the internal diffusion conductance (Parkhurst 1994), thereby potentially further curbing A_{mass} . Such a negative scaling of internal diffusion conductance with the fraction of leaf air space has been observed in some (Syvertsen et al. 1995; Hanba et al. 1999), but not in all studies (Hanba et al. 2001), indicating that the relative significance of various structural traits depends on the overall leaf constitution.

3.3 Structural Determinants of Leaf Water Transport Efficiency

Leaf stomatal conductance is a highly variable quantity, which in well-illuminated plants is primarily determined by plant water status. For the full employment of the structural and biochemical investments in the photosynthetic potentials in non-stressed conditions, A_{area} must be coordinated with the maximum stomatal conductance to water vapor (G_{max}). G_{max} varies with the total number of stomata (stomatal density) and average pore area of single stomata (Sack et al. 2003a), and accordingly, a coordination is expected between the stomatal pore area per unit leaf area, the thickness of mesophyll, and the internal mesophyll surface area (Sack et al. 2003a).

For leaves that operate at a given narrow range of leaf water potential, leaf hydraulic conductance per unit area (K_{leaf}) must further match the transpiration rate ($E = \Delta\psi K_{\text{leaf}}$, where $\Delta\psi$ is the water potential gradient between the evaporation sites in the leaf and the point of leaf attachment to the stem). In fact, recent studies have observed strong positive correlations between K_{leaf} and maximum stomatal pore area, and G_{max} and A_{area} (Aasamaa et al. 2001; Sack et al. 2003a; Brodribb and Holbrook 2004).

How does the coordination between G_{max} and K_{leaf} arise? The total leaf hydraulic conductance depends both on the conductances of leaf veins, and on the conductances of the apoplastic and symplasmic pathways of water movement from the xylem to the sites of evaporation in the mesophyll. Both

components of the hydraulic pathway are important in determining the overall hydraulic conductance (Cochard et al. 2004; Sack et al. 2004; Sack and Tyree 2005). The total hydraulic conductance of leaf venation, in turn, is mainly determined by the conductances of the higher order major veins and the minor veins (Fig. 6, Sack and Tyree 2005). This may possibly reflect the fact that the midrib and lower order major veins also function as structural support, and leaves tend to invest more biomass than needed for self-support to cope with the dynamic loads experienced during windy conditions. Thus, a large bottleneck in the venation system resides in the transition between vein orders or within the minor veins (Sack et al. 2004). Given the importance of minor veins and apoplastic and symplasmic pathways, total leaf hydraulic conductance is expected to scale with the venation density and with the total number of extravascular pathways, i.e. with internal mesophyll surface area. Currently, only limited data exist on the hydraulic conductance of different venation architectures, the leakiness of vein xylem conduits, membrane permeabilities, and conductances of apoplastic pathways. Nevertheless,

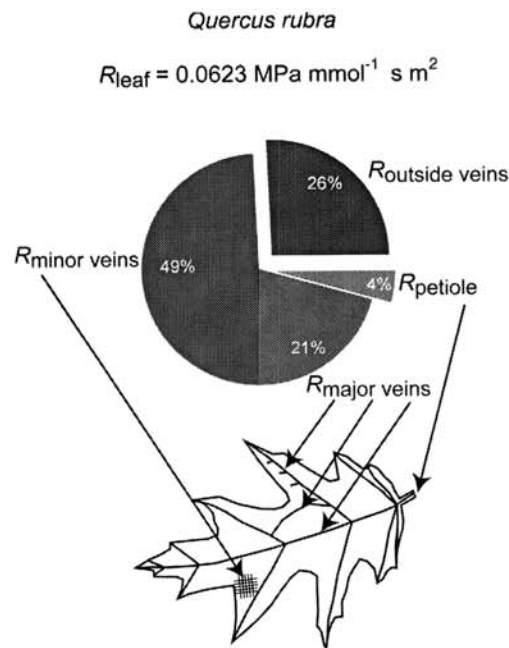


Fig. 6. Distribution of the total leaf hydraulic resistance (R_{leaf}) among different vascular components in the temperate deciduous tree *Quercus rubra* (modified from Sack et al. 2004). R rather than the inverse, hydraulic conductance (K_{leaf}), has been shown because the total pathway resistance is the sum of the component serial resistances

computer simulations (Roth et al. 1994, 1995) and observations of the occurrence of species with differing leaf venation densities in earth floras (Uhl and Mosbrugger 1999) support the control of K_{leaf} by venation density. In addition, the hypothetical scaling of K_{leaf} by the number of extravascular pathways is confirmed by a strong positive correlation of K_{leaf} with T (Fig. 7).

3.4 Leaf Size and Shape Effects on Photosynthesis: Only a Matter of Leaf Energy Balance?

Gradients in leaf size from tropical rain forests to deserts and temperate forests have been described in many studies (Grubb 1977; Medina 1984), and it is commonly thought that leaf size, and possibly leaf shape will mainly impact on A_{area} via modification of the leaf heat balance. A larger leaf will heat up more at a given air temperature, due to a thicker boundary layer and slower convective cooling. However, with higher temperature, the leaf will potentially show a higher rate of gas exchange at a given value of stomatal conductance (Parkhurst and Loucks 1972), and enhanced latent heat loss buffers against excessive leaf temperatures. As larger leaves are expected to optimize photosynthetic parameters at higher temperature, leaf size-mediated changes in leaf energy balance do not per se facilitate or inhibit photosynthetic potentials.

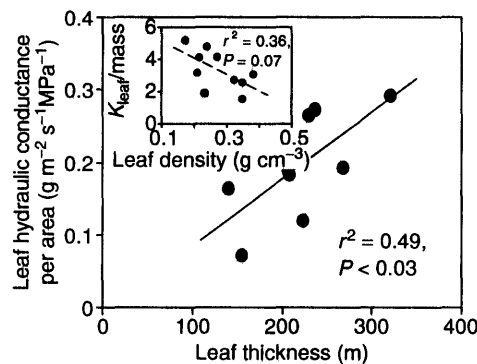


Fig. 7. Leaf hydraulic conductance (K_{leaf}) in relation to leaf thickness in exposed and shaded leaves of five temperate deciduous woody species (*Acer rubrum*, *A. saccharum*, *Betula papyrifera*, *Q. rubra*, *Vitis labrusca*) and in the evergreen vine *Hedera helix* (modified from Sack et al. 2003a). The inset demonstrates the correlation between K_{leaf} per unit mass (K_{leaf}/M_A ; $\text{mg g}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and leaf density. K_{leaf}/M_A characterizes the water supply of average leaf cells. Leaf thickness (T) and density (D) are related through M_A ($M_A = TD$). For other abbreviations, see Figs. 5 and 6

However, in natural conditions, the leaves are often constrained by the availability of water, and if the leaf temperature exceeds the level that can be optimized, water loss relative to C gain becomes uneconomical, and the maximum leaf size will be constrained by water supply.

Whether there is coordination between leaf shape and gas exchange is not yet fully established. While leaf shape affects the capacity to pack the leaves on a shoot for enhanced light capture, leaf shape per se may not play much of a role in modifying leaf energy balance. Classic work using six differently shaped copper model leaves indicated that dissected and lobed leaves may dissipate heat and exchange gases more effectively than entire leaves (Vogel 1970), especially in windless conditions (free convection) or under low wind velocities (mixed convection), which lead to more extensive temperature gradients across the surface of non-lobed leaves (Roth-Nebelsick 2001). The situation may be different under strong wind velocities (forced convection), when a common boundary layer develops above the entire surface of the dissected leaf or a collection of small leaves such as a conifer shoot (Germino and Smith 1999). However, the convection efficiency of different leaf shapes may also strongly depend on the wind direction (Roth-Nebelsick 2001). Lobed and dissected leaves tilted with respect to wind direction are more efficient than their non-lobed counterparts, because wind can freely gush through the interceptions (Vogel 1970; Roth-Nebelsick 2001). Furthermore, lobed leaves are often more jagged and folded, with protruding leaf margins. Such a leaf arrangement significantly increases leaf surface roughness and reduces the critical wind speed for turbulence, thereby potentially increasing leaf heat exchange at a common wind speed (Grace 1978).

Most of the previous experimental work on leaf heat exchange has focused on steady-state conditions. However, leaf light environment in the field strongly fluctuates in time leading to “heatflecks” (Singsaas et al. 1999), which suddenly rise leaf temperature strongly above the ambient temperature. Given that dissected and small leaves generally produce more “flecked” light field, and that lateral heat conductance is larger for dissected structures, coping with temporarily excessive temperatures also favors dissected and lobed leaf shapes.

Recent findings that more lobed leaves possess higher leaf hydraulic conductance, have led to suggestions that leaf lobation is an adaptive adjustment to improve K_{leaf} (Sisó et al. 2001; Zwieniecki et al. 2004). Higher hydraulic conductance of more lobed leaves was explained by a lower amount of mesophyll tissue between the major veins, minimizing the average distance of mesophyll cells from lower-order major veins (Sisó et al. 2001; Zwieniecki et al. 2004). However, this relationship between the complexity of leaf outline

and K_{leaf} is not universal (Sack et al. 2003a). In fact, when the conductance of higher-order veins and extravascular pathways limit K_{leaf} , minimization of the distance of mesophyll cells from major veins may have a limited effect on overall leaf hydraulic conductance.

3.5 A Further Linkage Between Leaf Size and A_{mass}

In addition to affecting light interception, leaf energy balance and hydraulic efficiency, differences in leaf size and shape also significantly modify leaf biomass partitioning between support and photosynthetic tissues. Larger leaves may have disproportionately greater biomass investments in vasculature and sclerenchyma to maintain lamina flatness and inclination angles and ensure effective water transport to mesophyll cells (Givnish 1984). Enhanced investment in vasculature is compatible with an efficient water-conducting pathway (Enquist et al. 1999; West et al. 1999), but also with lower photosynthetic rates (Poorter and Evans 1998; Garnier et al. 1999) and lower growth rates (Van Arendonk and Poorter 1994). So far, the biomass partitioning between major veins and the rest of the leaf lamina has been studied in a few broad-leaved species. The results indicate that the fraction of leaf biomass in major veins increases with increasing leaf size (Fig. 8, Niinemets et al. 2004a), which is the optimal strategy to maximize light harvesting and water supply to the mesophyll for a given biomass investment in mechanical support (Niinemets and Fleck 2002b). However, important interspecific differences in investments in major veins apparently also exist (Fig. 8). Given that major leaf veins can contain > 20% of lamina biomass (Fig. 8), scaling of fractional biomass investments in support with leaf size likely provides an important explanation for variation in foliage photosynthetic capacities of co-existing species that possess similar M_A and leaf longevity.

As the previous paragraphs indicate, the relationships between leaf structure and net assimilation primarily arise because leaves of varying structure and chemistry contain different fractions of photosynthetic mesophyll. Aside from modifications of thickness of cuticle, epidermis, and intercellular air space volume of interveinal leaf lamina areas, all leaves contain a significant fraction of vasculature, and also have petioles of varying thickness and length for the attachment to the stem. It is important to note that leaves of the same aggregated structural attributes such as M_A , density and thickness may contain different fractions of support tissues within a unit leaf mass, and accordingly possess contrasting foliar photosynthesis rates.

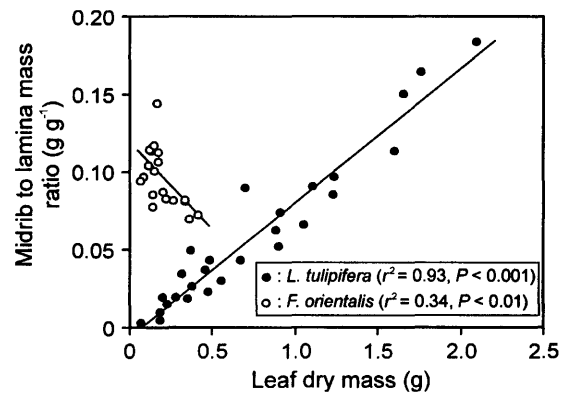


Fig. 8. Leaf midrib relative to the rest of the lamina biomass versus total leaf dry mass in *Liriodendron tulipifera* (data from Niinemets and Fleck 2002b) and *Fagus orientalis* (data from Niinemets and Fleck 2002a). Each point corresponds to an individual leaf. Data are fitted by linear regressions

3.6 Variation in PNUE due to Leaf Structure

The availability of limiting elements such as N may be a further factor shaping the structural coordination of leaf photosynthetic capacity. Because roughly half of leaf N is invested in the photosynthetic apparatus (Evans 1989), there is a strong correlation between A_{mass} and N_{mass} (Evans 1989; Wright et al. 2004b). Thus, the relations between leaf architecture and A_{mass} may be interpreted using N as a universal currency that limits maximum leaf photosynthetic capacity. From this perspective, A_{mass} can be expressed as the product of N_{mass} and PNUE ($=A_{\text{mass}}/N_{\text{mass}}$). Variation in N_{mass} occurs due to concentration or dilution of foliar N, and accordingly, due to variations in the thickness and density of mesophyll cell walls as well as support tissues such as epidermis, hypodermis, sclereids and veins. For instance, increases in foliar biomass investments in vasculature lead to lower foliar N concentrations of the entire lamina (Niinemets and Fleck 2002a, b), while increases in the volume fraction of photosynthetic mesophyll tissue increase N_{mass} (Reich 1998).

The variations in PNUE are associated with differences in the partitioning of leaf N among photosynthetic compounds (Hikosaka and Terashima 1996; Hikosaka et al. 1998), and overall partitioning of leaf N among photosynthetic and non-photosynthetic pools (Hikosaka and Terashima 1996; Hikosaka et al. 1998). The size of the non-photosynthetic pool may depend on leaf structure, as 10–15% of leaf N is associated with cell walls (Takashima et al. 2004), and a significant fraction of N with vasculature

(Niinemets and Fleck 2002b). Thus, as the fraction of support tissues increases, an increasing fraction of total N will be partitioned in non-photosynthetic compartments, reducing leaf PNUE. In addition to N partitioning, variation in internal CO_2 diffusion conductance further modifies the use efficiency of N invested in photosynthetic apparatus, implying a direct link between leaf structure and PNUE. Due to structural controls of leaf N partitioning within the leaf and structural controls on efficiency of diffusion, the slopes of A_{mass} versus N_{mass} may significantly vary for different species assemblages (Wright and Westoby 2002; Niinemets et al. 2004d).

Further, it may be of importance that low nutrient availability itself leads to larger M_A (Beadle 1966; Smith et al. 2004), and that this response enhances leaf nutrient conservation due to a longer leaf life-span (Wright and Westoby 2002, 2003; Wright et al. 2002, 2004a). The hypothesis of nutritional control of sclerophylly has been suggested by several studies, leading to interpretations that sclerophyllous leaf structure in Mediterranean shrublands, tropical heaths and tropical upper montane forests are driven by nutrient-limited soils (Grubb 1977; Turner 1994). However, only a few studies have investigated simultaneously nutrient and water limitations in these communities. Recent studies suggest that low water availability rather than nutrients provide the primary explanation for the occurrence of some sclerophyllous floras (Niinemets 2001; Lamont et al. 2002).

4 Structural Acclimation of Leaf Photosynthesis to Environment

In addition to understanding the broad patterns for species groups, it is important to recognize that a wide range in any leaf trait can be found within every community. The variation in leaf characteristics among species within a site is often as great or greater than the mean difference between the sites, even when the sites are spread out along a dramatic climatic gradient from a desert to a rain forest (Reich et al. 1997, 1999). There is always environmental heterogeneity within each specific site. Thus, scaling of plant photosynthetic productivity from the leaf to the global scale requires an understanding of the fundamental scaling relations as well as a consideration of within-species plasticity in these relations.

4.1 Adjustments to Light

As an acclimation response to the vertical light gradient, M_A varies several-fold in plant canopies (Fig. 9A; Meir et al. 2002). As the result of stacking of

the mesophyll with increasing irradiance, A_{area} scales positively with M_A in plant canopies (Fig. 9B), while A_{mass} may be relatively invariable (Fig. 9C).

The within-canopy variation in M_A results from increases in both T and D (Niinemets et al. 1999, 2003; Sack et al. 2003a). Contrary to the interspecific relationships (Niinemets 1999b), increases in density are positively associated with A_{area} within tree canopies (Niinemets et al. 1999), possibly because the light-mediated increase in D is associated with increases in the fraction of palisade tissues in leaf mesophyll more than with increases in cell wall thickness. Such adaptive modifications in leaf anatomy further increase leaf photosynthetic capacity at a common T .

Across habitats, species show similar plastic modifications of M_A and A_{area} to irradiance (Cao 2000; Evans and Poorter 2001; Sack et al. 2003b).

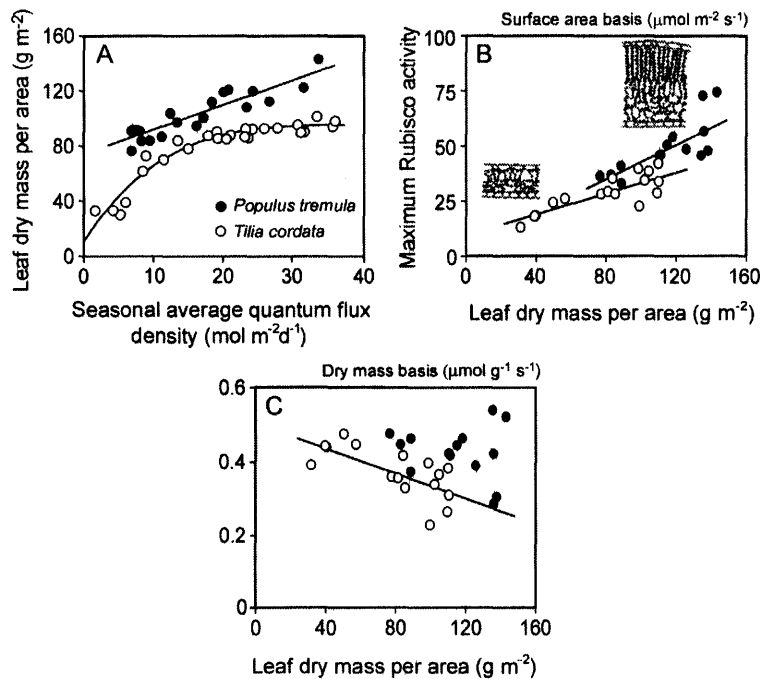


Fig. 9. Increases in M_A with long-term irradiance in the canopies of deciduous temperate trees (A), and correlations between M_A and maximum Rubisco carboxylase activity per unit area (B) and dry mass (C; modified from Niinemets et al. 1998). Analogous relationships were observed for the maximum photosynthetic electron transport rate. In B, corresponding changes in half thickness (T) are also shown. The idealized leaf cross-sections are scaled to correspond with the observed three-fold gradient in T in the mixed canopy of *P. tremula* and *T. cordata* (Niinemets et al. 1999). All linear and non-linear regressions are significant at $P < 0.005$. For abbreviations, see Figs. 5 and 7

Furthermore, at a global scale, M_A and T increase with increasing global solar radiation (Niinemets 2001), demonstrating evolutionary adjustments in leaf structure to irradiance. In fact, according to experimental studies, structural acclimation is a more effective way of increasing A_{area} in high-light environments than modification of N partitioning among the components of the photosynthetic apparatus (Niinemets et al. 1998; Sack et al. 2003b).

Within the canopy, K_{leaf} scales positively with M_A and its components, D and T (Sack et al. 2003a; Aasamaa et al. 2004), and the values of K_{leaf} also increase across habitats with varying irradiance (K. Aasamaa, A. Söber and Ü. Niinemets, unpublished data; L. Sack, N. M. Holbrook and M. T. Tyree, unpublished data). These co-variations among leaf structural characteristics and hydraulic conductance along light gradients further support the strong coordination of leaf assimilation and hydraulic characteristics.

4.2 Modifications due to Varying Moisture Supply

Plants adapted to limited moisture supply develop traits that either allow: (1) an early diurnal stomatal closure, or (2) maintenance of xylem function and leaf gas exchange despite falling soil water potentials. An array of structural modifications exists to maintain water flow from drying soil. Commonly, M_A increases in response to drought stress (Abrams et al. 1994; Abrams and Mostoller 1995; Sack 2004). Drought-related changes in M_A are mainly associated with increased cell wall thickness, cell wall lignification and decreased internal air space, collectively leading to larger D [see Niinemets (2001) for a review]. The adaptive significance of larger D in drought-adapted plants is that it rigidifies the plant leaves and accordingly renders them more resistant to pressure-driven changes in leaf volume and water content. The increase in rigidity can be physically measured as a greater bulk modulus of elasticity (ϵ ; pressure change per unit change of symplasmic leaf water content; Niinemets 2001). Thus, plants with higher ϵ lose less cell water for a common change in leaf water potential, and can in drying soils maintain water extraction with a greater degree of leaf hydration. Adjustment of leaf water extraction capacity through leaf rigidification may further protect the leaves from herbivory and the mechanical injuries that tend to accumulate over time. This suggests that increasing the resistance to mechanical lesions implies a greater leaf life-span in drought-adapted leaves. However, greater diffusion resistance and the resultant lower A_{mass} are the major penalties of more robust leaf design.

The resistance of K_{leaf} to drought-induced decline, or a resilient K_{leaf} via a xylem embolism refilling mechanism, are also the traits of paramount

significance in drought tolerance (Trifilo et al. 2003). Ample evidence of a greater safety margin of stem xylem conductance in plants acclimated to drought is available (e.g., Linton et al. 1998; Hacke et al. 2001a), but few data exist on the adjustments of leaf vein conductance to drought (Salleo et al. 2001). Inevitably, a greater safety margin with respect to cavitation is associated with decreased xylem conduit diameters (Linton et al. 1998; Hacke et al. 2001a), implying that the species with water-potential-insensitive K_{leaf} values are characterized by lower potential K_{leaf} . Nevertheless, species with “safe” K_{leaf} can more strongly modify $\Delta\psi$ between the leaf and the point of leaf attachment to the stem, thereby maintaining $E(\Delta\psi K_{\text{leaf}})$. Although drought-sensitive species may have a larger potential hydraulic conductance, K_{leaf} decreases with increasing $\Delta\psi$ in these species, typically with a threshold-type response (Salleo et al. 2001), and a certain transpiration rate cannot be maintained after the critical water potential for cavitation has been achieved (Nardini et al. 2001).

There is a trend of a negative scaling of K_{leaf}/M_A with D in six temperate species (Fig. 7, inset). Given that K_{leaf}/M_A is the conductance estimate characterizing the water supply of average leaf cells, this negative trend suggests coordination between leaf hydraulic (hydraulic “safety”) and structural variables (extraction of water with lower water loss) that improve leaf-drought tolerance. For stemwood, it has been demonstrated that increases in tissue density effectively prevent xylem implosion at low negative pressures (Hacke et al. 2001a), and an analogous linkage between low water potential tolerance and foliar structure is also feasible for leaves.

5 Age-Dependent Changes in Leaf Photosynthetic Capacity

5.1 Increases in the Functional Activity in Young Leaves: Biochemical Versus Structural Limits

The ontogenetic trajectory of a developing leaf consists of coordinated modifications in all leaf traits. During leaf area expansion and thickening both N_{area} and M_A increase (Hanba et al. 2001; Niinemets et al. 2004c). Although the young leaves have higher N_{mass} than mature leaves (Niinemets et al. 2004c), the N investment in Rubisco, in rate-limiting components of the photosynthetic electron transport chain and in chlorophyll is low, resulting in low C assimilation potentials (Eichelmann et al. 2004; Niinemets et al. 2004c). With advancing leaf ontogeny, N_{area} and the fraction of N in photosynthetic compounds increase, leading to the values of A_{area} typical of mature leaves. There is evidence that these changes are

controlled by photosystem I content, which first reaches the mature-leaf level (Eichelmann et al. 2004).

Apart from these biochemical modifications, the initial periods of leaf development are characterized by intensive cell division (Miyazawa and Terashima 2001; Miyazawa et al. 2003), resulting in tightly packed tissues with a low volume fraction of internal air space (Miyazawa and Terashima 2001). In the following intensive leaf expansion phase, the volume fraction of air space increases dramatically, leading to concomitant increases in the internal CO_2 diffusion conductance from the outer surface of cell walls to chloroplasts (Hanba et al. 2001; Miyazawa and Terashima 2001; Eichelmann et al. 2004). Thus, A_{max} in young leaves is co-limited by both the low content of photosynthetic enzymes as well as by the low efficiency of CO_2 diffusion.

Young leaves with weakly developed vasculature also have low values of K_{leaf} , suggesting that limited hydraulic conductance may also curb the photosynthetic efficiency of young leaves (Martre et al. 2000; K. Aasamaa, A. Söber and Ü. Niinemets, unpublished data). In addition, formation and differentiation of stomata on the leaf surface continues until leaf maturation (Kouwenberg et al. 2004). These findings suggests that inefficient water-conducting pathways and low stomatal pore area exert a further relevant limitation on C gain in young leaves.

5.2 Time-Dependent Deterioration of Leaf Physiological Activity in Mature Leaves and During Senescence

In non-senescent leaves, there are significant time-dependent decreases in photosynthetic rates due to decreases in N_{mass} (Wilson et al. 2001; Niinemets et al. 2004c), as foliar N is diluted by cell wall accretion, and possibly because of N resorption as a late-season N sink forms in the developing buds. Mesophyll diffusion conductance also decreases continuously in mature non-senescent leaves (Miyazawa and Terashima 2001). Decreases in diffusion conductance are associated with increases in the thickness of mesophyll cell walls (Miyazawa and Terashima 2001), and possibly also with decreases in the pore volume in cell walls due to accumulation of lignin and cutin (Suzuki and Itoh 2001; Miyazawa et al. 2003; Niinemets et al. 2004d). At a "macro-scale", the age-dependent changes reflecting decreased diffusion efficiency are the increase in M_A and leaf C content per unit dry mass (Miyazawa and Terashima 2001; Wilson et al. 2001; Niinemets et al. 2004d).

The declining biochemical and diffusion efficiencies occur simultaneously with a decline in K_{leaf} (Aasamaa et al. 2002; Salleo et al. 2002; Lo Gullo et al. 2004, 2005). As leaves age, repeated episodes of dehydration and

embolism in the veins may lead to a progressive loss of conductance (Brodribb and Holbrook 2003), a situation analogous to cavitation fatigue observed in stemwood xylem (Hacke et al. 2001b). The decrease in K_{leaf} is also dependent on the accumulation of tyloses in the leaf (Salleo et al. 2002). In evergreen conifers, the activity of secondary needle growth in non-elastic mature leaves may lead to compression of xylem vessels, thereby further reducing the efficiency of water transport (Gilmore et al. 1995). In addition to vascular limitations, the time-dependent decreases in K_{leaf} are amplified by potential losses of membrane conductances in the bundle sheaths, and in the apoplastic pathways, as cell walls thicken and accumulate hydrophobic constituents (Sack 2005). While decreases in leaf N and diffusion conductance decrease leaf photosynthetic capacity, the hydraulic limitations would result in decreased stomatal conductances, and decrease the realized leaf assimilation rates.

Overall, a series of time-dependent modifications with complex interactions and feedbacks and environmental dependencies occur during leaf aging (Fig. 10). Declining function may interact with a seasonal cue to precipitate leaf senescence (Salleo et al. 2002), finally leading to leaf abscission. In mature non-senescent leaves, changes in leaf functioning occur relatively slowly (Niinemets et al. 2004c), but the decrease in leaf assimilation potentials is fast during senescence due to regulated dismantling of cell organelles and resorption of N (Kitajima et al. 1997, 2002; Wilson et al. 2001; Niinemets et al. 2004c). In evergreens, the time at which the senescence phase commences apparently also depends on the rate of accumulation of mechanical damage, and on the speed of time-dependent changes in leaf diffusion conductance and hydraulics (Fig. 10), which would ultimately determine when the cost/benefit ratios of specific leaves become uneconomical. Furthermore, older leaves of evergreen species are being gradually shaded by new foliage, and the re-acclimation to the new light environment is a critical factor modifying the life-span of the foliage (Niinemets 1997, Fig. 10). Accordingly, leaf longevity depends on the speed and the extent of modifications in leaf structural and physiological traits in a complex manner (Fig. 10).

6 Outlook: a Network of Coordinated Leaf Traits

There are many examples of trait correlations, demonstrating that plant performance is optimized by simultaneous modifications in a series of key traits. We propose that coordinated variation among plant traits may be achieved in at least five ways. The traits can be *allometrically* coordinated,

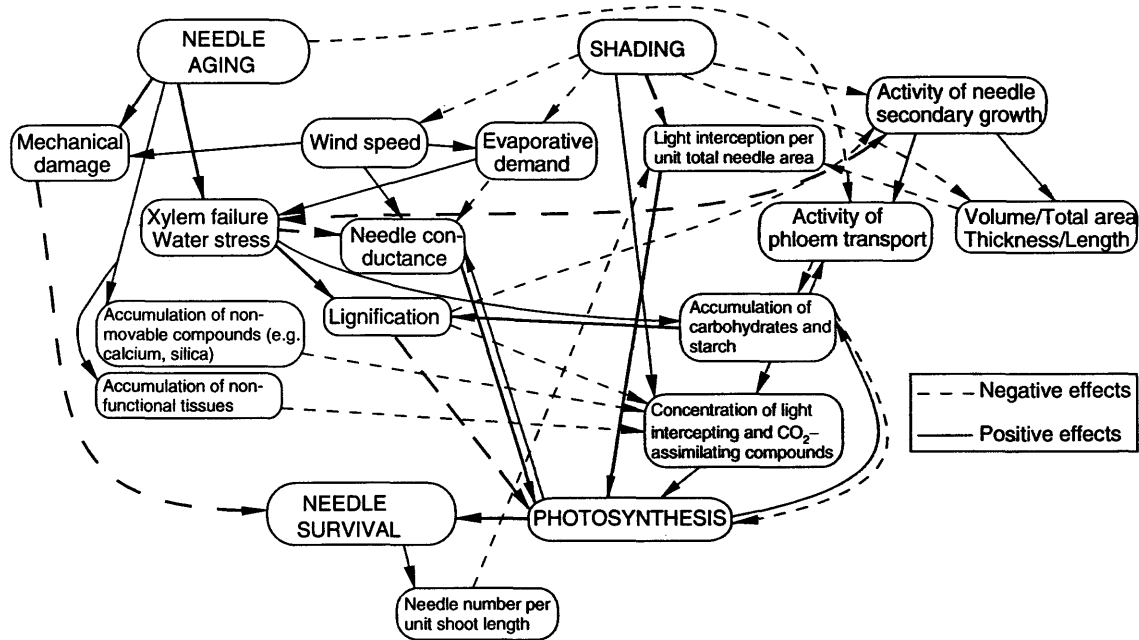


Fig. 10. Dependence of needle survival on the interplay between foliage shading and aging in conifers: a conceptual model. Aging of non-senescent mature needles results in enhanced lignification of cell walls, accumulation of non-structural carbohydrates, and ash minerals (primarily Ca), and deposition of dead tissues (Niinemets 1997). These chemical changes result in dilution of needle chemicals responsible for light interception and C acquisition. As wind speed, and air temperature, are positively correlated with irradiance, and air humidity is negatively correlated with irradiance [see Niinemets and Valladares (2004) for a review], the magnitude of environmental stresses decreases with increasing shading. For simplicity, the influences of tree growth on the foliage carbohydrate pool, and the effects of nutrient requirements for growth on needle life-span have been omitted. Activity of needle secondary growth is assumed to be controlled by the same factors affecting primary growth (Dale 1988). Shade-acclimation state achieved during needle primary growth is assumed to be a central factor controlling the velocity of the decline in C acquisition capacity of the needles during further shading. Most important links are shown with **bold lines**

especially if they are related to plant size, or to developmental age (Sack et al. 2002, 2003b). The traits can be *structurally* coordinated if they share an anatomical and/or a morphological basis. Whether or not the traits are structurally coordinated, they can be *functionally* coordinated. Functionally coordinated traits contribute to a given process in a co-dependent way or independently, and are therefore simultaneously abundant in a given set of conditions. For instance, leaf stomatal and hydraulic conductances are often functionally coordinated (Aasamaa et al. 2001; Brodribb and Holbrook 2003; Sack et al. 2003a). *Genetic* or *developmental* coordination of traits occurs if the expression of the traits during growth and/or during plant plastic responses to environmental stresses proceeds simultaneously. Many trait linkages will fall into multiple categories. Furthermore, observed covariations among simple and composite traits may reflect the way the composite traits have been defined. For example, M_A is the product of T and D (Witkowski and Lamont 1991; Niinemets 1999b), and accordingly varies if either of these variables changes.

To a certain extent, all traits may be considered as vertices linked by single or double-headed arrows, and path analysis and structural equation modeling can be used to indicate the causality among interrelated traits (Shipley 1995; Shipley and Lechowicz 2000). However, often the causal structure among the traits is less clear. For instance, A_{mass} is given as A_{area}/M_A , and accordingly, these traits are interlinked as in a triangle, with each vertex connected to the other two by double-headed arrows. Taking this further, a super-network of vertices and inter-relationships may be conceived for all possible leaf traits. This would be a purely conceptual framework, and whether the potential trait coordinations are expressed as tight correlations will depend on the set of species considered (Fig. 11). Eventually, when more sets of traits and their coordination are well understood for large species sets, the full potential network can be laid out, and it will allow scaling up from given traits to whole-plant performance.

As in many natural networks, certain vertices will be 'hubs' with a disproportionate number of arrows linking them to other vertices (Barabási 2002). One structural trait that is a notable 'hub' interconnected frequently with other traits is M_A , which connects all traits that are leaf-area based with those that are leaf-mass based. Which relationships of those in the super-network will be realized depends on the species set considered. For instance, there is generally a strong positive interspecific correlation between A_{area} and A_{mass} , while M_A is negatively associated with both estimates of foliar photosynthetic potential (Wright et al. 2004b). However, depending on the variation in M_A in a specific species set, there may be no relationship between A_{area} and A_{mass} (Fig. 11; Niinemets 1999b). In turn, while M_A is for all species the product of T and D ,

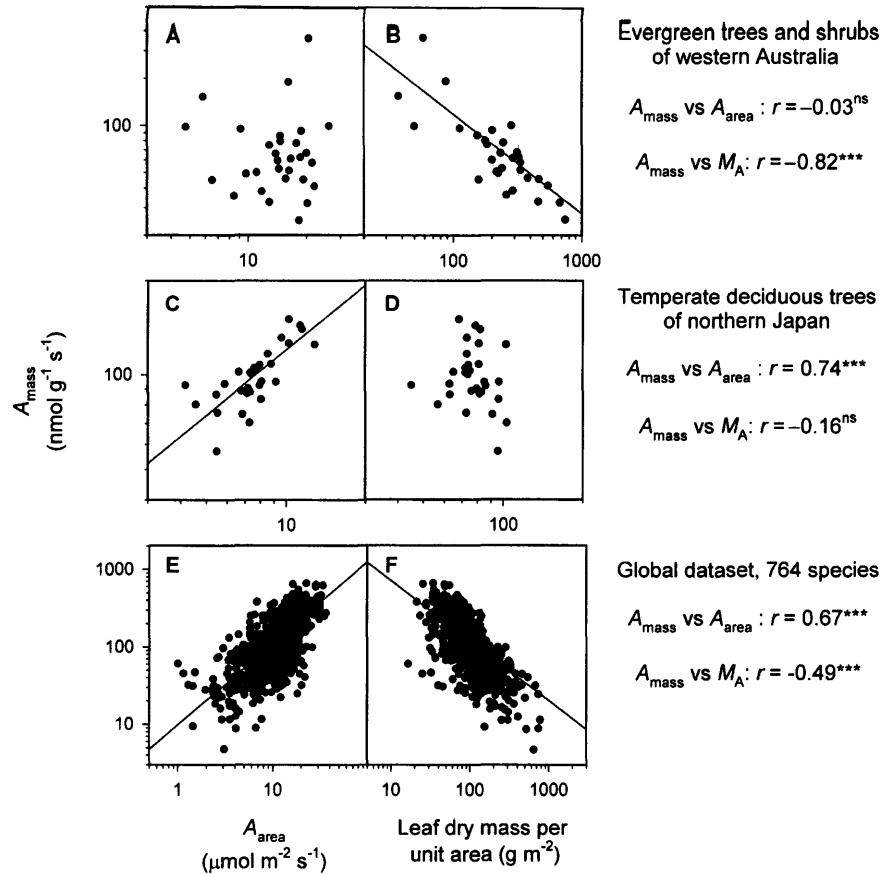


Fig. 11. Correlations among the A_{mass} and A_{area} (A, C, E) and A_{mass} and M_A (B, D, F) for evergreen trees and shrubs of western Australia (A, B; data from E. J. Veneklaas, published in Wright et al. 2004a, b), northern Japan (C, D; Koike 1988) and the global dataset (E, F; Wright et al. 2004b), which also includes the data presented in A–D. M_A links area- and mass-based quantities ($A_{\text{area}} = M_A A_{\text{mass}}$). Data were fitted by linear regressions. *** $P < 0.001$, ns $P > 0.05$. For abbreviations, see Figs 4, and 5

T is more variable in some cases, and thus more important in driving the differences in M_A , while for other species sets, the variation in M_A is driven by D (Niinemets 1999b; Shipley 2002). These examples further demonstrate the importance of structural characteristics in modifying the variations in leaf photosynthetic potentials, and underscore the significance of a functional understanding of covariation networks of plant traits.

7 Conclusions

Recently progress has been made in determining the constraints on photosynthesis at tissue, whole-leaf and shoot levels. Our model for a super-network of coordinated leaf traits enables a simultaneous consideration of the relationships of disparate traits. Traits show different coordination depending on whether leaves are compared within canopies, among individuals in different habitats, or across species sets, within or across habitats and life forms. In each case, the efficiency of light harvesting varies because of the structural limitations of the exposure of chlorophyll within the leaves and exposure of leaves according to their specific location in the canopy, while the variations in foliar photosynthetic potentials arise from the limitations of either area- or mass-based gas exchange. The area-based gas-exchange involves limitations to surface area for light capture, as well as limitations to gaseous CO₂ diffusion, including the hydraulic constraints that affect stomatal aperture. The mass-based gas-exchange involves constraints due to thick cell walls, as well as low cell wall porosity and a high degree of lignification, and a low fraction of internal leaf air space, which modify the photosynthetic potentials per unit leaf mass or N. Our review also emphasizes the importance of leaf size and shape in altering leaf physiological potentials. Leaf size not only influences leaf energy balance, but also affects the balance between photosynthetic and support biomass within the leaf, thereby changing mass-based leaf photosynthetic activity. Recent work has begun integration of leaf C and N economy traits and water-use traits, and understanding of the coordination of traits across shifting availabilities of irradiance, water, and nutrients is gradually emerging. Due to the large evolutionary and plastic modifications in foliar structure, structural limitations of foliar photosynthesis play at least as significant a role as physiological and biochemical constraints.

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