

# Photosynthesis and resource distribution through plant canopies

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## ABSTRACT

Plant canopies are characterized by dramatic gradients of light between canopy top and bottom, and interactions between light, temperature and water vapour deficits. This review summarizes current knowledge of potentials and limitations of acclimation of foliage photosynthetic capacity ( $A_{\max}$ ) and light-harvesting efficiency to complex environmental gradients within the canopies. Acclimation of  $A_{\max}$  to high light availability involves accumulation of rate-limiting photosynthetic proteins per unit leaf area as the result of increases in leaf thickness in broad-leaved species and volume:total area ratio and mesophyll thickness in species with complex geometry of leaf cross-section. Enhancement of light-harvesting efficiency in low light occurs through increased chlorophyll production per unit dry mass, greater leaf area per unit dry mass investment in leaves and shoot architectural modifications that improve leaf exposure and reduce within-shoot shading. All these acclimation responses vary among species, resulting in species-specific use efficiencies of low and high light. In fast-growing canopies and in evergreen species, where foliage developed and acclimated to a certain light environment becomes shaded by newly developing foliage, leaf senescence, age-dependent changes in cell wall characteristics and limited foliage re-acclimation capacity can constrain adjustment of older leaves to modified light availabilities. The review further demonstrates that leaves in different canopy positions respond differently to dynamic fluctuations in light availability and to multiple environmental stresses. Foliage acclimated to high irradiance respond more plastically to rapid changes in leaf light environment, and is more resistant to co-occurring heat and water stress. However, in higher light, co-occurring stresses can more strongly curb the efficiency of foliage photosynthetic machinery through reductions in internal diffusion conductance to  $\text{CO}_2$ . This review demonstrates strong foliage potential for acclimation to within-canopy environmental gradients, but also highlights complex constraints on acclimation and foliage functioning resulting from light  $\times$  foliage age interactions, multiple environmental stresses, dynamic light fluctuations and species-specific leaf and shoot structural constraints.

**Key-words:** acclimation kinetics, age effects, foliage aggregation, leaf longevity, leaf structure, light acclimation, nitrogen content, support costs, tocopherol content, xanthophyll cycle.

**Abbreviations:**  $A_{\max}$ , photosynthetic capacity (maximum photosynthesis rate);  $C_B$ , 'chlorophyll binding' (ratio of chlorophyll content to nitrogen content in light-harvesting pigments and pigment-binding complexes);  $C_C$ ,  $\text{CO}_2$  concentration in chloroplasts;  $\chi_A$ , leaf chlorophyll content per area (Eqn 2);  $D$ , foliage diameter;  $\delta$ , shoot inclination angle;  $\Delta_L$ , spatial clumping coefficient (Eqn 3);  $F_L$ , fraction of leaf nitrogen in light harvesting (Eqn 2);  $F_R$ , fraction of leaf nitrogen in ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco) (Eqn 4);  $G$ , extinction coefficient (Eqn 3);  $\gamma$ , angle between the normal to the shoot plain ( $0^\circ, 0^\circ$ ) and the direction of illumination (Eqn 3);  $g_i$ , internal  $\text{CO}_2$  diffusion conductance;  $J_{\max}$ , capacity for photosynthetic electron transport;  $L_B(\phi, \delta)$ , beam path-length in the shoot volume for specific shoot rotation ( $\phi$ ) and inclination ( $\delta$ ) angles (Eqn 3);  $M_A$ , foliage dry mass per unit area;  $N_A$ , foliage nitrogen content per area;  $N_M$ , foliage nitrogen content per dry mass;  $P(\phi, \delta)$ , probability of photon interception for specific shoot rotation ( $\phi$ ) and inclination ( $\delta$ ) angles (Eqn 3);  $\phi$ , shoot rotation angle;  $Q_{\text{ex}}$ , cumulative extra quantum flux density;  $Q_{\text{int}}$ , seasonal average daily integrated quantum flux density;  $\rho$ , foliage area density (total leaf area per shoot volume, Eqn 3);  $S_{\text{mes}}/S_C$ , inner mesophyll cell wall area to chloroplast exposed surface area ratio;  $S_P/S_T$ , foliage projected to total area ratio;  $S_T/V$ , foliage total area to volume ratio;  $\theta$ , lamina cross-sectional angle;  $\text{VAZ}$ , sum of xanthophyll cycle carotenoids (violaxanthin, antheraxanthin and zeaxanthin);  $V_{\text{cmax}}$ , maximum carboxylase activity of Rubisco;  $V_{\text{cr}}$ , specific activity of Rubisco (Eqn 4);  $\xi$ , leaf absorptance (Eqn 1).

## INTRODUCTION

Light availability typically varies ca. 50-fold within the canopies of closed vegetation stands, and significant variation in light occurs even within the crown of a free-standing plant (Le Roux *et al.* 2001a; Baldocchi, Wilson & Gu 2002; Valladares 2003). This extensive variation in within-canopy light availability induces extensive foliage structural and physiological modifications such that in the plant canopy,

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each leaf has unique combinations of trait values. Typically, foliage photosynthetic capacity ( $A_{\max}$ ) increases two- to fourfold from the bottom to the top of the canopy (e.g. Meir *et al.* 2002; Niinemets *et al.* 2006a). Although the range in foliage physiological capacities is impressive,  $A_{\max}$  still varies less than theoretically required to maximize canopy photosynthesis for a given total leaf nitrogen or foliar biomass (Field 1983; Hirose & Werger 1987; Badeck 1995; de Pury & Farquhar 1997; Schieving & Poorter 1999; Meir *et al.* 2002; Anten 2005), and the discrepancies between actual and theoretical canopy photosynthetic profiles are still poorly understood (Anten 2005).

Several factors can constrain plant acclimation in canopies. In fast-growing herbaceous stands, foliage developed in high light becomes rapidly shaded by newly developing foliage (Anten 2005; Hikosaka 2005). In a like manner, in evergreen species, foliage formed in a certain light environment becomes shaded by new foliage in subsequent seasons (Brooks, Sprugel & Hinckley 1996; Niinemets *et al.* 2006a; Wright *et al.* 2006). This interaction between light and age can importantly alter canopy profiles of  $A_{\max}$  through shading-dependent induction of senescence (Hikosaka 2005), anatomical constraints on re-acclimation of high light-acclimated foliage to low light and through enhanced internal diffusion resistance to  $\text{CO}_2$  (Ethier *et al.* 2006; Niinemets *et al.* 2006a). While potentially important, age-dependent modifications in foliage function are often ignored in scaling up leaf carbon gain potentials from leaf to canopy. Most of the available scaling up exercises for evergreen trees apply the physiology of current-year leaves to all leaf age classes in the canopy (Rambal *et al.* 2003). Although the available scaling up algorithms can potentially consider multiple age classes (Medlyn 2004), information of age-dependent changes is more often lacking than available (Grote 2007).

There are further important interactions between environmental factors within the canopies. In particular, both temperature and water vapour pressure deficit scale positively with canopy light availability (Baldocchi *et al.* 2002; Niinemets & Valladares 2004), implying that foliage can be exposed to simultaneous heat, water and high light stresses. Simultaneous acclimation to multiple stresses can significantly modify the profiles of  $A_{\max}$  within the canopy, but only few studies have investigated the interactions between the stress factors within plant canopies and the resulting modifications in foliage functioning. In addition, foliage adjusted to certain long-term average light environment has to cope with day-to-day light fluctuations that strongly deviate from average light conditions. Because re-acclimation of  $A_{\max}$  to changed light conditions may be limited by time-dependent and anatomical constraints (Oguchi, Hikosaka & Hirose 2005), light fluctuations, especially rapid increases in light availability, can further significantly enhance overall stress and alter leaf photosynthetic activity (Niinemets *et al.* 2003; García-Plazaola *et al.* 2004).

Modifications in  $A_{\max}$  have received the majority of attention in within-canopy acclimation studies, but canopy photosynthetic productivity also depends on acclimation of foliage light-harvesting efficiency to leaf irradiance

(Cescatti & Niinemets 2004) for a review). Adjustment in light-harvesting efficiency can modify whole canopy photosynthetic productivity to a similar degree than physiological changes, and needs consideration in scaling up foliage function from leaf to canopy (Ryel 1993; Werner *et al.* 2001b). It is further important that light-dependent structural and physiological modifications improving  $A_{\max}$  can reduce light-harvesting efficiency and vice versa (Valladares & Pugnaire 1999; Walters & Reich 2000; Pearcy, Muraoka & Valladares 2005). These possible trade-offs mean that individual foliage acclimation responses must be assessed in the context of specific canopy light availabilities and from the perspective of maximizing whole canopy performance. Species differ widely in the distribution of foliage between canopy micro-environments receiving relatively high and low light availabilities, and accordingly, the 'value' of specific traits affecting photosynthetic potential and light harvesting is species-specific.

The main aims of this review are to give an overview of the state of the art of within-canopy foliage acclimation, outline the gaps in knowledge, reconcile apparent controversies and suggest further experimental and theoretical work to enhance understanding of canopy functioning. This manuscript reviews the basic within-canopy acclimation responses in  $A_{\max}$  and light-harvesting efficiency to long-term light availability, re-acclimation of foliage to changed light conditions and modification of foliage function by interactions between age and light availability, by multiple interactions between different environmental factors and by foliage adjustment to dynamically changing canopy light environments. While all plants exhibit remarkable photosynthetic plasticity to light, within-canopy variation in photosynthetic potentials is achieved by various combinations of structural and physiological modifications in different plant life forms. Acclimation responses are reviewed separately for herbs, broad-leaved species and in needle-leaved species with complex geometry of foliage cross-section. Each of these plant life forms portrays unique anatomical constraints and structural acclimation responses to light environment.

## ACCLIMATION OF FOLIAGE LIGHT-HARVESTING CAPACITY WITHIN CANOPIES

### Variations in nitrogen partitioning in light harvesting

Changes in foliage light harvesting can occur through modifications in leaf pigment content and/or by alterations in the exposure of foliage to incident irradiance. Alterations in chlorophyll content affect leaf absorptance ( $\xi$ ) and thereby modify the amount of light intercepted at a given incident light intensity. How much is an increase in leaf chlorophyll content enhancing light absorption? Evans (1993b) derived an empirical relationship between leaf absorptance and chlorophyll content per area ( $\chi_A$ ,  $\text{mmol m}^{-2}$ ) for a wide range of species differing in foliage structure and chlorophyll content:

$$\xi = \frac{\chi_A}{\chi_A + 0.076}, \quad (1)$$

where  $0.076 \text{ mmol m}^{-2}$  is an empirical coefficient. Further work has demonstrated that foliage structure exerts only a moderate effect on leaf absorptance, but also that this equation is invalid for species having strongly waxy or hairy leaves with highly reflectant surface (Evans & Poorter 2001).

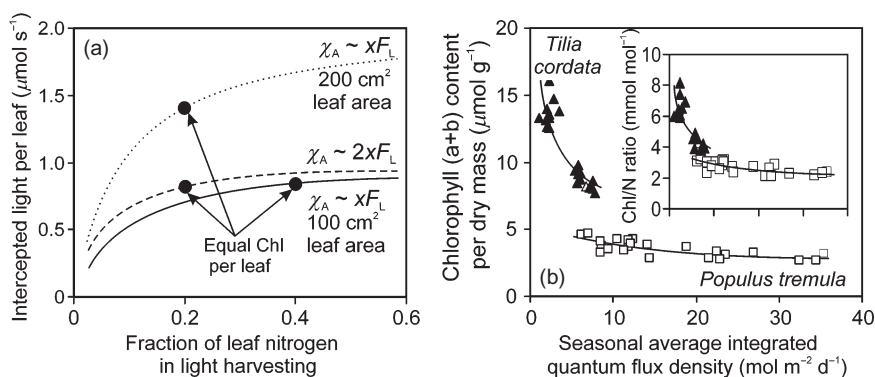
Nitrogen is the mineral element frequently limiting plant productivity in natural communities. Because of the large nitrogen cost of chlorophyll and chlorophyll-binding proteins, within-canopy modifications in light interception efficiency depend on variations in nitrogen investments in light harvesting. To evaluate the impact of varying nitrogen investments in chlorophyll and pigment-binding proteins on leaf light-harvesting efficiency, leaf chlorophyll content can be expressed in nitrogen equivalents as (Niinemets & Tenhunen 1997)

$$\chi_A = N_M M_A F_L C_B, \quad (2)$$

where  $N_M$  ( $\text{g g}^{-1}$ ) is leaf nitrogen content per dry mass;  $M_A$  ( $\text{g m}^{-2}$ ) is leaf dry mass per unit area;  $F_L$  is the fraction of leaf nitrogen in light harvesting, and  $C_B$  [ $\text{mmol Chl (g N)}^{-1}$ ] is the 'chlorophyll binding', that is, the amount of chlorophyll corresponding to a unit nitrogen invested in light harvesting.  $C_B$  considers the nitrogen cost of chlorophyll and chlorophyll-binding proteins and depends on the stoichiometry of light-harvesting pigment-binding protein

complexes, and is typically around  $2.1\text{--}2.5 \text{ mmol g}^{-1}$  (Niinemets & Tenhunen 1997; Niinemets, Kull & Tenhunen 1998b). Equation 2 provides a quantitative means to estimate leaf-level light-harvesting costs in equivalents of nitrogen and comparison of the cost of light harvesting with costs of achieving a certain photosynthetic capacity [fraction of nitrogen in ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and in photosynthetic electron transport components, see further].

Equations 1 and 2 demonstrate that the relationships between light interception and chlorophyll content and fractional nitrogen investments in light harvesting are strongly asymptotic. Thus, light-harvesting efficiency of leaves with moderately high chlorophyll content can only be enhanced to a minor degree by further increases in chlorophyll content and nitrogen investment in light harvesting. These equations predict that for an incident quantum flux density of  $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , a leaf of  $100 \text{ cm}^2$  area,  $M_A$  of  $20 \text{ g m}^{-2}$  and  $N_M$  of 2% and fractional nitrogen investment of 0.2 (20% of total N in light harvesting) will intercept  $0.725 \mu\text{mol s}^{-1}$  light per leaf. Increasing the fractional nitrogen investment twice ( $F_L = 0.4$ ) increases leaf light interception by 16% to  $0.84 \mu\text{mol s}^{-1}$  (Fig. 1a), while further doubling ( $F_L = 0.8$ ) improves light interception only by less than 6% ( $0.89 \mu\text{mol s}^{-1}$ ). In fact, because of the asymptotic nature of leaf absorptance versus chlorophyll relationship, the overall light absorption can be increased much more by spreading the same amount of chlorophyll over larger leaf area than by increasing the chlorophyll content of a given leaf. While increasing twice the chlorophyll content per unit area increases light interception by 16%, dispersing the



**Figure 1.** The amount of light intercepted by leaves with differing nitrogen investments in light harvesting ( $F_L$ ), structure and total area (a), and the dependencies of total chlorophyll content per dry mass and chlorophyll to N ratio (inset) on seasonal average integrated quantum flux density ( $Q_{\text{int}}$ ) in broad-leaved deciduous early-successional shade-intolerant species *Populus tremula* and late-successional shade-tolerant species *Tilia cordata* (b, modified from Niinemets *et al.* 2003). In (a), light interception was simulated according to Eqns 1 and 2 for an incident quantum flux density of  $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Leaf chlorophyll content per area for a given fraction of N in light harvesting ( $\chi_A \sim xF_L$ ) was calculated for the control scenario (solid line) using leaf nitrogen content per dry mass of 2%, leaf dry mass per unit area ( $M_A$ ) of  $20 \text{ g m}^{-2}$  and  $C_B$  (Eqn 2) of  $2.4 \text{ mmol g}^{-1}$ . These are typical values for shade leaves of broad-leaved deciduous species (Niinemets *et al.* 1998b). For high chlorophyll content scenario (dashed line),  $\chi_A$  was increased twofold ( $\chi_A \sim 2xF_L$ ) by increasing  $M_A$  to  $40 \text{ g m}^{-2}$ . In the third scenario (dotted line), the effect of increasing leaf size at the same  $\chi_A$  was explored by increasing the leaf area twice. Dots denote the same total leaf chlorophyll content per leaf of  $0.004 \text{ mmol}$ . In (b), data were fitted by non-linear regressions in the form of  $y = ab^x$  ( $r^2 = 0.60$  for *P. tremula* and  $r^2 = 0.81$  for *T. cordata* in the main panel, and  $r^2 = 0.47$  for *P. tremula* and  $r^2 = 0.71$  for *T. cordata* in the inset,  $P < 0.001$  for all). Chlorophyll to N ratio characterizes the fractional investment of nitrogen in light harvesting (Eqn 2).  $Q_{\text{int}}$  is determined by a method combining hemispherical photography and long-term measurements of instantaneous quantum flux density by quantum sensors (see Niinemets *et al.* 1998a for details). Chl, chlorophyll.

same amount of chlorophyll over twice larger leaf area results in an enhancement of total light interception by 100% (Fig. 1a).

Although spreading chlorophyll over larger foliar area is seemingly a superior strategy, construction of a larger leaf area is associated with greater carbon costs (Poorter *et al.* 2006), and there may be further constraints associated with efficient leaf exposure on the shoot. There is clearly a minimum leaf chlorophyll content below which leaf carbon cost becomes too high (Gutschick 1988). In fact, acclimation to low light in natural canopies is associated both with generation of larger leaf area relative to a given leaf dry mass (low  $M_A$ ), resulting in smearing of chlorophyll over larger area, as well as with enhanced investment of nitrogen in light harvesting. Leaf chlorophyll content per dry mass typically increases with decreasing light availability in the canopy (Fig. 1b; Grassi & Bagnaresi 2001; Le Roux *et al.* 2001b; Meyer *et al.* 2006), implying greater fractional nitrogen investments in chlorophyll and light-harvesting pigment-binding complexes (Fig. 1b inset; Evans & Poorter 2001; Grassi & Bagnaresi 2001; Warren *et al.* 2003). In lowest canopy irradiances, plants may invest up to 60% of total leaf nitrogen in light harvesting (Niinemets & Tenhunen 1997; Niinemets *et al.* 1998b; Evans & Poorter 2001; Grassi & Bagnaresi 2001). Such an enhanced nitrogen investment in light harvesting results in increases in light absorptance per dry mass and increases in light-harvesting efficiency of unit foliage mass (Hirose & Werger 1995). Although the overall effect of enhanced resource investment in light harvesting within the leaf can be moderate compared to distributing the same amount of chlorophyll over a larger area, even a slight improvement of leaf light-harvesting capacity can significantly improve leaf carbon balance in extremely light-limited lower canopy environments, where there may be simply not enough carbon for extra leaf area formation and support.

### Efficiency of leaf exposure: leaf three-dimensional architecture and rolling

Needle-leaved species are characterized by complex three-dimensional cross-section geometry that can importantly alter foliage light-harvesting characteristics (Jordan & Smith 1993; Cescatti & Niinemets 2004). Many studies investigating light-harvesting properties of needle-leaved species simplify the 'conifer problem' by using projected leaf area (e.g. Bond *et al.* 1999; Han *et al.* 2003). However, according to Cauchy's theorems that define the silhouette and exposed area of any convex solid, the pertinent area to characterize light-harvesting efficiency of convex foliage elements with complex geometry is half of the total area (Lang 1991; Chen & Black 1992). Implicit in this conclusion is that angular distribution of foliage on the shoot is spherical, that is, there is no preferential foliage orientation in space. Whenever leaves have a certain preferred orientation in space, Cauchy's theorems are not valid and the cross-sectional shape of the objects can also affect average leaf irradiance (Cescatti & Niinemets 2004). Thus, information

of total area relative to biomass investment in leaves (cost of light harvesting) and of foliage cross-sectional shape for horizontally or vertically oriented leaves is needed to evaluate the efficiency of light interception in species with complex foliage geometry.

Needle total area to volume ratio ( $S_T/V$ ) typically increases with decreasing leaf long-term light availability, reflecting reduced needle thickness in lower canopy (Sprugel, Brooks & Hinckley 1996; Stenberg *et al.* 1999; Niinemets *et al.* 2005b, 2007). Given that biomass investment scales with foliage volume, increases in  $S_T/V$  also denote greater foliage area per unit biomass investment in foliage. This relationship is qualitatively independent of whether or whether not the shape of leaf cross-section changes with light availability. For instance, in species with completely circular foliage cross-section as the cladodes in Australian *Casuarina* spp., the cross-sectional area of a cladode with diameter  $D$  is given as  $\pi D^2/4$ , and the circumference as  $\pi D$ , giving  $S_T/V$  as  $4/D$ . Thus, in such species, the biomass investment for formation of unit  $S_T$  decreases in direct proportion with shading-dependent reductions in  $D$  (Niinemets *et al.* 2005b).

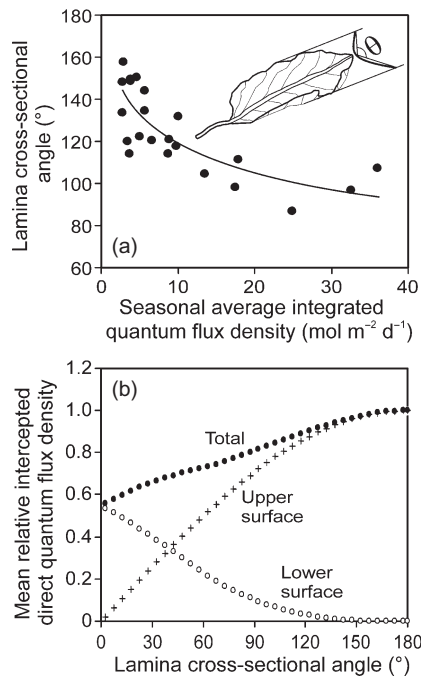
In several shade-tolerant conifers such as *Abies* and *Picea*, the shape of needle cross-section is also dependent on light availability. Specifically, needles become flatter at lower light, resulting in larger projected to total area ratio ( $S_P/S_T$ ) (Sprugel *et al.* 1996; Cescatti & Zorer 2003; Cescatti & Niinemets 2004). In these shade-tolerant conifers, needle angular distribution in low light is not spherical, but needles are positioned essentially side by side in a horizontal shoot plane, that is, the angular distribution of needle surface is horizontal (see further). Accordingly, an increase in  $S_P/S_T$  ratio implies greater exposed surface area to total surface area and improved light-harvesting efficiency in low light in these species.

Although such three-dimensional effects are generally considered of minor significance in broad-leaved species, foliage of broad-leaved species is hardly ever completely flat. More often, leaves of broad-leaved species are curled or rolled (Sinoquet, Mouliat & Bonhomme 1991; Sassenrath-Cole 1995; Sinoquet *et al.* 1998; Fleck, Cescatti & Tenhunen 2003). The degree of leaf rolling increases with increasing light availability in the canopy (Fig. 2a), radically reducing light-harvesting efficiency of leaves at high light, and altering the distribution of light interception between lower and upper leaf surfaces (Fig. 2b). Greater degree of leaf rolling in high light can be advantageous in reducing the risk of photoinhibition, especially when high light availabilities interact with water and heat stress (Werner *et al.* 2001a). In addition, rolling of upper canopy leaves results in penetration of light into deeper canopy layers, enhancing the availability of light in mid- and lower canopy.

### Efficiency of leaf exposure: angular distribution and degree of foliage aggregation

Foliage light-harvesting efficiency further depends on shoot architecture that determines the interactions among





**Figure 2.** Lamina cross-sectional angle ( $\theta$ ) in dependence on  $Q_{\text{int}}$  in broad-leaved deciduous tree *Fagus sylvatica* (a) and the effects of variations in  $\theta$  on relative direct quantum flux density intercepted by leaf upper and lower surface and on total intercepted light (b).  $\theta$  is defined in the inset of (a). In (b), the amount of light intercepted by a rolled leaf is expressed relative to the amount of light intercepted by a completely flat leaf. Data modified from Fleck *et al.* (2003). The non-linear regression fit in (a) is significant at  $P < 0.001$  ( $r^2 = 0.64$ ).

neighbouring leaves on the shoot and the angular distribution of leaf surface. Statistical radiative transfer models based on a turbid medium analogy describe plant shoot as a collection of shading objects aggregated in a defined volume (Cescatti & Zorer 2003; Niinemets, Sparrow & Cescatti 2005c). In statistical shoot models, the probability of photon interception in the shoot volume,  $P(\phi, \delta)$ , is simulated using a binomial model or a Markov model (Nilson 1971). According to the binomial model,  $P(\phi, \delta)$  depends on the angular distribution of leaf surface (G-function or so-called extinction coefficient) (Ross 1981), the spatial clumping index ( $\Delta_L$ ) (Nilson 1971), the leaf area density ( $\rho$ ) and the beam path-length in the shoot volume [ $L_B(\phi, \delta)$ ]:

$$P(\phi, \delta) = 1 - [1 - G(c, \gamma)\Delta_L]^{\frac{\rho L_B(\phi, \delta)}{\Delta_L}}, \quad (3)$$

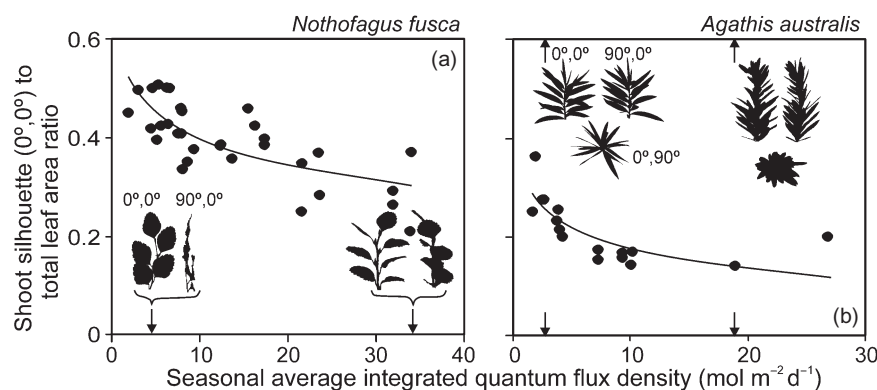
where  $\gamma$  is the angle between the normal to the shoot plain ( $0^\circ, 0^\circ$ ) and the direction of illumination, depending both on the angles  $\phi$  and  $\delta$ . Equation 3 can be applied to shoots of any structure and size and provides a straightforward way to separate various determinants of foliage light harvesting.

The G-function characterizes the angular distribution of leaf surface and is typically expressed using the ellipsoidal distribution, which assumes that foliage angles are distributed parallel to an oblate (ratio of ellipsoid horizontal to

vertical semi-axes,  $c > 1$ , horizontal distributions) or prolate ( $c < 1$ , vertical distributions) spheroid (Campbell 1986). The clumping index,  $\Delta_L$ , describes the departure of leaf dispersion from a random dispersion (Nilson 1971). For a random dispersion of foliage elements  $\Delta_L \rightarrow 0$ , and the binomial model simplifies to a Poisson model. Positive values of  $\Delta_L$  (positive binomial model) indicate that foliage elements are regularly dispersed. All else being equal, a shoot with a regular leaf dispersion has a lower shoot gap fraction, and accordingly intercepts more light than a shoot with a random dispersion. Negative values of  $\Delta_L$  (negative binomial model) indicate leaf aggregation. Shoots with aggregated foliage have a larger gap fraction, and hence intercept light less efficiently than shoots with a random dispersion. While the shoot light-harvesting efficiency can also be investigated using complex ray-tracing algorithms that explicitly describe every foliage element in space (Sinoquet *et al.* 2005), the advantage of Eqn 3 is that it uses simple characteristics with clear physical meaning that can be used to compare the light-harvesting efficiencies of shoots with widely varying size and geometry.

According to Eqn 3, the light-harvesting efficiency of shoots with the same foliage density can be increased by flatter foliage inclination angle distributions (larger G-function) and by increasing the regularity of foliage dispersion (larger positive values of  $\Delta_L$ ). Most research of shoot light-harvesting efficiency has been carried out in needle-leaved conifers. In needle-leaved conifers, the degree of leaf aggregation typically decreases with decreasing light availability in the canopy, resulting in less clumped, or occasionally even in regular needle dispersion at lowest quantum flux densities in the canopy (Bernier *et al.* 2001; Stenberg *et al.* 2001; Palmroth *et al.* 2002; Cescatti & Zorer 2003; Niinemets *et al.* 2006b). Such changes in needle aggregation imply lower needle overlap and greater light-harvesting efficiency in lower light availability. In shade-tolerant conifers such as *Abies* and *Picea*, but not necessarily in shade-intolerant conifers such as *Pinus*, foliage angular distributions become also flatter at lower light availability such that all needles are positioned essentially on the same horizontal plane, forming an analogue of a broad-leaved leaf (Stenberg *et al.* 1998, 1999; Cescatti & Zorer 2003; Niinemets *et al.* 2006b). These modifications of angular distribution of needle surface further enhance light-harvesting efficiency and partly explain superior light-harvesting efficiency of shade-tolerant conifers in low light.

While the outlined shoot architectural tuning plays a paramount role in enhancing foliage light-harvesting efficiency in the lower canopy, strongly clumped and radially symmetric shoots developed at high light availabilities often harvest light with only 15–20% efficiency relative to a flat broad-leaved leaf (Stenberg *et al.* 2001; Cescatti & Zorer 2003; Cescatti & Niinemets 2004; Niinemets *et al.* 2006b). To understand the significance of enhanced clumping in high light, it is important to consider that in the upper canopy, light availability is higher than needed to saturate photosynthesis. Even though foliage aggregation results in lower mean quantum flux densities on needle surface, this does



**Figure 3.** Shoot silhouette to total leaf area ratio in relation to  $Q_m$  in broad-leaved evergreen species *Nothofagus fusca* (a, data modified from Niinemets *et al.* 2004a) and broad-leaved evergreen conifer *Agathis australis* (b, data modified from Niinemets *et al.* 2005c). Shoot silhouettes corresponding to different light environments (denoted by an arrow) are also shown. The shoot silhouette projections are defined using rotation ( $\phi$ ), and inclination angle ( $\delta$ ) pairs ( $\phi, \delta$ ). For the projection ( $0^\circ, 0^\circ$ ), the upper face of the shoot is perpendicular to the view direction; shoot is rotated  $90^\circ$  around its axis for the projection ( $90^\circ, 0^\circ$ ) (side view), while the projection ( $0^\circ, 90^\circ$ ) corresponds to shoot axial view. Data are fitted by non-linear regressions [ $r^2 = 0.54$  for (a) and  $r^2 = 0.53$  for (b),  $P < 0.001$  for both].

not necessarily result in reduction of needle photosynthetic rates. Thus, an architectural pattern that concentrates photosynthetic biomass at high light where the photosynthetic gains are the largest results in enhanced upper canopy photosynthetic productivity as more foliage biomass can be positioned in high light. In addition, strongly aggregated upper canopy shoots with low light-harvesting efficiency let more light through to deeper canopy layers, improving the light availability in the light-limited lower canopy. Thus, the variation in shoot architecture with long-term shoot light environment is a major acclimation response that results in more uniform distribution of light within the canopy, and overall greater photosynthetic light use efficiency (photosynthetic production per incident light) of the entire canopy (Chen *et al.* 1999; Baldocchi & Amthor 2001; Cescatti & Niinemets 2004).

Shoot architecture is traditionally considered to modify mainly light harvesting in needle-leaved species with strongly aggregated small leaves. However, foliage can be clumped in broad-leaved species as well, resulting in low light-harvesting efficiencies, in the order of only 15–20% in the shoots developed in high light (Niinemets, Cescatti & Christian 2004a; Niinemets *et al.* 2005c). In broad-leaved species, shoot light interception efficiency responds to canopy light gradients similarly to needle-leaved conifers (Valladares & Pearcy 1999, 2000; Werner *et al.* 2001b; Suzuki 2002). In particular, broad-leaved shoots become increasingly flatter with decreasing light availability, resulting in enhanced light-harvesting efficiency in low light (e.g. Fig. 3 and Hutchinson *et al.* 1986). However, leaf clumping responses to long-term light availability vary among broad-leaved species. In agreement with general patterns in needle-leaved conifers, foliage became increasingly more regularly dispersed with decreasing light availability in broad-leaved conifer *Agathis australis* (Fig. 3b; Niinemets *et al.* 2005c). By contrast, foliage aggregation was weakly associated with light availability, or the leaves were even more strongly aggregated in low light in broad-leaved

evergreen *Nothofagus* species (Fig. 3a; Niinemets *et al.* 2004a). This contrasting response was mainly associated with limited carbon availability for shoot axis wood formation in low light, leading to greater overlap of neighbouring leaves in *Nothofagus* species (Fig. 3a; Niinemets *et al.* 2004a). Clearly, efficient light harvesting through adequate spacing of foliage along the shoot axis requires large biomass investments for foliage support. Such enhanced costs for shoot axis wood production can limit the potential light-harvesting efficiency in the lowest canopy irradiances.

## ACCLIMATION OF PHOTOSYNTHETIC POTENTIALS TO CANOPY LIGHT GRADIENTS IN BROAD-LEAVED SPECIES

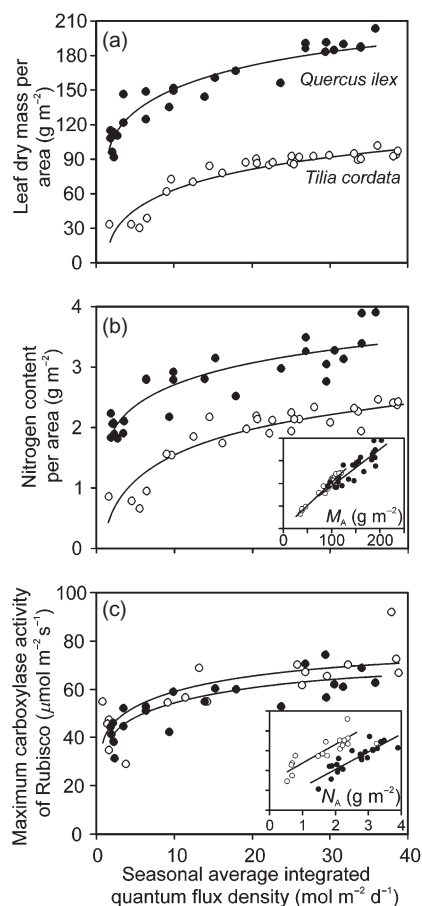
### Alterations in structure, nitrogen content and nitrogen partitioning

To assess the importance of various factors responsible for within-canopy modifications in leaf photosynthetic capacity ( $A_{\max}$ ), the partial determinants of  $A_{\max}$ , the maximum carboxylase activity of Rubisco ( $V_{\max}$ ) per unit area and the capacity for photosynthetic electron transport ( $J_{\max}$ ) per area can be expressed as the products of several independent characteristics. For  $V_{\max}$ ,

$$V_{\max} = 6.25 V_{\text{cr}} M_A F_R N_M, \quad (4)$$

where  $V_{\text{cr}}$  is the specific activity of Rubisco, that is, the maximum rate of ribulose-1,5-bisphosphate carboxylation per unit Rubisco protein;  $M_A$  is leaf dry mass per unit area;  $F_R$  is the fraction of leaf nitrogen in Rubisco;  $N_M$  is leaf nitrogen content per dry mass, and 6.25 is the nitrogen content of Rubisco protein (Niinemets & Tenhunen 1997).  $J_{\max}$  can be revealed analogously, with  $F_B$  characterizing the fraction of nitrogen in proteins limiting  $J_{\max}$  (Niinemets & Tenhunen 1997).  $A_{\max}$  is strongly correlated with both  $V_{\max}$  and  $J_{\max}$  (Wullschlegel 1993).

Leaf dry mass per unit area and leaf thickness increase with increasing light availability in canopies of a wide range of species spanning herbs, deciduous broad-leaved trees, evergreen warm-temperate and tropical broad-leaved trees, broad-leaved Mediterranean sclerophylls and evergreen conifers (see Fig. 4a for an illustration in two species of contrasting leaf longevity; Oberbauer & Strain 1986, Bond *et al.* 1999, Grassi & Bagnaresi 2001, Meir *et al.* 2002, Walcroft *et al.* 2002, Han *et al.* 2003; Terashima *et al.* 2006). As nitrogen contents per dry mass ( $N_M$ ) vary hardly along



**Figure 4.** Light-dependent modifications in leaf dry mass per unit area ( $M_A$ , a), nitrogen content per unit area ( $N_A$ , b) and maximum carboxylase activity of Rubisco ( $V_{cmax}$ , c) in Mediterranean broad-leaved evergreen species *Quercus ilex* (filled symbols, current-year foliage data modified from Niinemets *et al.* (2006a) and temperate deciduous broad-leaved species *Tilia cordata* (open symbols, data modified from Niinemets *et al.* 1998b). The inset in (b) demonstrates the correlations between  $N_A$  and  $M_A$ , and the inset in (c) the correlations between  $V_{cmax}$  and  $N_A$  (the same numerical scale as in main panels). Data were fitted by non-linear regressions in main panels and by linear regressions in the insets (all are significant at  $P < 0.001$ ,  $r^2 > 0.57$ ).  $V_{cmax}$  was calculated using  $CO_2$  concentration at the carboxylation sites in the chloroplasts ( $C_c$ ). In *Q. ilex*,  $C_c$  was determined using a combined chlorophyll fluorescence/gas-exchange approach (Niinemets *et al.* 2006a). In *T. cordata*,  $C_c$  was estimated using the method of Ethier & Livingston (2004) as discussed in Niinemets *et al.* (2006a).

canopy light gradients, an increase in  $M_A$  results also in a strong positive scaling of nitrogen content per area ( $N_A = M_A N_M$ ) with light (Fig. 4b). Typically,  $N_A$  is linearly related to  $M_A$  along canopy light gradients (Fig. 4b inset). Fractional allocation of nitrogen in Rubisco and in proteins limiting photosynthetic electron transport (Eqn 4) increases or is relatively constant with increasing light availability (Niinemets & Tenhunen 1997; Niinemets *et al.* 1998b; Evans & Poorter 2001; Grassi & Bagnaresi 2001; Le Roux *et al.* 2001b; Warren *et al.* 2003). Even if leaf nitrogen allocation were invariable along the light gradient, scaling of bulk nitrogen content per area would already mean accumulation of limiting photosynthetic enzymes per unit area, and positive scaling of maximum foliage photosynthetic rates ( $A_{max}$ ) and its partial determinants  $V_{cmax}$  and  $J_{max}$  (Fig. 4c). This response would be further amplified by positive scaling of  $F_R$  and  $F_B$  (Eqn 4) with light. Overall, it seems that in woody species, the structural adjustment through light-dependent modifications in  $M_A$  is responsible for most of the variation in  $V_{cmax}$  and  $J_{max}$ , while alteration in nitrogen partitioning plays a secondary role (Niinemets *et al.* 1998b; Evans & Poorter 2001) (but see Niinemets & Tenhunen 1997; Grassi & Bagnaresi 2001). In contrast, nitrogen partitioning seems to be more important in herbs (Pons *et al.* 1990; Evans 1993a; Hikosaka & Terashima 1995).

### Deviations from optimality predictions and species differences in canopy gradients in structural and functional traits

The increase in photosynthetic potentials with long-term light availability implies enhanced investment of resources where photosynthesis is potentially the highest because of higher light availability. Such a pattern results in higher canopy photosynthesis for given biomass or nitrogen in leaves than would a strategy with a constant  $A_{max}$  throughout the canopy (Gutschick & Wiegand 1988; Farquhar 1989; Chen *et al.* 1993; Baldocchi & Harley 1995; Sellers *et al.* 1996). The optimization models suggest one-to-one proportional scaling of  $A_{max}$  and long-term canopy light environment for maximization of canopy photosynthesis. Yet, the relationships of  $M_A$ ,  $N_A$  and  $A_{max}$  and light availability are often curvilinear (Fig. 4c). The ranges in  $M_A$ ,  $N_A$  and  $A_{max}$  are typically two- to fourfold for a 5- to 15-fold canopy light gradient (Fig. 4), reflecting curvilinearity and finite values of these characteristics in low light. Even when  $M_A$ ,  $N_A$  and  $A_{max}$  scale linearly with light, they have apparent finite values when light availability goes to zero (positive y-intercepts, Meir *et al.* 2002). This evidence collectively indicates that the gradients in  $A_{max}$  and  $N_A$  are generally much less profound than predicted by the optimality models (Badeck 1995; de Pury & Farquhar 1997; Schieving & Poorter 1999; Meir *et al.* 2002; Anten 2005).

What factors cause the discrepancy between theoretical predictions and experimental observations? So far, even the mechanisms responsible for light-dependent increases in  $M_A$  are poorly understood (Terashima *et al.* 2005). Enhanced transport of growth hormones such as cytokinins

via transpiration stream (Pons, Jordi & Kuiper 2001) or greater sugar availability per se (Terashima *et al.* 2005) has been suggested a possible mechanisms. Such a control by sugars has been implemented in canopy acclimation schemes (Kull & Kruijt 1999).

Light-dependent controls on hormone or sugar distributions alone may not be enough to explain the observed patterns in  $M_A$  and the deviations from theoretical optima. Curvilinearity in light versus  $A_{\max}$  relationships can be partly associated with other stress factors such as lower water availability and heat stress, typically interacting with light in plant canopies (Niinemets & Valladares 2004; see further). In general, growth is one of the most water stress-sensitive plant processes (Tardieu & Granier 2000). In addition, structural limitations apparently determine the minimum finite  $M_A$  a given species can form (Gutschick & Wiegel 1988; Meir *et al.* 2002), while the maximum values of  $M_A$  can be constrained by enhanced internal diffusion limitations and low light availabilities in the mid and bottom cell layers of thicker leaves. Furthermore, in some late-successional species,  $M_A$  can be partly driven by the light availability in the year preceding foliage formation (e.g. Uemura *et al.* 2000), suggesting that the way  $M_A$  scales with current light availability depends on 'memory effects', that is, on how well the current leaf light environment matches the light environment during bud formation.

World-scale interspecific relationships demonstrate that foliage photosynthetic capacities per dry mass are negatively associated with  $M_A$  (Wright *et al.* 2004), contrary to within-species patterns across the canopy light gradients. This negative relationship likely reflects greater cell wall fraction and greater internal diffusion limitations in species with structurally more robust leaves (Pons & Westbeek 2004; Takashima, Hikosaka & Hirose 2004; Terashima *et al.* 2005). In addition, the fraction of leaf nitrogen associated with cell walls is larger in species with greater  $M_A$  (Takashima *et al.* 2004), such that the photosynthetic nitrogen use efficiency (photosynthesis rate per unit leaf nitrogen) scales negatively with  $M_A$  in interspecific comparisons (Takashima *et al.* 2004). The comparison between broad-leaved deciduous species *Tilia cordata* and evergreen Mediterranean sclerophyll species *Quercus ilex* indicates that  $M_A$ ,  $N_A$  and photosynthetic capacity respond to light in a similar manner in both species, but also that photosynthetic nitrogen use efficiency is larger in the deciduous species (Fig. 4c inset), confirming the previous observations (Takashima *et al.* 2004). This difference partly resulted from ca. 80% lower internal diffusion conductance in *Q. ilex* (average  $\pm$  SE across the entire light gradient =  $0.0559 \pm 0.002 \text{ mol m}^{-2} \text{ s}^{-1}$ ) than in *T. cordata* ( $0.100 \pm 0.012 \text{ mol m}^{-2} \text{ s}^{-1}$ ), and possibly also from greater cell wall-bound nitrogen fraction in the evergreen species. This example demonstrates that species differences in light acclimation of foliage photosynthetic potentials to canopy light gradients are not only determined by light-dependent changes in  $M_A$  and  $N_A$ , but also can be affected by species-specific values of minimum  $M_A$ , internal

diffusion conductance to  $\text{CO}_2$  and fractional nitrogen distribution between photosynthetic apparatus and cell walls.

### Foliage re-acclimation potential

While the acclimation of foliage to long-term canopy light gradients has been studied extensively, the response of  $A_{\max}$  to an abrupt increase in leaf light environment has received less attention. In young developing leaves, photosynthetic potential can occasionally fully adjust to new light environment through increases in leaf thickness and  $M_A$  (Sims & Pearcy 1992; Yamashita, Koike & Ishida 2002; Oguchi *et al.* 2005) with the degree of re-acclimation depending on leaf age at the time of transfer (Sims & Pearcy 1992; Yamashita *et al.* 2002). As cell walls become cross-linked and lignified during and after cessation of leaf growth, most species have a limited potential for modifications of  $M_A$  and leaf thickness after leaf maturation (Sims & Pearcy 1992; Yamashita *et al.* 2002; Oguchi *et al.* 2005). Thus, the photosynthetic capacity of shade-acclimated fully mature leaves can mainly be increased by increasing the number of chloroplasts per unit leaf area and by increasing the fraction of nitrogen in Rubisco and limiting components of photosynthetic electron transport chain. As chloroplasts should be positioned at close vicinity of mesophyll cell walls to minimize internal diffusion resistance to  $\text{CO}_2$  transport from outer surface of cell walls to chloroplasts (Terashima *et al.* 2005), acclimation of shade-adapted leaves to high irradiance ultimately depends on availability of empty space along the cell wall, that is, on inner mesophyll cell wall area to chloroplast exposed surface area ratio ( $S_{\text{mes}}/S_C$ ) (Oguchi, Hikosaka & Hirose 2003; Oguchi *et al.* 2005). As even in low-light acclimated leaves, the outer mesophyll cell surface is often fully covered by chloroplasts ( $S_{\text{mes}}/S_C \approx 1$ ) (Oguchi *et al.* 2005), re-acclimation of such leaves to high irradiance is inherently limited by anatomical constraints.

Overall, it seems that high light-adapted species with intrinsically higher photosynthetic capacity have greater foliage re-acclimation potential than understorey species (Naidu & DeLucia 1997; Oguchi *et al.* 2003; Cai, Rijkers & Bongers 2005; Oguchi *et al.* 2005). While presence of open space along the mesophyll cell walls increases the responsiveness of low light-grown leaves to increases in light availability, it also requires greater biomass investment in cell walls. Such an extra investment will be essentially 'wasted' when no increase in light environment occurs during leaf lifespan. Thus, a less efficient design of foliage in high light-adapted species is the cost these species 'pay' for greater potential of re-acclimation.

### LIGHT-ACCLIMATION OF PHOTOSYNTHETIC CAPACITIES IN SPECIES WITH COMPLEX LEAF GEOMETRY

As light-harvesting scales with half-of-the-total area in needle-leaved species (see previous discussion), half-of-the-total or total area is the appropriate basis for expression of foliage photosynthetic activities in needle-leaved species.



However, as many studies express the rates per unit projected needle surface area, it is important to have information of projected to total area ratio ( $S_P/S_T$ ) as well. Because  $S_P/S_T$  can vary with long-term light environment, conclusions on light-dependent plasticity in  $A_{\max}$  (slope of the relationship between  $A_{\max}$  versus long-term light availability) can vary depending on the expression basis ( $A_{\max}$  per unit total area =  $A_{\max}$  per unit projected area  $\times S_P/S_T$ ).

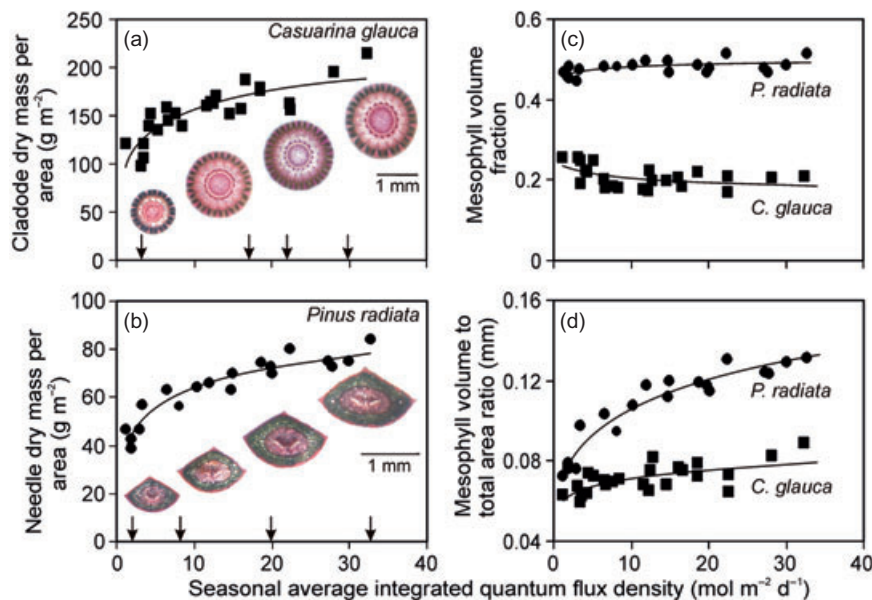
In needle-leaved species, both foliage dry mass per unit total and projected foliage area increase with increasing long-term foliage light availability, mainly reflecting increased volume to total area ratio ( $V/S_T$ , larger thickness) in higher light (Fig. 5a,b; Richardson *et al.* 2000; Warren *et al.* 2003). As the result of the increase of  $V/S_T$  and  $V$  per unit projected area,  $(V/S_T)/(S_P/S_T)$ , both nitrogen and photosynthetic capacity per unit projected and total area also generally scale positively with light availability (Grassi & Bagnaresi 2001; Warren *et al.* 2003; Niinemets *et al.* 2007). However, needle-leaved species are characterized by large fractions of foliar biomass and volume in support (Niinemets *et al.* 2005b, 2007). Therefore, scaling of foliage photosynthetic potentials with light can also depend on light-dependent modifications in the relative share of mesophyll and support biomass within the foliage.

In the cross-section of cylindrical cladodes of *Casuarina*, the mesophyll is constrained to outer cladode surface and is present as isolated 'islands' separated by thick-walled lignified sclerenchyma cells (Fig. 5a). In addition, lignified xylem and phloem fibers fill a large part of the cladode central

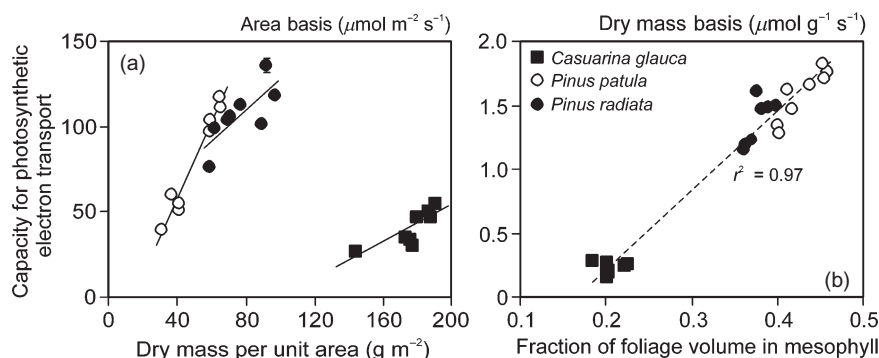
area. Altogether, the fraction of cladode volume in lignified tissues is 0.4–0.6 in this species (Fig. 5a; Niinemets *et al.* 2005b). In fact, the volume fraction of mechanical tissues tends to increase, and the volume fraction of mesophyll tends to decrease with increasing light availability within the canopy of *Casuarina* (Fig. 5c; Niinemets *et al.* 2005b). Despite the slight decrease of mesophyll volume fraction, the number of mesophyll 'islands' on cladode cross-section and the thickness of mesophyll islands increase with increasing light availability (Fig. 5a), resulting in a positive scaling of mesophyll volume to total area ratio (Fig. 5d) and cladode photosynthetic potential per unit area with light availability (Fig. 6a; Niinemets *et al.* 2005b).

Analogously, in *Pinus* needles, a large fraction of needle volume is in the central cylinder that accommodates vascular bundles and transfusion tissue, and in lignified epidermal and hypodermal cell layers on needle surface, with the overall volume fraction of mechanical tissues in central cylinder and needle dermal tissues being 0.3–0.4 (Fig. 5b, Niinemets *et al.* 2007). Differently from *Casuarina*, there is a slight increase in mesophyll volume fraction with increasing light availability (Fig. 5c), amplifying the light-dependent increase in mesophyll volume to total area ratio and photosynthetic capacity per unit total and projected area (Figs 5d & 6a).

These examples and other work (Bond *et al.* 1999; Grassi & Bagnaresi 2001) indicate that there are significant species differences in scaling of photosynthetic capacity per area with  $M_A$  and light availability (Fig. 6a). These



**Figure 5.** Light-driven changes in cladode dry mass per area in angiosperm conifer *Casuarina glauca* (a, data modified from Niinemets *et al.* 2005b), needle dry mass per unit area in conifer *Pinus radiata* (b, data modified from Niinemets *et al.* 2007), and mesophyll volume fraction (c) and mesophyll volume to total area ratio (d) in *C. glauca* (filled squares) and *P. radiata* (filled circles). Representative cladode and needle freehand cross-sections taken from different light environments (denoted by arrows) are shown in (a) and (b). The cross-sections taken from different light environments (denoted by arrows) are shown in (a) and (b). The cross-sections were stained with phloroglucinol that specifically reacts with aldehyde residues of lignin yielding reddish pigments in lignified tissues (Pomar, Merino & Ros Barceló 2002; Niinemets *et al.* 2005b). The tissue remaining green is the mesophyll. All non-linear regressions are significant at  $P < 0.001$ , except for the data of *C. glauca* in (c) ( $P < 0.01$ ).



**Figure 6.** Capacity for photosynthetic electron transport ( $J_{\max}$ ) per unit area in relation to  $M_A$  foliage dry mass per unit area (a) and  $J_{\max}$  per unit dry mass in relation to mesophyll volume fraction (b) in three needle-leaved species. The same data set as in Fig. 5. In addition, the data of long-needled subtropical evergreen conifer *Pinus patula* from Niinemets *et al.* (2007) are also depicted. Data were fitted by linear regressions ( $P < 0.01$  for all). The relationships were analogous with the maximum carboxylase activity of Rubisco ( $V_{\max}$ ) (Niinemets *et al.* 2005b; Niinemets *et al.* 2007).

differences in scaling depend on variations in mesophyll volume to total area ratio with light (Fig. 5d), but also denote important interspecific differences in needle biomass allocation between support and mesophyll. When data of species with contrasting share of needle volume between mechanical tissues and mesophyll are pooled, there is a strong positive relationship between foliage photosynthetic capacity per unit foliage dry mass and the fraction of foliage volume in mesophyll (Fig. 6b). This uniform relationship underscores the importance of anatomical modifications in tuning foliage photosynthetic potentials to different canopy light environments. Given that  $A_{\max}/\text{mass}$  scales with mesophyll volume fraction, foliage with the same integrated structural characteristics such as  $M_A$  or thickness may have widely differing photosynthetic potentials per area depending on the distribution of needle biomass between various tissues ( $A_{\max}/\text{area} = M_A A_{\max}/\text{mass}$ ).

The increase of foliage volume to surface area ratio with increasing irradiance is suggested to constitute the primary acclimation response that maximizes foliage photosynthetic activity per unit area along gradients of irradiance (Roderick *et al.* 1999), and broad trends in foliage functioning across environmental gradients have been outlined (Roderick, Berry & Noble 2000). However, the main conclusions of Roderick *et al.* (2000) were derived from work with flat-leaved species, where lamina interior between two epidermal layers is essentially filled with mesophyll tissue. In these species, increases in  $V/S_T$  ratio translate to a proportional increase of mesophyll volume per unit surface area. Foliage with complex three-dimensional shape typically has a large non-photosynthetic core (Fig. 5a,b; Groom, Lamont & Markey 1997), suggesting that  $V/S_T$  ratio may be poorly linked to photosynthetic performance, especially if species with widely varying mesophyll investments are compared and if mesophyll volume to  $S_T$  ratio and  $V/S_T$  respond differently to environment (Fig. 6). Therefore, in species with complex three-dimensional foliage geometry, mesophyll

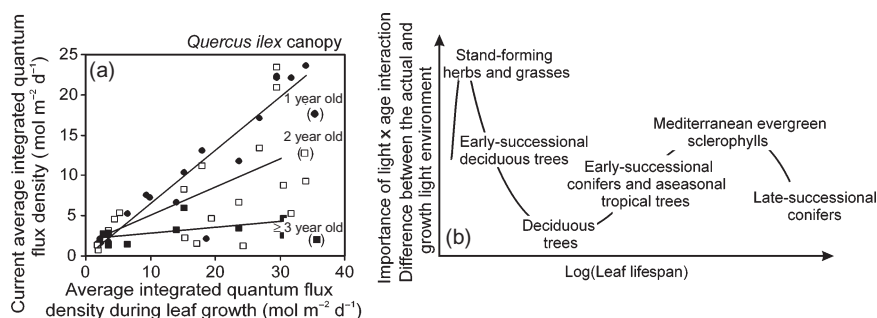
volume to surface area ratio rather than  $V/S_T$  is a more appropriate trait to scale foliage functional activity along environmental gradients.

## CANOPY PHOTOSYNTHETIC PERFORMANCE IN RELATION TO LEAF LONGEVITY

### Interaction of leaf age and light gradients

In woody species, foliage development is time consuming (Miyazawa & Terashima 2001), and foliage structural and photosynthetic characteristics –  $M_A$ ,  $N_A$  and photosynthetic capacity – are best correlated with the environmental signal averaged over a relatively long time period. Incident quantum flux density averaged over 30–60 d preceding the measurements explained the largest degree of within-canopy variation in foliage traits in temperate trees (Niinemets, Kull & Tenhunen 2004b). In most species in temperate deciduous forests and broad-leaved tropical drought-deciduous forests, all canopy leaves are formed at approximately the same time, and leaf production is negligible during the rest of the growing season. Thus, the leaves in different canopy positions experience similar average light environment throughout their lifespan. While leaf photosynthetic capacity decreases slowly during the season in mature non-senescent leaves of deciduous species, possibly reflecting enhanced internal diffusion limitations, this reduction is similar in upper and lower canopy with no strong age  $\times$  light interaction (Wilson, Baldocchi & Hanson 2000; Niinemets *et al.* 2004b; Grassi & Magnani 2005; Grassi *et al.* 2005).

In contrast, in herbaceous stands, stems and new leaves are formed continuously during most of the lifespan of the plants, such that lower canopy leaves formed first in high light are overtopped by younger leaves, resulting in simultaneous gradients in leaf age and light availability (Hirose, Werger & van Rhee 1989; Pons & Jordi 1998; Pons & de Jong-van Berkel 2004; Hikosaka 2005; Terashima *et al.* 2005;



**Figure 7.** Relationships between current leaf light availability and light availability during leaf growth for different-aged leaves of Mediterranean evergreen broad-leaved species *Quercus ilex* (a, modified from Niinemets *et al.* 2006a), and the difference between current and growth light environment and the importance of light  $\times$  leaf age interaction on foliage functioning in species with varying leaf longevity (b, arbitrary scales). In (a), the slopes of present versus past (during leaf development) average integrated quantum flux densities are 0.66 for 1-year-old leaves, 0.42 for 2-year-old leaves and 0.16 for 3-year-old leaves (regressions fitted through zero).

Terashima *et al.* 2006). Similarly, several early-successional species such as *Salix* spp., and coppiced *Populus* spp. from temperate climates and bamboo species from temperate to tropical climates can produce leaves continuously during the growing season, resulting in a strong age  $\times$  light interaction within the canopy (Liu *et al.* 1988; Kull, Koppel & Noormets 1998). In fact, leaf dry mass per unit area that generally exhibits strong light-driven within-canopy variation (see previous discussion) is poorly associated with leaf irradiance and leaf height in *Salix* spp. stands (Kull *et al.* 1998).

In evergreen species growing in seasonal climates, leaves produced at certain light environment become shaded by new leaves in subsequent seasons, resulting in drastically reduced light availabilities of older leaves. For instance, in evergreen Mediterranean species *Q. ilex*, light availability of 1-year-old leaves is on average 66% of that to which the leaves were exposed during their development; light availability of 2-year-old-leaves is 42% of that during the development, and light-availability of 3-year-old leaves is 16% of that during their development (Fig. 7a). Analogously, light availability is 18–60% lower for older leaves than for current-year leaves in 28 evergreen species from seasonally dry Australian mallee and *Eucalyptus*-dominated woodlands (Wright *et al.* 2006). Furthermore, evergreen late-successional conifers may support 8–16 needle cohorts (Reich *et al.* 1999; Harlow, Duursma & Marshall 2005), resulting in even more aggravated differences in leaf current and previous light environment. In most scaling up exercises, only photosynthesis measurements of current-year leaves are available, and current-year physiology is applied to all leaves in the canopy (e.g. Rambal *et al.* 2003). Given that in evergreen broad-leaved Mediterranean species more than 60% of foliage may be older than one season (Sala *et al.* 1994; Niinemets *et al.* 2005a) and current-year foliage can only comprise a small fraction of total leaf biomass in evergreen conifers (Kayama, Sasa & Koike 2002; Harlow *et al.* 2005), understanding the shading effects on older foliage has important consequences for predicting whole tree carbon balance.

### Significance of leaf age $\times$ light gradients in canopies of species with fast leaf turnover

Simultaneous age and light gradients can alter foliage functioning in canopies with short-living foliage such as herb and early-successional broad-leaved temperate deciduous canopies by several mechanisms. Firstly, a significant fraction of whole canopy foliage is anatomically acclimated to higher irradiance than the leaves experience during a large part of their lifespan. Secondly, extensive shading can speed up leaf ageing and senescence (Weaver & Amasino 2001). Both of these mechanisms can occur simultaneously and can dynamically modify the distribution of photosynthetic activity within the canopy.

Upon shading, leaves generally re-allocate photosynthetic nitrogen from Rubisco and electron transport components to light-harvesting proteins and chlorophyll, thereby enhancing light harvesting (Sims & Pearcy 1991). Yet, high light-developed leaves have large overall thickness and strongly developed palisade parenchyma consisting of tightly packed long cells. In such leaves, chloroplasts shade each other more strongly, and path length of light is longer than in leaves developed in low light with most of the mesophyll present as loosely distributed spongy parenchyma (Vogelmann & Martin 1993). This suggests that anatomical limitations may constrain the efficiency of light harvesting in high light-developed leaves re-acclimated to upper canopy shade.

Shading itself does not necessarily affect leaf ageing when the entire plant is shaded and plant growth and development is delayed (Weaver & Amasino 2001). However, in open-grown plants with fast growth and development, shading caused by canopy expansion often results in accelerated ageing, senescence and overall greater leaf turnover, especially in herbaceous species with rapid life cycle (Hikosaka 2003, 2005). Senescence of lower canopy leaves results in N re-mobilization from foliage and allocation to upper canopy leaves, leading to a strong gradient in foliage N contents per unit leaf area and dry mass, even when  $M_A$  and leaf anatomy are weakly related to current

light environment within such rapidly developing canopies (Hirose *et al.* 1989; Ackerly 1997; Kull *et al.* 1998). Clearly, re-mobilization of N from lower canopy leaves and allocation to upper canopy where light availability is larger enhances whole canopy photosynthesis for given total canopy N. Such adjustment of N contents through re-allocation is analogous to  $M_A$ -driven changes (Figs 4 & 5a,b), but it is important to recognize that leaf age rather than light acclimation per se can mainly control N allocation program in rapidly developing canopies (Field 1983). Continuous dynamic adjustment of foliage N contents can also be more costly because of energetic requirements of N re-mobilization and new foliage growth, than maintenance of a static gradient of N distribution resulting from structural acclimation during foliage growth. Because of the strong interaction of foliage senescence with light availability, it seems that age  $\times$  light interaction affects canopy performance to the largest degree in herb and early-successional deciduous woody stands, where shading results in rapid leaf turnover and leaf senescence (Fig. 7b).

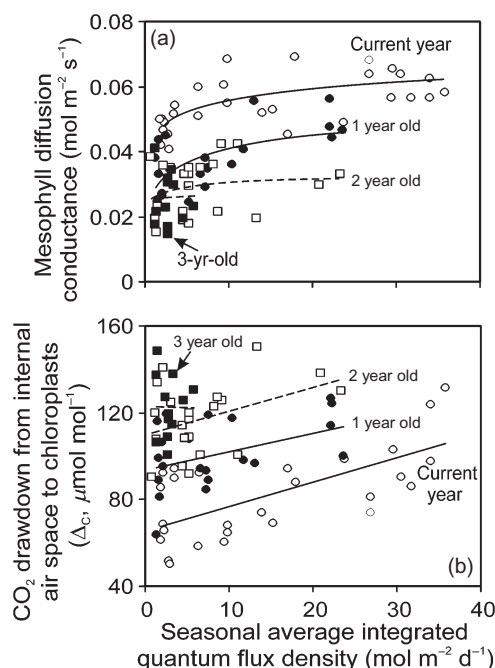
### Foliage age $\times$ light interactions in evergreen species

For species with evergreen long-living foliage, most of contemporary understanding of foliage light acclimation to canopy light gradients stems from studies on current-year foliage. Current-year leaves of evergreens respond to light availability gradients qualitatively similarly to the foliage in deciduous species (Fig. 4). However, significant decline in light availability during leaf lifespan suggests that the association of  $M_A$  and  $N_A$  of older leaves to current leaf light environment is notably weaker than these relationships for current-year leaves (Niinemets *et al.* 2006a). The whole concept of within-canopy foliage acclimation in evergreens has been challenged on the basis of circumstance that  $M_A$  and  $N_A$  of older leaves poorly depend on current canopy light environment (Wright *et al.* 2006). However, this poor relationship rather reflects the inability of fully mature foliage adapted to high irradiance to reduce thickness or  $M_A$  in response to shading, as well as to inherent constraints on re-allocation of cell wall-bound N that comprises a particularly large fraction of total N in evergreen species (Takashima *et al.* 2004).

In fact, foliage photosynthetic apparatus does re-adjust to changed light environment, and both  $V_{\max}$  and  $J_{\max}$  per unit area of older leaves are more strongly associated with current than with previous leaf light environment (Niinemets *et al.* 2006a). Such a modification of foliage photosynthetic capacity without strong alterations in foliage N content has also been observed in other species (Hikosaka 2005). In broad-leaved evergreens, the re-acclimation to low light is associated with shifting nitrogen allocation from Rubisco and proteins limiting electron transport to light-harvesting proteins, resulting in lower  $V_{\max}$  and  $J_{\max}$  per unit area and moderate increases in leaf absorptance (Niinemets *et al.* 2006a and unpublished data). In evergreen late-successional conifers, there is major age-dependent increase

in leaf chlorophyll content, reflecting re-allocation of nitrogen to light harvesting (Brooks, Hinckley & Sprugel 1994; Brooks *et al.* 1996), but possibly also some inactivation rather than dismantling of Rubisco (Ethier *et al.* 2006). Such possible inactivation without re-allocation is seemingly a wasteful strategy that reduces the overall nitrogen use efficiency of foliage. As there is significant re-mobilization of N from older conifer needles during new foliage formation (Weikert *et al.* 1989), Rubisco inactivation may be a temporary condition, reflecting somewhat higher light environment of older needles before new flush maturation, and limited N requirement of current-year needles after maturation.

Differently from herbs, leaf longevity of evergreens is often larger in shade than in high light (Harlow *et al.* 2005), indicating that senescence does not necessarily interact with shading in these species. However, increases in leaf age are associated with reductions in internal diffusion conductance from sub-stomatal cavities to chloroplasts ( $g_i$ ) (Fig. 8a; Ethier *et al.* 2006). This decline in  $g_i$  results in greater draw-down of  $\text{CO}_2$  from sub-stomatal cavities to chloroplasts (Fig. 8b, but see Ethier *et al.* 2006), signifying that foliage photosynthetic potentials are used less efficiently in older foliage. Such age-dependent reductions in  $g_i$  possibly reflect reductions in chloroplast surface to total leaf area ratio in older shaded foliage as well as enhanced lignification and thickening of cell walls. While  $g_i$  is positively associated with irradiance in younger leaves, this relationship vanishes in older leaves (Fig. 8), suggesting that inherent anatomical



**Figure 8.** Light- and age-dependent alterations in mesophyll diffusion conductance (a) and  $\text{CO}_2$  drawdown from sub-stomatal cavities to chloroplasts (b) in *Quercus ilex* (data modified from Niinemets *et al.* 2006a). Data were fitted by non-linear regressions in (a) and by linear regressions in (b). Non-significant regressions ( $P > 0.05$ ) are shown by a dashed line.



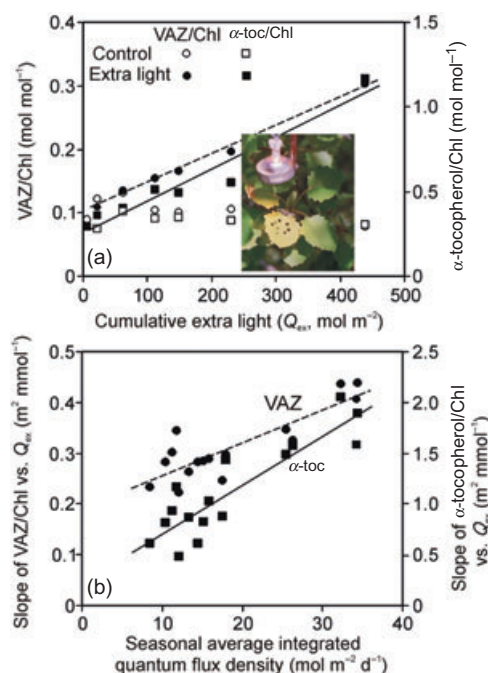
constraints limit  $g_i$  adjustment to altered light environment. These data collectively indicate that age-dependent modifications in cell wall structure and chemistry as well as inflexible leaf anatomical architecture that is adjusted to previous high light environment rather than to new low light environment can importantly constrain photosynthetic efficiency of older shaded foliage in evergreen species.

In addition to leaf-level alterations, in conifer shoots, needles with less favorable carbon balance on shoot top and bottom faces abscise first such that shoot morphology changes from axially symmetric to bilaterally symmetric with most needles positioned side by side on the same horizontal plane (Niinemets *et al.*, unpublished observations). As discussed earlier, such architectural adjustment maximizes shoot light harvesting in lower canopy where most light comes from high solar inclination angles. Because in late-successional conifers with extensive foliage area annual foliage production contributes less to total canopy leaf biomass than in broad-leaved evergreens, the shading of older foliage occurs with a relatively slower rate in conifers. Given further that re-acclimation of conifer foliage to reduced light availability can occur both at leaf and shoot level, overall significance of age  $\times$  light interaction seems to affect canopy performance less in conifers than in broad-leaved evergreens (Fig. 7b).

## DYNAMIC MODIFICATIONS OF FOLIAGE FUNCTIONING IN RESPONSE TO LIGHT FLUCTUATIONS

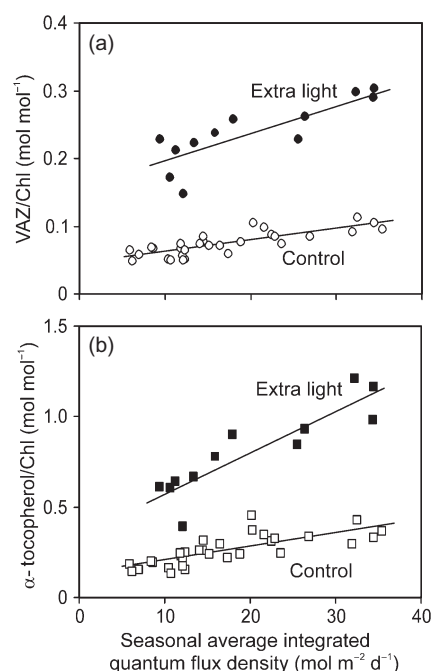
In natural conditions, environmental factors always fluctuate. Dynamic adjustment to such perturbations may critically affect plant resource harvesting efficiency and competitive potential in heterogeneous environments (Schurr, Walter & Rascher 2006). Although differences in average light environment between various canopy locations may be constant during most of the growing season, within every 'average' light micro-environment, light availability strongly fluctuates during and between the days. It is not yet fully clear whether leaves developed and exposed to differing long-term light availabilities respond similarly to such relatively short light fluctuations. As adjustment of photosynthetic capacity is relatively time consuming and full photosynthetic adjustment may be limited in mature leaves because of anatomical constraints, increases in light availability for few hours or few days above long-term average conventionally result in increased fraction of 'excess light' that cannot be used in photosynthesis and that is potentially damaging to photosynthetic apparatus. Thus, coping with dynamic light environments is an integral component of acclimation to within-canopy light regime.

Plants cope with excess light by increasing the capacity for non-radiative dissipation of absorbed light (see Demmig-Adams & Adams 2006 for a review). Enhancement of non-radiative dissipation of light energy partly relies on increases in the pool size of xanthophyll cycle carotenoids – violaxanthin, antheraxanthin and zeaxanthin (VAZ) – that play an



**Figure 9.** Representative sample responses of xanthophyll cycle carotenoid (VAZ) to chlorophyll (Chl) ratio (squares) and  $\alpha$ -tocopherol ( $\alpha$ -toc) to Chl ratio (circles) to cumulative extra light [ $Q_{ex}$  (a)], and the correlations between the slopes of the VAZ/Chl and  $\alpha$ -toc/Chl versus  $Q_{ex}$  [sample relationships in (a)] and long-term leaf light availability before the treatment (b). The experiment was conducted *in situ* in the canopy of temperate deciduous tree *Populus tremula* (data modified from Niinemets *et al.* 2003; and García-Plazaola *et al.* 2004). Additional illumination of 500–800  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> was provided by wide-beam halogen lamps [inset in (a)] between 0500–2100 h for 11 d, and cumulative extra light was calculated from the start of illumination until specific sampling event. In (a), VAZ/Chl and  $\alpha$ -toc/Chl of the control leaf exposed to natural illumination (no  $Q_{ex}$ , open symbols) and sampled for pigments at times corresponding to given  $Q_{ex}$  of the illuminated leaf are also shown. All linear regressions are significant at  $P < 0.001$ .

important role in non-photochemical quenching of light energy (see Demmig-Adams & Adams 2006 for a detailed review). In laboratory experiments, VAZ contents increase rapidly after stepwise increase of light, with the maximum VAZ content typically observed 3–5 d after the change of light level (Demmig-Adams *et al.* 1989; Eskling & Åkerlund 1998). Experimental studies *in situ* in field environments suggest that in strongly fluctuating natural environments, acclimation of VAZ contents to changed light regime takes longer (Logan, Demmig-Adams & Adams 1998; Niinemets *et al.* 2003). In temperate deciduous broad-leaved trees *Populus tremula* and *T. cordata*, VAZ content increased linearly with cumulative extra light during 11 d of the experiment without any signs of saturation (Fig. 9a). This experiment further demonstrated that the slope of the VAZ content versus cumulative extra light relationship was positively correlated with long-term leaf light environment (Fig. 9b), and that the overall increase in VAZ content was stronger at higher light (Fig. 10a). These data suggest that



**Figure 10.** Variation in VAZ/chlorophyll (Chl) (a) and  $\alpha$ -tocopherol to Chl (b) in response to long-term natural leaf light availability (open symbols) and changes in these characteristics induced by leaf exposure to extra irradiance of 500–800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  between 0500–2100 h in *Populus tremula* (filled symbols, the same data set as in Fig. 9). The leaves were exposed to extra light for 11 d, and pigment contents were determined on seven occasions during the experiment (Fig. 9a for the increase of pigments with cumulative extra light). The values reported here are final estimates at the end of the experiment. Data were fitted by linear regressions ( $P < 0.001$ ).

leaf xanthophyll cycle pool size is not necessarily in a steady state in field environments, but changes continuously as a result of day-to-day variability in light environment. These data further demonstrated a stronger capacity of upper canopy leaves to respond to light fluctuations (Fig. 9), suggesting that the potential to adjust to dynamic changes in light is the function of overall leaf light availability.

In addition to VAZ, extra illumination also increases  $\alpha$ -tocopherol content (García-Plazaola *et al.* 2004) and volatile isoprenoid release from the foliage (Hanson & Sharkey 2001b). As a lipid-soluble compound,  $\alpha$ -tocopherol plays a key role in detoxification of free radicals and oxidized compounds that can accumulate during high light stress in plant membranes (Havaux, Lütz & Grimm 2003). It has also been hypothesized that there is a certain free pool of zeaxanthin in thylakoid membranes and that this 'free' zeaxanthin acts synergistically with  $\alpha$ -tocopherol as membrane antioxidant (Havaux & Niyogi 1999; Müller-Moulé, Havaux & Niyogi 2003). In this regard, it is remarkable that increases in VAZ and  $\alpha$ -tocopherol content occurred simultaneously after increases in leaf light availability (Fig. 9). As with VAZ, the  $\alpha$ -tocopherol content of upper canopy leaves responded more strongly to the increase in light availability (Figs 9b & 10b).

What is the significance of light-dependent enhancement of volatile isoprenoid production in emitting species? Several studies demonstrate that isoprene and monoterpene emissions can enhance leaf thermal tolerance (Sharkey & Singsaas 1995; Singsaas *et al.* 1997; Loreto *et al.* 1998; Copolovici *et al.* 2005). As there is an interaction between temperature and light availability in plant canopies (see further), such an increase of volatile isoprenoid emissions may reflect higher leaf temperatures in the upper canopy. However, other studies demonstrate that lipid-soluble isoprene and volatile monoterpenes can also act as antioxidants reducing oxidative stress in membranes (Loreto & Velikova 2001; Loreto *et al.* 2004; Copolovici *et al.* 2005). Thus, rapid augmentation of volatile isoprenoid production in emitting species after increases in light level may also reflect an important acclimation response to enhance the antioxidative status of plant membranes.

These data jointly indicate that there are important within-canopy differences in the potential to adjust to rapid modifications in light environment. Such differences in acclimation to high light stress can significantly alter down-regulation of foliage photosynthetic potentials and light-harvesting efficiency, and thereby the realized daily photosynthesis in different canopy locations.

## ADJUSTMENT TO MULTIPLE ENVIRONMENTAL FACTORS IN PLANT CANOPIES

In natural canopies, both temperature and water vapour pressure deficit generally increase with increasing light availability from the bottom to the top of the canopy (Baldocchi *et al.* 2002; Niinemets & Valladares 2004). This co-variation of environmental drivers suggests that plants in the upper canopy are often exposed to greater heat stress and may suffer from greater water stress. There is evidence of lower leaf water potentials (Aasamaa *et al.* 2004; Sellin & Kupper 2004), and greater degree of midday and drought-dependent stomatal closure in the upper canopy leaves in temperate forests (Niinemets, Sonninen & Tobias 2004c; Sellin & Kupper 2004) (but see Tissue *et al.* 2006 for humid temperate rainforest). There is further evidence that foliage heats up to higher temperatures in the upper than in the lower canopy (Sharkey *et al.* 1996; Singsaas & Sharkey 2000), collectively suggesting that leaves are exposed to interacting stresses in the upper canopy.

Studies of plant acclimation to multiple interacting stresses have been rare (Björkman 1987; Havaux & Strasser 1990; Havaux 1992; Valladares & Pearcy 1997; Valladares *et al.* 2005). Exposure to one stress can amplify plant sensitivity to another stress factor (Valladares & Pearcy 1997; Valladares *et al.* 2005), but acclimation to a certain stress can also improve the resistance to other co-occurring stresses (Havaux & Strasser 1990; Havaux 1992). Water stress typically enhances the stability of photosynthetic electron transport to heat stress (Havaux 1992), possibly as the result of stabilization of membranes by ions and ubiquitous neutral osmotica such as sugars and specialized

organic osmotica such as proline and glycine betaine that tend to accumulate in water-stressed leaves (Seemann, Downton & Berry 1986; Sulpice *et al.* 1998; Bajji, Lutts & Kinet 2001; Hüve *et al.* 2006). Heat resistance of photosynthetic electron transport rate scales positively with leaf light availability within a temperate forest canopy (Niinemets, Oja & Kull 1999). As the contents of osmotica and sugars also increase with increasing canopy light availability (Aasamaa *et al.* 2004; Niinemets & Valladares 2004), greater heat resistance of photosynthetic machinery in the upper canopy may portray foliage co-acclimation to water and heat stress. However, modifications in membrane lipid composition (Guillot-Salomon *et al.* 1991), enhanced volatile isoprenoid emission (Harley, Guenther & Zimmerman 1996; Hanson & Sharkey 2001a; Grote 2007), and  $\alpha$ -tocopherol and zeaxanthin production (García-Plazaola *et al.* 2004) can also play a role in foliage thermal acclimation.

In addition to physiological alterations, adjustment to water limitations is associated with enhanced cell wall thickness and tighter packing of mesophyll cells to resist lower water potentials (Lu & Neumann 1998; Wu & Cosgrove 2000; Cramer, Schmidt & Bidart 2001; Grill *et al.* 2004). Such changes in cell size and cell wall architecture can have major impact on internal CO<sub>2</sub> diffusion conductance ( $g_i$ ). There is generally a strong positive linear scaling of  $g_i$  with leaf photosynthetic capacity (Evans & Loreto 2000) mainly mediated by enhanced chloroplast to exposed mesophyll surface area in leaves with higher photosynthetic capacity (Terashima *et al.* 2005). However,  $g_i$  increases only moderately with increasing light availability in Mediterranean evergreen species *Q. ilex* (Fig. 8a), possibly reflecting water stress-driven structural adjustments in cell walls and cell size at higher light availability. The light-dependent increase in  $g_i$  in *Q. ilex* is much less than the corresponding light-dependent increase in  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (cf. Figs 4c & 8a) such that CO<sub>2</sub> drawdown from sub-stomatal cavities to chloroplasts is larger in higher light (Fig. 8b).

Few other studies have examined the variation in  $g_i$  along light gradients. As with *Q. ilex* (Fig. 8b), CO<sub>2</sub> drawdown was higher in the upper than in the lower canopy leaves in evergreen broad-leaved species *Citrus paradisi* (Lloyd *et al.* 1992; Syvertsen *et al.* 1995), but the drawdown was similar in upper and lower canopy in mesophytic leaves of *Prunus persica* (Lloyd *et al.* 1992; Syvertsen *et al.* 1995) and *Juglans nigra* × *regia* (Piel *et al.* 2002), and in needles of *Pseudotsuga menziesii* (Warren *et al.* 2003). The scaling of CO<sub>2</sub> drawdown with light availability was species-dependent in three deciduous *Acer* species (Hanba, Kogami & Terashima 2002). The overall effect of canopy light environment on CO<sub>2</sub> drawdown caused by internal mesophyll resistance may depend on the way light and water availability gradients interact in specific canopies.

Attempts have been made to derive optimization algorithms that simultaneously optimize nitrogen and water use in the canopy (Buckley, Farquhar & Miller 2002). Such approaches provide invaluable insight into within-canopy adjustments in foliage structure and function that

simultaneously maximize the use of multiple resources. However, application of these models to examine the effects of multiple limitations in plant canopies clearly requires more experimental work to characterize the constraints and derive reliable parameterizations.

## CONCLUSIONS

Acclimation of foliage carbon gain capacities to within-canopy light gradients involves a vast variety of structural and physiological modifications that collectively improve foliage light-harvesting efficiency in low light and photosynthetic capacity in high light availability. While the positive scaling of photosynthetic capacity with long-term light availability is a universal phenomenon, plant life form affects the extent to which this acclimation response is controlled by structural and physiological characteristics and the extent to which age-dependent changes in foliage function interact with light acclimation. In rapidly expanding canopies, foliage structure may be similar for all leaves in the canopy, and within-canopy variation in photosynthetic rates is mainly driven by nitrogen re-allocation from lower canopy to upper canopy leaves as senescence is induced in shaded lower canopy leaves. In flush-type deciduous forest canopies, all leaves develop at about the same time, and variation in photosynthetic capacity is mainly driven by acclimation of leaf structure to growth light environment, whereas in evergreen species, canopy functioning is additionally complicated by enhanced internal CO<sub>2</sub> diffusion limitations in older leaves and constrained re-acclimation potential of foliage developed at high light and becoming shaded during subsequent seasons as canopy grows and new foliage is produced. Leaf function in canopy is further modified by dynamic acclimation to short-term light fluctuations and interactions between light, heat and water stress. Interactions between environmental drivers can significantly constrain foliage photosynthetic capacity and realized photosynthetic production in high irradiance.

While a series of optimization studies suggest that within-canopy variation in foliage structural and photosynthetic characteristics is less than predicted for a maximum photosynthetic production at given total canopy N and foliar biomass (Badeck 1995; Schieving & Poorter 1999; Meir *et al.* 2002; Anten 2005), age-dependent constraints, dynamic acclimation to light and simultaneous acclimation to interacting stresses can partly explain this discrepancy. To improve prediction of canopy photosynthetic productivity, canopy models should include age-dependent modifications in leaf internal conductance, foliage responses to light fluctuations and simultaneous acclimation to interacting environmental drivers.

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