Photosynthetic Acclimation to Simultaneous and Interacting Environmental Stresses Along Natural Light Gradients: Optimality and Constraints

Ü. Niinemets[1,2] and F. Valladares[3]

[1] Department of Plant Physiology, University of Tartu, Riia 23, Tartu, Estonia
[2] Centro di Ecologia Alpina, I-38040 Viote del Monte Bondone (TN), Italy
[3] Centro de Ciencias Medioambientales, C.S.I.C., Serrano 115 dpdo., 28006 Madrid, Spain

Abstract: There is a strong natural light gradient from the top to the bottom in plant canopies and along gap–understorey continua. Leaf structure and photosynthetic capacities change close to proportionally along these gradients, leading to maximisation of whole canopy photosynthesis. However, other environmental factors also vary within the light gradients in a correlative manner. Specifically, the leaves exposed to higher irradiance suffer from more severe heat, water, and photoinhibition stresses. Research in tree canopies and across gap–understorey gradients demonstrates that plants have a large potential to acclimate to interacting environmental limitations. The optimum temperature for photosynthetic electron transport increases with increasing growth irradiance in the canopy, improving the resistance of photosynthetic apparatus to heat stress. Stomatal constraints on photosynthesis are also larger at higher irradiance because the leaves at greater evaporative demands regulate water use more efficiently. Furthermore, upper canopy leaves are more rigid and have lower leaf osmotic potentials to improve water extraction from drying soil. The current review highlights that such an array of complex interactions significantly modifies the potential and realized whole canopy photosynthetic productivity, but also that the interactive effects cannot be simply predicted as composites of additive partial environmental stresses. We hypothesize that plant photosynthetic capacities deviate from the theoretical optimum values because of the interacting stresses in plant canopies and evolutionary trade-offs between leaf- and canopy-level plastic adjustments in light capture and use.

Key words: Humidity, leaf temperature, light availability, photoinhibition, photosynthesis acclimation, plasticity, stress, vapour pressure deficit.

Introduction

Globally changing environmental drivers have promoted an enhanced interest in the acclimation capacity of vegetation. Plants as sessile organisms are expected to be highly plastic in response to heterogeneous and changing environments, but the limits and determinants of plant acclimation are still not entirely understood. In addition to other climatic factors, there are long-term global changes in atmospheric clearness and diffuse to direct solar radiation ratio that both importantly modify photosynthetic productivity (Farquhar and Roderick, 2003; Gu et al., 2003). Thus, understanding plant photosynthetic plasticity to light is crucial to predict future changes in Earth carbon balance.

Light environment strongly varies within the leaves and within plant canopies and there is a strong variation in light availability along gap–understorey continua. Due to this great heterogeneity of growth light environments, plants have been traditionally thought to have a strong potential to adjust to different growth irradiances (Valladares, 2003). Cell photosynthetic activity significantly varies from the top to the bottom layers of a single leaf (e.g., Vogelmann et al., 1996), from the top to the bottom of plant canopies (e.g., Ellsworth and Reich, 1993; Niinemets et al., 1998; Le Roux et al., 2001), and along gap–understorey continua (e.g., Bazzaz and Wayne, 1994), demonstrating that photosynthesis physiology does plastically adjust to long-term light conditions.

Comparisons between leaf and whole canopy photosynthetic activities have shown a striking similarity between the acclimation of leaf photosynthetic characteristics within a single leaf and within the plant canopy (Terashima and Hikosaka, 1995). Assuming that photosynthetic acclimation results in an optimal distribution of limiting resources in the canopy, leaf level photosynthesis models may be directly applied to predict whole canopy photosynthesis rates (Farquhar, 1989; Sellers et al., 1992; Friend, 2001). Because of intrinsic simplicity, such "big leaf" models are widely applied to understand the response of plant canopies to globally changing environmental drivers (Amthor, 1994; Sands, 1995; Raulier et al., 1999). In fact, derivation of indices of leaf photosynthetic performance from ecosystem-level eddy covariance measurements, essentially rests on the assumption that plant canopy responds as a "big leaf" (Amthor et al., 1994; Leuning et al., 1998). Eddy covariance is today a standard method to understand sources of temporal and spatial variations of net ecosystem exchange (Aubinet et al., 2000), but the caveats and limitations of this approach are often not fully acknowledged.

The "big leaf" models only consider light acclimation, and postulate a direct proportionality between average leaf irradiance and leaf photosynthetic capacity, i.e., an "optimal" acclimation

(Friend, 2001; Meir et al., 2002). According to experimental studies, changes in leaf photosynthetic capacity with integrated irradiance are less than required for an "optimal" distribution (Friend, 2001; Meir et al., 2002; Niinemets et al., 2004 a), indicating inherent limitations of simple scaling routines. Although variation in light is the primary stress factor in plant canopies and along gap–understorey gradients, other environmental factors significantly interact with irradiance. In particular, there are strong interactions between temperature and light, and vapour pressure deficit and light (Bazzaz and Wayne, 1994; Singsaas et al., 1999; Jifon and Syvertsen, 2003). Thus, it is not only light, but multiple interacting environmental variables the leaves are faced with in plant canopies. This complicates understanding and prediction of acclimation in natural environments, because plants must adjust to multiple environmental stresses simultaneously. Modification of plant photosynthetic acclimation to light by co-varying environmental variables significantly alters realized plant photosynthesis rates (Valladares and Pearcy, 1997; Niinemets et al., 1999 b), but these important effects are still not included in contemporary canopy photosynthesis predictions.

In the current paper, we first review the changes in environmental factors within plant canopies and along gap–understorey continua, and suggest that the magnitude of the interactions between the environmental factors is large enough to significantly modify leaf physiology. Second, we outline the interactive effects of environmental variables on plant photosynthesis and demonstrate short- and long-term changes in plant photosynthetic functioning due to aggravated environmental stresses and acclimation to interacting environmental variables. We further show that interactive short-term effects may be more deleterious to leaf photosynthetic functioning than each stress factor acting separately, but also that acclimation to any single factor may improve the resistance to other stress factors as well. Finally, we illustrate the long-term homeostatic behaviour of plant canopies, where plants both modify and respond to their internal gradients of light in a phenotypic and evolutionary time-scale, leading to complex and dynamic patterns of carbon gain physiology of leaves that are separated by relatively short distances in plant canopies.

Variations in Light Environment in Space and Time

The spatial variation of light is primarily a function of leaf area index, inclination, and dispersion of foliage elements (Valladares, 2003). As the cumulative leaf area increases with increasing depth in the canopy, incident leaf irradiances progressively decline. Differences in incident irradiance between upper and lower canopy leaves are generally 10- to 20-fold for grasslands (Faurie et al., 1996; Tappeiner and Cernusca, 1996), 20- to 50-fold for temperate forest ecosystems (Fig. **1 A**; Eliáš et al., 1989; Niinemets et al., 1998a; Koike et al., 2001), and at the extreme, 50- to 200-fold for tropical rain forests (Chazdon and Fetcher, 1984; Brown, 1993; Barker, 1996). Although in several communities such as savanna-type ecosystems there may be large gaps between plant crowns, foliage is generally more strongly aggregated in shoots and branches in such communities (Asner and Wessman, 1997; Asner et al., 1998), implying that the gradients in incident irradiance are not necessarily less important in habitats with a discontinuous vegetation cover (e.g., Caldwell et al., 1986).

Even the communities with a closed overstorey canopy contain gaps with varying size distribution. This results in a continuous gap–understorey gradient in incident irradiance for the lower vegetation layer. Gap–understorey gradients are highly dynamic due to overstorey growth and mortality, and accordingly, there is a strong long-term interaction between the spatial and temporal variations in over- and understorey light environment. Apart from this interaction, the distribution and shape of the gaps in the overstorey affects diurnal and seasonal changes in the incident irradiance for the understorey (Wayne and Bazzaz, 1993 b; Bazzaz and Wayne, 1994; Pearcy, 1999).

Although the total variation of the light environment is larger for upper canopy leaves than for lower canopy leaves, and for larger than for smaller gaps in the understorey, relative variability that is characterized by the coefficient of variation, is larger for the shaded microsites (Brown, 1993; Bazzaz and Wayne, 1994). Large relative variability in the shaded environments is primarily because of greater relative importance of sunflecks (Bazzaz and Wayne, 1994). Furthermore, the average length of sunflecks decreases with decreasing total integrated irradiance as the overstorey gaps in solar paths become smaller (Valladares et al., 1997), demonstrating that temporal and spatial scales of light variability may also interact in a very short timescale (Baldocchi and Collineau, 1994; Tang and Washitani, 1995; Valladares, 2003). Taken together, these data highlight a major interaction between the spatial and temporal scales of light variation, and indicate that alteration in the quantity of light is associated with complex modifications in temporal distribution of incident quantum flux density.

Co-Variation of Environmental Factors Within and Along Natural Light Gradients

Canopy variation in irradiance of several orders of magnitude is accompanied by similar gradients in wind speed (Eliáš et al., 1989), and drag on leaves (Marcolla et al., 2003), implying that the mechanical stresses are disproportionately larger for the upper than for the lower canopy leaves (Niklas, 1996). Other environmental factors co-vary with light in plant canopies, with ranges of variation that may be physiologically significant (Fig. **1 B, C**).

Studies spanning temperate to tropical forests demonstrate that the gradient in air temperature (T_A) within the plant canopies is typically 3–5 °C (Fig. **1 B**; Chiariello, 1984; Eliáš et al., 1989; Barker, 1996; Niinemets et al., 1999b; Baldocchi et al., 2002). Although the daily average T_A may be only several degrees higher in the top than in the bottom of canopies (Niinemets et al., 1999 b), the daily air temperature maxima are significantly larger and minima lower in the upper canopy leaves, resulting in temperature gradients occasionally as high as 10 °C. This is important as plants may be more sensitive to the temperature extremes than to average temperatures (Bazzaz and Wayne, 1994; Box, 1996).

A relevant aspect in interpreting the measured gradients in air temperature is the extent to which T_A reflects leaf temperature. Due to greater wind speeds, leaf boundary layer conductances are higher in the upper than in the lower canopy, indicating a more advanced heat loss of exposed leaves. However, on calm days, the maximum leaf temperatures of sunlit leaves may be
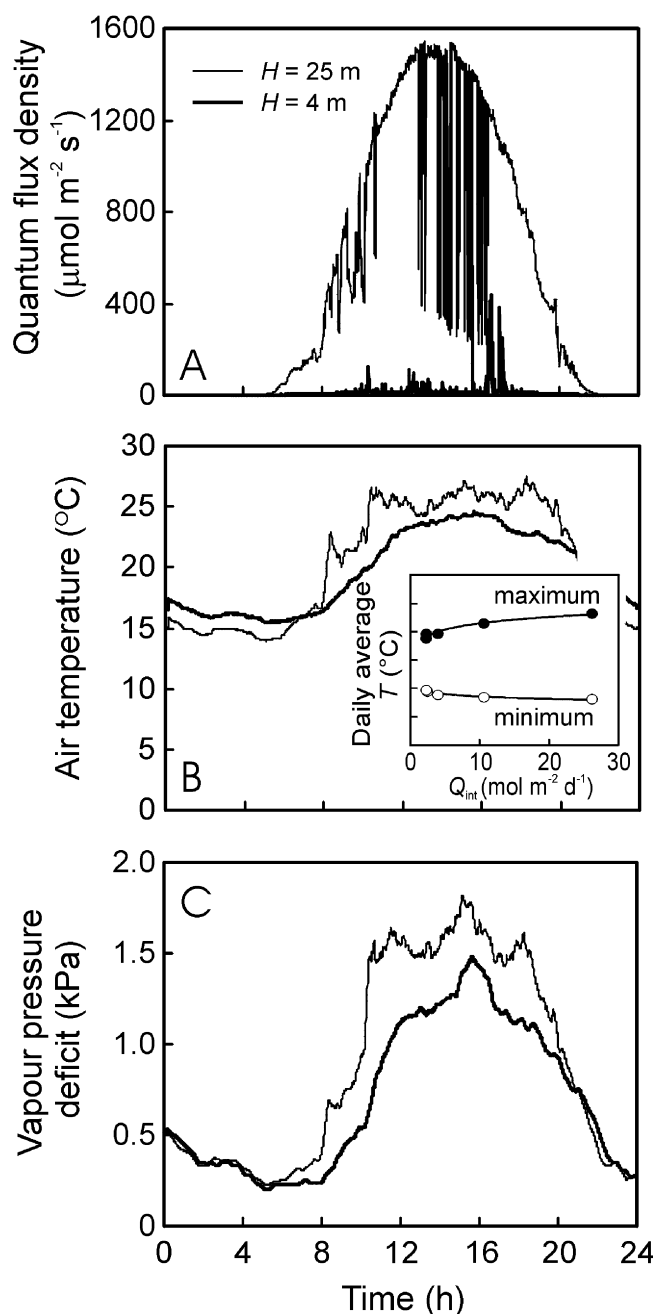
Fig. 1   Example of diurnal variations in (**A**) photosynthetic quantum flux density *(Q)*, (**B**) air temperature *(T),* and (**C**) vapour pressure deficit *(D)* in the upper (height = 25 m) and lower canopy (height = 4 m) on a clear day (July 30, 1995; unpublished data of Niinemets) in a mixed broadleaved deciduous forest dominated by *Populus tremula* in the upper canopy layer and *Tilia cordata* in the lower canopy layer as detailed in Niinemets et al. (1998 a). The inset in **B** demonstrates the correlations between seasonal average integrated quantum flux density (Q_{int}) and daily average maximum and minimum temperatures for the entire growing season (June 3 – October 1, 1995; modified from Niinemets et al., 1999 b).

more than 5 – 10 °C higher than ambient air temperatures (Gates, 1980; Hamerlynck and Knapp, 1994; Singsaas et al., 1999; Jifon and Syvertsen, 2003). Even in windy conditions, leaf temperatures may rise rapidly during lightflecks as the leaf energy balance has not yet reached the steady state (Sing-

saas et al., 1999). This signifies that leaf temperatures may fluctuate extensively during the day, similar to the incident quantum flux densities (Singsaas et al., 1999).

As an outcome of higher maximum temperatures, relative air humidity is lower and vapour pressure deficit larger in the upper canopy (Fig. **1 C**). The midday and afternoon values of relative humidity are typically 20 – 30 % lower for the upper than for the lower canopy layers (Chiariello, 1984; Eliáš et al., 1989; Barker, 1996; Niinemets, unpublished observations), and corresponding values of vapour pressure deficit of the ambient air may differ by 0.5 – 3 kPa between the upper and the lower canopy (Fig. **1 C**; Barker, 1996). This means that leaf evaporative demands increase with the irradiance in the canopy. Although larger wind speeds in the upper canopy may reduce leaf temperatures on windy days, a more advanced coupling of leaves to the atmosphere due to wind may also enhance leaf water loss.

The timing of peak quantum flux densities, temperatures, and vapour pressure deficits during the day is an important factor potentially altering the effect of interacting environmental variables on leaf functioning. Depending on leaf azimuthal orientation in the canopy and on understorey gap shape and orientation, environmental stresses are most severe at different times during the day, due to diurnal variation of the direction of direct solar radiation (Wayne and Bazzaz, 1993 b; Bazzaz and Wayne, 1994). According to the experimental observations, interacting stresses may be less detrimental for leaves receiving morning sun than for leaves exposed to direct radiation at midday or afternoon (Wayne and Bazzaz, 1993 b). This is possibly because the leaves have reached the equilibrium with soil water contents in the morning, allowing the leaves to function with full capacity at high quantum flux densities. Leaf water potentials significantly decrease during the rest of the day, leading to a stronger afternoon sensitivity of stomatal conductance to high temperatures and vapour pressure deficits, and decreases in photosynthetic productivity in high light.

In addition to environmental differences, there are significant ambient CO_2 mole fraction (C_a) gradients from the soil surface to the uppermost leaves that result from the variations in the balance between auto- and heterotrophic respiration and photosynthesis. The magnitude of such gradients depends on wind profiles and friction velocity. The strongest C_a gradient is generally within the first few meters from the soil surface (Buchmann et al., 1996), but C_a values may often be 20 – 50 μmol mol^{-1} higher for lower canopy leaves compared with upper canopy leaves (Eliáš et al., 1989; Barker, 1996; Buchmann et al., 1996; Koike et al., 2001; Baldocchi and Bowling, 2003).

Are the Within-Canopy and Gap–Understorey Environmental Gradients the Same?

The environmental factors co-vary with irradiance within plant canopies as well as along gap–understorey gradients, but there are important differences between these light gradients that may significantly alter plant responses. Specifically, soil water availability may be lower below tree crowns, due to canopy interception and water uptake by tree roots, than in intercanopy gaps (Breshears et al., 1997). Although leaf temperatures and vapour pressure deficits between the leaf and atmosphere are larger for plants growing in gaps than for plants

growing in deep canopy shade (Brown, 1993; Bazzaz and Wayne, 1994), potential differences in soil water availability may mean that, in years with extreme soil drought, water stress becomes more severe for seedlings and saplings growing under low light than for plants growing under high light (Valladares and Pearcy, 2002).

Seedlings and saplings of woody species, as well as herbs competing in the understorey gaps, also have shallower root systems compared with overstorey trees. Given that upper soil horizons dry out earlier in the season than the deeper soil horizons, temporal development of plant water stress may vary during the season for the overstorey and understorey species (Bazzaz and Wayne, 1994). Due to the lack of reserves at the beginning of the growing season, plants may more strongly respond to early season drought than to late season drought (Bazzaz and Wayne, 1994). This suggests that differences in drought timing between under- and overstorey plants may significantly modify plant responses to within canopy and gap–understorey light gradients.

Because growth is more limited by nutrients in high than in low light (Poorter and Nagel, 2000), and the competition for nutrients is more severe in high light early successional environments (Tilman, 1993), nutrient availability for growth is generally lower in large gaps than in deeply shaded understorey (Bazzaz and Wayne, 1994). Such a greater degree of nutrient limitation in larger gaps is supported by negative correlations between foliar nitrogen content per unit dry mass (N_M) and the integrated irradiance above the seedling's foliage (Ellsworth and Reich, 1992; Wayne and Bazzaz, 1993a). This is significant, because microsite differences in nutrient availability may more importantly alter species competitive potentials along the gap–understorey continuum than differences in species physiology (Bungard et al., 2000). There may also be important differences in timing of peak nutrient availabilities among exposed and shaded microsites, as seasonal variation in soil microbial activity is strongly linked to soil temperature and water contents (Cain et al., 1999; Kelly and Mays, 1999), further emphasising the complexity of gap–understorey gradients. In contrast, nitrogen availability is essentially the same for all leaves in a tree canopy, and leaf N_M values vary generally only to a minor extent in tree canopies (e.g., Ellsworth and Reich, 1993). However, some studies have demonstrated lower N_M values in the upper than in the lower canopy, because of changes in the fractions of structural versus photosynthetic leaf tissues within the canopy (Niinemets et al., 1999a). Such alterations in leaf composition commonly occur as the leaves adapt to water-limited environments (Lamont et al., 2002), and may be the outcome of interacting environmental stresses in plant canopies (see below).

Outline of the Basic Changes in Leaf Photosynthetic Functioning in Response to Light Gradients

Structural and physiological acclimation to enhance photosynthetic capacity

Adaptation to long-term changes in light availability involves extensive modifications in leaf anatomy (leaf thickness, fractional composition of various tissues) and morphology (leaf size, leaf dry mass per unit area; Fig. 2A; Koike et al., 2001). Stacking of foliar biomass per unit area brings about a positive
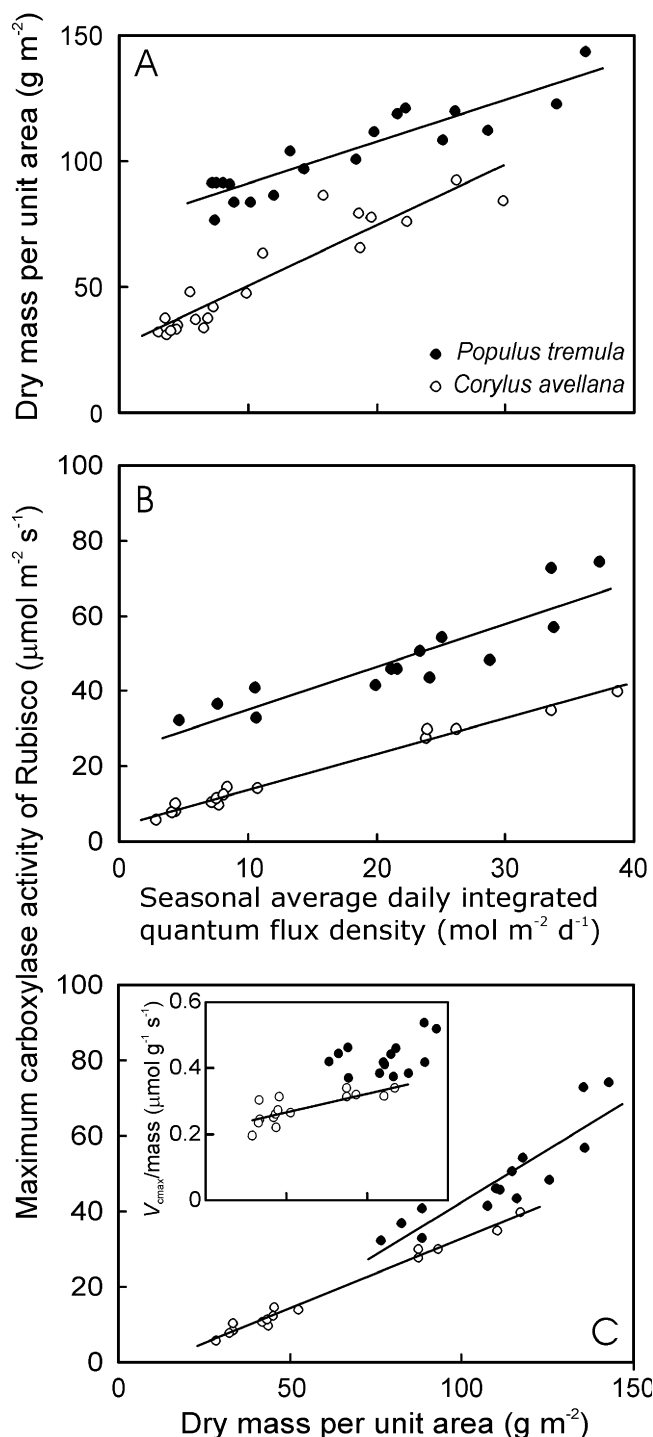
Fig. 2 Effects of seasonal average integrated quantum flux density (Q_{int}) on (**A**) leaf dry mass per unit area (M_A) and on (**B**) the maximum carboxylase activity of Rubisco per unit area (V_{cmax}/area), and (**C**) the correlation between V_{cmax}/area and M_A in deciduous temperate shade-intolerant tree species *Populus tremula,* and shade-tolerant species *Corylus avellana* (modified from Niinemets and Kull, 1998; Niinemets et al., 1998b). The inset in (**C**) demonstrates the correlation between mass-based maximum carboxylase activity of Rubisco and M_A. Data are fitted by linear regressions, and all regressions drawn are significant at $p < 0.001$.

scaling of leaf photosynthetic potentials per unit area with integrated irradiance (Fig. **2B**; Gutschick and Wiegel, 1988; Harley and Baldocchi, 1995; Koike et al., 2001), while photosynthetic potentials per unit dry mass vary significantly less with growth irradiance (Fig. **2C**). Increases in growth irradiance often also result in enhanced foliar nitrogen partitioning in Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and rate-limiting proteins of the photosynthetic electron transport chain (Evans, 1989; Niinemets and Tenhunen, 1997; Grassi and Bagnaresi, 2001). However, light-dependent modifications of leaf nitrogen partitioning among proteins of photosynthetic machinery appear to change leaf photosynthetic capacity less than anatomical and morphological alterations (Evans and Poorter, 2001).

Although there is a consensus that leaf photosynthetic potentials acclimate to integrated irradiance during leaf growth, it is important that plant acclimation capacity may be different for direct and diffuse irradiance (Wayne and Bazzaz, 1993a; Leakey et al., 2002) as well as may vary with the timing of peak irradiances (Wayne and Bazzaz, 1993a). Such variations in light environment occur both within tree canopies and along gap–understorey gradients, and may importantly modify the resulting gradation in photosynthetic capacities at a common integrated irradiance.

In addition to leaf level adjustments enhancing photosynthetic capacity, packing of the number of leaves, and leaf area per unit shoot axis length increases with increasing growth irradiance in conifers (Stenberg et al., 1998; Cescatti and Zorer, 2003) and broadleaved species (Valladares and Pearcy, 1999). Leaf area aggregation results in a lower mean irradiance on the leaf surface than a hypothetical shoot architecture without leaf overlap. A greater degree of leaf clustering in high light also implies a larger photosynthetic biomass investment per unit shoot length that may improve the total carbon gain of shoots exposed to high irradiances where photosynthetic returns are largest (Stenberg et al., 1998).

Differences in plastic modifications in photosynthetic capacity in multi-species stands

There are intriguing species differences in plastic modifications in foliage photosynthetic capacities to integrated irradiance (Fig. **2B**) that importantly affect the photosynthetic productivity of multi-species canopies. These species differences in photosynthetic capacity are primarily determined by species potentials to adjust foliage dry mass per unit area (M_A; Fig. **2C**), but the existence of mixed canopies that consist of species with contrasting plastic responses to light, is not fully understood (Valladares et al., 2002c). Species differences in leaf acclimation capacity hint at adaptive advantages of phenotypic stability in highly heterogeneous light environments and/or to compensating adjustments in other traits (Valladares et al., 2000). Clearly, species can occupy similar positions in the canopy and along gap–understorey continua deploying different suites of traits and thus, compensating for the lack of plasticity in some traits by enhanced plasticity in other traits (Bazzaz and Wayne, 1994). However, there seems to be a trade-off between the limited potential for adjustment of leaf photosynthetic capacity, and species competitive ability in high light (Fig. **3**). Enhanced physiological plasticity (photosynthetic capacity, maximum stomatal conductance), in turn,
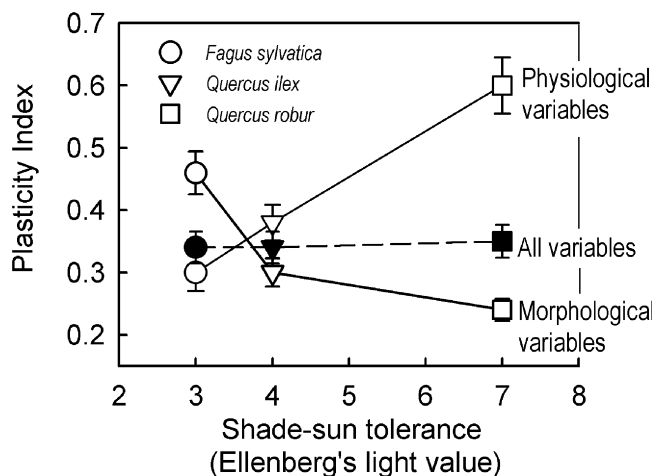

Fig. 3 Plastic response to light availability of seedlings of three widespread European tree species (*Fagus sylvatica* – circles, *Q. ilex* – triangles, and *Quercus robur* – squares) differing in shade tolerance. Lower value of Ellenberg's light index indicates higher shade tolerance (Ellenberg et al., 1991). Values of the plasticity index were calculated for all variables pooled (six variables; solid symbols), and separately for three physiological (photosynthetic capacity, maximum stomatal conductance, and Rubisco activity) and three morphological variables (root-to-shoot ratio, leaf size, and leaf mass ratio; open symbols). Error bars give ± SE. Elaborated from Valladares et al. (2002a, b).

appears to compromise the plasticity in whole plant morphological and architectural traits that enhances plant performance in low light (Fig. **3**; Valladares et al., 2002b).

Species differences in photosynthetic adjustments may also be linked to contrasting species responses to environmental drivers that interact with irradiance. For instance, foliage shade tolerance and water stress tolerance are negatively correlated across woody species (Abrams, 1990), underscoring the importance to consider multiple limitations in predicting whole canopy photosynthesis.

Plant responses to excess light

Even in leaves that are acclimated to full sun, foliar photosynthetic rates saturate at quantum flux densities of ca. 400 – 700 µmol m^{-2} s^{-1} rather than at daily peak light intensities of 1600 – 2000 µmol m^{-2} s^{-1}. Plants cope with the excess incident light that is above the photosynthetic saturation point by either avoidance of excess light interception or by enhancing the capacity for non-photochemical quenching of excess irradiance. In addition to leaf clumping effects that concentrate foliar photosynthetic biomass in the upper canopy, but reduce the mean irradiance on the leaf surface, foliage orientations become more vertical in the upper canopy (Valladares, 1999; Fleck et al., 2003). In canopies with varying leaf angles, steep leaf angles of the upper canopy result in interception of only 30 – 60% of incoming radiation, implying that the leaf angle plays a major role in photoprotection (Domingo et al., 2000). In addition, steeper angles of the upper canopy allow for enhanced light penetration to the lower leaves, and result in more homogeneous distribution of light among foliage units (Valladares and Pearcy, 1998; Werner et al., 2001b). Leaves in many species are also significantly curled or rolled in higher
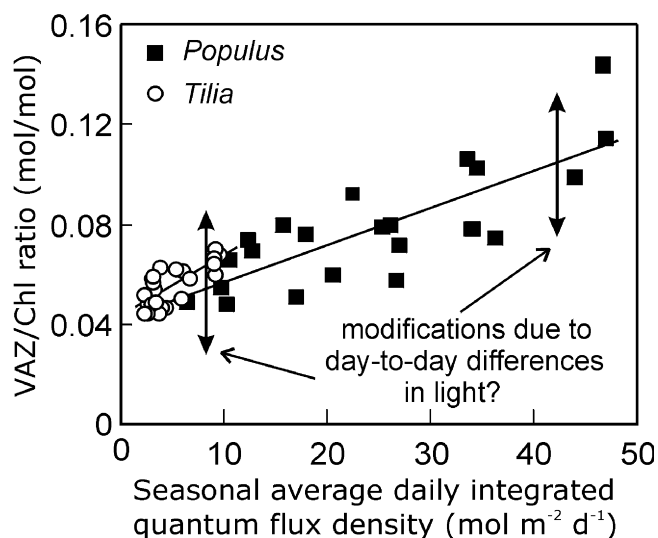
Fig. 4 Modification of the xanthophyll cycle carotenoid pool size (sum of violaxanthin, antheraxanthin, and zeaxanthin, VAZ) relative to total leaf chlorophyll by variation in irradiance in shade-intolerant species *Populus tremula* and shade-tolerant species *Tilia cordata*. The same stand as in Fig. **1**. Daily integrated quantum flux density was averaged for 3 days preceding foliar sampling. Modified from Niinemets et al. (1998 a).

The capacity for non-photochemical quenching of absorbed irradiance scales positively with incident integrated leaf irradiance (Demmig-Adams and Adams, 1996, 2000). These adjustments in excess light energy dissipation are thought to occur mainly through changes in the xanthophyll cycle carotenoid pool size (Fig. **4**; Demmig-Adams and Adams, 1996, 2000). Laboratory studies conducted under continuous illumination suggest that xanthophyll cycle pool size fully adjusts to stepwise changes in irradiance in 3 – 5 days after changes in light regime (Demmig-Adams et al., 1989; Bilger et al., 1995). However, currently it is unclear which frequencies of solar radiation variation drive modifications in the xanthophyll cycle pool size in field conditions. In strongly dynamic natural light environments, changes in xanthophyll cycle pool size were not completed even 11 – 17 days after alteration of the light regime (Logan et al., 1998; Fig. **5**). Furthermore, there is a significant interaction between previous leaf light environment and leaf capacity to adjust to rapid light changes, and this interaction is also species-dependent (Fig. **5A** versus Fig. **5B**). Overall, the recent experimental evidence indicates that the xanthophyll cycle pool is not in a steady-state in field conditions, and that leaves do not precisely track day-to-day fluctuations in irradiance.

Modification of Photosynthetic Acclimation by Interactions Among Environmental Variables

Interaction between light and temperature environments

Although the differences between average temperatures may be relatively minor among canopy top and bottom, maximum differences are significantly larger (Fig. **1 B** inset). Upper canopy leaves are exposed to extreme heat events, which are becoming more frequent in certain geographic areas as a result
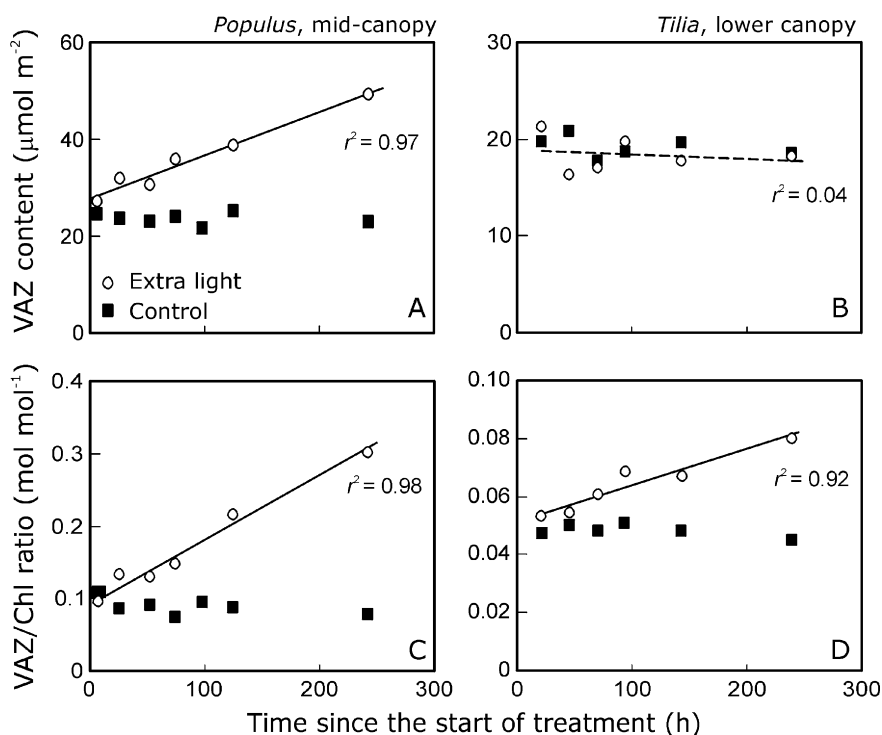
light, again strongly reducing leaf light interception (Fleck et al., 2003). Overall, this suite of morphological and architectural traits reduces the risk of exceeding the limits of physiological tolerance to heat and high light, which is particularly likely to threaten individual leaves when other resources such as water and nitrogen are scant (Valladares and Pearcy, 1997).

Fig. 5 Changes in xanthophyll cycle carotenoid content per unit area (**A, B**) and chlorophyll (**C, D**) due to extra light of 500 – 700 μmol m^{-2} s^{-1} for 12 h photoperiod in *Populus tremula* and *Tilia cordata*. Recalculated from Niinemets et al. (2003 a). Data were fitted by linear regressions. The regressions depicted with the solid line are significant at $p < 0.001$.
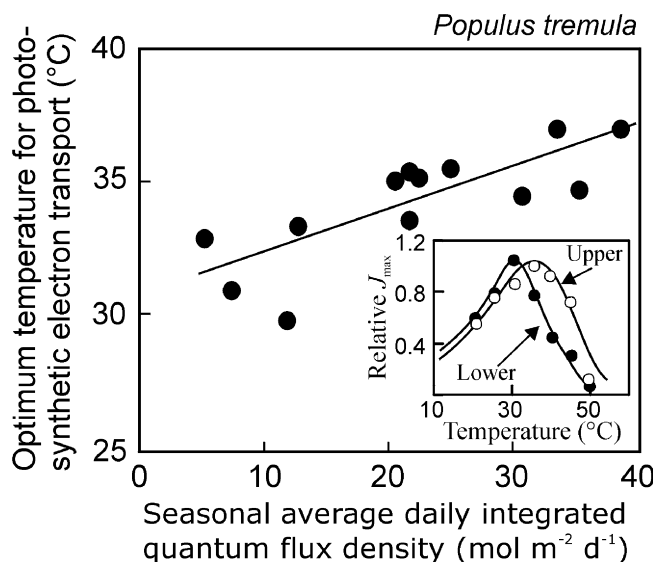
Fig. 6 Optimum temperature (T_{opt}) for the capacity of photosynthetic electron transport (J_{max}) in relation to Q_{int} in the canopy of *Populus tremula* (modified from Niinemets et al., 1999b). Inset demonstrates the representative J_{max} versus temperature response curves for an upper canopy leaf (Q_{int} = 22.5 mol m^{-2} d^{-1}, T_{opt} = 35.1 °C) and a lower canopy leaf (Q_{int} = 9.5 mol m^{-2} d^{-1}, T_{opt} = 30.4 °C). In these relations, J_{max} was normalised with respect to the optimum temperature.

of global climate changes (Valladares and Pearcy, 2002). These events can lead to leaf necrosis, threatening the survival of small and slow-growing plants (Valladares and Pearcy, 1997). However, it is the level of exposure to high irradiance that is the main determinant of leaf death after extreme heat events, so shade leaves at lower positions in the canopy are less affected (Groom et al., 2004).

Given that these extreme temperatures affect plant photosynthesis the most, especially in interaction with high irradiances (Havaux, 1992; Mishra and Singhal, 1992), leaf photosynthesis apparatus is expected to acclimate to the canopy temperature profile. This suggestion is supported by increases in the optimum temperatures (T_{opt}) for the capacity of photosynthetic electron transport (J_{max}) with increasing irradiance in the canopy (Fig. 6). Such increases imply that there is a spectrum of temperature responses of J_{max} within the canopy rather than a uniform temperature response, as assumed in the contemporary canopy photosynthesis models (e.g., Harley and Baldocchi, 1995; Friend, 2001).

The mechanism of the increase of heat tolerance of photosynthetic apparatus of leaves exposed to greater integrated irradiance is not entirely understood. Modification of membrane fluidity through changes in the saturation/desaturation state of membrane lipids, as well as lipid composition, is a major way for adjustment of J_{max} to long-term air temperatures (Santarius and Weis, 1988; Routaboul et al., 1997; Murata and Nishiyama, 1998), and may explain most of the within-canopy variation in the temperature responses of J_{max}.

As an alternative, Gruszecki and Strzalka (1991) and Havaux and Tardy (1996) suggested that the xanthophyll cycle plays an important role in modification of membrane fluidity. In par-
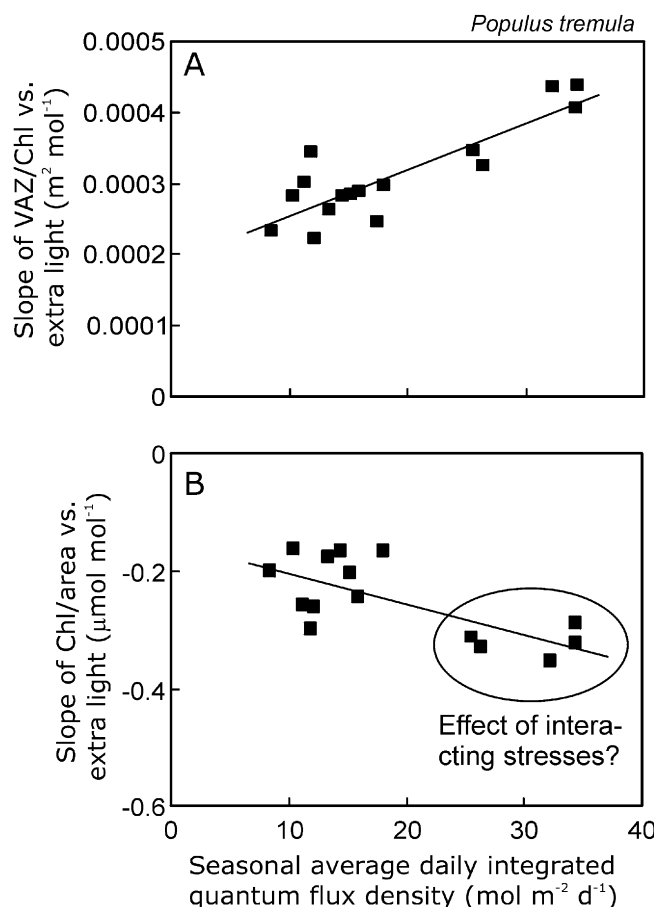
Fig. 7 Influences of integrated irradiance on (**A**) the slope of the VAZ/Chl versus cumulative extra light, and (**B**) the slope of leaf chlorophyll content versus cumulative extra light in *Populus tremula* (modified from Niinemets et al., 2003a). Extra light of 500–700 μmol m^{-2} s^{-1} was applied during a 12 h photoperiod for 11 days (Fig. 5), and the time-dependent increases in VAZ/Chl and Chl/area were fitted by linear regressions for every leaf developed under the specific irradiance environment. Data points in **A** and **B** were fitted by linear regressions. The relationships depicted were significant at $p < 0.001$ (**A**) and $p < 0.05$ (**B**).

ticular, they postulated that zeaxanthin dissolves in thylakoids and chloroplast outer membranes and thereby makes these membranes more rigid (Havaux and Tardy, 1996; Havaux, 1998). Thus, light-dependent changes in the pool size of xanthophyll cycle carotenoids may significantly enhance leaf tolerance of high temperatures. According to recent experimental evidence, increases in xanthophyll cycle pool size after light changes do not necessarily prevent chlorophyll photo-destruction, especially at higher integrated irradiances (Fig. 7), further suggesting that xanthophylls may play a role other than just photo-protection. Given that there is a certain fraction of xanthophyll cycle carotenoids that is not bound to pigment-binding proteins (Havaux, 1998; Anderson et al., 2001), the hypothesis of the changes in heat-tolerance of electron transport due to xanthophyll cycle activity is promising for further experiments.

Some plant species are also important emitters of volatile isoprenoids, such as isoprene and monoterpenes, that may also protect plant membranes from heat damage (Sharkey and
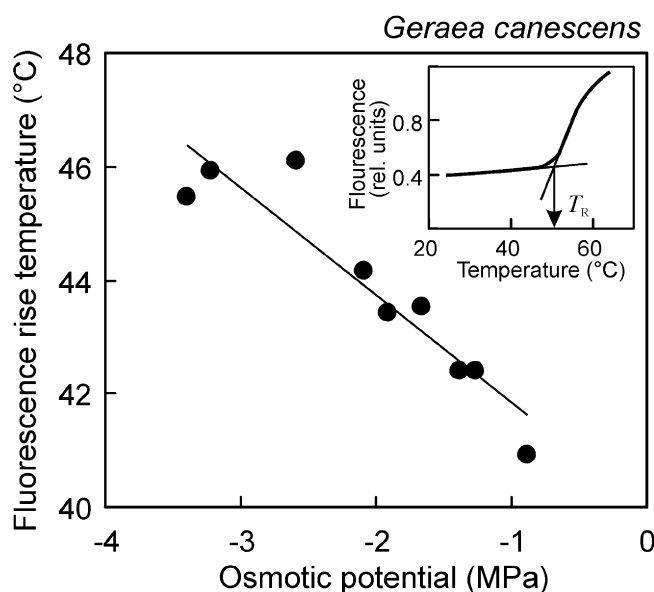
Fig. 8 Temperature (T_R) for the rise of dark fluorescence in the presence of far red light (F_0) in relation to leaf osmotic potential in the desert plant *Geraea canescens* (modified from Seemann et al., 1986). T_R is correlated with the temperature for phase change of thylakoid membranes and thus, the membrane damage due to heat stress (Santarius and Weis, 1988). Inset shows a representative dark fluorescence versus temperature response curve and determination of T_R value in *P. tremula* (Hüve, Bichele and Niinemets, unpublished data).

Fig. 9 Canopy variation in the leaf osmotic potentials due to the presence of sugars in mid-season in *P. tremula* and *C. avellana* (calculated from the data of Niinemets and Kull, 1998).

Singsaas, 1995; Loreto et al., 1998). Given that the emission rates of these compounds increase with increasing light availability in the canopy (Harley et al., 1997; Staudt et al., 2003), enhanced isoprenoid emission potential of leaves developed at higher irradiance may synergistically protect plant membranes from heat stress in the emitting species.

Interaction between temperature, light, and water

Sensitivity of leaf photosynthetic activity to high temperatures is lower in leaves experiencing water stress (Seemann et al., 1984; Havaux, 1992; Epron, 1997; Lu and Zhang, 1999), although such an interaction is not evident in all experiments (Jagtap et al., 1998). Given that decreases in cell sap osmotic potential are a major leaf response to water stress, increases in the concentration of leaf osmotica have been hypothesised to directly affect the stability of plant membranes (Seemann et al., 1984; Santarius and Weis, 1988). Shifts in the phase change temperatures for plant membranes demonstrate that elevated concentrations of osmotically active substances do stabilise plant membranes, and decrease the sensitivity of photosynthetic electron transport rates to heat stress (Fig. **8**). Both the ions of neutral salts as well as neutral osmotica such as sugars enhance leaf heat resistance (Seemann et al., 1986; Santarius and Weis, 1988).

In plant canopies, there is a large gradient in leaf osmotic potentials (Niinemets et al., 1999c) that, to a large degree, results from a variation in leaf sugar concentrations due to differences in foliar photosynthetic productivity at varying total daily irradiances (Fig. **9**). Furthermore, in water-stressed conditions, starch and oligosaccharide concentrations decrease while the
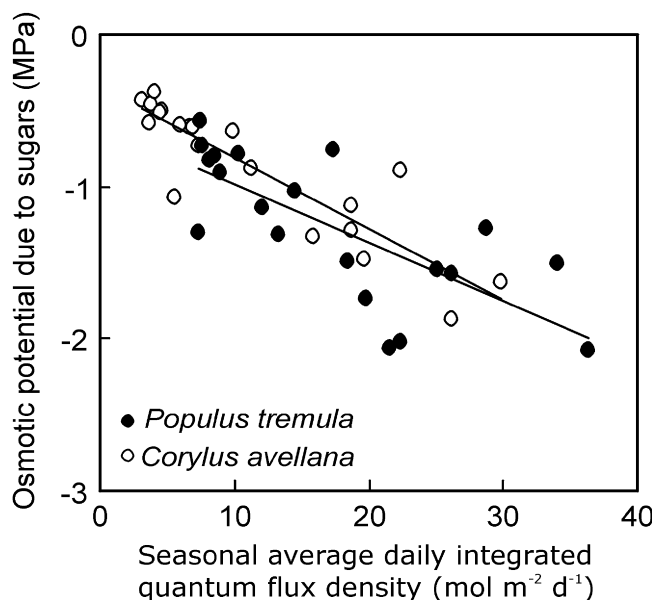
concentrations of monosaccharides increase, underscoring the important role of carbohydrates in osmotic adjustment (Epron and Dreyer, 1996). This large gradient in cell sap osmolarity (Fig. **9**) suggests that modifications in the temperature optima of J_{max} may partly result from light effects on cumulative photosynthesis, and possibly also from water stress effects on leaf carbohydrate concentrations.

Canopy variation in leaf water stress and implications for photoinhibition

The gradient in sugar concentrations within the canopy may just result from canopy differences in daily photosynthesis integrals. However, as discussed above, evaporative demands are inevitably larger in higher light due to greater leaf temperatures and lower relative humidity. Greater evaporative demands still do not mean that the leaves at higher irradiance must necessarily cope with a more severe water stress. Maximum stomatal conductances scale positively with growth irradiance, and upper canopy leaves may not suffer from a more severe water stress than lower canopy leaves, provided the soil water availability and stem, branch and petiole hydraulic conductivities are not limiting. In general, the hydraulic conductivity of shoots of the same diameter is larger for light-acclimated shoots (Cochard et al., 1999; Lemoine et al., 2002), indicating that the water conduction capacities scale with growth irradiance. In fact, upper canopy shoots can also sustain lower water potentials (Cochard et al., 1999; Niinemets et al., 1999c; Lemoine et al., 2002) and are less vulnerable to cavitation (Cochard et al., 1999; Lemoine et al., 2002).

Nevertheless, during prolonged soil water stress, longer pathway lengths and greater evaporative demands do lead to a relatively stronger stomatal closure in leaves exposed to greater irradiance (Fig. **10**; Lemoine et al., 2002; Jifon and Syvertsen, 2003). This decrease is species-dependent (Fig. **10**; Hanba et
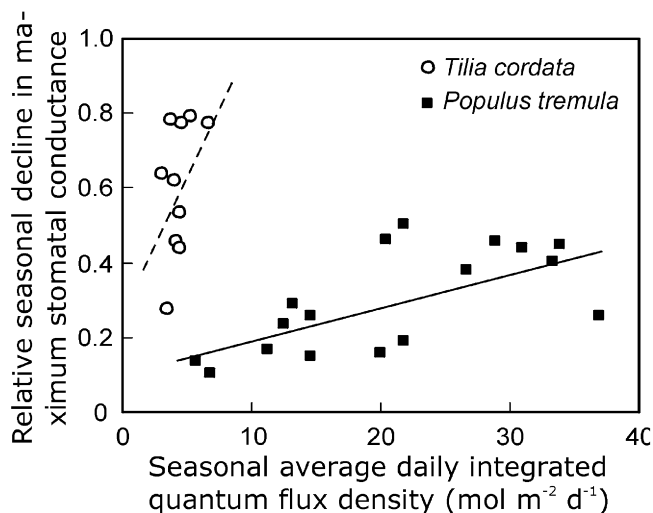
Fig. 10 Relative decline in maximum stomatal conductance (G_{max}) because of developing soil water stress at different growth irradiances in the canopy of *Populus tremula* (filled symbols, modified from Niinemets et al., 2004 b) and *Tilia cordata* (open symbols; the same stand as in Fig. 1, Niinemets, unpublished data). Relative seasonal decrease in the potential G_{max} was calculated as (G_{max} [non-stressed] – G_{max} [stressed]) / G_{max} (non-stressed).

al., 2002), possibly because of species-specific root system architectures and sensitivity of conducting pathways to cavitation (Oren et al., 1999). According to simulation analyses, the larger degree of stomatal closure of the upper canopy leaves results in a proportionally greater decrease of potential leaf daily photosynthetic productivity (Niinemets et al., 2004 b). Such a canopy variation in the difference between the potential and actual foliage photosynthetic productivity may be further enhanced by lower air CO_2 mole fractions in the upper canopy (Buchmann et al., 1996; Baldocchi and Bowling, 2003).

In addition, water stress leads to greater fractions of excess excitation energy, and may significantly amplify leaf carbon losses due to photoinhibition (Havaux, 1992; Lu and Zhang, 1999). Experimental data demonstrate greater photoinhibition of upper canopy leaves, especially if photosynthetic activity of upper canopy leaves is limited by interacting water and temperature stresses (Niinemets and Kull, 2001; Jifon and Syvertsen, 2003). There are large differences in species sensitivity to photoinhibition (Osmond et al., 1999) that are linked to species tolerance of heat and water stress. In multispecies canopies, the species that keep the stomata less open during periods of moderate water stress also have less open PSII centres, and are more sensitive to photoinhibition developing during the day (Niinemets and Kull, 2001).

Although the scaling of photoinhibition of photosynthetic electron transport rate *(J)* with integrated light is unequivocal, it is currently unclear what is the effect of inhibition of *J* on photosynthesis. In the upper canopy and on clear days, photosynthesis is limited by Rubisco (CO_2-limited photosynthesis) during most of the day, while the regeneration of ribulose-1,5-bisphosphate (RUBP; light-limited photosynthesis) constrains carbon assimilation mainly early and late in the day, when the incident quantum flux densities are below the saturation point of photosynthesis. This is different in the lower

canopy where photosynthesis is limited by low light during almost the entire day. Thus, any decrease in the rate of photosynthetic electron transport of lower canopy leaves leads to concomitant changes in daily photosynthesis integral, while for upper canopy leaves, photoinhibition may constrain carbon gain mainly in the afternoon. Simulation analyses have suggested that photoinhibition still has the largest effect, in the order of 8 – 10% of potential carbon gain, on upper canopy carbon gain and a marginal effect, in the order of 3%, for lower canopy leaves (Werner et al., 2001 a). However, these simulations did not account for the interactions among environmental factors and for the larger degree of water stress in the upper canopy. More severe water stress likely results in a lower internal CO_2 concentration of upper canopy leaves, thereby effectively shifting the transition point of Rubisco to RUBP-limited assimilation to lower irradiances. Although counterintuitive, in conditions of severe soil drought, photoinhibition constrains photosynthetic carbon gain more severely in low light environments (Valladares and Pearcy, 2002).

Water stress, wind speed, and rearrangements in leaf structure

To maintain the water flow from drying soil, water potential must be lower at any point downstream. As the measurements demonstrate, minimum leaf water potentials are lower in higher irradiance (Niinemets et al., 1999 c). This is in part achieved by lower leaf osmotic potentials in higher light (Fig. 9; Myers et al., 1987; Niinemets et al., 1999 c). However, low leaf osmotic potentials may significantly curb leaf photosynthesis rates due to direct effects on Calvin cycle enzyme activity, especially if the decrease in leaf osmotic potential results from accumulation of salt ions within the leaves (Kaiser et al., 1981). Thus, osmotic adjustment of leaf water potentials clearly has a physiological limit.

An alternative way to enhance the water potential gradient between the soil and the leaves is to increase the rigidity of cell walls, which can be measured as an increase in the bulk leaf elastic modulus (change in leaf pressure potential per unit change of symplasmic leaf water, ε). Increases in ε allow the leaf to achieve a larger drop in leaf water potential for a given change in leaf water content. Thus, this kind of elastic adjustment contributes towards maintenance of water flow through the leaves without augmenting leaf osmotic stress. There are several lines of evidence demonstrating more rigid cell walls in leaves growing at higher irradiance. First, leaf density (mass per unit volume, Fig. 11) and leaf dry to fresh mass ratio, that characterizes the fraction of structural tissues within the leaves, increase with increasing integrated irradiance (Niinemets and Kull, 1998). An increase in both of these leaf variables leads to a larger ε (Fig. 11; Niinemets, 2001), hinting at a positive correlation between ε and integrated light. Second, leaf lignin concentrations increase with increasing growth irradiance (Niinemets and Kull, 1998), again supporting the suggestion that cell wall characteristics change within the light gradients. Finally, direct measurements do demonstrate that ε increases with increasing light availability in the canopy (Oberbauer et al., 1987).

Because wind speeds are also larger in the upper canopy, structural changes in leaves at higher growth irradiance may partly reflect leaf acclimation to cope with enhanced mechanical stresses (Niklas, 1996; Niinemets and Fleck, 2002). In small-
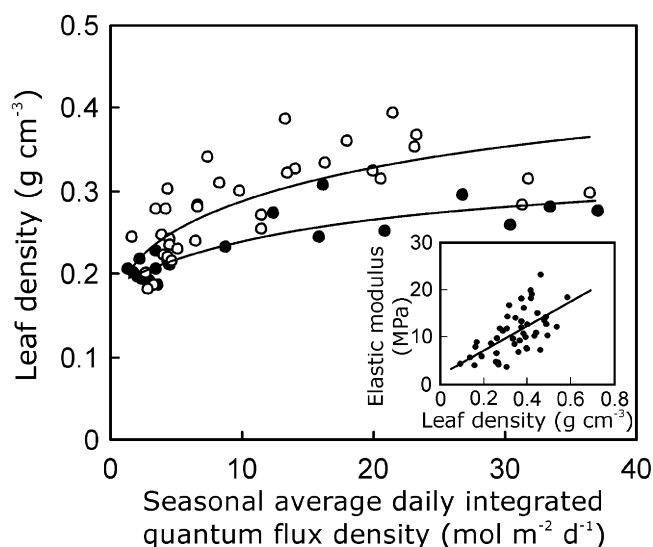
Fig. 11 Relationships between leaf density and Q_{int} in *Rhododendron ponticum* (open symbols) and *Ilex aquifolium* (filled symbols) sampled in the Alcornocales Natural Park, Sierra del Aljibe, South Spain (modified from Niinemets et al., 2003 b). Inset demonstrates the correlation between leaf density and bulk leaf elastic modulus (ε) determined for a series of species with differing leaf structure (modified from Niinemets, 2001). Bulk leaf elastic modulus is the change in leaf turgor pressure per unit change of symplasmic leaf water. For a common water loss, increases in ε result in a larger change in leaf water potential, and accordingly, in a greater water potential gradient between the soil and the leaves. Data are fitted by non-linear or linear (inset) regressions and are all statistically significant at $p < 0.001$.

leaved herb species, increases in wind speed may bring about enhanced biomass investment in support (Retuerto and Woodward, 1992). However, in trees with large leaves on long petioles, a lower value of ε (larger elasticity) may be more advantageous as it reduces leaf drag coefficient and leaf sensitivity to high wind. In particular, larger leaf elasticity would allow the leaf to bend away from the strong wind or achieve a rolled conformation with lower effective surface (Vogel, 1989).

Trade-off between leaf carbon gain capacity and acclimation to water stress

An increase in the content of non-assimilative tissues improves leaf water status and stiffness, but results in a lower fraction of photosynthesising tissues, and thus, has a cost in terms of leaf photosynthetic capacity. Especially, in water stress-sensitive species, leaf photosynthetic capacity per unit dry mass may significantly decrease at high growth irradiance relative to low light (Niinemets and Kull, 1998; Niinemets et al., 1998 b; Turnbull et al., 2002). Given that acclimation to high growth irradiance increases the fractional distribution of leaf nitrogen in proteins limiting the light-saturated net assimilation rate, while acclimation to low growth irradiance increases the fraction of leaf nitrogen in light harvesting (Niinemets and Tenhunen, 1997), a decrease instead of the expected increase in mass-based photosynthetic potentials in leaves acclimated to high light provides indirect evidence of the trade-off between acclimation to irradiance and water stress.

Apart from modifications in the distribution of leaf biomass between assimilative and support tissues, thicker cell walls and enhanced cell wall lignification may bring about a larger internal diffusion resistance to CO_2 in leaves acclimated to higher light. Although the internal diffusion conductance per unit leaf area (g_i) appears to increase with increasing leaf growth irradiance (Hanba et al., 2002; Piel et al., 2002), this increase is curvilinear and levels off at higher growth irradiances (Hanba et al., 2002). Moreover, it is the conductance per unit mass rather than per unit area that scales with the average CO_2 supply of leaf cells. In fact, the internal conductance per unit dry mass (g_i/M_A) was significantly lower in full light-grown leaves in two out of three *Acer* species (Hanba et al., 2002). Such scaling of diffusion resistance with growth irradiance implies a lower efficiency of leaf photosynthetic apparatus at a common investment of leaf resources in photosynthetic proteins. This suggestion is supported by lower values of chloroplastic CO_2 concentrations in full light-grown leaves relative to shaded leaves (Hanba et al., 2002).

"Optimal" Canopy Carbon Gain and the Interacting Environmental Factors

Optimality hypothesis of leaf photosynthetic adjustment to growth irradiance predicts that leaf photosynthetic capacities are directly proportional to average irradiance (Farquhar, 1989; Friend, 2001). However, such proportionality is not supported by field data (Fig. **12**; Meir et al., 2002) that exhibit a significant intercept of leaf photosynthetic capacity versus light relations. Such intercepts indicate that either the leaf photosynthetic capacity of lower canopy leaves is too high (Meir et al., 2002) or that the photosynthetic capacity of the upper canopy leaves is too low (Fig. **12**; Friend, 2001; Turnbull et al., 2002) compared with an "optimal" distribution of photosynthetic capacity. Because changes in leaf structure and physiological capacities due to interacting stress factors appear to limit leaf photosynthetic adjustment to high growth irradiances, our analysis suggests that deviation of the within-canopy variation of leaf photosynthetic capacity from an "optimal" pattern may at least partly result from interacting environmental constraints.

The residuals between the observed light-dependent changes in foliage photosynthetic potentials and the "optimal" pattern increase with increasing growth irradiance (Fig. **12**). This is fully consistent with the assumption that the deviations from "optimal" distribution are caused by interactions among environmental drivers, because the magnitude of interacting stresses gradually increases with growth irradiance in the canopy (Fig. **1 B**). Furthermore, departure from the "optimal" distribution becomes larger with developing soil water stress (Turnbull et al., 2002), supporting the argument that "non-optimal" plant performance may result from other constraints.

So far, we were primarily focused on plants that form a single leaf flush at the beginning of the growing season, and maintain the foliage during the rest of the season. However, acclimation of leaf photosynthetic capacities may be further complicated by confounding canopy gradients of leaf age, which are common in temperate herb (Anten et al., 1998) or conifer (Brooks et al., 1996) species or in tropical rain forest species (Ishida et al., 1999). The age gradients in the canopy occur as older leaves become gradually overtopped and shaded by the development of new leaves. Such age gradients may further modify leaf ac-
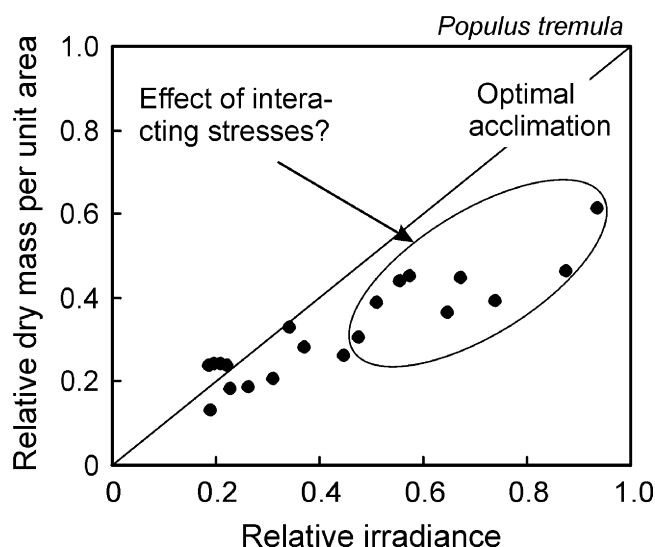
Fig. 12 Correlation between the relative irradiance (Q_R) and leaf dry mass per unit area (M_A) standardized with respect to the maximum M_A (R_{MA}) in *Populus tremula* (the same data as in Fig. **2**). Relative M_A values were adjusted such that the intercept of R_{MA} versus Q_R was zero. For an optimal variation in leaf photosynthetic potentials, R_{MA} should be directly proportional to Q_R (Sands, 1995; Friend, 2001).

climation to light and interacting environmental factors, because leaf capacity for physiological changes and anatomical and morphological modifications decreases with increasing leaf age (Valladares and Pearcy, 1999; Yamashita et al., 2002). Experimental manipulations of the light environment of young and old leaves indicate that the plant realized photosynthesis is dominated by photosynthetic acclimation to light, but also that leaf ageing plays an important role in canopy photosynthetic performance (Hikosaka et al., 1993). In certain evergreen, open canopies with low total N and photosynthetic capacities, photosynthetic capacity gradients are even more distant from an "optimal" distribution than these gradients are in even-aged canopies (Valladares and Pearcy, 1999).

Plants Altering their Light Environment: Evolutionary Limits to "Optimal" Carbon Gain

In addition to interactions with other environmental drivers and age gradients, plants may not track the theoretical optima, because the time for full acclimation is limited during a single individual lifetime or because highly fluctuating environments select for phenotypic stability. Advantages of phenotypic stability in heterogeneous light environments are currently far from being fully understood, but experimental data do demonstrate that not all components of diurnal, day-to-day and seasonal variability in quantum flux densities induce acclimation responses. For instance, differences in duration and intensity of sunflecks significantly modify plant carbon gain, but plants do not possess specific acclimation responses to light regimes with a high degree of unpredictability (Sims and Pearcy, 1993; Leakey et al., 2002). In a like manner, values of leaf dry mass per unit area do not track short-term fluctuations in light climate (Ackerly, 1997; Niinemets et al., 2004 a).

By responding to environment, plants can modify and control, to some extent, the environment they experience. Optical properties of leaves, meristem growth, and branching patterns are affected by light, but these characteristics also influence light harvesting and the within-canopy light environment. The half-times of canopy level adjustments after changes in incident irradiance vary between 3 – 10 days in seedlings of tropical tree species that continuously form new leaves (Ackerly, 1997), highlighting a large potential for adjustments of leaf light environment by plastic canopy level modifications.

In this way, plant phenotypic plasticity in response to light can be considered a form of niche construction or habitat selection (Donohue, 2003). The evolution of niche construction traits may result in a correlated selection for other traits. The trade-off between the ability to be plastic and the ability to perform optimally in a given environment is a universal limitation to the evolution of plasticity (Sultan, 1992). However, plasticity in niche construction characteristics smoothes the environmental variation experienced within the canopy, suggesting that plasticity at a canopy scale can lead to specialisation at smaller scales (leaves or tissues within a leaf). As an example, shade-tolerant plants have greater morphological plasticity (Fig. **3**) that decreases the environmental variation experienced by individual leaves within the crown or tissues within the leaves, but enhanced morphological plasticity is associated with a specialised leaf physiology (Fig. **3**). Such trade-offs between the suites of traits may significantly alter species dispersal patterns in the canopy and along gap–understorey gradients. For instance, the invasive nature of certain plant populations or species is linked to an enhanced plastic response to light (Niinemets et al., 2003 b), while phenotypic stability under varying light conditions seems to mirror adaptations to unpredictable and adverse habitats (Valladares et al., 2002 a). These considerations and experimental data outlined suggest that there is a significant trade-off between enhanced plasticity in foliage production that results in different light micro-environments within the plant crown, and plasticity of single leaves that alters the photosynthetic capacity of leaves.

Conclusions

Although variation in light within plant canopies constitutes the most dramatic environmental gradient which plants commonly experience, wind speeds, temperature and water availability co-vary with light. These interactions become especially amplified during soil water stress, which leads to limited transpiratory foliar cooling and extreme leaf temperatures. Our review highlights that the interactions among environmental variables result in large within and among canopy differences in excess energy quenching capacity, and modified temperature responses of photosynthesis and leaf water stress sensitivity. Interactions between light and other environmental factors, and trade-offs between the suites of traits, greatly complicate our capacity to interpret plant adaptations to optimize photosynthesis in heterogeneous and changing environments. Modelling canopy performance and predicting its potential evolution under different global change scenarios requires both theoretical and empirical work, addressing not only the acclimation to interacting environmental factors but also the evolution of plasticity for correlated characters.

Acknowledgements

References

Abrams, M. D. (1990) Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology 7, 227 – 238.

Ackerly, D. (1997) Allocation, leaf display, and growth in fluctuating light environments. In Plant resource allocation (Bazzaz, F. A. and Grace, J., eds.), San Diego: Academic Press, Inc., pp. 231 – 264.

Amthor, J. S. (1994) Scaling CO_2-photosynthesis relationships from the leaf to the canopy. Photosynthesis Research 39, 321 – 350.

Amthor, J. S., Goulden, M. L., Munger, J. W., and Wofsy, S. C. (1994) Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. Australian Journal of Plant Physiology 21, 623 – 651.

Anderson, J. M., Chow, W. S., Park, Y.-I., Franklin, L. A., Robinson, S. P.-A., and van Hasselt, P. R. (2001) Response of *Tradescantia albiflora* to growth irradiance: change versus changeability. Photosynthesis Research 67, 103 – 112.

Anten, N. P. R., Miyazawa, K., Hikosaka, K., Nagashima, H., and Hirose, T. (1998) Leaf nitrogen distribution in relation to leaf age and photon flux density in dominant and subordinate plants in dense stands of a dicotyledonous herb. Oecologia 113, 314 – 324.

Asner, G. P. and Wessman, C. A. (1997) Scaling PAR absorption from the leaf to landscape level in spatially heterogeneous ecosystems. Ecological Modelling 103, 81 – 97.

Asner, G. P., Wessman, C. A., and Archer, S. (1998) Scale dependence of absorption of photosynthetically active radiation in terrestrial ecosystems. Ecological Applications 8, 1003 – 1021.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P. H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grunwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T. (2000) Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. Advances in Ecological Research 30, 113 – 175.

Baldocchi, D. D. and Bowling, D. R. (2003) Modelling the discrimination of CO_2 above and within a temperate broad-leaved forest canopy on hourly to seasonal time scales. Plant, Cell and Environment 26, 231 – 244.

Baldocchi, D. and Collineau, S. (1994) The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. In Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground (Caldwell, M. M. and Pearcy, R. W., eds.), San Diego: Academic Press, pp. 21 – 71.

Baldocchi, D. D., Wilson, K. B., and Gu, L. (2002) How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broad-leaved deciduous forest – an assessment with the biophysical model CANOAK. Tree Physiology 22, 1065 – 1077.

Barker, M. G. (1996) Vertical profiles in a Brunei rain forest. I. Microclimate associated with a canopy tree. Journal of Tropical Forest Science 8, 505 – 519.

Bazzaz, F. A. and Wayne, P. M. (1994) Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap – understory continuum. In Exploitation of Environmental Heterogeneity by Plants. Ecophysiological Processes Above- and Belowground (Caldwell, M. M. and Pearcy, R. W., eds.), San Diego: Academic Press, pp. 349 – 390.

Bilger, W., Fisahn, J., Brummet, W., Kossmann, J., and Willmitzer, L. (1995) Violaxanthin cycle pigment contents in potato and tobacco plants with genetically reduced photosynthetic capacity. Plant Physiology 108, 1479 – 1486.

Box, E. O. (1996) Plant functional types and climate at the global scale. Journal of Vegetation Science 7, 309 – 320.

Breshears, D. D., Rich, P. M., Barnes, F. J., and Campbell, K. (1997) Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications 7, 1201 – 1215.

Brooks, J. R., Sprugel, D. G., and Hinckley, T. M. (1996) The effects of light acclimation during and after foliage expansion on photosynthesis of *Abies amabilis* foliage within the canopy. Oecologia 107, 21 – 32.

Brown, N. (1993) The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. Journal of Tropical Ecology 9, 153 – 168.

Buchmann, N., Kao, W.-Y., and Ehleringer, J. R. (1996) Carbon dioxide concentrations within forest canopies – variation with time, stand structure, and vegetation type. Global Change Biology 2, 421 – 432.

Bungard, R. A., Press, M. C., and Scholes, J. D. (2000) The influence of nitrogen on rain forest dipterocarp seedlings exposed to a large increase in irradiance. Plant, Cell and Environment 23, 1183 – 1194.

Cain, M. L., Subler, S., Evans, J. P., and Fortin, M.-J. (1999) Sampling spatial and temporal variation in soil nitrogen availability. Oecologia 118, 397 – 404.

Caldwell, M. M., Meister, H.-P., Tenhunen, J. D., and Lange, O. L. (1986) Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portugese macchia: measurements in different canopy layers and simulations with a canopy model. Trees: Structure and Function 1, 25 – 41.

Cescatti, A. and Zorer, R. (2003) Structural acclimation and radiation regime of silver fir (*Abies alba* Mill.) shoots along a light gradient. Plant, Cell and Environment 26, 429 – 442.

Chazdon, R. L. and Fetcher, N. (1984) Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. Journal of Ecology 72, 553 – 564.

Chiariello, N. (1984) Leaf energy balance in the wet lowland tropics. In Physiological Ecology of Plants of the Wet Tropics (Medina, E., Mooney, H. A., and Vásquez-Yánes, C., eds.), Tasks for Vegetation Science, 12. The Hague: Dr. W. Junk Publishers, pp. 85 – 98.

Cochard, H., Lemoine, D., and Dreyer, E. (1999) The effects of acclimation to sunlight on the xylem vulnerability to embolism in *Fagus sylvatica* L. Plant, Cell and Environment 22, 101 – 108.

Demmig-Adams, B. and Adams, W. W., III. (1996) Xanthophyll cycle and light stress in nature: uniform response to excess direct sunlight among higher plant species. Planta 198, 460 – 470.

Demmig-Adams, B. and Adams, W. W., III. (2000) Photosynthesis – harvesting sunlight safely. Nature 403, 371 – 374.

Demmig-Adams, B., Winter, K., Winkelmann, E., Krüger, A., and Czygan, F.-C. (1989) Photosynthetic characteristics and the ratios of chlorophyll, β-carotene, and the components of the xanthophyll cycle upon a sudden increase in growth light regime in several plant species. Botanica Acta 102, 319 – 325.

Domingo, F., Villagarcía, L., Brenner, A. J., and Puigdefábregas, J. (2000) Measuring and modelling the radiation balance of a heterogeneous shrubland. Plant, Cell and Environment 23, 27 – 38.

Donohue, K. (2003) Setting the stage: phenotypic plasticity as habitat selection. International Journal of Plant Sciences 164, S79 – S92.

Eliáš, P., Kratochvílová, I., Janouš, D., Marek, M., and Masarovichová, E. (1989) Stand microclimate and physiological activity of tree leaves in an oak-hornbeam forest. I. Stand microclimate. Trees: Structure and Function 4, 227–233.

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., and Pauliβen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa, Scripta Geobotanica, Vol. 18. Göttingen: Verlag Erich Goltze KG.

Ellsworth, D. S. and Reich, P. B. (1992) Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. Functional Ecology 6, 423–435.

Ellsworth, D. S. and Reich, P. B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. Oecologia 96, 169–178.

Epron, D. (1997) Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*). Journal of Experimental Botany 48, 1835–1841.

Epron, D. and Dreyer, E. (1996) Starch and soluble carbohydrates in leaves of water-stressed oak saplings. Annales des Sciences Forestières 53, 263–268.

Evans, J. R. (1989) Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9–19.

Evans, J. R. and Poorter, H. (2001) Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell and Environment 24, 755–767.

Farquhar, G. D. (1989) Models of integrated photosynthesis of cells and leaves. Philosophical Transactions of the Royal Society of London, Series B. Biological Sciences 323, 357–367.

Farquhar, G. D. and Roderick, M. L. (2003) Pinatubo, diffuse light, and the carbon cycle. Science 299, 1997–1998.

Faurie, O., Soussana, J. F., and Sinoquet, H. (1996) Radiation interception, partitioning and use in grass-clover mixtures. Annals of Botany 77, 35–45.

Fleck, S., Niinemets, Ü., Cescatti, A., and Tenhunen, J. D. (2003) Three-dimensional lamina architecture alters light harvesting efficiency in *Fagus*: a leaf-scale analysis. Tree Physiology 23, 577–589.

Friend, A. D. (2001) Modelling canopy CO_2 fluxes: are "big-leaf" simplifications justified? Global Ecology and Biogeography 10, 603–619.

Gates, D. M. (1980) Biophysical ecology. New York: Springer-Verlag.

Grassi, G. and Bagnaresi, U. (2001) Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. Tree Physiology 21, 959–967.

Groom, P. K., Lamont, B. B., Leighton, S., Leighton, P., and Burrows, C. (2004) Heat damage in sclerophylls is influenced by their leaf properties and plant environment. Écoscience 11, in press.

Gruszecki, W. I. and Strzalka, K. (1991) Does the xanthophyll cycle take part in the regulation of fluidity of the thylakoid membrane? Biochimica et Biophysica Acta 1060, 310–314.

Gu, L., Baldocchi, D. D., Wofsy, S. C., Munger, J. W., Michalsky, J. J., Urbanski, S. P., and Boden, T. A. (2003) Response of a deciduous forest to the Mount Pinatubo eruption: enhanced photosynthesis. Science 299, 2035–2038.

Gutschick, V. P. and Wiegel, F. W. (1988) Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. The American Naturalist 132, 67–86.

Hamerlynck, E. P. and Knapp, A. K. (1994) Leaf-level responses to light and temperature in two co-occurring *Quercus (Fagaceae)* species: implications for tree distribution patterns. Forest Ecology and Management 68, 149–159.

Hanba, Y. T., Kogami, H., and Terashima, I. (2002) The effect of growth irradiance on leaf anatomy and photosynthesis in *Acer* species differing in light demand. Plant, Cell and Environment 25, 1021–1030.

Harley, P. C. and Baldocchi, D. D. (1995) Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parametrization. Plant, Cell and Environment 18, 1146–1156.

Harley, P., Guenther, A., and Zimmerman, P. (1997) Environmental controls over isoprene emission in deciduous oak canopies. Tree Physiology 17, 705–714.

Havaux, M. (1992) Stress tolerance of photosystem II *in vivo*. Antagonistic effects of water, heat and photoinhibition stress. Plant Physiology 100, 424–432.

Havaux, M. (1998) Carotenoids as membrane stabilizers in chloroplasts. Trends in Plant Science 3, 147–151.

Havaux, M. and Tardy, F. (1996) Temperature-dependent adjustment of the thermal stability of photosystem II *in vivo*: possible involvement of xanthophyll-cycle pigments. Planta 198, 324–333.

Hikosaka, K., Okada, K., Terashima, I., and Katoh, S. (1993) Acclimation and senescence of leaves: their roles in canopy photosynthesis. In Photosynthetic Responses to the Environment (Yamamoto, H. Y. and Smith, C. M., eds.), Madison: American Society of Plant Physiologists, pp. 1–13.

Ishida, A., Toma, T., and Marjenah (1999) Leaf gas exchange and chlorophyll fluorescence in relation to leaf angle, azimuth, and canopy position in the tropical pioneer tree, *Macaranga conifera*. Tree Physiology 19, 117–124.

Jagtap, V., Bhargava, S., Streb, P., and Feierabend, J. (1998) Comparative effect of water, heat and light stresses on photosynthetic reactions in *Sorghum bicolor* (L.) Moench. Journal of Experimental Botany 49, 1715–1721.

Jifon, J. L. and Syvertsen, J. P. (2003) Moderate shade can increase net gas exchange and reduce photoinhibition in citrus leaves. Tree Physiology 23, 119–127.

Kaiser, W. M., Kaiser, G., Prachuab, P. K., Wildman, S. G., and Heber, U. (1981) Photosynthesis under osmotic stress. Inhibition of photosynthesis of intact chloroplasts, protoplasts, and leaf slices at high osmotic potentials. Planta 153, 416–422.

Kelly, J. M. and Mays, P. A. (1999) Nutrient supply changes within a growing season in two deciduous forest soils. Soil Science Society of America Journal 62, 226–232.

Koike, T., Kitao, M., Maruyama, Y., Mori, S., and Lei, T. T. (2001) Leaf morphology and photosynthetic adjustments among deciduous broad-leaved trees within the vertical canopy profile. Tree Physiology 21, 951–958.

Lamont, B. B., Groom, P. K., and Cowling, R. M. (2002) High leaf mass per area of related species assemblages may reflect low rainfall and carbon isotope discrimination rather than low phosphorus and nitrogen concentrations. Functional Ecology 16, 403–412.

Leakey, A. D. B., Press, M. C., Scholes, J. D., and Watling, J. R. (2002) Relative enhancement of photosynthesis and growth at elevated CO_2 is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. Plant, Cell and Environment 25, 1701–1714.

Lemoine, D., Cochard, H., and Granier, A. (2002) Within crown variation in hydraulic architecture in beech (*Fagus sylvatica* L.): evidence for a stomatal control of xylem embolism. Annals of Forest Science 59, 19–27.

Le Roux, X., Walcroft, A. S., Daudet, F. A., Sinoquet, H., Chaves, M. M., Rodrigues, A., and Osorio, L. (2001) Photosynthetic light acclimation in peach leaves: importance of changes in mass:area ratio, nitrogen concentration, and leaf nitrogen partitioning. Tree Physiology 21, 377–386.

Leuning, R., Dunin, F. X., and Wang, Y.-P. (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements. Agricultural and Forest Meteorology 91, 113–125.

Logan, B. A., Demmig-Adams, B., and Adams, W. W. III. (1998) Antioxidants and xanthophyll cycle-dependent energy dissipation in *Cucurbita pepo* L. and *Vinca major* L. upon a sudden increase in growth PPFD in the field. Journal of Experimental Botany 49, 1881 – 1888.

Loreto, F., Förster, A., Dürr, M., Csiky, O., and Seufert, G. (1998) On the monoterpene emission under heat stress and on the increased thermotolerance of leaves of *Quercus ilex* L. fumigated with selected monoterpenes. Plant, Cell and Environment 21, 101 – 107.

Lu, C. and Zhang, J. (1999) Effects of water stress on Photosystem II photochemistry and its thermostability in wheat plants. Journal of Experimental Botany 50, 1199 – 1206.

Marcolla, B., Pitacco, A., and Cescatti, A. (2003) Canopy architecture and turbulence structure in a coniferous forest. Boundary-Layer Meteorology 108, 39 – 59.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A., and Jarvis, P. G. (2002) Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. Plant, Cell and Environment 25, 343 – 357.

Mishra, R. K. and Singhal, G. S. (1992) Function of photosynthetic apparatus of intact wheat leaves under high light and heat stress and its relationship with peroxidation of thylakoid lipids. Plant Physiology 98, 1 – 6.

Murata, N. and Nishiyama, Y. (1998) Molecular mechanisms of the low-temperature tolerance of the photosynthetic machinery. In Stress Responses of Photosynthetic Organisms (Satoh, K. and Murata, N., eds.), Amsterdam: Elsevier Science Publishers B. V., pp. 93 – 112.

Myers, B. J., Robichaux, R. H., Unwin, G. L., and Craig, I. E. (1987) Leaf water relations and anatomy of a tropical rainforest tree species vary with crown position. Oecologia 74, 81 – 85.

Niinemets, Ü. (2001) Climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs at the global scale. Ecology 82, 453 – 469.

Niinemets, Ü., Bilger, W., Kull, O., and Tenhunen, J. D. (1998 a) Acclimation to high irradiance in temperate deciduous trees in the field: changes in xanthophyll cycle pool size and in photosynthetic capacity along a canopy light gradient. Plant, Cell and Environment 21, 1205 – 1218.

Niinemets, Ü. and Fleck, S. (2002) Leaf biomechanics and biomass investment in support in relation to long-term irradiance in *Fagus*. Plant Biology 4, 523 – 534.

Niinemets, Ü., Kollist, H., García-Plazaola, J. I., and Becerril, J. M. (2003 a) Do the capacity and kinetics for modification of xanthophyll cycle pool size depend on growth irradiance in temperate trees? Plant, Cell and Environment 26, 1787 – 1801.

Niinemets, Ü. and Kull, O. (1998) Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiology 18, 467 – 479.

Niinemets, Ü. and Kull, O. (2001) Sensitivity to photoinhibition of photosynthetic electron transport in a temperate deciduous forest canopy: Photosystem II centre openness, non-radiative energy dissipation and excess irradiance under field conditions. Tree Physiology 21, 899 – 914.

Niinemets, Ü., Kull, O., and Tenhunen, J. D. (1998 b) An analysis of light effects on foliar morphology, physiology, and light interception in temperate deciduous woody species of contrasting shade tolerance. Tree Physiology 18, 681 – 696.

Niinemets, Ü., Kull, O., and Tenhunen, J. D. (1999 a) Variability in leaf morphology and chemical composition as a function of canopy light environment in co-existing trees. International Journal of Plant Sciences 160, 837 – 848.

Niinemets, Ü., Kull, O., and Tenhunen, J. D. (2004 a) Within canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. Plant, Cell and Environment 27, 293 – 313.

Niinemets, Ü., Oja, V., and Kull, O. (1999 b) Shape of leaf photosynthetic electron transport versus temperature response curve is not constant along canopy light gradients in temperate deciduous trees. Plant, Cell and Environment 22, 1497 – 1514.

Niinemets, Ü., Sõber, A., Kull, O., Hartung, W., and Tenhunen, J. D. (1999 c) Apparent controls on leaf conductance by soil water availability and via light-acclimation of foliage structural and physiological properties in a mixed deciduous, temperate forest. International Journal of Plant Sciences 160, 707 – 721.

Niinemets, Ü., Sonninen, E., and Tobias, M. (2004 b) Canopy gradients in leaf intercellular CO_2 mole fractions revisited: interactions between leaf irradiance and water stress need consideration. Plant, Cell and Environment, in press.

Niinemets, Ü. and Tenhunen, J. D. (1997) A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. Plant, Cell and Environment 20, 845 – 866.

Niinemets, Ü., Valladares, F., and Ceulemans, R. (2003 b) Leaf-level phenotypic variability and plasticity of invasive *Rhododendron ponticum* and non-invasive *Ilex aquifolium* co-occurring at two contrasting European sites. Plant, Cell and Environment 26, 941 – 956.

Niklas, K. J. (1996) Differences between *Acer saccharum* leaves from open and wind-protected sites. Annals of Botany 78, 61 – 66.

Oberbauer, S. F., Strain, B. R., and Riechers, G. H. (1987) Field water relations of a wet-tropical forest tree species, *Pentaclethra macroloba (Mimosaceae)*. Oecologia 71, 369 – 374.

Oren, R., Sperry, J. S., Katul, G. G., Pataki, D. E., Ewers, B. E., Phillips, N., and Schafer, K. V. R. (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant, Cell and Environment 22, 1515 – 1526.

Osmond, C. B., Anderson, J. M., Ball, M. C., and Egerton, J. G. (1999) Compromising efficiency: the molecular ecology of light-resource utilization in plants. In Physiological Plant Ecology. The 39th Symposium of the British Ecological Society held at the University of York, 7 – 9 September 1998 (Press, M. C., Scholes, J. D., and Barker, M. G., eds.), Oxford: Blackwell Science, pp. 1 – 24.

Pearcy, R. W. (1999) Responses of plants to heterogeneous light environments. In Handbook of Functional Plant Ecology (Pugnaire, F. I. and Valladares, F., eds.), New York: Marcel Dekker, pp. 269 – 314.

Piel, C., Frak, E., Le Roux, X., and Genty, B. (2002) Effect of local irradiance on CO_2 transfer conductance of mesophyll in walnut. Journal of Experimental Botany 53, 2423 – 2430.

Poorter, H. and Nagel, O. (2000) The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology 27, 595 – 607.

Raulier, F., Bernier, P. Y., and Ung, C.-H. (1999) Canopy photosynthesis of sugar maple *(Acer saccharum):* comparing big-leaf and multilayer extrapolations of leaf-level measurements. Tree Physiology 19, 407 – 420.

Retuerto, R. and Woodward, F. I. (1992) Effects of windspeed on the growth and biomass allocation of white mustard *Sinapis alba* L. Oecologia 92, 113 – 123.

Routaboul, J.-M., Vijayan, P., and Browse, J. (1997) Lack of trienoic fatty acids in an *Arabidopsis* mutant increases tolerance of photosynthesis to high temperature. In Physiology, Biochemistry and Molecular Biology of Plant Lipids (Williams, J. P., Khan, M. U., and Lem, N. W., eds.), Dordrecht: Kluwer Academic Publishers, pp. 200 – 202.

Sands, P. J. (1995) Modelling canopy production. I. Optimal distribution of photosynthetic resources. Australian Journal of Plant Physiology 22, 593 – 601.

Santarius, K. A. and Weis, E. (1988) Heat stress and membranes. In Plant Membranes – Structure, Assembly and Function (Harwood, J. L. and Walton, T. J., eds.), London: The Biochemical Society, pp. 97 – 112.

Seemann, J. R., Berry, J. A., and Downton, W. J. S. (1984) Photosynthetic response and adaptation to high temperature in desert plants. A comparison of gas exchange and fluorescence methods for studies of thermal tolerance. Plant Physiology 75, 364 – 368.

Seemann, J. R., Downton, W. J. S., and Berry, J. A. (1986) Temperature and leaf osmotic potential as factors in the acclimation of photosynthesis to high temperature in desert plants. Plant Physiology 80, 926 – 930.

Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., and Hall, F. G. (1992) Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. Remote Sensing of Environment 42, 187 – 216.

Sharkey, T. D. and Singsaas, E. L. (1995) Why plants emit isoprene. Nature 374, 769.

Sims, D. A. and Pearcy, R. W. (1993) Sunfleck frequency and duration affects growth rate of the understorey plant, *Alocasia macrorrhiza.* Functional Ecology 7, 683 – 689.

Singsaas, E. L., Laporte, M. M., Shi, J.-Z., Monson, R. K., Bowling, D. R., Johnson, K., Lerdau, M., Jasentuliytana, A., and Sharkey, T. D. (1999) Kinetics of leaf temperature fluctuation affect isoprene emission from red oak *(Quercus rubra)* leaves. Tree Physiology 19, 917 – 924.

Staudt, M., Joffre, R., and Rambal, S. (2003) How growth conditions affect the capacity of *Quercus ilex* leaves to emit monoterpenes. The New Phytologist 158, 61 – 73.

Stenberg, P., Smolander, H., Sprugel, D. G., and Smolander, S. (1998) Shoot structure, light interception, and distribution of nitrogen in an *Abies amabilis* canopy. Tree Physiology 18, 759 – 767.

Sultan, S. E. (1992) What has survived of Darwin's theory? Phenotypic plasticity and the Neo-Darwinian legacy. Evolutionary Trends in Plants 6, 61 – 71.

Tang, Y. and Washitani, I. (1995) Characteristics of small-scale heterogeneity in light availability within a *Miscanthus sinensis* canopy. Ecological Research 2, 189 – 197.

Tappeiner, U. and Cernusca, A. (1996) Microclimate and fluxes of water vapour, sensible heat and carbon dioxide in structurally differing subalpine plant communities in the Central Caucasus. Plant, Cell and Environment 19, 403 – 417.

Terashima, I. and Hikosaka, K. (1995) Comparative ecophysiology of leaf and canopy photosynthesis. Plant, Cell and Environment 18, 1111 – 1128.

Tilman, D. (1993) Community diversity and succession: the roles of competition, dispersal, and habitat modification. In Biodiversity and Ecosystem Function (Schulze, E.-D. and Mooney, H. A., eds.), Ecological Studies, 99. Berlin: Springer Verlag, pp. 327 – 344.

Turnbull, M. H., Whitehead, D., Tissue, D. T., Schuster, W. S., Brown, K. J., Engel, V. C., and Griffin, K. L. (2002) Photosynthetic characteristics in canopies of *Quercus rubra, Quercus prinus* and *Acer rubrum* differ in response to soil water availability. Oecologia 130, 515 – 524.

Valladares, F. (1999) Architecture, ecology, and evolution of plant crowns. In Handbook of Functional Plant Ecology (Pugnaire, F. I. and Valladares, F., eds.), New York: Marcel Dekker, Inc., pp. 121 – 194.

Valladares, F. (2003) Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. In Progress in Botany, Vol. 64 (Esser, K., Lüttge, U., Beyschlag, W., and Hellwig, F., eds.), Berlin: Springer Verlag, pp. 439 – 471.

Valladares, F., Allen, M. T., and Pearcy, R. W. (1997) Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occurring along a light gradient. Oecologia 111, 505 – 514.

Valladares, F., Balaguer, L., Martínez-Ferri, E., Perez-Corona, E., and Manrique, E. (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? The New Phytologist 156, 457 – 467.

Valladares, F., Chico, J. M., Aranda, I., Balaguer, L., Dizengremel, P., Manrique, E., and Dreyer, E. (2002 a) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. Trees: Structure and Function 16, 395 – 403.

Valladares, F. and Pearcy, R. W. (1997) Interactions between water stress, sun-shade acclimation, heat tolerance and photoinhibition in the sclerophyll *Heteromeles arbutifolia.* Plant, Cell and Environment 20, 25 – 36.

Valladares, F. and Pearcy, R. W. (1998) The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub. Oecologia 114, 1 – 10.

Valladares, F. and Pearcy, R. W. (1999) The geometry of light interception by shoots of *Heteromeles arbutifolia:* morphological and physiological consequences for individual leaves. Oecologia 121, 171 – 182.

Valladares, F. and Pearcy, R. W. (2002 b) Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. Plant, Cell and Environment 25, 749 – 759.

Valladares, F., Skillman, J. B., and Pearcy, R. W. (2002 c) Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. American Journal of Botany 89, 1275 – 1284.

Valladares, F., Wright, S. J., Lasso, E., Kitajima, K., and Pearcy, R. W. (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81, 1925 – 1936.

Vogel, S. (1989) Drag and reconfiguration of broad leaves in high winds. Journal of Experimental Botany 40, 941 – 948.

Vogelmann, T. C., Nishio, J. N., and Smith, W. K. (1996) Leaves and light capture: light propagation and gradients of carbon fixation within leaves. Trends in Plant Science 1, 65 – 70.

Wayne, P. M. and Bazzaz, F. A. (1993 a) Birch seedling responses to daily time courses of light in experimental forest gaps and shade-houses. Ecology 74, 1500 – 1515.

Wayne, P. M. and Bazzaz, F. A. (1993 b) Morning vs afternoon sun patches in experimental forest gaps: consequences of temporal incongruency of resources to birch regeneration. Oecologia 94, 235 – 243.

Werner, C., Ryel, R. J., Correia, O., and Beyschlag, W. (2001 a) Effects of photoinhibition on whole-plant carbon gain assessed with a photosynthesis model. Plant, Cell and Environment 24, 27 – 40.

Werner, C., Ryel, R. J., Correia, O., and Beyschlag, W. (2001 b) Structural and functional variability within the canopy and its relevance for carbon gain and stress avoidance. Acta Oecologica 22, 129 – 138.

Yamashita, N., Koike, N., and Ishida, A. (2002) Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. Plant, Cell and Environment 25, 1341 – 1356.

Ü. Niinemets

Department of Plant Physiology
University of Tartu
Riia 23
51011 Tartu
Estonia
E-mail: ylo@zbi.ee