

Chapter 4

Within-Canopy Variations in Functional Leaf Traits: Structural, Chemical and Ecological Controls and Diversity of Responses

Ülo Niinemets*

*Environmental Sciences, Estonian University of Life Sciences,
Tartu, Estonia*

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*Author for correspondence, e-mail: ylo.niinemets@emu.ee

Summary

Plant canopies are characterized by extensive gradients in light availability that importantly alter the photosynthetic productivity of leaves in different canopy layers and result in acclimatory changes in leaf structural, chemical and physiological traits. These within-canopy variations are further importantly driven by species functional type and ecological characteristics such as shade tolerance (ecological controls). This chapter explores the within-canopy variations in key functional traits among different plant functional types and in species with different ecological potentials using a simple methodology to separate the importance of different leaf-level traits in foliage photosynthetic acclimation. As a major acclimatory change, foliage photosynthetic capacity per leaf area (A_{\max}^A) increases with increasing long-term average integrated quantum flux density (Q_{int}) in the canopy. Within-canopy variation in A_{\max}^A results in a greater whole canopy carbon gain than having A_{\max}^A constant through the canopy. The increase in A_{\max}^A with Q_{int} can potentially result from increases in leaf dry mass per unit area (M_A), nitrogen content per unit dry mass (N_M) and nitrogen allocation to rate-limiting photosynthetic proteins. This analysis indicates that the importance of these three key factors varies among plant functional types. In species with relatively low rates of canopy expansion and leaf turnover such as woody evergreens and woody deciduous species, within-canopy variation in A_{\max}^A is primarily determined by M_A , while in herbaceous species with high rates of canopy growth and leaf turnover, the variation is mainly driven by changes in N_M and nitrogen allocation to rate-limiting proteins of photosynthetic machinery. Furthermore, there are large within-canopy modifications in structural traits such as leaf angles and spatial aggregation modulating light harvesting and light avoidance, and in chemical traits such as xanthophyll cycle carotenoid content and isoprene emission contributing to abiotic stress resistance. As the result of light-dependent alterations in these

Abbreviations: A – Net assimilation rate; $A_{c,\text{con}}$ – Canopy photosynthesis for constant leaf biochemical potentials; $A_{c,\text{var}}$ – Canopy photosynthesis for variable leaf biochemical potentials; A_{\max} – Photosynthetic capacity; A_{\max}^A – Photosynthetic capacity per unit area; A_{\max}^M – Photosynthetic capacity per unit dry mass; B_C – Chlorophyll binding (amount of chlorophyll per unit nitrogen invested in light harvesting Eq. 4.4); Chl – Chlorophyll; C_a – Ambient CO_2 concentration; C_c – Chloroplasmic CO_2 concentration; C_i – CO_2 concentration in the intercellular air space; E_N – Photosynthetic nitrogen use efficiency; F_B – Fraction of leaf nitrogen in rate-limiting proteins of photosynthetic electron transport; F_L – Fraction of leaf nitrogen in light harvesting; F_R – Fraction of leaf nitrogen in Rubisco; g_m – Mesophyll diffusion conductance; g_s – Stomatal conductance; J_{\max} – Capacity for photosynthetic electron transport; J_{\max}^A – Capacity for photosynthetic electron transport per unit area; J_{mc} – Capacity for photosynthetic electron transport per unit cytochrome f ; k – Light extinction coefficient; L – Leaf area index; LHC II – Light harvesting complex II; M_A – Leaf dry mass per unit area; N_A – Nitrogen content per unit area; N_M – Leaf nitrogen content per unit dry mass; PS I – Photosystem I;

PS II – Photosystem II; Q – Photosynthetic quantum flux density; Q_0 – Above-canopy Q ; Q_{int} – Incident integrated Q during leaf growth and development; R_c – Light-dependent change of a given trait (Eq. 4.5); SC – Shade tolerance score; S_T/S_P – Total to projected leaf area ratio; VAZ – Xanthophyll cycle carotenoids (violaxanthin antheraxanthin and zeaxanthin); V_{cmax} – Maximum carboxylase activity of Rubisco; $V_{\text{cmax,b}}$ – V_{cmax} at the bottom of the canopy; $V_{\text{cmax,t}}$ – V_{cmax} at the top of the canopy; V_{cmax}^A – Maximum carboxylase activity of Rubisco per unit area; V_{cr} – Specific activity of Rubisco (maximum rate of ribulose-1,5-bisphosphate carboxylation per unit Rubisco protein); V_i – Trait value at a seasonal average quantum flux density of i ($Q_{\text{int},i}$); α – Initial quantum yield for photosynthetic electron transport; $\alpha_{p,a}$ – Initial quantum yield of photosynthesis for an absorbed light; $\alpha_{p,i}$ – Initial quantum yield of photosynthesis for an incident light; θ – Lamina cross-sectional angle; ξ – Leaf absorptance; χ_A – Chlorophyll content per unit area; χ_M – Chlorophyll content per unit dry mass; φ_F – Leaf lamina inclination angle at leaf fall-line; $|\varphi_L|$ – Absolute lamina inclination angle (average angle between the normal to the leaf plane and the vertical direction); φ_P – Petiole inclination angle; Ω – Leaf clumping index

traits, lower canopy leaves have a greater light harvesting efficiency, while upper canopy leaves have a greater capacity for excess radiation dissipation and resistance to abiotic stress. Plasticity for foliar modifications varies among woody species of different ecological potentials with shade-intolerant species tending to have a greater photosynthetic plasticity, while shade-tolerant species greater leaf areas and higher canopy light interception. This review emphasizes the overall large within-canopy variation in key foliage functional traits and underscores the important differences among plant functional types and in species with different ecological potentials in their acclimation to within-canopy environment.

Keywords Acclimation • Chlorophyll content • Carotenoids • Dry mass per unit area • Isoprene emission • Leaf age • Leaf life span • Leaf morphology • Nitrogen content • Nitrogen partitioning • Optimization • Photosynthetic capacity • Shade tolerance

I. Introduction

Variation in light availability is one of the most conspicuous features of plant canopies. Daily integrated average light flux varies often more than 50-fold between canopy top and bottom in dense plant canopies (Fig. 4.1, Hirose et al. 1988; Koike et al. 2001; Valladares 2003; Niinemets and Anten 2009; Chap. 9, Hikosaka et al. 2016b), but unexpectedly, the gradient is still 10–20-fold in relatively open canopies (Hirose et al. 1988; Werger and Hirose 1988; Rambal 2001; Joffre et al. 2007). Even in free-standing plants, foliage is importantly aggregated within the canopy envelope, and leaves at the top shade the leaves positioned lower in the canopy, resulting in major light gradients (e.g., Le Roux et al. 1999; Chap. 11, Disney 2016).

Foliage photosynthetic capacities acclimate to these extensive long-term light gradients through plant canopies such that whole canopy photosynthetic response cannot be predicted from “an average leaf response”, but is the integrated response of leaves in different canopy positions with different physiological potentials tuned to their specific light environment (Hirose and Werger 1987b; Ellsworth and Reich 1993; Anten 1997; Pons and Anten 2004; Niinemets and Anten 2009; Chap. 5, Pons 2016). In fact, multiple leaf structural and chemical traits vary between canopy top and bottom, including leaf dry mass per unit area, leaf nitrogen content and nitrogen

partitioning among proteins of photosynthetic machinery (Hirose and Werger 1987b; Ellsworth and Reich 1993; Anten 1997; Pons and Anten 2004; Niinemets and Anten 2009; Chap. 5, Pons 2016). Variations in these key functional traits ultimately drive within-canopy photosynthetic acclimation. Various structural and chemical traits have inherently different plasticities to within-canopy light conditions in different plant life forms and in species with different ecological potentials, leading to a spectrum of within-canopy photosynthetic acclimation responses across species (Niinemets and Anten 2009 for a review).

In addition to long-term variations in light availability, the environmental setting in plant canopies is much more complex. Light is a highly dynamic environmental factor that varies strongly during the day and among the days and seasons. Despite photosynthetic acclimation, leaves at the top of the canopy can be exposed to excess irradiance on clear days, resulting in photoinhibition and oxidative stress (Osmond et al. 1999; Werner et al. 2001b; Demmig-Adams and Adams 2006). Photoinhibition can become particularly pronounced when photosynthesis rates are reduced due to other abiotic stress factors such as soil drought (Ramalho et al. 2000; Werner et al. 2002; Valladares et al. 2005; Niinemets and Keenan 2014). There are major within-canopy gradients in the leaf capacity to adjust to dynamically changing light conditions (Niinemets et al. 2003; García-Plazaola et al. 2004), indicating that

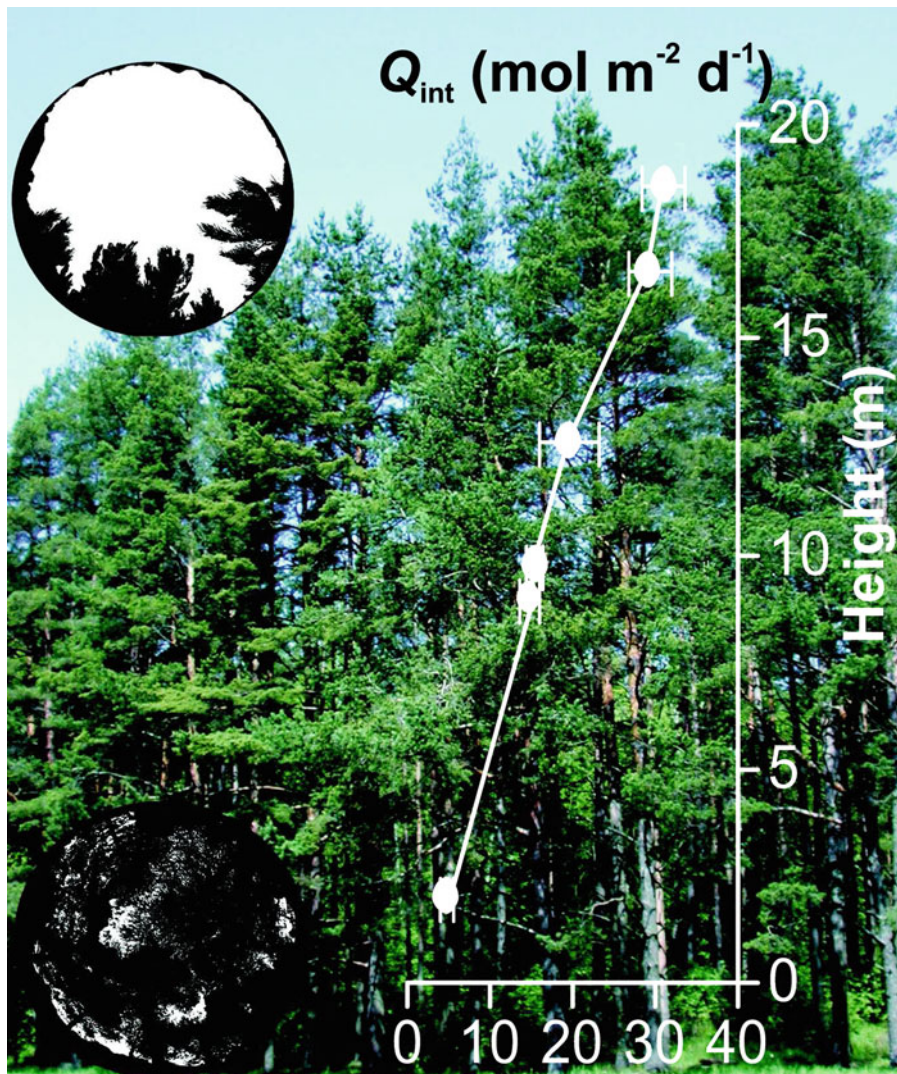


Fig. 4.1. Illustration of within-canopy variation in incident seasonal average integrated quantum flux density (Q_{int}) in a temperate evergreen conifer *Pinus sylvestris* canopy in Ahunapalu (58°19' N, 27°17' E, elevation ca. 60 m). Niinemets et al. (2001) provides further details of the stand. Hemispherical photographs taken from the upper part of the canopy (height of 18 m, $Q_{int} = 31.2 \text{ mol m}^{-2} \text{d}^{-1}$) and lower part of the canopy within the shrub layer (height of 1.5 m, $Q_{int} = 3.85 \text{ mol m}^{-2} \text{d}^{-1}$) are also demonstrated. Error bars show \pm SD of average Q_{int} at each height level. Q_{int} is defined as the average daily integrated quantum flux density during foliage growth and development. Hemispherical photo analysis is a classic method for obtaining the relative potential penetrating quantum flux density in different locations of the canopy (e.g., Anderson 1964). The obtained relative potential values of incident diffuse and direct light availability need to be calibrated by long-term quantum flux density measurements to estimate Q_{int} for each canopy location (e.g., Niinemets et al. 1998a). Note that for illustrative purposes, the y-axis crosses with the x-axis at the highest Q_{int} value

coping with excess light can be importantly determined by past leaf light regime.

In addition to light, air temperatures increase from canopy bottom that receives less radiation toward canopy top that is exposed to greater radiation (Niinemets et al. 1999b; Zhang et al. 2010; Krédl

et al. 2012; Pinheiro Prado et al. 2013; Zhang et al. 2013). These gradients in temperature are also associated with gradients in relative air humidity (Chiariello 1984; Krédl et al. 2012; Zhang et al. 2013). Lower humidity coupled with greater temperature and radiation input leads to greater

evaporative demands and potentially greater water stress in the upper canopy (Niinemets et al. 1999c; Hubbard et al. 2002; Aasamaa et al. 2004; Niinemets et al. 2004d; Sellin and Kupper 2004). In fact, the hydraulic conductivity of stem and branches can limit water transport to upper canopy in clear days with high radiation input (Joyce and Steiner 1995; Brodribb et al. 2005; Renninger et al. 2006; Ewers et al. 2007; Peltoniemi et al. 2012; Chap. 7, Woodruff et al. 2016). Thus, upper canopy leaves may become water-stressed even in situations with ample soil water supply (Joyce and Steiner 1995; Lemoine et al. 2002; Ewers et al. 2007). Stronger water stress in turn can lead to more severe photoinhibition and oxidative stress in leaves in the upper canopy.

This evidence suggests that, apart from changes in photosynthetic capacity, acclimation to within-canopy light gradients also involves structural and chemical adjustments to avoid excess light interception and increase the resistance to photoinhibition and oxidative stress in the upper canopy leaves (Rasmuson et al. 1994; Hikosaka and Hirose 1997; During 1999; Ishida et al. 1999a; James and Bell 2000; Werner et al. 2001b; Niinemets et al. 2003; García-Plazaola et al. 2004). It has been even suggested that interactions among environmental drivers and co-occurrence of multiple stresses can constrain the photosynthetic acclimation to within-canopy light environment, and as the result, “full acclimation” to within-canopy light is principally not possible (Niinemets and Valladares 2004; Niinemets 2012; Peltoniemi et al. 2012).

This chapter describes within-canopy variations in leaf photosynthetic rates and analyzes underlying sources of variation due to modifications in leaf structural, chemical and physiological characteristics. First, a methodology to separate structural, chemical and allocational controls on the variations in foliage photosynthetic rates within plant canopies is introduced. Then a short meta-analysis in broad-leaved evergreen species *Quercus ilex* is carried out to highlight the many facets of within-canopy

foliage structural, chemical and physiological acclimation. The compiled dataset of *Q. ilex* foliar characteristics is unique in that it covers variations in all key leaf functional traits including diffusion conductances from ambient air to chloroplasts. The comprehensive analysis of the variation patterns in *Q. ilex* with high leaf longevity is used as a baseline to compare within-canopy acclimation responses in other plant functional types with higher leaf turnover.

This review also analyses the overall significance of variations in photosynthetic capacity in altering the whole canopy carbon gain and considers the possible structural and chemical constraints on the acclimation of photosynthetic capacity. This chapter further focuses on structural traits determining efficient light harvesting in the lower canopy and avoidance of excess radiation interception in the upper canopy, and on chemical traits responsible for safe dissipation of excess light and increasing resistance to enhanced oxidative stress in the upper canopy. The review emphasizes that there is an important within-canopy variation in how the stress resistance traits respond to dynamic alterations in light availability. Finally, this chapter analyses the variations in plasticity in whole-canopy acclimation among species with different shade tolerance that characteristically colonize habitats with varying light availability. This review emphasizes the strong within-canopy acclimation in key leaf traits and outlines the richness of responses in different plant functional types and in species with different shade tolerance.

II. Evaluation of the Role of Different Leaf Functional Traits Involved in Variation of Photosynthesis Through Plant Canopies

Variation in environmental drivers through plant canopies, in particular, variation in average daily incident integrated quantum

flux density during foliage growth and development (Q_{int}) alters a plethora of foliage structural, chemical and photosynthetic traits (Terashima and Hikosaka 1995; Anten et al. 1996, 1998; Koike et al. 2001; Lemoine et al. 2002; Meir et al. 2002; Wright et al. 2006; Niinemets 2007). As a key change, foliage photosynthetic capacity (A_{max}) typically increases with increasing Q_{int} from canopy bottom to top (Terashima and Hikosaka 1995; Anten et al. 1998; Koike et al. 2001; Lemoine et al. 2002; Meir et al. 2002; Wright et al. 2006; Niinemets 2007). Apart from A_{max} that determines foliage assimilation rate at high light, foliage light harvesting efficiency importantly drives photosynthesis at lower light intensities. The initial quantum yield of photosynthesis also often varies, although the within-canopy variation in quantum yield is less than in A_{max} , at least under non-stressed conditions (Cartechini and Palliotti 1995; Sands 1996; Niinemets and Kull 2001; Werner et al. 2001b).

To gain mechanistic insight into sources of within-canopy variation in A_{max} and the initial quantum yield of photosynthesis, the steady-state photosynthesis model of Farquhar et al. (1980) is typically used (Chap. 3, Hikosaka et al. 2016a). According to Farquhar et al. (1980) photosynthesis model, A_{max} is determined by the biochemical potentials of photosynthesis, the maximum carboxylase activity of Rubisco (V_{cmax}) and the capacity for photosynthetic electron transport (J_{max}), and by the stomatal (g_s) and mesophyll diffusion (g_m) conductances for photosynthesis, while the initial quantum yield of photosynthesis is mainly determined by the initial quantum yield for photosynthetic electron transport (α).

Within-canopy acclimation of J_{max} , V_{cmax} and α results from changes in multiple underlying traits. In the following, I define the modeling framework to evaluate the role of different leaf traits responsible for variations in J_{max} , V_{cmax} and α . The modeling framework will be used further through the chapter to gain insight into the importance of within-canopy variations in leaf structure and chemistry.

A. Determinants of Foliage Biochemical Potentials

Changes in biochemical photosynthesis potentials are determined by modifications in leaf structural and chemical traits, and the key question is to what extent different traits control variations in V_{cmax} and J_{max} . To separate among the effects of various structural and chemical traits on foliage biochemical potentials, V_{cmax} and J_{max} can be expressed as composites of several independent characteristics. For V_{cmax} :

$$V_{\text{cmax}} = 6.25V_{\text{cr}}M_A F_R N_M, \quad (4.1)$$

where V_{cr} is the specific activity of Rubisco, i.e., the maximum rate of ribulose-1,5-bisphosphate carboxylation per unit Rubisco protein ($\mu\text{mol g}^{-1} \text{s}^{-1}$), M_A is the leaf dry mass per unit area (g m^{-2}), F_R is the fraction of leaf nitrogen in Rubisco, N_M is the leaf nitrogen content per unit dry mass (g g^{-1}) and 6.25 (g g^{-1}) is the nitrogen content of Rubisco protein (Niinemets and Tenhunen 1997). Analogously, J_{max} is given as:

$$J_{\text{max}} = 8.06J_{\text{mc}}M_A F_B N_M, \quad (4.2)$$

where J_{mc} is the capacity for photosynthetic electron transport per unit cytochrome f , F_B is the fraction of nitrogen in rate-limiting proteins of photosynthetic electron transport, and the factor 8.06 considers the nitrogen content of proteins and molar stoichiometry relative to cytochrome f (Niinemets and Tenhunen 1997). Implicit in this expression is that the capacity for linear electron transport rate is determined by electron carriers between photosystems I and II (Niinemets and Tenhunen 1997 for a discussion).

Estimates of J_{max} and V_{cmax} are typically obtained from net assimilation vs. CO_2 response curves, ideally from net assimilation (A) vs. chloroplastic CO_2 concentration (C_c) response curves. In the past, C_c was not routinely estimated due to difficulties with estimation of mesophyll diffusion conductance ($C_c = C_i - A/g_m$, where C_i is the CO_2 concentration in the intercellular air space).

Thus, in the majority of past studies, V_{cmax} and J_{max} estimates were derived from A vs. C_i response curves assuming that g_m is infinite. However, recent work has demonstrated that g_m is finite, and that it varies among species and can limit photosynthesis as significantly as stomatal conductance (Flexas et al. 2012 for a review). Thus, estimates of foliage biochemical potentials from A vs. C_i response curves provide apparent, underestimated, values of V_{cmax} and J_{max} , and accordingly F_R and F_B according to equations 4.1 and 4.2 are also apparent fractions of N in rate-limiting proteins.

Apart from CO_2 response curves, inverse modeling techniques can be used to estimate J_{max} and V_{cmax} from light response curves of photosynthesis (e.g., Niinemets and Tenhunen 1997; Niinemets et al. 1999d; Patrick et al. 2009) and estimate V_{cmax} from the light-saturated net assimilation rate (e.g., Niinemets 1999). However, for inverse modeling, one needs an estimate of CO_2 concentration in the chloroplasts or at least an estimate of C_i . Alternatively, many studies have calculated the photosynthetic nitrogen use efficiency (E_N), the ratio of A_{max} to foliage N content (Hirose and Werger 1987a, 1994; Hikosaka et al. 1998; Hirose and Bazzaz 1998; Yasumura et al. 2002; Escudero and Mediavilla 2003; Pons and Westbeek 2004). Photosynthetic nitrogen use efficiency provides another estimate of the allocation of N to rate-limiting components of photosynthesis, but differently from F_R that is standardized for variations in g_s and g_m (C_c -based estimate of F_R) or g_s (C_i -based apparent F_R), within-canopy and species differences in E_N can be affected by differences in diffusion conductances.

B. Traits Affecting Light Harvesting and Initial Quantum Yield

Classic studies have demonstrated that the initial quantum yield of photosynthesis for an absorbed light measured at a given chloroplastic CO_2 and oxygen concentration and temperature ($\alpha_{\text{p},a}$) is remarkably constant among C_3 plants (Ehleringer and Björkman 1977; Leverenz 1987, 1988, 1994). However,

quantum yields for an incident light ($\alpha_{\text{p},i}$) importantly vary due to differences in leaf absorptance (ξ) that modifies the amount of light intercepted at a given incident light intensity, thereby altering the quantum yield ($\alpha_{\text{p},i} = \xi\alpha_{\text{p},a}$) (Leverenz 1987, 1988, 1994; Long et al. 1993; Oberhuber et al. 1993).

Leaf absorptance is primarily a function of leaf chlorophyll content per unit area (χ_A , mmol m^{-2}) (Evans 1993a; Evans and Poorter 2001), except for hairy or waxy leaves that often have enhanced reflectance (Ehleringer and Björkman 1978; Evans and Poorter 2001; Cescatti and Niinemets 2004). For leaves without such highly reflective epidermal characteristics, Evans (1993a) developed an empirical relationship between ξ and χ_A that describes well variations in ξ for a broad range of species with differing foliage architectures (Evans and Poorter 2001):

$$\xi = \frac{\chi_A}{\chi_A + 0.076}, \quad (4.3)$$

where 0.076 mmol m^{-2} is an empirical constant.

Leaf chlorophyll (Chl) and chlorophyll-binding proteins contain a large fraction of foliar nitrogen, and therefore, it is pertinent to express leaf chlorophyll content in nitrogen equivalents (Niinemets and Tenhunen 1997) as:

$$\chi_A = N_M M_A F_L B_C, \quad (4.4)$$

where F_L is the fraction of leaf nitrogen invested in light harvesting, and B_C ($\text{mmol Chl (g N)}^{-1}$) is the chlorophyll binding defined as the amount of chlorophyll per unit nitrogen invested in light harvesting. It depends on the nitrogen cost of chlorophyll and specific chlorophyll-binding proteins, on the number of chlorophyll-binding sites in each chlorophyll-binding protein and on the stoichiometry of light-harvesting pigment-binding protein complexes (Hikosaka and Terashima 1996; Niinemets and Tenhunen 1997; Bassi and Caffarri 2000). In particular, B_C increases with increasing the share of chlorophyll associated with light-harvesting complex of photosystem II (LHC II) that

binds more chlorophyll than the centers of photosystems I and II (PS I and PS II) (Bassi and Caffarri 2000; Jackowski et al. 2001; Paulsen 2001). Since the bulk of chlorophyll *b* is associated with LHC II and minor light harvesting complexes of PS II (Bassi and Caffarri 2000), increases in B_C are also associated with decreases in chlorophyll *a/b* ratio.

The chlorophyll binding is normally about 2.1–2.5 mmol (g N)⁻¹ in vascular plants (Niinemets and Tenhunen 1997; Niinemets et al. 1998b), and it increases and chlorophyll *a/b* ratio decreases with decreasing light availability in the canopy (e.g., Evans 1993a, b; Niinemets and Tenhunen 1997; Niinemets et al. 1998b; Pons and Anten 2004), reflecting increases in the amount of chlorophyll associated with LHC II relative to that contained in PS I and PS II. This is an important acclimatory modification as it reduces the N cost of light harvesting (Hikosaka and Terashima 1995). While values of B_C are not routinely reported in the literature, chlorophyll *a/b* ratio is characteristically assessed in studies investigating light acclimation, and can be used as a proxy of light-driven modifications in thylakoid stoichiometry.

III. Light-Dependent Variations in Photosynthesis and Underlying Traits Across Plant Canopies

Equations 4.1, 4.2, 4.3, and 4.4 provide a simple means to analyze the effects of variations in foliage structure, nitrogen content and nitrogen partitioning on foliage photosynthetic potentials and initial quantum yield. In this section, I analyze how leaf structural and chemical traits vary in plant canopies and what are the implications for foliage photosynthetic potentials. As realized net assimilation rates are importantly driven by CO₂ diffusion conductances from ambient atmosphere to chloroplasts, I also consider within-canopy variations in stomatal and mesophyll conductances.

This section provides first a meta-analysis of within-canopy variations in leaf traits in the Mediterranean evergreen sclerophyll

Quercus ilex. This species grows in water-limited open ecosystems where the variation in light availability as a source for foliage functional differentiation has been traditionally neglected. This meta-analysis serves to identify the basic scaling relationships between key foliage traits and irradiance in the canopy and make the general point that even in species growing in open ecosystems, there can be major within-canopy variations in foliage characteristics. This meta-analysis also serves as an example demonstrating how fragmentary information present in multiple studies can be summarized to gain insight into within-species variability. Overall, there is less data available for broad-leaved evergreen woody species than for herbaceous species and needle-leaved evergreen and winter-deciduous woody species (Niinemets and Anten 2009 for a review), making this analysis particularly pertinent. Furthermore, the data summarized in *Q. ilex* include all key functional leaf-level traits covering structural, biochemical and diffusional limits of photosynthesis, making the analysis truly comprehensive. In particular, within-canopy variation in mesophyll diffusion conductance has not been routinely studied with a few exceptions (Niinemets et al. 2006a; Cano et al. 2013; Niinemets 2015).

Although the meta-analysis in *Q. ilex* highlights the basic within-canopy leaf trait variation patterns, evergreens such as *Q. ilex* support multiple age cohorts. This is significant as in evergreens, older foliage becomes gradually shaded with canopy expansion and formation of new leaves. Accordingly, within-canopy trait patterns of older leaves are importantly driven by the capacity of older foliage to reacclimate to new light conditions. Thus, in the following, I analyze the within-canopy trait variations in older leaf age classes in evergreens primarily focusing on modifications in the overall plastic variations and on the strength of trait vs. light climate relationships.

After highlighting the basic within-canopy variation patterns in evergreens, I further ask how do the within-canopy gradients in foliage traits vary among different plant functional types? Different plant

functional types are characterized by varying rates of foliage and canopy growth and turnover and such differences in the rates of canopy expansion and leaf longevity can alter the gradients of light through the canopy, leaf lifetime intercepted light integral and the extent of variation in light availability during leaf lifetime (Schulze 1981; Jarvis and Leverenz 1983; Woodward et al. 1994; Niinemets et al. 2012; Niinemets and Keenan 2012). This may significantly alter the degree of within-canopy variation in different leaf-level traits in different plant functional types.

Finally, I analyze the overall significance of within-canopy variations in photosynthetic potentials for whole-canopy net assimilation rates using a simple modeling approach. This model-based analysis further underscores the importance of within-canopy trait variation and emphasizes the need to include phenotypic plasticity in large-scale photosynthesis models.

A. A Meta-Analysis of Within-Canopy Variations in the Mediterranean Evergreen *Quercus ilex*

1. Data and Methods

A thorough literature survey identified eight studies that provided information on within-canopy variation in light vs. foliage traits in *Q. ilex* (Eckardt et al. 1975; Rambal 1992; Sala et al. 1994; Rambal et al. 1996; Niinemets et al. 2002b, 2006a; Davi et al. 2008; Vaz et al. 2011). For these studies, average seasonal average incident integrated quantum flux density for 50 days after bud burst (Q_{int}) was used as an estimate of light availability. In studies reporting leaf dry mass per unit area (M_A) in relation to directly measured cumulative leaf area index, relative quantum flux density was derived according to Lambert-Beer's law using an extinction coefficient of 0.5 (Sala et al. 1994), while for optical leaf area index obtained by LAI-2000 instrument (Rambal et al. 1996), an extinction coefficient of 0.8 (Niinemets et al. 2010) was used. The above-

canopy Q_{int} was derived for the year of foliage sampling using global radiation databases as in Niinemets and Keenan (2012). Q_{int} vs. foliage trait relationships were fitted by non-linear regressions in the form $y = ax^b$ and $y = a\text{Ln}(x) + b$. As leaf dry mass per unit area is strongly correlated with within-canopy variations in Q_{int} (e.g., Fig. 4.2a and Meir et al. 2002; Niinemets 2007; Niinemets and Anten 2009), M_A was used as a substitute of light for studies explicitly investigating variations in foliage chemistry within the canopy light gradients, but lacking direct light measurements. This analysis only included mature fully-expanded current year foliage. The relationships in older leaf age classes are analyzed in Sect. III.B.

2. Variations in key Functional Traits

Analysis of all published within-canopy patterns of foliage traits in *Q. ilex* highlights several broad trends in plastic modifications in foliage structural, chemical and photosynthetic characteristics. First of all, M_A strongly increased with increasing average quantum flux density during leaf growth, 1.5–2.4-fold between canopy top and bottom (Q_{int} , Fig. 4.2a). Nitrogen content per unit area (N_A) also increased, 1.7–2.7-fold, with increasing Q_{int} ($r^2 = 0.77\text{--}0.93$, $P < 0.001$), but nitrogen content per unit dry mass (N_M) varied little within the canopy ($r^2 = 0.00\text{--}0.12$, $P > 0.2$, average \pm SD = 1.57 % \pm 0.25 % across the studies analyzed). Foliage photosynthetic capacity per unit area (A_{max}^A , $r^2 = 0.64$, $P < 0.001$ for the data of Niinemets et al. 2006a) and foliage photosynthetic potentials, the maximum carboxylase activity of Rubisco (V_{cmax}^A) and the capacity for photosynthetic electron transport per unit area (J_{max}^A , Fig. 4.2b) scaled positively with Q_{int} (ca. 2.5-fold change of foliage photosynthetic potentials between canopy top and bottom for the data in Fig. 4.2b and 1.8-fold change in Vaz et al. 2011), but mass-based photosynthetic characteristics varied little within the canopy ($r^2 = 0.00\text{--}0.06$ for these three traits). Furthermore, the fractions

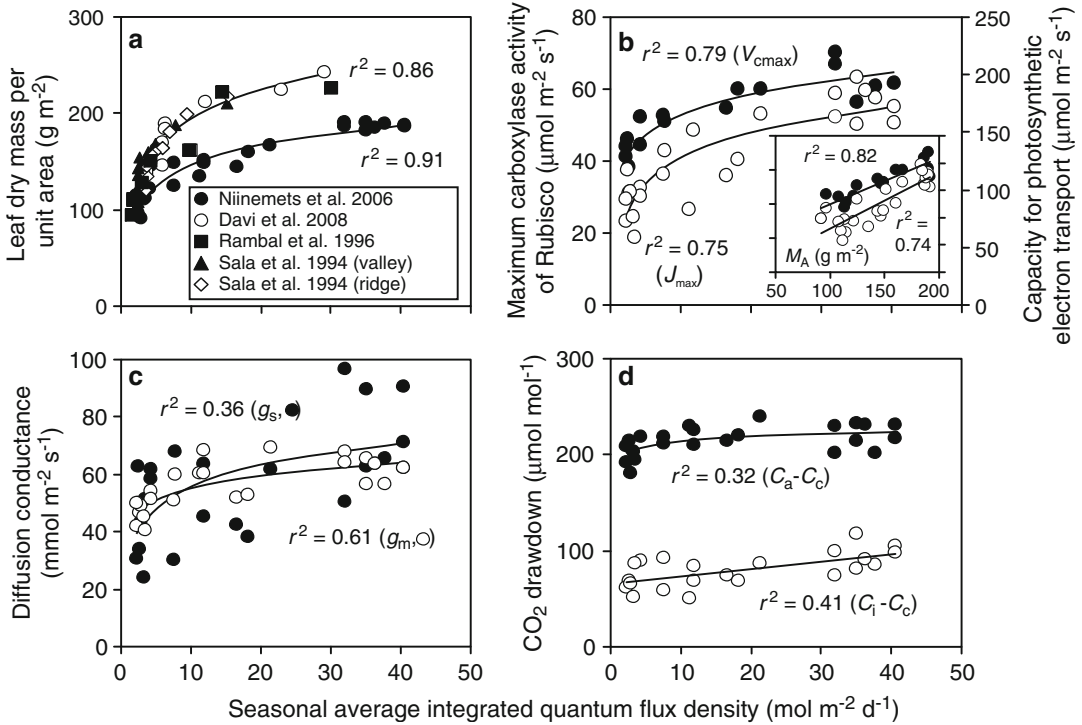


Fig. 4.2. Effects of within-canopy variation in average integrated quantum flux density (Q_{int}) on (a) leaf dry mass per unit area (M_A), (b) maximum carboxylase activity of Rubisco (V_{cmax}) and capacity for photosynthetic electron transport (J_{max}), (c) stomatal conductance to water vapor (g_s) and mesophyll diffusion conductance (g_m) and (d) CO_2 drawdown from ambient air to chloroplasts ($C_a - C_i$) and from intercellular air space to chloroplasts ($C_i - C_c$) in current-year leaves of Mediterranean broad-leaved evergreen sclerophyll *Quercus ilex*. The inset in (b) demonstrates the correlations of V_{cmax} and J_{max} with leaf dry mass per unit area. The data were fitted by linear (panel inset) and non-linear regressions in the form $y = ax^b$ and $y = a\text{Ln}(x) + b$, whichever of the two provided a higher r^2 ($P < 0.01$ for all regressions). Data sources in panel a as indicated, all other data are from Niinemets et al. (2006a). The sampling locations were: 41.73°N, 3.58°E, elevation 270 m (Davi et al. 2008), 41.25°N, 1°E, elevation 700 m (valley) and 975 m (ridge) (Sala et al. 1994), 43.74°N, 3.59°E, elevation 270 m (Rambal et al. 1996) and 45.88°N, 10.87°E, elevation 300 m (Niinemets et al. 2006a). Q_{int} corresponds to average daily integrated incident quantum flux density for 50 days after bud burst

of nitrogen in Rubisco (Eq. 4.1, average \pm SD = 0.154 ± 0.025 for the data of Niinemets et al. 2006a) and in bioenergetics (Eq. 4.2, 0.039 ± 0.007 for the data of Niinemets et al. 2006a and 0.036 ± 0.009 for the data of Rambal et al. 1996) were independent of Q_{int} ($P > 0.1$ for both variables and both datasets). Given the invariability of nitrogen allocation and considering that the area-based traits are the products of mass-based traits and M_A , within-canopy variation in N_A and foliage photosynthetic potentials was mainly driven by light-dependent variations in M_A (Fig. 4.2b inset).

Both stomatal and mesophyll conductances were greater in the upper canopy (Fig. 4.2c). The CO_2 drawdown from ambient air (C_a) to intercellular air space (C_i) was independent of Q_{int} ($r^2 = 0.01$), indicating that stomata limited photosynthesis similarly through the canopy. However, the CO_2 drawdown from intercellular air space to chloroplasts (C_c , $C_i - C_c$), and the overall drawdown ($C_a - C_c$) increased with increasing Q_{int} (Fig. 4.2d), demonstrating that g_m limited photosynthesis more in the upper canopy. Thus, increases in M_A were not only associated with stacking of photosynthesizing biomass per unit area,

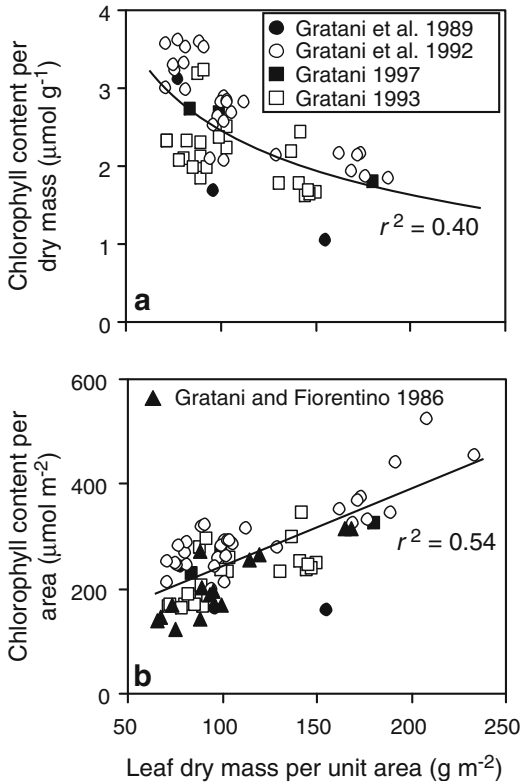


Fig. 4.3. Correlations of leaf chlorophyll content per unit leaf dry mass (a) and per unit leaf area (b) with leaf dry mass per unit area in current-year leaves of *Quercus ilex*. Variations in dry mass per unit area are due to within-canopy differences in light environment (Fig. 4.2a). Data from multiple studies investigating within-canopy variation in leaf traits (Gratani and Fiorentino 1986, Table 1 for site locations; Gratani et al. 1989, 1992; Gratani 1993, 1997) were pooled and fitted by a non-linear regression in the form $y = ax^b$ (a) and with a linear regression (b). $P < 0.001$ for both regressions

but increased foliage robustness also resulted in reduced efficiency of use of resources invested in photosynthetic machinery. Such enhanced diffusion limitations might reflect increases in cell wall thickness, an acclimation response contributing to withstanding low leaf water potentials in the upper canopy (see Sect. 1), but also reducing CO_2 diffusion rate through leaf liquid phase (e.g., Terashima et al. 2011; Tosens et al. 2012a, b; Tomás et al. 2013).

As light measurements were not available in studies investigating within-canopy variation in chlorophyll contents, M_A was used as a proxy of within-canopy light conditions.

Across these studies, foliage chlorophyll content per unit dry mass (χ_M) scaled negatively with M_A (Fig. 4.3a). Given that N_M was not correlated with within-canopy variation in light, this result also suggests that N in light harvesting (F_L , Eq. 4.4) increases with increasing shading in the canopy. Nevertheless, in this species, within-canopy variation in M_A was greater than the variation in χ_M such that leaf chlorophyll content per unit area was positively correlated with M_A (Fig. 4.3b).

B. Leaf Age-Dependent Variations in Foliage Plasticity in Evergreens

1. Why Should Plasticity Depend on Leaf Age?

Evergreen species support multiple leaf age cohorts, e.g., *Q. ilex* supports leaves up to 6 years old (Niinemets et al. 2005a), and several conifers can support leaves more than 10 years old (Ewers and Schmid 1981; Schoettle 1989; Schoettle and Fahey 1994; Niinemets and Lukjanova 2003). Increases in leaf age are characteristically associated with increases in leaf dry mass per unit area and in reductions in N_M and photosynthetic capacity (Teskey et al. 1984; Brooks et al. 1994, 1996; Niinemets 1997b; Niinemets et al. 2005a). On the other hand, older foliage initially developed at higher light becomes gradually shaded by new foliage and the key question is to what extent the older foliage can reacclimate to the modified light conditions. Although there is some secondary leaf growth at least in conifers (Ewers 1982; Gilmore et al. 1995), rigidification of cell walls after foliage maturation strongly curbs further foliage expansion growth. Thus, foliage structural reacclimation to modified light conditions is inherently limited. However, foliage may reacclimate to altered light conditions by changing nitrogen content and nitrogen allocation among the components of photosynthetic machinery within the leaf (Brooks et al. 1996; Niinemets 1997b; Escudero and Mediavilla 2003; Oguchi et al. 2005, 2006; Muller et al. 2009). Given the structural constraints, it is

plausible that foliage photosynthetic plasticity to light is decreasing with increasing foliage age.

2. Analyzing Plasticity Changes

To compare plastic changes in foliage traits of leaves of different age, I calculated the relative light-dependent change (R_c) of a given trait as (Niinemets et al. 2015):

$$R_c = \frac{V_{i+x} - V_i}{\Delta Q_{\text{int}}(V_{i+x} + V_i)/2}, \quad (4.5)$$

where V_i is the trait value at a seasonal average quantum flux density of i ($Q_{\text{int},i}$) and V_{i+x} is the trait value at $Q_{\text{int},i} + x$ ($Q_{\text{int},i+x}$). R_c is normalized with respect to the average trait value across the given light range, $(V_{i+x} + V_i)/2$, to account for age-dependent changes in absolute trait values. The plasticity to within-canopy variations in light increases with increasing the R_c value. In the following analysis, R_c was calculated with $Q_{\text{int},i} = 6 \text{ mol m}^{-2} \text{ d}^{-1}$ and $Q_{\text{int},i+x} = 12 \text{ mol m}^{-2} \text{ d}^{-1}$. Foliage trait vs. Q_{int} relationships are curvilinear (Fig. 4.2), and this is a moderately high light range positioned in the strongly increasing part of foliage trait vs. Q_{int} relationships. In the following, age-dependent changes in plasticity are analyzed in three species, *Q. ilex* and conifers *Abies amabilis* and *Pinus contorta*.

3. Experimental Evidence of Plasticity Modifications

Examination of R_c values in leaves of different age indicated that the plasticity in N_A (Fig. 4.4a), M_A (data not shown) and A_{max}^A (Fig. 4.4b) decreased with increasing leaf age in the three species analyzed. The reduction in plasticity was also associated with reduction in the degree of explained variance (Fig. 4.4c, d), indicating that the relationships became weaker and more scattered with increasing leaf age.

However, the age-dependent reduction in the plasticity in A_{max}^A was less than in N_A and M_A (cf. Fig. 4.4a, b). This suggests that

differently from structural traits and total nitrogen content, foliage photosynthetic traits of older shaded foliage can adapt to modified light regime (Brooks et al. 1994; Niinemets et al. 2006a). In fact, in *Q. ilex*, photosynthetic capacity of 1-year-old foliage was even more plastic than photosynthetic capacity of current-year foliage (Fig. 4.4b). This was associated with within-leaf changes in nitrogen allocation among proteins limiting photosynthetic capacity. Differently from current-year leaves (Sect. III.A.2), both F_R (Eq. 4.1, $r^2 = 0.29$, $P < 0.05$) and F_B (Eq. 4.2, $r^2 = 0.45$, $P < 0.01$ for the data of Niinemets et al. 2006a) increased with Q_{int} in 1-year-old leaves of *Q. ilex*. Nevertheless, in these leaves, the within-canopy variation in nitrogen allocation, F_R and F_B , 1.4–1.5-fold for the whole canopy, was still less than for nitrogen content and leaf dry mass per unit area.

In *Abies amabilis*, it has been further demonstrated that reacclimation to reduced light conditions results in increased nitrogen allocation to light harvesting (Brooks et al. 1994, 1996). This evidence collectively indicates that older foliage of evergreens can reacclimate to altered light conditions primarily due to modifications in nitrogen allocation within leaves, but also that the overall photosynthetic plasticity to light is lower for older leaves (Fig. 4.4). Thus, the modifications in nitrogen allocation cannot fully compensate for the structural inadequacy of shaded older foliage morphologically acclimated to higher past irradiance.

This analysis indicates that in evergreens, foliage photosynthetic characteristics of any canopy layer depend both on the structural, chemical and physiological acclimation to growth light conditions as well as on the reacclimation capacity. Interactions of leaf age with light availability and limited reacclimation capacity can clearly blur light vs. foliage structure and physiological activity relationships (Niinemets et al. 2006a). For example, such a confounding variation in leaf age and within-canopy light regime might explain why the correlations of leaf structural characteristics with light were weak for Australian broad-leaved evergreens (Wright et al. 2006) and in conifer *Pinus*

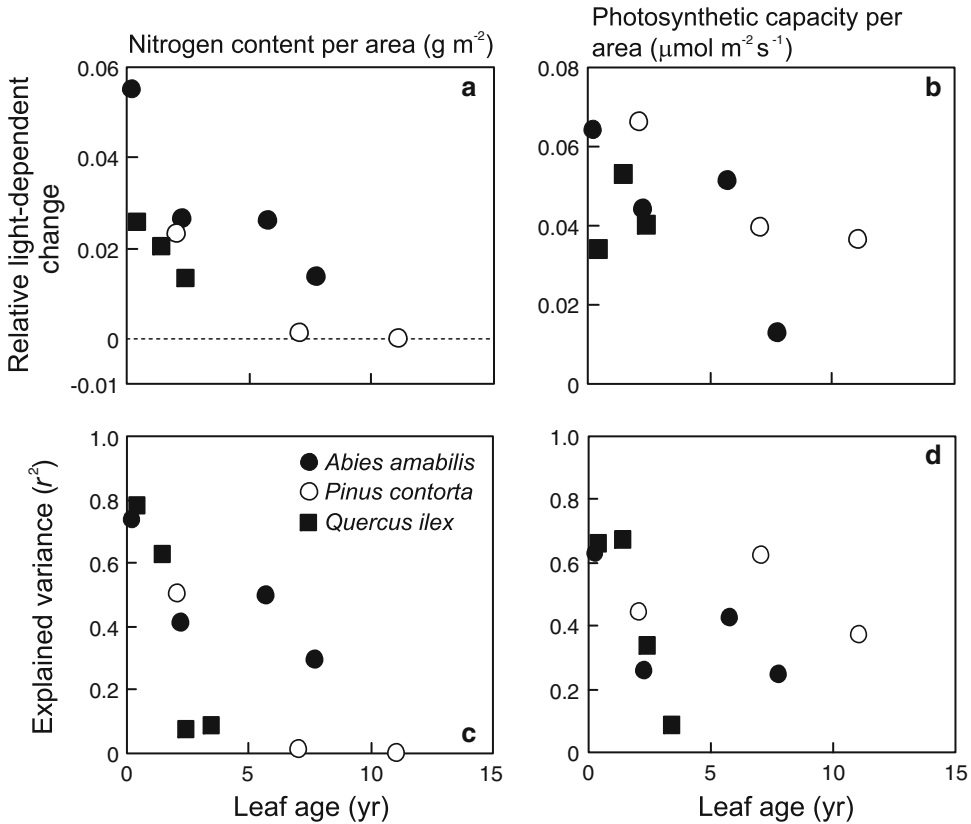


Fig. 4.4. Modifications in relative light-dependent changes in foliage nitrogen content per unit area (a) and photosynthetic capacity per unit area (b) with leaf age and concomitant changes in the explained variance (r^2 , c and d) in the temperate evergreen conifers *Abies amabilis* (Data of Brooks et al. 1996) and *Pinus contorta* (Data of Schoettle and Smith 1999) and in the Mediterranean evergreen broad-leaved species *Quercus ilex* (Data of Niinemets et al. 2006a). Relative light-dependent change (R_c) of a given trait is defined by Eq. 4.5 and characterizes the light-dependent plasticity normalized with respect to the average trait value to directly compare plasticities in species with different average trait values. The plasticity increases with increasing the R_c value. Here R_c was calculated for a moderately high light range (Q_{int}) of 6–12 $\text{mol m}^{-2} \text{d}^{-1}$ (Fig. 4.2 for the full light responses). Q_{int} is defined as in Fig. 4.2

pinaster (Warren and Adams 2001) when all leaves of different age were analyzed together.

C. Qualitative Differences among Trait Relationships between Plant Functional Types

1. Species with Low to Moderately High Leaf Turnover

The meta-analysis in the broad-leaved evergreen sclerophyll *Q. ilex* underscores the strong within-canopy variation in foliage structural, chemical and photosynthetic

characteristics (Figs. 4.2 and 4.3) as is typical in plant canopies (Hirose and Werger 1987a, b; Ellsworth and Reich 1993; Pons et al. 1994; Meir et al. 2002; Niinemets 2007). The overall range of variation in M_A between canopy top and bottom in *Q. ilex* was 1.5–2.4 in the eight studies analyzed (Fig. 4.2a). The within-canopy variation in M_A was associated with similar variations in area-based contents of nitrogen and chlorophyll (Fig. 4.3), mass-based photosynthetic potentials (Fig. 4.2b) and stomatal conductance (Fig. 4.2c). In contrast, mass-based nitrogen content and photosynthetic potentials were not associated with light

availability and chlorophyll content per unit dry mass even decreased with increasing light availability. Overall, this evidence demonstrates that within-canopy increase in area-based characteristics in *Q. ilex* primarily reflected accumulation of tissue with similar chemical composition and physiological activity per unit leaf area (most traits) or that the stacking trend dominated over the trend of dilution of the chemicals (chlorophyll).

These observations in *Q. ilex* are in a broad agreement with past observations in other broad-leaved evergreens. Differently from *Q. ilex*, a moderate increase in N_M with Q_{int} has been observed in temperate evergreen *Ilex aquifolium* (Aranda et al. 2004) and in several temperate *Nothofagus* species (Niinemets et al. 2004b), and in tropical species *Ficus insipida* (Posada et al. 2009). Analogously, photosynthetic capacity per unit dry mass (A_{max}^M) (Chazdon and Field 1987; Ishida et al. 1999b; Posada et al. 2009) and nitrogen partitioning coefficients, F_R and F_B (Evans and Poorter 2001), can either moderately decrease or increase in different evergreen species. Nevertheless, all these studies emphasize that the light-dependent increase in M_A is the key factor responsible for within-canopy increases in N_A and A_{max}^A in broad-leaved evergreens.

The relationships are analogous in evergreen needle-leaved conifers. In conifers, the variations in foliage nitrogen content and photosynthetic capacity per unit area are also dominated by M_A (Sprugel et al. 1996; Niinemets 1997a; Stenberg et al. 1999; Palmroth and Hari 2001; Han et al. 2003; Leal and Thomas 2003; Han et al. 2004, 2006). Furthermore, similar relationships have been demonstrated in other species with needle-like assimilative organs such as cladodes in the angiosperm *Casuarina* (Niinemets et al. 2005b). However, an increase in N_M with increasing Q_{int} has been observed in some conifers, and this was associated with increased mesophyll volume fraction and enhanced photosynthetic capacity per leaf dry mass at higher Q_{int} (Niinemets et al. 2007). So far,

light-dependent modifications in tissue fractional composition have been studied only in a few conifers (e.g., Aussenac 1973; Kovalyev 1980; Niinemets et al. 2007), and clearly more studies on three-dimensional needle anatomy are called for. Furthermore, in conifers with complex three-dimensional leaf cross-section, foliage photosynthetic capacity per unit projected area also depends on modifications in total to projected leaf area ratio (S_T/S_B , Sect. IV.A).

The relationships of leaf traits with Q_{int} are qualitatively similar in broad-leaved deciduous species that form all leaves simultaneously in the beginning of growing season, and thus, are characterized by a relatively high leaf longevity (Ellsworth and Reich 1993; Tjoelker et al. 1995; Niinemets and Kull 1998; Niinemets et al. 1998b; Koike et al. 2001; Meir et al. 2002; Iio et al. 2005). Although in some species, N_M (Niinemets et al. 1998b), A_{max}^M (Niinemets et al. 1998b) and nitrogen partitioning in photosynthetic machinery, F_B and F_R (Niinemets et al. 1998b, 2010) increase with increasing Q_{int} , in other species, N_M (Ellsworth and Reich 1993; Niinemets 1995; Fleck et al. 2003), A_{max}^M (Ducrey 1981; Ellsworth and Reich 1993; Niinemets et al. 1998b), and nitrogen partitioning coefficients (Niinemets et al. 2010) can also moderately decrease with increasing Q_{int} . Thus, again the overall photosynthetic response to within-canopy variations in Q_{int} primarily results from modifications in M_A . Nevertheless, upon sudden changes in irradiance, woody deciduous species can significantly change foliage photosynthetic capacity through changes in nitrogen partitioning (Naidu and DeLucia 1997; Niinemets et al. 2003; Oguchi et al. 2005, 2006), albeit the acclimation is limited due to anatomical constraints as in evergreen species (Sect. III.B, Oguchi et al. 2005, 2006) and can be relatively time-consuming (Naidu and DeLucia 1997; Kull and Kruijt 1999; Niinemets et al. 2003).

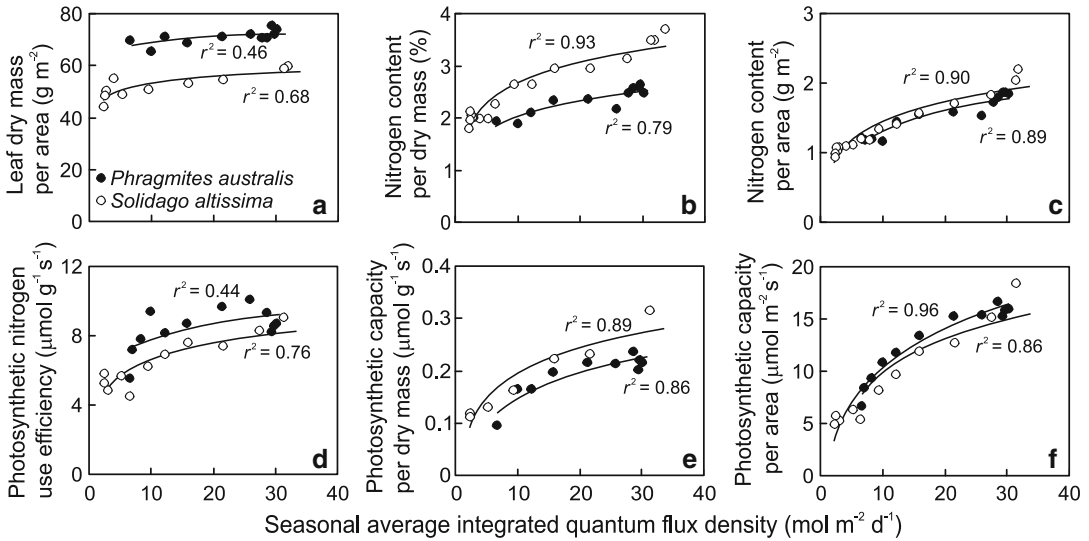


Fig. 4.5. Light-dependent variations in leaf dry mass per unit area (a), nitrogen content per unit dry mass (b) and area (c), photosynthetic nitrogen use efficiency (photosynthetic capacity per unit nitrogen, (d), and light-saturated net assimilation rate at ambient CO_2 concentration (photosynthetic capacity) per unit dry mass (e) and area (f) in the grass *Phragmites australis* (Data of Hirose and Werger 1994, 1995) and in the herb *Solidago altissima* (Data of Hirose and Werger 1987a, b; Werger and Hirose 1988). Data were fitted by non-linear regressions in the form of $y = a\text{Ln}(x) + b$ (all regressions are significant at least at $P < 0.02$). Seasonal average integrated quantum flux density (Q_{int}) is defined as in Fig. 4.2

2. Species with High Leaf Turnover

The situation is qualitatively different for broad-leaved deciduous woody species with continuous canopy expansion such as in fast-growing dense young *Salix* stands or coppice plantations. In such stands, foliage developed earlier becomes shaded by newly developed foliage analogously to different-aged foliage in evergreen canopies (Sect. III.B). Thus, there are strong leaf age and light gradients within the fast-expanding canopies of deciduous species. In fact, in such canopies, most leaves could have been exposed to high light during their development at the top of the canopy. As the result, M_A is relatively invariable in fast-growing woody canopies, and the within-canopy variation in N_A is primarily driven by a strong gradient in N_M (Vapaavuori et al. 1989; Vapaavuori and Vuorinen 1989; Noormets et al. 1996; Kull et al. 1998), while the within-canopy variation in A_{max}^A is driven by increases of A_{max}^M with Q_{int} (Vapaavuori et al. 1989; Vapaavuori and Vuorinen 1989).

The situation is similar in the canopies of herbaceous species where the entire canopy is formed during a single growing season and there is a continuous canopy growth until the onset of inflorescence formation. Examination of leaf trait vs. Q_{int} relationships in representative grass (*Phragmites australis*) and herb (*Solidago altissima*) species (Data of Hirose and Werger 1987a, 1994, 1995, Werger and Hirose 1988) demonstrates that although M_A does increase with increasing Q_{int} (Fig. 4.5a), the increase is much less than the corresponding change of N_M through the canopy (Fig. 4.5b) such that the increase of N_A (Fig. 4.5c) is mainly dependent on within-canopy gradient in N_M . In addition to N_A , the light-dependent increase of A_{max}^A (Fig. 4.5f) is determined by increases in nitrogen allocation (photosynthetic nitrogen use efficiency, E_N , Fig. 4.5d), i.e., $A_{\text{max}}^A = E_N N_A$. Increases in both N_M and photosynthetic nitrogen use efficiency are responsible for the strong increase of A_{max}^M with Q_{int} (Fig. 4.5e; $A_{\text{max}}^M = E_N N_M$). Given further that

$A_{\max}^A = E_N N_M M_A$, this evidence collectively indicates that nitrogen reallocation among the leaves and modification in nitrogen partitioning within the leaves are the primary mechanisms determining acclimation of herbaceous canopies to within-canopy light gradients, while changes in M_A play a less important role.

Overall, the strong gradients in N_M , photosynthetic nitrogen use efficiency and A_{\max}^M in species with high leaf turnover partly reflect reacclimation to modified light conditions, but also greater leaf turnover and senescence of older leaves at the bottom of plant canopy (Vapaavuori et al. 1989; Vapaavuori and Vuorinen 1989; Pons and Pearcy 1994; Hikosaka 1996; Anten et al. 1998; Weih 2009). In fact, in species with short leaf life-span and fast leaf turnover, it has been demonstrated that shading, especially shading of individual leaves, can introduce programmed cell death, leading to rapid reductions of leaf photosynthetic capacity and leaf abscission (Burkey and Wells 1991; Pons and Pearcy 1994; Ackerly and Bazzaz 1995; Ono et al. 2001; Vos and van der Putten 2001; Boonman et al. 2006). On the other hand, compared with species with low rate of leaf turnover, photosynthetic capacity in species with high leaf turnover can relatively rapidly respond to increases in light availability (Pons and Pearcy 1994; Boonman et al. 2006).

D. Variations in Photosynthetic Plasticity Among Plant Functional Types

In *Q. ilex*, the relationships of M_A and photosynthetic potentials with Q_{int} were strongly curvilinear, with most of the change in foliage characteristics occurring over the light range of 2–12 mol m⁻² d⁻¹ (Fig. 4.2). In the case of M_A , clear site differences were evident at the saturating part of M_A vs. Q_{int} relationships, at Q_{int} values higher than ca. 12 mol m⁻² d⁻¹ (Fig. 4.2a). Although extensive, the ranges of variation in M_A , N_A and photosynthetic potentials in broad-leaved evergreens are somewhat smaller than the

within-canopy variations in these traits of two- to four-fold in the canopies of winter-deciduous forest trees (see Sect. V; e.g., Ellsworth and Reich 1993; Niinemets and Kull 1998; Iio et al. 2005; Niinemets and Anten 2009; Niinemets et al. 2015). In fact, in several deciduous broad-leaved species, there is only a moderate curvilinearity in leaf trait vs. Q_{int} relationships (Niinemets and Kull 1998; Meir et al. 2002; Aranda et al. 2004; Niinemets et al. 2015). The range of variation in trait vs. Q_{int} relationships is also high, more than two- to four-fold in several evergreen shade-tolerant conifers from genera *Abies* and *Picea* (Niinemets 1997a; Stenberg et al. 1998; Cescatti and Zorer 2003). However, there was a low within-canopy plasticity of 1.3–1.7-fold in two *Picea* species in the study of Ishii et al. (2003), and in *Pseudotsuga menziesii* and *Tsuga heterophylla* in the study of Bond et al. (1999). Low foliage plasticity 1.3–2-fold has been reported for several *Pinus* species (Bond et al. 1999; Niinemets et al. 2001, 2002a).

In the case of herbaceous species, high photosynthetic plasticity, typically two- to four-fold (Fig. 4.5f; Hirose and Werger 1994; Anten et al. 1995b; Niinemets et al. 2015), in exceptional cases close to or even more than an order of magnitude (Pons et al. 1993; Hirose and Werger 1994; Anten et al. 1995b, Chap. 5, Pons 2016) has been reported. This high plasticity is associated with moderate changes in leaf dry mass per unit area (Fig. 4.5a) and nitrogen allocation (Fig. 4.5d) and moderate to extensive changes in leaf nitrogen content per unit dry mass (Fig. 4.5b; Hirose et al. 1989; Lemaire et al. 1991; Evans 1993a, b; Hirose and Werger 1994; Niinemets et al. 2015; Chap. 5, Pons 2016).

Overall, there is evidence of greater photosynthetic plasticity in leaves with shorter life-span. The differences among evergreen and deciduous woody species mainly result from the circumstance that evergreens can reduce their M_A when growing in shade conditions less than deciduous species,

resulting in correspondingly narrower range in photosynthetic potentials in evergreens. High photosynthetic plasticity in herbaceous canopies is mainly associated with moderate to high gradients in all three determinants of photosynthetic capacity (Eqs. 4.1 and 4.2): M_A , nitrogen allocation and partitioning. In particular, gradients in nitrogen allocation in herbaceous species reflect the inherent strategy of resource remobilization from shaded leaves undergoing senescence to young developing leaves at the top of the canopy (Werger and Hirose 1988; Hikosaka et al. 1994; Hirose and Werger 1994; Hikosaka 1996; Franklin and Ågren 2002, Chap. 5, Pons 2016).

E. Importance of Within-Canopy Biochemical Modifications in Whole Canopy Photosynthesis

Within-canopy variation in key leaf traits allows for investment of photosynthesizing biomass in environments where the pay-back is higher, and has therefore been considered as an adaptive feature. Several studies have explored the quantitative benefits of trait variation using either numerical integration or optimality analyses (Field 1983; Hirose and Werger 1987b; Gutschick and Wiegell 1988; Farquhar 1989; Sands 1995; Anten 2005; Peltoniemi et al. 2012; Hikosaka 2014; Chap. 13, Anten 2016). There can be several target variables for optimization of canopy photosynthesis for given biomass investment in leaves (Gutschick and Wiegell 1988), maximization of canopy photosynthesis for given total canopy nitrogen content (Field 1983; Hirose and Werger 1987b; Farquhar 1989; Anten 2005; Chap. 13, Anten 2016) or maximization of canopy photosynthesis with given nitrogen and water use (Buckley et al. 2002; Farquhar et al. 2002; Peltoniemi et al. 2012). Overall, all optimality analyses have suggested that foliage photosynthetic capacity and nitrogen content should increase with average quantum flux density

in the canopy and that such “optimal” distribution of resources results in a higher carbon gain than a constant photosynthetic capacity for all leaves in the canopy (Fig. 4.6; Niinemets 2012 for a review).

Comparisons of predicted and observed canopy gradients, however, indicate that unconstrained optimality analyses predict too strong gradients in nitrogen content and foliage photosynthetic capacity (Niinemets and Anten 2009 and Chap. 13, Anten 2016 for reviews). Various hypotheses have been put forward to explain the discrepancies from full optimality. First of all, the condition of optimality can differ depending on the time scale and light characteristics, e.g., for diffuse and direct light (Hikosaka 2014). Thus, definition of the pertinent light (diffuse vs. direct, incident vs. absorbed, instantaneous vs. integrated) driving within-canopy acclimation can importantly modify the predicted optimal distribution. It has further been hypothesized that changes in foliage traits from canopy top to bottom are not only driven by light, but also by other co-varying environmental characteristics (Sect. I), in particular, by variations in evaporative demand (e.g., Niinemets and Valladares 2004). Meeting the needs for hydraulic and structural adjustment to ensure water flux to photosynthetically more active leaves and cope with potentially enhanced water availability limitations in the upper canopy can compromise full photosynthetic acclimation to high light (Peltoniemi et al. 2012; Chap. 7, Woodruff et al. 2016).

There are also biophysical limitations on the minimum and maximum thickness of leaves and their N content per unit dry mass, constraining leaf M_A and N_A values and ultimately leaf photosynthetic capacity in both high and low light (Gutschick and Wiegell 1988; Dewar et al. 2012; Niinemets 2012). Clearly, including constraints on M_A and N_A has resulted in more realistic predictions of within-canopy gradients in M_A , N_A and photosynthetic capacity (Gutschick and Wiegell 1988; Dewar et al. 2012) than assuming unconstrained variation in leaf traits (e.g., Farquhar 1989; Sands 1995).

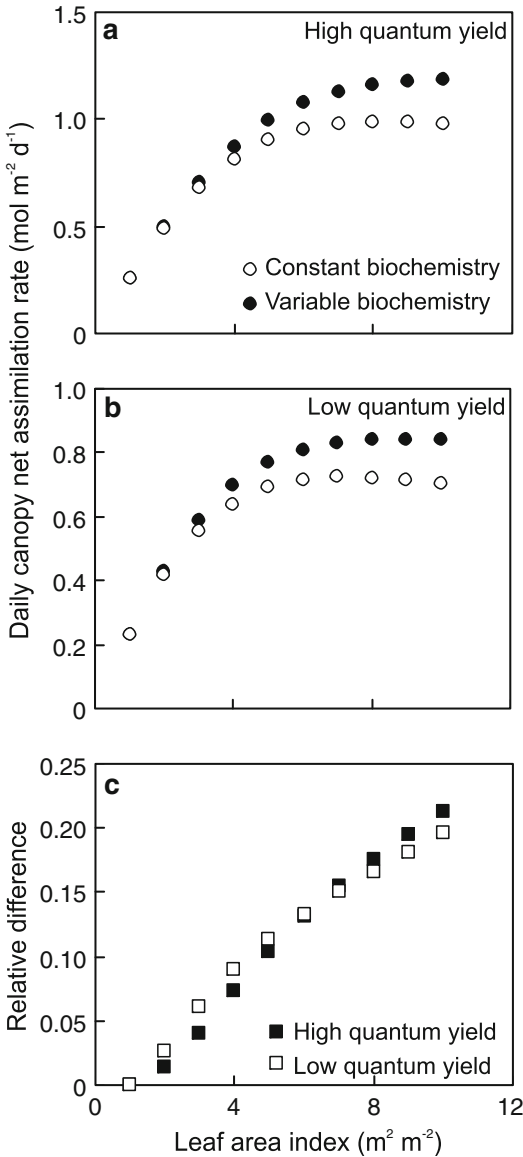


Fig. 4.6. Simulated whole canopy daily integrated photosynthesis (a, b) in dependence on canopy leaf area index (L) for hypothetical canopies with constant foliage biochemical potentials (canopy photosynthesis, $A_{c,\text{con}}$) and in canopies with light-dependent variation in foliage biochemical potentials ($A_{c,\text{var}}$), and (c) relative differences in daily canopy photosynthesis among canopies with constant and variable biochemistry, $(A_{c,\text{var}} - A_{c,\text{con}})/A_{c,\text{con}}$, in relation to L . The simulations were conducted for canopies with high initial quantum yield for photosynthetic electron transport for an incident light of $0.248 \text{ mol mol}^{-1}$ (a) and in canopies with a low quantum yield $0.15 \text{ mol mol}^{-1}$. The high quantum yield scenario corresponds to non-photoinhibited leaves with moderately high leaf absorbance of 0.85, while the low quantum yield

Using either constrained or unconstrained optimization algorithms, it is possible to analyze what is the possible significance of within-canopy variation in foliage traits in canopies of different leaf area index (L) and structure (Fig. 4.6; Anten et al. 1995a; Anten 2005; Chap. 13, Anten 2016). In the case of constrained optimization, the within-canopy gradient in A_{max}^A was fixed at a moderately high level of 2.6-fold between canopy top and bottom. In the case of unconstrained optimization, A_{max}^A was set directly proportional to Q_{int} . In all simulations, the whole-canopy leaf area-weighted average A_{max}^A was a given fixed constant value ($A_{\text{max},c}^A$). Thus, the “unconstrained” optimization used the greatest gradient to yield the given $A_{\text{max},c}^A$ value.

Independent of the way of modeling, these analyses suggest that the possible benefits of foliage acclimation to Q_{int} are greater for canopies with stronger light gradients, i.e.,

scenario corresponds to photoinhibited and/or highly reflective leaves. Foliage net assimilation rates were modeled according to Farquhar et al. (1980) photosynthesis model for constant values of leaf temperature of 25°C and CO_2 concentration in chloroplasts (C_c) of $280 \mu\text{mol mol}^{-1}$ and using the Rubisco kinetic characteristics as in Niinemets and Tenhunen (1997). In the case of the simulation with constant biochemistry, the maximum carboxylase activity of Rubisco was set at a value of $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the capacity for photosynthetic electron transport was scaled as $2.5V_{\text{cmax}}$, and non-photorespiratory respiration rate as $0.015V_{\text{cmax}}$ (see Niinemets et al. 1998b). A sine function with a maximum quantum flux density (Q) of $1,400 \mu\text{mol m}^{-2} \text{s}^{-1}$ was used to approximate the diurnal variations in above-canopy Q (Q_0). Variation in Q through the canopy was simulated according to a simple Lambert-Beer model assuming that foliage is randomly dispersed (the clumping index $\Omega = 1.0$): $Q = Q_0 e^{-k\Omega L}$, where k is the extinction coefficient ($k = 0.5$ in this simulation). In the case of variable biochemistry, V_{cmax} vs. daily integrated Q (Q_{int}) relationships were fitted for canopies with different L by linear regressions such that the ratio of the values of V_{cmax} at the top of the canopy ($V_{\text{cmax},t}$) and at the bottom ($V_{\text{cmax},b}$) was 2.6 (moderately high within-canopy variation in foliage biochemical potentials) and the whole-canopy leaf area-weighted average V_{cmax} was $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. All other characteristics of Farquhar et al. (1980) photosynthesis model were varied with V_{cmax} as in the simulations with the constant biochemistry

in canopies with a larger leaf area index (Fig. 4.6a, b) and in canopies with higher light extinction coefficient (data not shown, see Chap. 9, Hikosaka et al. 2016b for gradients of cumulative L and light). In the case of the constrained optimization, the optimal distribution was expected to increase whole canopy photosynthesis between 1.5 and 21 % compared with all leaves having a constant photosynthetic capacity equal to $A_{\max,c}^A$. The effect of considering within-canopy variation in leaf traits increased with increasing L (Fig. 4.6c). Of course, the stronger the within-canopy gradient in photosynthetic characteristics, the greater is the overall whole-canopy photosynthetic benefit. In the case of “unconstrained” optimization of A_{\max}^A , whole-canopy photosynthetic rate was predicted to be ca. 50 % greater than in the simulation with a constant A_{\max}^A (data not shown).

The photosynthetic benefit might seem relatively small for open canopies (Fig. 4.6a), especially when the whole-canopy gradient in A_{\max}^A is moderate as for instance in the Mediterranean evergreen *Q. ilex* (Fig. 4.2). Nevertheless, even a moderate improvement of long-term carbon gain can importantly benefit the plant in highly stressful environments where the annual carbon gain is significantly reduced due to soil drought. Furthermore, drought stress often leads to photoinhibition, importantly reducing the initial quantum yields of photosynthetic electron transport and carbon assimilation (Niinemets and Keenan 2014 for a review). The implication of such a reduction in the initial quantum yields is that the light saturation point of photosynthesis is shifted to higher quantum flux densities, and thus higher quantum flux densities appear limiting to photosynthesis. The overall effect in terms of whole-canopy photosynthesis is that the canopy photosynthesis decreases with a reduction of the quantum yield (cf. Fig. 4.6a, b). However, photosynthesis of canopies with low to moderate L , becomes much more sensitive to within-canopy variations in A_{\max}^A (Fig. 4.6b, c). Thus, within-canopy differences in photosynthetic capacity can

importantly benefit photosynthesis in relatively open canopies as well, especially under conditions leading to reduction of quantum yields of photosynthesis such as drought and photoinhibition stresses.

IV. Variations in Traits Improving Light Harvesting and Protecting from Excess Light

Apart from the major within-canopy modifications in foliage functional traits that result in alterations in foliage photosynthetic potentials, variations in a number of leaf traits also alter leaf light harvesting efficiency and/or play a role in avoidance of excess light harvesting. Given the interaction of light with other environmental drivers (Sect. I), there are also significant within-canopy gradients in abiotic stress. In particular, leaves exposed to high irradiances can be severely heat- and drought-stressed, especially in conditions of soil drought, while in the lower canopy, the photosynthetic productivity is still most severely limited by light availability. The interactive effects of environmental drivers are further complicated by highly dynamic nature of light in plant canopies. In this section, I analyze variations in structural and chemical traits responsible for alterations in light harvesting and abiotic stress tolerance, and further consider the dynamic responses of leaf traits to rapid changes in light availability.

A. Structural Traits as Determinants of Light Harvesting and Avoidance

Section III.A indicated that acclimation to low light availability in the bottom of a plant canopy is associated with enhanced investment of nitrogen in chlorophyll and pigment-binding complexes (see Fig. 4.3), and analogous relationships have been observed in a number of species (Niinemets and Anten 2009 for a review). Such enhanced investment of nitrogen in light harvesting within the leaf enhances light harvesting per unit mass, i.e., increases

light availability of an average mesophyll cell (e.g., Niinemets 2007). Although researchers seldom think of light harvesting as a mass-based phenomenon, mass basis characterizes the cost of light harvesting in terms of resource investment.

Differently from the mass basis, area-based chlorophyll contents may increase (Fig. 4.3b), be invariable or decrease with increasing Q_{int} (e.g., Hallik et al. 2009a). Nevertheless, due to non-linear dependence of leaf absorptance on leaf chlorophyll content (Eq. 4.3), effects of such changes in area-based chlorophyll content generally result in minor within-canopy modifications in leaf absorptance (e.g., St-Jacques et al. 1991; St-Jacques and Bellefleur 1993; Poorter et al. 1995). Given this, major reductions in M_A in woody species in low light constitute an important acclimation response leading to greater light intercepting surface area, and thus, enhanced light interception with given biomass investment in leaves.

Light harvesting efficiency in needle-leaved species can also be enhanced by changes in total to projected leaf area ratio (S_T/S_P). S_T/S_P decreases strongly with decreasing Q_{int} in some shade-tolerant conifers such as in *Picea* and *Abies* (Niinemets and Kull 1995; Sprugel et al. 1996; Cescatti and Zorer 2003), increasing the light harvesting surface area at the given total surface area in lower light. However, minor modifications or invariable S_T/S_P have been observed in intolerant conifers from the genus *Pinus* (Niinemets et al. 2001, 2002a) and in the angiosperm *Casuarina* with needle-like cladodes (Niinemets et al. 2005b).

Furthermore, at the shoot scale, the degree of foliage spatial aggregation in shoots decreases with decreasing Q_{int} , implying reduction of within-shoot shading (Stenberg 1996, 1998; Smolander and Stenberg 2001; Cescatti and Zorer 2003; Niinemets et al. 2006b). In addition, foliage inclination angle distributions within shoots become more horizontal in the lower canopy in several shade-tolerant conifers, thereby improving interception of light from vertical

inclination angles that constitute a more prevalent source of both diffuse and direct radiation in the lower canopy (Stenberg 1996, 1998; Cescatti and Zorer 2003; Niinemets et al. 2006b). On the other hand, greater foliage aggregation and more vertical foliage inclination angles at higher irradiances reduce mean irradiance on leaf surface, and thus reduce the degree of foliage photoinhibition and severity of heat stress (Cescatti and Zorer 2003; Niinemets et al. 2006b). This implies that modifications in needle and shoot structure play a dual role, improving light harvesting in low light and avoiding excess radiation interception at high light.

In broad-leaved species, there are also classic changes in leaf inclination angle distributions analogous to conifers (Fig. 4.7a; for reviews see Niinemets 2010; Chap. 2, Goudriaan 2016). In addition to changes in average leaf inclination angle from vertical to horizontal with decreasing light availability in the canopy, there are also important modifications in the degree of lamina flatness in several broad-leaved species. In particular, leaves tend to be increasingly rolled at the top of plant canopies (Fig. 4.7b). Such increases in the degree of foliage rolling can strongly reduce leaf light interception and also change the share of light interception by leaf lower and upper surface (Fleck et al. 2003). Consideration of both the within-canopy changes in leaf inclination angle and degree of leaf rolling indicates that the overall efficiency of light interception may vary more than two-fold within the canopy of broad-leaved species due to modifications in these structural traits (Fig. 4.7c). Thus, modifications in inclination angles and degree of rolling play a major role in altering the balance between light interception and avoidance. Overall, these case studies suggest that avoidance of excess light interception leads to a more uniform illumination of foliage in the canopy, i.e., greater penetration of light into deeper canopy layers. Simulations studies indicate that more uniform light distribution strongly benefits the whole canopy carbon gain

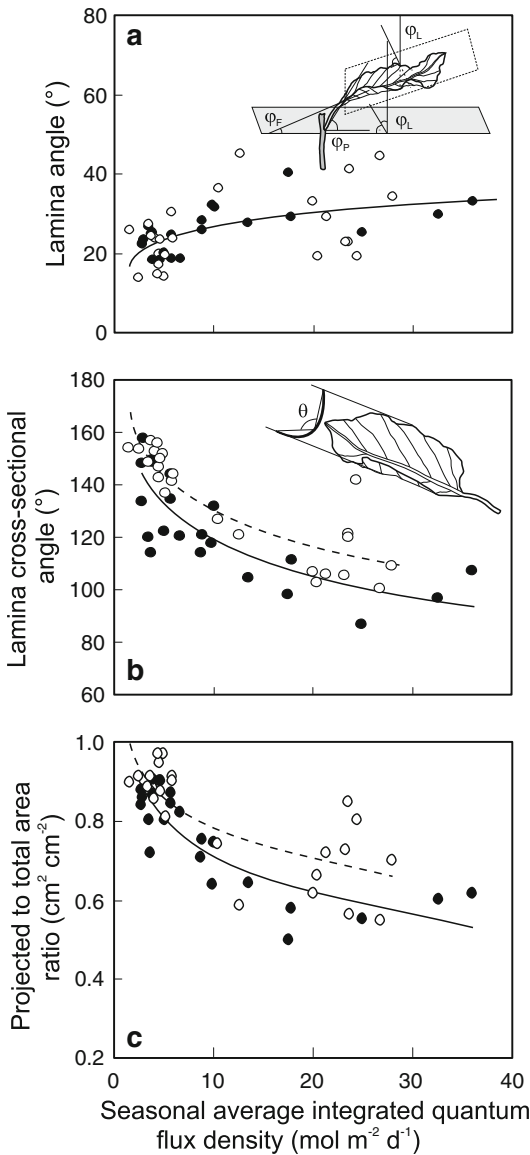


Fig. 4.7. Effects of seasonal average daily integrated quantum flux density (Q_{int}) on (a) the absolute lamina inclination angle, i.e., the average angle between the normal to the leaf plane and the vertical direction ($|\phi_L|$, inset in (a) for the definition), (b) lamina cross-sectional angle (θ , inset in (b) for the definition) and (c) lamina projected to total area ratio in a dominant (filled circles) and a sub-dominant tree (open circles) of the temperate deciduous species *Fagus sylvatica*. Inset in (a) also demonstrates the definition of inclination angles of petiole (ϕ_P) and leaf lamina at leaf fall-line (ϕ_F). Data fitting as in Fig. 4.5 ($P < 0.001$ for all). In (a), the slopes and intercepts of $|\phi_L|$ vs. $\ln Q_{int}$ relationships did not differ among the trees according to covariation analyses, and thus, the data for both trees were fitted by a common regression. Modified from Fleck et al. (2003)

(Ryel et al. 1994; Hikosaka and Hirose 1997; Werner et al. 2001a; Cescatti and Niinemets 2004; Valladares and Niinemets 2007), and thus, “optimization” of canopy structure constitutes an important means to maximize canopy carbon gain.

B. Chemical Traits Improving Abiotic Stress Tolerance

Excess light intercepted during midday on clear days can result in severe photooxidative damage of photosynthetic apparatus compromising photosynthetic activity in the morning and evening periods and on overcast days when light intensities are lower. Temporal exceeding of leaf heat stress limits during lighflecks and upon sustained exposure to high radiation loads can further result in heat damage of photosynthetic apparatus. All such adverse effects are expected to be more significant in the upper canopy due to greater radiation loads (Sect. I).

Plants cope with excess energy by increasing the capacity for non-photochemical quenching (non-radiative dissipation of excess light energy), in particular, through xanthophyll cycle. In the xanthophyll cycle, the xanthophyll violaxanthin is converted into xanthophylls antheraxanthin and zeaxanthin under strong light by violaxanthin deepoxidase enzyme (Demmig-Adams and Adams 1994, 1996b, 2006). This process is activated by acidification of chloroplast lumen when photosynthetic electron transport exceeds the capacity for electron use in dark reactions of photosynthesis, and ultimately, zeaxanthin formation together with acidification result in thylakoid conformational changes that lead to enhanced non-radiative dissipation of excess light (Demmig-Adams and Adams 1994, 1996, 2006; Gilmore et al. 1994; Arnoux et al. 2009). The capacity for non-radiative energy dissipation depends on the pool size of xanthophyll cycle carotenoids, violaxanthin, antheraxanthin and zeaxanthin (VAZ) (Demmig-Adams and Adams 1996a; Demmig-Adams et al. 1998; Logan et al. 1996).

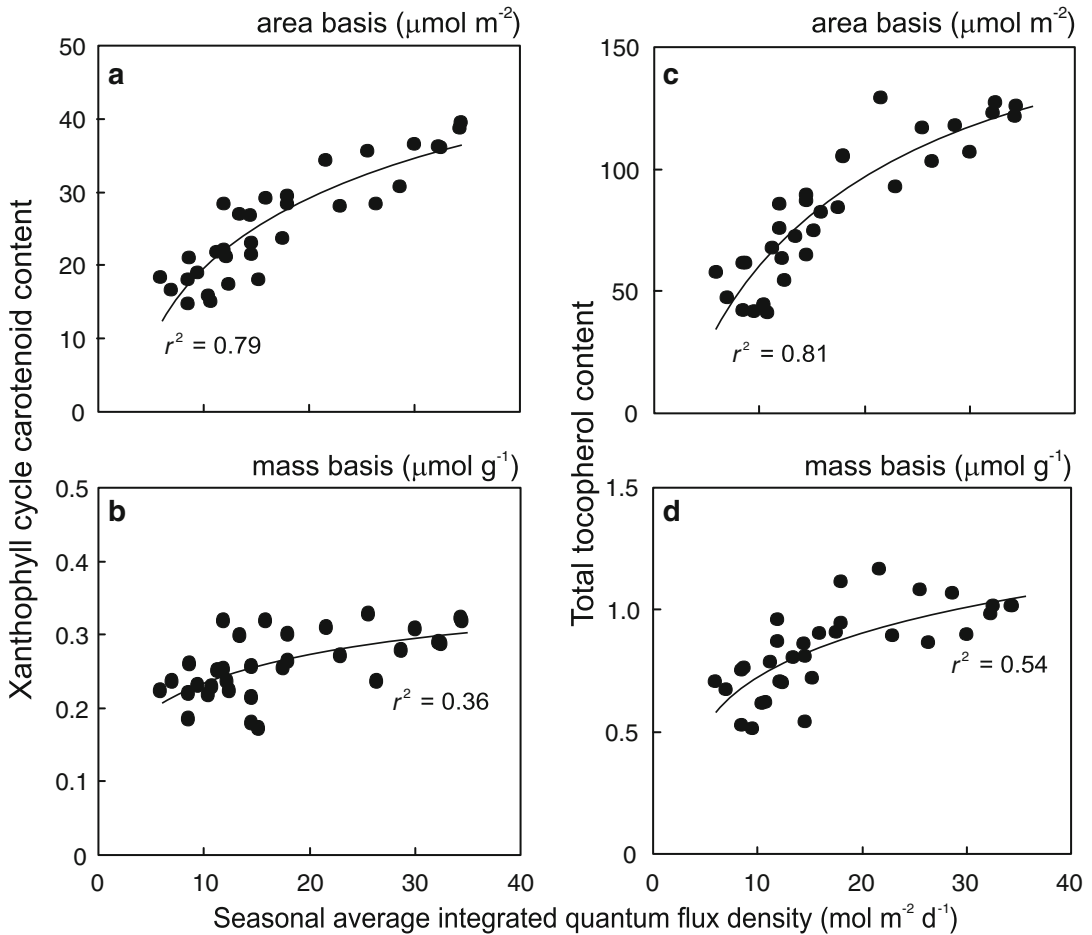


Fig. 4.8. Correlations of xanthophyll cycle carotenoids (VAZ) (a, b) and total tocopherol (c, d) contents per unit area (a, c) and dry mass (b, d) with seasonal average integrated incident quantum flux density (Q_{int}) in the canopy of the temperate deciduous tree *Populus tremula*. VAZ is the sum of contents of violaxanthin, antheraxanthin and zeaxanthin (Data of Niinemets et al. 2003), and total tocopherol content is the sum of contents of α -, β -, δ - and γ -tocopherol (Data of García-Plazaola et al. 2004). Data were fitted by non-linear regressions as in Fig. 4.5 ($P < 0.001$ for all)

Acclimation to high irradiance typically results in increases in VAZ pool size (Fig. 4.8a, b; Demmig-Adams et al. 1999; Demmig-Adams and Adams 2006). The within-canopy range of variation in leaf area-based VAZ pool size is often three- to four-fold (Fig. 4.8a). Since VAZ content per unit dry mass also increases with increasing light availability (Fig. 4.8b), this increase does reflect greater VAZ content and higher capacity for safe dissipation of excess excitation energy of single mesophyll cells at higher light (e.g., Niinemets et al. 1998a,

2003). However, differently from foliage photosynthetic capacity and nitrogen allocation that are relatively invariable during growing season in temperate trees (Niinemets et al. 2004c; Grassi and Magnani 2005; Grassi et al. 2005), the adjustment in VAZ pool size to changed light conditions is much faster, occurring typically in a few days (Sect. IV.C). The pool sizes of other carotenoids, for example β -carotene and lutein pools, can also change along the light gradients, but the changes are typically only moderate compared with modifications in

VAZ. In fact, VAZ to carotenoid ratio also increases with increasing light availability in the canopy (e.g., Niinemets et al. 1998a, 1999a, 2003; Hansen et al. 2002).

Free non-protein-bound, VAZ, in particular zeaxanthin, has also been implicated in direct protection against photooxidative stress (Havaux and Niyogi 1999). In fact, plants have multiple antioxidant systems to cope with oxidative stress, including ascorbate and glutathione in leaf liquid phase and tocopherols in leaf lipid phase (Barclay et al. 1997; Noctor and Foyer 1998; Havaux and Niyogi 1999). In addition to VAZ, the contents of these specific liquid- and lipid-phase antioxidants increase with increasing light in the canopy (García-Plazaola and Becerril 2001; Hansen et al. 2002, 2003; García-Plazaola et al. 2004). However, the within-canopy variation seems to be larger for lipophilic antioxidants than for water-soluble antioxidants (García-Plazaola et al. 2004). For instance, in *Populus tremula*, total tocopherol content per unit area varied more than three-fold within the canopy (Fig. 4.8c), while total ascorbate and glutathione contents per leaf area varied only ca. 1.5-fold within the canopy (García-Plazaola et al. 2004). In fact, the within-canopy variation of total tocopherol content per unit dry mass was more than two-fold (Fig. 4.8d), while no strong canopy gradient was evident for liquid-soluble antioxidants expressed on a dry mass basis (García-Plazaola et al. 2004).

Some of the lipid-phase antioxidant systems have been implicated in heat stress resistance as well. In particular, zeaxanthin has been demonstrated to play an important role in maintaining membrane integrity in heat-stressed leaves (Havaux et al. 1996; Havaux and Tardy 1997). Furthermore, constitutive isoprene emissions have been demonstrated to improve foliage heat stress resistance in isoprene-emitting species (Sharkey and Singaas 1995; Singaas et al. 1997). Improvement of heat resistance by isoprene has been suggested to be due to direct involvement of isoprene in stabilization of membranes at higher temperatures or/and due to antioxidative properties of

isoprene that avoids peroxidation of membrane lipids in heat-stressed leaves (Sharkey et al. 2008; Vickers et al. 2009; Possell and Loreto 2013). Although isoprene is emitted constitutively only in a few emitting species (Kesselmeier and Staudt 1999; Fineschi et al. 2013), in the emitting species, there are extensive within-canopy gradients in isoprene emission rate (Harley et al. 1996, 1997; Funk et al. 2006; Niinemets et al. 2010). For example, in deciduous broad-leaved trees, the variation between canopy top and bottom was 27-fold for isoprene emission rate per leaf area (Fig. 4.9a) and 17-fold for isoprene emission rate per leaf dry mass (Fig. 4.9b). Furthermore, the fraction of photosynthetic carbon used for isoprene emission varied 12-fold (Fig. 4.9c), indicating that the plasticity in isoprene emission rate was more than a magnitude larger than the plasticity in net assimilation rate.

Taken together, the evidence summarized here demonstrates presence of major gradients in photoprotective pigment and antioxidant pools and isoprene emissions in plant canopies. These gradients in protective chemicals likely play key roles in coping with excess irradiance and recurrent heat stress events, whereas the protective capacity is particularly high at the top of plant canopies where the abiotic stress is often the greatest. Presence of such an extensive array of defenses plays a major role in preserving the integrity of foliage photosynthetic capacity through stress periods and allows for rapid onset of photosynthesis when the stress is relieved.

C. Dynamics in Protective Traits After Rapid Changes in Light Availability

As mentioned in Sect. IV.B, VAZ pool size adjusts to changes in light regime much faster than leaf structure, nitrogen content and allocation and photosynthetic capacity, although the rate of change in photosynthetic traits depends on plant growth form (Sect. III.C). In fact, it seems that the acclimation to potentially damaging high

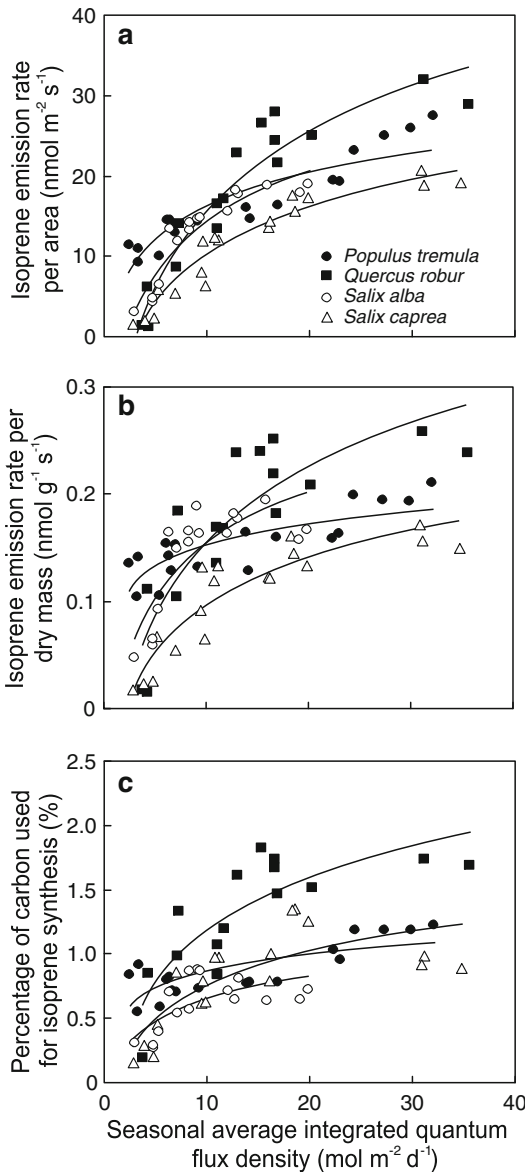


Fig. 4.9. Light-dependent variations in isoprene emission rate per unit leaf area (a) and dry mass (b) and the percentage of photosynthetic carbon used for isoprene emission (c) within the canopies of four temperate deciduous species. Data fitting as in Fig. 4.2 ($P < 0.001$ for all relationships). Measurements of isoprene emission and net assimilation rates were conducted at an ambient CO_2 concentration of $380 \mu\text{mol mol}^{-1}$, light intensity of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and leaf temperature of $25 \text{ }^\circ\text{C}$. Modified from Niinemets et al. (2010)

irradiance is governed by adjustments in foliar photosynthetic capacity in long-term, while the safe dissipation of excess light energy is accomplished by changes in xanthophyll cycle pool size during short-term weather fluctuations. However, as discussed in the Sect. III.C, acclimation to altered light conditions not always occurs, and either shading or exposure to excessive light can result in a continuous time-dependent decline in foliage photosynthetic rates and pigment contents, and ultimately leaf abscission.

Provided leaves do acclimate to the modified conditions, the key questions are what is the overall capacity for adjustment of VAZ content and antioxidant pools to changes in light conditions and whether the rate of acclimation varies within the canopy? Field data can to some extent be used to study the speed of xanthophyll cycle acclimation in ecosystems with significant day-to-day variations in quantum flux densities. For instance, in temperate humid forests, clear days are commonly intervened with overcast days such that day-to-day variation in above-canopy irradiance is several-fold (Niinemets et al. 2004c). Averaging quantum flux density over various number of days preceding measurement of physiological and chemical characteristics and using these various estimates of average integrated light can be used to test the strength of correlations of integrated light vs. leaf trait relationships in dependence on the length of light integration period (Ögren and Sjöström 1990; Niinemets et al. 1998a, 1999a; Geron et al. 2000; Werner et al. 2001b).

Using such an approach, it was observed that integrated light for 3 days preceding foliage sampling best explained the within-canopy variation in VAZ pool size in a temperate deciduous tree canopy (Niinemets et al. 1998a, 1999a). This result indicates that VAZ pool size can rapidly adjust to day-to-day variations in light conditions, thereby quickly regulating the capacity for non-photochemical quenching of excess

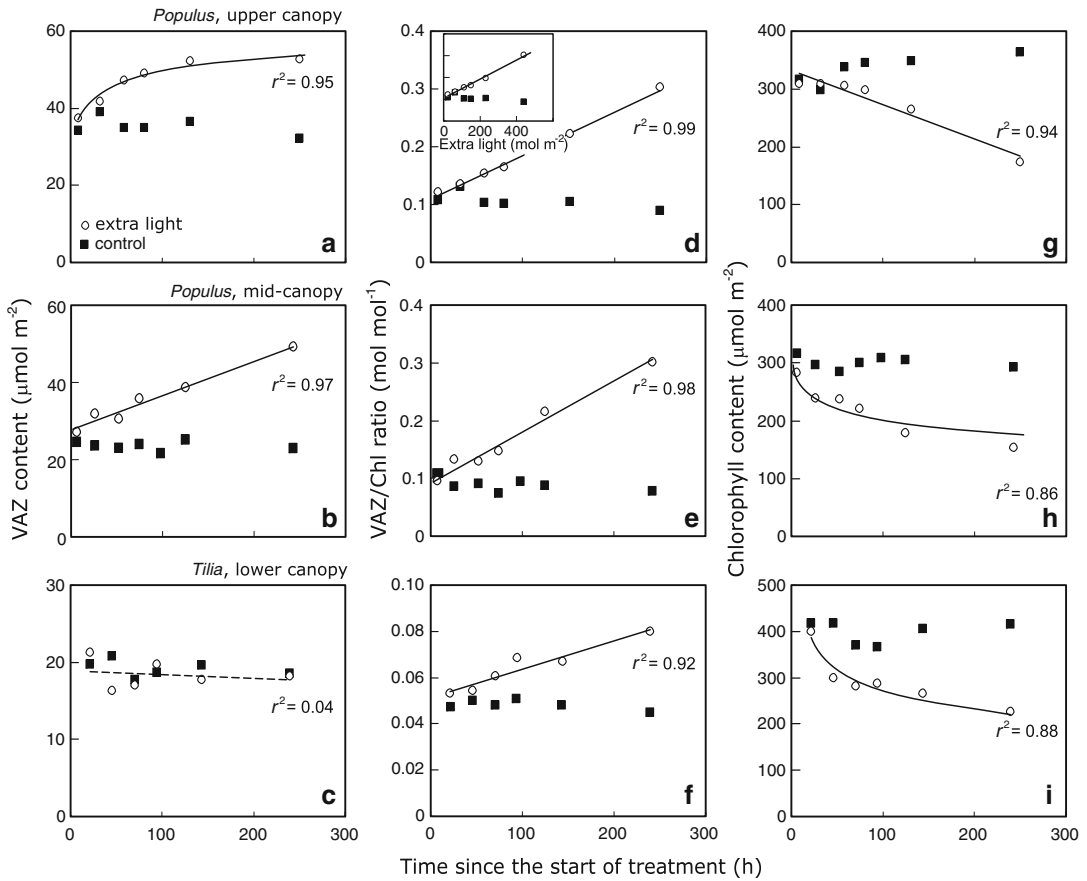


Fig. 4.10. Effects of illumination with extra light of ca. $40\text{--}50\text{ mol m}^{-2}\text{ d}^{-1}$ upon foliage pigment contents at different positions in the tall tree canopy: time-dependent changes in xanthophyll cycle carotenoid (VAZ) content per unit area (a–c), ratio of VAZ to chlorophyll (Chl) content (VAZ/Chl, d–f) and chlorophyll content (g–i) for representative control and illuminated leaves of temperate deciduous trees *Populus tremula* from the upper (a, d, g) and the mid-canopy (b, e, h) and *Tilia cordata* from the lower canopy (c, f, i). In addition, the inset in (d) demonstrates the variation in VAZ/Chl ratio in relation to cumulative extra irradiance in *P. tremula* (the control treatment corresponds to leaves without extra light sampled at the same time as the treated leaves). The data were fitted by non-linear (a, h, i) or linear (all others) regressions. The non-significant regression ($P > 0.8$) in (c) is drawn by a dashed line. In the upper-canopy leaves of *P. tremula* (height 23 m), the seasonal average natural integrated irradiance (Q_{int}) was $34.4\text{ mol m}^{-2}\text{ d}^{-1}$ for both the control and the treated leaf, and the extra irradiance was $40.8\text{ mol m}^{-2}\text{ d}^{-1}$. In the mid-canopy leaves of *P. tremula* (height 19 m), Q_{int} was $22.5\text{ mol m}^{-2}\text{ d}^{-1}$ for the control and $18\text{ mol m}^{-2}\text{ d}^{-1}$ for the treated leaf, and the extra irradiance was $50.6\text{ mol m}^{-2}\text{ d}^{-1}$. In the lower canopy leaves of *T. cordata* (height 17 m), Q_{int} was $6.03\text{ mol m}^{-2}\text{ d}^{-1}$ for the control and $6.10\text{ mol m}^{-2}\text{ d}^{-1}$ for the treated leaf, and the extra irradiance of the illuminated leaf was $48.0\text{ mol m}^{-2}\text{ d}^{-1}$. Data of Niinemets et al. (2003)

light to match the changed light conditions. However, using illumination with extra light, it was further demonstrated that the degree of acclimation in VAZ pool size varies through the canopy and that there are different response kinetics in leaves developed at different light availabilities in the canopy (Niinemets et al. 2003). In particular, VAZ

pool size was less responsive in the lower canopy species *Tilia cordata* than in the upper canopy species *Populus tremula*, and the initial increase in VAZ pool size tended to be faster in the upper canopy of *Populus tremula* (Fig. 4.10a–c). Furthermore, the ratio of VAZ to chlorophyll content was more responsive to extra illumination in the

upper canopy leaves in both species (Niinemets et al. 2003; Fig. 4.10d–f), reflecting within-canopy differences in the response of chlorophyll contents to extra illumination (Niinemets et al. 2003, Fig. 4.10g–i). Foliage tocopherol contents responded even stronger to extra illumination than leaf pigments, and the rate of increase of tocopherol content was greater in upper canopy leaves (García-Plazaola et al. 2004). These results together demonstrate that the overall degree of adjustment in pigment pools and foliage antioxidative capacity after light changes can importantly depend on leaf past acclimation status.

Although pigment and antioxidant pool sizes dynamically respond to variations in light input among days, the experiment with extra illumination in the canopies of deciduous trees demonstrated that full acclimation was not reached even after 11 days of exposure to extra light (Fig. 4.10). This delayed response is in agreement with several other experimental studies that have indicated that the response to stepwise increase in light in the field conditions may not even be fully completed in 17 days after start of exposure to enhanced illumination (Logan et al. 1998a, b). This differs from experiments in growth chambers under constant environmental conditions where changes in VAZ and antioxidant pools were completed in 5–7 days after stepwise increases in irradiance (Demmig-Adams et al. 1989; Bilger et al. 1995; Eskling and Åkerlund 1998). This suggests that in natural plant canopies under strongly fluctuating light, temperature and humidity conditions, pigment and antioxidant systems are inherently in non-steady-state conditions. Although pigment pools do rapidly adjust to environmental changes, the period of environmental fluctuations is often shorter than is needed to reach the steady-state pigment and antioxidant pool sizes. Furthermore, the rate of response to altered conditions significantly varies through the canopy, being likely an important factor determining leaf abiotic stress resistance in the canopy.

V. Photosynthetic Acclimation in Relation to Species Shade Tolerance

The term “economics spectrum” characterizes the covariation of foliage traits associated with superior performance in low resource environments such as structurally more robust foliage, and traits that improve fitness in high resource environments such as enhanced photosynthetic capacity (e.g., Wright et al. 2004, 2005). However, shading is associated both with reduced foliage robustness and reduced photosynthetic capacity, especially within single species, but also for several plant functional types (Lusk et al. 2008; Hallik et al. 2009b; Niinemets and Anten 2009). Thus, compared with other stresses, shading constitutes an outlying low resource environment. Here I analyzed within-canopy patterns in key foliage functional traits from the perspective of the leaf economics spectrum with main focus on Northern hemisphere temperate species.

A. Evidence from the Case Studies

Section III demonstrated that there are important differences in the within-canopy variations in different leaf traits among plant functional types and that these differences are associated with differences in leaf turnover. Apart from differences among plant functional types, plant stands are often composed of species with different ecological potentials. Characteristically, species in the lower canopy layers and in dense late-successional communities have greater shade tolerance than species in the upper canopy positions and in more open early-successional communities (Valladares and Niinemets 2008). Differences in community position among shade-tolerant and intolerant species are also associated with differences in leaf trait vs. Q_{int} relationships. In broad-leaved deciduous trees, M_A often responds less plastically to Q_{int} in more shade-tolerant than in less tolerant species (Fig. 4.11, Kull and Niinemets 1998; Niinemets et al. 1998b;

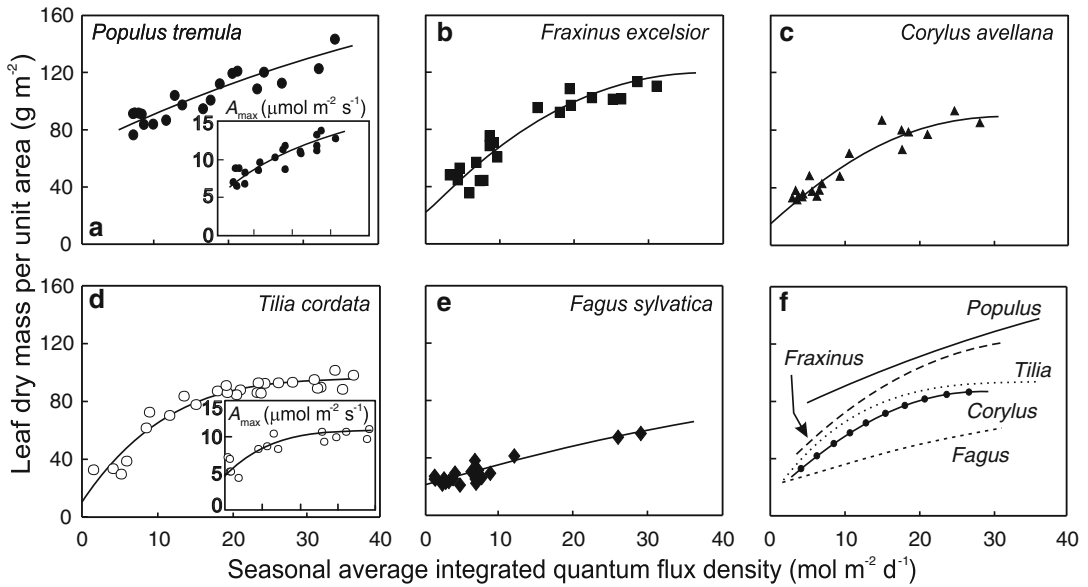


Fig. 4.11. Comparison of light-dependent variations in leaf dry mass per unit area within the canopies of five temperate deciduous woody species of contrasting shade tolerance. The insets demonstrate variations in leaf photosynthetic capacity with Q_{int} . Data fitting as in Fig. 4.5 (all relationships are significant at $P < 0.001$). Species are ranked according to shade tolerance score (SC, Niinemets and Valladares 2006) from the least tolerant to the most tolerant as: *Populus tremula* (SC = 2.3), *Fraxinus excelsior* (2.9), *Corylus avellana* (3.5), *Tilia cordata* (4.2) and *Fagus sylvatica* (4.6). Shade tolerance score is a relative measure varying from 1 (least tolerant) to 5 (most tolerant) that characterizes species capacity to endure shade relative to other species (Niinemets and Valladares 2006 for a detailed definition; Valladares and Niinemets 2008. Data for *Fagus sylvatica* are from Niinemets (1995) and for the four other species from Niinemets et al. (1998b)

Valladares and Niinemets 2008). However, such a pattern is not always observed (e.g., very intolerant *Populus tremula* in Fig. 4.11a vs. very tolerant *Fagus sylvatica* in Fig. 4.11e). Although shade-intolerant species can maintain leaves at low light availabilities when grown in monocultures (Nygren and Kellomäki 1983; Niinemets et al. 2004a), the situation is different in multi-species canopies where shade-tolerant species gradually grow into the upper canopy, and the foliage of intolerant species competes for light availability with foliage of tolerant species in the lower and mid-canopy. Thus, the apparent low plasticity in *P. tremula* in Fig. 4.11a might reflect the general circumstance that in multispecies canopies intermixed with shade-tolerant species, the intolerant species may not simply be able to maintain leaves below a certain Q_{int} value (ca. 7–8 mol m⁻² d⁻¹ for *P. tremula* in Fig. 4.11a).

As in broad-leaved deciduous woody species, within-canopy plasticity in foliage photosynthetic potentials is mainly driven by changes in M_A that result in stacking of rate-limiting photosynthetic proteins per unit leaf area (Sect. III.C), lower within-canopy plasticity in M_A is also associated with lower photosynthetic plasticity in less shade-tolerant species (Kull and Niinemets 1998; Niinemets et al. 1998b). It has further been demonstrated that the sensitivity to photoinhibition is greater in more shade-tolerant species (Lovell et al. 1994; Chazdon et al. 1996; Naidu and DeLucia 1997) that also generally possess lower photosynthetic capacities (Bazzaz 1979; Lovell et al. 1994).

On the other hand, shade-tolerant temperate species can support foliage at lower Q_{int} than intolerant species and have both smaller minimum and maximum M_A values (Fig. 4.11). Thus, despite lower

photosynthetic plasticity, shade-tolerant species can form a greater leaf area with given foliage biomass in leaves, improving light interception of the canopy. Such a greater light interception capacity not only improves the whole canopy carbon gain, but the shading by more extensive canopy itself can serve as an important competitive attribute constraining the survival of seedlings and saplings of less shade-tolerant competitors and ultimately leading to dominance of shade-tolerant late-successional plants in the canopy (Küppers 1985; Schieving and Poorter 1999; Anten 2002).

Much less data are available for within-canopy gradients in tropical and southern hemisphere temperate evergreen species. In three tropical species, within-canopy plasticity in M_A , N_A and A_{\max}^A was greater in shade-intolerant evergreen species *Ficus insipida* than in more tolerant *Luehea seemannii*, whereas the highest plasticity was observed in the shade-intolerant drought-deciduous species *Castilla elastica* (Posada et al. 2009). Among the tropical *Piper* species of varying shade tolerance, the within-canopy plasticity in M_A , N_A and A_{\max}^A of shade tolerant *P. aequale* and *P. lapathifolium* was less than in moderately tolerant *P. hispidum* and intolerant *P. auritum* and *P. umbellatum* (Chazdon and Field 1987). Among southern hemisphere temperate evergreen *Nothofagus* species, more shade tolerant *Nothofagus solandri* var. *cliffortoides* had a greater within-canopy plasticity in M_A than less tolerant *N. fusca*, but the plasticity in N_A did not differ among species (Niinemets et al. 2004b). In another study in temperate southern hemisphere evergreens, more tolerant *Nothofagus solandri* var. *cliffortoides* had a greater plasticity in M_A than very intolerant species *Kunzea ericoides* (White and Scott 2006). However, in this study, other moderately shade-tolerant species had a similar within-canopy plasticity in M_A as the very intolerant *K. ericoides* (White and Scott 2006). Clearly more comparative studies are needed to gain conclusive insight into the controls of foliage plasticity by shade tolerance in tropics and in southern hemisphere temperate ecosystems.

B. Generalizing the Patterns

The conclusions drawn from the case studies in temperate deciduous broad-leaved species seem to be valid more widely. Broad-scale analyses of structural, chemical and physiological variation in high-light-developed leaves across Northern hemisphere temperate woody flora indicate that M_A decreases with increasing species shade-tolerance also in broad-leaved and needle-leaved evergreen species (Fig. 4.12a). Thus, formation of an extensive leaf area is also the key competitive strategy in shade-tolerant evergreen species (Niinemets 2010; Warren et al. 2012). However, in temperate evergreens, greater canopy leaf area in more tolerant species is also importantly driven by enhanced leaf longevity (Hallik et al. 2009b; Niinemets 2010).

Differently from M_A , nitrogen content per unit area (Fig. 4.12b) and photosynthetic capacity per unit area (Fig. 4.12c) were not correlated with species shade tolerance in temperate evergreens. However, the patterns developed for leaves exposed to high light do not necessarily provide insight into variations in within-canopy plasticity in foliage structure and photosynthetic potentials. Given the higher leaf longevity in shade-tolerant species and reduction in leaf-level plasticity with leaf age (Fig. 4.4), canopy-level photosynthetic plasticity across leaves of different age might be lower in more shade-tolerant species.

Differently from Northern hemisphere temperate species, M_A of tropical evergreens and southern hemisphere temperate evergreens is typically higher in more shade tolerant species than in less tolerant species (Chazdon 1992; Kitajima 1994; Lusk 2004; Lusk et al. 2008; Houter and Pons 2012). Thus, higher biomass investment is needed for a given plastic change in M_A in more shade tolerant species, implying that the high initial M_A may limit both structural and photosynthetic plasticity in shade tolerators. Further studies are needed to generalize within-canopy plastic changes in evergreens of different shade tolerance in both temperate and tropical ecosystems.

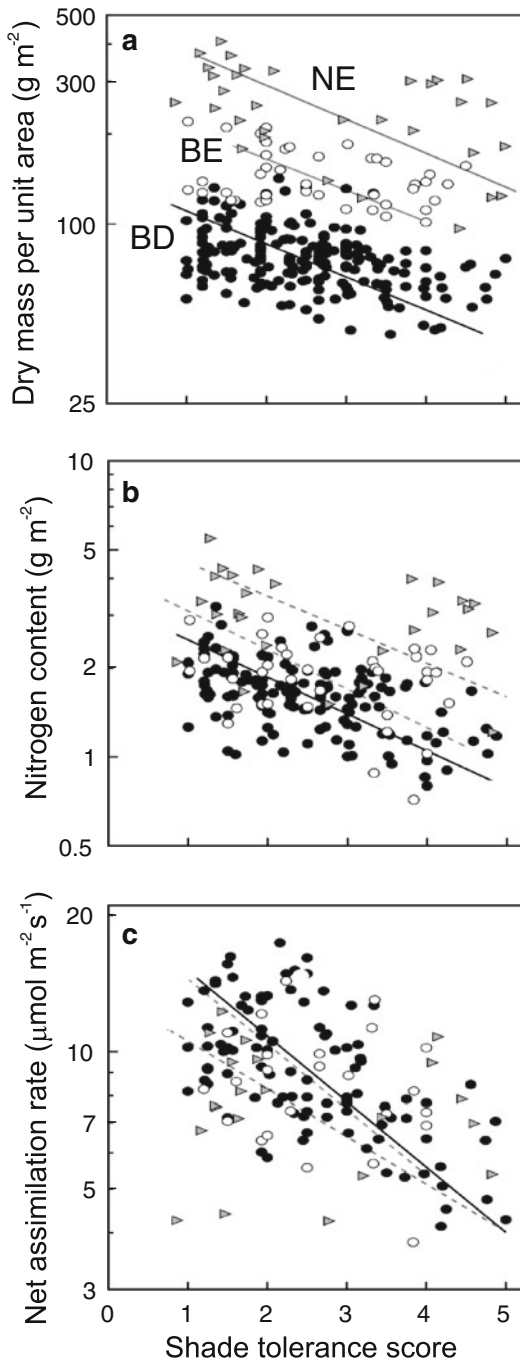


Fig. 4.12. Correlations of leaf dry mass per unit area (a), nitrogen content per unit area (b) and light-saturated net assimilation rate per unit area (photosynthetic capacity, c) with species shade tolerance score in Northern hemisphere broad-leaved deciduous (BD), broad-leaved evergreen (BE) and needle-leaved evergreen (NE) trees and shrubs ($n = 341$, modified from

VI. Conclusions

This review highlights major within-canopy modifications in foliage photosynthetic capacity that improve the whole canopy carbon gain compared with a hypothetical canopy with constant photosynthetic capacity for all leaves in the canopy. While scaling of photosynthetic capacity with long-term average integrated quantum flux density is a ubiquitous response in plants, there are important plant functional type differences in the scaling of key foliage functional traits with light availability. The rate of foliage turnover increases in the sequence evergreens < deciduous woody species with deterministic growth < deciduous woody species with indeterminate growth < herbaceous species. The evidence summarized here indicates that plant functional type differences in canopy growth phenology and differences in leaf turnover importantly alter the significance of various leaf traits in determining the within-canopy acclimation of foliage photosynthetic capacity.

This chapter also emphasizes that environmental gradients are typically complex in plant canopies. Leaves at the top of plant canopies often can suffer from more severe water, photoinhibition and oxidative stresses that can constrain photosynthetic acclimation to canopy light regime. Furthermore, coping with such interacting stresses typically leads to structural adaptations reducing excess light interception in the upper canopy, and chemical modifications improving the stress resistance. In fact, within-canopy variations in protective traits can be much larger than in photosynthetic characteristics, and there are further significant within-canopy variations in the degree and rate of adjustment of the pools of protective chemicals to dynamically changing light conditions.

Hallik et al. 2009b). Species shade tolerance score defined as in Fig. 4.11. Data were fitted by standardized major axis regressions using SMATR 2.0 (Warton et al. 2006) and non-significant regressions ($P > 0.05$) are shown by dashed lines

There is still a limited understanding of species differences in foliage plasticity to within-canopy environmental gradients, but the evidence summarized suggests that shade tolerance is an important driver of species plasticity. Shade-tolerant species growing in understory and in late-successional communities characteristically form a greater foliage area and have superior light harvesting capacity, but their photosynthetic capacity and plasticity seem to be lower than in less tolerant species growing in more open communities and in early-successional habitats where rapid carbon gain capacity is the primary attribute of competition. Further studies are needed to gain insight into the generality of suggested variation patterns of foliage plasticity with species ecological potentials. Understanding such plastic variations is not only fundamentally important, but would allow construction of more realistic carbon gain models capable of simulating ecosystem carbon gain through ecosystem development.

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