**Plant responses to heterogeneous environments**

Ülo Niinemets

# A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance

**Abstract** Changes in the efficiency of light interception and in the costs for light harvesting along the light gradients from the top of the plant canopy to the bottom are the major means by which efficient light harvesting is achieved in ecosystems. In the current review analysis, leaf, shoot and canopy level determinants of plant light harvesting, the light-driven plasticity in key traits altering light harvesting, and variations among different plant functional types and between species of different shade tolerance are analyzed. In addition, plant age- and size-dependent alterations in light harvesting efficiency are also examined. At the leaf level, the variations in light harvesting are driven by alterations in leaf chlorophyll content modifies the fraction of incident light harvested by given leaf area, and in leaf dry mass per unit area ($M_A$) that determines the amount of leaf area formed with certain fraction of plant biomass in the leaves. In needle-leaved species with complex foliage cross-section, the degree of foliage surface exposure also depends on the leaf total-to-projected surface area ratio. At the shoot scale, foliage inclination angle distribution and foliage spatial aggregation are the major determinants of light harvesting, while at the canopy scale, branching frequency, foliage distribution and biomass allocation to leaves ($F_L$) modify light harvesting significantly. $F_L$ decreases with increasing plant size from herbs to shrubs to trees due to progressively larger support costs in plant functional types with greater stature. Among trees, $F_L$ and stand leaf area index scale positively with foliage longevity. Plant traits altering light harvesting have a large potential to adjust to light availability. Chlorophyll per mass increases, while $M_A$, foliage inclination from the horizontal and degree of spatial aggregation decrease with decreasing light availability. In addition, branching frequency decreases and canopies become flatter in lower light. All these plastic modifications greatly enhance light harvesting in low light. Species with greater shade tolerance typically form a more extensive canopy by having lower $M_A$ in deciduous species and enhanced leaf longevity in evergreens. In addition, young plants of shade tolerators commonly have less strongly aggregated foliage and flatter canopies, while in adult plants partly exposed to high light, higher shade tolerance of foliage allows the shade tolerators to maintain more leaf layers, resulting in extended crowns. Within a given plant functional type, increases in plant age and size result in increases in $M_A$, reductions in $F_L$ and increases in foliage aggregation, thereby reducing plant leaf area index and the efficiency of light harvesting. Such dynamic modifications in plant light harvesting play a key role in stand development and productivity. Overall, the current review analysis demonstrates that a suite of chemical and architectural traits at various scales and their plasticity drive plant light harvesting efficiency. Enhanced light harvesting can be achieved by various combinations of traits, and these suites of traits vary during plant ontogeny.

**Keywords** Bifurcation ratio · Biomass allocation · Foliage distribution · Leaf structure · Light interception · Review analysis · Shade tolerance · Shoot architecture · Stand age

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## Introduction

In deeply shaded understories, plant carbon gain can be improved most by capturing more light (Pearcy and Sims 1994). Thus, efficient light harvesting is of paramount importance for plants growing in competition in dense stands under natural conditions (Pearcy et al. 2004; Valladares and Niinemets 2008). At ecosystem scale, strong, close to linear, positive relationships between canopy productivity and the amount of intercepted light

have often been found (Duursma and Mäkelä 2007; Jarvis and Leverenz 1983; Lagergren et al. 2004), further demonstrating that light is the major ecosystem-scale driver of productivity.

There are inherent genetic (leaf structure, biomass allocation, maximum plant height) and mechanical (biomass requirements for efficient leaf exposure) limitations to the maximum efficiency of light harvesting. For instance, biomass costs for leaf exposure become increasingly larger as the leaves are positioned farther apart in twigs, stems and branches, and are allocated higher up along the stem. Because of such genetic and mechanical constraints, plants cannot ever expose all their foliage to full light. The incident quantum flux density declines exponentially with increasing canopy leaf area index ($L$, leaf area per unit ground area), and there are always extensive light gradients from the top to the bottom of plant canopies. The percentage of above-canopy light reaching through the tree foliage to the herb and moss layer on the forest floor is often less than 1% in tropical rainforests (see, e.g., Torquebiau 1988) and less than 2–5% in moderately humid temperate deciduous forests (see, e.g., Niinemets et al. 1998a). Even in heavily water-limited and relatively open Mediterra-nean and savanna woodlands, canopy transmittance is also frequently less than 20% (Bégué et al. 1994; Le Roux et al. 1997; Rambal 2001).

Plant species have a large capacity to alter leaf, shoot, and canopy level traits to cope with this large gradient in irradiance (for reviews, see Cescatti and Niinemets 2004; Kawamura 2009; Niinemets 2007; Pearcy and Sims 1994; Valladares and Niinemets 2007). However, there is generally a gradual change in species and life-form spectra with changing light availability, suggesting that, in competitive environments, single species are appar-ently not able to acclimate to the whole natural light range. World forests are characterized by highly layered architecture, and whole ecosystem light harvesting is driven by the complementary contributions of different plant functional types (Ishii and Asano 2009). For instance, in moderately humid temperate and tropical forests, a moss layer is overtopped by sparse herb cover, above which is the shrub and tree layer. The deciduous tree canopy may further consist of an upper layer with shade-intolerant species, and of a lower layer with shade-tolerant tree species (Niinemets et al. 1998a, 1999), while in mixed forests, deciduous and evergreen species with contrasting ecological potentials can occupy different canopy positions (Ishii and Asano 2009). In a similar manner, mosses grow below the herb layer in grassland communities, and herb and grass species may occupy different positions in the layered grassland can-opy (Aan et al. 2006; Fliervoet and Werger 1984; Hirose and Werger 1995; Kull and Aan 1997). At the same time, neither herbs nor mosses are constrained to grow in low-light understory environments only. For instance, herb species often dominate open and relatively dry early-successional habitats as well as wet habitats like bogs. In contrast, overstory tree species cannot grow under forest understory light availabilities that are sufficient for shade-tolerant herb and moss species. Despite the qualitative understanding of species and life-form changes in plant canopies, the ecophysiological and genetic constraints limiting the acclimation to low light in shade intolerant species in forest and herb communities are still not entirely understood. Why cannot single species occupying the uppermost positions in the canopy just increase the canopy light interception by adding more leaf layers? Why is it not possible to further tune foliar morphology and leaf chlorophyll content to enhance light interception efficiency? Identification of the determinants and constraints on plant light harvesting efficiency is highly relevant, contributing to the under-standing of the functioning of multi-storied forest and herb communities.

Extensive work has been conducted on species-spe-cific determinants of light harvesting, but few studies have investigated simultaneously the suites of traits at various hierarchical scales (e.g., Farque et al. 2001; Hemmerlein and Smith 1994; Kawamura 2009; Paquette et al. 2007; Selaya et al. 2008). Leaf, shoot and canopy level traits all contribute to light harvesting and it is important to gain quantitative insight into the role of various traits on plant light harvesting in different plant functional types as well as on the light-dependent plas-ticity of these traits (Ishii and Asano 2009). Species-specific trait values along with the plasticity in these traits likely importantly drive species differentiation along gap-understory gradients, but the combinations of traits responsible for species shade tolerance are still not fully understood (Valladares and Niinemets 2008). In addition, plant age and size affect plant structural characteristics at leaf, shoot and canopy levels (Green-wood et al. 2009; Niinemets 2002; Niinemets et al. 2005c; Nock et al. 2008; Richardson et al. 2000; Sumida and Komiyama 1997; Vanninen et al. 1996). The extent and rate of such dynamic alterations in plant structure have important consequences for changes in the efficiency of light harvesting in species with differing environmental requirements and, thus, for the dynamics of multi-spe-cies stands. However, these important modifications have not been considered in a systematic manner in studies analyzing stand dynamics and alterations in stand productivity with stand age.

The current review analyzes the determinants of plant light harvesting at leaf, shoot and canopy levels, and the light-driven plasticity and age- and size-dependent variations in the key traits responsible for total plant light interception (amount of light intercepted per plant) and plant light harvesting efficiency (amount of incident light harvested per unit plant leaf area) in different plant functional types and species with differing shade toler-ance. The analysis demonstrates that it is important to consider the suites of traits at various hierarchical levels, and dynamic modifications in these traits during plant ontogeny in order to understand the replacements of species and plant functional types within and along gradients in light availability.

## Chemical and structural adjustments of leaves for efficient light harvesting

Traditionally, leaf-level traits have been considered as important determinants of leaf light harvesting. In particular, foliage chlorophyll content ($\chi$) determines the leaf absorptance, and thus the fraction of light absorbed for any given incident light availability. Typically, across habitats of varying light availability, and for within-canopy light gradients in plants forming all leaves in the canopy at about the same time, foliage chlorophyll content per unit dry mass ($\chi_M$) increases with decreasing light availability (e.g., Fig. 1b; Evans and Poorter 2001; Hallik et al. 2009a; Iio et al. 2005), resulting in improved leaf absorptance per unit leaf mass and higher light availability of mesophyll cells for given incident light.

As any increase in chlorophyll content is associated with concomitant increases in the pigment-binding protein complexes that are expensive in terms of leaf nitrogen, the increase in $\chi_M$ in low light brings about large increases in the amount of leaf nitrogen invested in light harvesting. $\chi_M$ can be expressed as the product of the fraction of leaf nitrogen invested in light harvesting ($P_L$), nitrogen content per dry mass ($N_M$) and the amount of chlorophyll formed with a given amount of nitrogen invested in light harvesting [$C_B$, mmol Chl (g N)$^{-1}$] (Niinemets and Tenhunen 1997):

$$\chi_M = P_L N_M C_B, \tag{1}$$

$C_B$ considers that all leaf chlorophyll is associated with chlorophyll-binding proteins. $C_B$ depends on the stoichiometry of pigment-binding proteins (Niinemets et al. 1998b; Niinemets and Tenhunen 1997). $N_M$ is generally relatively invariable along understory and within-canopy light gradients (e.g., Ellsworth and Reich 1993; Kull and Niinemets 1993; Takahashi et al. 2005), while $C_B$ tends to increase with decreasing light availability (Niinemets et al. 1998b; Niinemets and Tenhunen 1997), reflecting a larger fraction of chlorophyll associated with the light-harvesting antenna system that binds more chlorophyll for a given amount of N invested in pigment-binding complexes than the reaction centers PSI and PSII (Anderson and Osmond 1987; Bassi and Caffarri 2000; Hikosaka and Terashima 1996). Nevertheless, $C_B$ varies only between 2.1 and 2.5 mmol g$^{-1}$ along the light gradients (Niinemets et al. 1998b; Niinemets and Tenhunen 1997). Given the low variability in $N_M$ and $C_B$, the strong increase in $\chi_M$ in low light reflects mainly the increase in $P_L$ (Eq. 1) with decreasing light availability (Fig. 1d, Grassi and Bagnaresi 2001; Huang et al. 2007). In fact, plants can invest a large part of foliar nitrogen in light harvesting in low light—even up to 30–60% of total leaf nitrogen (Fig. 1d, Niinemets and Tenhunen 1997)—demonstrating that enhanced light harvesting is expensive in terms of leaf nitrogen.
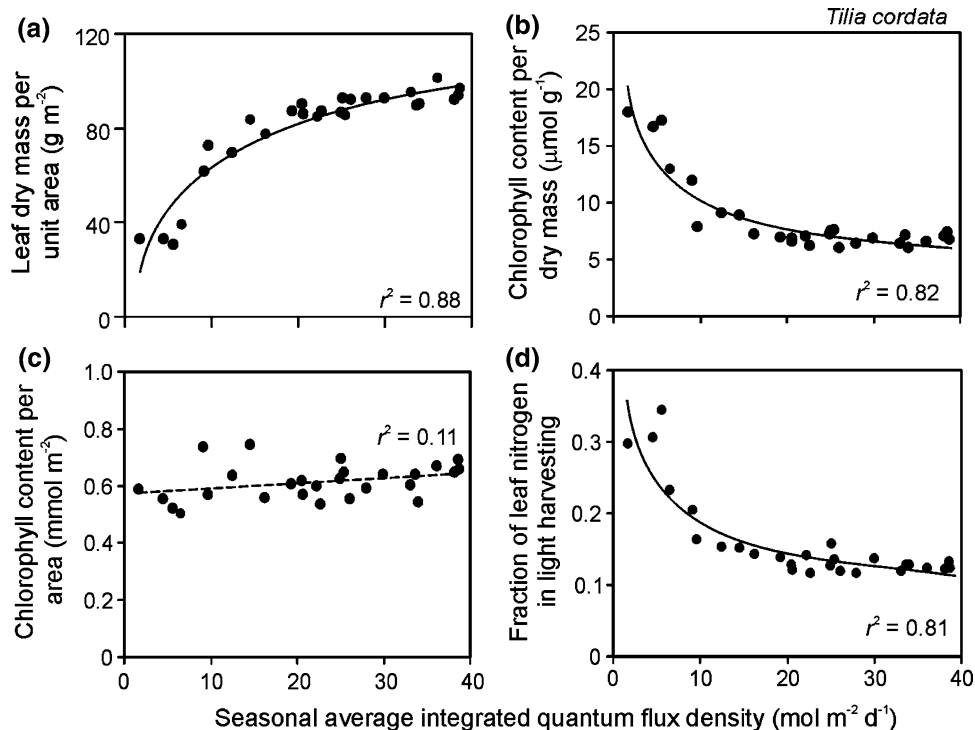


Fig. 1 Effects of incident light availability ($Q_{int}$) on leaf dry mass per unit area ($M_A$) (a), foliage chlorophyll content per unit leaf dry mass ($\chi_M$) (b) and area ($\chi_A$) (c), and the fraction of leaf nitrogen invested in light harvesting ($P_L$, Eq. 1) (d) in temperate deciduous tree *Tilia cordata* (modified from Niinemets and Kull 1998; Niinemets et al. 1998b). Chlorophyll content per area is the product of $\chi_M$ and $M_A$. $Q_{int}$ is the measure of average light availability during leaf growth and development (average value between 1 May and 31 July). Data were fitted by linear regressions (c) and non-linear regressions in the form $y = ax^b$ (a, b, d). All relationships are significant at $P < 0.001$, except for the correlation between $\chi_A$ and $Q_{int}$ in (c) ($P = 0.10$)

Differently from chlorophyll content per mass, chlorophyll content per area, $\chi_A$, varies significantly less along light gradients. The relationships between $\chi_A$ and light may be positive, negative or, most commonly, non-significant (Fig. 1c, Gracia 1987; Hallik et al. 2009a; Hansen et al. 2002; Niinemets 1997b). As $\chi_A$ is the product of leaf dry mass per unit area ($M_A$) and $\chi_M$, the difference between light-dependent variations in the area- and mass-based characteristics is due to opposite changes in $\chi_M$, which scales negatively (Fig. 1b), and $M_A$, which scales positively with light availability (Figs. 1a, 2a, b, Ellsworth and Reich 1993; Meir et al. 2002; Niinemets et al. 1998b).

Lower leaf dry mass per unit area ($M_A$) in deeper shade allows the plants to construct a greater leaf surface area for light interception at a certain biomass investment in foliage and, as such, is a key modification enhancing the harvesting of low light (see also "Whole plant determinants of light harvesting"; Gutschick and Wiegel 1988). In fact, due to the asymptotic relationship between leaf chlorophyll content per area and light interception (Evans 1993; Niinemets 2007), leaf light harvesting increases progressively less with increasing leaf chlorophyll content per area in leaves with larger $\chi_A$. For instance, it can be predicted (Evans 1993; Niinemets 2007) that, for leaves with a low $\chi_A$ of 0.2 mmol m$^{-2}$, increasing leaf chlorophyll content by 20% increases leaf absorptance by 4.2%, while for leaves with moderate–high $\chi_A$ of 0.6 mmol m$^{-2}$, the same increase results in an increase in leaf absorptance of only 1.9%. Due to this strongly asymptotic response of "diminishing returns", light harvesting can be increased much more by "smearing" the given amount of chlorophyll over larger leaf surface area that can be achieved by thinner leaves with smaller $M_A$ (Niinemets 2007).

Previous discussion has focused on modifications that improve light harvesting efficiency, but why then do all leaves not have low $M_A$ and high $\chi_M$? Greater $M_A$ at higher light can be also viewed as "sun acclimation" as thicker leaves with higher $M_A$ have greater photosynthetic capacity and use higher quantum flux densities in photosynthesis more efficiently (Niinemets 2007; Terashima et al. 2006, 2001). Given the high nitrogen cost of photosynthesis, higher chlorophyll concentrations would also not necessarily improve photosynthesis at higher light as fully exposed leaves typically intercept more light than can be potentially used to drive photosynthesis (Demmig-Adams and Adams 2006). Instead, investing more nitrogen in proteins limiting the light-saturated rate of photosynthesis, such as ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco), and components of photosynthetic electron transport (Hikosaka and Terashima 1995; Niinemets and Tenhunen 1997; Terashima et al. 2006) can improve photosynthesis under high light much more than investing this extra nitrogen in chlorophyll. Thus, full interpretation of foliage chemical and structural modifications along light gradients requires consideration also of plant photosynthetic acclimation to high light availabilities.

## Differences in foliage chemical and structural plasticity in species with differing shade tolerance and leaf life-span

The light-driven plasticity in a given trait can be defined as the slope of the relationship between the trait and light availability, whereas light can be non-transformed or log-transformed depending on the shape of the response (Portsmuth and Niinemets 2007). Species with different shade tolerance differ surprisingly little in the plastic responses of $\chi_M$ and $P_L$ to light availability (Grassi and Bagnaresi 2001; Niinemets 1997b; Niinemets et al. 1998b, 2003), underscoring the convergent nature of the foliar light-harvesting pigment system in vascular plants. However, the relationships of $M_A$ with light availability vary more among species. In some studies, the light-driven plasticity in $M_A$ has been observed to be larger in shade-intolerant than in shade-tolerant species (Bloor and Grubb 2004; Groninger et al. 1996; Oguchi et al. 2005; Portsmuth and Niinemets 2007; Sánchez-Gómez et al. 2006). In contrast, other studies have found the opposite (Chen 1997; Delagrange et al. 2004; Niinemets and Kull 1998; Paz 2003; Valladares et al. 2002) or have not found clear-cut patterns (Paquette et al. 2007). These contrasting variation patterns suggest that, in addition to leaf-level traits, whole plant light harvesting and plant fitness also depend on higher level (shoots, canopy) traits that can compensate for limited chemical and structural variations at the leaf level.

The plastic light-dependent modifications in $M_A$ and chlorophyll content outlined above pertained to species forming leaves at about the same time as such a simultaneous leaf formation leads to steep within-canopy light gradients during foliage development. This is the case, for instance, with broad-leaved temperate deciduous species having only a single leaf growth flush in the beginning of the growing season. In species with continuous leaf development, such as many herbs and grasses, and fast-growing tree and shrub species, older leaves formed first are continuously overtopped by younger leaves (Kikuzawa 2003). This means that all leaves in the canopy having continuous leaf formation develop essentially at the same light availability, explaining why the vertical gradients in $M_A$ are weaker in fast-growing canopies (Anten and Hirose 1998; Kull et al. 1998; Niinemets and Anten 2009; Werger and Hirose 1988). Furthermore, in continuously growing canopies, within-canopy light gradients are accompanied by simultaneous gradients in leaf age and senescence. As limiting nutrients, such as nitrogen, are retranslocated from senescing leaves and chlorophyll is destroyed, $N_M$ and $\chi_M$ may be actually positively related to light availability in such canopies (Anten and Hirose 1998; Ciganda et al. 2008; Niinemets and Anten 2009; Rousseaux et al. 2000). This evidence collectively suggests that acclimation to low light availability is inherently limited in fast-growing canopies with high leaf turnover. Apparently, there is a fundamental

compromise in light-acclimation potential and leaf longevity. Leaves in continuously developing canopies consisting of leaves with short life-span can only moderately adjust to rapidly changing light availabilities, while foliage in canopies having more distinct growth period and leaves with a longer life-span strongly acclimates to a less dynamic canopy light environment. In general, species with continuous foliage development are characteristic of open early-successional habitats, while "single-flush" species are characteristic of shaded late-successional communities (Kikuzawa 2003).

## Foliage structural modifications in species with complex leaf-cross section

In species with complex three-dimensional leaf cross-section as in evergreen conifers or in needle-leaved angiosperms, changes in foliage cross-section can also importantly alter foliage light harvesting efficiency. Because the currently widely used optical planimeters and imaging systems measure projected leaf area, projected

area is commonly used to characterize light-interception capacity in such species. On the other hand, many earlier studies employing morphological needle measurements for leaf area determination have used total needle surface area. This difference is important as the ratio between leaf total to projected surface area ($A_T/A_P$) can vary significantly, between ca. 2.2 and 4 in needle-leaved species (Fig. 2c, Barclay and Goodman 2000; Niinemets et al. 2002b; Niinemets and Kull 1995a; Sellin 2000), implying large differences in plant leaf area and stand leaf area index ($L$) based on projected or total area. In addition, variations in $A_T/A_P$ also result in significant differences in derived characteristics such as $M_A$ expressed per unit projected or total area (Fig. 2a,b).

Importantly, the $A_T/A_P$ ratio decreases with decreasing light availability in some shade-tolerant conifer species such as the species from the genera *Abies* and *Picea* (Fig. 2c, Cescatti and Zorer 2003; Stenberg et al. 1999) due to greater changes in vertical leaf dimension than in horizontal leaf dimension, indicating modifications in the shape of leaf cross-section. In the interior of plant canopies, most light comes from high
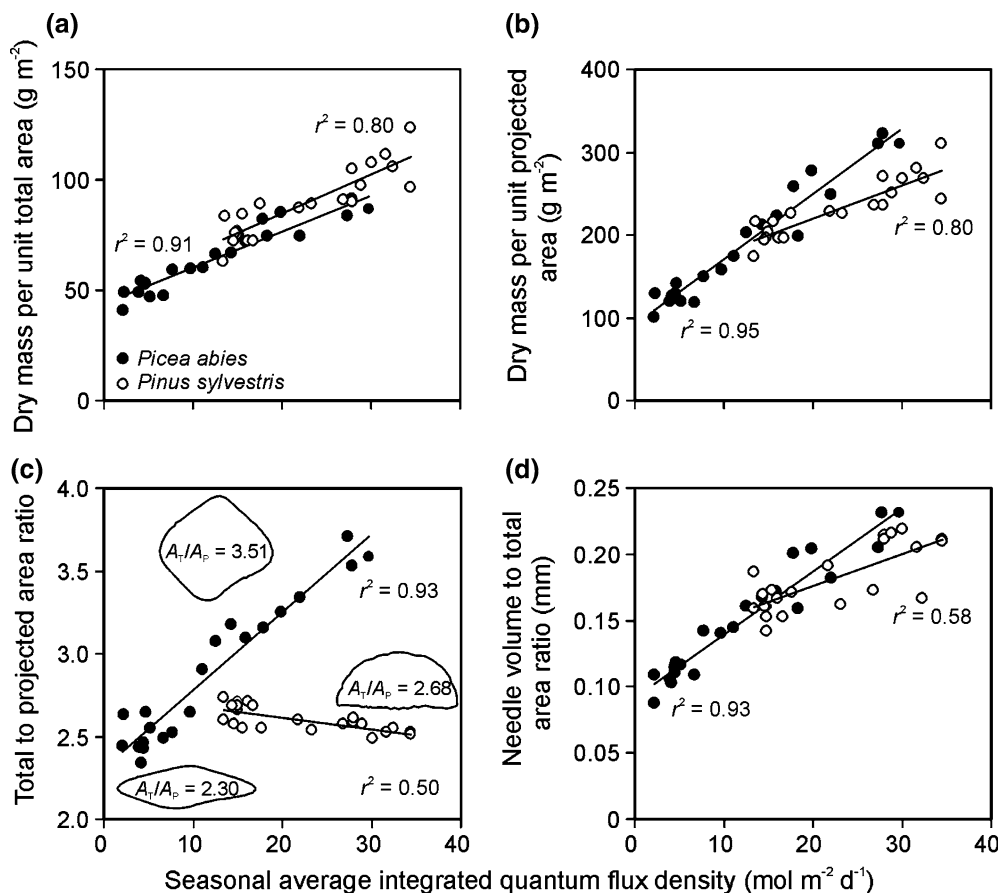


**Fig. 2** Correlations of needle dry mass per unit total ($M_{A,T}$) (**a**) and projected ($M_{A,P}$) (**b**) area, total ($A_T$) to projected ($A_P$) needle area ratio ($A_T/A_P$) (**c**), and needle volume ($V$) to $A_T$ ratio (**d**) with light availability in temperate evergreen conifers *Picea abies* (*filled symbols*, modified from Niinemets 1997a, data for 17 m tall trees) and *Pinus sylvestris* (*open symbols*, modified from Niinemets et al. 2001, data for the fertile site, 17–21 m tall trees). $M_{A,P}$ is equal to $M_{A,T}A_T/A_P$. Representative needle cross-sections with corresponding $A_T/A_P$ values are also shown in (**c**) for low- and high-light-acclimated needles of *P. abies* and for medium- to high-light-acclimated needles in *P. sylvestris*. Light availability as defined in Fig. 1. Data are fitted by linear regressions (all significant at $P < 0.001$)

solar elevation angles from above rather than from lateral directions (see below "Foliage inclination angle and aggregation"). Thus, lower $A_T/A_P$ ratio in weaker light combined with preferential orientation of needles horizontally with wider leaf dimension facing upwards, implies greater exposed surface area at the given total leaf surface area and, as such, is an important acclimation response improving leaf light harvesting efficiency (Cescatti and Niinemets 2004).

Decreases in $M_A$ with decreasing light availability in needle-leaved species are associated primarily with reductions in the thickness of foliage elements, or, more correctly for needle-leaved species, with reductions in volume to total leaf area ratio (Fig. 2d, Niinemets and Kull 1995a; Niinemets et al. 2005b; Poorter et al. 2009; Witkowski and Lamont 1991). While in species with relatively invariable $A_T/A_P$, foliage dimensions decrease with decreasing light availability in both vertical and horizontal dimensions to a similar degree (Fig. 2c for *Pinus sylvestris*; Niinemets et al. 2001), in species with strong reductions in $A_T/A_P$ in low light (Fig. 2c for *Picea abies*; Niinemets 1997a; Niinemets and Kull 1995a), vertical leaf dimension decreases relatively more than the horizontal leaf dimension. In the latter species, the traits on the basis of projected area are also driven by changes in cross-sectional leaf shape. For instance, $M_A$ expressed per projected area ($M_{A,P}$) is the product of dry mass per total area ($M_{A,T}$) and $A_T/A_P$. Accordingly, if $A_T/A_P$ scales positively with light, $M_{A,P}$ will vary more along the light gradients than $M_{A,T}$ (cf. Fig. 2a, b for variations in $M_A$ expressed on the basis of total and projected area in *P. abies* and *P. sylvestris*). In contrast, $A_T/A_P$ can also scale negatively with light in some intolerant conifers (Niinemets et al. 2001, 2002b). In this case, the plasticity in $M_{A,P}$ is less than in $M_{A,T}$.

As the comparison between two wide-spread temperate conifer species, shade-tolerant *P. abies* and shade-intolerant *P. sylvestris*, demonstrates, conifer species differ largely in the light-driven plastic modifications in foliage cross-sectional shape (Fig. 2c), $M_A$ (Fig. 2a, b) and the thickness of foliage elements (Fig. 2d). The shade-tolerant conifer *P. abies* had greater plasticity in most foliage structural traits (Fig. 2b–d) than the intolerant *P. sylvestris*. Analogously, in other studies, low morphological plasticity has been reported for other shade-intolerant pine species (Niinemets et al. 2002b), while high plasticity has been observed for shade-tolerant *Abies* and *Picea* species (Cescatti and Zorer 2003; Sprugel et al. 1996; Stenberg et al. 1999). In contrast, Bond et al. (1999) found few differences in morphological, chemical and physiological plasticity in three conifers with contrasting shade tolerance. However, in their study, all foliage characteristics were expressed only per unit projected leaf area. As the comparison between *P. abies* and *P. sylvestris* demonstrates (Fig. 2a,b), the apparent plasticity in traits expressed per unit total and projected area may be different due to the varying light responses of the $A_T/A_P$ ratio. While both species had similar plasticity in $M_A$ expressed per total area (statistically non-significantly different slope, Fig. 2a), *P. abies* had larger plasticity (greater slope) in $M_A$ expressed per unit projected area (Fig. 2b). This example demonstrates that it is necessary to report data on $A_T/A_P$ ratio together with the traits expressed either per unit projected or per total surface area. Although such structural modifications play a major role in needle light-harvesting efficiency, still only limited data are available for different conifer species. Especially rare have been studies measuring needle light environment together with structural traits in needle natural location in the canopy (e.g., Greenwood et al. 2009 for comparison of plasticity using ambiguous non-quantitative "sun"/"shade" dichotomy). Clearly, more work on the plasticity of needle cross-sectional shape and biomass accumulation per unit leaf area is needed for different conifer species in order to generalize the trends.

## Foliage inclination angle and shoot-scale aggregation in relation to light interception

Among other factors, the efficiency of foliage exposure is the function of foliage inclination angle and leaf spatial aggregation (Cescatti 1997; Cescatti and Niinemets 2004; Givnish 1979; Hikosaka and Hirose 1997). The probability of beam interception, $F$, in the shoot volume can be expressed for any given solar zenith angle $\phi$ as (Cescatti and Niinemets 2004; Cescatti and Zorer 2003; Niinemets et al. 2002a):

$$F = 1 - e^{-G(\phi)\Omega\rho D(\phi)}, \tag{2}$$

where $G(\phi)$ is the extinction coefficient (Ross 1981), $\Omega$ is the clumping factor (Markov coefficient for spatial aggregation, Nilson 1971), $\rho$ is the leaf area density in the shoot volume, and $D(\phi)$ is the beam path-length in the shoot volume. $G(\phi)$ depends on the foliage inclination angle distribution. Commonly, ellipsoidal foliage inclination angle distribution that assumes that foliage inclination angles are distributed parallel to the surface of a prolate (erectophile distributions) or an oblate (planophile distributions) spheroids used (Campbell 1986; Norman and Campbell 1989). $\Omega$ characterizes the degree of foliage spatial aggregation. For random foliage dispersion, $\Omega = 1$, for clumped foliage dispersions $\Omega < 1$ and for regular dispersions $\Omega > 1$ (Nilson 1971). Foliage with clumped dispersion intercepts less, and foliage with regular dispersion more light than the foliage with random dispersion.

It has been frequently observed that leaf inclination angle from the horizontal, $\theta$, changes gradually from more vertical in the upper canopy and in high light habitats to more horizontal in the lower canopy and in low light habitats (e.g., McMillen and McClendon 1979). As in the lower canopy most light arrives from above with low solar zenith angles, such a variation in $\theta$ significantly improves light interception in the lower

**Fig. 3** Foliage inclination angle ($\theta$) in relation to average seasonal integrated quantum flux density (log-scale, **a**) and foliage inclination angle distributions (**b**–**d**) in a mixed temperate deciduous canopy composed of shade tolerant *Tilia cordata* (*Tc*) in the lower layer and shade intolerant *Populus tremula* (*Pt*) in the upper canopy layer (modified from Niinemets 1998a). Leaf inclination angle distributions are shown separately for *T. cordata* (**b**) and *P. tremula* (**c**) canopy layers [*lower* and *upper* layer for both species as shown in (**a**)] and for the entire canopy combining the foliage inclination angles for both species (**d**). In **b** and **c**, lower canopy (canopy height, $H_C$, 4–12 m, growing season average light availability, $Q_{int}$, 2.2–4.6 mol m$^{-2}$ day$^{-1}$ for *T. cordata* and $H_C$ = 15–21 m, $Q_{int}$ = 5.9–12.4 mol m$^{-2}$ day$^{-1}$ for *P. tremula*) is shown by *grayscale wide bars*, and upper canopy ($H_C$ = 12–17.8 m, $Q_{int}$ = 4.6–8.8 mol m$^{-2}$ day$^{-1}$ for *T. cordata* and $H_C$ = 21–26.5 m, $Q_{int}$ = 12.4–36.8 mol m$^{-2}$ day$^{-1}$ for *P. tremula*) by *grayscale narrow bars*. A least squares fit to whole canopy leaf inclination angle distribution by ellipsoidal leaf distribution function is also provided. Ellipsoidal distribution assumes that leaf inclination angles are distributed parallel to a surface of an ellipsoid (Campbell 1986). Only one parameter, $c$, the ratio between the horizontal and vertical semi-axes of the ellipsoid, is needed to describe the ellipsoidal leaf angle distribution ($c$ = 2.3 for the whole canopy, $r^2$ = 0.47, $P$ = 0.02). In *P. tremula*, most leaves had negative inclination angles ($\theta < 0$), i.e., were hanging downwards (Niinemets 1998a), but in all cases, the absolute leaf inclinations, abs($\theta$), are demonstrated as leaf light harvesting scales with cos($\theta$) that is independent of the sign of $\theta$



canopy. In contrast, more erectophile leaves in the upper canopy intercept less potentially damaging mid-day solar radiation with highest peak intensities, and permit more light to reach the lower canopy. Thus, such variations in inclination angles result in more uniform distribution of light within the canopy and improve whole canopy light interception (Cescatti and Niinemets 2004; Gutschick and Wiegel 1988; Valladares and Niinemets 2007).

However, $\theta$ is a complex trait that varies significantly at any light level in the canopy. Thus, the overall correlation between light availability and $\theta$ can be poor (Fig. 3a, Niinemets 1998a). Therefore, it is more appropriate to consider leaf angle distributions. Experimental evidence demonstrates that, in many species, foliage inclination angles become more planophile in lower canopy (Fig. 3a–c, Baldocchi et al. 1985; Cescatti and Zorer 2003; Kull et al. 1999; Niinemets et al. 2004, 2005c; Planchais and Sinoquet 1998; Utsugi 1999; Utsugi et al. 2006), indicating that the foliage light extinction coefficient changes throughout the canopy. Contrary to these observations, foliage inclination angles can be relatively insensitive and essentially spherical throughout the canopy in some shade-intolerant conifers (Niinemets et al. 2002a), demonstrating important variation among species in light-driven plasticity in the adjustment of foliage inclination angles.

Although the ellipsoidal distribution function has become a popular model to fit the distributions of foliage inclination angles for the entire canopy and at different canopy positions, it can poorly perform at specific canopy light availability. At any given light availability, inclination angles can vary less than predicted by the model (e.g., Kull et al. 1999; Utsugi et al. 2006). For instance, in a mixed deciduous forest dominated by shade tolerant *Tilia cordata* in the lower canopy and
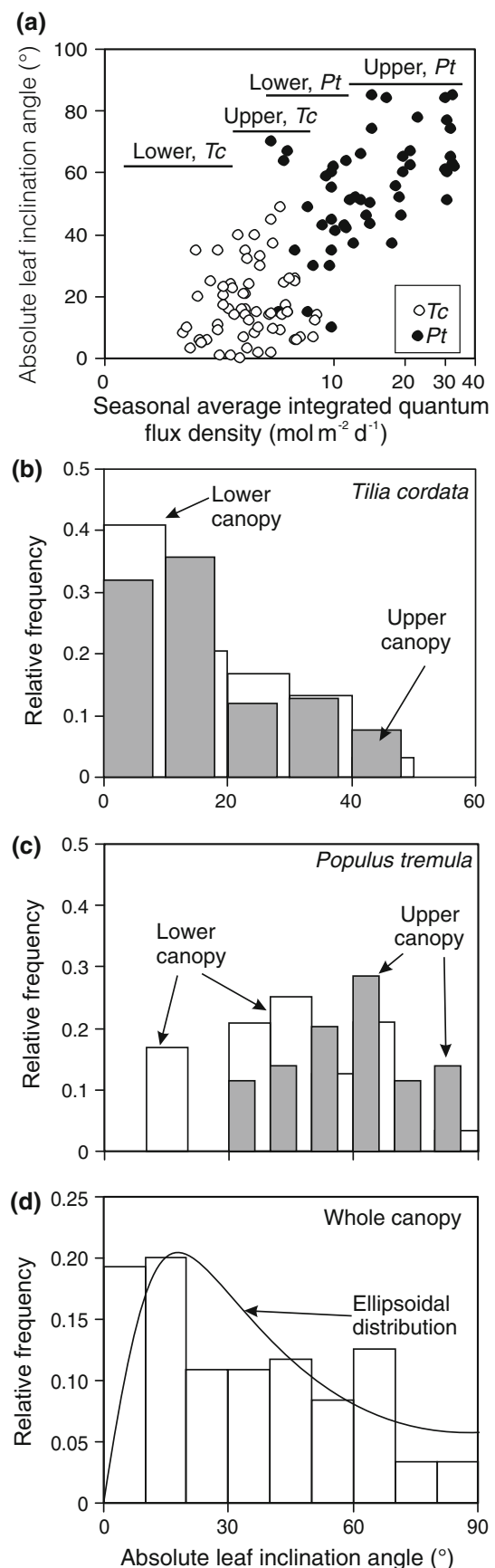
shade intolerant *Populus tremula* in the upper canopy, the ellipsoidal distribution function provided a reasonable fit for the entire canopy (Fig. 3d). However, *T. cordata* with planophile foliage possessed no leaves with $\theta > 50°$, while the best ellipsoidal distribution fit would predict a certain fraction of leaves with any inclination angle class up to 90°; *P. tremula* with more erectophile foliage possessed less leaves than predicted in leaf inclination angle classes $\theta < 50°$ (e.g., Fig. 3b,c). There are a number of alternative leaf angle distribution functions (Thomas and Winner 2000; Wang et al. 2007) and, in fact, a combination of several alternative foliage distribution functions are needed to fit foliage distributions in mixed species canopies consisting of species with planophile and erectophile foliage.

The comparisons between *T. cordata* and *P. tremula* (Fig. 3), and other studies (Falster and Westoby 2003; McMillen and McClendon 1979; Ryel and Beyschlag 1995) demonstrate that species can differ greatly in $\theta$. In particular, late-successional stands dominated by shade-tolerant species often have more horizontal foliage inclination angles (Fleck 2003; McMillen and McClendon 1979; Pearcy et al. 2004). Optimization models have been used to derive the optimal distribution of foliage inclination angles in the canopies (e.g., Gutschick and Wiegel 1988). Optimal foliage inclination angles maximizing canopy photosynthesis are predicted to be relatively steep as in such canopies more leaf layers with positive carbon balance can be supported (Hikosaka and Hirose 1997). The key question is why do plant canopies often have planophile inclination angle distributions when this does not maximize canopy photosynthesis? As planophile leaves cast deeper shade, competitive optimization based on game theory has suggested that species with planophile leaves can invade a stand with vertical leaves by reducing the carbon gain of erectophile-leaved species more than its own carbon gain (Hikosaka and Hirose 1997). Therefore, evolutionarily stable stands that cannot be invaded by species with different inclination angles have more horizontal leaves than would maximize single plant productivity (Hikosaka and Hirose 1997). Although not being the most productive strategy, greater capacity to shade out the species with vertical foliage orientation and higher foliage shade tolerance likely explain the dominance of shade-tolerant species with planophile leaves in late-successional forests.

Foliage is considered to be dispersed randomly in many stand carbon gain models, but in real plant stands foliage is often aggregated at shoot, branch and canopy levels, and thus intercepts less light than foliage with random dispersion. Such an aggregation at different scales is an adaptive feature for high-light exposed foliage as it allows allocation of more foliage in high light where photosynthetic returns are the largest, while larger self-shading shields the foliage from potentially damaging high irradiances. In contrast, inevitably higher self-shading in the care of aggregated foliage is obviously disadvantageous under low light. In many species, the degree of foliage aggregation within the shoot decreases with
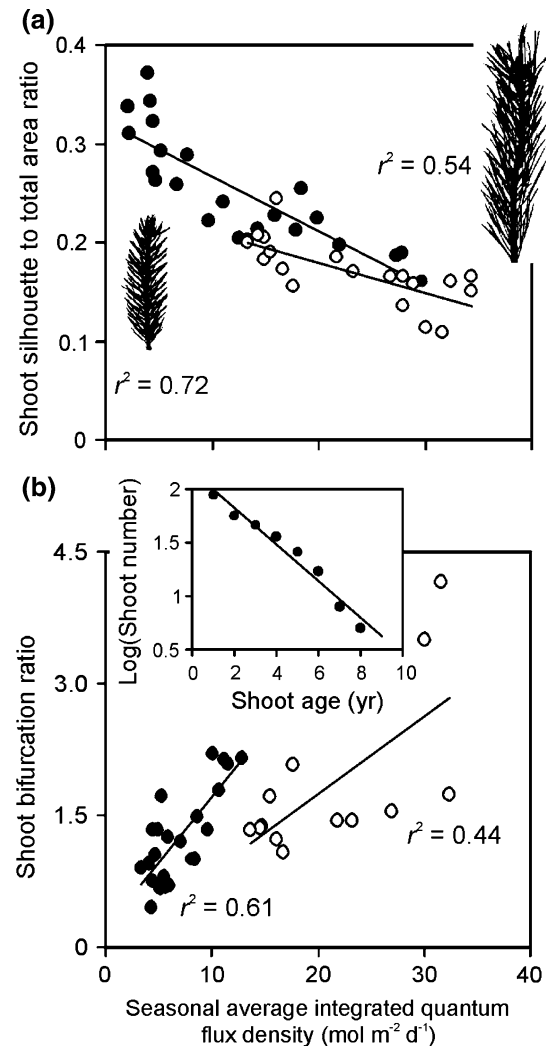


**Fig. 4** Dependencies of shoot silhouette to total needle area ratio (**a**) and shoot bifurcation ratio (**b**) on seasonal average quantum flux density in temperate evergreen conifers *Picea abies* and *Pinus sylvestris*. Shoot silhouette to total area ratio ($S_S$) is provided for shoots facing the view direction (both inclination and rotation angles are 0°). This projection commonly provides the maximum value of $S_S$ (Stenberg et al. 1999). Shoot bifurcation ratio ($R_b$) characterizes the frequency of branching and is defined as the ratio of the number of shoots in given age class relative to the number of shoots in the next older age class. The slope of Log(shoot number) vs shoot age relationship (*inset* in **b** for a sample relationship in *P. sylvestris*) is equal to $-\text{Log}R_b$ ($R_b = 1.48$ for the sample shoot in the *inset*). All relationships are significant at $P < 0.01$. Data sources for **a** as in Fig. 2, for **b** modified from Niinemets and Lukjanova (2003b)

decreasing light availability in the canopy (Cescatti and Zorer 2003; Niinemets et al. 2002a, 2006b), implying that the shoot light harvesting efficiency increases in lower light. In some broad-leaved species, leaves in shoots may become even regularly dispersed in lowest light availabilities, where leaves are positioned side by side, filling the gaps between the neighboring leaves (Niinemets et al. 2004, 2005c; Pearcy et al. 2004; Planchais and Sinoquet 1998), while leaves are often strongly rolled in higher irradiance, implying a greater degree of aggregation (Fleck et al. 2003).

Conifers and needle-leaved angiosperms exhibit the largest degree of shoot-level foliage clumping, discernible in very low shoot silhouette to shoot total needle area ratios, even below 0.1 in some shade-intolerant conifer species (Fig. 4a; Niinemets et al. 2006b; Smolander et al. 1994; Stenberg et al. 2001). Again, shade-tolerant conifer species seem to have higher plasticity for modification of shoot architecture than intolerant conifers (Fig. 4a compares the shade-tolerant conifer *Picea abies* and intolerant conifer *Pinus sylvestris*) (see Cescatti and Zorer 2003; Stenberg et al. 1999, 2001 for shoot-level plasticity in different conifers; Stenberg et al. 1998). In particular, shade-tolerant conifers commonly have a higher shoot silhouette to total area ratio in low light availability and form flat shoots with planophile inclination angle distribution and less clumped dispersion with needles positioned side by side, resembling the leaves in broad-leaved species (Fig. 4a, Cescatti and Zorer 2003; Niinemets 1997a; Stenberg et al. 1998, 1999). The capacity to construct shoots with high shoot silhouette to needle area ratio has been considered to be an important trait allowing shade tolerant species to maintain foliage in deeper shade, thereby supporting large leaf area indices and harvest more light than intolerant species (Leverenz 1992; Leverenz and Hinckley 1990; Leverenz et al. 2000; see below for the other determinants of species leaf area index).

## Branching and leaf area distribution in the canopy

Branching architecture can also greatly alter the packing of foliage and the efficiency of foliage exposure. The angle of branching has been denoted as an important adaptive feature determining the degree of overlap between neighboring branches and leaves (Fisher 1986; Honda and Fisher 1978; Kennedy 2009). In addition, the frequency of branching can alter foliage aggregation. Bifurcation ratio, the number of branches formed per unit mother shoot or branch (Borchert and Slade 1981; Whitney 1976), is often used to characterize the frequency of branching (see inset in Fig. 4b for derivation of bifurcation ratio), and basic tree geometric features can be simulated on the basis of the bifurcation ratio (Kennedy 2009; Kull et al. 1999; Küppers 1994). The bifurcation ratio commonly increases with increasing light availability (Fig. 4b, Banez et al. 1999; Kull et al. 1999; Kull and Tulva 2000; Niinemets and Lukjanova 2003a, b; Steingraeber et al. 1979; Veres and Pickett 1982; Whitney 1976), resulting in denser canopies with larger degree of foliage aggregation and lower efficiency of light interception in higher irradiance. Nevertheless, light-driven plasticity in branching frequency has not been always observed (Ali and Kikuzawa 2005; Harris and Bassuk 1993).

The frequency of branching and distribution of branching activity throughout the canopy shape the branch scaffolding that supports the leaf canopy (Sterck and Schieving 2007). Horn (1971) distinguished between two idealized tree crown geometries: 'monolayer' and 'multilayer'. Growth activity mainly in the upper canopy and stronger horizontal growth combined with low bifurcation ratio results in the horizontal extension of branches primarily in the upper canopy (Gratzer et al. 2004; Kempf and Pickett 1981; Pickett and Kempf 1980). Such a growth pattern leads to a flat umbrella-shaped crown—a so-called 'monolayer' with regular foliage dispersion—that harvests light very efficiently. Strong vertical extension growth, combined with a high bifurcation ratio and branch formation throughout the canopy results in a 'multilayer' canopy. 'Multilayer' canopy can support more leaf layers than 'monolayer', but due to stronger self-shading between the leaf layers, the light-harvesting efficiency is lower than that of a 'monolayer'. Due to these characteristic features, foliage is distributed uniformly throughout the crown in 'multilayer' canopies, while in 'monolayer' canopies, foliage is allocated more strongly to the upper canopy layers. 'Monolayers' are typically considered to be shade-tolerant late-successional species, while 'multilayers' are shade-intolerant early-successional species (Gratzer et al. 2004; Horn 1971; Valladares and Niinemets 2008), but contrasting patterns have found in the literature (Poorter et al. 2000, 2006).

Three important aspects need consideration when correlations are sought between crown architecture and species shade tolerance. First, 'monolayer' and 'multilayer' are the extremes of a spectrum of tree canopies, and strict 'monolayer' versus 'multilayer' dichotomy is rare among species differing in shade tolerance. Nevertheless, in young plants, crowns in shade-intolerant species tend to be longer and foliage tends to be distributed more evenly across the crowns than in shade-tolerant species (Niinemets 1996; Poorter and Werger 1999).

Second, the conditions under which crown architectures are compared are also important. When species of different shade tolerance are compared under natural conditions, it may be hard to find species under comparable light conditions. There is evidence of a gradual shift from 'multilayer' canopies in high light to 'monolayer' canopies in low light (Fig. 5, Gratzer et al. 2004; Kohyama 1980; Mori et al. 2008; O'Connell and Kelty 1994; Saito et al. 2004). Such plastic changes in foliage distribution enhance light harvesting in low light, while maximizing canopy photosynthetic production under high light. Species can also differ significantly in their capacity to alter foliage distribution in response to low light. Foliage distribution in saplings of the shade-tolerant temperate deciduous tree *Acer platanoides* responded significantly to light availability, but no significant effect of light was observed in saplings of the shade-intolerant tree *Quercus robur* (Niinemets 1996). Although both species have a 'multilayer' crown arrangement under high light, species differences in crown architecture under low light were linked to shade tolerance. These data demonstrate that it is important to
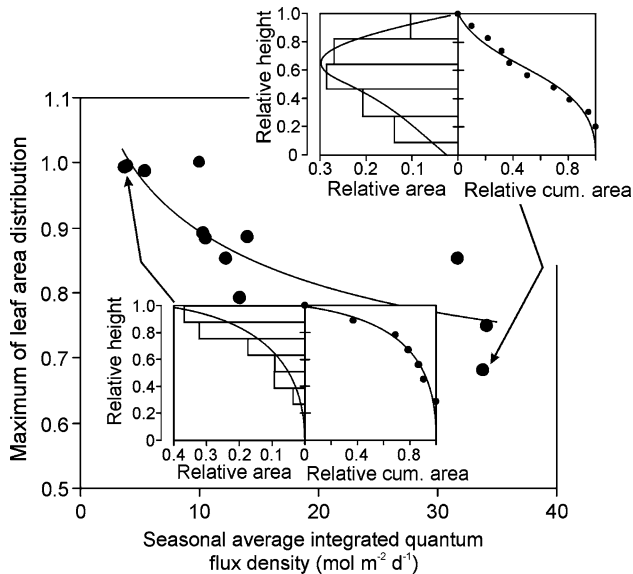
**Fig. 5** Maximum of within-canopy relative leaf area distributions ($R_{H,max}$, relative to the total tree height) in saplings (total height 0.5–1.5 m) of the temperate deciduous tree *Acer platanoides* in relation to above-canopy light availability ($r^2 = 0.72$, $P < 0.001$; data modified from Niinemets 1996). To compare directly the shape of the distributions, both leaf area at any given height and cumulative leaf area were normalized with respect to total plant leaf area, and height in the canopy was normalized with respect to total plant height. Leaf area distributions were fitted by Weibull functions, and $R_{H,max}$ was calculated for each sapling (see Niinemets 1996 for further discussion). Greater values of $R_{H,max}$ demonstrate that more foliage is present higher in the canopy. Light availability is defined as in Fig. 1. *Insets* Sample distributions of relative leaf area at any given height, and relative cumulative leaf area together with the Weibull function fits for representative plants grown under low light ($R_{H,max} = 1.0$) and high light ($R_{H,max} = 0.68$)

compare species at the same and ecologically relevant light availability to gain conclusive insight into the relationships between shade tolerance and crown structure.

Finally, the situation can be different again for large trees growing in dense stands with tree tops being exposed to high irradiance and canopy bottom to low irradiance. Given the low shade tolerance of foliage in intolerant species, foliage is expected to be shifted gradually upwards in canopies of shade-intolerant species, while shade-tolerant species can support extended crowns. Such contrasting patterns in foliage distribution among species with differing shade tolerance can be observed especially for evergreen species accumulating particularly high leaf area indices. For example, Fig. 2 demonstrates that the foliage in the shade intolerant conifer *Pinus sylvestris* requires at least 10 mol m$^{-2}$ day$^{-1}$ light, while foliage in the shade tolerant conifer *Picea abies* can be found at ca. 2 mol m$^{-2}$ day$^{-1}$ light, and this difference in foliage shade tolerance is associated with extended crowns in *Picea* and short crowns in *Pinus* when grown in dense stands. Analogously, mature shade-tolerant tropical evergreen trees typically have extended crowns while intolerant species have short

crowns (Poorter et al. 2000, 2006; see also "Plant age and light harvesting from leaf to stand").

## Whole plant determinants of light harvesting and differences in light harvesting among plant functional types

Total foliage area per plant dry mass, LAR (m$^2$ g$^{-1}$), depends both on leaf mass fraction (leaf dry mass per unit total plant dry mass), $F_L$, and leaf dry mass per unit area, $M_A$ as:

$$LAR = \frac{F_L}{M_A}. \tag{3}$$

Stand leaf area index $L$ and LAR are further related as:

$$L = LAR B_S, \tag{4}$$

where $B_S$ is the standing biomass per unit ground area (g m$^{-2}$). Combining Eqs. 3 and 4, $L$ can be expressed as

$$L = \frac{F_L}{M_A} B_S. \tag{5}$$

This equation demonstrates that the fraction of leaves in total biomass and leaf dry mass per unit area are the key traits altering whole community leaf area index. In addition to within-canopy variation in $M_A$ (see "Chemical and structural adjustments of leaves for efficient light harvesting"), $M_A$ varies greatly among species. In saplings and mature individuals of temperate trees, shade-tolerant species commonly have lower $M_A$ at given light availability than shade-intolerant species (Hallik et al. 2009b; Niinemets 2006) and thus, can construct a larger foliar area with given biomass investment in leaves. Analogously, shade-tolerant herb species often also possess lower $M_A$ (Olff 1992; Pons 1976, 1977). However, seedlings of shade-intolerant temperate tree species tend to have lower $M_A$ than the seedlings of shade-tolerant species (Reich et al. 1998; Walters and Reich 1999). In tropical evergreen and temperate Southern hemisphere species, $M_A$ tends to be associated positively with species shade tolerance independently of plant ontogenetic status (Kitajima 1994; Lusk et al. 2008b; Lusk and Warton 2007). As $M_A$ correlates positively with plant age and size (see "Plant age and light harvesting"), smaller seed size and smaller initial size likely explain the lower $M_A$ in seedlings of shade-intolerant temperate species (Niinemets 2006). In contrast, larger $M_A$ in shade tolerators in tropical evergreens has been associated with the structural adjustment improving foliage mechanical robustness and resistance to herbivores and pathogens, changes that collectively lead to greater leaf longevity (Kitajima 1994; Lusk 2004; Lusk et al. 2008b). In these species, enhanced leaf longevity results in accumulation of foliage and increases in $F_L$ (see "Light harvesting in plant species with varying leaf longevity").

Plant functional types vary significantly in average $M_A$ values, ranking according to $M_A$ as herbs < deciduous woody species < evergreen angiosperms < evergreen gymnosperms (Poorter et al. 2009). Plant functional types that can construct leaves more cheaply can form higher foliar area with a given biomass investment in leaves, and thereby intercept more light. However, plant costs for light harvesting consist not only of carbon and nutrient costs required for foliage construction, but also costs associated with construction of petioles, branches and stems to support the foliage. To sustain extensive foliar areas, large investments in support structures are also necessary. Furthermore, it is not just extensive foliage area that is important, but the leaves must be exposed to light. In understory environments, where a few gaps penetrate the upper canopy, branch and petiole costs associated with effective leaf spacing become especially important. From a mechanical perspective, the support costs required to keep a leaf in a horizontal position are considerably larger than the costs for keeping a vertical leaf with the same mass and size (Givnish and Vermeij 1976; Niklas 1994). Thus, when the leaves become more horizontal with decreasing light availability, the costs for constructing petioles and branches should increase.

As efficient light harvesting is expensive in terms of biomass investment in support tissues, the efficiency with which foliage can be supported can be a major factor determining species ability to grow under low light environments. Although plants tend to allocate more biomass into leaves under low light (e.g., King 2003; Portsmuth and Niinemets 2007), large support investments in low light to improve the efficiency of light harvesting (low degree of self-shading and efficient exposure of foliage) likely explain why $F_L$ is sometimes not associated significantly with light availability, or may even be lower under low light (e.g., Mori and Takeda 2004; Quero et al. 2007; Walters et al. 1993). Intrinsic limitations associated with too high costs for foliar support may constrain species to higher light environments, where carbon for foliage construction is cheaper. Givnish (1988) provided a quantitative analysis of whole plant light compensation points in relation to plant size and biomass allocation to foliage. This analysis demonstrated that larger plants with a greater fraction of biomass in support and a lower fraction in foliage require progressively higher light availabilities for survival (Givnish 1988), emphasizing the importance of considering the scaling of support investments with plant size (see also "Plant age and size effects on light harvesting from leaf to stand").

There are inherent differences between various plant functional types in foliar support costs and fractional investment in foliage (Fig. 6). The costs for foliar support are lowest (largest $F_L$) in herbs, where there are no woody support tissues, and largest in tree species with long-living expensive branch and stem framework. At the extreme, deciduous trees constructing their leaf canopy each year have on average almost 98% of above-ground biomass in stems, branches and twigs (Fig. 6). At the same time, the
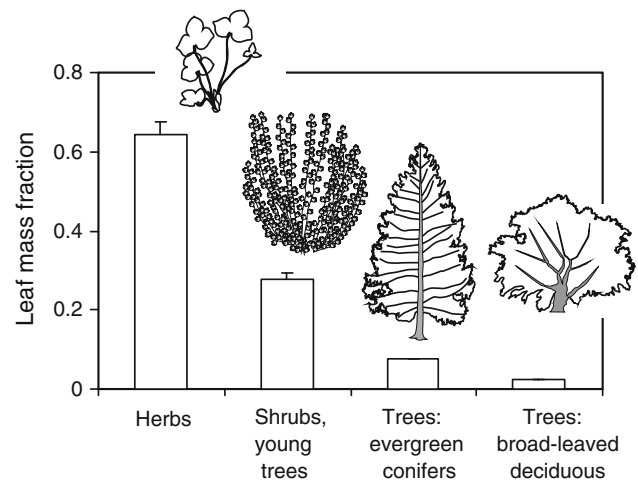


**Fig. 6** Variation in the average ($\pm$ SE) fraction of above-ground plant dry mass in leaves ($F_L$) among temperate Northern hemisphere herbs ($n = 21$), shrubs and young trees ($n = 51$), evergreen coniferous trees ($n = 102$) and broad-leaved deciduous trees ($n = 216$). For herbs, the data were obtained from Niinemets et al. (2006a), for shrubs and young trees (saplings up to height 2.6 m) from Niinemets (1998b) and Niinemets et al. (2006a). For trees, $F_L$ was determined from allometric regressions between tree diameter and above-ground biomass components. The database of allometric regression equations prepared by Jenkins et al. (2004) was used predominantly, but additional studies were also included (Kubota 2006; Shibuya et al. 2005). For all allometric regressions in trees, $F_L$ was determined for the tree diameter at breast height of 30 cm, which corresponds to medium-sized trees

support tissues remain largely alive in perennial herbaceous species, in contrast to woody species, in which much of the stem and branch biomass may consist of dead wood and bark. This means that the maintenance requirements per unit biomass investment in support tissues can be lower in trees than in herbs, making trees potentially more competitive after they have become established in the community and paid for the initial costs of woody biomass construction. Furthermore, growing taller than the neighbors results in higher light availabilities and in shading out competitors. Although gaining height results in high support costs and reduced whole plant efficiency of light interception, plants competing for light with the neighbors commonly grow taller than the heights that would maximize plant productivity in a non-competitive situation (Givnish 1982; Iwasa et al. 1984; Pronk et al. 2007), underscoring the importance of height growth strategy as a means to enhance fitness in highly competitive natural communities.

The importance of support costs for whole plant carbon balance is exemplified by the high competitive ability of lianas, the "support"-parasites. Because lianas use the support system generated by trees, their own support investments are minimal. This allows a considerably greater biomass investment in foliage than that in co-existing trees (Cai et al. 2007; Schulze 1982; Selaya et al. 2007; Toledo-Aceves and Swaine 2008), and results in rapid height growth and proliferation in the tree canopy. Nevertheless, depending on the suite of other traits affecting light interception, such as $M_A$ and

canopy architecture, young co-existing tree species may achieve whole plant light harvesting efficiencies similar to that of lianas (Selaya et al. 2007).

Although there has been much insightful theoretical reasoning about the importance of support investments in determining whole plant light harvesting efficiency and whole plant light compensation points (Givnish 1988), studies on the whole plant light compensation points in saplings have started only recently (Baltzer and Thomas 2007). Clearly, more quantitative work on plant light harvesting in relation to support costs is needed to gain insight into the functioning of multi-species, highly structured plant stands that support a variety of species with widely varying support investments (Pearcy et al. 2004).

## Light harvesting in plant species with varying leaf longevity

In the previous section, stand leaf area index, $L$, was expressed in relation to total stand biomass (Eq. 5). To analyze the impact of variations in leaf longevity $L$, it is more convenient to express it in relation to annual biomass production per unit ground area, $B_A$. For deciduous species,

$$L = \frac{F_A}{M_A} B_A, \qquad (6)$$

where $F_A$ is the fraction of annual biomass production invested in foliage. In closed stands supporting a steady-state $L$, the amount of foliage formed every year has been called the basic amount of foliage ($B_B$) (Tadaki 1966). It has been suggested that high foliage construction cost limits the amount of foliage formed annually ($B_B$), and thus, the maximum leaf area indices that can be supported in deciduous species (Schulze et al. 1977). Contrary to deciduous species, multiple leaf age classes can be supported in evergreens, resulting in several-fold higher amounts of leaf biomass than that formed annually (Tadaki 1966, 1991). However, the total amount of foliage supported in evergreens is not directly the product of $B_B$ and leaf life-span, but also depends on foliage mortality, $\alpha$. Assuming that the annual biomass production, and the fraction of biomass invested in foliage do not vary among different years, and that the mortality rate is a constant:

$$L = \frac{F_A}{M_{A,F}} B_A \sum_{\Lambda=1}^{\Lambda=\Lambda_{max}} e^{-\alpha(\Lambda-1)}, \qquad (7)$$

where $\Lambda$ (years) is leaf age ($\Lambda = 1$ for current year leaves) and $\Lambda_{max}$ is the maximum leaf life-span. As leaf dry mass per unit area may increase with leaf age (Bond-Lamberty et al. 2002; Niinemets 2002; Niinemets et al. 2005a; Poorter et al. 2009), $M_{A,F}$ in this equation refers to the value of $M_A$ in the year of foliage formation. From this equation, it is possible to calculate that, for a given annual biomass investment in foliage, $F_A B_A$, a canopy composing of leaves with annual mortality rate of 0.1 and $\Lambda_{max}$ of 15 years has 5.2-fold higher $L$ than a canopy composed of current year leaves only, while a canopy with a mortality rate of 0.3 and $\Lambda_{max}$ of 10 years has an $L$ value that is 3.7-fold higher.

These examples demonstrate that increasing leaf longevity provides an important way to accumulate foliage and enhance canopy light harvesting. It has been demonstrated that increases in foliage life-span result in greater sapling foliage area in temperate evergreen species (Lusk 2004; Lusk and Contreras 1999). Analogously, saplings of tropical tree species with greater leaf longevity accumulated more leaf area than saplings with lower leaf longevity (Selaya et al. 2008). Although in all these studies, greater longevity was associated with more robust leaves with larger $M_A$, which negatively affects $L$ (Eq. 7), accumulation of foliage biomass driven by extended leaf life-span was a more important determinant of leaf area than $M_A$, such that species with greater longevity also had greater foliage area and intercepted more light (Lusk 2004; Selaya et al. 2008).

So far, studies investigating the relationships between foliage longevity, biomass allocation to leaves and stand leaf-area index have been rare (Gower et al. 1993; Reich et al. 1992). This lack of information is associated with limited data on leaf area index in mono-specific stands, and information about foliage longevity is lacking even in extensive multi-species trait databases (e.g., Wright et al. 2004). To test for the correlations between average foliage life-span ($\Lambda_{av}$), fraction of biomass in leaves and stand leaf area index, an extensive dataset of Northern hemisphere conifers with varying $\Lambda_{av}$ was composed ("Appendix", $n = 40$ for $F_L$ and $n = 42$ for $L$). As optical measurements of $L$ with hemispherical photography or portable devices such as a Li-Cor plant canopy analyzer (LI-2000; Li-Cor, Lincoln, NE) require assumptions about the degree of foliage aggregation (Chen 1996; Stenberg et al. 1994), direct measurements of stand leaf area were used in all cases. In this dataset, $\Lambda_{av}$ varied from 6 months in deciduous conifers such as *Larix* spp. to 110 months in evergreen conifer *Picea mariana* (Greenway et al. 1992). As expected, the fraction of biomass in foliage (Fig. 7a), and stand leaf area index (Fig. 7b) were positively correlated with $\Lambda_{av}$. Although foliage clumping may also increase with increasing $L$, studies have demonstrated that conifer canopies with greater $L$ do intercept more light (Gersonde et al. 2004; Parker et al. 2002), indicating that leaf life-span is a key determinant of stand-level variations in light interception.

Despite the general correlations, outlying observations suggested that species environmental requirements also affect relationships between leaf longevity and biomass accumulation. For instance, subarctic to boreal conifer *Picea mariana* has the highest $\Lambda_{av}$, but this species does not form dense canopy in its native stressful environment (Bégin and Filion 1999; Mugasha et al. 1991). Similarly, *Pinus edulis* colonizes dry stressful sites and has a relatively high leaf life-span of 66 months, but supports smaller leaf area index than predicted by the regression fitted to all data. Trade-offs between biomass investment
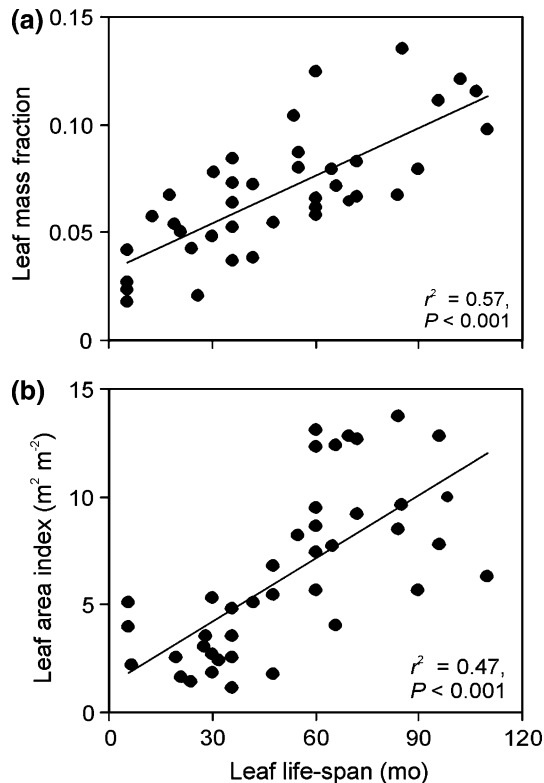
**Fig. 7** The fraction of leaf mass in above-ground biomass (**a**, $n = 40$) and stand leaf area index (**b**, $n = 42$) in relation to average leaf life-span ($\Lambda_{av}$) in Northern hemisphere temperate conifers. Each data point corresponds to an individual species. Whenever multiple estimates were available for a given species, averages were calculated. Average leaf life-span is defined as the leaf age-class retaining at least 50% of leaves (Cordell et al. 2001; Kayama et al. 2002; Prior et al. 2003). See legend to Fig. 6 for the key data sources for $F_L$. In addition, for deciduous conifers, additional $F_L$ estimates were obtained from Kajimoto et al. (2006) and Satoo (1974). Again, $F_L$ was calculated from allometric regressions for tree diameter at breast height of 30 cm. Stand leaf area index and $\Lambda_{av}$ data with corresponding references are reported in the "Appendix"

in foliage in fertile sites with ample water availability, and in roots in infertile dry sites (Givnish 2002; Montague and Givnish 1996; Smith and Huston 1989) are most likely responsible for such variations among species.

## Plant age and size effects on light harvesting from leaf to stand

Plant light harvesting is often studied independently of plant age and size, but aging and size both greatly affect plant structure and biomass allocation in herbaceous and woody perennials with profound implications for light harvesting. Any age-dependent change in leaf phenotype is called heteroblasty (Diggle 1999; Greenwood 1995; Greenwood et al. 2009). For light harvesting, it is significant that leaf dry mass per unit area increases with increasing plant age in herbaceous perennials (Niinemets 2004, 2005) and with increasing plant age and size in woody shrubs and trees (Claveau et al. 2005; Day et al. 2001; Greenwood et al. 2009;

Niinemets 2002, 2006; Rijkers et al. 2000). In some species, age-dependent changes in $M_A$ are also associated with major alterations in leaf size and shape (Gould 1993; Greenwood 1995; Lee and Richards 1991). In species with heteroblastic alterations in leaf size and shape, leaves are typically smaller in mature plants (Gould 1993; Lee and Richards 1991). In extreme cases, as in certain conifers, juvenile foliage has a needle-like appearance, as, for instance, in the Northern hemisphere species *Juniperus occidentalis* (Miller et al. 1995) and in the Southern hemisphere species *Podocarpus dacrydioides* and *Halocarpus kirkii* (Hay and Dellow 1952), while leaves in mature plants have been reduced to scale-like structures strongly appressed to the shoot axis (Hay and Dellow 1952; Miller et al. 1995).

How within-canopy plasticity in $M_A$ is affected by plant size and age is currently unclear. Some studies have found greater within-canopy plasticity in $M_A$ in older trees (Day et al. 2001; Richardson et al. 2001), while the opposite has been observed in other studies (Richardson et al. 2000). However, in these studies, foliage light environment has been specified in an ambigous manner as "upper" versus "lower" canopy. Given that canopy density can vary with plant size and age (Nock et al. 2008), and larger trees can intercept higher quantum flux densities in their natural forest environment, actual light measurements are crucial to the study of age-driven plasticity changes. In studies where long-term leaf irradiance has been measured directly, in most cases no differences in plastic changes in $M_A$ versus light availability among trees with varying size have been observed (Niinemets 2006; Niinemets and Kull 1995a; Niinemets et al. 2005c).

With accumulation of support structures, the fraction of biomass in leaves decreases with increasing age in herbaceous perennials (Niinemets 2004, 2005) and with age and size in woody species (Fig. 8; Bartelink 1998; Delagrange et al. 2004; Miller et al. 1995; Peichl and Arain 2007; Vanninen et al. 1996). These modifications in foliage structure and biomass allocation together lead to strong reductions in stand $L$ with increasing plant age and size (Bond-Lamberty et al. 2002; Delzon and Loustau 2005; Frazer et al. 2000; Nock et al. 2008; Ryan et al. 1997) and overall reduced canopy light interception (Frazer et al. 2000; Nock et al. 2008). On the other hand, reductions in the overstory $L$ in aging trees create windows of opportunity for early-successional forest species and understory shrubs. There is a negative correlation between overstory and understory $L$ across the chronosequence of temperate forest stands (Bond-Lamberty et al. 2002; Vertessy et al. 2001), demonstrating that age-related changes in forest canopy transmittance play an important role in the dynamics of forest stands.

The rate of ontogenetic changes in both $M_A$ (Niinemets 2006) and $F_L$ (Fig. 8, King 2003) varies significantly among woody species, likely providing explanation for species differences in age-dependent modifications in foliage biomass and $L$ observed across the studies (e.g., Ryan et al. 1997, 2004). In particular,
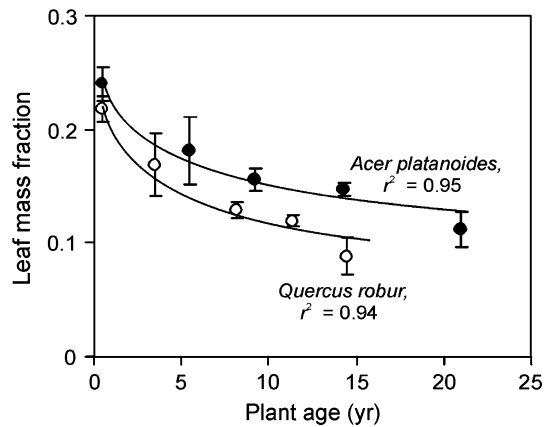
**Fig. 8** Age-dependent changes in the average ($\pm$ SE) mass fraction of leaves in above-ground biomass in relation to plant age in saplings (total height up to 2.6 m) of the temperate deciduous shade tolerant tree *Acer platanoides* and intolerant tree *Quercus robur* (data modified from Niinemets 1998b; Portsmuth and Niinemets 2007—only the control treatment from the latter study). The non-linear regressions in the form of $y = a + b\text{Log}x$ are significant for both species at $P < 0.001$

there is evidence that $M_A$ and $F_L$ decrease at a slower rate in shade-tolerant species than in intolerant species (Fig. 8; King 2003; Lusk et al. 2008a; Niinemets 2006). Such delayed ontogenetic modifications in foliage structure and allometry imply that shade tolerant species of a given size accumulate more foliar area than intolerant species (Paquette et al. 2007; Takahashi and Lechowicz 2008), and that their light harvesting capacity decreases at a slower rate. This can provide an explanation for the increasingly superior performance of shade-tolerant species in forest understories as co-existing plants of varying tolerance increase in age and size (Harcombe et al. 2002; Stephens and Ward 1992; Ward and Stephens 1993).

In addition to modifications in leaf structure and fractional biomass allocation to foliage, in some broad-leaved species, there is evidence of more vertical foliage inclination angles in older trees (James and Bell 1996, 2000), reducing the efficiency of light harvesting in lower light availabilities. Furthermore, foliage is aggregated more strongly in larger trees. At shoot level, greater foliage aggregation is associated with denser packing of leaves in shorter shoots (Frazer et al. 2000; Niinemets and Kull 1995b; Niinemets et al. 2005c; Sterck and Bongers 2001). In addition, in the heteroblastic conifers, the scale-like mature foliage closely adhering to the shoot axis also increases effective foliage aggregation. At stand scale, data indicate that foliage aggregation increases with increasing stand age (Frazer et al. 2000; Mencuccini and Grace 1996). These observations collectively suggest that enhanced foliage aggregation should be added to the list of factors reducing light harvesting efficiency of older trees.

Initially, crown depth may increase with increasing tree size but, beyond a certain critical tree size, relative crown depth decreases in many species, implying a shift of foliage to higher irradiances in the upper canopy

(Hashimoto 1991; Niinemets 1996; Osunkoya et al. 2007; Sterck and Bongers 2001; Sumida and Komiyama 1997; Xu and Harrington 1998). Such changes can be particularly significant in dense stands (Xu and Harrington 1998). Given further that foliage in older trees with larger $M_A$ is less "shade adapted" than foliage in younger trees, such an upward movement of foliage in older trees may reflect reductions in foliage tolerance of low light availabilities. If so, shortening of canopy extension is expected to occur with a slower rate in more shade-tolerant species. Current data on the ontogenetic modifications in crown architecture among species with contrasting shade tolerance are very limited. Nevertheless, the available data suggest that the height of the first living branch increases and canopy depth decreases more slowly in more shade-tolerant species (Niinemets 1996; Sumida and Komiyama 1997). Greater foliage tolerance of within-canopy shade in more shade-tolerant species may explain why older plants of shade-tolerant species have more extended 'multilayer' canopies, in contrast to younger plants, which tend to have 'mono-layer' canopies (see "Branching and leaf area distribution in the canopy").

Overall, this information demonstrates that age- and size-dependent dynamic modifications in foliage, shoot and canopy architecture play a paramount role in ontogenetic changes in plant leaf area accumulation, light harvesting efficiency and plant survival in forest understories. Plant survivorship in the understory decreases dramatically with increasing plant age (Metcalfe et al. 1998; Rikhari et al. 1998), reflecting greater light requirement of older and larger trees (Niinemets 2006; Sheil et al. 2006). To understand the functioning of different-aged plant stands, and to be able to simulate plant stand development, it is critical to consider age- and size-dependent alterations in leaf, shoot and canopy architecture.

## Conclusions and outlook

The current analysis emphasizes the importance of structural controls at various hierarchical scales in determining plant light harvesting and modifications in species distribution along understory-gap gradients. Due to species-specific trait values and limited plasticity, there is a fundamental trade-off between a species' ability to acclimate to low and high light environments. Universal suites of traits improving species tolerance of low light conditions and species' capacity to shade out competitors are high chlorophyll content, low foliage aggregation and low leaf inclination angle. Deciduous species further achieve high foliage accumulation through reduced $M_A$, while evergreens increase foliage longevity. At a canopy level, young shade-tolerant plants enhance light harvesting by flat crowns, while older plants enhance accumulation of shade-tolerant foliage in multi-layered crowns. Although there is broad consensus on the traits improving light harvesting, much

less is known of the relative importance of various traits in altering species shade tolerance. All traits altering light harvesting vary with long-term light availability, but information of plasticity of many important plant traits is currently scarce, calling for more quantitative studies along light gradients.

Different combinations of traits characterize various plant functional types with an apparent trade-off between biomass investment in support biomass vs foliage, a pattern that likely causes the increase in plant light requirement with increasing adult stature (herbs < shrubs < trees). Along the lines of this trade-off, biomass allocation to foliage decreases with increasing plant age and size. Plant aging and increase in size further leads to modifications in foliage structure, reducing the amount of leaf area formed with a given amount of foliar biomass in leaves. In addition, foliage is aggregated more strongly in older and larger plants. These changes collectively decrease the light harvesting efficiency with increasing plant age and size. Overall, these ontogenetic changes demonstrate that studies on leaf, shoot and canopy level attributes at certain moments in time provide only a snapshot of canopy light harvesting. Understanding the causes of variation of species dominance along light gradients requires consideration of age-dependent modifications in plant light harvesting. Clearly more experimental work on ontogenetic modifications in plant light harvesting is needed to improve our knowledge of the functioning of differently-aged multi-species natural plant communities.

## Appendix

See Table 1.

**Table 1** Estimates of stand projected leaf area index in essentially mono-specific stands ($L$) and average leaf life-span ($\Lambda_{av}$) for 41 temperate conifer species

| Species | $\Lambda_{av}$ (mo)[a] | $L$ (m$^2$ m$^{-2}$)[b] | Reference |
|---|---|---|---|
| *Abies alba* | 98 | 10.0 | Bindiu (1981), Cescatti and Zorer (2003) |
| *Abies amabilis* | 70 | 12.8 | Grier and Running (1977) |
| *Abies balsamea* | 96 | 7.8 | Mathieu (2006) |
| *Abies concolor* | 42 | 5.1 | Peterson et al. (1987) |
| *Abies firma* | 72 | 9.2 | Ando (1981) |
| *Abies fraseri* | 84 | 13.7 | Barker et al. (2002), Whittaker (1966) |
| *Abies lasiocarpa* | 96 | 12.8 | Jack and Long (1992) |
| *Abies sibirica* | 84 | 8.5 | Chen et al. (2005) |
| *Abies veitchii* | 60 | 9.5 | Tadaki et al. (1970) |
| *Chamaecyparis obtusa* | 48 | 5.4 | Tadaki et al. (1966), Utsugi et al. (2006) |
| *Cryptomeria japonica* | 48 | 6.8 | Tadaki and Kawasaki (1966), Tadaki et al. (1965, 1967) |
| *Juniperus communis* | 36 | 3.6 | Dahlberg et al. (2004) |
| *Juniperus monosperma* | 48 | 1.8 | Grier et al. (1992) |
| *Juniperus occidentalis* | 24 | 1.4 | Grier and Running (1977), Peterson et al. (1987) |
| *Juniperus virginiana* | 36 | 1.2 | Kiniry (1998) |
| *Larix decidua* | 6 | 5.1 | Gower et al. (1993) |
| *Larix kaempferi* | 6 | 4.0 | Liang et al. (2004), Satoo (1974) |
| *Picea abies* | 85 | 9.7 | Andersson (1973), Jarvis and Leverenz (1983), Leverenz and Hinckley (1990), Møller (1946) |
| *Picea engelmannii* | 90 | 5.7 | Nel and Wessman (1993) |
| *Picea mariana* | 110 | 6.3 | Bond-Lamberty et al. (2002), Gower et al. (1997) |
| *Picea rubens* | 72 | 12.7 | Gordon (1976) |
| *Picea sitchensis* | 60 | 12.3 | Grier and Running (1977), Leverenz and Hinckley (1990) |
| *Pinus banksiana* | 30 | 1.8 | Fassnacht and Gower (1997), Magnussen et al. (1986), Vogel and Gower (1998) |
| *Pinus contorta* | 60 | 5.7 | Jack and Long (1992), Leverenz and Hinckley (1990) |
| *Pinus edulis* | 66 | 4.0 | Classen et al. (2007) |
| *Pinus elliottii* | 19 | 2.5 | Gholz et al. (1991), Scurlock et al. (2001) |
| *Pinus halepensis* | 30 | 2.7 | López-Serrano et al. (2000) |
| *Pinus palustris* | 32 | 2.4 | Holder (2000) |
| *Pinus ponderosa* | 36 | 2.5 | Fassnacht et al. (1994), McLeod and Running (1988), Oren et al. (1987), Peterson et al. (1987), Pierce and Running (1988) |
| *Pinus radiata* | 28 | 3.5 | Myers et al. (1996) |
| *Pinus resinosa* | 36 | 4.8 | Deblonde et al. (1994), Fassnacht et al. (1994), Gower et al. (1993) |
| *Pinus strobus* | 30 | 5.3 | Gower et al. (1993), Vose and Swank (1990) |
| *Pinus sylvestris* | 28 | 3.1 | Jarvis and Leverenz (1983), Leverenz and Hinckley (1990), Møller (1946), Ovington (1957) |
| *Pinus taeda* | 21 | 1.7 | Albaugh et al. (1998) |
| *Pseudotsuga menziesii* | 65 | 7.7 | Borghetti et al. (1986), Gower et al. (1992), Leverenz and Hinckley (1990), Marshall and Waring (1986), Runyon et al. (1994) |
| *Taxodium distichum* | 7 | 2.2 | Oren et al. (1999) |

**Table 1** continued

| Species | $\Lambda_{av}$ (mo)[a] | $L$ (m$^2$ m$^{-2}$)[b] | Reference |
|---|---|---|---|
| *Thuja occidentalis* | 55 | 8.2 | Pronk (2004) |
| *Tsuga canadensis* | 60 | 13.1 | Whittaker (1966) |
| *Tsuga heterophylla* | 66 | 12.4 | Gholz (1982), Grier and Running (1977), Runyon et al. (1994) |
| *Tsuga mertesiana* | 60 | 8.7 | Grier and Running (1977), Peterson et al. (1987) |
| *Tsuga sieboldii* | 60 | 7.4 | Ando (1981) |

[a] $\Lambda_{av}$ is defined as the leaf age-class retaining at least 50% of leaves (Cordell et al. 2001; Kayama et al. 2002; Prior et al. 2003). The data for $\Lambda_{av}$ come mainly from the compilation of Hallik et al. (2009b) reporting estimates of $\Lambda_{av}$ for 27 species in the dataset. For species missing from their compilation, data were obtained from the literature—*Abies amabilis* (Hessl et al. 2004), *Abies balsamea* (Niinemets and Lukjanova 2003b) and *Pinus elliottii* (Holder 2000), and for the remaining 11 species, $\Lambda_{av}$ was determined by counting the number of leaf age-classes with at least 50% of foliage remaining in representative species habitats

[b] As optical measurements of $L$ require assumptions about the aggregation of foliage (Chen 1996; Sampson and Allen 1995; Stenberg et al. 1994), only direct measurements of $L$ were used in all cases. Averages were calculated whenever multiple estimates of $L$ were available

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