

Does shade improve light interception efficiency? A comparison among seedlings from shade-tolerant and -intolerant temperate deciduous tree species

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Summary

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- Here, we tested two hypotheses: shading increases light interception efficiency (LIE) of broadleaved tree seedlings, and shade-tolerant species exhibit larger LIEs than do shade-intolerant ones. The impact of seedling size was taken into account to detect potential size-independent effects on LIE. LIE was defined as the ratio of mean light intercepted by leaves to light intercepted by a horizontal surface of equal area.
- Seedlings from five species differing in shade tolerance (*Acer saccharum*, *Betula alleghaniensis*, *A. pseudoplatanus*, *B. pendula*, *Fagus sylvatica*) were grown under neutral shading nets providing 36, 16 and 4% of external irradiance. Seedlings (1- and 2-year-old) were three-dimensionally digitized, allowing calculation of LIE.
- Shading induced dramatic reduction in total leaf area, which was lowest in shade-tolerant species in all irradiance regimes. Irradiance reduced LIE through increasing leaf overlap with increasing leaf area. There was very little evidence of significant size-independent plasticity of LIE.
- No relationship was found between the known shade tolerance of species and LIE at equivalent size and irradiance.

Key words: forest regeneration, light interception efficiency (LIE), phenotypic plasticity, shade tolerance, silhouette : total area ratio (STAR).

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Introduction

To acquire the energy required for the numerous processes involved in the conversion of atmospheric CO₂ into biomass, plants need to capture solar radiation within their surrounding environment. In a forest understory, where light is often highly variable in time and in space (Runkle, 1982; Canham *et al.*, 1990; Gendron *et al.*, 2001), growth and survival of regenerating seedlings are closely linked to their capacity to intercept light efficiently under contrasting light environments, and this capacity may be critical to seedling survival.

At the individual tree scale, light interception efficiency (LIE) can be defined as the ratio of mean light intercepted by leaves to light intercepted by a horizontal surface of equal area. The integral of this ratio over the whole sky hemisphere and over time defines LIE. Following this definition, LIE is governed by the combination of: (i) arrangement of the leaf surface within the crown volume; (ii) optical properties of leaves and the soil surface; and (iii) light distribution over the sky hemisphere. Crown shape and particularly branching pattern (Sipe & Bazzaz, 1994), leaf number, size and shape (Niklas, 1989; Ackerly & Bazzaz, 1995; Farnsworth & Niklas, 1995), leaf

distribution (Planchais & Sinoquet, 1998) and leaf orientation (Planchais & Sinoquet, 1998; Farque *et al.*, 2001; Falster & Westoby, 2003; Gálvez & Pearcy, 2003) contribute to a large extent to an efficient intercepting leaf surface.

Significant differences in LIE are expected among species since fine-scale studies of crown morphology and architecture usually reveal numerous interspecific differences (Hallé *et al.*, 1978; Sterck, 1997; Beaudet & Messier, 1998; King & Maindonald, 1999; Poorter, 1999; Kawamura & Takeda, 2002). Indeed, potential differences in the sum of numerous fine-scale crown traits are likely to result in contrasting LIEs among species which may be critical for survival in forest understory. Such differences might, in turn, contribute to the degree of shade tolerance observed among forest tree species (Baker, 1949; Forcier, 1975). Recent evidence nevertheless showed that only small interspecific differences in light interception abilities occurred among species under similar environments (Poorter & Werger, 1999; Valladares *et al.*, 2002; Pearcy *et al.*, 2004). It is still debatable whether shade-tolerant species have an intrinsically larger LIE than shade-intolerant ones.

Differences in irradiance received during development resulted in a large intraspecific diversity in LIE for single branches or whole crowns (phenotypic plasticity) (Planchais & Sinoquet, 1998; Valladares & Pearcy, 1998; Farque *et al.*, 2001; Fleck *et al.*, 2003; Gálvez & Pearcy, 2003). Under low irradiance regimes, LIE is frequently increased because of smaller leaf inclination angles (i.e. horizontal leaves) or a smaller number of leaf layers or petiole twisting, the two latter processes limiting the detrimental effect of self-shading among leaves. Conversely, LIE is decreased under higher irradiance regimes because of denser crowns and larger leaf area that increase leaf overlap and self-shading. However, this decrease in LIE with higher irradiance regimes is often counterbalanced by a deeper light penetration within the crown and results in reduced interception of damaging high and direct sunlight radiations.

Until now, little attention has been paid to the variability of LIE of woody species with respect to their ontogeny or development in size (but see Ackerly & Bazzaz, 1995; Farque *et al.*, 2001; Niinemets *et al.*, 2005), despite the recognized importance of tree size on crown morphology and biomass allocation (Messier & Nikinmaa, 2000; Naumburg *et al.*, 2001; Sterck & Bongers, 2001; Claveau *et al.*, 2002; Delgrange *et al.*, 2004). Kawamura and Takeda (2002) reported, for two *Vaccinium* species, the critical importance of individual height and ontogeny for determining crown dimensions and branching patterns, respectively, whereas light availability mostly affected phyllotactic traits. Recently, Niinemets *et al.* (2005) concluded that increasing size or age of *Agathis australis* (Araucariaceae) resulted in a decreased LIE. Consequently, in addition to acclimation to diverse irradiance conditions, intra- and interspecific differences in LIE are likely to occur during the early development of regenerating trees because of ontogenetic constraints.

Here, we examined the variation in leaf organization and integrated crown light interception of five different broadleaved

species: (i) two North American species, the shade-tolerant *Acer saccharum* and the moderately shade-tolerant *Betula alleghaniensis*; and (ii) three western European species, the shade-tolerant *Fagus sylvatica*, the moderately shade-tolerant *A. pseudoplatanus*, and the pioneer and shade intolerant *B. pendula*. We used direct measurements and spatially explicit three-dimensional model simulations to compute light interception. For this purpose, we digitized the crown of 1- and 2-year-old seedlings grown in a nursery under three contrasting light regimes (36, 16 and 4% of full sunlight, provided by neutral shading nets) to assess the precise organization of leaves within the crown volume. Then, using reconstructed three-dimensional images of digitized seedlings in the plant functional and structural model VegeSTAR (Adam *et al.*, 2004), silhouette to total leaf area ratio was estimated for single directions (STAR_Ω) or integrated at crown level over the whole sky (STAR_{sky}) and then used for estimating whole-plant LIE.

This study had three main objectives: (i) to assess the plasticity of leaf organization and resulting crown LIE in relation to contrasting irradiance microclimates and seedling age (ontogenic processes); (ii) to compare species for the degree of plasticity they show in LIE; and (iii) to check whether shade-tolerant species differ from shade-intolerant ones with respect to LIE.

Materials and Methods

Plant material and experimental design

Two North American broadleaved tree species, *Acer saccharum* Marsh (sugar maple: AS) and *Betula alleghaniensis* Britton (yellow birch: BA), and three European ones, *Acer pseudoplatanus* L. (sycamore: AP), *Betula pendula* Roth (European white birch: BP) and *Fagus sylvatica* L. (European beech: FS) were used. Germinated seedlings were transplanted into 10 l pots filled with a mixture of peat and sand (1/3 v/v) and placed in a nursery at Champenoux (48°44' N, 6°14' E) near Nancy, France. We used three aluminized neutral shading nets (OLS screens, Ludvig Svensson, Kinna, Sweden) which provided three contrasting irradiance regimes [high light (HL), 36% of the corresponding external irradiance; intermediate light (IL), 16%; and low light (LL), 4%; further discussed later]. Seedlings were placed at least 30 cm from each other to limit mutual shading. They were fertilized twice during the growing season (during May and at the beginning of August) with 40 g (4 g l⁻¹ substrate) of a slow-release fertilizer (Nutricote® 100+, 13/13/13 N/P/K+ oligo-elements). Water was provided every day to field capacity using drip irrigation controlled by a time switch. Three series of 30 seedlings per species and treatment were planted during May 2000, 2001 and 2002 under the same shading nets so as to obtain simultaneously 1- and 2-year-old seedlings for measurements. During the summer, one to six healthy individuals were selected for digitization. Table 1 provides details of seedling dispatching among years, ages and species.

Table 1 Number of digitized saplings according to species, light regime, age and installation year

Installation	Age	AP			AS			BA			BP			FS		
		HL	IL	LL	HL	IL	LL	HL	IL	LL	HL	IL	LL	HL	IL	LL
2000	1 years	5	5	5							5	5	5	5	5	5
	2 years	5	5	5							5	4	4	6	5	5
2001	2 years	4	4		2	2	2	1	2	2	4	4		4	4	
2002	1 years				2	2	2	2	2	2						

HL, high light; IL, intermediate light; LL, low light; AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, *Fagus sylvatica*.

Measurement of irradiance microclimate below shading nets

Two linear PAR sensors (amorphous silicium sensors, Solems, Palaiseau, France) recorded continuously (pace: 1 s, averaged values over 30 mn stored in a CR10X data logger, Campbell Scientific, Logan, UT, USA) photon flux density in the PAR (PPFD) below each net, while a similar sensor was used for incident irradiance outside the net. Sensors were calibrated every year with a Li-Cor reference quantum sensor (Li-190, Li-Cor Biosciences, Lincoln, NE, USA). A Delta-T BF2 sensor (Delta T, Cambridge, UK) was used to record diffuse and direct PPFD. Transmittance in the PAR below the shading nets was calculated as the ratio of the sum of PPFD below and above the nets. Resulting levels were as follows: HL, 36%, IL, 16%, LL, 4%.

During August 2000, a linear PAR sensor Li-Cor Li-191 (Li-Cor Biosciences) and a diffuse-direct sensor Delta-T BFS (Delta T) were used during two clear days (17 and 23/08/00) between 10:00 and 15:00 h local time, to assess diffuse and direct irradiance above and below the nets. Transmittances for direct and diffuse irradiance were expressed as a fraction of the incident PPFD: HL, 25.5% direct and 121% diffuse incident PPFD; IL, 8.8% direct and 60.0% diffuse PPFD; LL, 1.0% direct and 29.7% diffuse PPFD. The greater than 100% diffuse PPFD estimated below HL shading nets was attributable to redistribution of direct PPFD by multiple scattering inside the aluminized nets. This shows that the nets altered significantly the ratio diffuse/direct irradiance, the latter component being minor under the nets. Spectral composition of the light was not modified by the nets, and the red/far red ratio remained unaffected (data not shown).

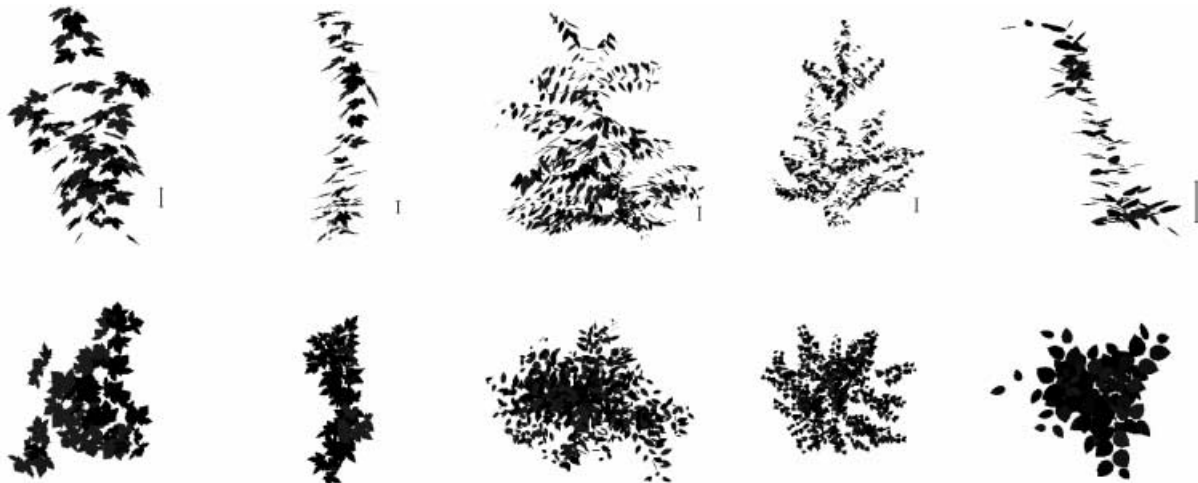
Seedling digitization

A total of 136 seedlings with two ages, four irradiance regimes and five species (i.e. between one and six replicates per individual treatment) were digitized during the 2000, 2001 and 2002 growing seasons (Table 1). Spatial distribution and geometry of leaves within the crown volumes was recorded using a Fastrak electromagnetic 3D apparatus (Polhemus Inc.,

Colchester, VT, USA) as described by Sinoquet *et al.* (1998). This apparatus associated with the 3A computer software (Adam *et al.*, 1999) allowed a precise positioning of each leaf. Position and orientation as given by the three Euler angles (leaf midrib elevation, θ ; leaf inclination around midrib, Φ ; and leaf midrib azimuth, Ψ) were recorded for each individual leaf assumed to be flat. This method, first tested by Sinoquet and Rivet (1997), was recently applied to describe the canopy structure of a range of plant species (Sinoquet *et al.*, 1998; Rakocevic *et al.*, 2000; Falster & Westoby, 2003; Sonohat *et al.*, 2006). To prevent canopy movements induced by wind and interferences within the electromagnetic measurement field (Sinoquet & Rivet, 1997), digitization was performed inside a small wood cabin that contained no metallic elements. One measurement at the lamina-petiole junction described the leaf spatial coordinates and Euler angles since the sensor was held along the midrib and parallel to the leaf blade. For the North American species, leaf length was estimated by recording spatial coordinates of lamina extremity (error < 1 mm, Sinoquet *et al.*, 1998), whereas for the European species, leaf length and width were measured to the nearest mm with a ruler. Time required for digitization was from 10 min in the case of a 20-cm-high *A. saccharum* to 2 d for a 190-cm-high *B. alleghaniensis*.

Canopy reconstruction of digitized individuals and light interception simulations

The geographically oriented x , y and z coordinates, and the three Euler angles recorded for each leaf after seedling digitization were used to reconstruct the crown of each individual using the three-dimensional explicit model VegeSTAR 3.02 (Adam *et al.*, 2004; Fig. 1). For each species, the specific relationship between leaf area (a), leaf length (l) and leaf width (w) was computed from a sample of leaves (c. 30 leaves per species) from the seedlings. The resulting relationships ($r^2 \geq 0.95$) were as follows: $a = 0.75l^2$, *A. saccharum*; $a = 0.34l^2$, *B. alleghaniensis*; $a = 0.61lw$, *B. pendula*; $a = 0.57lw$, *A. pseudoplatanus*; $a = 0.73lw$, *F. sylvatica*. These relationships were used to compute total leaf area per seedling. For each species, leaf surfaces were visualized in the model by a polygonal leaf prototype that



Acer pseudoplatanus *Acer saccharum* *Betula alleghaniensis* *Betula pendula* *Fagus sylvatica*

Fig. 1 Examples of reconstructed virtual saplings grown under the high irradiance regime (36% external irradiance) viewed from horizontal (above) and vertical (below) directions. Bar, 10 cm.

mimicked real leaf shape and obeyed the relationship between leaf area and dimensions.

To assess LIE, we used the ratio STAR (Carter & Smith, 1985; Oker-Blom & Smolander, 1988). The use of STAR to estimate LIE is based on several assumptions: (i) light scattering is neglected, i.e. leaf absorptance equals 1; and (ii) light interception by branches and twigs is negligible. Directional STAR was computed with the VegeSTAR 3.02 software (Adam *et al.*, 2004; Sinoquet *et al.*, 2005) as the ratio of projected leaf area in a given direction, as viewed by an orthographic camera (i.e. a camera with parallel beams), to the total leaf area. We used 46 directions pointing from the sky hemisphere to the three-dimensional model, with approximately equal adjacent solid angles (*c.* $2\pi/46$ steradians) and penta- and hexagonal facets (Den Dulk, 1989). The distribution is further referred to as 'turtle sky'. Each direction Ω was defined by elevation (Ω_{El}) and azimuth (Ω_{Az}) angles.

In a second step, STAR was decomposed as a product of leaf inclination (L_i) and leaf overlapping or clumping (L_o) components (Pearcy & Yang, 1996; Farque *et al.*, 2001):

$$STAR_{\Omega} = \frac{A_{\Omega}}{A_t} = \frac{\sum a_{\Omega}}{A_t} \times \frac{A_{\Omega}}{\sum a_{\Omega}} = L_i \times L_o \quad \text{Eqn 1}$$

(a_{Ω} , projected area of a leaf with area a along the direction Ω ; A_{Ω} , the projected canopy area; A_t , total leaf area, i.e. corresponds to $\sum a$). Low values of L_o indicate large leaf overlapping.

For every leaf, a_{Ω} was calculated from a as:

$$a_{\Omega} = \cos(\alpha) \times a \quad \text{Eqn 2}$$

where α is the angle between the leaf normal and the direction Ω calculated as:

$$\alpha = \arccos[\cos(\Phi)\sin(\theta)\cos(\Psi) + \sin(\Phi)\sin(\Psi)\cos(\Omega_{El})\cos(\Omega_{Az}) + \cos(\Phi)\sin(\theta)\sin(\Psi) - \sin(\theta)\cos(\Psi)\cos(\Omega_{El})\sin(\Omega_{Az}) + \cos(\Phi)\cos(\theta)\sin(\Omega_{El})] \quad \text{Eqn 3}$$

This can be simplified in:

$$\alpha = \arccos[(\cos(\Phi)\sin(\theta)\cos(\Psi - \Omega_{Az}) + \sin(\Phi)\sin(\Psi - \Omega_{Az}))\cos(\Omega_{El}) + \cos(\Phi)\cos(\theta)\sin(\Omega_{El})] \quad \text{Eqn 3a}$$

where Φ , θ and Ψ are the leaf rolling, elevation and azimuth angles, respectively.

STAR and the leaf inclination component L_i were integrated over the whole sky hemisphere ($STAR_{Sky}$ and L_{iSky}). For this purpose, the 46 values of STAR and L_i were weighted using an estimate of the contribution of cumulated irradiance incoming from each turtle sky facet [I_{Ω} where $\sum_{\Omega} I_{\Omega} = 1$] below the shading nets during the growing season (1 May to 30 September):

$$STAR_{Sky} = \sum_{\Omega} STAR_{\Omega} I_{\Omega} \quad \text{Eqn 4}$$

$$L_{iSky} = \sum_{\Omega} L_{i\Omega} I_{\Omega} \quad \text{Eqn 5}$$

L_{oSky} , leaf overlap component integrated over sky hemisphere, was calculated from L_{iSky} and $STAR_{Sky}$ as follows:

$$L_{oSky} = STAR_{Sky} / L_{iSky} \quad \text{Eqn 6}$$

LIE as defined in the introduction was calculated as follows:

$$LIE = \frac{\sum_{\Omega} STAR_{\Omega} I_{\Omega}}{\sum_{\Omega} I_{\Omega} \sin(\Omega_{El})} = \frac{STAR_{Sky}}{\sum_{\Omega} I_{\Omega} \sin(\Omega_{El})} \quad \text{Eqn 7}$$

According to this definition, LIE is equivalent to $STAR_{Sky}$ (weighted average of directional STAR) scaled so that a horizontal leaf has a LIE value equal to one under the considered light regime. Multipliers for converting $STAR_{Sky}$ to LIE are 1.91, 1.93 and 1.96 for HL, IL and LL regimes, respectively.

Cumulated irradiance incoming from each turtle sky facet was calculated using Gap Light Analyser (GLA) software (Frazer *et al.*, 1999). The sky hemisphere was divided into 4050 sectors (90 azimuth \times 45 zenith angles) and incident irradiance computed for each sector. We used a virtual open sky photograph (i.e. with white pixels only) and attributed each GLA sector to a turtle sky facet. In the open, the fraction direct irradiance (%Direct_{Open}) was 50% (integrated measurements from 16 June to 30 September 2002). The fraction of direct irradiance below shading nets was derived from %Direct_{Open} and the measured relative direct PPFD below each net. Total diffuse radiation was computed from the measured relative diffuse PPFD of each net. The spatial distribution of diffuse irradiance was set to Uniform OverCast (UOC) because large redistribution of light beams occurs below the nets.

Statistical analyses

All statistical analyses were performed with the statistical software R version 2.0.1 (R Development Core Team, 2004). Linear models were fitted for testing species, age and irradiance regime effects on response variables. When required, an additional covariate was included in the model for scaling the response variable to plant size. The log-transformed total leaf area A_t appeared to be the most suitable covariate as most size-dependent variables responded linearly to it (see the Results section). Our general approach was first to fit the main model with every interaction between factors and possibly covariate, up to the highest order, of the form:

$$R_{ijk} = \mu + (a_i + b_j + c_k + d_{ij} + e_{ik} + f_{jk} + g_{ijk}) + \epsilon_{ijk} \quad \text{Eqn 8}$$

or, when the covariate was present:

$$R_{ijk} = \mu + (a_i + b_j + c_k + d_{ij} + e_{ik} + f_{jk} + g_{ijk}) + (\alpha + a'_i + b'_j + c'_k + d'_{ij} + e'_{ik} + f'_{jk} + g'_{ijk})V_{ijk} + \epsilon_{ijk} \quad \text{Eqn 9}$$

(indices i , j and k , first, second and third factor levels, respectively; r , replicates; μ , intercept; a_i , b_j and c_k , main effects on intercept; d_{ij} , e_{ik} and f_{jk} , second-order interactions; g_{ijk} , third-order interaction effects on intercept, α , slope; a'_i , b'_j , c'_k , d'_{ij} , e'_{ik} , f'_{jk} and g'_{ijk} , effects on slope; R_{ijk} , response; V_{ijk} , covariate; ϵ_{ijk} , error term).

Then a cascade of nested models were fitted by setting to zero or equalizing the parameters that were not significantly different ($P < 0.05$) from zero or not significantly different among each other. Highest-order interaction parameters were checked first. At the end of the procedure, the most parsimonious (i.e. with the lowest number of parameters) model that was not significantly different (F -test between main and sub-model) from the main model was retained. At this stage, and if required, multiple comparison tests using the multivariate t distributions of the parameters were performed on parameters of interest with the multcomp R-package (Bretz *et al.*, 2004). Only the results of this final model are detailed in this paper.

Normality and homoscedasticity were checked graphically by plotting residuals against predicted and by normal quantile to quantile plots.

Results

Total leaf area

Total leaf area of saplings (A_t) differed significantly among irradiance regimes and among species at all ages (Table 2). The general pattern was an increase in A_t with increasing irradiance. During the first year *A. pseudoplatanus* and *B. pendula* developed largest A_t as compared with the other species under all irradiance regimes. During the second year, *B. alleghaniensis* had a large growth and as a result the largest leaf area, followed by *B. pendula*. After two growing seasons, the two *Acer* species were intermediate in almost all treatments. Meanwhile, *F. sylvatica* had dramatically low values of A_t as compared with any other species and exhibited an eightfold difference with *B. alleghaniensis* under high irradiance (HL, Fig. 2).

Table 2 Results of a two-way ANOVA on \log_e (total leaf area) and light interception efficiency (LIE) of 1- and 2-year-old seedlings as a function of irradiance regime (36, 16 and 4% of external irradiance) and species

	\log_e (total leaf area)		LIE	
	1-year-old	2-year-old	1-year-old	2-year-old
<i>n</i>	57	80	57	80
Irradiance regime				
df ₁ , df ₂	2, 42	2, 65	2, 42	2, 65
<i>F</i>	85.6	45.8	18.9	22.3
<i>P</i> > <i>F</i>	< 0.001	< 0.001	< 0.001	< 0.001
Species				
df ₁ , df ₂	4, 42	4, 65	4, 42	4, 65
<i>F</i>	56.2	30.4	0.83	3.4
<i>P</i> > <i>F</i>	< 0.001	< 0.001	0.513	0.014
Interaction				
df ₁ , df ₂	8, 42	8, 65	8, 42	8, 65
<i>F</i>	5.0	1.0	4.01	0.9
<i>P</i> > <i>F</i>	< 0.001	0.46	0.0013	0.52

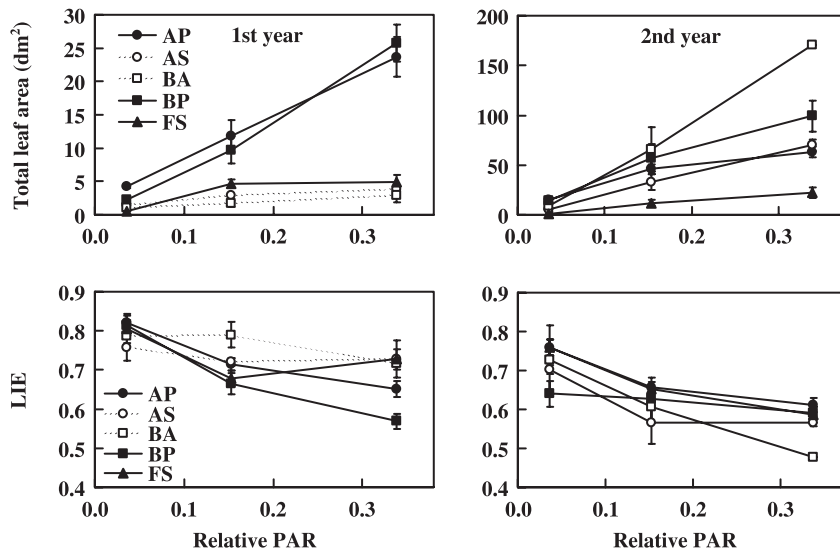


Fig. 2 Total leaf area (A_t) and computed light interception efficiency (LIE) as a function of irradiance regimes during growth (36, 16 and 4% of external irradiance) for 1-year-old (left) and 2-year-old (right) seedlings from five different broadleaved tree species: AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, *Fagus sylvatica*. Mean values from two to 10 trees per treatment \pm SE, except for 2-year-old BA, HL (high irradiance regime) (one tree). PPFD, photon flux density in the PAR.

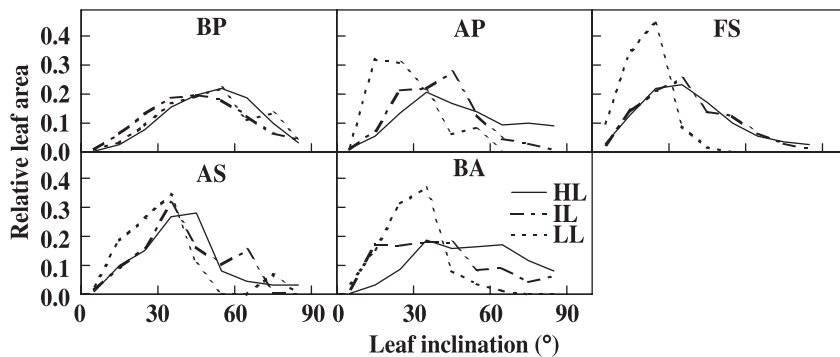


Fig. 3 Distribution of leaf inclinations, expressed as a fraction of total leaf area. Leaves of 2-year-old seedlings were pooled for each species and irradiance regime. Seedlings from five different broadleaved tree species grown under three different light regimes (HL, high; IL, intermediate; LL, low irradiance regimes). BP, *Betula pendula*; AP, *Acer pseudoplatanus*; FS, *Fagus sylvatica*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*. Angle classes with a 5° width.

Leaf inclination distribution

In order to document the leaf inclination component of STAR_{sky} , we calculated the distribution of leaf inclination, defined as the angle between the leaf normal and the vertical, and calculated as $\arccos(|\cos(\Phi)\cos(\theta)|)$, relative to leaf area (and not to leaf number to limit the influence of small nonrepresentative leaves) in 2-year-old seedlings (Fig. 3). All species but *B. pendula* showed a shift toward less horizontal leaves with increasing irradiance regimes. *B. pendula* showed a more evenly distributed leaf inclination than other species with no clear evidence of a shift attributable to irradiance regime.

Light interception efficiency

Light interception efficiency differed significantly among irradiance regimes and species during both the first and second years, according to a two-way ANOVA (Table 2). However patterns of variation were much less straightforward than for A_t (Fig. 2). Nevertheless a general decrease in LIE was detected with increasing irradiance both during the first and during the second year. Moreover, second-year values were smaller than corresponding first-year values. Differences among species

were difficult to detect, as the species ranking depended on age and irradiance microclimate. This complex pattern was attributable to pronounced age- and size-related effects that interacted with irradiance-induced plasticity and with species effects.

Light interception efficiency decreased severely with increasing A_t (Fig. 4), and effects of irradiance regime and age on LIE might be confounded with ontogenic effects mediated by size (i.e. by A_t). We therefore introduced $\log_e(A_t)$ as a covariable into the main linear model, according to Eqn 9 ($n = 137$, d.f. = 78, $r^2 = 0.849$). The most parsimonious model ($n = 137$, d.f. = 129, $r^2 = 0.703$) that was not significantly different from the main model ($F = 1.484$, d.f. = 51 and 78, $P = 0.057$) led to the relationships drawn in Fig. 4, and to the following conclusions: (i) no irradiance regime effect could be detected independently from that mediated by total leaf area; (ii) no age effect could be detected except for slope of 1-year-old *B. pendula* ($P = 0.024$); (iii) the slopes were not significantly different among species, except for the slope of the 1-year-old *B. pendula* ($P = 0.024$), that is, the size-induced plasticity of LIE was of similar amplitude in all species except 1-year-old *B. pendula*; (iv) there were significant differences in intercepts ($P < 0.001$) – multiple comparison tests produced the following ranking of species: $\text{FS}^a < \text{AS}^b < \text{BA}^b < \text{BP}$ (second

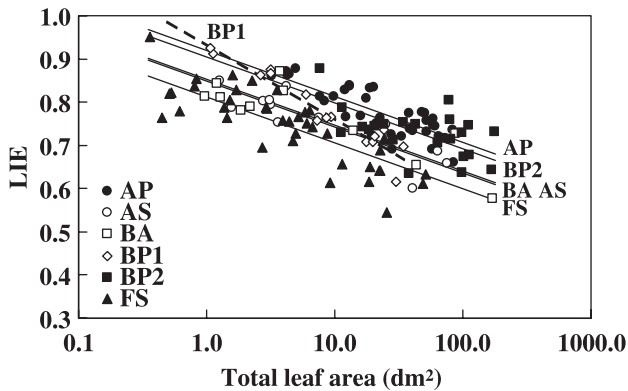


Fig. 4 Relationship between total leaf area (A_t) and computed light interception efficiency (LIE) for 1- or 2-year-old seedlings from five different broadleaved tree species grown under three different irradiance regimes (36, 16 and 4% of external irradiance). AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, *Fagus sylvatica*; BP1, 1-year-old *B. pendula*; BP2, 2-year-old *B. pendula*. Each point refers to an individual tree. Regression lines (dashed line, 1-year-old *B. pendula*) are from the retained linear model (see the 'Materials and Methods' section).

year)^c < AP^c (species sharing same letter are not significantly different). This means that *F. sylvatica* seedlings showed, after removal of the size effect, a smaller LIE in all treatments and all ages. The largest LIE was recorded in *A. pseudoplatanus* and *B. pedula*.

Leaf inclination component (L_{iSky})

Comparison of models according to Eqn 9 (all effects and interactions plus covariate) and Eqn 8 (all effects and interactions without covariate) revealed no significant effect of A_t on L_{iSky} ($F = 1.00$, d.f. = 29 and 78, $P = 0.479$). This leads to the following conclusions: (i) the effect of leaf inclination on STAR remained constant with A_t ; (ii) despite a very narrow range of L_{iSky} (0.496–0.523), there were significant main effects of species, irradiance and age and significant interactions, age × irradiance and age × species, in the model according to Eqn 4 (Fig. 5); multiple comparison tests on irradiance led to LL < IL = HL, and on species to BP^a < AS^a < BA^{ab} < AP^{ab} < FS^b (treatments sharing the same letters are not significantly different).

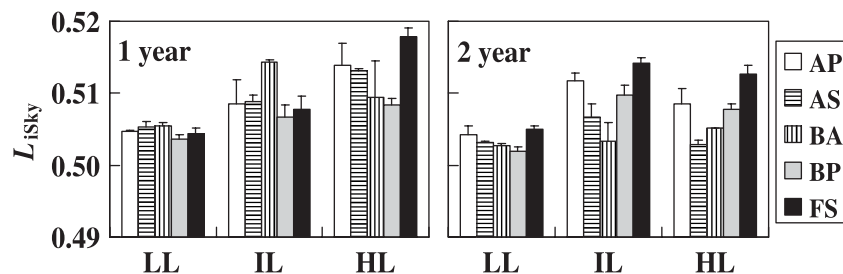


Fig. 5 Leaf inclination component of integrated silhouette : total leaf area ratio (L_{iSky}) (see Eqn 1) of five different broadleaved tree species grown under three different irradiance regimes (4, 16 and 36% of external irradiance, LL, IL and HL, respectively). AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, *Fagus sylvatica*. Left panel, 1-year-old seedlings; right panel, 2-year-old seedlings. Mean values ± SE, except for 2-year-old BA, HL (one tree).

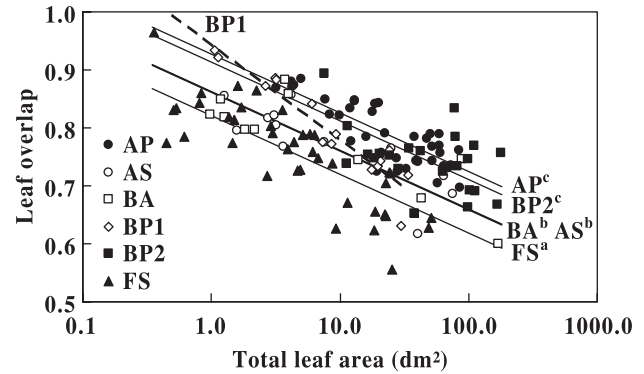


Fig. 6 Leaf overlap component of integrated silhouette : total leaf area ratio ($STAR_{sky}$) (see Eqn 1) as a function of total leaf area in seedlings from five different broadleaved tree species grown under three different irradiance regimes (36, 16 and 4% of external irradiance). AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, and *Fagus sylvatica*; BP1, 1-year-old *B. pendula*; BP2, 2-year-old *B. pendula*. Each point refers to an individual tree. Regression lines (dashed line, 1-year-old *B. pendula*) are from the retained linear model (see the 'Materials and Methods' section).

Leaf overlap component (L_{oSky})

Contrary to L_{iSky} , L_{oSky} decreased linearly with $\log(A_t)$ (Fig. 6) in all species. A model according to Eqn 9 ($n = 137$, d.f. = 78, $r^2 = 0.835$) was fitted to the data. The most parsimonious model ($n = 137$, d.f. = 129, $r^2 = 0.680$) that was not significantly different from the main model ($F = 1.331$, d.f. = 51 and 78, $P = 0.078$) led to the linear regression lines drawn in Fig. 6 and to the following conclusions: (i) no irradiance regime effect could be detected independently from that mediated by total leaf area; (ii) no age effect except for slope of 1-year-old *B. pendula* ($P = 0.028$); (iii) the slopes were not significantly different between species, except for slope of 1-year-old *B. pendula* ($P = 0.028$), that is, the size-induced plasticity of L_{oSky} was of similar amplitude in all species except 1-year-old *B. pendula*; (iv) significant differences in intercepts – multiple comparison tests produced the following ranking of species: FS^a < AS^b = BA^b < BP (2nd year)^c = AP^c (species sharing the same letter are not significantly different) ($P < 0.001$).

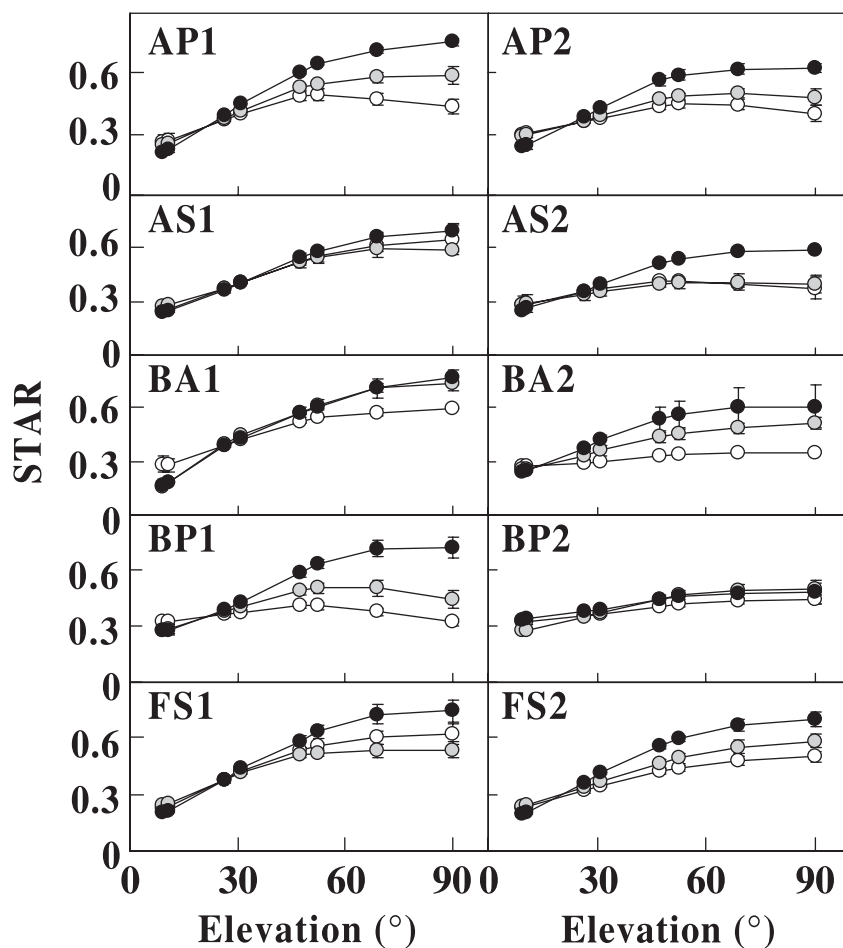


Fig. 7 Impact of the incidence elevation (0° , horizontal; 90° , vertical) on the silhouette : total leaf area ratio (STAR) integrated over the different azimuths. Seedlings from five different broadleaved tree species. Left panel, 1-year-old; right panel, 2-year-old seedlings. High light regime (HL), white circles; intermediate light regime (IL), grey circles; low light regime (LL), black circles. AP, *Acer pseudoplatanus*; AS, *Acer saccharum*; BA, *Betula alleghaniensis*; BP, *Betula pendula*; FS, *Fagus sylvatica*. Mean values from two to 10 trees per treatment \pm SE, except for 2-year-old BA, HL (one tree).

Directional effects on STAR

The results of the simulation presented above may be modified because of irradiance geometry, which changes dramatically from open spaces (similar contributions of direct and diffuse radiation) to deep shade below canopies (diffuse radiation dominant except during light flecks). To document this question, STAR was computed as a function of the elevation of incident irradiance (directional STAR, Fig. 7). In all species, STAR generally increased with elevation. Irradiance microclimate induced some changes, and STAR from highest elevations was smaller in plants grown under high irradiance regimes except in 2-year-old *B. pendula*.

Discussion

A simple framework for analysing LIE variations

In this study, we used Pearcy's LIE decomposition (Pearcy & Yang, 1996) in order to distinguish light interception ability attributable to foliage orientation – the more horizontal leaves, the more efficient foliage – and foliage overlapping.

Alternative frameworks relating to the theory of radiative transfer have been proposed to assess the effect of structural parameters on light interception properties (e.g. space occupation, leaf area density, foliage dispersion; Planchais & Sinoquet, 1998). However, the application of the radiative transfer theory to isolated plants depends on the definition of a canopy envelope filled with the vegetation elements (Norman & Welles, 1983; Cescatti, 1997). Recent studies have reported how subjective the definition of such canopy envelopes is, because the canopy volume depends on the shape of the envelope (e.g. bounding box vs convex envelope vs parametric shapes; Boudon, 2004) and also because of the fractal nature of canopies making canopy volume change with measurement scale (Phattaralerphong & Sinoquet, 2005). This is especially crucial in small plants like seedlings with a small number of leaves (Farque *et al.*, 2001) because it is unclear if air space between leaves belongs to the canopy volume or not. As parameters like canopy porosity, leaf area density and, consequently, clumping depend on how canopy volume is defined, they have a similar uncertainty as canopy volume (Sinoquet *et al.*, 2005). This is the reason that we have used a simple but robust framework – as

previously proposed by Pearcy and colleagues – rather than an apparently more detailed one, but which shows some drawbacks (especially the scale-dependence of the canopy envelope).

Comparison between YPLANT and VegeSTAR

YPLANT (Percy & Yang, 1996) is a widely used model and, before further discussion, it may be useful to compare YPLANT with VegeSTAR. VegeSTAR only computes STAR, which is the ratio of projected leaf area to total leaf area (called E_D in YPLANT). $STAR_{sky}$ is derived after summing directional values over the sky vault, weighed by cumulative irradiance. By contrast, YPLANT also computes light absorption and interception efficiency, called E_a and E_i , respectively. Absorption computations involve leaf reflection and transmission processes, which are treated in a simplistic manner – in particular, the directional redistribution of scattered light is neglected. Interception efficiency assumes leaves as black bodies, i.e. leaf absorbance is 1. In conclusion, similar variables between VegeSTAR and YPLANT are directional STAR (in VegeSTAR) and E_D (display efficiency in YPLANT). All other parameters in YPLANT such as E_i (LIE in this study), except for those implying absorption, can be calculated from the VegeSTAR output.

Total leaf area

The different irradiance regimes imposed on the seedlings from five European and North American broadleaved tree species induced large differences in growth. There was at least a sevenfold difference between minimum and maximum mean total leaf area (A_t) at the diverse ages vs irradiance regime combinations. This value needs to be compared with the range of values affecting LIE: the variation encompassed only a maximal range of 1.3-fold. Therefore, total leaf area developed by the seedlings accounts for most of the interspecific diversity of total light interception. LIE plays only a minor role in this variability.

Species ranking for total leaf area remained stable among the different irradiance regimes, but changed with age. During the second year of growth, the ranking from smaller to larger total leaf area overlapped with the ranking for shade tolerance. The shade-tolerant *F. sylvatica* had, in all cases, the lowest total leaf area. *A. pseudoplatanus* and *A. saccharum*, with intermediate tolerance, ranked intermediate and the two more shade-intolerant birches (*B. pendula* and *B. alleghaniensis*) had the largest leaf areas. Similar findings have been reported by Kitajima (1994), Walters and Reich (1999) and Poorter (1999), but this is not a general rule (Montgomery & Chazdon, 2002). This large difference in sapling size (estimated from leaf area) among species is probably one of the clues to shade tolerance/intolerance, as discussed later.

Interspecific variability of LIE

Static observations and descriptions of fine-scale tree traits generally show a large diversity in crown morphology and architecture among tree species (Hallé *et al.*, 1978; Sterck, 1997; Millet *et al.*, 1998; Percy *et al.*, 2004; Claveau *et al.*, 2005). Indeed, our seedlings revealed a large diversity in growth and branching patterns, with a sympodial growth in beech and a monopodial growth in the other species, with differences in ramification, leaf sizes and leaf inclination. But with respect to LIE, our results are in line with some recent findings (Valladares *et al.*, 2002; Percy *et al.*, 2004) that revealed only small differences when comparing species under similar irradiance environments and similar sizes/ages. This suggests a strong interspecific convergence in crown light capture capability (Poorter & Werger, 1999; Valladares *et al.*, 2002), possibly attributable to constraints imposed by the other functions of the crown, such as water transport and mechanical resistance (Percy *et al.*, 2005).

Irradiance-induced vs ontogenic plasticity of LIE

Light interception efficiency was found to vary dramatically in all species with changes in size (leaf area being an estimator of size); that is, there was a large ontogenic plasticity in LIE. A large fraction of the effect of shading on total light interception and LIE was therefore induced by delayed growth in shade vs high light grown saplings (Coleman *et al.*, 1994). Indeed, as leaf area accumulated during growth, leaf overlap severely depressed LIE, as was observed by Farque *et al.* (2001) in oaks. By contrast, irradiance-induced changes in leaf inclination tended to have a small influence on LIE, owing to the spatial integration over a sky hemisphere where irradiance distribution is essentially homogeneous after light redistribution below the shading nets. This result contradicts some earlier studies that reported a large impact of leaf inclination in the modulation of LIE (Takenaka *et al.*, 2001; Valladares *et al.*, 2002). However, these latter findings referred to particular species such as understory fruit plants, steep-leaved herbs, palms or lianas, where individual architecture does not experience equivalent mechanical and functional constraints to those of long-lived and potentially tall forest trees and to understory grown plants undergoing much more heterogeneous light distribution than found under our shading nets. In these examples, the plants were also small, with few leaves, so that leaf overlap was of less influence on LIE than leaf inclination. Nevertheless, saplings with higher leaf area (i.e. 2-year-old saplings and saplings grown under higher irradiance) had more leaves with larger inclination angles, which might increase interception of irradiance from more horizontal directions. We found that this effect remained small in all conditions. Moreover, the largest differences attributable to irradiance regimes occurred at the highest angular elevations. Generally the leaf overlapping component of STAR decreased (i.e.

there was more leaf overlap), while the leaf inclination component increased with increasing elevation of incident irradiance. For plants grown under higher irradiance, the smaller STAR at directions close to vertical is again attributable to leaf overlap. It is not compensated for in the horizontal directions by a shift in leaf inclination distribution to more vertical inclinations because, despite this shift, there was still a majority of leaves whose inclination is closer to horizontal than to vertical. A noticeable exception was *B. pendula*, the most shade-intolerant among the studied species, where the STAR gradient from horizontal to vertical directions was smooth and not influenced by irradiance regime. This is attributable to the conical crown shape of this species (Fig. 1), combined with its even leaf inclination distribution and its ability to shed its innermost shaded leaves: its foliage is distributed like a carapace, allowing light interception to be equally efficient whatever the direction of incident light, which might give an advantage in open sites.

Light interception and seedling functional ecology

Similar conclusions describing little or no interspecific differences in light interception abilities under similar environments (Poorter & Werger, 1999; Valladares *et al.*, 2002; Pearcy *et al.*, 2004) do not rule out the supposed importance of LIE in the diversity of species functional ecology or shade tolerance. Indeed, small differences between species in instantaneous or daily light capture may lead to rather large differences in final carbon gain over the whole growing season. Here, substantial differences between the five species (in LIE or L_{oSky}) demonstrated that slight architectural and phyllotaxic species-specific traits were maintained even if the whole-crown LIE was similarly affected among species by dimensional constraints. However, the ranking of species for LIE differed largely from that for shade tolerance. Noticeably, the most shade-tolerant species, *F. sylvatica*, had the lowest LIE among the five species studied.

LIE was larger in individuals grown under low than under high irradiance. This was mainly an effect of irradiance-induced differences in seedling sizes rather than a light-driven acclimation of architectural and phyllotaxic traits. As demonstrated in several earlier studies, individual size greatly affects morphological and allocational patterns, and apparent plasticity in response to environmental factors such as light, nutrients or water may be at least partly attributed to such ontogenetic shifts during plant ontogeny (Huber & Stuefer, 1997; McConnaughay & Coleman, 1999; Müller *et al.*, 2000). Specifically, tree size modulates the ratio of photosynthetic to nonphotosynthetic tissues (Messier & Nikinmaa, 2000; Naumburg *et al.*, 2001; Claveau *et al.*, 2002; Delagrangé *et al.*, 2004). This is of particular interest with regard to seedling early development in various understory environments. Decreasing LIE with increasing individual size and leaf area tends to support the hypothesis that at the establishment stage, seedlings are more efficient in light capture, especially in elevations with potentially

high returns in direct light (i.e. vertical directions) than at further developmental stages. Then, as seedlings are growing and accumulating biomass and leaves, leaf overlap increases and the ratio of photosynthetic to nonphotosynthetic tissues declines, so that the plants may require more light for achieving a positive carbon balance or, under constant light, reach a maximum size over which carbon balance becomes negative, leading to the death of the tree (Messier *et al.*, 1999; Messier & Nikinmaa, 2000). Therefore, long-term survival under shade can be achieved either by delaying the time when maximum size is reached through low growth or by allowing a greater maximum size through minimizing carbon costs of leaf display and carbon assimilation or both.

Thus, species-specific patterns of carbon allocation under contrasting light environments might be critical for their LIE and resulting functional ecology. Species allocating carbon preferentially to above-ground growth even under shaded environments will reduce their LIE, since they are increasing their size and leaf area, whereas species maintaining lower growth rates under shaded conditions might increase their survival by maintaining a more efficient leaf display with a low carbon cost. These specific differences may help to explain the larger shade tolerance of *F. sylvatica*, *A. pseudoplatanus* and *A. saccharum* compared with *Betula* species in the forest understory. Indeed, *Acer* species are able to control apical and especially lateral meristem development when suppressed in order to maintain very slow growth rates under very low light conditions (Sipe & Bazzaz, 1994; Goulet *et al.*, 2000; Delagrangé *et al.*, 2004). *F. sylvatica* controls its development through polycyclism: in shaded environments this species exhibits only a single flush in spring, then buds enter dormancy and no leaf production occurs later on. By contrast, *Betula* species continuously produce new leaves while possibly shedding the older, shaded ones: species that continuously allocate biomass to height and lateral growth of crown, even in shaded environments, are likely to increase carbon costs and self-shading dramatically (Kikuzawa, 2003).

Furthermore, minimizing the cost of leaf display through architectural traits could give an advantage under shade. The studied species differed greatly according to their developmental patterns which, as pointed out by Beaudet and Messier (1998), may act as important constraints to morphological acclimation to the light regime. For instance, *Acer* species which have long petioles and large leaves may improve their leaf display efficiency at lower cost (Beaudet & Messier, 1998; Takenaka *et al.*, 2001) than highly branched *Fagus* species with small leaves and short petioles and where one possible way to decrease leaf overlap would be through increasing internode length but it could rapidly have a detrimental effect on carbon balance (Pearcy *et al.*, 2005). Crown shape may also be important for light capture as horizontally spread crowns such as those of *Fagus* are expected to have a higher efficiency for intercepting light incoming from vertical directions than erect crowns such as those of *Acer* or, to a lesser extent, *Betula*.

But, as *Fagus* has the lowest LIE among the species studied, this trait cannot alone account for LIE interspecific variability. Obviously, LIE and its leaf overlap component are the outcome of a complex combination of architectural traits constrained by developmental pattern and associated carbon costs; more research, especially on carbon costs and gains associated to architectural traits, is needed to understand shade tolerance in trees better.

Finally, another essential factor associated with LIE and possibly linked to species functional ecology is the potential partitioning between direct and diffuse light capture among species. Although it is difficult to draw general conclusions, Fig. 7 clearly indicates that some species are able to adjust their diffuse vs direct light capture. Generally, 1-year-old seedlings preferentially intercept light from vertical directions, while 2-year-old seedlings do it mainly from all directions. Similarly, except for the shade-intolerant *B. pendula*, efficiency of interception in vertical directions increases with decreasing light regimes. Several studies have reported the ability of some tree species seedlings to preferentially intercept direct (Muraoka *et al.*, 2003) or diffuse light (Ackerly & Bazzaz, 1995; Valladares *et al.*, 2002). However, to estimate the advantage of enhancing diffuse light compared with direct light interception (or the reverse) in a given light environment and conclude on its impact on the survival of those species in forest understory, more research is needed: (i) to develop long-term light capture models based on realistic and highly variable cloudy/sunny conditions; and (ii) to improve our understanding of sun-fleck use (i.e. photosynthetic apparatus activation and de-activation).

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References

- Ackerly DD, Bazzaz FA. 1995. Seedling crown orientation and interception of diffuse radiation in tropical forest gaps. *Ecology* 76: 1134–1146.
- Adam B, Donès N, Sinoquet H. 2004. *VegeSTAR3.1. Calcul de l'Interception Lumineuse et de la Photosynthèse*. Technical Notice. Clermont-Ferrand, France: UMR INRA-UBP PIAF.
- Adam B, Sinoquet H, Godin C, Donès N. 1999. *3A – Software for the Acquisition of Plant Architecture, Version 2.0*. Clermont-Ferrand, France: UMR INRA-UBP PIAF.
- Baker FS. 1949. A revised tolerance table. *Journal of Forestry* 47: 179–181.
- Beaudet M, Messier C. 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 28: 1007–1015.
- Boudon F. 2004. Représentation géométrique multi-échelles de l'architecture des plantes. Montpellier, France: Université Montpellier II. *PhD Thesis*.
- Bretz F, Hothorn T, Westfall P. 2004. *Multcomp: Multiple Tests and Simultaneous Confidence Intervals. R Package, Version 0.4-8*.
- Canham CD, Denslow JS, Platt WJ, Runkle JR, Spies T, White PS. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 20: 620–631.
- Carter GA, Smith WK. 1985. Influence of shoot structure on light interception and photosynthesis in conifers. *Plant Physiology* 79: 1038–1043.
- Cescatti A. 1997. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. 1. Model structure and algorithms. *Ecological Modelling* 101: 263–274.
- Claveau Y, Messier C, Comeau PG. 2005. Interacting influence of light and size on aboveground biomass distribution in sub-boreal conifer saplings with contrasting shade tolerance. *Tree Physiology* 25: 373–384.
- Claveau Y, Messier C, Comeau PG, Coates KD. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 32: 458–468.
- Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology & Evolution* 9: 187–191.
- Delagrange S, Messier C, Lechowicz MJ, Dizengremel P. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiology* 24: 775–784.
- Den Dulk JA. 1989. The interpretation of remote sensing, a feasibility study. Wageningen, the Netherlands: Wageningen University. *PhD Thesis*.
- Falster DS, Westoby M. 2003. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist* 158: 509–525.
- Farnsworth KD, Niklas KJ. 1995. Theories of optimization, form and function in branching architecture in plants. *Functional Ecology* 9: 355–363.
- Farque L, Sinoquet H, Colin F. 2001. Canopy structure and light interception in *Quercus petraea* seedlings in relation to light regime and plant density. *Tree Physiology* 21: 1257–1267.
- Fleck S, Niinemets U, Cescatti A, Tenhunen JD. 2003. Three-dimensional lamina architecture alters light-harvesting efficiency in *Fagus*: a leaf-scale analysis. *Tree Physiology* 23: 577–589.
- Forcier LK. 1975. Reproductive strategies and the co-occurrence of climax tree species. *Science* 189: 808–810.
- Frazer GW, Canham CD, Lertzman KP. 1999. *Gap Light Analyzer (GLA): Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation*. Burnaby, British Columbia, Canada: Simon Fraser University (also Millbrook, New York, USA: Institute of Ecosystem Studies).
- Gálvez D, Pearcy RW. 2003. Petiole twisting in the crowns of *Psychotria limonensis*: implications for light interception and daily carbon gain. *Oecologia* 135: 22–29.
- Gendron F, Messier C, Comeau PG. 2001. Temporal variations in understory photosynthetic photon flux density of a deciduous stand: effects of canopy development, solar elevation & sky conditions. *Agricultural and Forest Meteorology* 106: 23–40.
- Goulet J, Messier C, Nikinmaa E. 2000. Effect of branch position and light availability on shoot growth of understory sugar maple and yellow birch saplings. *Canadian Journal of Botany-Revue Canadienne de Botanique* 78: 1077–1085.

- Hallé F, Oldeman RAA, Tomlinson PB. 1978. *Tropical Trees and Forests: an Architectural Analysis*. New York, NY, USA: Springer Verlag.
- Huber H, Stuefer JF. 1997. Shade-induced changes in the branching pattern of a stoloniferous herb: functional response or allometric effect? *Oecologia* 110: 478–486.
- Kawamura K, Takeda H. 2002. Light environment and crown architecture of two temperate *Vaccinium* species: inherent growth rules versus degree of plasticity in light response. *Canadian Journal of Botany-Revue Canadienne de Botanique* 80: 1063–1077.
- Kikuzawa K. 2003. Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. *Functional Ecology* 17: 29–38.
- King DA, Maindonald JH. 1999. Tree architecture in relation to leaf dimensions and tree stature in temperate and tropical rain forests. *Journal of Ecology* 87: 1012–1024.
- Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98: 419–428.
- McConaughay KDM, Coleman JS. 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80: 2581–2593.
- Messier C, Doucet R, Ruel JC, Claveau Y, Kelly C, Lechowicz MJ. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. *Canadian Journal of Forest Research* 29: 812–823.
- Messier C, Nikinmaa E. 2000. Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. *Écoscience* 7: 345–356.
- Millet J, Bouchard A, Edelin C. 1998. Plagiotropic architectural development of four tree species of the temperate forest. *Canadian Journal of Botany-Revue Canadienne de Botanique* 76: 2100–2118.
- Montgomery RA, Chazdon RL. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131: 165–174.
- Müller I, Schmid B, Weiner J. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3: 115–127.
- Muraoka H, Koizumi H, Percy RW. 2003. Leaf display and photosynthesis of tree seedlings in a cool-temperate deciduous broadleaf forest understory. *Oecologia* 135: 500–509.
- Naumburg E, Ellsworth DS, Percy RW. 2001. Crown carbon gain and elevated [CO₂] responses of understory saplings with differing allometry and architecture. *Functional Ecology* 15: 263–273.
- Niinemets U, Sparrow A, Cescatti A. 2005. Light capture efficiency decreases with increasing tree age and size in the southern hemisphere gymnosperm *Agathis australis*. *Trees-Structure and Function* 19: 177–190.
- Niklas KJ. 1989. The effect of leaf-lobing on the interpretation of direct solar radiation. *Oecologia* 80: 59–64.
- Norman JM, Welles JM. 1983. Radiative transfer in an array of canopies. *Agronomy Journal* 75: 481–488.
- Oker-Blom P, Smolander H. 1988. The ratio of shoot silhouette area to total needle area in Scots pine. *Forest Science* 34: 906.
- Percy RW, Muraoka H, Valladares F. 2005. Crown architecture in sun and shade environments: assessing function and trade-offs with a three-dimensional simulation model. *New Phytologist* 166: 791–800.
- Percy RW, Valladares F, Wright SJ, de Paulis EL. 2004. A functional analysis of the crown architecture of tropical forest Psychotria species: do species vary in light capture efficiency and consequently in carbon gain and growth? *Oecologia* 139: 163–177.
- Percy RW, Yang WM. 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia* 108: 1–12.
- Phattaralerphong J, Sinoquet H. 2005. A method for 3D reconstruction of tree crown Volume from photographs: assessment with 3D-digitized plants. *Tree Physiology* 25: 1229–1242.
- R Development Core Team. 2004. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: Foundation for Statistical Computing.
- Planchais I, Sinoquet H. 1998. Foliage determinants of light interception in sunny and shaded branches of *Fagus sylvatica*. *Agricultural and Forest Meteorology* 89: 241–253.
- Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* 13: 396–410.
- Poorter L, Wêrger MJA. 1999. Light environment, sapling architecture, and leaf display in six rain forest tree species. *American Journal of Botany* 86: 1464–1473.
- Rakocevic M, Sinoquet H, Christophe A, Varlet-Grancher C. 2000. Assessing the geometric structure of a white clover (*Trifolium repens* L.) canopy using 3-D digitising. *Annals of Botany* 86: 519–526.
- Runkle JR. 1982. Pattern of disturbance in some old-growth mesic forests of eastern north America. *Ecology* 63: 1533–1546.
- Sinoquet H, Rivet P. 1997. Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitising device. *Trees-Structure and Function* 11: 265–270.
- Sinoquet H, Sonohat G, Phattaralerphong J, Godin C. 2005. Foliage randomness and light interception in 3-D digitized trees: an analysis from multiscale discretization of the canopy. *Plant Cell and Environment* 28: 1158–1170.
- Sinoquet H, Thanisawanyangkura S, Mabrouk H, Kasemsap P. 1998. Characterization of the light environment in canopies using 3D digitising and image processing. *Annals of Botany* 82: 203–212.
- Sipe TW, Bazzaz FA. 1994. Gap partitioning among maples (*Acer*) in central New-England – shoot architecture and photosynthesis. *Ecology* 75: 2318–2332.
- Sonohat G, Sinoquet H, Kulandaivelu V, Combes D, Lescouret F. 2006. Three-dimensional reconstruction of partially 3D digitized peach tree canopies. *Tree Physiology* 26: 337–351.
- Sterck FJ. 1997. Trees and light: tree development and morphology in relation to light availability in a tropical rain forest in French Guiana. Wageningen, the Netherlands: Wageningen Agricultural University. *PhD Thesis*.
- Sterck FJ, Bongers F. 2001. Crown development in tropical rain forest trees: patterns with tree height and light availability. *Journal of Ecology* 89: 1–13.
- Takenaka A, Takahashi K, Kohyama T. 2001. Optimal leaf display and biomass partitioning for efficient light capture in an understory palm, *Licuala arbuscula*. *Functional Ecology* 15: 660–668.
- Valladares F, Percy RW. 1998. The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub. *Oecologia* 114: 1–10.
- Valladares F, Skillman JB, Percy RW. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. *American Journal of Botany* 89: 1275–1284.
- Walters MB, Reich PB. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist* 143: 143–154.