Tree Physiology 23, 577–589

Three-dimensional lamina architecture alters light-harvesting efficiency in *Fagus*: a leaf-scale analysis

STEFAN FLECK,[1] ÜLO NIINEMETS,[2,3] ALESSANDRO CESCATTI[4] and JOHN D. TENHUNEN[1]

[1] *Department of Plant Ecology, University of Bayreuth, D-95440 Bayreuth, Germany*

[2] *Department of Plant Physiology, Institute of Molecular and Cell Biology, University of Tartu, Riia 23, EE 51010 Tartu, Estonia*

[3] *Author to whom correspondence should be addressed (ylo@zbi.ee)*

[4] *Centro di Ecologia Alpina, I-38040 Viote del Monte Bondone (TN), Italy*

Received July 23, 2002; accepted November 16, 2002; published online May 15, 2003

Summary Modification of foliage exposition and morphology by seasonal average integrated quantum flux density (Q_{int}) was investigated in the canopies of the shade-tolerant late-successional deciduous tree species *Fagus orientalis* Lipsky and *Fagus sylvatica* L. Because the leaves were not entirely flat anywhere in the canopy, the leaf lamina was considered to be three-dimensional and characterized by the cross-sectional angle between the leaf halves (θ). Both branch and lamina inclination angles with respect to the horizontal scaled positively with irradiance in the canopy, allowing light to penetrate to deeper canopy horizons. Lamina cross-sectional angle varied from 170° in the most shaded leaves to 90–100° in leaves in the top of the canopy. Thus, the degree of leaf rolling increased with increasing Q_{int}, further reducing the light-interception efficiency of the upper-canopy leaves. Simulations of the dependence of foliage light-interception efficiency on θ demonstrated that decreases in θ primarily reduce the interception efficiency of direct irradiance, but that diffuse irradiance was equally efficiently intercepted over the entire range of θ values in our study. Despite strong alteration in foliage light-harvesting capacity within the canopy and greater transmittance of the upper crown compared with the lower canopy, mean incident irradiances varied more than 20-fold within the canopy, indicating inherent limitations in light partitioning within the canopy. This extensive canopy light gradient was paralleled by plastic changes in foliar structure and chemistry. Leaf dry mass per unit area varied 3–4-fold between the canopy top and bottom, providing an important means of scaling foliage nitrogen contents and photosynthetic capacity per unit area with Q_{int}. Although leaf structure versus light relationships were qualitatively similar in all cases, there were important tree-to-tree and species-to-species variations, as well as evidence of differences in investments in structural compounds within the leaf lamina, possibly in response to contrasting leaf water availability in different trees.

Keywords: acclimation, carbon content, dry mass per unit area, leaf inclination, leaf rolling, light interception, nitrogen content.

Introduction

Plants have a large potential for structural adjustment in canopy light-interception capacity through modifications of branch and foliage orientation and leaf structural attributes (Planchais and Sinoquet 1998, Pearcy and Valladares 1999). An important acclimation response is alteration of leaf inclination angle with respect to the horizontal, which often increases along understory–gap gradients (Niklas and Owens 1989, Midgley et al. 1992, Planchais and Sinoquet 1998, Valladares and Pearcy 1998) as well as from the bottom to the top of canopies (Pearcy and Yang 1998, Niinemets and Fleck 2002*b*). At high irradiances, vertically oriented leaves allow efficient reduction of mean intercepted quantum flux densities that may be potentially damaging to foliar photosynthetic apparatus, whereas horizontal leaves are advantageous for harvesting low quantum flux densities (Valladares and Pearcy 1998).

It is currently unclear whether leaf inclination responses to long-term irradiance are constant in the canopy within and between species. The inclination of free-hanging leaves apparently depends on leaf characteristics that determine the lamina load on the petiole, such as lamina and petiole lengths and mass (Niklas 1992*b*, Niinemets and Fleck 2002*a*, 2002*b*), as well as on lamina and petiole stiffness, which alter the extent to which the leaf bends under its own mass (Niklas 1991, 1992*b*). In addition, tropic responses to irradiance may alter petiole angle and thereby lamina inclination (Niklas 1996, Niinemets and Fleck 2002*b*). Thus, leaf inclination in static equilibrium is an integrated response of lamina and petiole structural characteristics to interacting environmental variables, suggesting that lamina inclination angles at a common irradiance may vary depending on the magnitude of the gradients of other environmental factors within the canopy.

Apart from the inclination angle, many grass species commonly reduce mean radiation loads on the leaf surface by lamina folding or rolling, particularly under conditions of water stress (Begg 1980, Heckathorn and DeLucia 1991). The leaves of broad-leaved species are also often curled and rolled (Innes 1992, Muraoka et al. 1998, Sinoquet et al. 1998). Although the curvature and folding of the lamina surface may significantly affect whole-plant light absorption, current 3-D canopy light interception models generally consider that the leaves of broad-leaved trees are completely flat (Pearcy and Yang 1996, Cescatti 1997, Sinoquet et al. 1998, Takenaka et al. 1998). The potential significance of leaf curling for leaf light-interception capacity has been studied in only a few cases (Sinoquet et al. 1998, Farque et al. 2001), and modification of the degree of leaf rolling within the tree canopy has not been examined. Given that both potential excess irradiances and foliar water stress scale with height in the canopy, the degree of leaf rolling may also vary within the canopy light gradient.

We investigated variability in branch and foliage inclination angles, leaf architecture and chemistry in relation to irradiance in *Fagus sylvatica* L. and *Fagus orientalis* Lipsky (*Fagus sylvatica* ssp. *orientalis* Greuter & Burdet (Shen 1992)). We demonstrate a strong control of light availability on foliage inclination angles and lamina architecture as well as on the degree of leaf rolling, and important tree-to-tree and interspecific variability in the relationship between irradiance and leaf light-interception capacity. To understand further the functional significance of foliage folding in *Fagus*, we also estimated the potential effect of leaf rolling on light interception per unit leaf area for seasonal average angular distributions of diffuse and direct radiation.

Materials and methods

Study species

Fagus sylvatica is a canopy dominant species in lowland and montane forests in central to southern Europe, and *F. orientalis* is a widespread canopy species typical in montane forests of south-western Asia and south-eastern Europe (Mayer and Aksoy 1986, Tosun and Özpay 1996, Peters 1997). The distribution patterns of these species in the southeastern Balkans suggest that *F. orientalis* may occur on drier and warmer sites than *F. sylvatica* (Mayer 1984). Both species have medium-sized, simple, elliptic to obovate leaves on short petioles. The leaves of *F. orientalis* are generally 9–14 cm long with 7–12 pairs of second-order pinnate veins, whereas leaves of *F. sylvatica* are 5–10 cm long with 5–9 pairs of veins (Peters 1997). All *Fagus* species grow in similar habitats and are shade-tolerant late-successional forest components throughout the world (Peters 1992, 1997). Canopy leaves of *F. sylvatica* occur at irradiances as low as 5% or less of above-canopy irradiance (Ducrey 1981). For *F. orientalis*, the amount of irradiance penetrating the mature canopy is on the order of 1–2% (Koval and Bityukov 1969).

Study sites

Fagus sylvatica was studied at Buchenallee, Fichtelgebirge, Germany (50°03′ N, 11°52′ E, elevation 900–915 m, inclination 13.5°). The site is located on the SSW aspect of the highest peak of Schneeberg (elevation 1051 m) in the Fichtelgebirge. Mean annual long-term precipitation at the site is 1200 mm (Bayerischer Klimaforschungsverbund 1998), and the mean annual (1995–1999) temperature is 6.0 °C with a mean monthly minimum of –4.5 °C and a mean monthly maximum of 17.1 °C (O. Klemm, BITÖK, University of Bayreuth, Germany, unpublished data). The site supports a monotypic 120-year-old *Fagus* stand with a dominant height of 26 m, stem density of 520 ha^{-1} and leaf area index of 8.1. The understory primarily consists of *Deschampsia flexuosa* (L.) Trin and *Oxalis acetosella* L. with a mean coverage of only 2%. The pseudopodsolic brown soil (Dystric Cambisol) is a loamy sand formed on granite. The humus (A) layer is on average 5.7 ± 0.8 cm thick with a $\mathrm{pH_{H_2O}}$ of 4.75 ± 0.13 and a molar C/N ratio of 20.5 ± 0.5.

Fagus orientalis was studied at the Botanical Garden of the University of Bayreuth, Germany (49°55′ N, 11°35′ E, elevation 365 m). Mean annual precipitation (1992–1999) is 688 mm, and mean annual temperature is 8.3 °C with a mean monthly minimum of –0.4 °C and a mean monthly maximum of 17.9 °C, (O. Klemm, unpublished data).

Foliage sampling and measurement of inclination angles

At each site, two representative trees were chosen, and foliage was collected in July 1997 at Buchenallee and in July 1999 at the Botanical Garden of the University of Bayreuth. Both *F. sylvatica* trees were 22 m tall and about 50 years old, but the dominant tree had greater lateral crown dimensions and a larger stem diameter at breast height (40 cm) than the subdominant tree (30 cm). The subdominant tree was also partly shaded by neighboring older and taller beech trees. The first foliated branch in the dominant tree was located 14 m above ground, whereas foliage started at 9.5 m in the subdominant tree. The two *F. orientalis* study trees were 12–14 years old and 5–8 m tall, with the live canopy starting at about 1.2 m above ground. For all study trees, leaves were sampled along the vertical canopy light gradient using a mobile lift for *F. sylvatica* and a ladder for *F. orientalis*. Thus, for *F. sylvatica*, we could sample the topmost leaves exposed to full sunlight, whereas for *F. orientalis*, we reached the uppermost leaves at a height of about 6.5 m, which received more than 75% of the above-canopy irradiance.

In *F. sylvatica*, lamina inclination angles (φ_L) relative to the horizontal of freely hanging leaves were measured with a protractor and plumb line for 5–10 leaves from each specific canopy location. Because the leaves were often curled and the leaf lamina was not necessarily planar, we defined φ_L as the vertical angle between the normal to a hypothetical leaf plane and zenith (see Figure 1 for definitions). Given that light-interception capacity of a plane is proportional to $\cos(\varphi_L)$, and the value of a cosine function does not depend on the sign of the angle, only the absolute values of φ_L ($|\varphi_L|$) were recorded and means for all leaves per sample location were calculated. In addition to φ_L, mean branch angle was estimated from at least 10 measurements of twigs and branches of 0.8–3.0 cm diameter in the immediate vicinity (< 0.8 m) of the shoot, leaves of which were measured for lamina inclination angles.

In *F. orientalis*, we measured φ_L as well as petiole (φ_P) and leaf midrib (φ_F) inclination angles, and always recorded the actual rather than absolute values of inclinations of foliage ele-

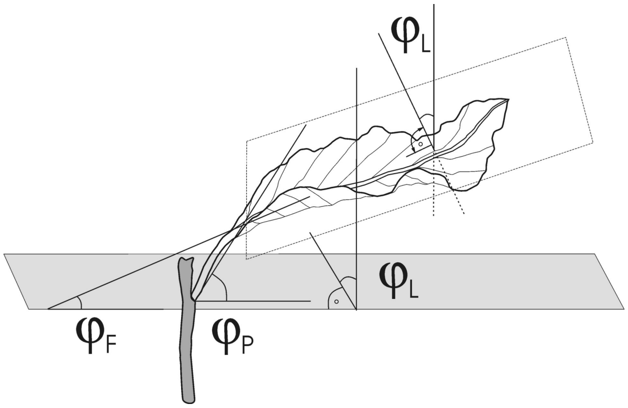

Figure 1. Measurement of petiole (φ_P) and lamina (φ_F, φ_L) vertical inclination angles with respect to the horizontal. The angle φ_P is defined as the angle between the attachment points of the petiole to the twig and to the lamina, φ_F as the horizontal angle of leaf mid-rib, and φ_L as an average angle between the normal to the leaf plane and the vertical direction ($\varphi_L \geq \varphi_F$).

ments. All angles were measured with a precision of ± 5°.

To quantitatively characterize curving and rolling of the leaf lamina, height (H_S) and width (W_S) of the leaf space were measured in the middle of each leaf as described in Figure 2A. The mean (± SD) relative error of H_S measurements was 7.5 ± 3.7%, and that of W_S measurements was 1.2 ± 0.3%. After these measurements, leaves were removed, put in plastic bags and immediately transported to the laboratory for foliage morphological measurements.

Determination of daily integrated incident quantum flux density for leaves

Hemispherical photographs were taken with a Minolta MF camera equipped with 0.15× fisheye adapter (Soligor, Leinfelden-E., Germany) above a leaf cluster of about 10 neighboring leaves in *F. sylvatica* and above each sampled leaf in *F. orientalis* to determine seasonal (May 1 to June 30) mean daily integrated photosynthetically active quantum flux densities (Q_{int}; mol m^{-2} day^{-1}) above the sampled foliage. From the hemispheric images, the canopy transmittance to diffuse (I_D, diffuse site factor) and potential direct solar radiation (I_B, direct site factor) were calculated as outlined by Niinemets and Fleck (2002*b*). In essence, the relative area of canopy gaps (nine sky bands, 36 radial sectors per sky band) for uniformly overcast sky conditions was estimated for I_D, whereas I_B was found as the canopy gap fraction along solar tracks between May 15 and June 30. Calculations of both I_D and I_B considered the angular distribution of diffuse and direct radiation over the sky, and the angular fractions were also cosine corrected to determine the radiation incident on a horizontal plane.

Based on mean (May 1 to June 30) estimates of the direct (R_B; MJ m^{-2} day^{-1}) and diffuse (R_D) components of global solar radiation measured both in the Botanical Garden and Fichtelgebirge (O. Klemm, unpublished data), we computed Q_{int} as (see Niinemets and Fleck 2002*b* for details):

$$Q_{int} = I_D R_D \gamma_D + I_B R_B \gamma_B \qquad (1)$$

where γ_D and γ_B (mol MJ^{-1}) are the conversion factors for diffuse and direct solar radiation, respectively (Ross and Sulev 2000). The relative error of Q_{int} estimates is less than 5% at high irradiance (Q_{int} > 20 mol m^{-2} day^{-1}), but increases to ~20% at low irradiance (Q_{int} < 2 mol m^{-2} day^{-1}; Koppel and Frey 1985 and Niinemets et al., unpublished observations).

Additional foliage morphological and chemical characteristics

The maximum projected area of each leaf laid flat (A_T) was es-

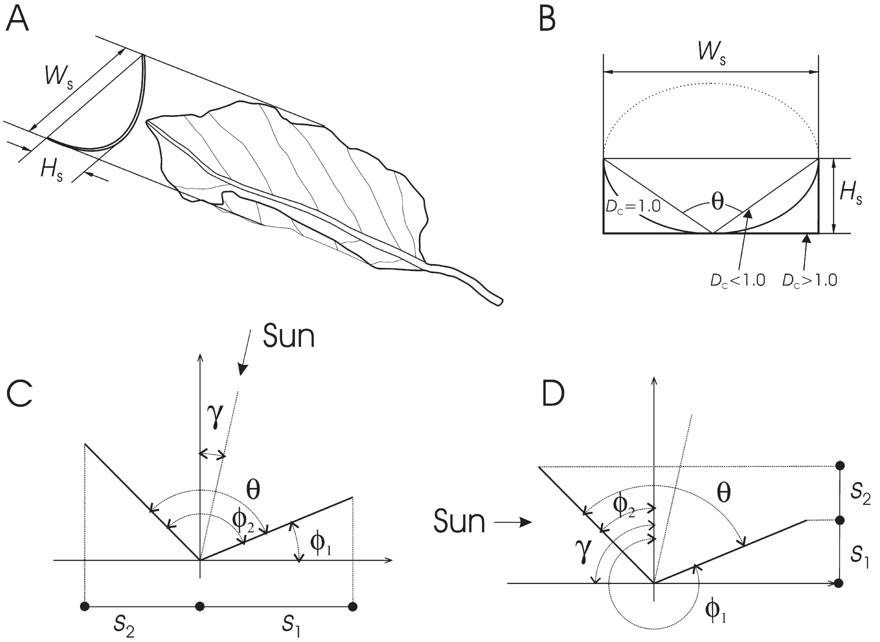

Figure 2. Scheme of the leaf cross section. Leaf space width (W_S) and height (H_S) were measured in the widest leaf position (A), and the lamina cross-sectional angle (θ, B) was computed by Equation 5. As demonstrated in the idealized axial view of the leaf lamina (B), the shape of the leaf cross section may vary for the same combination of W_S and H_S values. This variability was characterized by the shape coefficient, D_C, calculated from the maximum width of the leaf laid flat and the length of the hypothetical half ellipse defined by W_S and H_S (Equations 3–4). In (C) and (D), a geometrical model of a leaf cross section that allows characterization of the effects of leaf rolling on foliage light-interception capacity is outlined (Equations 5–11). Depending on the angle between the sun and the leaf normal (γ), leaf halves may (D) or may not (C) overlap.

timated with a portable leaf area meter (CI-202, CID, Vancouver, WA). Maximum leaf width (W_T) and length of the unrolled laminae were also measured, and the in situ leaf area projection onto a horizontal surface (A_P) was computed as:

$$A_P = \cos(\varphi_L) A_T \frac{W_S}{W_T} \tag{2}$$

Leaf dry mass was determined after drying at 70 °C for at least 48 h, and leaf dry mass per unit A_T (M_A) was calculated. Total leaf nitrogen and carbon contents were determined with an elemental analyzer (CHN-O-Rapid, Foss Heraeus, Hanau, Germany).

To describe the geometry of the leaf cross section, we considered the cross section of the curved leaf lamina to be a half-ellipse. Thus, the hypothetical length of the curved surface at the widest position along the leaf (L_C) is given as (Bartsch 1966, Figures 2A and 2B):

$$L_C = \frac{\pi}{2}\left(\frac{3}{2}\left(H_S + \frac{W_S}{2}\right) - \sqrt{\frac{H_S W_S}{2}}\right) \tag{3}$$

The shape coefficient of leaf lamina (D_C), characterizing the extent to which a leaf cross section deviates from a half-ellipse, was calculated as:

$$D_C = W_T / L_C \tag{4}$$

where W_T is maximal leaf width of the unrolled leaf lamina. Values of $D_C > 1$ suggest that the lamina curvature is larger at the edges than in the middle of the lamina, or that, apart from the enrolling characterized by H_S, the lamina is also locally curled. Values of $D_C < 1$ may indicate that the leaf cross section more closely approximates a V-shape with the leaf lamina clasped at the midrib (Figure 2B). Alternatively, as the degree of leaf rolling increases, H_S may become larger than the length of the semi-axis of the ellipse, also resulting in values of $D_C < 1$. When the leaves are entirely rolled, H_S is equal to the length of the ellipse axis. However, inward curving of leaf lamina edges was not observed in our study, indicating that H_S was not larger than the length of the corresponding semi-axis.

Estimation of effect of leaf rolling on foliage light-interception capacity

In our study, mean (± SE) D_C was 0.9613 ± 0.0007 (range 0.86–1.13) for all data pooled. For a rectangular open leaf cross section, the expected mean D_C was 1.1943 ± 0.0009 (range 1.05–1.27), and for a V-shape it was 0.9360 ± 0.0003 (range 0.90–0.96), indicating that the V-shape (Figure 2B) most closely approximated the measurements. Thus, we assumed that leaf cross sections are triangular to simplify the analysis. For a V-shaped leaf, the cross-sectional angle (θ, Figures 2B and 2C) is equal to:

$$\theta = 2\arctan\left(\frac{W_S}{2H_S}\right) \tag{5}$$

The probability of photon interception in a plant canopy, $F(\omega,\gamma)$, can be estimated according to the theory of light penetration in a turbid medium (Nilson 1971). The model predicts $F(\omega,\gamma)$ as a function of the extinction coefficient (G-function, Ross 1981), of the Markov index for spatial aggregation (λ_0, Nilson 1971), of the leaf area density in the medium (ρ), and of the beam path-length for specific solar azimuth (ω) and zenith (γ) angles, $L(\omega,\gamma)$:

$$F(\omega,\gamma) = 1 - \exp(-G(\gamma)\lambda_0 \rho L(\omega,\gamma)) \tag{6}$$

The G-function is defined as the ratio between the area projected onto a plane orthogonal to the view direction and the actual leaf area (Ross 1981), and can be estimated analytically for several theoretical distributions of leaf angles (Campbell and Norman 1989) assuming planar or convex leaves. For concave (rolled) leaves, these analytical formulations cannot be applied. Light-interception characteristics of 3-D objects with specific shapes can be studied by Monte Carlo ray-tracing approaches (Sinoquet et al. 1998, Disney et al. 2000). However, there are no analytical solutions for these models, and therefore, they are difficult to parameterize for estimation of canopy radiative regime.

We derived an analytical formulation to characterize the effect of leaf rolling on light-interception capacity by using several simplifying assumptions. Assuming that the beam is orthogonal to the leaf midrib and that the bisector of the cross-sectional angle θ is pointing to the zenith, the effect of lamina rolling can be computed as a function of θ and γ. Defining the angles ϕ_1 and ϕ_2 (Figures 2C and 2D) as:

$$\phi_1 = \pi/2 - \gamma - \theta/2 \tag{7a}$$

$$\phi_2 = \pi/2 - \gamma + \theta/2 = \phi_1 + \theta \tag{7b}$$

the corresponding projections S_1 and S_2 of a leaf lamina with a width W_T are given as:

$$S_1 = \frac{W_T}{2}\cos(\phi_1) \tag{8a}$$

$$S_2 = \frac{W_T}{2}\cos(\pi - \phi_2) \tag{8b}$$

The G-function of a V-shaped leaf (Figures 2C and 2D) is computed as the ratio of the leaf projected area on a plane perpendicular to the view direction to the actual leaf area. Thus, the G-function is:

$$G(\gamma,\theta) = \left| \begin{array}{ll} \dfrac{|S_1 + S_2|}{W_T}, & if\ S_1 S_2 \geq 0 \\ \dfrac{\max(|S_1|,|S_2|)}{W_T}, & if\ S_1 S_2 < 0 \end{array} \right. \tag{9}$$

The condition $S_1S_2 > 0$ corresponds to no overlap between the lamina sides (Figure 2C), and $S_1S_2 < 0$ corresponds to overlapping lamina sides (Figure 2D). Equation 9 can be written in a concise form as:

$$G(\gamma,\theta) = \frac{|S_1 + S_2| + |S_1| + |S_2|}{2W_T} \qquad (10)$$

We calculated the G-function as dependent on the zenith angle of the incoming radiation by varying the angle γ in the range of 0–90° (Figure 2C). We further expressed the G-function as the sum of the contributions of the upper (G_U) and lower (G_L) sides of the leaf lamina to evaluate the importance of leaf rolling on the relative distribution of irradiance on different leaf sides:

$$G(\gamma,\theta) = G_U(\gamma,\theta) + G_L(\gamma,\theta) \qquad (11)$$

Contributions of upper and lower sides for specific geometric situations are given in Table 1.

To determine the effect of varying cross-sectional angles on foliage light-interception capacity over the entire growing season, we calculated the daily total intercepted irradiance relative to the irradiance on a flat leaf (ξ):

$$\xi = \frac{\int_0^{\pi/2} Q(\gamma)G(\gamma,\theta)d\gamma}{\int_0^{\pi/2} Q(\gamma)G(\gamma,\pi)d\gamma} \qquad (12)$$

where $Q(\gamma)$ is either the direct (D) or diffuse (d) irradiance at zenith angle γ. The calculations were performed separately for D and d, and for the upper and lower leaf sides. Mean zenith distributions of direct and diffuse radiation were computed for the period May 1–June 30, 1999 using the above-canopy solar radiation measurements in Fichtelgebirge (O. Klemm, unpublished data) and the radiative transfer model of Cescatti (1997) to calculate the incident light above the canopy. In these calculations, we assumed that both the folded and flat leaves lay horizontal ($\varphi_L = 0$) at the top of the canopy, and that the foliage azimuth angle distribution is spherical. Although leaf light-interception efficiency also varies with leaf inclination angle and leaf clumping, our simulation analysis allows us to gain functional insight into the effects of leaf rolling independently of other co-existing sources of variability in the light climate.

Data analysis

The statistical significance of light effects on foliage morphological and chemical characteristics were tested by linear and nonlinear ($y = a\log x + b$) regression analyses. Analyses of covariance (ANCOVA) were employed to compare the relationships between various trees and species. For comparison of nonlinear relationships, the explaining variable, Q_{int}, was log-transformed before the analysis. Slopes of the linear and linearized relationships were compared by separate slope ANCOVA model. If the interaction term was nonsignificant, the analysis was continued according to the common-slope model. Initial analyses demonstrated that there were no statistical differences in foliar characteristics between the trees of *F. orientalis*. Therefore, the final analysis compared only *F. orientalis* and dominant and subdominant trees of *F. sylvatica*. Differences between the groups were separated by the Bonferroni test. All relationships were considered significant at $P < 0.05$ (Wilkinson 1990).

Results

Variation in branch and foliage inclination angles within the canopy

Branch inclination angle was strongly related to canopy height (Figure 3A) and to Q_{int} (Figure 3B). The relationships were stronger for canopy height than for Q_{int} (cf. Figures 3A and 3B), suggesting that the previous rather than the current light environment determined mean branch inclination angle, or that other factors, such as hydraulics, influence branch angle. Compared with branches in the dominant tree, branches in the subdominant tree, which had a narrower and taller crown, had a more upward orientation ($P < 0.001$ for common-slope ANCOVA analyses with the actual data in Figure 3A and with $\log(Q_{int})$ for the data in Figure 3B).

Absolute lamina inclination angle ($|\varphi_L|$, see Figure 1 for definition) in both species (Figure 4A) and actual inclination

Table 1. Values of the G-function (Equation 10) and contributions of the upper (G_U) and lower (G_L) leaf sides for varying positions of a V-shaped leaf lamina with respect to the sun. Variations in the projections of leaf halves, S_1 and S_2, due to leaf cross-sectional angle θ and the angle γ between the leaf normal and the sun are illustrated in Figures 2C and 2D.

$G(\gamma,\theta)$	$G_U(\gamma,\theta)$	$G_L(\gamma,\theta)$	Condition
$\lvert S_1 + S_2\rvert / W_T$	$(S_1 + S_2)/W_T$	0	$S_1 > 0$ and $S_2 > 0$
$\lvert S_1 + S_2\rvert / W_T$	0	$-(S_1 + S_2)/W_T$	$S_1 < 0$ and $S_2 < 0$
$\max(\lvert S_1\rvert,\lvert S_2\rvert)/W_T$	$(S_1 + S_2)/W_T$	$-S_2/W_T$	$S_1 > 0$ and $S_2 < 0$ and $\lvert S_1\rvert > \lvert S_2\rvert$
$\max(\lvert S_1\rvert,\lvert S_2\rvert)/W_T$	0	$-S_2/W_T$	$S_1 > 0$ and $S_2 < 0$ and $\lvert S_1\rvert < \lvert S_2\rvert$
$\max(\lvert S_1\rvert,\lvert S_2\rvert)/W_T$	0	$-S_1/W_T$	$S_1 < 0$ and $S_2 > 0$ and $\lvert S_1\rvert > \lvert S_2\rvert$
$\max(\lvert S_1\rvert,\lvert S_2\rvert)/W_T$	S_2/W_T	$(S_1 + S_2)/W_T$	$S_1 < 0$ and $S_2 > 0$ and $\lvert S_1\rvert < \lvert S_2\rvert$

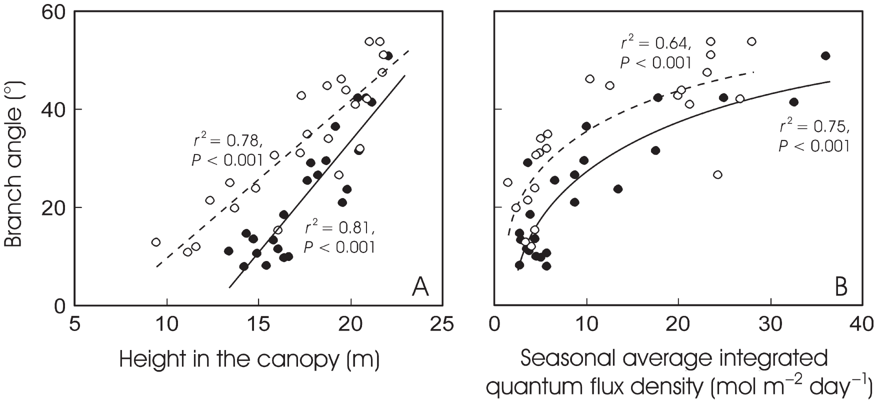

Figure 3. Branch angle in relation to height in the canopy (A) and seasonal integrated quantum flux density (Q_{int}) (B) in *F. sylvatica*. A dominant (●) and a subdominant (○) tree were investigated, and linear (A) or logarithmic (B) regressions were fitted to the data.

angle in *F. orientalis* ($r^2 = 0.41$, $P < 0.001$) were positively related to Q_{int}. Covariance analyses demonstrated that neither the slopes ($P > 0.9$) nor the intercepts ($P > 0.1$) of the absolute lamina inclination angle versus Q_{int} relationships were significantly different between *F. orientalis* and the dominant and subdominant trees of *F. sylvatica*. Because the regression lines for different *F. sylvatica* trees essentially coincided, a single regression was used to fit the data ($r^2 = 0.42$, $P < 0.001$ for the dominant tree and $r^2 = 0.22$, $P < 0.01$ for the subdominant tree).

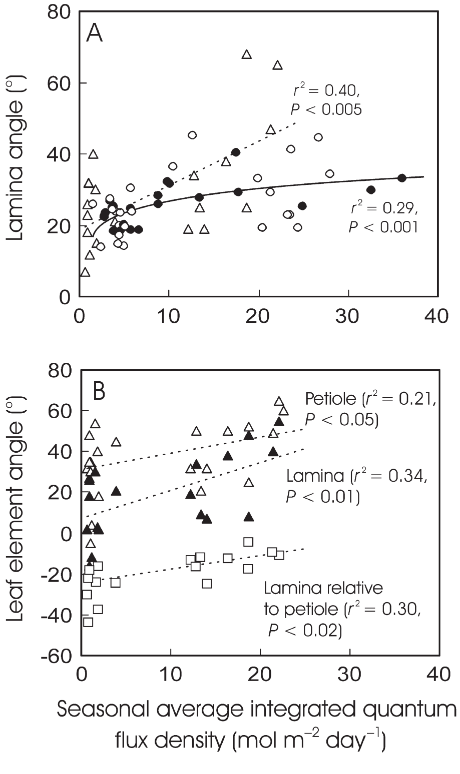

Figure 4. Effects of integrated quantum flux density (Q_{int}) on (A) the absolute lamina inclination angle (Figure 1, $|\varphi_L|$) in *F. sylvatica* (circles) and *F. orientalis* (triangles), and on (B) the actual inclination angles of petiole (φ_P, △), leaf lamina at leaf fall-line (φ_F, ▲) and the angle of leaf lamina relative to the petiole ($\varphi_D = \varphi_F - \varphi_P$, □) in *F. orientalis*. Data were fitted by linear or logarithmic regressions. Because lamina inclination angle versus Q_{int} relationships in (A) were not significantly different between dominant (●) and subdominant (○) trees of *F. sylvatica* ($P > 0.05$ according to covariance analyses with log-transformed data), the data for both trees were fitted by the same regression.

In *F. orientalis*, petiole (φ_P) and leaf midrib (φ_F) inclination angles were positively related to Q_{int} (Figure 4B). Petiole inclination angle was strongly correlated with φ_L and φ_F (Figure 5). However, there was evidence that lamina angle relative to petiole angle increased with Q_{int} as well (Figure 4B), indicating that the dependencies of lamina and leaf midrib inclination angles on irradiance were not attributable to light effects on φ_P alone.

Foliage inclination angles generally scaled less strongly with canopy height than with Q_{int}. For example, the fraction of explained variance (r^2) was only 0.15 ($P < 0.001$) for the canopy height versus lamina absolute inclination angle in *F. sylvatica* (cf. Figure 4A).

Irradiance effects on three-dimensional foliage architecture

We observed that leaf laminas were never completely planar, and that they became increasingly rolled with increasing Q_{int} (Figure 6). As indicated by the ratios of leaf space height (H_S, see Figure 2 for definition) to leaf space width (W_S, Figure 6B), W_S to total leaf width (Figure 6C), and the angle of lamina cross section (Equation 5, Figure 6D), the degree of leaf rolling was larger at greater irradiances. Analyses of covariance demonstrated that both slopes (Figures 6B and 6C, $P < 0.001$ for both dependencies) and intercepts (Figure 6A, $P < 0.001$) of the logarithmic relationships differed significantly between the *Fagus* species, and between the dominant and the subdominant *F. sylvatica* trees.

The leaf shape coefficient (D_C, Equation 4, Figure 2B) decreased from about 1.0 at low irradiances to 0.91–0.92 in the highest light environment in *F. orientalis* ($r^2 = 0.54$, $P < 0.01$). In the dominant tree of *F. sylvatica*, D_C was weakly and positively related to irradiance ($r^2 = 0.16$, $P > 0.05$), but it was independent of irradiance in the subdominant tree ($r^2 = 0.00$, $P > 0.5$).

Simulated effect of lamina folding on leaf light interception capacity

We simulated (Equations 7–12) the effects of leaf folding for

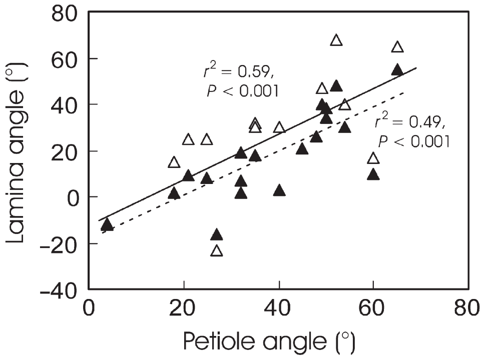

Figure 5. Correlation between lamina (▲ = φ_F; △ = φ_L; see Figure 1 for definitions) and petiole inclination angles in *F. orientalis*. Data were fitted by linear regressions.

two hypothetical leaf architectures. A flat leaf with an angle of leaf cross section (θ, Figures 2B and 2C) of 180° is typical in the shaded part of the canopy, and a leaf with θ = 100° is common in the upper part of the *Fagus* crown (Figure 6D). As the simulation indicates, the dependence of light interception of a flat leaf on the beam angle of radiation can be simply described by a cosine function (Figure 7). Although light interception is generally lower for the folded leaf than for the flat leaf (Figure 7), the folded leaf exhibits a more uniform interception capacity that is less strongly affected by solar zenith angle of the incoming radiation. Furthermore, compared with the flat leaf, the folded leaf has a higher G at higher solar zenith angles, from which most of the diffuse radiation comes (inset in Figure 8B), and a lower G at lower angles, from which most of the direct radiation penetrates.

The simulation of mean seasonal intercepted irradiance by leaves of varying cross-sectional angle (Figure 8) further underscores the importance of leaf rolling in avoidance of excessive radiation interception. The analysis demonstrates that the interception efficiency of direct radiation decreases with increasing leaf curvature (Figure 8A), reducing the risk of photoinhibition and increasing the light availability for the shaded canopy layers, but also that leaf curvature over the range observed within the *Fagus* canopy (Figure 6D) does not significantly reduce the interception efficiency of diffuse irradiance at the top of the canopy (Figure 8B). In particular, the decreased interception of diffuse light by the upper leaf surface is partly compensated by increased interception by the lower leaf surface (Figure 8B).

These simulations (Figures 7–8) are based on a simplified leaf cross-sectional geometry (Figure 2C) that may often be elliptical rather than V-shaped (Figure 2B). Given that, in terms of G, an elliptical cross section is more similar to a flat leaf than a V-shape, the values of G for leaves with elliptical cross sections are expected to be closer to the G-value of a flat leaf. Nevertheless, these effects are likely to be minor, and do not qualitatively alter our conclusions with respect to the performance of real leaves in the canopy.

Correlation of degree of leaf rolling with leaf structural characteristics

Leaf dry mass per unit area (M_A) scaled strongly with Q_{int} (Figure 9A). Analysis of covariance with log(Q_{int}) as covariate suggested that the slope was larger in *F. orientalis* than the slopes in either the dominant or subdominant trees of *F. sylvatica* ($P < 0.001$). The dominant *F. sylvatica* tree had a larger slope than the subdominant tree ($P < 0.05$, Figure 9A).

Maximal leaf length ($r^2 = 0.12$, $P > 0.1$), width (W_T, $r^2 = 0.00$, $P > 0.9$) and total area (Figure 9B) were independent of

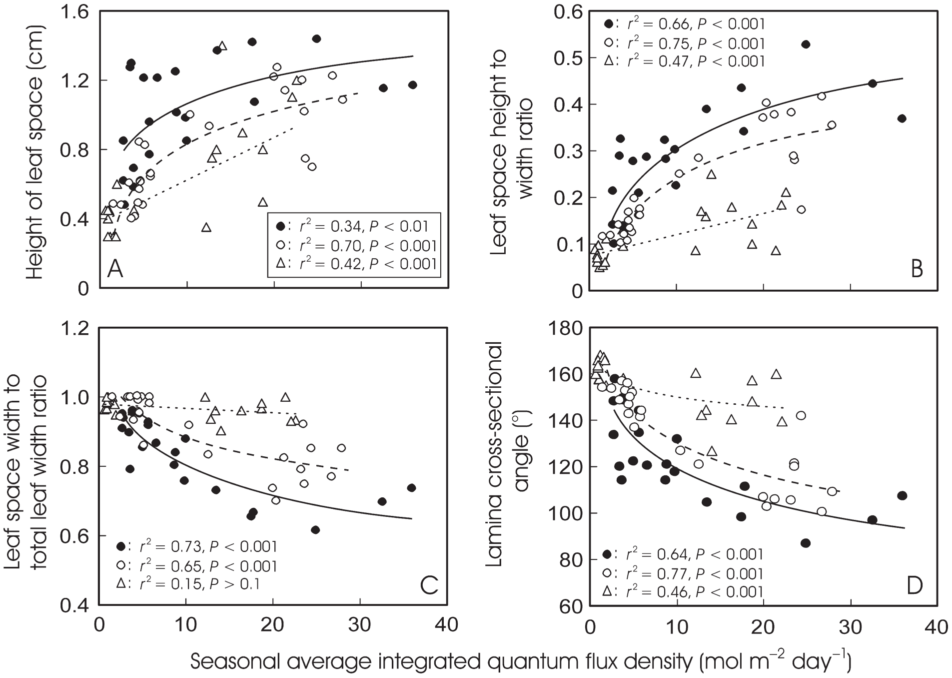

Figure 6. Dependence of the height of leaf space (H_S, A), the ratio of H_S to the width of leaf space (W_S, B), the W_S to maximal leaf width ratio (C) and lamina cross-sectional angle (θ, D) on Q_{int} in *F. sylvatica* and *F. orientalis*. The height and width of leaf space, and lamina cross-sectional angle are defined in Figure 2, and the symbols are as in Figure 4A.

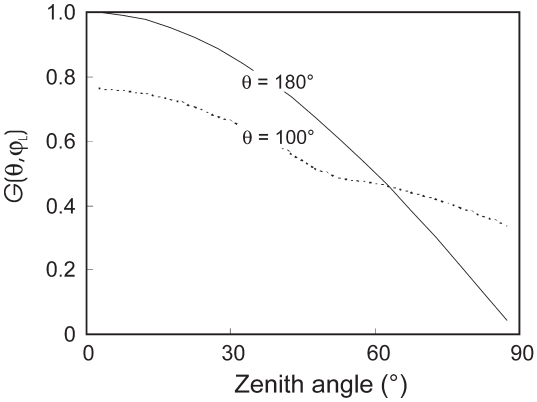

Figure 7. Dependence of simulated values of the G-function (the ratio between the projected area on a surface orthogonal to the direction of the projection and total leaf surface, Equation 10) on the solar zenith angle in the case of a flat leaf (cross-sectional angle, θ = 180°) and a leaf with θ = 100°. The G-function is the major determinant of light-interception capacity of single leaves. Leaf cross-sectional angles of around 100° are typical for sunlit leaves of *Fagus* (Figure 6D).

irradiance in *F. orientalis*. However, W_T ($r^2 = 0.32$, $P < 0.005$) and leaf area (Figure 9B) were negatively related to irradiance in the dominant *F. sylvatica* tree, but not in the subdominant tree (Figure 9B, $r^2 = 0.05$, $P > 0.2$ for W_T). Nevertheless, when the data for both *F. sylvatica* trees were pooled, both leaf area ($r^2 = 0.10$, $P < 0.05$) and W_T ($r^2 = 0.15$, $P < 0.01$) were negatively related to irradiance. Maximal leaf width and area were larger in *F. orientalis* than in both trees of *F. sylvatica* ($P < 0.001$). In *F. sylvatica*, the area (Figure 9B, $P < 0.05$) and width ($P < 0.001$) were larger in the dominant tree than in the subdominant tree.

In *F. sylvatica*, projected leaf area (Equation 2) was negatively related to irradiance ($r^2 = 0.62$, $P < 0.001$ for the dominant tree and $r^2 = 0.18$, $P < 0.05$ for the subdominant tree). This resulted from decreases in both foliage inclination angles (Figure 4A) and the width of leaf space (W_S; $r^2 = 0.65$, $P < 0.001$ for the dominant and $r^2 = 0.56$, $P < 0.001$ for the subdominant tree) with increasing irradiance in this species. Although W_S also scaled negatively with irradiance in *F. orientalis* ($r^2 = 0.33$, $P < 0.01$), its projected leaf area was independent of irradiance ($r^2 = 0.11$, $P > 0.1$). Given the weak change in total leaf area with irradiance, projected to total leaf area ratio (A_P/A_T) scaled negatively with irradiance in all cases (Figure 9C). For the linearized relationships, neither the slopes nor the intercepts differed among the groups ($P > 0.05$).

Leaf rolling and foliage chemistry

Foliage nitrogen concentration per unit dry mass (N_M) was positively related to Q_{int} in the subdominant *F. sylvatica* tree, but negatively related in the *F. orientalis* trees (Figure 10A). Despite the contrasting N_M versus Q_{int} relationships, nitrogen content per area (N_A) was always positively related to irradiance ($r^2 = 0.85$ for the dominant and $r^2 = 0.88$ for the subdominant tree of *F. sylvatica*, and $r^2 = 0.88$ for *F. orientalis*, $P < 0.001$ for all), indicating that the positive effect of light on M_A (Figure 9A) was also primarily responsible for the scaling of N_A with light. As with M_A, the relationships between N_A and irradiance were curvilinear in *F. sylvatica*, but linear in *F. orientalis*.

Foliage carbon content per unit dry mass (C_M) and Q_{int} were positively correlated for both *F. sylvatica* trees, but a negative relationship was observed in *F. orientalis* (Figure 10B). Given that proteins contain more carbon (53.5%, cf. Vertregt and Penning de Vries 1987) than leaves on average (mean ± SD of C_M was 48.5 ± 1.0% for *Fagus sylvatica* and 46.03 ± 0.45 for *F. orientalis*), and that foliar nitrogen content provides an estimate of foliar protein content, the decrease in C_M with Q_{int} in *F. orientalis* may have resulted from decreases in N_M with irradiance. To test this possibility, the protein-free carbon content (structural carbon, C_S) was computed as:

$$C_S = \frac{C_M - 6.25 \times 53.5 \times N_M / 100}{1 - 6.25 N_M / 100} \tag{13}$$

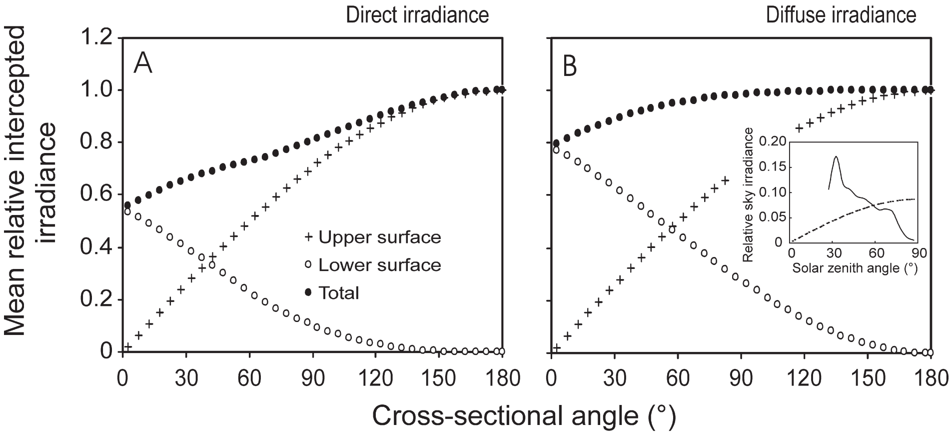

Figure 8. Mean daily relative direct (A) and diffuse (B) irradiance intercepted by upper and lower leaf sides, and the total intercepted irradiance in relation to the lamina cross-sectional angle. The irradiance was expressed relative to the value determined for a flat leaf (Equation 12), and the contributions of upper and lower leaf sides were separated according to Table 1. The inset in (B) demonstrates mean (May 1–June 30, 1999) zenithal distributions of direct (solid line) and diffuse irradiance (dashed line) employed in simulations of light-interception efficiency. In these calculations, both the diffuse and direct irradiance were computed for a surface orthogonal to the beam direction as $Q_F/\cos(\gamma)$, where Q_F is the irradiance measured by a flat sensor and γ is the zenith angle. The irradiances in the inset were normalized such that the integrals of both distributions were equal to 1.0.

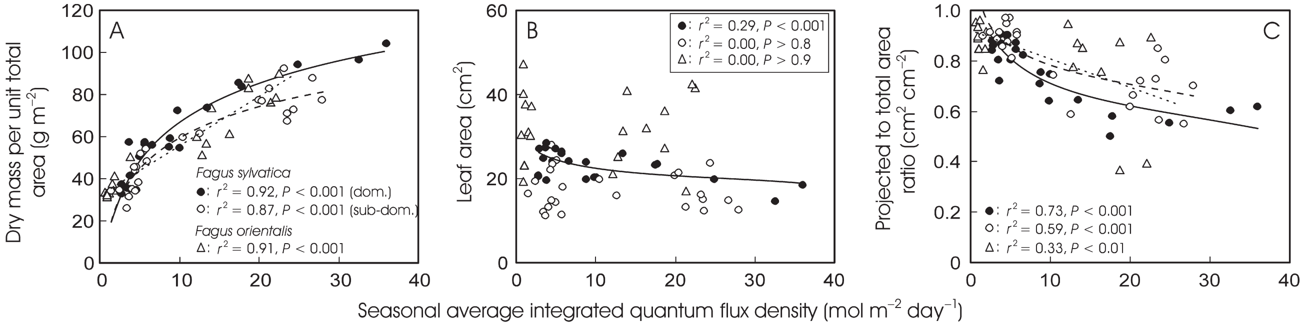

Figure 9. Lamina dry mass per unit area (A), leaf area (B) and projected to total leaf area ratio (A_P/A_T, C) in relation to Q_{int} in *F. sylvatica* and *F. orientalis*. Only the significant ($P < 0.05$) regressions are depicted. The projected leaf area, A_P, was computed according to Equation 2. The symbols are as in Figure 4A.

where the constant 6.25 converts nitrogen content to protein content. The structural carbon content was independent of Q_{int} in *F. orientalis* ($r^2 = 0.06$), indicating that the decline in C_M resulted from changes in N_M.

Structural carbon content was positively related to leaf morphological characteristics. Given the positive effects of light on foliage morphological variables and structural carbon content, these correlations may have resulted from covariation of foliar structural and chemical variables with irradiance. Among the leaf carbon versus morphology relationships, various data generally did not conform to a single fit, suggesting that these correlations existed because of covariation. However, for the relationships between C_S and H_S/W_S (Figure 11), C_S and the cross-sectional angle ($r^2 = 0.59$, $P < 0.001$), and C_S and the W_S to maximal leaf width ratio ($r^2 = 0.44$, $P < 0.001$), different sets of data were seemingly a part of the same correlation (slopes and intercepts were not significantly different at $P < 0.05$ according to ANCOVA analysis), hinting at possible causal relationships.

Discussion

Changes in branch and foliage inclination angles

Increases in branch (Figures 3A and 3B) and foliage (Figure 4A) inclination angles relative to the horizontal with increasing Q_{int} in *Fagus* confirm the trends observed in other broad-leaved tree species (Baldocchi et al. 1984, James and Bell 1996, Niinemets and Fleck 2002*b*). Although the integrated effect of leaf inclination angle on total daily integrated light may be relatively minor because solar azimuth and zenith angles vary during the day, simulations (Gutschick and Wiegel 1988, Valladares and Pearcy 1998) and measurements (Ishida et al. 1999) demonstrate that increases in foliage inclination angle significantly reduce the daily amount of intercepted light. Furthermore, higher leaf inclination angles allow efficient reduction of average irradiance incident to the leaf surface at midday (Ishida et al. 1999), when the probability of photoinhibition is greatest due to interactions of low atmospheric humidity and high temperature with excess quantum flux densities. Given that the net assimilation rate versus incident quantum flux density (Q) relationships of the upper canopy leaves of *F. sylvatica* saturate at Q values of 350–600 µmol m^{-2} s^{-1} (Rees and Stickan 1991, Schulte 1993), i.e., at considerably lower Q than the irradiances of about 2000 µmol m^{-2} s^{-1} incident to completely horizontal leaves at midday, increases in foliage inclination angle provide an important architectural mechanism to decrease the probability of photoinhibition of upper-canopy leaves. In contrast, horizontal leaves in the shaded part of the canopy can effectively increase the total absorbed radiation because the light is mainly coming from the low zenithal angles (Gutschick and Wiegel 1988).

The measurements in *F. orientalis* indicated that the positive effect of light on lamina inclination angle relative to the horizontal (Figure 4A) was primarily attributable to increases in

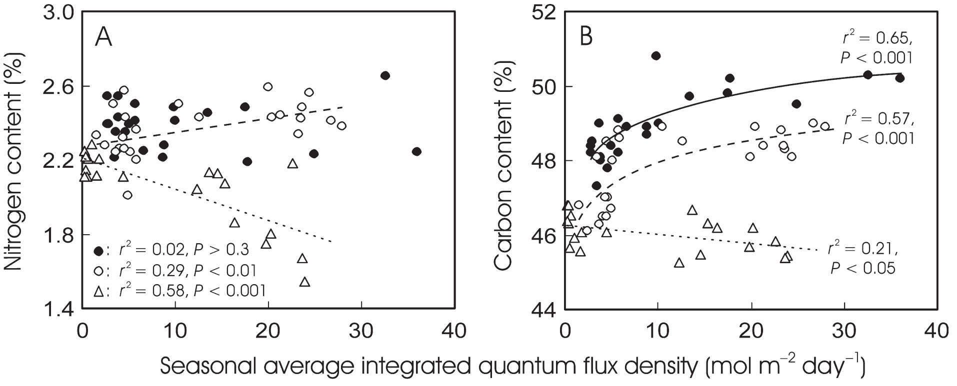

Figure 10. Relationships of foliar nitrogen content (A) and carbon content (B) with irradiance in *F. sylvatica* and *F. orientalis*. The symbols are as in Figure 4A.

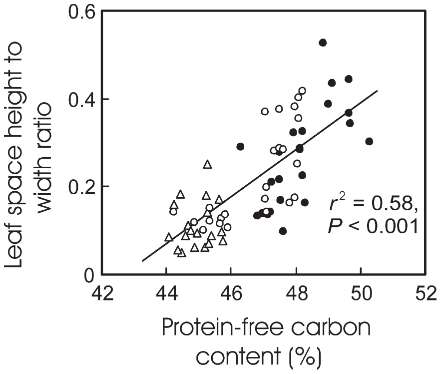

Figure 11. Correlation between leaf protein-free carbon content and the leaf space height to width ratio (H_S/W_S, Figure 2) in *Fagus sylvatica* and *Fagus orientalis*. Symbols are as in Figure 4A. All data were fitted by a single linear regression line. Separate linear regressions gave $r^2 = 0.46$ ($P < 0.001$, ●) and $r^2 = 0.55$ ($P < 0.001$, ○) for *F. sylvatica* and $r^2 = 0.00$ ($P > 0.8$) for *F. orientalis*.

petiole angle, possibly manifesting a photo- or gravitropic response of petioles to irradiance (Halstead and Dutcher 1987, Niklas 1992*a*). However, increases in the angle of the leaf lamina with respect to the petiole (Figures 4B and 5) also played a role in leaf inclination, suggesting that leaf biomechanical attributes such as lamina load on petiole, petiole stiffness and biomass investment in mechanical support within the lamina affected leaf inclination angle in the canopy (cf. Niinemets and Fleck 2002*a* for a detailed analysis).

Functional significance of the variation in lamina flatness within the canopy

In addition to changes in foliage inclination angle, inward rolling of leaves significantly altered unit leaf area projection. Leaves were not entirely flat anywhere in the canopy, and the degree of leaf curling strongly increased with increasing irradiance in the canopy in both *Fagus* species (Figure 6). Leaf margins of many important forest woody species such as *Acer*, *Carpinus*, *Carya*, *Cornus*, *Frangula*, *Fraxinus*, *Hedera*, *Juglans*, *Prunus* and *Sorbus* (authors' personal observations) are often folded upward. Although lamina rolling in broad-leaved trees may significantly alter foliage light-interception capacity, very few canopy light-interception models account for the non-flatness of tree leaves (Sinoquet et al. 1998).

To quantitatively describe the effect of leaf rolling on foliage potential for light harvesting, we calculated the *G*-value, which provides an estimate of the light interception efficiency per unit foliar area for a specific beam direction (Equations 6 and 9) for two leaves differing in degree of lamina rolling (Figure 7). The simulations indicated that leaf rolling may be an effective strategy to decrease direct irradiance on the leaf surface, and simultaneously optimize the interception of diffuse light with moderate irradiances, thereby further reducing the risk of photoinhibition in the upper canopy.

Foliage dry mass per area (M_A) in relation to irradiance

Although extensive modifications in leaf light-harvesting capacity within the canopy lead to a more uniform light gradient and allow greater light penetration to the lower canopy compared to a situation in which all leaves are completely flat and horizontal, incident irradiances varied more than 20-fold between the canopy top and bottom (cf. the light scale in Figure 4A). To adjust foliage physiological potentials with leaf specific orientation and canopy location, M_A generally increases with light availability in the canopy (e.g., Niinemets and Kull 1998), providing a primary explanation for increases in foliage photosynthetic capacities per unit area with leaf irradiance (Hollinger 1996). Moreover, decreases in M_A are compatible with a more extensive foliar area, and accordingly with greater light interception per unit biomass investment in leaves. We observed that leaf dry mass per unit area varied fourfold along the light gradient in *F. sylvatica*, and threefold for a less extensive light gradient in *F. orientalis* (Figure 9A). In comparison, lower ranges of variation of 1.5–3-fold have been observed for less shade-tolerant species (Niinemets and Kull 1998), suggesting that high plasticity in orientation of foliage surface and in M_A may partly explain the extreme shade tolerance of *Fagus* species.

Leaf carbon investments and leaf rolling

Leaf rolling is generally considered to be a specific response of leaves to water limitations (Begg 1980). Thus, the opposite relationship between water and light availability in the canopy may provide a mechanistic explanation for the scaling of degree of leaf rolling with irradiance (Figures 2 and 6). In many grasses, leaf rolling results from water loss in specific bulliform cells in the leaf epidermis (Begg 1980), and there are strong correlations between leaf water potential and the degree of leaf rolling in these species (Begg 1980, Heckathorn and DeLucia 1991, Fernandez and Castrillo 1999). In some grass species, leaf rolling may also be facilitated by anatomical differentiation and turgor gradients between the leaf halves at both sides of the midrib (Singh and Singh 1989). Importantly, leaf rolling is readily reversible in grasses, and strong diurnal variability may occur in the degree of leaf rolling (Begg 1980), thereby allowing adjustment in light interception and water loss under specific environmental conditions.

The degree of leaf rolling also increases in response to water stress in broad-leaved tree species (Castel and Fereres 1982, Gill and Mahall 1986, Ruiz-Sánchez et al. 1997), but little is known about the mechanism of leaf rolling in these species. In the deciduous water-stress sensitive *Juglans regia* L. (Tyree et al. 1993), detached leaves roll readily as foliage water content decreases (A. Cescatti, unpublished data), suggesting a mode of action similar to that in the grass species. However, the leaves of *Juglans* spp. have a particularly low bulk modulus of elasticity and readily wilt at the turgor loss point. This is in marked contrast to the leaves of *Fagus*, which do not wilt even after turgor loss (Ü. Niinemets, unpublished observations). Thus, it is unlikely that, in species with stiff leaves, the degree of leaf rolling is directly controlled by leaf water potentials. Differential regulation of the growth of upper and lower leaf sides by means of a complex signal transduction pathway (Pickard 1985) may be involved in the leaf rolling response in deciduous woody species. There is ample evidence indicating that curling and rolling of plant leaves is often driven by the plant stress hormone ethylene (Righetti 1996, Jackson 1997, Kosugi et al. 2000), possibly because of ethylene effects on auxin or gibberellin gradients through the leaf (Pickard 1985, Mattoo and Suttle 1991).

Although the exact mechanism of leaf rolling in *Fagus* remains to be discovered, for modeling daily light-interception capacity of the foliage, it is important that whenever the rolling mechanism involves differential growth regulation between upper and lower leaf surfaces, once developed, the leaf rolling should not be readily reversible. Although there were tree-to-tree and interspecific differences in the leaf rolling and carbon content versus Q_{int} relationships, we observed that the variables characterizing the degree of leaf rolling—H_S/W_S (Figure 11), W_S/W_T and the cross-sectional lamina angle—each gave a single relationship with structural leaf carbon content. This may indicate that the degree of leaf rolling depends directly on increases in lamina lignification to support the curved lamina.

Tree-to-tree and interspecific variability in the leaf structure versus light relationships

We found significant tree-to-tree and interspecific differences in the degree of leaf rolling (Figure 6), dry mass per unit area (Figure 9A), leaf size (Figure 9B) and leaf carbon contents (Figure 10B). Increases in M_A, degree of leaf rolling and carbon contents are typical responses to water limitation in many species (Castel and Fereres 1982, Witkowski and Lamont 1991, Abrams et al. 1994). Thus, larger values of foliar carbon contents, M_A and degree of leaf rolling at a common irradiance in the dominant relative to the subdominant tree of *F. sylvatica* may indicate that leaves in the dominant tree were subject to greater water stress. Leaf size, on the other hand, was greater in the subdominant *F. sylvatica* tree than in the dominant tree (Figure 9B); however, leaf size is determined early in the season, whereas M_A, leaf carbon contents and leaf rolling may increase throughout the season (Castel and Fereres 1982, Reich et al. 1991, Grossoni et al. 1998). These data collectively suggest that the tree-to-tree variability in foliage structure versus irradiance relationships resulted from more severe water limitations in the dominant tree than in the subdominant tree. Such tree-to-tree differences in water availability may be related to greater total foliage area, lower stem and branch hydraulic conductivities, differences in rooting systems, or micro-site heterogeneity in water availability.

Conclusions

In addition to modifications in leaf inclination angles, changes in the degree of leaf rolling may significantly alter foliage light-interception capacity and distribution of light throughout the canopy. The projected leaf area to total leaf area ratio, which provides an estimate of the combined effects of foliage inclination angle and leaf rolling on the interception efficiency of unit foliar area, varied from 0.97 to 0.37 within the canopy (Figure 9C), indicating a large plasticity for canopy structural acclimation. This response is functionally convergent with the large decreases in projected needle surface area to total needle surface area ratio with increasing Q_{int} in conifers (Niinemets et al. 2002). It provides an important mechanism for maintaining the efficiency of light harvesting in diffuse light, and for reducing the interception of peaks of beam irradiance that could lead to photoinhibition.

Although leaf rolling responses are commonly observed in broad-leaved trees, little is known about the mechanisms and controls of these phenomena. Because of the importance of leaf rolling for whole-canopy light interception, further research is needed to unravel the potential associations between foliage water potential, leaf structure and lignification on the degree of leaf rolling in the canopy.

Our study also highlighted significant differences in leaf structure and chemistry versus irradiance relationships among trees of varying social status in the same canopy. A tree stand consists of a size hierarchy of individuals, and may exhibit strong micro-heterogeneity in belowground resources. For scaling of leaf structure and physiology versus irradiance relationships from trees to an entire stand, we suggest that potential tree-specific controls on leaf structure should be elucidated and incorporated.

Acknowledgments

We thank Triin Niinemets for help in the field and in the lab, and Dr. Otto Klemm (Chair of Microclimatology, BITÖK, Universität Bayreuth, Germany) for sharing with us the unpublished climatic data from the field sites. Financial support was provided by the Estonian Science Foundation (Grant 4584), the Estonian Minister of Education (Grant 0180517s98), the German Federal Minister of Research and Technology (BMFT, grants BEO 51-0339476A (BITÖK), EST 001-98), and the CaRiTRo Foundation.

References

Abrams, M.D., M.E. Kubiske and S.A. Mostoller. 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology 75:123–133.

Baldocchi, D.D., D.R. Matt, B.A. Hutchinson and R.T. McMillen. 1984. Solar radiation within an oak–hickory forest: an evaluation of the extinction coefficients for several radiation components during fully leafed and leafless periods. Agric. For. Meteorol. 32: 307–322.

Bartsch, H.-J. 1966. Mathematische Formeln. 5th Edn. VEB Fachbuchverlag, Leipzig, 508 p.

Bayerischer Klimaforschungsverbund. 1998. Klimakarte: Niederschläge 1961–1990. Karten zur Wasserwirtschaft. Bayerisches Landesamt für Wasserwirtschaft, München.

Begg, J.E. 1980. Morphological adaptations of leaves to water stress. *In* Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J. Kramer. John Wiley, New York, pp 33–42.

Campbell, G.S. and J.M. Norman. 1989. The description and measurement of plant canopy structure. *In* Plant Canopies: Their Growth, Form and Function. Eds. G. Russell, B. Marshall and P.G. Jarvis. Society for experimental biology seminar series. 31. Cambridge University Press, Cambridge, pp 1–19.

Castel, J.R. and E. Fereres. 1982. Responses of young almond trees to two drought periods in the field. J. Hortic. Sci. 57:175–187.

Cescatti, A. 1997. Modelling the radiative transfer in discontinuous canopies of asymmetric crowns. I. Model structure and algorithms. Ecol. Model. 101:263–274.

Disney, M., P. Lewis and P. North. 2000. Monte Carlo ray tracing in optical canopy reflectance modelling. Remote Sens. Rev. 18: 163–196.

Ducrey, M. 1981. Bioclimatological studies in a broad leaf high stand (*Fagus sylvatica* L. and *Quercus sessiliflora* Salisb.). III. Photosynthetic rates of leaves from various levels in the stand. Ann. Sci. For. 38:71–86. In French.

Farque, L., H. Sinoquet and F. Colin. 2001. Canopy structure and light interception in *Quercus petraea* seedlings in relation to light regime and plant density. Tree Physiol. 21:1257–1267.

Fernandez, D. and M. Castrillo. 1999. Maize leaf rolling initiation. Photosynthetica 37:493–497.

Gill, D.S. and B.E. Mahall. 1986. Quantitative phenology and water relations of an evergreen and a deciduous chaparral shrub. Ecol. Monogr. 56:127–143.

Grossoni, P., F. Bussotti, C. Tani, E. Gravano, S. Santarelli and A. Bottacci. 1998. Morpho-anatomical alterations in leaves of *Fagus sylvatica* L. and *Quercus ilex* L. in different environmental stress conditions. Chemosphere 36:919–924.

Gutschick, V.P. and F.W. Wiegel. 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. Am. Nat. 132:67–86.

Halstead, T.W. and F.R. Dutcher. 1987. Plants in space. Annu. Rev. Plant Physiol. 38:317–345.

Heckathorn, S.A. and E.H. DeLucia. 1991. Effect of leaf rolling on gas exchange and leaf temperature of *Andropogon gerardii* and *Spartina pectinata*. Bot. Gaz. 152:263–268.

Hollinger, D.Y. 1996. Optimality and nitrogen allocation in a tree canopy. Tree Physiol. 16:627–634.

Innes, J.L. 1992. Observations on the condition of beech *Fagus sylvatica* L. in Britain in 1990. Forestry 65:35–60.

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

Jackson, M. 1997. Hormones from roots as signals for the shoots of stressed plants. Trends Plant Sci. 2:22–28.

James, S.A. and D.T. Bell. 1996. Leaf orientation of juvenile *Eucalyptus camaldulensis*. Aust. J. Bot. 44:139–156.

Koppel, A.T. and T.E.-A. Frey. 1985. On study of radiation regime within Norway spruce crown. Lesovedenie 4:3–8. In Russian.

Kosugi, Y., K. Shibuya, N. Tsuruno, Y. Iwazaki, A. Mochizuki, T. Yoshioka, T. Hashiba and S. Satoh. 2000. Expression of genes responsible for ethylene production and wilting are differently regulated in carnation (*Dianthus caryophyllus* L.) petals. Plant Sci. 158:139–145.

Koval, I.P. and N.A. Bityukov. 1969. Light conditions under the beech forest canopy. Lesovedenie 5:46–56. In Russian.

Mattoo, K. and J.C. Suttle. 1991. The plant hormone ethylene. CRC Press, Boca Raton, FL, 265 p.

Mayer, H. 1984. Wälder Europas. Gustav Fischer Verlag, Stuttgart, 691 p.

Mayer, H. and H. Aksoy. 1986. Wälder der Türkei. Gustav Fischer Verlag, Stuttgart, 290 p.

Midgley, G.F., M.C. Rutherford, G.W. Davis and J. de W. Bösenberg. 1992. Photosynthetic responses of heliophilus *Rhus* species to environmental modification by invasive shrubs. Funct. Ecol. 6: 334–345.

Muraoka, H., A. Takenaka, Y. Tang, H. Koizumi and I. Washitani. 1998. Flexible leaf orientations of *Arisaema heterophyllum* maximize light capture in a forest understorey and avoid excess irradiance at a deforested site. Ann. Bot. 82:297–307.

Niinemets, Ü. and S. Fleck. 2002*a*. Leaf biomechanics and biomass investment in support in relation to long-term irradiance in *Fagus*. Plant Biol. 4:523–533.

Niinemets, Ü. and S. Fleck. 2002*b*. Petiole mechanics, leaf inclination, morphology, and investment in support in relation to light availability in the canopy of *Liriodendron tulipifera*. Oecologia 132:21–33.

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

Niinemets, Ü., D.S. Ellsworth, A. Lukjanova and M. Tobias. 2002. Dependence of needle architecture and chemical composition on canopy light availability in three North American *Pinus* species with contrasting needle length. Tree Physiol. 22:747–761.

Niklas, K.J. 1991. Flexural stiffness allometries of angiosperm and fern petioles and rachises: evidence for biomechanical convergence. Evolution 45:734–750.

Niklas, K.J. 1992*a*. Gravity induced effects on material properties and size of leaves on horizontal shoots of *Acer saccharum* (Aceraceae). Am. J. Bot. 79:820–827.

Niklas, K.J. 1992*b*. Petiole mechanics, light interception by lamina, and “Economy in Design.” Oecologia 90:518–526.

Niklas, K.J. 1996. Differences between *Acer saccharum* leaves from open and wind-protected sites. Ann. Bot. 78:61–66.

Niklas, K.J. and T.G. Owens. 1989. Physiological and morphological modifications of *Plantago major* (Plantaginaceae) in response to light conditions. Am. J. Bot. 76:370–382.

Nilson, T. 1971. A theoretical analysis of the frequency of gaps in plant stands. Agric. Meteorol. 8:25–38.

Pearcy, R.W. and F. Valladares. 1999. Resource acquisition by plants: the role of crown architecture. *In* Physiological Plant Ecology. Eds. M.C. Press, J.D. Scholes and M.G. Barker. Blackwell Science—MPG Books Ltd., Cornwall, pp 45–66.

Pearcy, R.W. and W. Yang. 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. Oecologia 108:1–12.

Pearcy, R.W. and W. Yang. 1998. The fuctional morphology of light capture and carbon gain in the redwood forest understorey plant, *Adenocaulon bicolor* Hook. Funct. Ecol. 12:543–552.

Peters, R. 1992. Ecology of beech forests in the northern hemisphere. Ph.D. Diss., Landbouwuniversiteit Wageningen, 125 p.

Peters, R. 1997. Beech forests. Geobotany 24. Kluwer Academic Publishers, Dordrecht, 169 p.

Pickard, B.G. 1985. Early events in geotropism of seedling shoots. Annu. Rev. Plant Physiol. 36:55–75.

Planchais, I. and H. Sinoquet. 1998. Foliage determinants of light interception in sunny and shaded branches of *Fagus sylvatica* L. Agric. For. Meteorol. 89:241–253.

Rees, U. and W. Stickan. 1991. Untersuchungen zum C-Haushalt von Jungbuchen—CO_2-Assimilation in Abhängigkeit von der Einstrahlung. Ber. FZ Waldökosyst., Reihe B 22:138–141.

Reich, P.B., M.B. Walters and D.S. Ellsworth. 1991. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. Plant Cell Environ. 14:251–259.

Righetti, B. 1996. Chlorophyll, ethylene and biomass determination in *Prunus avium* cv. Victoria cultivated *in vitro* under different atmospheric conditions. J. Hortic. Sci. 71:249–255.

Ross, J. 1981. The radiation regime and architecture of plant stands. Dr. W. Junk, The Hague, 342 p.

Ross, J. and M. Sulev. 2000. Sources of errors in measurements of PAR. Agric. For. Meteorol. 100:103–125.

Ruiz-Sánchez, M.C., R. Domingo, R. Savé, C. Biel and A. Torrecillas. 1997. Effects of water stress and rewatering on leaf water relations of lemon plants. Biol. Plant. 39:623–631.

Schulte, M. 1993. Saisonale und interannuelle Variabilität des CO_2-Gaswechsels von Buchen (*Fagus sylvatica* L.)—Bestimmung von C-Bilanzen mit Hilfe eines empirischen Modells. Ph.D. Diss., Universität Göttingen, 165 p.

Shen, C.F. 1992. A monograph of the genus *Fagus* Tourn ex L. (Fagaceae). Ph.D. Diss., City Univ. New York, 390 p.

Singh, G. and T.N. Singh. 1989. Mechanism of leaf rolling in rice. Curr. Sci. 58:804–806.

Sinoquet, H., S. Thanisawanyangkura, H. Mabrouk and P. Kasemsap. 1998. Characterization of the light environment in canopies using 3D digitising and image processing. Ann. Bot. 82:203–212.

Takenaka, A., Y. Inui and A. Osawa. 1998. Measurement of three-dimensional structure of plants with a simple device and estimation of light capture of individual leaves. Funct. Ecol. 12:159–165.

Tosun, S. and Z. Özpay. 1996. Propositions to solve the regeneration problems in the pure and mixed oriental beech (*Fagus orientalis* Lipsky.) stands covered by high dense rhododendrons. *In* Approaches to Extension in Forestry—Experiences and Future Developments. Proc. IUFRO Workshop Party S6.06-03 Extension, Symposium 30.09.–04.10.96, Freising, Germany. Eds. R. Hubner and R. Beck. IUFRO, pp 1–6.

Tyree, M.T., H. Cochard, P. Cruiziat, B. Sinclair and T. Ameglio. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. Plant Cell Environ. 16:879–882.

Valladares, F. and R.W. Pearcy. 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.

Vertregt, N. and F.W.T. Penning de Vries. 1987. A rapid method for determining the efficiency of biosynthesis of plant biomass. J. Theor. Biol. 128:109–119.

Wilkinson, L. 1990. SYSTAT: The system for statistics. SYSTAT, Evanston, IL, 677 p.

Witkowski, E.T.F. and B.B. Lamont. 1991. Leaf specific mass confounds leaf density and thickness. Oecologia 88:486–493.