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# Adjustment of foliage structure and function to a canopy light gradient in two co-existing deciduous trees.

## Variability in leaf inclination angles in relation to petiole morphology

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**Abstract** Foliar inclination angles, petiole morphology and dry matter partitioning between assimilative and support biomass were studied in shade-intolerant *Populus tremula* L. and shade-tolerant *Tilia cordata* Mill. along a natural light gradient across the canopy. The leaves of sub-canopy species *T. cordata* were on average exposed to lower irradiances, and they were also more horizontal with greater blade inclination angles ( $\phi_B$ , defined as the angle between the leaf fall-line and the horizon;  $\phi_B$  was positive for the leaves inclined upwards, and negative for the leaves inclined downwards) than those in *P. tremula*. Seasonal average daily integrated quantum flux density ( $Q_{int}$ , mol m<sup>-2</sup> day<sup>-1</sup>) and  $\phi_B$  were not related in *T. cordata*, and only a weak negative effect of  $Q_{int}$  on  $\phi_B$  was detected in *P. tremula*. Nevertheless, when both species were pooled, there was a strong negative relationship between  $Q_{int}$  and  $\phi_B$ , implying that the leaves became progressively vertical with increasing height in the canopy. Interspecific differences in foliage inclination were mainly related to petiole morphology, in particular to petiole length, rather than to contrasting biomass investment patterns between assimilative and support tissues within the leaf. It was suggested that more horizontal leaves, resulting from the species-specific structure of petioles, partly explain the superior performance of shade-tolerant *T. cordata* in the understory and the sub-canopy.

**Key words** Acclimation · Canopy architecture · Light interception · *Populus tremula* · *Tilia cordata*

### Introduction

Tree canopies possess a highly organized structure that is adjusted towards effective interception and use of light at different canopy heights. Leaves at the top and bottom of a canopy are often exposed to a more than 20-fold differ-

ence in irradiance averaged over long-term (Ellsworth and Reich 1993; Niinemets 1995; Niinemets and Kull 1998). A vast number of tree acclimation responses to light – including changes in crown architecture (Kohyama 1980), foliage distribution (Niinemets 1996), inclination (McMillen and McClendon 1979; Hollinger 1989), and morphology and anatomy of leaves (Ellsworth and Reich 1993; Kull and Niinemets 1993; Pearcy and Sims 1994; Niinemets 1995, 1996) – have been identified and suggested to be adaptive, since the plastic changes in these plant traits optimise the light use efficiency of the whole plant in the heterogeneous canopy environment (Gutschick and Wiegel 1988; Bazzaz and Wayne 1994).

Leaf blade inclination angle from the horizontal ( $\phi_B$ ) is an important variable affecting the efficacy of light interception. There is evidence that foliar inclination angles change continuously along the light gradient in the canopy. As light becomes increasingly deficient with increasing canopy depth, foliar inclination angles become progressively horizontal (McMillen and McClendon 1979; Hutchinson et al. 1986; Hollinger 1989), thereby improving the efficiency of direct light absorption from vertical solar elevation angles. Yet, the variability in foliage inclination angles at a common irradiance is generally large (e.g., Miller 1967; Baldocchi et al. 1984; Hutchinson et al. 1986; Hollinger 1989), and the mechanisms underlying the correlation between foliar inclination angle and long-term irradiance are currently poorly understood.

Without dynamic stresses, petiole deflection from the horizontal is determined by petiole mechanical properties and the lamina load imposed on petiole (Niklas 1991d, 1992). Thus, light-determined alterations in petiole architecture, lamina load and biomass partitioning between petioles and lamina may be responsible for the relationship between lamina inclination angle and irradiance. An increase in leaf dry mass per area ( $M_A$ ) with increasing irradiance is the major light-related modification in leaf morphology (Percy and Sims 1994; Niinemets 1995, 1997; Niinemets and Tenhunen 1997). Given

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that foliar area per leaf is relatively independent of long-term light conditions along the canopy (Niinemets 1997; Niinemets and Kull 1998), the change of  $M_A$  with irradiance is likely to lead to a positive correlation between blade mass and irradiance. This, in turn, increases the static load imposed on the petiole, and unless petiole linear dimensions do not scale with irradiance, may be a reason for the observed negative correlations between inclination angle and irradiance. However, studies indicate that the fractional foliar biomass investments in petioles are insensitive to irradiance or even decrease with increasing light availability (Niinemets 1998).

The objectives of the current study were to find out (1) whether foliar inclination angles become more horizontal with increasing canopy depth in a mixed deciduous forest dominated by shade-intolerant early-successional species *Populus tremula* and shade-tolerant late-successional *Tilia cordata*, and (2) what biomechanical attributes of petioles and biomass partitioning patterns are responsible for the observed variability across the canopy. It was expected that the results of this study provide important insight into the acclimation responses of tree canopies, and contribute towards a functional description of tree canopy architecture.

## Material and methods

### Study area

The work was conducted in a deciduous mixed stand at Järvselja (58° 22' N, 27° 20' E, elevation 38–40 m), Estonia in July and August 1995. Overstory (17–27 m) was dominated by *P. tremula* and *Betula pendula* Roth., *T. cordata* was the subcanopy species (4–17 m), and *Corylus avellana* L. and the coppice of *T. cordata* dominated the understory. The soil was a gleyed pseudopodsol formed on a loamy till with average ( $\pm$ SE) C/N molar ratio of 23.8 $\pm$ 2.2, pH<sub>KCl</sub> of 4.19 $\pm$ 0.10, and cation exchange capacity of 0.61 $\pm$ 0.15 mol/kg (base saturation 23 $\pm$ 7%) in the humus horizon.

### Foliage sampling and morphological analyses

The leaves were taken between 1200–1400 hours along a vertical light gradient across the canopy. Trees were accessed from perma-

nent scaffoldings (height 25 m) located at the study site, and the highest sampling height per total tree height was always >0.97. Mean ( $\pm$ SE) height of the sampled trees was 26.5 $\pm$ 0.3 m in *P. tremula* (4 trees) and 7.4 $\pm$ 2.4 m in *T. cordata* (11 trees). In *T. cordata*, 90% of foliar samples were taken from 4 sub-canopy trees, which were on average 17.1 $\pm$ 0.2 m tall. Canopy and subcanopy trees of *P. tremula* and *T. cordata* were of the same age (ca. 40 year), the saplings of *T. cordata* studied in the understory were 4–12 years old.

Petiole length ( $L_p$ ) was measured with a rule, and petiole diameter(s) with the micrometer. *T. cordata* was considered to possess cylindrical petioles, and all measurements along the petiole (6–22, average $\pm$ SE=11.5 $\pm$ 0.3) were averaged to obtain the mean petiole diameter ( $P_D$ ). *P. tremula* has elliptical petioles (cf. Niklas 1991d) and both the minor ( $a$ ) and the major axes ( $b$ ) of the petiole cross-section were measured in perpendicular directions in 6–16, on average 10.7 $\pm$ 0.3, locations along the petiole. Minimum values of  $P_D$ , and the minor ( $a$ ) and major ( $b$ ) axes were defined as the minimum detected values among the whole set of measurements in the given petiole. All morphological measurements were conducted with fresh plant material.

Fresh mass of laminae and petioles was determined immediately after collection, and dry mass after oven-drying at 70 °C for at least 48 h. To calculate petiole density ( $\rho_p$ , dry mass per volume), petiole volume was found from length ( $L_p$ ) and petiole diameter ( $L_p \frac{\pi \cdot P_D^2}{4}$ ) in *T. cordata*, and from  $L_p$  and minor and major semi-axes of the ellipse ( $L_p \frac{\pi \cdot a \cdot b}{4}$ ) in *P. tremula*.

### Petiole and blade inclination from the horizontal

Petiole and lamina inclination angles with respect to horizon were measured with a protractor (Dasco Pro, Rockford Ill., USA) as depicted in Fig. 1. The reported values are the averages of five determinations per leaf. The angles below the horizon (0°) are considered negative, the angles above it are positive. The angle measurements were conducted only in windless conditions in free-hanging leaves. Thus, leaf position was considered to reflect the static load imposed on the petiole. Petiole second moment of area ( $I$ ) was calculated according to Wainwright et al. (1976):

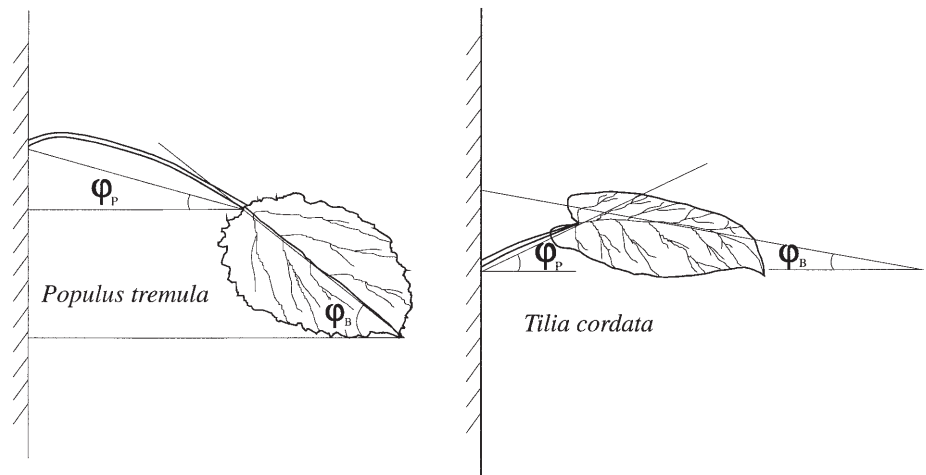
$$I = \frac{\pi \cdot P_D^4}{64} \quad (T. cordata)$$

$$I = \frac{\pi \cdot a^3 \cdot b}{64} \quad (P. tremula) \quad (1)$$

and an estimate of petiole deflection from the horizontal due to static bending (for a flexurally uniform cantilever),  $\delta_{\max}$ , as (Wainwright et al. 1976; Niklas 1991d):

$$\delta_{\max} = \frac{M_f \cdot L_p^3}{3E \cdot I} \quad (2)$$

**Fig. 1** Examples of the measurements of blade and petiole inclination angles in *Tilia cordata* and *Populus tremula*. Petiole inclination angle ( $\phi_p$ ) was measured as the angle between the points of petiole attachment to the twig and lamina attachment to the petiole. Blade inclination angle ( $\phi_b$ ) was measured at the fall-line of the blade (approximately in the middle of the blade when the fall-line was non-linear)



where  $M_f$  is leaf fresh mass (petiole + lamina), and  $E$  is petiole elastic modulus.  $E$  was not directly measured, but was assumed to be constant across the environmental gradients and petiole morphologies for each species. Thus,  $\delta_{\max}$  was normalized with respect to maximum and minimum calculated values across the whole set of data and is given in relative units. Since there is generally a positive correlation between petiole density and its elastic modulus (Niklas 1991a, b), observed patterns in petiole density suggested that these assumptions were correct (cf. Results). Moreover, previous research has demonstrated that the absolute values of petiole flexural stiffness (the product of  $E$  and  $I$ ) are generally dominated by  $I$  (Niklas 1991c–e).

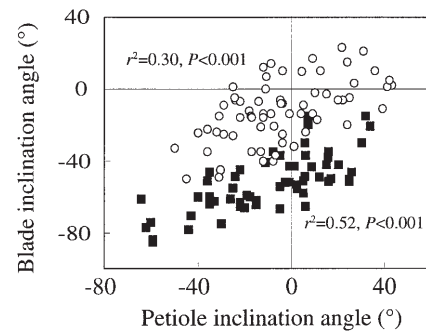
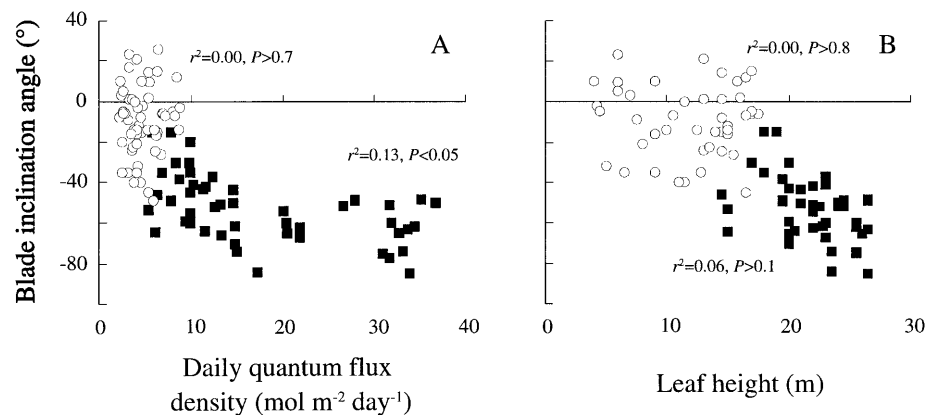
Estimations of mean incident integrated quantum flux density ( $Q_{\text{int}}$ )

Continuous measurements of photosynthetically active quantum flux density ( $Q$ ) with quantum sensors, and estimations of fractional penetration of irradiance at sensor locations with hemispherical photography were combined to derive long- and short-term average quantum flux densities incident to the leaves.  $Q$  was monitored at 18 canopy heights with 8 GaAsP photodiodes (G1118, Hamamatsu Photonics, Shizuoka, Japan) and 10 silicon photodiodes (OPT-21, Burr-Brown, Tucson, Ariz., USA). Both types of photodiodes were calibrated against a quantum sensor (LI-190SA, Li-Cor, Lincoln, Neb., USA). Daily integrated  $Q$  was calculated from the sensor readings taken in 1 min steps. Mean seasonal quantum flux density ( $Q_{\text{int}}$ ,  $\text{mol m}^{-2} \text{ day}^{-1}$ ) for the sensor position was found as the average daily integrated  $Q$  between the completion of lamina expansion-growth ( $\sim 3$  June, 1995) and the date of foliage sampling. Hemispherical photographs were taken just above the sensor locations in weekly intervals. The fractions of penetrating diffuse ( $I_{\text{dif}}$ , diffuse site factor) and of potential penetrating direct solar radiation of open sky ( $I_{\text{dir}}$ , direct site factor) were calculated from these photographs as described previously (Niinemets and Kull 1998). Hemispherical photographs were also taken above the leaf just before the leaf was harvested for morphological analyses. Integrated average quantum flux densities for sample locations were calculated from multiple linear regression equations in the form of  $Q_{\text{int}} = c \times I_{\text{dif}} + d \times I_{\text{dir}}$ . The regression coefficients,  $c$  and  $d$ , were estimated from actual  $Q_{\text{int}}$  measurements with the quantum sensors ( $r^2 = 0.99$ ,  $P < 0.001$ ).

#### Data analysis

Sample sizes were 60 in *P. tremula* and 68 in *T. cordata*. Linear regression and product-moment correlation techniques were used for simplicity throughout. Petiole second moment of area ( $I$ , Eq. 1) was logarithmed before statistical analysis. Species were compared by Model I ANOVA or by ANCOVA (Fig. 3, species as the main effect and petiole inclination angle as covariate) where appropriate. In the case of the covariation analysis, common slope

**Fig. 2** Blade inclination angle in *P. tremula* (■) and *T. cordata* (○) in relation to (A) seasonal integrated incident daily quantum flux density ( $Q_{\text{int}}$ ) and (B) leaf height in the canopy. Inclination angles were measured as depicted on Fig. 1,  $Q_{\text{int}}$  was estimated by a method combining hemispherical photography and direct light measurements with quantum sensors.  $r^2$ -s denote the explained variances of linear regression analyses within species



**Fig. 3** Correlations between blade and petiole inclination angles (cf. Fig. 1).  $r^2 = 0.30$  ( $P < 0.001$ ) in *T. cordata* and  $r^2 = 0.52$  ( $P < 0.001$ ) in *P. tremula*. Symbols as in Fig. 2

model was applied, because the interaction terms was insignificant ( $P > 0.2$ ). The relationships were considered significant at  $P < 0.05$  (Wilkinson 1990).

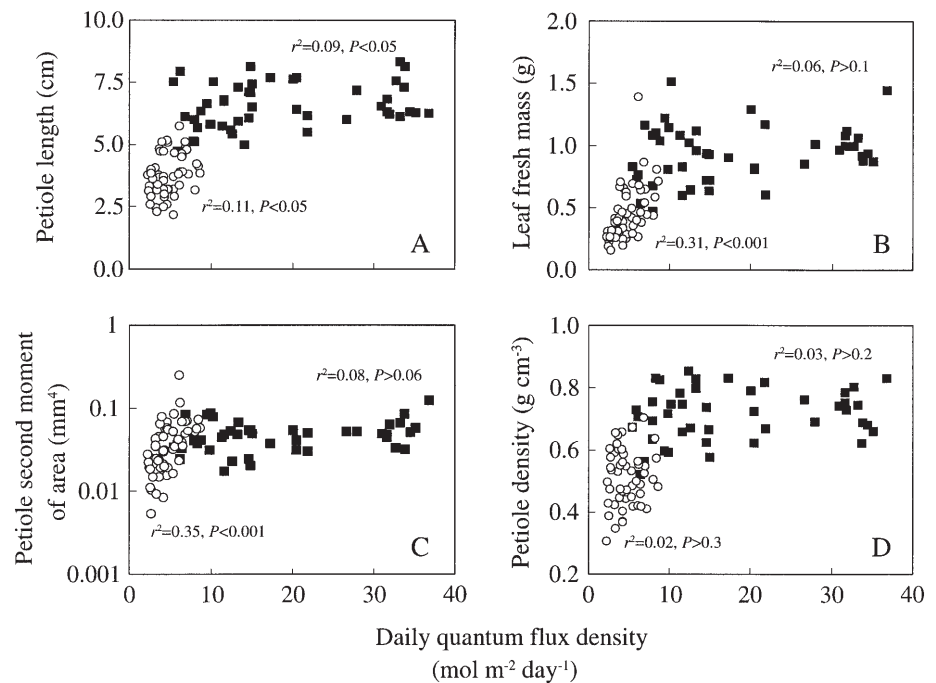
## Results

### Leaf inclination angles

The foliar layers of both *T. cordata* and *P. tremula* spanned over more than 10 m, but the trees of *P. tremula* were taller. Because of the exponential decline of light with increasing cumulative foliar area, the range of the integrated daily quantum flux densities ( $Q_{\text{int}}$ ) was also larger in *P. tremula*.

Within species, foliar inclination angles ( $\phi_B$ ) were relatively insensitive to long-term incident irradiance (Fig. 2A) and leaf height (Fig. 2B) in the canopy. A weak negative correlation was detected between  $\phi_B$  and  $Q_{\text{int}}$  only in *P. tremula* (Fig. 2). Petiole inclination angles ( $\phi_P$ ) were independent of irradiance and leaf height in both species (data not shown).  $\phi_B$  and  $\phi_P$  were positively correlated with each other, yet, the relationships were scattered (Fig. 3). The variability in blade inclination angle ( $\phi_B$ ) was 2- to 3-fold at a common integrated daily quantum flux density (Fig. 2A). In *P. tremula*,  $\phi_B$  ranged from  $-20$  to  $-70^\circ$  among the leaves emerged from the same bud (data not shown, cf. Fig. 2A).

**Fig. 4** Effects of integrated incident daily quantum flux density on (A) petiole length, (B) leaf fresh mass (petiole+lamina), (C) second moment of area (Eq. 1), and on (D) petiole density (dry mass per volume). Petiole second moment of area depends on linear dimensions and the geometry of petiole transverse section, and determines petiole mechanical characteristics for constant petiole material properties. Petiole density is used as an estimate of its elastic modulus (e.g., Niklas 1991a, b) in the current analysis. Symbols as in Fig. 2



Since the absolute values of negative and positive angles are equivalent in terms of light interception, the correlations between light, leaf height and leaf angles were also calculated using the absolute values, but the relations were similar to those observed among the original data set (results not shown).

When the data of both species were pooled (Fig. 2),  $\phi_B$  was negatively correlated with both  $Q_{int}$  ( $r^2=0.41$ ,  $P<0.001$ ), and leaf height ( $r^2=0.47$ ,  $P<0.001$ ), but  $\phi_P$  was still poorly related to light ( $r^2=0.03$ ,  $P>0.06$ ) and height ( $r^2=0.05$ ,  $P<0.05$ ). At a common  $\phi_P$ , *T. cordata* had a larger  $\phi_B$  than *P. tremula* (Fig. 3,  $P<0.001$ ), indicating that there is a considerable flexibility in adjusting lamina angles independent of petiole position and inclination.

#### Morphological determinants of lamina angle

Only moderate effects of light were detected on petiole mass and metric and leaf (petiole+lamina) mass variables (Fig. 4). Petiole length increased with increasing  $Q_{int}$  in *T. cordata* and *P. tremula*, and petiole second moment of area and leaf fresh mass in *T. cordata* (Fig. 4). *P. tremula* had generally larger leaves (Fig. 4B) with longer (Fig. 4A) and denser (Fig. 4D) petioles than *T. cordata*. However, petiole second moment of area was comparable between the species (Fig. 4C). Within species, petiole inclination angle was negatively correlated with petiole length in both *P. tremula* ( $r^2=0.23$ ,  $P<0.001$ ) and *T. cordata* ( $r^2=0.25$ ,  $P<0.001$ ), but negatively with leaf fresh mass ( $r^2=0.21$ ,  $P<0.001$ ) and petiole second moment of area ( $r^2=0.14$ ,  $P<0.001$ ) only in *T. cordata*. This negative correlation of  $\phi_P$  with  $I$  (Eq. 1), large values of which actually increase the mechanical stability of petioles

(Eq. 2), resulted from a positive correlation between  $I$  and petiole length ( $r^2=0.42$ ,  $P<0.001$ ) in *T. cordata*.

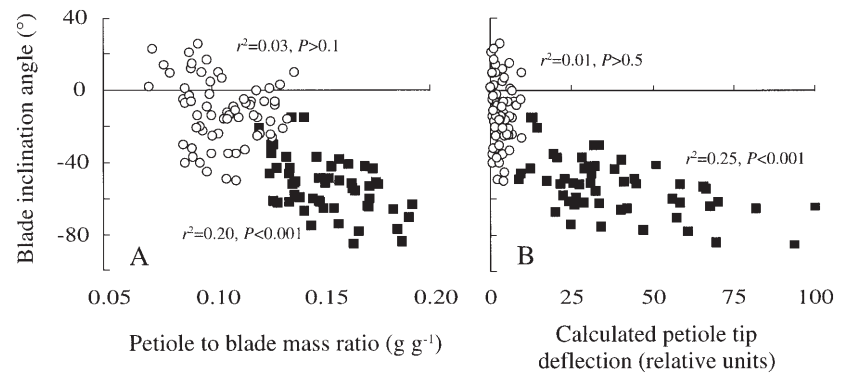
$\phi_B$  was negatively related to petiole length in *P. tremula* ( $r^2=0.32$ ,  $P<0.001$ ), but not in *T. cordata* ( $r^2=0.03$ ,  $P>0.1$ ), and was also not correlated with other structural variables depicted on Fig. 4. For the whole material,  $\phi_B$  scaled negatively with petiole length ( $r^2=0.59$ ,  $P<0.001$ ), leaf fresh mass ( $r^2=0.34$ ,  $P<0.001$ ), and petiole density ( $r^2=0.30$ ,  $P<0.001$ ), but was independent of petiole second moment of area ( $r^2=0.02$ ,  $P>0.1$ ). Again, the negative relationship between  $\phi_B$  and petiole density resulted from a positive correlation between petiole density and petiole length ( $r^2=0.40$ ,  $P<0.001$ ).

Contrary to expectations, the leaves with the greatest fractional leaf biomass investment in petioles had the most negative  $\phi_B$ -s (Fig. 5A). This was because the petiole to blade mass ratio was positively correlated with petiole length ( $r^2=0.82$ ,  $P<0.001$ ) and leaf fresh mass ( $r^2=0.47$ ,  $P<0.001$  for the whole material). A negative relationship between  $\phi_P$  and relative petiole tip deflection from the horizontal calculated from morphological variables (Eq. 2) was observed in both species ( $r^2=0.22$ ,  $P<0.001$  in *P. tremula* and  $r^2=0.14$ ,  $P<0.005$  in *T. cordata*). However, the tip deflection was negatively related to  $\phi_B$  only in *P. tremula* (Fig. 5B). Both the negative correlations of  $\phi_B$  with petiole to blade mass ratio and with petiole tip deflection were highly significant when both species were pooled (Fig. 5,  $r^2=0.53$ ,  $P<0.001$  for both correlations).

The relationships were not significantly improved by using minimum petiole diameter or minimum lengths of petiole axes instead of average values in the aforementioned calculations (data not shown).



**Fig. 5** Blade angle vs foliar biomass investment in (A) petioles, and (B) calculated static petiole tip deflection from the horizontal (Eq. 2, relative units). Tip deflection is computed for free-hanging leaves taking account of petiole morphology and lamina load on petiole. Symbols as in Fig. 2



## Discussion

### Correlations of blade inclination angle with light

In the simplest case, the fractional penetration of quanta is given by (Duncan et al. 1967):

$$\frac{Q}{Q_0} = e^{\frac{-LG}{\sin \theta}} \quad (3)$$

where  $Q_0$  is the quantum flux density above the canopy,  $L$  the cumulative foliar area,  $\theta$  the sun elevation above the horizon, and  $G$  is the projection of unit leaf area. Though it is a general praxis to use a single value of  $G$  for the whole canopy, the current study (Fig. 2) and a number of earlier observations demonstrate that  $G$  varies along the canopy in a deterministic manner; increasing  $\phi_B$ -s with increasing height are commonly observed in tree canopies (cf. Introduction). According to the modelling studies, such a pattern optimizes whole canopy carbon gain (Kuroiwa 1970; Trenbath and Angus 1975), because vertically inclined leaves in the upper canopy allow light to penetrate the deeper canopy layers during midday hours with high direct light flux, and allow a more uniform light distribution across the canopy. By contrast, horizontal leaves in the lower canopy maximize the surface area projection, and thereby improve the efficiency of direct light interception when solar elevation angles are high.

### Influences of petiole structure on leaf inclination

Petiole tip deflection from the horizontal may be described by basic physical relationships (e.g., Niklas 1991e). As the mechanical theory evinces (Eq. 2), leaf support costs in terms of biomass investment in petioles increase as leaves become more horizontal, because such leaves require petioles with large  $I$ . At a common absolute inclination angle, the leaves inclined downwards possess the same  $G$  (Eq. 3) as those inclined upwards, but the leaves with negative inclination angles require lower biomass investments in petioles for the same absolute  $\phi_B$ .

Given that the lamina area per leaf was independent of irradiance, but a strong positive correlation was ob-

served between the leaf dry mass per area and  $Q_{\text{int}}$  in these species (Niinemets and Kull 1998, unpublished observations of Niinemets 1995), lamina load on petiole also tended to increase with increasing  $Q_{\text{int}}$  (Fig. 4B). By no doubt, light effects on lamina load affected blade angle, but the calculations with petiole and blade mass and metric variables demonstrated that petiole length was the major determinant of  $\phi_B$ , and was also partly responsible for the observed interspecific differences in  $\phi_B$ . Though *P. tremula* had more dense petioles than *T. cordata* (Fig. 4D), its petioles were also longer and the blade loads on petioles were larger, resulting in lower foliar inclination angles in this species (Fig. 2).

What is the ecological significance of the longer petioles in *P. tremula*? According to simulation studies, increasing petiole length decreases shading within the shoot in broad-leaved species, and may significantly increase shoot light interception, especially in species with short internodes (Takenaka 1994) like *P. tremula*. Though long petioles sacrifice the ability to form a planar light-intercepting display advantageous in low light, they result in a lower shading within the shoots. Thus, in high light environments, long petioles allow the plant to support higher foliar areas on shorter shoots, and accordingly, such design requires lower biomass investments in carbon-expensive framework of woody branches.

The previous discussion has focused on the effects of static bending on foliage inclination. However, long elliptic petioles of *P. tremula* cause the blade to flutter even in a light wind (Niklas 1991d). Therefore, in this species, the blade angles are highly variable temporally and very different from those determined for free-hanging leaves in windless conditions. Leaf flutter of *Populus* leaves decreases the amount of light intercepted by upper canopy leaves, but tends to increase the number of light-flecks in the lower canopy, and may lead to a spatially more even light distribution within the canopy (Roden and Pearcy 1993).

### Implications on species composition of the canopy

The previous analysis demonstrated that the highly significant correlation between  $\phi_B$  and  $Q_{\text{int}}$  for the pooled set of data (Fig. 2A) was mostly the result of interspecific-

ic differences in petiole architecture (Fig. 4) combined with species dispersal patterns across the canopy – shade-intolerant *P. tremula* in the overstory and shade-tolerant *T. cordata* in the sub-canopy and the understory. Increasingly more horizontal leaves with increasing canopy depth have been observed in a number of multispecies forest canopies (cf. Introduction). Extending the previous discussion on the economy of light harvesting to species performance along the vertical light gradients, it is concluded that (1) more horizontal leaves of *T. cordata* play an important part in the greater shade-tolerance of this species, and (2) interspecific differences in  $\phi_B$  partly explain the co-existence of the studied species in different layers in the same mixed canopy.

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