

Distribution of leaf photosynthetic properties in tree canopies: comparison of species with different shade tolerance

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Summary

1. Parameters of the photosynthesis vs CO_2 response curve, nitrogen and chlorophyll contents were studied in *Populus tremula*, *Tilia cordata* and *Corylus avellana* leaves along a natural light gradient in the canopy.

2. In all species, leaf nitrogen content per unit area (N_s) declined with decreasing fractional transmission of photon flux density (K_{sum}), measured by a hemispheric photographic technique. However, the shape of the relationship between N_s and K_{sum} depended on species. N_s was almost linearly related to K_{sum} in the most light-demanding species *P. tremula* but this relationship was curved in two other species. *Populus tremula* possessed the largest values of N_s at given K_{sum} , while *C. avellana*, the most shade-tolerant species, had the lowest values of N_s .

3. Both the initial slope, characterizing the maximum carboxylation efficiency, and the plateau value, providing an estimate of the photosynthetic electron transport capacity, of the photosynthesis vs CO_2 response curves, were linearly related to N_s and only minor differences were observed among the studied species. Leaf chlorophyll content per area was also related to N_s but the ratio of Chl/N increased substantially at low K_{sum} in the lower canopy. It was concluded that the partitioning of nitrogen between light harvesting, electron transport and carboxylation components of the photosynthetic apparatus may change with depth in the canopy as a result of a relative increase in the light-harvesting complexes in relation to the rest of the photosynthetic apparatus.

4. The interspecific differences in species' photosynthetic potentials are mainly associated with different nitrogen distribution patterns along the canopy and in minor part with differences in nitrogen partitioning among photosynthetic machinery.

Key-words: Canopy, carbohydrates, *Corylus avellana*, leaf nitrogen, photosynthesis, *Populus tremula*, *Tilia cordata*

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Introduction

Scaling up photosynthesis from single leaf to canopy requires information on the qualitative changes in photosynthetic apparatus caused by changes in average light environment of the leaf as well as of the overall distribution of the photosynthetic apparatus between the leaves in the canopy.

Leaf photosynthetic properties are well correlated with leaf nitrogen content (Evans 1989; Hollinger 1992; Reich *et al.* 1994). Ultimate exploitation of this relationship has led to the conclusion that, because of parallel changes of leaf nitrogen content and irradiance inside the canopy, a canopy behaves like a big leaf on the time-scale over which acclimation has occurred (Kull & Jarvis 1995). This is a very attractive result as it simplifies substantially calculations of whole-canopy photosynthesis but it requires verification by

actual measurements. It may be argued that a leaf nitrogen vs leaf photosynthesis relationship cannot be universal in leaves from different light environments, because nitrogen partitioning between the proteins determining the capacity for ribulosebisphosphate (RUBP) regeneration (determined by photosynthetic electron transport capacity), RUBP carboxylation and light harvesting depends on irradiance during leaf growth and development (Evans 1989). Owing to the differences in nitrogen partitioning, maximum rate of photosynthetic electron transport (J_{max}) and maximum rate of carboxylation (V_{max}) may depend differently on leaf nitrogen content (N_s) in leaves developed in different light environments (Niinemets & Tenhunen 1997). This dissimilarity in photosynthesis vs nitrogen relationships has been exploited in several models of canopy photosynthesis (Chen *et al.* 1993; Luo, Field & Mooney 1994).

There is strong evidence indicating that the distribution patterns of foliage photosynthetic properties along a canopy is mainly determined by light distribution (Chazdon & Field 1987; Pearcy & Sims 1994). There are even more data available demonstrating parallel decreases in leaf nitrogen content per area and irradiance with depth in a canopy (DeJong & Doyle 1985; Hirose *et al.* 1988; Ackerly 1992; Evans 1993; Hikosaka, Terashima & Katoh 1994; Niinemets 1995, 1997a). On the basis of these relationships, and the assumption that nitrogen content and photosynthetic parameters are well correlated, several attempts have been made to calculate canopy photosynthesis. On the other hand, theoretical nitrogen distributions, in close agreement with actual ones, can be derived from leaf photosynthesis models assuming that whole-canopy carbon gain or energy consumption are maximized for a given total nitrogen content (Field 1983; Givnish 1986; Hirose & Werger 1987; Hilbert, Larigauderie & Reynolds 1991). Unfortunately, all these models can be employed to describe the actual distribution patterns of nitrogen and photosynthesis within the canopy only when canopy leaf area index as well as the total amount of foliar nitrogen per unit ground area are known. This is because these models lack a clear mechanism responsible for the parallel changes in irradiance, photosynthetic properties and leaf nitrogen within the canopy.

Life form also alters the relationship between the pattern of foliar nitrogen distribution and light environment (Field & Mooney 1986; Hirose & Werger 1994; Kull, Aan & Sõelsepp 1995), and it varies across woody species with different light requirements as well (Chazdon & Field 1987; Hollinger 1992; Kull & Niinemets 1993; Niinemets 1997b). Although the contrasting distribution patterns of photosynthetic parameters within the plant canopies composed of species with widely varying growth forms and light requirements might provide important insight into the nature of the mechanisms responsible for the appearance of observed patterns of distribution of leaf photosynthetic properties and leaf nitrogen within canopies, few data concerning such differences are currently available.

The main aim of this study was to find out how, and to what extent, woody species with contrasting light requirements differ in the distribution of leaf photosynthetic properties and nitrogen along the canopy light gradient. Photosynthetic parameters (maximum photosynthesis at CO₂ saturated conditions, the initial slope of photosynthesis vs CO₂ response curve) and leaf chlorophyll content, which characterize main limiting processes imposed on foliar carbon acquisition, were studied in relation to leaf nitrogen content and light distribution.

Materials and methods

The study was conducted near Tartu, Estonia (58° 15' N and 26° 45' E) in August 1994. The average

annual rainfall is 650 mm, and the average temperature in July is 17.0 °C and in January is – 6.7 °C. The vegetation period usually lasts 175–180 days from mid-April to October.

Three woody species were chosen for investigation. *Populus tremula* L. is a light-demanding tree with a maximal height of about 30 m; *Tilia cordata* Mill. is a shade-tolerant tree with a maximal height of about 25 m, usually growing in the understorey of natural Estonian forests and rarely reaching the overstorey; *Corylus avellana* L. is a shade-tolerant shrub with a maximal height of about 8 m, and is a very common species in the Estonian natural forests. The *P. tremula* and *C. avellana* investigated were growing in the same mixed forest with *Alnus incana* (L.) Moench, *Betula pendula* Roth. and *Fraxinus excelsior* L. *Populus tremula* dominated the overstorey with a height of 15–18 m, while *C. avellana* and *Sorbus aucuparia* L. were in the understorey. The trees of *T. cordata* that were investigated were growing as a small group some km away from the former stand. The soils were a sandy pseudopodsol with pH_{KCl} of 4.0–4.5 in the topsoil in the *P. tremula* and *C. avellana* site, and a loamy brown pseudopodsol with pH_{KCl} of 6.0–6.3 in the *T. cordata* site.

A mobile lift was used for foliar sampling for chemical analyses as well as for photosynthesis measurements. From each sample point in the canopy, eight to 10 leaves were collected for analysis of nitrogen, chlorophyll, leaf area and dry mass, and light conditions were measured immediately.

The light environment of each sample point was assessed with the hemispherical (fish-eye) canopy photographic technique (Percy & Pfitsch 1991; Rich *et al.* 1993). A camera (model OM-2S, Olympus Optical Co., Ltd, Shinjuku-ku, Tokyo, Japan) with an 8 mm fish-eye lens was vertically aligned with the top of the camera facing north. Enlarged images were processed manually to estimate the contribution of diffuse and direct components of photosynthetically active quantum flux density (PPFD). From every photograph, the relative areas of canopy gaps were measured with respect to zenith angle and, assuming a uniformly overcast sky distribution, the relative transmission of diffuse irradiance in the horizontal plane (K_{dif}) was calculated. The potential amount of direct solar radiation (K_{dir}) was estimated with respect to zenith angle along solar tracks within 2 month intervals from the summer solstice. Relative transmission of summary PPFD in the horizontal plane (or the 'global site factor', Rich *et al.* 1993) was calculated as $K_{\text{sum}} = p_{\text{dif}}K_{\text{dif}} + (1 - p_{\text{dif}})K_{\text{dir}}$, where p_{dif} is the proportion of total PPFD above the canopy that is diffuse. According to our estimates (unpublished data), p_{dif} for our study area is 0.67. Actually, the value of K_{sum} is relatively insensitive to the value of p_{dif} insofar as K_{dif} and K_{dir} are highly correlated with each other ($r^2 = 0.77$, $P < 0.001$ for the whole set of data).

Shoots for gas-exchange measurements were cut under water, transported to the laboratory and photosynthesis vs CO_2 response (A/C_i) curves measured immediately. Measurements were made using a modified open system, previously described by Söber & Moldau (1977). A 9.62 cm² leaf area was enclosed in the leaf cuvette. Leaf temperature, measured by an infra-red radiation thermometer, regulated at $26 \pm 1^\circ\text{C}$. CO_2 concentration was monitored with an infra-red gas analyser (Infralyt IV, Junkalor VEB, Dresden, Germany) and water vapour partial pressure was measured with a home-made dry-bulb/wet-bulb micropsychrometer (Oja 1983). Light was supplied by a 75 W halogen lamp with optical condenser. A PPFD of $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ was used. This was sufficient to saturate photosynthesis at high partial pressures of CO_2 and did not result in any photodamage even in the most shade-grown leaves. A two channel gas-mixing system was used to prepare gas mixtures with different CO_2 partial pressures. The first channel, with a CO_2 partial pressure of 32 Pa, was used for stabilizing leaf gas exchange at the beginning of the measurement series and also between measurements at other CO_2 partial pressures. In the second channel, gas mixtures with different CO_2 concentrations were prepared in the sequence of 6, 1, 103 and 160 Pa. The assimilation

chamber was switched into the second channel for only 5 min at each CO_2 partial pressure, after allowing 10–15 min to stabilize photosynthesis at 32 Pa in the first channel between the sequential measurements. Such manipulation avoided possible depletion of the Calvin cycle at low CO_2 concentrations and downregulation of photosynthesis at high CO_2 concentrations owing to the limited utilization of triose phosphates (Sharkey 1985). Leaf gas-exchange parameters were calculated according to von Caemmerer & Farquhar (1981). The initial slope of the A/C_i curve was calculated using the gas-exchange data measured at CO_2 concentrations of 1 and 6 Pa; the maximum photosynthetic rate (P_{max}) is the measured rate at 160 Pa of CO_2 .

Total nitrogen content was estimated with an elemental analyser (CHN-O-Rapid, Foss Heraeus GmbH, Hanau, Germany). Chlorophyll concentration was determined in 80% aqueous acetone (v/v) with a spectrophotometer (SF-16, Lomo, St. Petersburg, Russia) using the equations of Porra, Thompson & Kriedemann (1989). To avoid the conversion of chlorophylls to pheophytins, leaves were ground in the presence of magnesium carbonate during the extraction of chlorophylls. Total non-structural carbohydrate content (TNC, sum of ethanol-soluble carbohydrates and starch) was determined colorimetrically by anthrone reaction using glucose standard as described previously (Niinemets 1995).

Leaf area was measured on a computer graphic tablet and dry mass was determined after drying at 70°C for 48 h.

Differences in linear regressions between species were tested by analysis of covariance (ANCOVA, Sokal & Rohlf 1995).

Results

The CO_2 compensation partial pressure was almost invariable in leaves from different positions in the canopy (Fig. 1a). The overall average CO_2 compensation partial pressure was slightly, but statistically significantly, lower for *T. cordata* than for the other species ($P < 0.05$). The ratio of intercellular to ambient CO_2 concentrations (C_i/C_a ratio) had a slight tendency to increase in the lower part of the canopy (Fig. 1b) and, again, the leaves of *T. cordata* were characterized by the lowest values.

The relationships between K_{sum} and the slope of the A/C_i curve or P_{max} were species dependent (Fig. 2a,c). These parameters were always highest in *P. tremula* than in the other species at the same PPFD. Both the slope of the A/C_i curve and P_{max} were better correlated with leaf nitrogen content than with K_{sum} (Fig. 2b,d). Although the relationships did not differ qualitatively among the species, the slopes were species dependent (Table 1). The slope was largest in *C. avellana* and smallest in *T. cordata*. For the pooled data, the linear regression equations between N_s and the slope of the A/C_i curve or P_{max} had negative

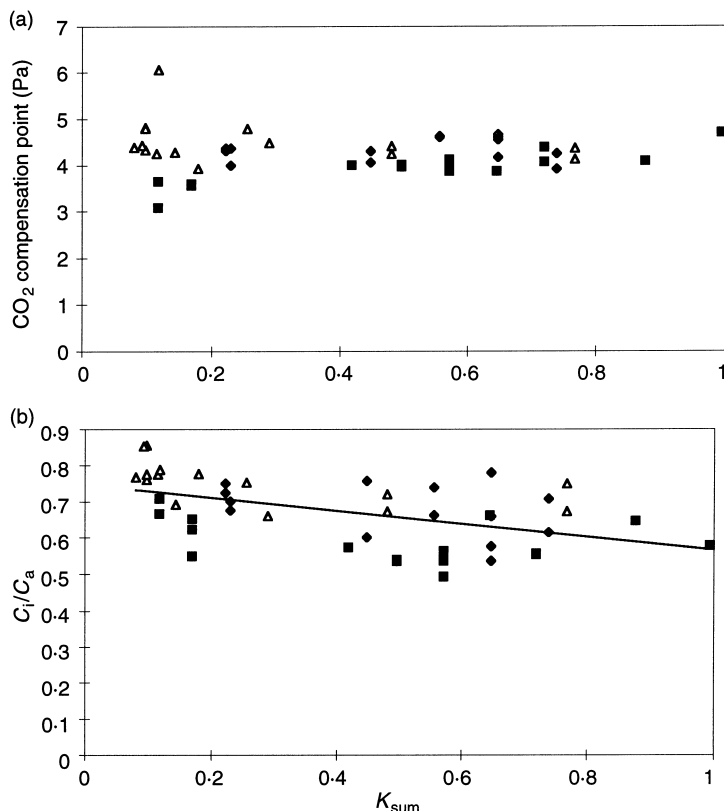


Fig. 1. (a) CO_2 compensation partial pressure and (b) the ratio of internal CO_2 partial pressure to ambient (C_i/C_a), measured at an ambient CO_2 of 32 Pa, in leaves from different light environments in the canopy characterized by relative transmission of irradiance in photosynthetically active spectral region (K_{sum}). Parameters of the regression line on (b): $C_i/C_a = -0.182K_{\text{sum}} + 0.747$ ($r^2 = 0.26$, $P < 0.01$). Species: *Populus tremula* (◆), *Tilia cordata* (■) and *Corylus avellana* (△).

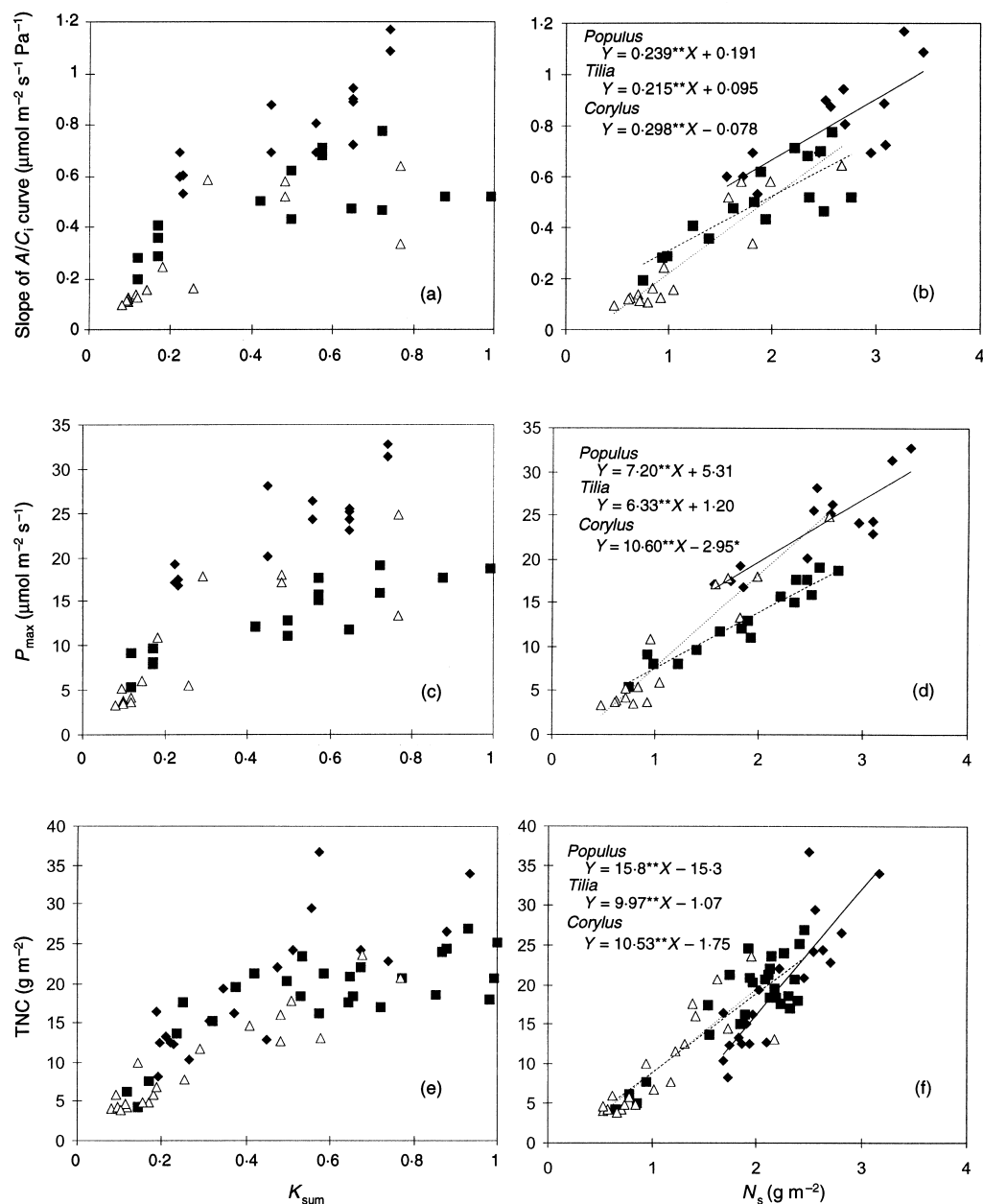


Fig. 2. (a,b) The initial slope, (c,d) plateau value (P_{max}) of the A/C_i curve, and (e,f) leaf TNC content as functions of the light environment at the leaf, K_{sum} (a,c,e) or leaf nitrogen content per area, N_s (b,d,f). Species: *Populus tremula* (\blacklozenge , solid line), *Tilia cordata* (\blacksquare , broken line) and *Corylus avellana* (\triangle , dotted line). Significance of the regression coefficients is denoted by asterisks: $^{**}P < 0.01$; $^{*}P < 0.05$. Regression equations for the pooled data: A/C_i slope $= 0.309^{**}N_s - 0.056$; $P_{max} = 9.02^{**}N_s - 1.52$; $TCN = 117^{**}N_s - 185^{**}$. The results of the statistical comparison of the regression lines are given in Table 1.

intercepts, demonstrating that photosynthesis capacity per nitrogen (an estimate of photosynthetic nitrogen-use efficiency) increases with increasing N_s . Both the slope of the A/C_i curve and P_{max} had similar dependence on leaf nitrogen content clearly indicating proportionality between these two photosynthetic parameters (Fig. 3).

The dependencies of leaf TNC content on leaf nitrogen or on K_{sum} were similar to those with photosynthetic parameters (Fig. 2e,f). With increasing PPFD leaf TNC content tended to saturate but the relationship between TNC and leaf nitrogen content was more or less linear.

Because leaf photosynthetic parameters were almost linearly related to leaf nitrogen content, we suggest that the reason why the distributions of the photosynthetic parameters in the canopy were strongly affected by species lies in the species differences in nitrogen distribution pattern (Fig. 4) rather than in nitrogen partitioning at the same N_s (Fig. 2). The differences in the N_s vs K_{sum} relationship are both quantitative and qualitative. The leaves of *P. tremula* always contained more nitrogen (at the same PPFD) than the other species and the shape of this relationship also differed between species. We tried to choose sample points to include the most shady conditions in the canopy where leaves

were present. Thus, the lower limit of the leaves was at the K_{sum} value of about 0.2 for *P. tremula*, about 0.1 for *T. cordata* and about 0.08 for *C. avellana* (Fig. 4).

The distribution of leaf chlorophyll ($a + b$) in the canopy differed qualitatively from the light relationships of the photosynthetic parameters (cf. Figs 2 and 5). The linear regression between total chlorophyll and nitrogen content has a significant intercept on the chlorophyll axis in all studied species and the data for different species are closely grouped (Fig. 5). However, these differences between species disappear when the ratio of total chlorophyll to leaf nitrogen is plotted against the value of K_{sum} (Fig. 6a). It appears that the amount of chlorophyll per unit of leaf nitrogen increases hyperbolically at low values of relative PPFD. This increase is accompanied by a slight decrease in chlorophyll a to chlorophyll b ratio (Fig. 6b).

Discussion

The most remarkable of the detected interspecific differences in photosynthetic parameters was the occurrence of a greater CO_2 compensation partial

pressure and a lower ratio of C_i/C_a at the normal ambient CO_2 concentration in *T. cordata*. We do not know whether this difference is attributable to species or to site.

The ratio C_i/C_a constantly decreases with height in the canopies (Garten & Taylor 1992). Although the detached shoots were used in the same PPFD, CO_2 and humidity conditions, the same relationship was also observed here. Statistically different C_i/C_a ratios suggest that stomatal regulation may differ between the species.

Despite small differences in the values of CO_2 compensation partial pressure and C_i/C_a ratio, the photosynthesis was similar in different species when evaluated on leaf nitrogen basis. The slope of the A/C_i response curve close to the CO_2 compensation partial pressure is proportional to the maximal rate of carboxylation (V_{max}) and photosynthesis at high CO_2 partial pressure provides an estimate of the electron transport capacity (J_{max}) (von Caemmerer & Farquhar 1981). Although the data points from different species gave slightly variable regression parameters for the regressions between N_s and P_{max} (Table 1), these differences are not large (Fig. 2b,d). The slope of the A/C_i curve and P_{max} changed simultaneously with changing leaf nitrogen, such that the ratio of these two parameters was almost constant (Fig. 3). In general the capacities for RUBP carboxylation and regeneration are in balance (Wullschlegel 1993).

Although total leaf chlorophyll content was also correlated with leaf nitrogen content, this relationship differed from that of the other investigated photosynthetic parameters. A linear approximation gives a large intercept on the chlorophyll axis at zero leaf nitrogen and this intercept differs remarkably between the studied species (Fig. 5). Because it is likely that there is no chlorophyll without any nitrogen, we used an hyperbolic function to fit the pooled data of the chlorophyll vs N_s relationship. The differences between the species disappeared when, in addition to leaf nitrogen content, the variability in light environment was also accounted for (Fig. 6a). Thus, we conclude that the fraction of leaf nitrogen in light-harvesting complexes has a direct dependence on leaf light environment. A relative increase in the content of light-harvesting proteins at low PPFD may be related to the requirements to maintain the high value of quantum yield of photosynthesis for an incident irradiance at low light. In his classic work, Gabrielsen (1948) showed that the apparent quantum yield declines if chlorophyll content drops below $\approx 220 \mu\text{mol m}^{-2}$ and this is the lower limit of chlorophyll content in the leaves studied here.

Evans (1989) estimated changes in nitrogen partitioning between different parts of the photosynthetic apparatus with respect to changing PPFD. He assumed that foliar nitrogen investment in electron transport capacity changes in proportion to leaf chlorophyll content. Our study demonstrates that it is

Table 1. Comparison of the linear regressions of photosynthetic parameters vs leaf nitrogen content between the species: analysis of covariance (ANCOVA)

Source of variation	df	SS	MS	F
1. P_{max} on N_s				
Among slopes	2	58.96	29.48	6.73**
Within regressions	39	170.76	4.38	
2. Slope of A/C_i curve on N_s				
Among slopes	2	0.000222	0.000111	1.03
Within regressions	39	0.004197	0.000108	
3. Leaf TNC on N_s				
Among slopes	2	86.53	43.26	3.69*
Within regressions	39	715.45	11.73	
4. Total chlorophyll on N_s				
Among slopes	2	8206	4103	1.50
Within regressions	39	167119	2740	

* $P < 0.05$; ** $P < 0.01$

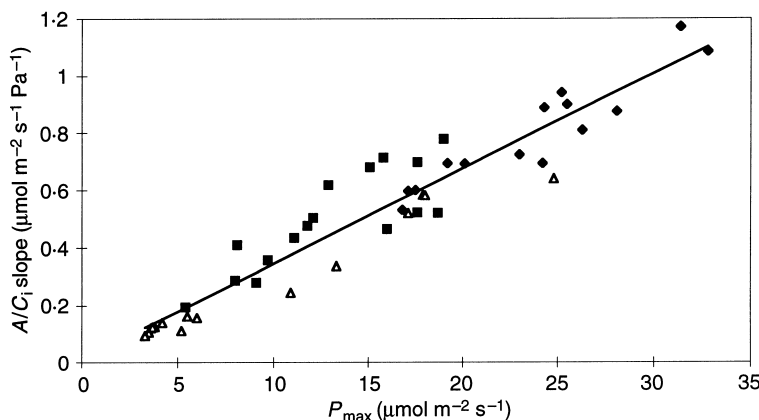


Fig. 3. The correlation between P_{max} and the slope of the A/C_i curve. Parameters of the regression line: slope = $0.0332P_{\text{max}} + 0.0121$ ($r^2 = 0.91$, $P < 0.001$). Symbols as Fig. 1.

more likely that only the amount of light-harvesting apparatus changes along the canopy light gradient. Amount of chlorophyll per nitrogen increases with decreasing PPFD (Fig. 6a), but electron transport capacity per leaf nitrogen remains almost constant. This finding is in accordance with the data of Pons & Percy (1994), who showed that when growth PPFD was decreased, the partitioning of nitrogen increased only relative to light-harvesting complex whereas nitrogen partitioning to the Calvin cycle and photosynthetic electron transport chain proteins decreased. Evidently, changes in nitrogen partitioning between different parts of the photosynthetic apparatus are not as large as proposed by Evans (1989) and this shift in partitioning seems to be particularly important at low PPFD to maintain the apparent quantum yield. In the model developed by Hikosaka & Terashima (1995) nitrogen is partitioned between five functional groups of photosynthetic proteins. Our data support their conclusion that under shade conditions the amount of nitrogen allocated to chlorophyll-protein complexes increases.

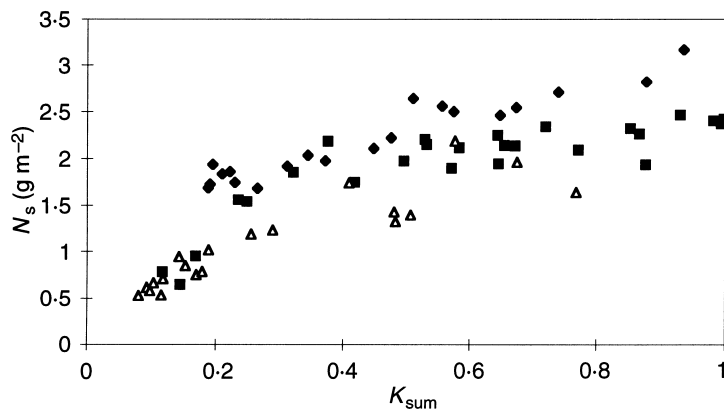


Fig. 4. Leaf nitrogen content as a function of K_{sum} . Symbols as Fig. 1.

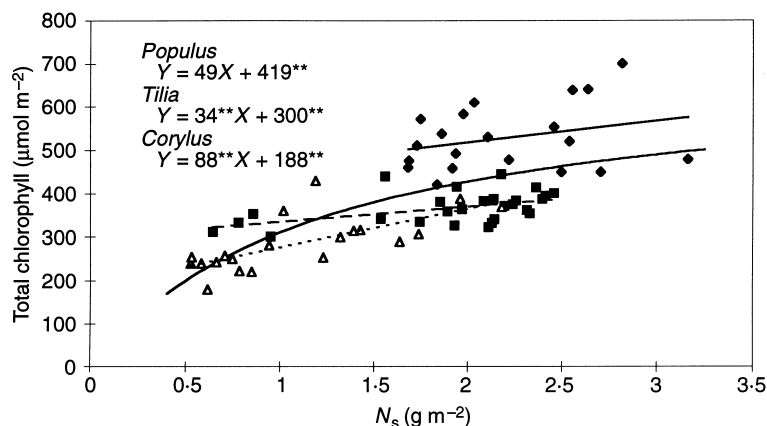


Fig. 5. Leaf total chlorophyll content as a function of leaf nitrogen content, N_s . The curve fitted through the pooled data is a hyperbola: $\text{Chl } (a + b) = 689N_s / (1.22 + N_s)$ ($r^2 = 0.46$, $P < 0.001$). Symbols as Fig. 2.

In general, leaf nitrogen content per area follows the light distribution along the canopy, as has been shown in a vast number of studies (cf. Introduction). But the interspecific differences in the distribution pattern of N_s are evident in the current study (Fig. 4), especially between *P. tremula* and *C. avellana* which were growing together in the same canopy. At the same light environment, the leaves of the light-demanding *P. tremula* always contained more nitrogen per area and, consequently, more photosynthetic apparatus than the leaves of the shade-tolerant *C. avellana*. The relationship between nitrogen and K_{sum} (Fig. 4) was almost linear in *P. tremula* but clearly declined from linear in the case of *C. avellana* and *T. cordata*. In several earlier studies, N_s vs PPFD relationship has been fitted with a straight line in trees (DeJong & Doyle 1985; Kull & Niinemets 1993; Niinemets 1995, 1997a,b), whereas in many herbaceous canopies and in vines this relationship has frequently been fitted with an exponential function (Hirose *et al.* 1988; Hikosaka *et al.* 1994; Hirose & Werger 1994). Thus, it seems that the shape of this relationship is growth-form dependent.

In our earlier studies, we have used the intercept of the N_s -PPFD relationship on the nitrogen axis as an estimate of the non-photosynthetic nitrogen in the leaf (Kull & Jarvis 1995). On the bases of the current study it becomes clear that such an estimate might be erroneous because this intercept is much larger than the estimate of non-photosynthetic nitrogen made on the basis of the relationship between P_{max} or the slope of the A/C_i curve and N_s (Fig. 2). Thus, we may conclude that even the lowest leaves in a canopy contain a considerable amount of photosynthetic apparatus, especially in a light-demanding species such as *P. tremula*.

TNC level in the mature leaf reflects the balance between carbon acquisition and export (Chapin, Schulze & Mooney 1990). Because carbon translocation also occurs when it is dark (Geiger & Servaites 1994), this balance will be achieved at higher values of TNC at high rather than at low intensities of photosynthesis. Thus, TNC can be used as an estimate of *in situ* photosynthesis integral and according to our data N_s is a better predictor of the photosynthetic production than leaf light environment (Fig. 2e,f). This may be explained by the existence of a dual link between the photosynthesis and N_s . From one side, the amount of leaf nitrogen reflects the content of photosynthetic enzymes, but from the other side, acquisition of this nitrogen consumes energy captured in photosynthesis.

Two important questions remain from this study. First, what causes the actual distribution pattern of nitrogen, as well as photosynthetic apparatus in a canopy, and second, why is this pattern, as well as the lower limit of the foliage, different in different species. Nitrogen distribution in canopies has been found to be optimal with respect to canopy carbon

gain (e.g. Field 1983; Hirose & Werger 1987). It is always likely that some function exists that is maximized by the canopy but such an approach usually does not involve the mechanism that is responsible for the particular distribution of N_s and photosynthetic properties. Chen *et al.* (1993) proposed the 'coordination theory', which is based on the assumption that the maximal rates of carboxylation, V_{\max} and electron transport capacity, J_{\max} , have different dependencies on N_s , and showed that real nitrogen distributions in canopies can be described on this basis. In our study there is no evidence that the basic assumption of the 'coordination theory' holds in reality. Moreover, we conclude that the reason for the particular nitrogen and photosynthesis profiles in a canopy lays not in photosynthetic apparatus, which is fairly conservative among the studied species, but some other species properties, e.g. assimilate costs related to nitrogen acquisition and construction of unit surface area with similar biomass investment in leaves. Previous studies have demonstrated that shade-tolerant species tend to possess lower leaf dry mass per area (LMA) (Kull & Niinemets 1993; Niinemets & Kull 1994) than intolerant species. Given that N_s is the product of LMA and leaf nitrogen per dry mass, shade-tolerant species require greater nitrogen concentrations to attain the same N_s .

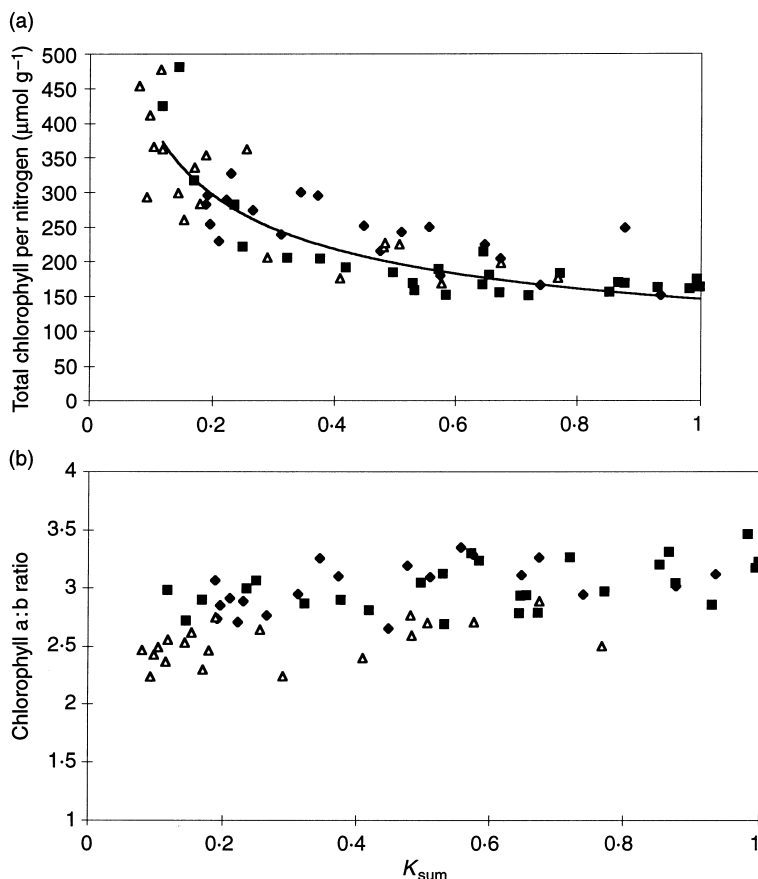


Fig. 6. Dependencies of (a) the ratio of total chlorophyll to leaf nitrogen (Chl/N_s) and (b) ratio of chlorophyll *a* to chlorophyll *b* on K_{sum} . Parameters of the fitted line on (a): $\text{Chl}/N_s = 150K_{\text{sum}}^{-0.439}$ ($r^2 = 0.81$, $P < 0.001$). Symbols as Fig. 1.

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