

Seasonal changes in leaf nitrogen pools in two *Salix* species

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Summary Leaf nitrogen distribution pattern was studied four times during the growing season in a 2-year-old *Salix viminalis* L. and *Salix dasyclados* Wimm. plantation in Estonia. We measured the vertical distributions of leaf nitrogen concentration, dry mass, leaf area and light environment (as fractional transmission of diffuse irradiance, a_d) in the canopy. The light-independent nitrogen pool was evaluated as the intercept of the leaf nitrogen concentration versus a_d relationship, and the nondegradable nitrogen pool was evaluated as the nitrogen remaining in abscised leaves. A strong vertical gradient of mass-based leaf nitrogen concentration was detected at the beginning of the growing season, and decreased steadily during canopy development. This decline had at least three causes: (1) the amount of nitrogen in the foliage was larger at the beginning of the growing season than at the end of the growing season, probably because of pre-existing root systems; (2) with increasing leaf area index (LAI) during the growing season, the proportion of leaf nitrogen in total canopy nitrogen that could be redistributed (light-dependent nitrogen pool) decreased; and (3) the photosynthetic photon flux density gradient inside the canopy changed during the season, most probably because of changes in leaf area and leaf angle distributions. Total canopy nitrogen increased almost proportionally to LAI, whereas the light-dependent nitrogen pool had a maximum in August. Also, the proportion of the light-dependent nitrogen pool in the total canopy nitrogen decreased steadily from 65.2% in June to 17.2% in September in *S. dasyclados* and from 63.3 to 15.1% in *S. viminalis*. The degradable nitrogen pool was always bigger than the light-dependent nitrogen pool.

Keywords: acclimation, leaf nitrogen concentration, light extinction, light interception, willow.

Introduction

Inside a plant canopy, the vertical distribution of foliar nitrogen parallels the distribution of photosynthetic photon flux density (PPFD). Parallel changes in nitrogen and PPFD distribution profiles have been demonstrated in herbaceous (Lemaire et al. 1991, Evans 1993, Hirose and Werger 1994) and woody canopies (Field 1983, DeJong and Doyle 1985, Ellsworth and Reich 1993, Kull and Niinemets 1993). This pattern of nitrogen distribution has been explained in terms of maximizing total

canopy photosynthesis (Field 1983), whole-plant carbon gain (Hirose and Werger 1987a, Hilbert et al. 1991), or energy consumption (Givnish 1988). All of these explanations are based on the finding that leaf nitrogen content and photosynthetic properties are closely correlated (Field and Mooney 1986, Evans 1989). However, experimental evidence shows that actual nitrogen distribution differs slightly from the theoretical optimal distribution (Field 1983, Hirose and Werger 1987a). This discrepancy can be accounted for by the inadequate optimization scheme used and by the existence of several nitrogen pools in leaves (Kull and Jarvis 1995). Charles-Edwards et al. (1987) have divided leaf nitrogen into two pools, degradable and nondegradable, and associated the degradable nitrogen pool with the photosynthetic apparatus of the leaf. However, biochemical distinction between these nitrogen pools can be difficult and problematic. When calculating optimal nitrogen distribution it is important to consider that leaves have several physiological functions besides photosynthesis in which nitrogen is involved, and that not all of the nitrogen in foliage may be distributed similarly to PPFD distribution. The leaf nitrogen–PPFD relationship usually has a positive intercept on the nitrogen axis (DeJong and Doyle 1985, Hirose and Werger 1987b, Percy and Sims 1994). We define the leaf nitrogen associated with this intercept as the light-independent nitrogen pool.

In tree canopies where both buds and leaves develop at different PPFDs, there is a strong relationship between leaf nitrogen and PPFD, and there is also a possibility of distinguishing between light-dependent and light-independent nitrogen pools, if leaf nitrogen is evaluated on a leaf area basis. In such a canopy, area-based nitrogen content changes along the vertical gradient mainly as a result of changes in the leaf mass to area ratio (LMA), whereas the nitrogen dry mass proportion may increase, decrease or remain constant (e.g., Ackerly 1992, Ellsworth and Reich 1993, Kull and Niinemets 1993, Reich and Walters 1994). A completely different situation occurs in herbaceous dicotyledonous canopies and in young developing tree canopies where all new leaves are formed at the top of the canopy in full sunlight and become gradually shaded during canopy development. In this situation, retranslocation of leaf nitrogen occurs together with the acclimation of leaves to changing PPFD (Pons and Percy 1994).

In some circumstances, nitrogen retranslocation may serve as the main nitrogen source for new foliage (Jonasson and Chapin 1985, Lemaire et al. 1991).

Data on changes in leaf nitrogen distribution in a developing tree canopy are scarce. Kull et al. (1995) compared different tree canopies and showed that total foliar nitrogen increased more rapidly with increasing canopy leaf area index (LAI) than did light interception. Based on the assumptions that the cost of acquiring a unit of nitrogen is constant in units of photosynthesis, and that photosynthesis is proportional to intercepted light, Kull and Jarvis (1995) hypothesized that there exists a critical value of the ratio of total canopy nitrogen to intercepted PPFD that cannot be exceeded.

The purpose of this study was to follow leaf nitrogen and PPFD distributions in a developing tree canopy during the growing season, and to evaluate the possibility of identifying the structural nitrogen pool based on the leaf nitrogen–PPFD relationship. Another objective of the study was to evaluate nitrogen redistribution during leaf acclimation to PPFD in the canopy, and to determine how closely changes in total foliar nitrogen are correlated with the amount of PPFD intercepted by the canopy.

Materials and methods

The study was conducted in 1994 at the Kambja energy forest plantation which was established in May 1993 under the auspices of the Estonian–Swedish Energy Forest Project. The plantation is located in southern Estonia, at 58°15' N and 26°45' E, on well decomposed organic soil. The basic soil parameters (in the upper 20-cm layer) include: a pH (KCl) of 5.7, a total nitrogen content of 1.8%, and phosphorus and potassium contents (estimated as soluble in 0.2 N HCl) of 5.7 and 13.4 mg/100 g soil, respectively. No additional fertilizer was applied. Mean annual rainfall in this area is 650 mm, the mean temperature in July is 17.0 °C, and in January it is –6.7 °C. The vegetation period usually lasts 175–180 days from mid-April to October.

Two willow clones originating from the Swedish Energy Forestry Project, *Salix dasyclados* Wimm., Clone 81090, and *Salix viminalis* L., Clone 78183, were studied. The plantation was established from cuttings at a density of 20,000 plants per hectare (double rows, distance between rows 0.75 and 1.25 m, distance between plants in a row 0.5 m). Weed control was performed mechanically three times in 1993 and once in May 1994. In March 1994, the first-year shoots were cut at a height of 5 cm above the ground to promote denser sprouting. Thus, the shoots investigated in the present study were of current-year growth on 1-year-old roots. The mean number of shoots without secondary branches that developed from each root system was seven in *S. dasyclados* and 12 in *S. viminalis*.

Measurements were made four times during summer 1994: on June 15, July 15, August 15 and September 9 before the first autumn frosts. On every measurement occasion, eight randomly chosen shoots per clone were studied. Each shoot was divided into three to five vertical sections depending on shoot height. In every section, one leaf was selected for detailed

investigation. A “fish-eye” photograph was taken from the position of attachment of every marked leaf; leaf height from the ground and the sequential number from the top were determined. The leaves were removed and dried (at 70 °C for 48 h) and dry mass and leaf area were measured. Leaf area was determined with a computer scanner. After leaf area measurements, the same leaves were sampled for nitrogen analysis. For each species and harvest date, all investigated shoots were combined and total foliar and stem dry masses were determined. Starting in July, recently abscised leaves were also collected for nitrogen analysis.

Light environment at the leaf surface was determined by using hemispherical “fish-eye” photographs (Anderson 1964). From each photograph, canopy gap fraction distribution was determined with respect to the zenith angle. Fractional transmission of diffuse irradiance on the horizontal plane (a_d) was calculated as:

$$a_d = \frac{\pi}{9} \sum_{\alpha=5^\circ, 15^\circ, \dots}^{85^\circ} g_\alpha \sin \alpha \cos \alpha, \quad (1)$$

where g_α is the gap fraction within a 10° zenith angle interval ($\alpha - 5^\circ, \alpha + 5^\circ$). The value of a_d was used as the measure of relative PPFD on the leaf. No correction for direct sunlight was made. Canopy relative light interception was estimated from the mean a_d value of the lowest leaves of the eight shoots.

Total leaf area and the foliar nitrogen of shoots were calculated with data obtained from the sampled leaves and the number of leaves per shoot. To obtain the canopy LAI and total canopy nitrogen per ground area (N_g), data on single shoots were multiplied by shoot density and the mean value was calculated.

Leaf nitrogen was determined with the standard Kjeldahl method by using a Tecator Kjeltec Auto 1030 analyzer (Tecator, Hogänäs, Sweden). The light-independent nitrogen pool in a leaf was determined as the intercept of the a_d versus leaf nitrogen regression line and was assumed to be the same for all leaves in the canopy at the time of the measurements. The total canopy light-dependent nitrogen pool was calculated as the difference between N_g and the total canopy light-independent nitrogen pool. The nondegradable nitrogen pool in a leaf was taken to be equal to the nitrogen concentration in abscised leaves, and this pool was assumed to be the same for all leaves in the canopy.

Results

A distinct vertical gradient occurred in mass-based leaf nitrogen concentration in both willow species (Figure 1). The gradient was especially steep at the beginning of the growing season with nitrogen concentration differing more than two-fold between the upper and lower leaves. During the season this difference gradually decreased. The same pattern was observed for the mass-based leaf nitrogen concentration versus a_d relationship (Figure 2). The slope of this relationship declined considerably during canopy development (Table 1).

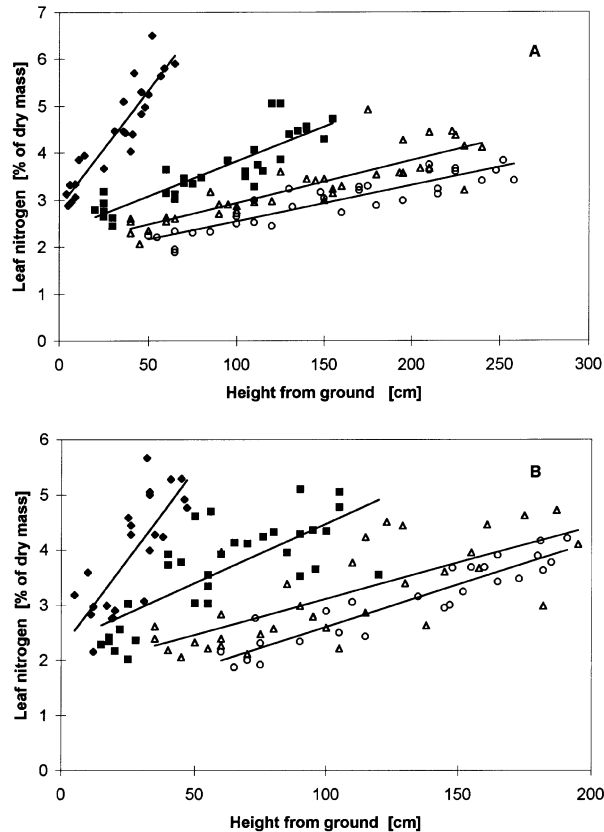


Figure 1. Seasonal changes in the vertical distribution of leaf nitrogen concentration. A: *S. dasyclados*; and B: *S. viminalis*; \blacklozenge = June 15; \blacksquare = July 15; \triangle = August 15; and \circ = September 9.

Table 1 also presents mean nitrogen concentrations of the lowest leaves in the canopy and the abscised leaves.

No obvious vertical gradient was detected in LMA (data not shown). In *S. dasyclados*, LMA increased during the growing season (Table 2), and the increase occurred almost simultaneously in old leaves at the bottom of the canopy and in young developing leaves at the top of the canopy. A steady increase in fully developed leaf size was the most pronounced change during the season (Figure 3). In *S. dasyclados*, the relationship between leaf height and the dry mass of fully developed leaves was almost linear.

The seasonal increase in total foliage nitrogen was almost proportional to the increase in total LAI, hence the ratio N_g/LAI changed little during the season, although it exhibited a maximum at the beginning of the season (Table 2). Both total canopy nitrogen and LAI increased simultaneously during the vegetation period. A comparison of the acquisition of the two main resources, nitrogen and light energy, revealed that the young developing canopy intercepted light per unit of foliar nitrogen very efficiently; however, the amount of foliar nitrogen increased up to the end of the season, whereas canopy light interception had a maximum in August (Figure 4). This difference in the dynamics of light interception and LAI was mainly caused by temporal changes in the canopy light extinction pattern. Although LAI increased during the season, the efficiency of a mean leaf area unit to absorb light decreased (Figure 5). The scattering of data points in Figure 5 was caused mainly by the calculation of LAI from the leaf area data of the shoot, without considering spatial variability in shoot size.

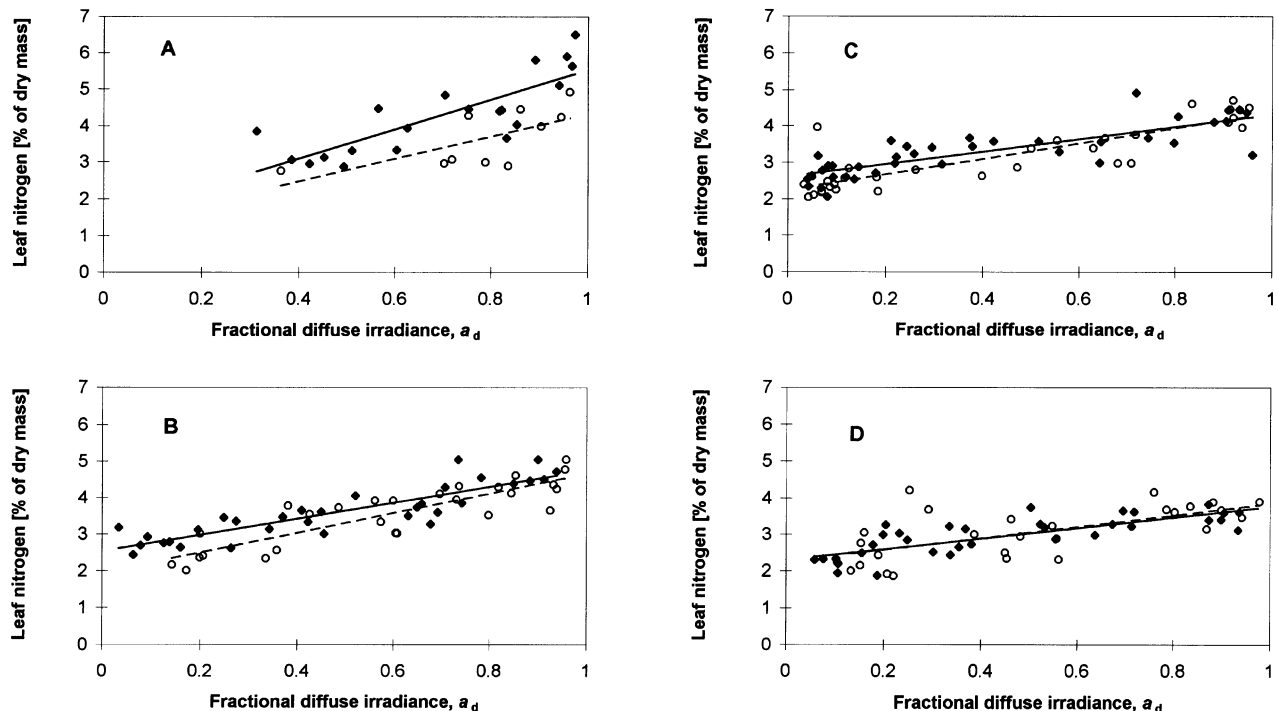


Figure 2. Relationship between leaf nitrogen concentration and fractional diffuse irradiance (a_d) in *S. dasyclados* (\blacklozenge , and solid line) and *S. viminalis* (\circ , and dashed line). A: June 15; B: July 15; C: August 15; and D: September 9. Regression parameters are given in Table 1.

Table 1. Seasonal changes in basic leaf nitrogen parameters: linear regression parameters for relationship of leaf mass-based nitrogen concentration versus fractional transmission of diffuse irradiance (a_d), and mass-based leaf nitrogen concentration (%) in the lowest attached and abscised leaves.

Species	Date	Leaf N concentration versus a_d regression parameters			Leaf N concentration (%)	
		Slope \pm SE	Intercept \pm SE	R^2 %	Lowest leaves	Abscised leaves
<i>Salix dasyclados</i>	June 15	4.06 \pm 0.68	1.47 \pm 0.50	66.1	3.31 \pm 0.14	–
	July 15	2.20 \pm 0.22	2.53 \pm 0.12	76.9	2.75 \pm 0.08	1.05 \pm 0.04
	August 15	1.71 \pm 0.20	2.60 \pm 0.10	66.7	2.45 \pm 0.07	1.32 \pm 0.06
	September 9	1.46 \pm 0.20	2.30 \pm 0.10	63.0	2.17 \pm 0.07	1.30 \pm 0.07
<i>Salix viminalis</i>	June 15	3.08 \pm 1.21	1.25 \pm 0.97	44.9	2.89 \pm 0.14	–
	July 15	2.69 \pm 0.31	1.96 \pm 0.20	75.0	2.39 \pm 0.11	1.43 \pm 0.18
	August 15	2.13 \pm 0.21	2.24 \pm 0.12	76.5	2.27 \pm 0.06	1.68 \pm 0.06
	September 9	1.58 \pm 0.39	2.26 \pm 0.23	40.8	2.14 \pm 0.16	1.89 \pm 0.07

Table 2. Leaf, nitrogen and light parameters calculated for the whole canopy: a_d = fractional transmission of diffuse irradiance; LMA = leaf mass to area ratio; N_g = total canopy N per ground area; LAI = leaf area index.

Species	Date	a_d at the lowest leaves	LMA (g m^{-2})	N_g (g m^{-2})	LAI	N_g/LAI (g m^{-2})
<i>Salix dasyclados</i>	June 15	0.48 \pm 0.04	65.9 \pm 1.0	0.45 \pm 0.06	0.16 \pm 0.02	2.78
	July 15	0.12 \pm 0.03	62.3 \pm 1.2	2.24 \pm 0.15	1.09 \pm 0.08	2.06
	August 15	0.08 \pm 0.01	74.8 \pm 2.1	6.16 \pm 0.72	2.41 \pm 0.19	2.55
	September 9	0.11 \pm 0.02	91.1 \pm 2.0	6.49 \pm 0.68	2.57 \pm 0.26	2.53
<i>Salix viminalis</i>	June 15	0.58 \pm 0.21	67.5 \pm 2.2	0.28 \pm 0.04	0.12 \pm 0.02	2.29
	July 15	0.23 \pm 0.03	62.4 \pm 1.4	2.00 \pm 0.27	0.94 \pm 0.14	2.13
	August 15	0.06 \pm 0.01	73.0 \pm 1.3	4.33 \pm 0.57	1.94 \pm 0.25	2.23
	September 9	0.17 \pm 0.01	62.7 \pm 1.5	5.03 \pm 0.56	3.01 \pm 0.20	1.67

The calculated values of light-dependent and degradable canopy nitrogen pools are given in Table 3. The size of the degradable nitrogen pool was not calculated for June because there were no abscised leaves at that time. In all cases, the degradable nitrogen pool was bigger than the light-dependent nitrogen pool, because the nitrogen concentration of the abscised leaves was always lower than the intercept value of the nitrogen versus a_d relationship (Table 1). The relative proportion of both light-dependent and degradable pools of nitrogen in the total canopy nitrogen decreased considerably during canopy development (Table 3). Moreover, although total foliar nitrogen increased monotonically with increasing LAI, the absolute amount of light-dependent nitrogen reached a maximum at LAI values of 2–2.5 (Figure 6). Hence, the light-dependent nitrogen pool changed in parallel with canopy light interception with a maximum in August. The absolute value of the degradable nitrogen pool of the canopy also had a distinct maximum in August.

Discussion

During leaf canopy development in two *Salix* species, several changes occurred in foliage parameters, light interception and nitrogen distribution. Although abscision of the lower leaves began in July, total canopy LAI increased until September. Total foliar nitrogen increased almost in proportion to leaf

area. The relatively high total nitrogen to LAI ratio in June (Table 2) can be accounted for by the development of shoots from the existing root systems. At the beginning of the growing season, the amount of nitrogen available to leaves was probably high as a result of both nitrogen stored in roots and the relatively high root to shoot ratio. The vertical nitrogen gradient, which changed markedly during the season, appeared as a result of changes in mass-based leaf nitrogen concentration, because LMA changed little. In contrast, in a closed forest canopy where leaves within the canopy develop under different PPFDs, a vertical nitrogen gradient appears mainly because of changes in LMA (Kull and Niinemets 1993).

When the nitrogen gradient was defined as a change in mass-based leaf nitrogen concentration per plant height unit (Figure 1), it decreased with increasing LAI and canopy closure. This result contrasts with studies where the opposite pattern has been shown (DeJong and Doyle 1985, Hirose et al. 1988, Schieving et al. 1992). In the present study, we identified several causes leading to decreases in the nitrogen gradient over the growing season. The steepness of the nitrogen gradient depends on the portion of the total nitrogen pool to be distributed in relation to PPFD, provided that the PPFD gradient is the sole predictor of nitrogen distribution inside the canopy. During the vegetation period, growth of leaf area and the light-independent nitrogen pool, as well as the uptake of nitrogen, were related in a way that caused a steady decline in

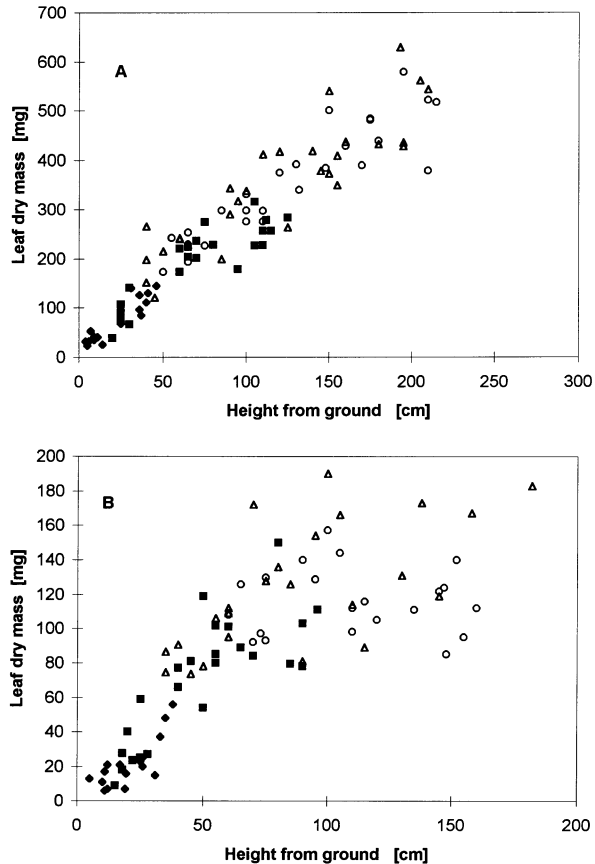


Figure 3. Seasonal changes in the dry mass of sampled leaves as a function of leaf attachment height. Only data for fully developed leaves are shown. A: *S. dasyclados*; and B: *S. viminalis*; \blacklozenge = June 15; \blacksquare = July 15; \triangle = August 15; and \circ = September 9.

the proportion of total canopy nitrogen to be distributed according to PPFD. In addition to changes in the size of the relocatable nitrogen pool, the PPFD gradient and its distribution pattern also changed during the season. Substantial clumping as well as the relatively small size and mainly horizontal position of leaves in the young developing plants resulted in a strong PPFD gradient in June. Later in the season, leaf area distribution and probably also leaf angle distribution became more random as a result of the bigger leaves, and the PPFD absorption efficiency of the unit leaf area declined. This decline in the PPFD gradient was an additional cause of the decrease in canopy nitrogen gradient.

The light-independent nitrogen pool in leaves, measured as the intercept of the leaf nitrogen versus a_d relationship (Table 1), approximated the amount of nitrogen measured in the lowest leaves. Data from June were the only exception, but in June the lowest leaves were relatively well exposed to light. The nondegradable nitrogen pool, measured as nitrogen in recently abscised leaves, was substantially smaller than the light-independent nitrogen pool, especially in *Salix dasyclados*. When considering optimal nitrogen distribution, it is important to know whether photosynthetic nitrogen is more closely related to the light-dependent or to the degradable

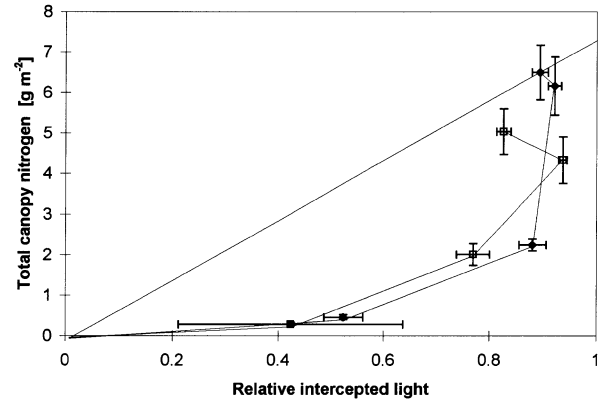


Figure 4. Seasonal changes in relationship between total canopy nitrogen per ground area unit and canopy relative light interception in *S. dasyclados* (\blacklozenge) and *S. viminalis* (\square). Bars show standard errors of the estimate ($n = 8$). The straight line denotes the maximum ratio of total canopy nitrogen/intercepted light in the studied canopies.

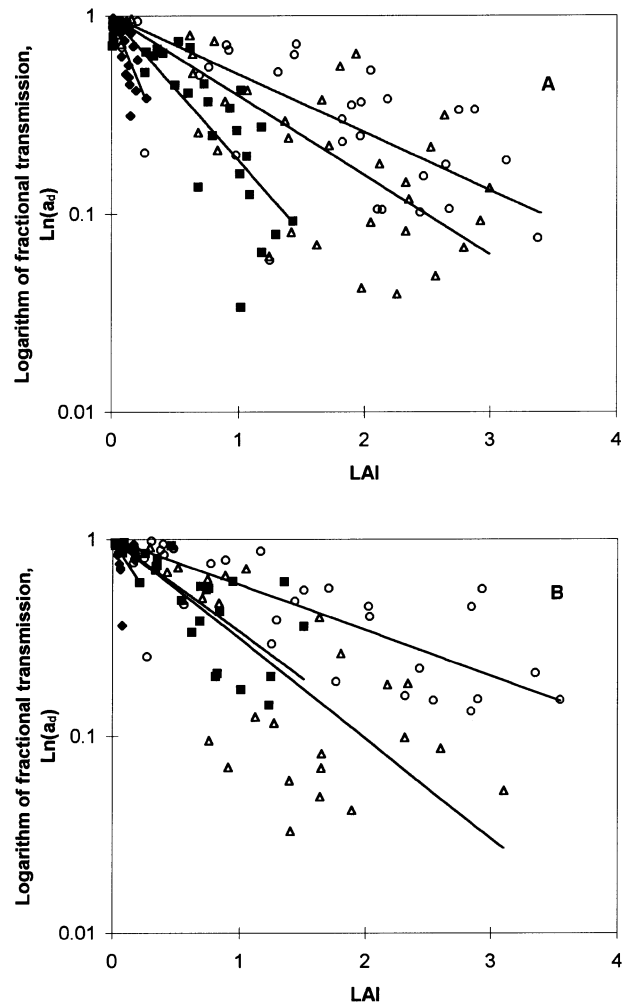


Figure 5. Seasonal changes in relationship between the leaf area index (LAI) and fractional transmission of diffuse radiation. A: *S. dasyclados*; and B: *S. viminalis*; \blacklozenge = June 15; \blacksquare = July 15; \triangle = August 15; and \circ = September 9. Data are fitted with exponential trendlines.

Table 3. Seasonal changes in light-dependent and degradable nitrogen pools calculated per ground area unit.

Species	Date	Light-dependent N pool		Degradable N pool	
		g m^{-2}	% of total canopy N	g m^{-2}	% of total canopy N
<i>Salix dasyclados</i>	June 15	0.30	65.2	—	—
	July 15	0.53	23.6	1.53	68.3
	August 15	1.47	23.9	3.78	61.4
	September 9	1.11	17.2	3.45	53.2
<i>Salix viminalis</i>	June 15	0.18	63.3	—	—
	July 15	0.85	42.6	1.16	58.0
	August 15	1.16	26.7	1.95	45.0
	September 9	0.76	15.1	1.46	29.0

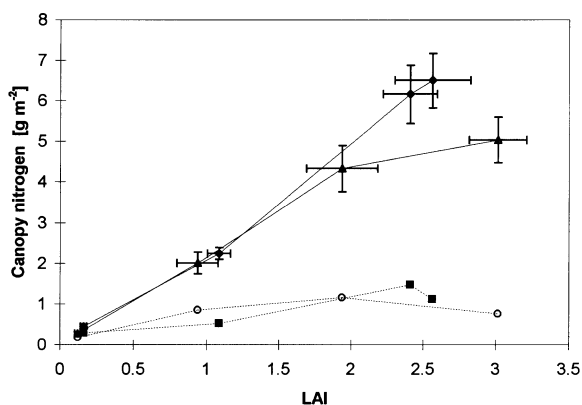


Figure 6. Total leaf nitrogen (solid line) and light-dependent nitrogen pool (dotted line) in relation to total canopy leaf area index (LAI) in *S. dasyclados* (◆, ■) and *S. viminalis* (▲, ○). Bars show standard errors of the estimate ($n = 8$).

nitrogen pool. Several modeling approaches have led to the conclusion that canopy photosynthesis is maximized if distribution of the photosynthetic apparatus approximates the PPFD profile inside the canopy (Marshall and Porter 1991, Wu 1993). However, there is some evidence that the leaf photosynthetic nitrogen pool is bigger than the light-dependent nitrogen pool. Only a few studies have presented both photosynthesis versus leaf nitrogen and leaf nitrogen versus PPFD relationships for the same species (DeJong and Doyle 1985, Hirose and Werger 1987b). These studies show that leaf nitrogen content is higher if it is extrapolated to zero PPFD than if it is extrapolated to zero photosynthesis. Thus, it is possible that the nonphotosynthetic nitrogen pool in the leaf is smaller than the estimated light-independent pool. Also, the photosynthetic apparatus may be distributed in such a way that a relatively larger part of it, expressed by its nitrogen content, is in shaded leaves compared with illuminated leaves, as was suggested by Evans (1989). Vapaavuori and Vuorinen (1989) obtained data from a similar *Salix* plantation showing that qualitative changes in the photosynthetic apparatus occurred in response to increased shading during canopy development, and this may complicate the relationship between total leaf nitrogen and leaf photosyn-

thesis. Based on numerous data, Field and Mooney (1986) demonstrated that, if photosynthesis and leaf nitrogen are evaluated on the basis of dry mass, extrapolation of nitrogen concentration to zero photosynthesis yields a positive intercept on the nitrogen axis, equal to 0.5 mmol g^{-1} , which is about 0.7% of the dry mass. This value is half of that obtained for abscised leaves in our study and indicates that the real nonphotosynthetic nitrogen pool may be smaller than the nondegradable nitrogen pool.

Kull and Jarvis (1995) hypothesized that there is a limit to the ratio of total canopy nitrogen to intercepted PPFD, because energy for acquiring nitrogen originates from intercepted PPFD. This limit probably depends on nitrogen availability in the soil and on the plant growth form, as well as on available light energy. In *Salix dasyclados*, the maximum total canopy nitrogen per unit of intercepted PPFD occurred in August and equalled $7 \text{ g nitrogen m}^{-2}$ of ground area, assuming that all available light is intercepted (Figure 4). This value is within the limits ($3.5\text{--}8.5 \text{ g m}^{-2}$) of total foliar nitrogen estimated for a range of Estonian natural and seminatural plant communities (Kull et al. 1995). Although the total nitrogen pool in the foliage increased up to the end of the growing season, the light-dependent pool as well as canopy PPFD interception culminated in August. The proportion of nitrogen in the light-dependent pool decreased from almost 65% of the total canopy nitrogen in June to 15% in September. Because the nondegradable nitrogen pool, estimated as the amount of nitrogen in abscised leaves, was smaller than the light-independent nitrogen pool, the degradable or retranslocatable nitrogen pool decreased from 68% in *S. dasyclados* in June to 29% in *S. viminalis* in September. These values lie in the range of foliar nitrogen retranslocation (24–81%) measured in other tree species (Chapin and Moilanen 1991, Escudero et al. 1992). Thus, at least 30% of total foliar nitrogen is neither degradable nor light-dependent. This figure may even reach 70% of total canopy nitrogen at high LAIs in closed canopies. Consequently, the amount of total canopy nitrogen that is not distributed according to the PPFD profile may be significant and should be taken into account when applying any optimal-ity scheme to describe nitrogen distribution inside a canopy.

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References

- Ackerly, D.D. 1992. Light, leaf age, and leaf nitrogen concentration in a tropical vine. *Oecologia* 89:596–600.
- Anderson, M.C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. *J. Ecol.* 52:27–41.
- Chapin, F.S., III and L. Moilanen. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. *Ecology* 72:709–715.
- Charles-Edwards, D.A., H. Stutzel, R. Ferraris and D.F. Beech. 1987. An analysis of spatial variation in the nitrogen content of leaves from different horizons within a canopy. *Ann. Bot.* 60:421–426.
- DeJong, T.M. and J.F. Doyle. 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). *Plant Cell Environ.* 8:701–706.
- Ellsworth, D.S. and P.B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96:169–178.
- Escudero, A., J.M. del Arco, I.C. Sanz and J. Ayala. 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients in the leaf biomass of different woody species. *Oecologia* 90:80–87.
- Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C₃ plants. *Oecologia* 78:9–19.
- Evans, J.R. 1993. Photosynthetic acclimation and nitrogen partitioning within a lucerne canopy. I. Canopy characteristics. *Aust. J. Plant Physiol.* 20:55–67.
- Field, C. 1983. Allocating leaf nitrogen for the maximisation of carbon gain: leaf age as a control on the allocation programme. *Oecologia* 56:341–347.
- Field, C. and H.A. Mooney. 1986. The photosynthesis–nitrogen relationship in wild plants. *In* On the Economy of Plant Form and Function. Ed. T. Givnish. Cambridge University Press, Cambridge, pp 25–55.
- Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. *In* Ecology of Photosynthesis in Sun and Shade. Eds. J.R. Evans, S. von Caemmerer and W.W. Adams, III. CSIRO, Melbourne, Australia, pp 63–92.
- Hilbert, D.W., A. Larigauderie and J.F. Reynolds. 1991. The influence of carbon dioxide and daily photon-flux density on optimal leaf nitrogen concentration and root:shoot ratio. *Ann. Bot.* 68:365–376.
- Hirose, T. and M.J.A. Werger. 1987a. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72:520–526.
- Hirose, T. and M.J.A. Werger. 1987b. Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiol. Plant.* 70:215–222.
- Hirose, T. and M.J.A. Werger. 1994. Photosynthetic capacity and nitrogen partitioning among species in the canopy of a herbaceous plant community. *Oecologia* 100:203–212.
- Hirose, T., M.J.A. Werger, T.L. Pons and J.W.A. van Rheenen. 1988. Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecologia* 77:145–150.
- Jonasson, S. and F.S. Chapin, III. 1985. Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. *Oecologia* 67:511–518.
- Kull, O. and P.G. Jarvis. 1995. The role of nitrogen in a simple scheme to scale up photosynthesis from leaf to canopy. *Plant Cell Environ.* 18:1174–1182.
- Kull, O. and Ü. Niinemets. 1993. Variations in leaf morphometry and nitrogen concentration in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L. *Tree Physiol.* 12:311–318.
- Kull, O., A. Aan and T. Söelsepp. 1995. Light interception, nitrogen and leaf mass distribution in a multilayer plant community. *Funct. Ecol.* 9:589–595.
- Lemaire, G., B. Onillon, G. Gosse, M. Chartier and J.M. Allirand. 1991. Nitrogen distribution within a lucerne canopy during re-growth: relation with light distribution. *Ann. Bot.* 68:483–488.
- Marshall, B. and J.R. Porter. 1991. Concepts of nutritional and environmental interactions determining plant productivity. *In* Plant Growth: Interactions with Nutrition and Environment. Eds. J.R. Porter and D.W. Lawlor. Cambridge University Press, Cambridge, pp 99–124.
- Pearcy, R.W. and D.A. Sims. 1994. Photosynthetic acclimation to changing light environments: scaling from the leaf to the whole plant. *In* Exploitation of Environmental Heterogeneity by Plants. Eds. M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego, pp 145–174.
- Pons, T.L. and R.W. Pearcy. 1994. Nitrogen reallocation and photosynthetic acclimation in response to partial shading in soybean plants. *Physiol. Plant.* 92:636–644.
- Reich, P.B. and M.B. Walters. 1994. Photosynthesis–nitrogen relations in Amazonian tree species. II. Variation in nitrogen vis-à-vis specific leaf area influences mass- and area-based expressions. *Oecologia* 97:73–81.
- Schieving, F., T.L. Pons, M.J.A. Werger and T. Hirose. 1992. The vertical distribution of nitrogen and photosynthetic activity at different plant densities in *Carex acutiformis*. *Plant Soil* 14:9–17.
- Vapaavuori, E.M. and A.H. Vuorinen. 1989. Seasonal variation in the photosynthetic capacity of a willow (*Salix* cv. *Aquatica gigantea*) canopy. I. Changes in the activity and amount of ribulose 1,5-bisphosphate carboxylase-oxygenase and the content of nitrogen and chlorophyll at different levels in the canopy. *Tree Physiol.* 5:423–444.
- Wu, R. 1993. Simulated optimal structure of a photosynthetic system: implication for the breeding of forest crop ideotype. *Can. J. For. Res.* 23:1631–1638.

