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Tight coupling between leaf area index and foliage N content in arctic plant communities

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Abstract The large spatial heterogeneity of arctic landscapes complicates efforts to quantify key processes of these ecosystems, for example productivity, at the landscape level. Robust relationships that help to simplify and explain observed patterns, are thus powerful tools for understanding and predicting vegetation distribution and dynamics. Here we present the same linear relationship between Leaf area index (LAI) and Total foliar nitrogen (TFN), the two factors determining the photosynthetic capacity of vegetation, across a wide range of tundra vegetation types in both northern Sweden and Alaska between leaf area indices of 0 and $1 \text{ m}^2 \text{ m}^{-2}$, which is essentially the entire range of leaf area index values for the Arctic as a whole. Surprisingly, this simple relationship arises as an emergent property at the plant community level, whereas at the species level a large variability in leaf traits exists. As the relationship between LAI and TFN exists among such varied ecosystems, the arctic environment must impose tight constraints on vegetation canopy development. This relationship simplifies the quantification of vegetation productivity of arctic vegetation types as the two most important drivers of productivity can be estimated reliably from remotely sensed NDVI images.

Keywords Arctic ecosystems · Productivity · Vascular plants

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Introduction

Arctic terrestrial ecosystems are important components of the global C cycle (Callaghan and Maxwell 1995; Oechel et al. 1993), and, of all terrestrial vegetation types, are expected to undergo the greatest degree of future climate change (Maxwell 1992; Chapin et al. 1995). However, the Arctic is a mosaic of diverse ecosystems; its plant communities differ in species, growth form, biomass, and productivity (Bliss et al. 1981; Shaver et al. 1996), and its soils vary in organic matter content, nutrient stocks, depth to permafrost, and depth to water table (Giblin et al. 1991; Walker and Everett 1991; Walker et al. 1994). Despite this variability, previous research in the Alaskan Arctic indicated a relatively strong correlation between plant community level leaf area index (LAI, $\text{m}^2 \text{ Leaf area m}^{-2} \text{ ground area}$) and Total foliar nitrogen (TFN, $\text{g N m}^{-2} \text{ ground area}$) (Williams and Rastetter 1999), the key vegetation parameters controlling carbon uptake via photosynthesis in Arctic environments during the growing season. We set out to investigate the existence and generality of this correlation by collecting new data in the arctic of northern Sweden, and by analyzing the previously collected data in more detail, at both the community and the species level. The tundras in the two regions differ in species and plant type composition, biomass, productivity, climate, and geology (Walker et al. 1995; Walker et al. 1989; Shaver and Jonasson 1999; Graglia et al. 2001; Michelsen et al. 1996; Van Wijk et al. 2004). In comparing these two regions, we tested whether the LAI-TFN correlation is a local phenomenon, or whether it could be a more general emergent property in arctic plant communities.

Materials and methods

Near Toolik Lake ($68^{\circ}38'N$, $149^{\circ}34'W$, elevation 720 m), Alaska, between 19 and 26 July 1997, and near Abisko ($68^{\circ}21'N$, $18^{\circ}49'E$, above the tree line, elevation

between 540 and 1,000 m), Sweden, between 15 and 30 July 2002, different dominant arctic vegetation types were sampled in 20×20 cm quadrats. Climatic information about the two regions is given in Table 1.

The Alaskan sites were selected in such a way that the whole range of vegetation types occurring in the northern foothills of the Brooks Range were represented in the dataset. The vegetation types were wet sedge tundra, tussock tundra, heath tundra, and shrub tundra. The Alaskan data were published earlier in a summarized form (Williams and Rastetter 1999). Also in northern Sweden, the most important vegetation types were defined and sampled in an area of 5 km². The most important vegetation types here were heath tundra, shrub tundra, wet sedge tundra and peat tundra. For both regions the individual quadrats were located in separate spatial clusters of the different vegetation types within the area to avoid possible problems with pseudoreplication. The distance between the sample points was highly variable, but never less than 4 m. Peat tundra in Sweden was less abundant than the other vegetation types around Abisko above the tree line, therefore only five independent samples (meaning not within the same spatial cluster of a vegetation type) could be taken. Care was taken that for each vegetation type the samples were distributed in such a way that the whole range of vegetation densities present was sampled.

We sampled 94 20×20 cm quadrats in the Toolik Lake region and 92 quadrats in the Abisko region. Of each of the harvested 20×20 cm quadrats, we removed and separated green foliage by species (except graminoids, which were sampled as a combined group). In total we sampled 24 plant species in the Abisko region and 26 plant species in the Toolik Lake region. We did not collect woody material. We determined one-sided projected leaf area of vascular plants using a Li-Cor LI-3000 leaf area meter in Alaska, and with a camera (JVC TK-S310) and accompanying software (Delta-T digital Analysis System, version 1.1) in Sweden. All samples were oven-dried at 60°C for 3 days, weighed, and %N determined in a Perkin-Elmer CHN analyzer. For %N determination we selected the minimum set of species that accounted for 85% of the total leaf area at each quadrat (mean number of species sampled per quadrat = 4.9). For those species at a site that were not sampled for %N (because for these species there was not enough leaf biomass to be able to determine %N) we made estimates using the N concentration determined for that

species at a nearby location. We calculated Total foliar N per ground area (TFN) in each quadrat for each site, using data on foliar N concentration (% by mass) and leaf mass per ground area (g m²).

Results

The vegetation types we investigated in this study are different in the contributions that the several plant types made to the total leaf area of the vascular plant communities (Table 2). The wetland vegetation type is dominated by graminoid plant species (especially *Carex* and *Eriophorum* species). The shrub vegetation type is dominated by deciduous shrubs (especially *Betula nana* and *Salix* species), whereas the heath vegetation type is dominated by both evergreen (especially *Vaccinium vitis-idaea*, *Empetrum nigrum* and in Alaska *Ledum palustre*) and deciduous shrubs (especially *B. nana*). The Alaskan tussock tundra is a mixture of the aforementioned graminoid, evergreen and deciduous species. In the Swedish peat systems *R. chaemaemorus* is also very important.

Despite this large difference in plant type composition between the vegetation types investigated, we found for both regions a very strong relationship between site LAI and total vascular-plant foliar N per ground area (TFN) (Fig. 1a). For the two regions the measurements of site LAI and TFN show the same relationship for LAI values up to 1 m² m⁻² [Fig. 1a; linear regression lines for LAI values up to 1 m² m⁻² are for Sweden $y = 1.87x$ and for Alaska $y = 1.95x$; difference in slope is not statistically significant; the explained variance of the regression for both sites for LAI up to 1 m² m⁻² was 0.90; if the region was used as an extra co-variate the explained variance increased to 0.93, a non-significant increase in model-fit ($P = 0.09$)]. In the TFN versus leaf biomass scatter plot, clear data-clustering was visible among individual regions and different vegetation types (Fig. 1b; the regression line between TFN and leaf mass

Table 1 Climate information for the Toolik Lake and Abisko regions

Region	Abisko, Sweden	Toolik Lake, AL, USA
Annual precipitation (mm) (percentage that falls as snow)	225–475 (47%)	200–400 (45%)
Average annual temperature (°C)	–1	–10
Average January temperature (°C)	–12	–24
Average July temperature (°C)	11	14

Table 2 Contribution in percentages to total plant community leaf area by the dominant plant types in the vegetation types investigated in this study

Vegetation type	Plant type	Percentage of total leaf area of the vascular plant community	
		Alaska	Sweden
Wetland	Graminoids	85–90	85–95
	Pteridophytes	0–10	0–5
Shrubs	Deciduous	70–100	60–90
	Evergreen	0–30	10–35
Heath	Evergreen	35–60	45–100
	Deciduous	30–60	0–50
Tussock tundra	Graminoids	10–60	–
	Evergreen	30–60	–
Peat tundra	Deciduous	5–40	–
	Graminoids	–	25–70
			20–40

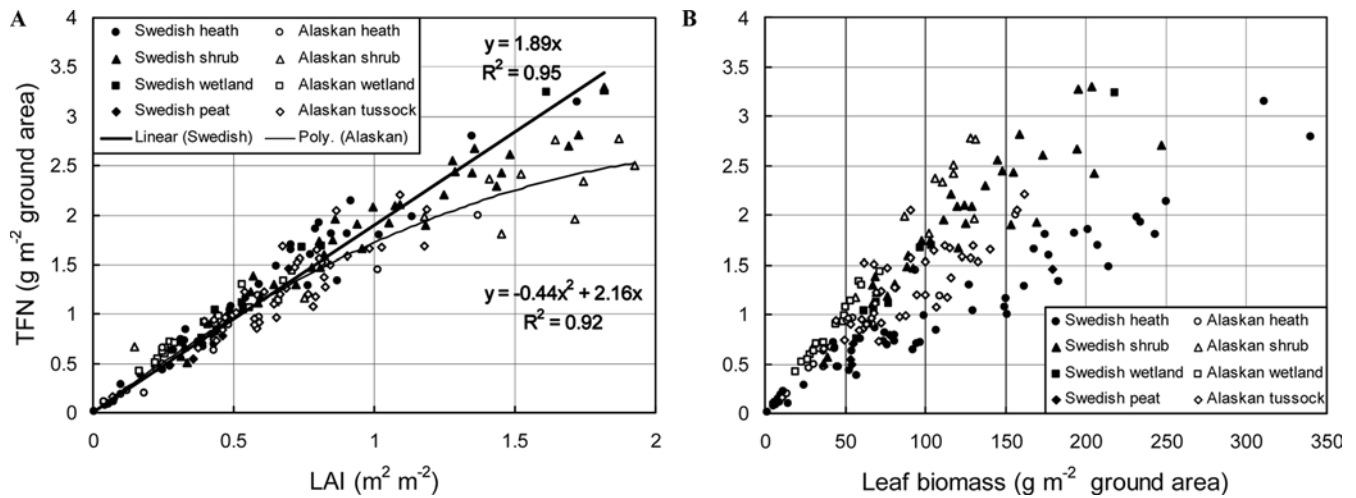


Fig. 1 Relationships between Total vascular plant foliar N (*TFN*) and Leaf area index (*LAI*) (a) and total vascular plant foliar N (*TFN*) and leaf mass (b) for both Alaska and northern Sweden; each data-point represents the results of a 20×20 cm quadrat

had an R^2 of 0.58), whereas this clustering was absent for *TFN* versus *LAI* scatter plots.

The strong coupling between foliar N and leaf area is absent at species level, as is shown by the large range of values for the key variable foliar N per unit leaf area (*NLA*; Table 3); the *NLA* values vary with a factor close to 3, whereas the within species variation is relatively small. There were also strong differences in other important leaf traits at species level like specific leaf area (*SLA*) and foliar N per unit leaf mass (*NLM*). For each individual species a consistent value of *NLA* can be derived with a relatively low uncertainty, but between species there are clear consistent differences (Fig. 2a,b).

Discussion

The tight correlation of the data up to LAI $1 \text{ m}^2 \text{ m}^{-2}$ in both regions shows that in the arctic vegetation types the relative amounts of canopy N and leaf area seem to be

controlled within similar constraints, and suggests a single controlling process for the pan-Arctic region. This relationship up to *LAI*-values of $1 \text{ m}^2 \text{ m}^{-2}$ covers essentially the entire range of *LAI*-values that occurs in the Arctic as a whole. We have chosen the vegetation types that were sampled in order to represent the widest possible range of leaf area and productivity at both the Toolik and Abisko regions, but the high-*LAI* vegetation types do not cover a large proportion of the landscape—most of the landscape is covered with low-*LAI* vegetation (Bliss and Matveyeva 1992; Walker et al. 2003; Dahlberg et al. 2004). This means that we can predict foliar N from *LAI* estimates using a relationship that has a coefficient of determination that is unusually high for ecological data. This tight correlation at community level occurs along a whole range of vegetation types with different species composition, both within and between the two regions, and despite the differences in climate (see Table 1 and Van Wijk et al. 2004) between the two regions. As the slopes of the regression

Table 3 Leaf traits of important plant species in Alaska and Sweden. Values given are mean and between parentheses the standard error. *SLA* Specific leaf area, *NLA* foliar nitrogen per unit leaf area, *NLM* foliar nitrogen per unit leaf mass

Species (no. of replicates)	Plant type	<i>SLA</i> ($\text{m}^2 \text{ kg}^{-1}$)	<i>NLA</i> (g m^{-2})	<i>NLM</i> (g kg^{-1})
Alaska				
<i>Betula nana</i> (26)	Deciduous	14.4 (0.5)	1.50 (0.09)	20 (1)
<i>Vaccinium vitis-idaea</i> (44)	Evergreen	6.5 (0.2)	1.46 (0.11)	9.2 (0.4)
<i>Vaccinium uliginosum</i> (16)	Deciduous	14.5 (0.5)	1.34 (0.09)	19 (1)
<i>Ledum palustre</i> (38)	Evergreen	6.5 (0.1)	2.10 (0.11)	14.2 (0.2)
<i>Arctostaphylos alpinus</i> (14)	Deciduous	13.5 (0.1)	1.27 (0.11)	17.3 (0.1)
<i>Equisetum spec.</i> (10)	Pteridophyte	5.5 (0.5)	3.32 (0.22)	17.1 (0.2)
Sweden				
<i>Betula nana</i> (50)	Deciduous	10.0 (0.2)	1.72 (0.03)	17.0 (0.3)
<i>Vaccinium vitis-idea</i> (36)	Evergreen	5.3 (0.3)	1.42 (0.04)	7.4 (0.2)
<i>Vaccinium uliginosum</i> (56)	Deciduous	10.4 (0.2)	1.43 (0.03)	14.7 (0.3)
<i>Empetrum nigrum</i> (62)	Evergreen	4.1 (0.1)	2.21 (0.04)	8.8 (0.2)
<i>Andromeda polifolia</i> (45)	Evergreen	5.7 (0.3)	2.14 (0.07)	12.0 (0.2)
<i>Carex bigelowii</i>	Graminoid	7.6 (0.6)	2.5 (0.2)	16 (1)
<i>Equisetum spec.</i> (18)	Pteridophyte	5.6 (0.4)	3.17 (0.24)	16.6 (0.5)

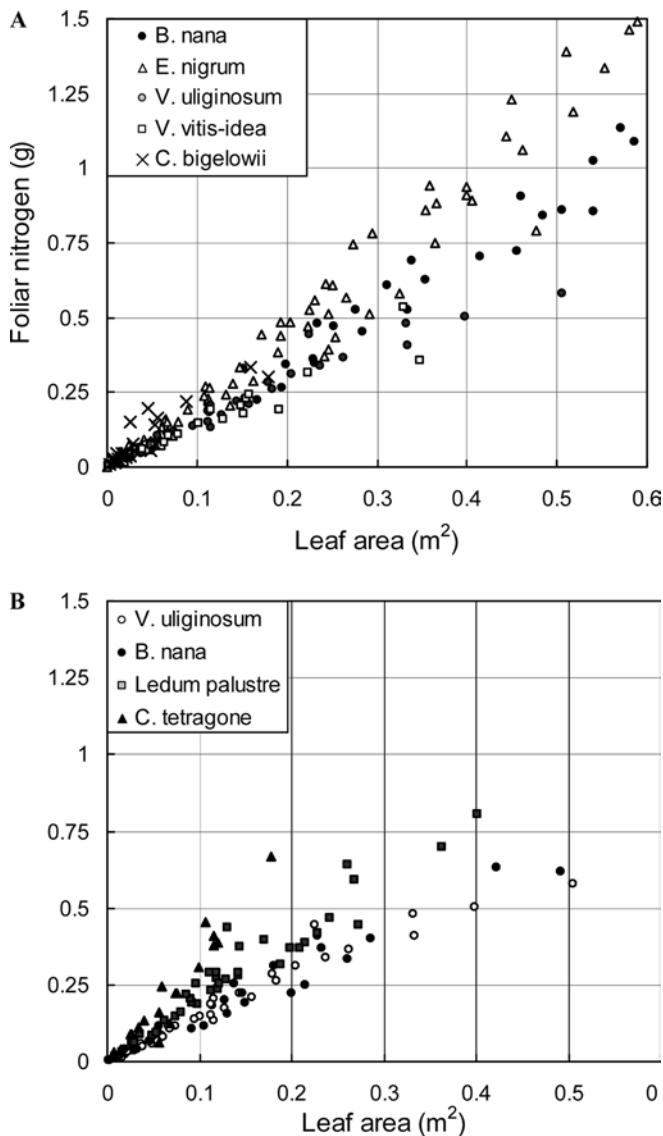


Fig. 2 Scatter plots of foliar N and leaf area of key species of and the Abisko region (a) and northern Alaska (b)

lines are not significantly different, the same relationship can be used for both regions to predict leaf nitrogen from the variable LAI.

The LAI-TFN relationship would not be surprising if it occurred in a plant canopy with a single species (e.g. Field and Mooney 1986; Field 1983), but this study shows that the relationship exists over a variety of arctic community types with different groups of species. An important conclusion of this work is that because the relationship between LAI and TFN is so tight across a range of LAI values and among such varied functional plant types, the arctic environment must impose tight constraints on vegetation canopy development. The latitude of the two regions is similar, maybe suggesting that radiation is the determining factor controlling the relationship between LAI and total foliar N, although there could be differences in cloudiness between the two

regions. It would be interesting to make the same measurements in similar arctic vegetation but at different latitudes (e.g. at Svalbard, or at an alpine system at lower latitude, for example in southern Norway). As LAI and foliar N concentration are the key biotic controls on ecosystem carbon accumulation via photosynthesis (Williams and Rastetter 1999; Williams et al. 2001; Van Wijk et al. 2003), the coupling results in a tight control of ecosystem photosynthetic capacity, independent of species composition.

Surprisingly, the signature of this control only shows up at the community level; important individual species in both arctic regions showed clear differences in their leaf traits. The tight LAI—total foliar N relationship at the community level is an emergent property, arising out of the complex interactions of individual plants, which one would not expect to occur given the large variability at the species level. The whole range of arctic plant communities investigated here, despite having different species composition and different dominant species, are composed of plant species in such a way that the overall community LAI-TFN value remains close to 1.90 g N m⁻² leaf area (Fig. 1a). Somehow, plant communities are never composed solely of plant species with low or high NLA values.

The small data set on individual species present in both Sweden and Alaska (Table 2), suggests that, compared to the measurements of Sweden, higher N per leaf mass values in Alaska are offset by higher specific leaf area values, thereby resulting in more similar N per leaf area values (see Table 3; data of *B. nana*, *V. vitis-idea* and *V. uliginosum*).

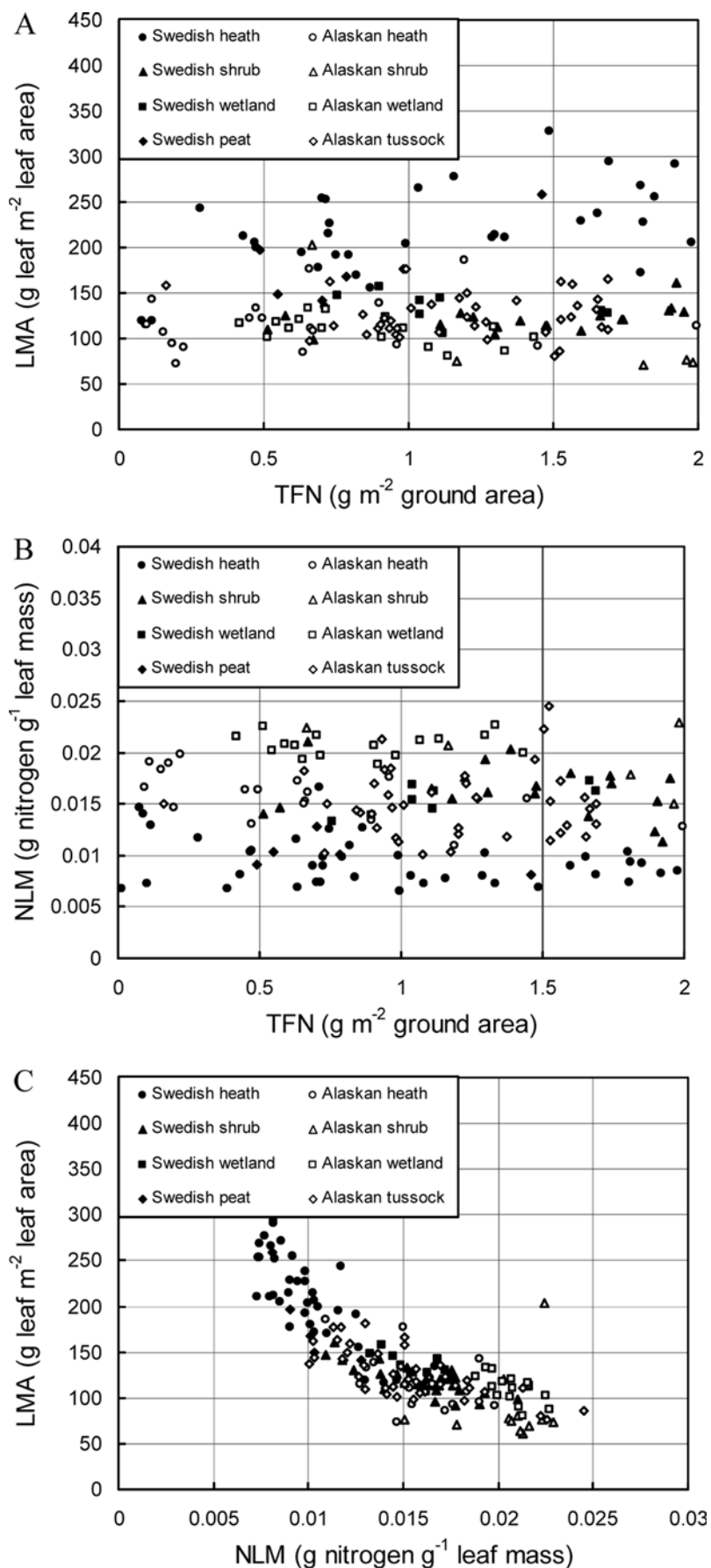
The conclusion that plant communities are never composed solely of plant species with low or high NLA values is also important when Figs. 1 and 2 are compared. If we construct plant communities of a certain LAI artificially by taking randomized draws of the plant characteristics of species present in the Arctic, this also results in an average slope of LAI-TFN relationship at community level of 1.90 g N m⁻² leaf area. However, the spread around this line using such a randomizer is larger than the spread shown in reality, as communities are formed with species that have similar low or high NLA values. Such a randomizer for example results in values of the community foliar N values at an LAI of 0.5 m² m⁻² between the extremes of 0.45 and 1.65 g m⁻² ground area, a range that is more than twice the range found in the field.

If we consider the three components of Table 3, we can define the following relationship:

$$\text{TFN} = \text{NLM} \times \text{LMA} \times \text{LAI}$$

where TFN is total foliar nitrogen (g m⁻² ground area) and LMA is the amount of leaf mass per unit leaf area (g m⁻² leaf area), the inverse of the SLA given in Table 3. The relatively tight relation between TFN and LAI as shown in Fig. 1a means that at ecosystem level

Fig. 3 Relationships between leaf mass per unit leaf area (*LMA*) and total vascular plant foliar N (*TFN*) (a), nitrogen per unit leaf mass (*NLM*) and total vascular plant foliar N (*TFN*) (b), and leaf mass per unit leaf area (*LMA*) and nitrogen per unit leaf mass (*NLM*) (c) for both Alaska and northern Sweden; each data-point represents the results of a 20×20 cm quadrat



NLM and LMA are negatively correlated. The scatter plots of NLM and LMA versus TFN, and of NLM versus LMA are shown in Fig. 3. Clearly visible is the negative correlation between NLM and LMA, and that the individual vegetation types have different values of NLM and LMA. The negative correlation between NLM and LMA was already known for individual plant species (e.g. Wright et al. 2004), but here we show that this correlation also exists at ecosystem level across a range of LAI values in the Arctic.

The difference in coupling between TFN and LAI, and TFN and leaf biomass (Fig. 1) shows that the tight coupling between LAI and total foliar N is not just simply an auto-correlation. At the community level, there is a much stronger coupling of the plant functional characteristics LAI, important for radiation interception, and foliar N, an important indicator of photosynthetic capacity, than with a structural variable like leaf mass. The much tighter relationship between LAI and TFN is remarkable from a measurement point of view, as leaf mass together with leaf nitrogen content of individual species determines total foliar N, whereas foliar N and LAI are more independent measurements.

The occurrence of the LAI–TFN relationship over a wide range of different vegetation types in two different regions shows that these communities seem to balance the relative costs and benefits of C and N in much the same way. Previous studies in the Arctic have indicated niche differentiation in plant nitrogen uptake: plant species have been shown to differ in the chemical form in which they capture nitrogen, as well as in the timing and in the spatial distribution of this capture (McKane et al. 2001). It has also been shown that in herbaceous plant communities in temperate regions, different morphological strategies for light capture can result in similar efficiencies in terms of light ‘foraging’ (Hirose and Werger 1995; Anten and Hirose 1999). However, our data suggest that at the plant community level in arctic systems, there is only one optimal relationship between leaf area and amount of N in the canopy. The tight relationship indicates that nutrient availability limits the total amount of foliage that can be produced and sustained, while the strong competition for the capture of light assures that this upper limit for leaf area is attained. If this relationship is truly conservative, there are important implications for the response of current arctic plant communities to global change. Any response will be restricted so that the novel canopy structure conforms to the relationship we have observed, and thereby to the tight control on productivity. The close relationship between LAI and N is also of interest because it aids our interpretation of remotely sensed vegetation data and simplifies the information required to generate landscape-level predictions of canopy production (Williams et al. 2001). In the latter case, LAI data can be used to infer canopy foliar N up to LAI values of around $1 \text{ m}^2 \text{ m}^{-2}$. The existence of a linear relationship between LAI and foliar N simplifies the task of generating a regional C budget, because it removes the need for

species level data and for chemical analyses of foliage. Furthermore, Williams et al. (2001) showed that the slope of the LAI–N relationship has a relatively large effect on the gross primary production (GPP) predicted at landscape level: a shift of 1 standard error (SE) of the slope of the LAI–N regression line resulted in a change of 8–9% in predicted landscape level GPP. The implication of the study presented in this paper could be that we can use the same relationships as in Williams et al. (2001) to make predictions along continents, although further research in more locations (e.g., Canada, Greenland and Siberia) should be performed before we can really state with confidence that the LAI–TFN relationship is a general relationship in arctic vegetation.

For LAI values greater than $1 \text{ m}^2 \text{ m}^{-2}$ the relationships for the two regions slightly deviate, mainly because of the curvature of the LAI and foliar N relationship found in Alaska (Fig. 1a). The deviation between the regions at higher LAI-values indicates that the tight control of foliar N and LAI is only present in situations in which nutrients are the most important limiting factor in the ecosystems; at higher foliar N and higher LAI values other factors also come into play, and the relationships in the two regions deviate. There are various explanations possible for this deviation, and they will have to be tested in future research. First, the deviations may be caused by permafrost in the Alaskan tundra. In terms of optimization of carbon this could mean that at certain values of N in the ecosystem, investment of plant C into roots is not effective any more in the Alaskan tundra, and relative investment in leaves can be increased, whereas this belowground limitation is absent in northern Sweden. A second factor could be the difference in climate (see Table 1); possibly this difference does not lead to large deviations in LAI versus foliar N tradeoffs at low leaf area values, but at larger values it could be that differences in photosynthesis and respiration caused by the differences in for example air temperature lead to other values of C and N allocation (Körner 1989). A third explanation could be the difference in carbon investment by the plant in secondary components in more productive vegetation. Graglia et al. (2001) showed that the phenolics concentration in *B. nana* leaves was significantly higher in Swedish tundra, possibly caused by heavier grazing, as compared to the Alaskan tundra. A fourth possible explanation could be differences in soil nitrogen cycling and hydrology between the two regions. The Toolik Lake region is characterized by permafrost and thick layers of organic matter in the soil, whereas in the Abisko region there is permafrost only in some small bog areas near Lake Torneträsk and the soil is generally characterized by good drainage (Jonasson et al. 1999).

Until now, as far as we know, no other consistent comparisons of total vascular leaf nitrogen and leaf area over different ecosystems exist. This is mainly due to the difficulty of measuring in a reliable manner total living leaf area and total leaf nitrogen of an ecosystem; we have not found individual datapoints for other ecosystems in which both variables were

quantified at ecosystem level; always only parts of the ecosystem were measured. The divergence of the Abisko and Toolik datasets at higher LAI-values suggests that the tight relationship between leaf nitrogen and leaf area breaks down at nutrient richer systems, but further research must be performed to confirm this.

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