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Determination of Leaf Area Index, Total Foliar N, and Normalized Difference Vegetation Index for Arctic Ecosystems Dominated by *Cassiope tetragona*

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Abstract

Leaf area index (LAI) and total foliar nitrogen (TFN) are important canopy characteristics and crucial variables needed to simulate photosynthesis and ecosystem CO_2 fluxes. Although plant communities dominated by *Cassiope tetragona* are widespread in the Arctic, LAI and TFN for this vegetation type have not been accurately quantified. We address this knowledge gap by (i) direct measurements of LAI and TFN for *C. tetragona*, and (ii) determining TFN-LAI and LAI–normalized difference vegetation index (NDVI) relationships for typical *C. tetragona* tundras in the subarctic (Sweden) and High Arctic (Greenland and Svalbard).

Leaves of *C. tetragona* are 2–6 mm long and closely appressed to their stems forming parallelepiped shoots. We determined the LAI of *C. tetragona* by measuring the area of the leaves while still attached to the stem, then doubling the resulting one-sided area. TFN was determined from leaf N and biomass. The LAI-NDVI and TFN-LAI relationships showed high correlation and can be used to estimate indirectly LAI and TFN. The LAI-NDVI relationship for *C. tetragona* vegetation differed from a generic LAI-NDVI relationship for arctic tundra, whereas the TFN-LAI relationship did not. Overall, the LAI of *C. tetragona* tundra ranged from 0.4 to 1.1 m^2 m^{-2} and TFN from 1.4 to 1.7 g N m^{-2}.

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Introduction

Cassiope tetragona (L) D. Don is an ericaceous evergreen dwarf-shrub common throughout the Arctic. It is a dominant species in many mesic and dry tundras with a moderate snow cover in winter, particularly on fellfields and heaths (Havström et al., 1993). Whereas information about species composition (Nams and Freedman, 1987a; Graglia et al., 2001); plant physiology (Baddeley et al., 1994; Michelsen et al., 1996); plant-microbial interactions (Jonasson et al., 1999a, 1999b); standing crop, growth dynamics, and production (Bliss et al., 1987; Nams and Freedman, 1987a, 1987b; Campioli et al., 2009); and biogeochemistry and responses to environmental perturbations (Molau, 1997; Jonasson et al., 1999b; Illeris et al., 2004; Grogan and Jonasson, 2005) are available for many *C. tetragona*–dominated sites, little attention has been given to canopy characteristics such as the leaf area index (LAI; m^2 leaf m^{-2} ground) and total foliar nitrogen (TFN; g N m^{-2} ground) in vegetation dominated by *C. tetragona*. LAI is a key controller of the amount of light intercepted by the vegetation and therefore, of photosynthesis, plant production, and of the carbon (C) accumulated by the ecosystem. In addition to the C cycle, LAI determines many other crucial aspects of the canopy microclimate, energy, and water exchange, such as radiation extinction, rainfall interception, and evapotranspiration (van Wijk and Williams, 2005). TFN is another key driver of photosynthesis and C cycle. Whereas LAI indicates the light absorptive capacity of the vegetation, TFN indicates the canopy's photosynthetic capacity (Williams and Rastetter, 1999). Furthermore, LAI and TFN are ecosystem indices independent of species composition which facilitate the generalization and scaling up of ecosystem properties at landscape and regional levels (van Wijk et al., 2005). Modeling studies have shown that LAI and TFN are key model parameters in simulating photosynthesis and net C exchange in arctic ecosystems (Williams and Rastetter, 1999; Williams et al., 2000; Rennermalm et al., 2005; Shaver et al., 2007). Lack of knowledge of these parameters represents a significant obstacle to accurate prediction of C cycling in the widespread *C. tetragona* tundra, the scaling up of C exchange in the heterogeneous arctic landscape, and its feedback to global change.

The lack of LAI estimates for vegetation dominated by *C. tetragona* is likely due to difficulties in measuring the leaf area of *C. tetragona*, which does not possess flat leaves (Baddeley et al.,

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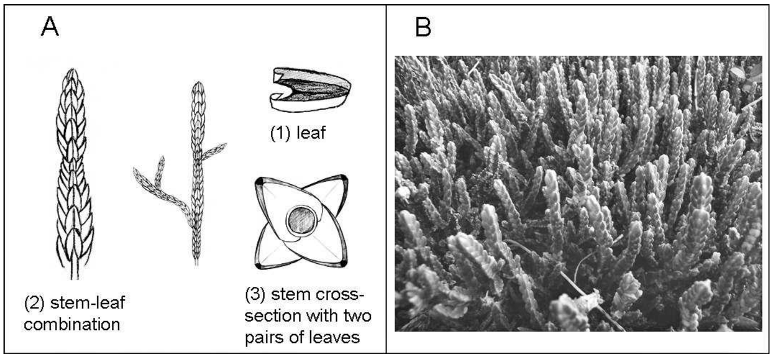

FIGURE 1. Morphology and leaf structure of *Cassiope tetragona* (A) for a shoot (drawings by Tommy Blommaert) and (B) at a subarctic tree-line heath (photo by Matteo Campioli).

1994). In fact, leaves of *C. tetragona*, with a life-span of 3–10 years (Molau, 1997), are 2–6 mm long, closely appressed to their stem, imbricate scale-like, and occur in opposite pairs (Callaghan et al., 1989) forming a parallelepiped green shoot which comprises leaf and stem biomass (Fig. 1). For leaves of such morphology, LAI cannot be determined following the classical method of Watson (1947) from the one-side area of the leaf tissue. Instead, the LAI should be determined as half of the total leaf intercepting area as proposed by Chen and Black (1992) for leaves of any shape (see review of Jonckheere et al., 2004). For the parallelepiped *C. tetragona*, half of the total leaf intercepting area is equivalent to two sides of the green biomass (Fig. 1). In this study, we used the latter account to determine directly LAI for different tundra sites dominated by *C. tetragona*: a tree-line heath, a fellfield, an abrasion plateau, a snow bed, and contrasting high-arctic heaths. From a subset of such observations, TFN was determined from measurements of leaf N concentration and biomass. Because of the correlation between LAI and TFN for arctic tundra (Williams and Rastetter, 1999; van Wijk et al., 2005), we investigated such a relationship for tundra dominated by *C. tetragona* also, which might provide an indirect method to estimate TFN.

The normalized difference vegetation index (NDVI) is a function of the land surface reflectance in the near-infrared (ca. 750–1000 nm) and red (ca. 625–740 nm). Because different land covers (e.g. vegetation, soil, snow, standing water), vegetation types (e.g. vegetation with different canopy structure, leaf morphology, soil background), and vegetation conditions (e.g. health and phenological status) present differences in reflectance in these two spectral regions, NDVI can be used to identify ecosystem type and quantify many vegetation properties, including LAI, biomass, chlorophyll content, and productivity. A strong correlation between LAI and NDVI was found for many types of tundra (van Wijk and Williams, 2005; Williams et al., 2006; Shaver et al., 2007; Street et al., 2007). In this study, the relationship between LAI and NDVI for vegetation dominated by *C. tetragona* was investigated to provide an indirect method of LAI determination.

In summary, the main objectives of this study are: (i) the development of a direct method to determine LAI for *C. tetragona*, and (ii) the determination of LAI, TFN, and the TFN-LAI and LAI-NDVI relationships for typical *C. tetragona* tundras in the subarctic and High Arctic. In addition, auxiliary data on canopy biomass, leaf traits (e.g. leaf N concentration and specific leaf area), and the relationship LAI-biomass for *C. tetragona* will also be presented.

Methods

STUDY SITES

Communities dominated by *C. tetragona* were investigated in northern Sweden near Abisko (68°18′N, 18°51′E), in Svalbard near Longyearbyen (78°25′N, 15°40′E), and in northeast Greenland near Zackenberg (74°47′N, 20°55′W) (Fig. 2). At Abisko the climate is subarctic montane, at Longyearbyen north Atlantic–Arctic, at Zackenberg continental high Arctic. Mean annual temperature and precipitation are −1.0, −5.7, and −9.4 °C, and 304, 180, and 228 mm, at Abisko, Longyearbyen, and Zackenberg, respectively (www.linnea.com/~ans, www.met.no; Sigsgaard et al., 2006). The growing season is about three months at Abisko and two months at Zackenberg and Longyearbyen. The sampling took place in mid season: at Abisko in late July–mid August 2005 and 2007, at Longyearbyen in mid–late July 2005, and at Zackenberg in mid July–early August 2006. The glacial history of the sites does not differ substantially with deglaciation and emergence from sea level occurring around 8000–10,000 years Before Present (Christiansen and Humlum, 1993; Berglund et al., 1996, Lønne and Nemec, 2004).

Two plant communities were investigated at Abisko: (i) a tree-line heath at 450 m a.s.l., and (ii) a high-elevation fellfield at 1150 m a.s.l. The tree-line heath is characterized by species-rich dwarf shrub vegetation and a sub-canopy cover of mosses and lichens. Sampling took place in areas with uniform, mostly *C. tetragona* cover, avoiding particularly productive or unproductive spots. At the fellfield, the vegetation is sparse, with few vascular species scattered among a discontinuous cover of mosses and

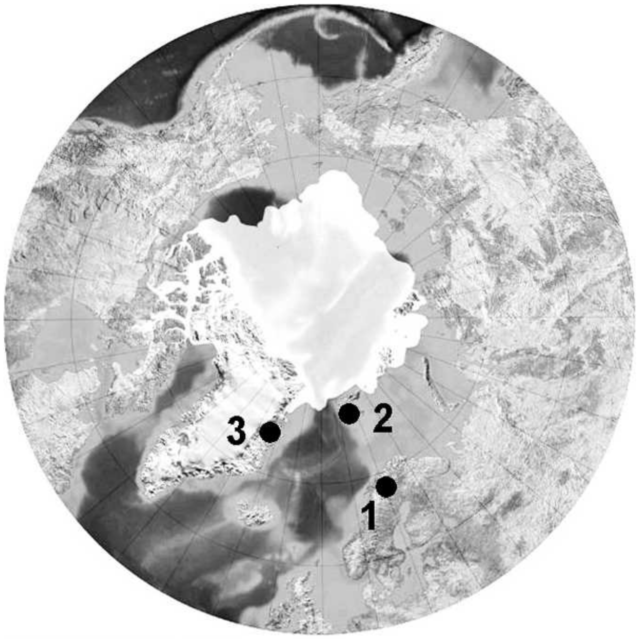

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FIGURE 2. Arctic locations investigated in this study: (1) Abisko, (2) Longyearbyen, and (3) Zackenberg (modified from ACIA, 2004).

lichens; we sampled within patches dominated by *C. tetragona*. The population of *C. tetragona* at the tree-line heath is truly subarctic and near the lower distributional limit of the species. On the other hand, because of the marked elevation, the *C. tetragona* population at the fellfield has physiological and environmental characteristics similar to that of *C. tetragona* at high-arctic locations (Callaghan et al., 1989; Havström et al., 1993). Further information about Abisko sites can be found in Havström et al. (1993), Michelsen et al. (1996), Jonasson et al. (1999b), Graglia et al. (2001), and Campioli et al. (2009).

At Zackenberg, we sampled a dry sparse heath on the valley bottom, a heath facing south, an abrasion plateau[1], and a snow bed, all at about 30–40 m a.s.l. (Bay, 1998). At Longyearbyen, we investigated a dry heath and a species-rich dwarf shrub heath. At Zackenberg and Longyearbyen, samples comprised a range of vegetation cover, varying from sparse to lush spots of *C. tetragona*. All data from the Zackenberg and Longyearbyen sites are available at http://ecosystems.mbl.edu/arc/terrest/tracegas/index.shtml.

LAI AND BIOMASS

We estimated LAI and biomass by harvesting replicate plots representative of each plant community. Harvesting took place after measurements of reflectance were completed as described below. At Abisko, we selected 0.04 m^2 plots (n = 15–16). Deciduous shrubs and herbs (forbs plus graminoids) are patchy at the sites and we sampled their leaves for the entire 0.04 m^2 plot. On the other hand, the cover of evergreen species (mostly *C. tetragona*) is uniform and we sampled it only in a representative 0.01 m^2 subplot. At Zackenberg and Longyearbyen, covers are more heterogeneous and we selected plots of 0.09 m^2 (n = 2–8). However, due to time limitation, for most of the replicates (ca. 70%) only representative 0.03–0.05 m^2 subplots were harvested. Samples were brought to the laboratory, kept refrigerated in sealed bags, and processed within two days after collection. For each plant community, LAI was calculated as the sum of (i) LAI of deciduous shrubs, herbs, and evergreen shrubs other than *C. tetragona*, determined from measurements of one-sided leaf area as in Street et al. (2007); and (ii) LAI of *C. tetragona*, which was determined using the new method (see below). All green biomass used in the LAI assessment was dried at 70 °C for 48 h and subsequently weighed.

LAI of species other than C. tetragona

The green leaves of species other than *C. tetragona* were detached from the stem and divided into (i) deciduous shrubs, (ii) evergreen shrubs (with the most common shrubs sorted at species level), and (iii) herbs. LAI of these plants was determined as the one-sided projected area of the leaves (Street et al., 2007), measured with a camera (JVC TK-S310, Tokyo, Japan) and combined software (Delta-T Digital Analysis System, version 1.1, Cambridge, U.K.) at Abisko, or with a scanner (CanoScan LiDE 30, Canon, Lake Success, U.S.A.) and combined software (WinFOLIA, Regent Instruments Inc., Quebec City, Canada) at Zackenberg and Longyearbyen.

LAI of C. tetragona

The green, parallelepiped, apical portions of *C. tetragona* plants (intact green leaves attached to stems) were scanned or photographed as described above to determine their one-sided area per unit area of ground surface (m^2 green biomass area m^{-2} ground). We estimated LAI as twice the one-sided area of this green biomass (Chen and Black, 1992) using three assumptions: (i) green leaf tissue of *C. tetragona* is packed without overlapping or gaps, (ii) green biomass of *C. tetragona* has a square-based parallelepiped shape (Fig. 1), and (iii) auxiliary green branches and small stems of *C. tetragona* with a more flat shape can be considered square-based parallelepipeds as the main stems.

To check these assumptions, we performed tests on *C. tetragona* material from the two Abisko sites, the tree-line heath and the fellfield. After measurement of green biomass area as described above, we divided the green biomass into two cohorts: (i) stems with cross section of 2 mm or larger (i.e. plant parts with a marked square-based parallelepiped shape), and (ii) auxiliary green branches and smaller *C. tetragona* stems (i.e. plant parts with a flatter shape). Leaf area was measured again separately for the two cohorts and LAI was recalculated as the sum of twice the one-side surface of the first cohort and the one-side surface of the second cohort. These recalculated LAI were compared for statistical difference to original LAI estimations.

VEGETATION REFLECTANCE AND NDVI

We determined NDVI from measurements of vegetation reflectance in the near infrared (R_{NIR}; reflectance at 0.725–1.0 μm) and red light (R_{RED}; reflectance at 0.56–0.68 μm) following the equation:

$$\mathrm{NDVI} = (\mathrm{R_{NIR}} - \mathrm{R_{RED}})/(\mathrm{R_{NIR}} + \mathrm{R_{RED}}) \qquad (1)$$

R_{NIR} and R_{RED} were measured for a subset of the plots harvested for the LAI assessment (8 plots at Abisko, 17 at Zackenberg, and 4 at Longyearbyen) as described by Street et al. (2007) using a UniSpec Spectral Analyser (PP Systems International, Amesbury, Massachusetts, U.S.A.) at Zackenberg, or a Skye Instruments SpectroSense2 (Skye Instruments, Powys, U.K.) at Abisko and Longyearbyen. The UniSpec analyzer records complete reflectance spectra from 0.3 μm to 1.0 μm; we selected wavebands of R_{NIR} (0.725–1.0 μm) and R_{RED} (0.56–0.68 μm). The Skye sensor measures total reflected radiation R_{NIR} and R_{RED}. The two instruments agreed well in cross-calibration (Street et al., 2007).

LEAF TRAITS

Leaf traits of *C. tetragona* and other common shrub species (*Betula nana*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Salix polaris* × *herbacea*) were analyzed in detail for material from the plots used for the LAI assessment at the Abisko tree-line heath and the fellfield sites. Specific leaf area (SLA; m^2 leaf kg^{-1} leaf) was determined from measurement of leaf area and biomass. SLA of *C. tetragona* was calculated using area of leaves attached to stems and biomass of leaves detached from stems by peeling. Leaf N concentration (mg N g^{-1} biomass) was determined with a TruSpec CN Determinator (LECO Corporation, St. Joseph, Missouri, U.S.A.) on ground leaf samples. Because peeling of *C. tetragona* is very time-consuming and N analyses costly, we determined SLA and leaf N concentration only for subsets of the

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[1] Wind-exposed site with sparse vegetation (less than ~20% of the total cover) and very dry soil.

TABLE 1

Mean values (with SE when appropriate) of leaf area index (LAI), canopy biomass, total foliar nitrogen (TFN), and nitrogen per leaf area (NLA) obtained by plot harvesting of different plant communities dominated by *Cassiope tetragona* in the subarctic (Abisko) and High Arctic (Zackenberg and Longyearbyen). Plot size varied from 0.01 to 0.04 m^2 at Abisko and 0.03 to 0.09 m^2 at Zackenberg and Longyearbyen.

Area	Plant community (replicates)	LAI m^2 leaf m^{-2} ground	Biomass g m^{-2} ground	TFN g N m^{-2} ground	NLA g N m^{-2} leaf
Abisko	tree-line heath (16)	1.10 (0.06)	150 (10)	1.73 (0.16)[a]	1.67 (0.07)[a]
	fellfield (15)	0.78 (0.05)	112 (7)	1.36 (0.11)[b]	1.83 (0.06)[b]
Zackenberg	valley bottom heath (8)	0.40 (0.05)	54 (11)	n.d.	n.d.
	south facing heath (5)	0.50 (0.07)	56 (8)	n.d.	n.d.
	abrasion plateau (3)	0.41 (0.05)	63 (15)	n.d.	n.d.
	snow bed (2)	0.46	78	n.d.	n.d.
Longyearbyen	dry heath (2)	0.65	98	1.45	2.23
	species-rich heath (2)	0.85	127	1.69	1.99

n.d. = not determined.

[a] 9 replicates.

[b] 8 replicates.

LAI plots ($n = 8$–9). However, for 3 plots of such subsets, we performed extra analyses on *C. tetragona* to test for N concentration differences between (i) current-year vs. non current-year leaves, and (ii) total green leaves vs. total green biomass. Because *C. tetragona* produces smaller leaves in spring than in summer (Callaghan et al., 1989), we considered as current-year growth the biomass from the shoot apex till the first double pair of small leaves. For these samples, the biomass ratio of leaf or stem vs. total green biomass was additionally determined. The water content of the green biomass of *C. tetragona* was determined gravimetrically from measurements of fresh- and dry weight of extra plant samples collected randomly at the tree-line heath and at the fellfield in mid August 2007 ($n = 6$–8).

TFN

TFN was estimated from leaf N concentration and leaf standing biomass specific for each plot and species. As mentioned above, because of time and financial constraints on N analyses, TFN was estimated only for a subset of the plots sampled for LAI ($n = 8$–9 at Abisko and $n = 2$ at Longyearbyen). For plots at Abisko, we used leaf N concentrations as determined above, whereas leaf N concentrations at Longyearbyen were determined with a 2400 Series II CHNS/O analyzer (PerkinElmer, Waltham, U.S.A.). For species not analyzed for N concentration (7% of the total leaf biomass), leaf N concentration was obtained from samples of the same species close to the investigated plot (2% of the total leaf biomass) or assumed equal to leaf N concentration of the dominant species (evergreen for evergreen species; deciduous shrubs for deciduous shrubs and herbs; 5% of the total leaf biomass). Bias due to the last assumption was considered negligible because of the small amount of leaf biomass involved and because leaf N concentration of species of the same functional type (or deciduous and herbs) at the study sites, or at similar plant communities, are comparable, i.e. never exceed a twofold difference (Wielgolaski et al., 1975; Jonasson et al., 1999b; van Wijk et al., 2005; Campioli, 2008).

STATISTICAL ANALYSES

Statistical analyses were conducted using S-PLUS 6.1 (Insightful Corporation, Seattle, U.S.A.). The difference between values of LAI or leaf N concentration was tested with the Student *t*-test (for comparison of two samples) or with one-way ANOVA (for comparison of more than two samples) ($p = 0.05$).

Results and Discussion

LAI, TFN AND CANOPY BIOMASS

LAI was 0.8–1.1 m^2 m^{-2} at Abisko, 0.4–0.5 m^2 m^{-2} at Zackenberg, and 0.7–0.9 m^2 m^{-2} at Longyearbyen (Table 1). LAI of the subarctic heath was substantially larger (1.3–2.8 fold) than LAI of the fellfield and high arctic heaths. This is in agreement with biometric measurements which revealed lower growth and leaf area for *C. tetragona* populations in harsher environments (Havström et al., 1993). Except for Abisko, LAI of communities sampled in the same area did not differ significantly (Table 1). The contribution of *C. tetragona* to total LAI was substantial, varying from 54% to 90% of the community total across all sites. LAI at Zackenberg was larger than indirect estimates reported for *C. tetragona* vegetation in the area (0.2–0.3 m^2 m^{-2}; Soegaard et al., 2000; Groendahl et al., 2007). Apart from these, we are not aware of any other information in the literature about LAI of *C. tetragona* tundras. The LAI of the subarctic tree-line heath is comparable to the LAI of other alpine and subarctic mesic-dry sites such as *Empetrum hermaphroditum* heath (1.3 m^2 m^{-2}; Street et al., 2007) and dry meadow and birch forest understory (about 1.0 and 1.2 m^2 m^{-2}; Berg et al., 1975). On the other hand, the LAI of the fellfield and high arctic *C. tetragona* tundras is similar to the LAI of low elevation heaths in northern Alaska (0.6–0.8 m^2 m^{-2}; Williams and Rastetter, 1999; Williams et al., 2000, 2006) and of mesic-dry tundras dominated by dwarf-shrub vegetation (e.g. *Dryas* spp. and *Salix* spp.) near the study sites in Svalbard and Greenland (0.4–0.5 m^2 m^{-2}; Soegaard et al., 2000; http://ecosystems.mbl.edu/arc/terrest/tracegas/index.shtml).

TFN of *C. tetragona* communities ranged from 1.4 to 1.7 g N m^{-2} ground (Table 1), similar to the TFN of the vascular component of many shrub and heath tundras in northern Sweden and Alaska (Williams and Rastetter, 1999; van Wijk et al., 2005). Canopy biomass was highest for the tree-line heath (150 g m^{-2}), intermediate for the fellfield and high arctic heath at Longyearbyen (100–130 g m^{-2}), and lowest for the high arctic sites at Zackenberg (50–80 g m^{-2}) (Table 1). These estimations match similar records for mesic-dry sites in Alaska (Williams and Rastetter, 1999), high arctic Canada (Svoboda, 1987; Bliss et al., 1987), and Svalbard and Greenland (http://ecosystems.mbl.edu/arc/terrest/tracegas/index.shtml).

METHODOLOGY OF LAI DETERMINATION

Methods of LAI determination based on leaf collection and direct measurement of leaf area are the most accurate and are

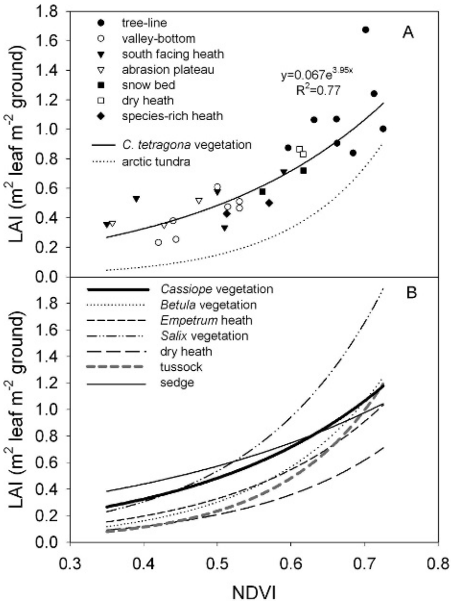

FIGURE 3. Relationship of leaf area index (LAI) vs. normalized difference vegetation index (NDVI) for (A) arctic tundras dominated by *Cassiope tetragona* and generic arctic tundra, and (B) different types of arctic tundras (the LAI-NDVI relationship for generic arctic tundra and for tundras dominated by species other than *C. tetragona* are from Shaver et al., 2007, and Street et al., 2007, respectively). The equation of exponential regression does not include one outlier at LAI = 1.67 m^2 m^{-2}.

important for calibration and corroboration of indirect methods (Jonckheere et al., 2004). The most important assumption of our method to estimate LAI of *C. tetragona*, i.e. that green leaf tissue of *C. tetragona* does not overlap or present gaps along the stems, was corroborated by visual inspection (Campioli, personal observation). In particular, the arrowhead shape of the leaves (Fig. 1A(1)) assures a negligible overlapping between the bottom of an upper leaf and the top of a lower leaf in the leaf scale-like composition of the shoots (Fig. 1A(2)). The absence of significant overlap and gap agrees with basic physiological principles: (i) continuous self-shading of energy-costly green tissue is inefficient, and (ii) a leaf structure with large gaps and increased water losses contrasts to the xeromorphic nature of *C. tetragona*. An accurate comparison between LAI estimates obtained from the surface of the *C. tetragona* leaf-stem combinations and from the total area of *C. tetragona* leaves peeled off the stems cannot be done because removing individual leaves causes leaf damage and leaf desiccation. Furthermore, the assumption that auxiliary green branches and small stems with a rather flat shape can be considered square-based parallelepipeds, as the main stems, does not affect the LAI estimation. Because of their low amount (5% of the total green biomass), the LAI overestimation caused by neglecting such evidence is minor (3–8%) and not significant. These considerations and, as shown above, the very close agreement between the LAI of *C. tetragona* vegetation and the LAI of other mesic-dry arctic sites with similar climate and soil fertility make us confident about the soundness of the method applied.

LAI-NDVI RELATIONSHIP

LAI and NDVI for *C. tetragona* tundras showed a high correlation ($p < 0.0001$), with a low root mean squared error of LAI prediction (0.14 m^2 m^{-2}) (Fig. 3a), as observed for other tundra plant communities (van Wijk and Williams, 2005; Williams et al., 2006; Street et al., 2007). Such a relationship can therefore be used to determine indirectly LAI of plant communities dominated by *C. tetragona* from measures of vegetation reflectance.

The LAI-NDVI relationship may vary significantly between tundra vegetation types according to canopy structure (e.g. vertical vs. horizontal canopy development, exposed ground fraction, presence of nonvascular vegetation and litter) and leaf characteristics (e.g. structure, orientation, and color) (Steltzer and Welker, 2006; Street et al., 2007). *Cassiope tetragona* communities generally have low NDVI (especially for LAI $<$ 0.8 m^2 m^{-2}; Fig. 3b), likely due to the erect nature of its green shoots which do not cover the bare ground and the light-grayish and very abundant attached dead leaves. The LAI-NDVI relationship for *C. tetragona* was, however, similar to those of other tundra vegetation types characterized by low NDVI such as sedge, affected also by abundant litter, and, at low LAI, *Salix* vegetation, characterized by gray-green leaves (Fig. 3b; Street et al., 2007). On the other hand, the LAI-NDVI relationship for *C. tetragona* vegetation differed markedly from generic LAI-NDVI relationships for arctic tundra (van Wijk et al., 2005; Shaver et al., 2007; Fig. 3a), which are therefore inadequate to estimate *C. tetragona* LAI. Such discrepancy was recorded because tussock, *B. nana*, and heath communities showed, for similar values of NDVI, much lower LAI (Fig. 3b).

Soegaard et al. (2000) estimated LAI for a high arctic *C. tetragona* heath by using a linear relationship between LAI and the ratio between reflectance in the near infrared and red light. However, tests revealed that the correlation between LAI and the R_{NIR}/R_{RED} ratio at our sites was low ($R^2 = 0.18$) and therefore inadequate to be used as an indirect method to estimate LAI. Regression of measured LAI vs. predicted LAI using the model of Soegaard et al. (2000) revealed that it performs rather poorly at our sites (slope of 0.97 but intercept of 0.34; $n = 29$).

LEAF TRAITS

SLA of *C. tetragona* was 12 m^2 kg^{-1} (Table 2), which is similar to or less than the SLA of deciduous species common at the investigated sites (11–17 m^2 kg^{-1}) but larger than the SLA of arctic evergreen shrubs (4–7 m^2 kg^{-1}; van Wijk et al., 2005). These results agree with observations on leaf thickness, found for *C. tetragona* to be intermediate between leaf thickness of evergreen and deciduous shrubs (Kudo et al., 1999). SLA of *C. tetragona* did not differ significantly between the subarctic tree-line heath and the fellfield (Table 2). Populations of *C. tetragona* growing in different climatic conditions might vary in leaf size because of trade-offs between protection against desiccation and light interception, but larger leaf size regularly corresponds to larger leaf biomass and thus constant SLA in *C. tetragona* (Havström et al., 1993).

Nitrogen concentration of current-year leaves of *C. tetragona* was significantly larger than N concentration of older *C. tetragona* leaves (Table 2), as observed for other evergreen species (Jonasson, 1989; Campioli, 2008). Similarly, the leaf N concentration of *C. tetragona* was comparable to other arctic evergreen shrubs (van Wijk et al., 2005; Campioli, 2008) but lower than in deciduous species at the same sites (e.g. *Betula nana* at the tree-line heath: 14.8 mg N g^{-1}; *Salix polaris* × *herbacea* at the fellfield: 17.4 mg N g^{-1}) or at other arctic locations (van Wijk et al., 2005). The leaf N concentration of *C. tetragona* at the fellfield was larger than at the tree-line heath (Table 2), likely because of the shorter growing season at the fellfield. Nitrogen concentration of the total green

TABLE 2

Leaf traits of *Cassiope tetragona* at a subarctic tree-line heath and fellfield: nitrogen per leaf mass (NLM; mean and SE; $n = 3–9$), leaf area per mass (LAM; mean and SE; $n = 8–9$) and nitrogen per leaf area (NLA; derived from NLM and LAM) (samples taken in late July–mid August). LAM coincides with the specific leaf area (SLA) when the mass of total green leaves rather than total green mass is considered.

	Tissue *C. tetragona*	NLM mg N g^{-1} mass	LAM m^2 leaf kg^{-1} mass	NLA mg N m^{-2} leaf
Tree-line heath	current-year leaves	12.6 (0.2)	n.d.	n.d.
	old green leaves	8.2 (0.3)	n.d.	n.d.
	total green leaves	10.1 (0.2)	11.9 (1.6)	0.85[b]
	total green biomass[a]	9.8 (0.2)	5.2 (0.1)	1.89
Fellfield	current-year leaves	14.2 (0.4)	n.d.	n.d.
	old green leaves	11.0 (1.0)	n.d.	n.d.
	total green leaves	11.9 (0.8)	12.1 (0.7)	0.98[b]
	total green biomass[a]	10.7 (0.5)	5.5 (0.1)	1.94

n.d. = not determined.

[a] Total green biomass: green leaves plus stem covered by green leaves.

[b] This value of NLA is not to be compared to ecosystem NLA or NLA of other species because it is derived from detached leaves of *Cassiope tetragona* and it does not account for the peculiar leaf morphology of *C. tetragona* and the parallelepiped shape of its leaf-stem combination.

biomass of *C. tetragona* was slightly lower than the N concentration of the total green leaves (3–10%), because of the lower N content of the stem (e.g. 7.9 mg N g^{-1} stem at the tree-line heath) which accounted for about 14–15% of the total green biomass. However, the difference was not significant and therefore N concentration of the total green tissue can be used as a surrogate of foliar N for *C. tetragona*.

The water content of the green biomass of *C. tetragona* at the tree-line heath and at the fellfield did not differ significantly (67–73 g H_2O 100 g^{-1} green biomass).

LEAF AREA-BIOMASS RELATIONSHIP

The constancy of SLA and water content for *C. tetragona* and the strong correlation between leaf area and green biomass ($p < 0.0001$; Fig. 4), allow the latter relationship to be used to estimate leaf area of *C. tetragona* from measurement of biomass. The leaf area–green biomass relationship for *C. tetragona* can be used as a straightforward indirect method to estimate LAI in case of time limitation (e.g. for communities with lush *C. tetragona* vegetation, the direct measurement of leaf area is time consuming) or when a planimeter for leaf area detection is not readily available at the field laboratory for a quick processing of the samples.

TFN-LAI RELATIONSHIP

The relationship between TFN and LAI showed high correlation ($p < 0.0001$; Fig. 5), indicating that TFN can be derived from measurements of LAI for *C. tetragona* tundras. The slope of the TFN-LAI relationship, i.e. the nitrogen per leaf area (NLA), was 1.78 g N m^{-2} (Fig. 5), with some variation across communities (1.7–2.2 g N m^{-2}; Table 1). At species level, the NLA of *C. tetragona* (1.89–1.94 g N m^{-2}; Table 2) was larger than the NLA of the deciduous species (1.30–1.78 g N m^{-2}).

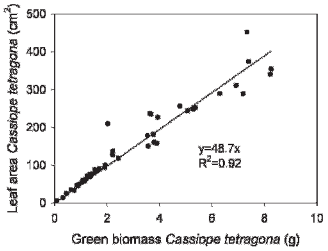

FIGURE 4. Relationship of leaf area vs. green biomass of *Cassiope tetragona* for arctic tundras dominated by *C. tetragona*.

A tight correlation between TFN and LAI is common for tundra ecosystems (Williams and Rastetter, 1999; van Wijk et al., 2005). Furthermore, van Wijk et al. (2005) found a generic TFN-LAI relationship for both Swedish and Alaskan tundra up to an LAI of 1 m^2 m^{-2}. A comparison of our data with the ones published by van Wijk et al. (2005) revealed no significant difference in the slope of our TFN-LAI relationship for *C. tetragona* tundra and their generic value for arctic tundra (1.9 g N m^{-2}). The inclusion of *C. tetragona* tundra would have a minimal impact (1% variation) on the slope and the correlation parameters of the generic relationship. Thus, the latter can be used to derive TFN also in arctic landscapes with plant communities dominated by *C. tetragona*.

Conclusions

LAI of *C. tetragona* can be determined from area measurement of leaves attached to the stem. This is easily done by doubling the one side area of the *C. tetragona* leaf-stem combinations. Furthermore, LAI of *C. tetragona* tundra can be determined from measurements of vegetation reflectance through a LAI-NDVI relationship. TFN can be determined in two ways also: directly, from measurement of leaf N concentration and biomass, or indirectly, by using a TFN-LAI relationship and measurements of LAI. However, the LAI-NDVI relationship for *C. tetragona* differs from the LAI-NDVI generic relationship for

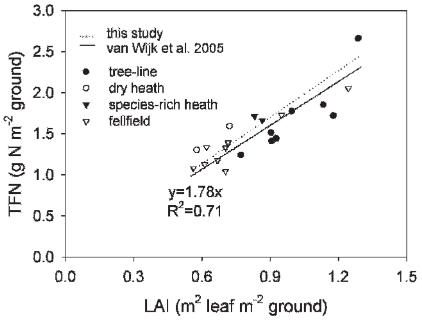

FIGURE 5. Relationship of total foliar nitrogen (TFN) vs. leaf area index (LAI) for different arctic communities dominated by *Cassiope tetragona*. The TFN-LAI relationship for generic arctic tundra (van Wijk et al., 2005) is also shown.

arctic tundra. This complicates the problem of scaling up in heterogeneous arctic landscapes because a single LAI-NDVI relationship does not seem to be appropriate for the entire Arctic. On the other hand, the TFN-LAI relationship for *C. tetragona* tundra does not differ from the generic TFN-LAI relationship for arctic communities and, therefore, a single relationship is adequate to derive regional value of TFN from regional averages of LAI.

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References Cited

ACIA, 2004: *Impact of a Warming Arctic: Arctic Climate Impact Assessment*. Cambridge and New York: Cambridge University Press, 140 pp.

Baddeley, J. A., Woodin, S. J., and Alexander, I. J., 1994: Effects of increased nitrogen and phosphorus availability on the photosynthesis and nutrient relations of three arctic dwarf shrubs from Svalbard. *Functional Ecology*, 8: 676–685.

Bay, C., 1998: *Vegetation mapping of Zackenberg valley, Northeast Greenland.* Danish Polar Center and Botanical Museum, University of Copenhagen, 29 pp, http://www.dpc.dk/sw13186.asp.

Berg, A., Kjelvik, S., and Wielgolaski, F. E., 1975: Measurements of leaf areas and leaf angles of plants in Hardangervidda, Norway. *In* Wielgolaski, F. E. (ed.), *Fennoscandian Tundra Ecosystems. Part 1: Plants and Microorganisms* Springer-Verlag: Berlin, 103–110.

Berglund, B. E., Barnekow, L., Hammarlund, D., Sandgren, P., and Snowball, I. F., 1996: Holocene forest dynamics and climate changes in the Abisko area, northern Sweden—The Sonesson model of vegetation history reconsidered and confirmed. *Ecological Bulletins*, 45: 15–30.

Bliss, L. C., Kerik, J., and Peterson, W., 1987: Primary production of dwarf shrub heath communities, Truelove Lowland. *In* Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem*. Edmonton: University of Alberta Press, 217–224.

Callaghan, T. V., Carlsson, B. A., and Tyler, N. J. C., 1989: Historical records of climate-related growth in *Cassiope tetragona* from the Arctic. *Journal of Ecology*, 77: 823–837.

Campioli, M., 2008: *Carbon allocation in ecosystems: an experimental and modelling approach for tundra and forest vegetations. PhD thesis*. Ghent, Belgium: Ghent University, 177 pp.

Campioli, M., Michelsen, A., Demey, A., Vermeulen, A., Samson, R., and Lemeur, R., 2009: Net primary production and carbon stocks for subarctic mesic-dry tundras with contrasting microtopography, altitude, and dominant species. *Ecosystems*, 12: 760–776.

Chen, J. M., and Black, T. A., 1992: Defining leaf area index for non-flat leaves. *Plant Cell and Environment*, 15: 421–429.

Christiansen, H. H., and Humlum, O., 1993: Glacial history and periglacial landforms of the Zackenberg area, Northeast Greenland: Preliminary results. *Geografisk Tidsskrift*, 93: 19–29.

Graglia, E., Jonasson, S., Michelsen, A., Schmidt, I. K., Havström, M., and Gustavsson, L., 2001: Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography*, 24: 5–12.

Groendahl, L., Friborg, T., and Soegaard, H., 2007: Temperature and snow-melt controls on interannual variability in carbon exchange in the High Arctic. *Theoretical and Applied Climatology*, 88: 111–125.

Grogan, P., and Jonasson, S., 2005: Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biology*, 11: 465–475.

Havström, M., Callaghan, T. V., and Jonasson, S., 1993: Differential growth-responses of *Cassiope tetragona*, an arctic dwarf shrub, to environmental perturbations among three contrasting high sites and sub-arctic sites. *Oikos*, 66: 389–402.

Illeris, L., König, S. M., Grogan, P., Jonasson, S., Michelsen, A., and Ro-Poulsen, H., 2004: Growing-season carbon dioxide flux in a dry subarctic heath: responses to long-term manipulations. *Arctic Antarctic, and Alpine Research*, 36: 456–463.

Jonasson, S., 1989: Implications of leaf longevity, leaf nutrient reabsorption and translocation for the resource economy of five evergreen plant species. *Oikos*, 56: 121–131.

Jonasson, S., Michelsen, A., and Schmidt, I. K., 1999a: Coupling of nutrient cycling and carbon dynamics in the Arctic; integration of soil microbial and plant processes. *Applied Soil Ecology*, 11: 135–146.

Jonasson, S., Michelsen, A., Schmidt, I. K., and Nielsen, E. V., 1999b: Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. *Ecology*, 80: 1828–1843.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., and Baret, F., 2004: Review of methods for *in situ* leaf area index determination—Part I. Theories, sensors and hemispherical photography. *Agricultural and Forest Meteorology*, 121: 19–35.

Kudo, G., Nordenhall, U., and Molau, U., 1999: Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: comparisons along a snowmelt gradient in northern Sweden. *Ecoscience*, 6: 439–450.

Lønne, I., and Nemec, W., 2004: High-arctic fan delta recording deglaciation and environment disequilibrium. *Sedimentology*, 51: 553–589.

Michelsen, A., Jonasson, S., Sleep, D., Havström, M., and Callaghan, T. V., 1996: Shoot biomass, delta C^{13}, nitrogen and chlorophyll responses of two arctic dwarf shrubs to *in situ* shading, nutrient application and warming simulating climatic change. *Oecologia*, 105: 1–12.

Molau, U., 1997: Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. *Global Change Biology*, 3: 97–107.

Nams, M. L. N., and Freedman, B., 1987a: Ecology of heath communities dominated by *Cassiope tetragona* at Alexandra Fiord, Ellesmere Island, Canada. *Ecography*, 10: 22–32.

Nams, M. L. N., and Freedman, B., 1987b: Phenology and resource allocation in a high arctic evergreen dwarf shrub, *Cassiope tetragona*. *Ecography*, 10: 128–136.

Rennermalm, A. K., Soegaard, H., and Nordstroem, C., 2005: Interannual variability in carbon dioxide exchange from a high arctic fen estimated by measurements and modeling. *Arctic, Antarctic, and Alpine Research*, 37: 545–556.

Shaver, G. R., Street, L. E., Rastetter, E. B., van Wijk, M. T., and Williams, M., 2007: Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, 95: 802–817.

Sigsgaard, C., Petersen, D., Groendahl, L., Thorsøe, K., Meltofte, H., Tamstorf, M., and Hansen, B. U., 2006: The Climate Basis and GeoBasis programmes. *In* Klitgaard, A. B., Rasch, M., and Caning, K. (eds.), *Zackenberg Ecological*

Research Operations, 11th Annual Report, 2006. Copenhagen: Danish Polar Center, 11–35.

Soegaard, H., Nordstroem, C., Friborg, T., Hansen, B. U., Christensen, T. R., and Bay, C., 2000: Trace gas exchange in a high-arctic valley 3. Integrating and scaling CO_2 fluxes from canopy to landscape using flux data, footprint modeling, and remote sensing. *Global Biogeochemical Cycles*, 14: 725–744.

Steltzer, H., and Welker, J. M., 2006: Modeling the effect of photosynthetic vegetation properties on the NDVI-LAI relationship. *Ecology*, 87: 2765–2772.

Street, L. E., Shaver, G. R., Williams, M., and van Wijk, M. T., 2007: What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems? *Journal of Ecology*, 95: 139–150.

Svoboda, J., 1987: Ecology and primary production of raised beach communities, Truelove Lowland. *In* Bliss, L. C. (ed.), *Truelove Lowland, Devon Island, Canada: a High Arctic Ecosystem*. Edmonton: University of Alberta Press, 185–216.

van Wijk, M. T., and Williams, M., 2005: Optical instruments for measuring leaf area index in low vegetation: application in arctic ecosystems. *Ecological Applications*, 15: 1462–1470.

van Wijk, M. T., Williams, M., and Shaver, G. R., 2005: Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia*, 142: 421–427.

Watson, D. J., 1947: Comparative physiological studies in the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Annals of Botany*, 11: 41–76.

Wielgolaski, F. E., Kjelvik, S., and Kallio, P., 1975: Mineral content of tundra and forest plants in Fennoscandia. *In* Wielgolaski, F. E. (ed.), *Fennoscandian Tundra Ecosystems. Part 1: Plants and Microorganisms*. Berlin: Springer-Verlag, 316–332.

Williams, M., and Rastetter, E. B., 1999: Vegetation characteristics and primary productivity along an arctic transect: implications for scaling-up. *Journal of Ecology*, 87: 885–898.

Williams, M., Eugster, W., Rastetter, E. B., McFadden, J. P., and Chapin, F. S., 2000: The controls on net ecosystem productivity along an arctic transect: a model comparison with flux measurements. *Global Change Biology*, 6: 116–126.

Williams, M., Street, L. E., van Wijk, M. T., and Shaver, G. R., 2006: Identifying differences in carbon exchange among arctic ecosystem types. *Ecosystems*, 9: 288–304.

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