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Topographic controls on the leaf area index and plant functional type of a tundra ecosystem

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Summary

1. Leaf area index (LAI) is an emergent property of vascular plants closely linked to primary production and surface energy balance. LAI can vary by an order of magnitude among Arctic tundra communities and is closely associated with plant functional type.

2. We examined topographic controls on vegetation type and LAI distribution at two different scales in an Arctic tundra ecosystem in northern Sweden. 'Micro-scale' measurements were made at 0.2-m resolution over a 40 m × 40 m domain, while 'macro-scale' data were collected at approximately 10-m resolution over a 500 m × 500 m domain. Tundra LAI varied from 0.1–3.6 at the micro-scale resolution and from 0.1–1.6 at the macro-scale resolution.

3. The correlation between dominant vascular species and LAI at the micro-scale ($r^2 = 0.40$) was greater than the correlation between dominant vegetation and LAI at the macro-scale ($r^2 = 0.14$). At the macro-scale, LAI was better explained by topographic parameters and spatial auto-correlation (pseudo $r^2 = 0.32$), than it was at the micro-scale ($r^2 = 0.16$). Exposure and elevation were significantly but weakly correlated with LAI at the macro-scale, whereas the most significant explanatory topographic variable was elevation ($r^2 = 0.12$).

4. The distribution of plant communities at both scales was significantly associated with topography. Shrub communities, dominated by *Betula nana*, were associated with low elevation sites, while more exposed and higher elevation sites were dominated by cryptogams.

5. Synthesis. Dominant vegetation, topography, and LAI were linked at both scales of investigation. But, for explaining LAI, topography became more important and dominant vegetation less important at the coarser scale. The explanatory power of dominant species/functional type for LAI variation was weaker at coarser scales, because communities often contained more than one functional type at 10 m resolution. The data suggest that remotely sensed topography can be combined with remotely sensed optical measurements to generate a useful tool for LAI mapping in Arctic environments.

Key-words: Arctic vegetation, geostatistics, leaf area index, multi-scale analysis, terrain indices, topography, spatial auto-regression

Introduction

The recent rate of warming in the Arctic has been two to three times the global average rate (Kattsov & Källén 2005), and may be accelerated by a vegetation-albedo feedback (Chapin et al. 2005). Warming is likely to result in significant changes in the distribution and structure of Arctic vegetation (Sturm et al. 2005), with important implications for land surface properties such as the leaf area index (LAI). Predicting future changes in LAI requires a better understanding of the present distribution of Arctic vegetation, its physical and biological determinants, and the relationship between LAI and vegetation composition.

Leaf area index (LAI) is an emergent property of assemblages of vascular plants, strongly linked to albedo, primary production, evapotranspiration, surface energy balance and biogeochemical cycling (Williams et al. 2001; Shaver et al. 2007; Street et al. 2007). To predict the ecosystem exchange of
CO₂ in Arctic ecosystems, it is not necessary to identify species or describe the vegetation, other than to estimate leaf area (Shaver et al., 2007). This primary importance of LAI in carbon (C) cycling is consistent with recent studies demonstrating a powerful convergence in vegetation-canopy architecture, specifically between ecosystem LAI and total foliar nitrogen (N), among diverse low Arctic ecosystems (Williams & Rastetter, 1999; Van Wijk et al., 2005). However, uncertainty in the temporal and spatial distribution of LAI (Williams & Rastetter, 1999; Van Wijk et al., 2005) limits efforts to predict Arctic photosynthesis and C cycling at multiple spatial scales (Williams et al., 2001). Asnentiel (2003) found that spatial LAI variability in the Arctic was higher than any of the other 13 Biomes investigated. It is therefore necessary to improve understanding of the spatial distribution of Arctic LAI to estimate reliably the effects of climate change on tundra ecosystems.

The high variability in LAI in Arctic ecosystems is related to high diversity in plant functional types (PFTs). These deciduous, evergreen, woody, and herbaceous species (Shaver & Chapin, 1991) and high degrees of spatial heterogeneity in PFTs across a range of scales within Arctic ecosystems (Williams et al., 2008). Vegetation assemblages are governed through the selection of individual plants through series of environmental filters (for example, resources, conditions, disturbance), operating on a hierarchial scale (Lavorel & Garnier, 2002). The filters in Arctic ecosystems have generally been identified as primarily nutritional (Shaver et al., 1986; Shaver, 1992; Van Wijk, 2004), but with other important factors including tolerance to winter desiccation, soil freezing, and water logging (Shaver & Chapin, 1991). The heterogeneity in vegetation suggests a highly variable distribution of environmental filters at similar scales. These exposed heaths tend to be dominated by evergreen, deciduous shrubs, which are the most competitive in terms of light capture and utilisation (Shaver, 1996). Tolerance of these exposed sites, which may have shallow or no snow cover, to extreme low winter temperatures, thus increasing rates of nutrient cycling (Nobrega & Grogan, 2007) and development that determine spatial patterns of LAI in Arctic ecosystems: (i) snow cover; (ii) climate, through direct effects of temperature, insolation and wind on plant development; (iii) hydrology, through its effect on soil moisture; (iv) soil/substrate variability, determining soil nutrients and soil water status; (v) biodiversity, determining the species pool and (vi) disturbance and site history, including the effects of herbivory and ecosystem management.

The first four controls are broadly related to the topography and form the focus of this study. We examine four related hypotheses to test the relative importance of topographical controls on LAI distribution in Arctic ecosystems. Our hypotheses (H1–H4) are that the primary constraint on LAI distribution is through environmental filters determined by either (H1) topographic parameters like elevation, slope and aspect, (H2) estimated landscape soil moisture, (H3) topographic exposure and associated likelihood of snow cover or (H4) derived potential isolation.

The relationships between topographic variables and LAI may vary with scale. The relationships between insolation, exposure and micro-topographical (0.1–1 m) versus macro-topographical (50–100 m) scales, Hydrological variability may be important across a range of scales, from hummocks to hill slopes. There are close links among the controls, which complicate attribution. For instance, soil conditions affect infiltration, hydraulic conductivity, and plant-water availability (Darmody et al., 2004).

We tested the hypothesis that at two different scales, defined by the horizontal resolution of a given LAI data set, the first scale was with 0.2 m horizontal resolution LAI data within a 40 m × 40 m micro-scale area, and the second was with approximately 10 m resolution LAI data within a 500 m × 500 m macro-scale area. Detailed digital elevation maps (DEM) were available at both scales with inappropriate resolutions. Vegetation community information was collected at both scales, allowing investigation into the connection between topography, dominant species and LAI.

This study is novel in that it uses a uniquely detailed data set, on plant community distribution, LAI and topography, to investigate vegetation-environment interactions. The data were collected at two resolutions, allowing the influence of scale and topography to be properly determined for the first time in Arctic tundra. We used statistical techniques that quantify spatial auto-correlation for appropriate fitting of geostatistical models. An additional goal of the paper was to demonstrate how topographic data can be used to improve landscape mapping of LAI, that is most frequently undertaken using remote sensing of land surface reflectance (Raynolds et al., 2006).

**Methods**

**STUDY SITE**

The study was located on the south-eastern slope of the Abisko ‘intensive valley’ site (IV), lies within a
small (approximately 30 ha) catchment in a tr ansition zone that intersects the local tree line (Williams et al. 2008). The IV has a gentle (approximately 5%) slope from south to north with an average elevation of approximately 620 m (Fig. 1). A stream runs through the centre of the study area. The Abisko weather station recorded an average annual rainfall of 300–400 mm per annum and an average temperature of –1°C (ASRS 2007). The hill slopes surround the IV reflecting an extensive cover of glacial and fluvial glacial deposits, with hummocks and depressions at spatial frequencies on the order of several metres.

VEGETATION DESCRIPTION

An herb-rich, low-diversity, cryptogam community dominated by grey-leaved Salix spp., with Betula nana understory. Dwarf birch was a community dominated by Betula nana, with the evergreen dwarf shrubs Empetrum hermaphroditum and to a lesser extent Vaccinium vitis-idaea. The hea th community comprised the same species as observed in the dwarf birch community, but was lower-growing and dominated by E. hermaphroditum. Themoss communities were typified by Sphagnum spp. and characterised by the presence of Rubus chamaemorus, among other herb and graminoid species as observed in the dwarf birch community, but was lower-growing and dominated by E. hermaphroditum.

INSTRUMENTS

Obtained with a Skye Instruments 2 Channel Sensor SKR1800 (Skye Instruments, UK), channel 1 = 0.56–0.68 nm, channel 2 = 0.725–1.1 nm) with the diffuser off, held 0.9 m above the ground for each microplot (Fig 1b). Withineach f the ninemicro-scale-plot, indirect NDVI measurements were obtained by combining: (i) Normalised Difference Vegetation Index (NDVI) obtained with a SkyE Instruments 2 Channel Sensor SKR1800 (Skye Instruments, Po wys, UK, channel 1 = 0.56–0.68 nm, channel 2 = 0.725–1.1 nm) with the diffuser off, held 0.9 m above the ground (referreredtohereafterasSkyeNDVI); and (ii) LAI estimate by LI-COR LAI-2000 (Canopy Analyzer, LI-COR, Lincoln, NE), collecting one above- and one below- canopy measurement (referredtoas LAI-2000 LAI). The pair ed LAI-2000 and NDVI measurements were conducted on regular grid.4 m x 4 m grid in every 4th microplot, giving a total of 5625 measurements. Subsequent y, needledriver harvest measurements (0.2 m x 0.2 m) f vascular plant LAI were taken for each micro-scale-plot (n=81). With ese results, we selected data to calibrate a model that combined the NDVI and LAI-2000 observations to generate an improved LAI estimate (van Wijk & Williams 2005). The 95% confidence interval of the direct LAI estimation varied from 0.07 to 0.2 over a range of LAI from 0–1.5 (Van Wijk & Williams 2005). Before each destructive harvest the dominant vascular plant species in each 0.2 m x 0.2 m quadrat were determined by visual cover. We defined the dominant vascular species as the most abundant based on cover.

Macro-scale measurements were collected on 14–25 August 2004, in a 500 m x 500 m area encompassing the micro-scale study site. The macro-scale area was subdivided into one hundred 50 m x 50 m plots. Sixteen of these plots were further subdivided into nine intensive 10 m x 10 m plots, giving 228 measurement locations (Fig. 1). The central intensive plots corresponded with the sample plots at the micro-scale area. At the centre of each of the macro-scale sampling points, an NDVI measurement was made using the Skye sensor with the diffuser on and suspended at 2 m above ground level, resulting in a nominal resolution of approximately 10 m in diameter. Macro-scale measurements of LAI were obtained using the calibration developed from the micro-scale data (Van Wijk & Williams 2005), with a detailed recalibration tool. The NDVI measurements (Williams et al. 2008). The root-mean-square error of LAI determination was not reported in the study. We thus believe that our results are robust to the differences.

LAI MEASUREMENTS

Measurementsof LAI were conducted on a nested sampling grid at two spatial scales in the IV (Fig. 1) during the Arctic summer. All location measurements were recorded in the Universal Transverse Mercator (UTM) projection; zone 34 North, WGS 1984 datum.

Micro-scale measurements were collected from 10–31 July 2002 within a 40 m x 40 m area centred on the stream in the foot slopes of the IV. The micro-scale measurements were made in 10 m x 10 m plots, giving a total of 5625 measurements. Subsequent y, needledriver harvest measurements (0.2 m x 0.2 m) f vascular plant LAI were taken for each micro-scale-plot (n=81). With ese results, we selected data to calibrate a model that combined the NDVI and LAI-2000 observations to generate an improved LAI estimate (van Wijk & Williams 2005). The 95% confidence interval of the direct LAI estimation varied from 0.07 to 0.2 over a range of LAI from 0–1.5 (Van Wijk & Williams 2005). Before each destructive harvest the dominant vascular plant species in each 0.2 m x 0.2 m quadrat were determined by visual cover. We defined the dominant vascular species as the most abundant based on cover.

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DIGITAL ELEVATION MODEL

A digital elevation model (DEM) was produced for the micro-scale site by manually surveying each of the 5625 sample locations with a level and a survey pole. The software SURFER was used to determine the 3D surface. The location of each plot was determined to an accuracy of ±6 m using a handheld GPS. Some plots (n=31) had overlapping birch treestorey and were excluded from all subsequent analyses. We considered only the remaining 197 tundra vegetation plots in this study. The data set included a visual estimate of cover, the rank density of the main vegetation cover types, including vascular plants, mosses, and lichens, for each plot. We defined the dominant vegetation based on the vegetation with the most abundant cover.

LAI surveys at the two scales were conducted two years apart. However, both surveys were conducted in the peak season of maximum vegetation growth, based on phenological studies at this site (Street et al. 2007). We thus believe that our results are robust to the differences in sampling time.

Fig. 1. (a) Digital elevation model of study site near Abisko, Sweden, showing the extent of the ‘macro-scale’ study area. Macro-scale measurements of LAI and vegetation type were recorded at each location marked with a black circle. The location of the nine micro-scale plots are indicated by black circles. The coordinates are in UTM (m), with east on the x axis and north on the y-axis. The contours are in m above a local datum.

(b) Digital elevation model of study site near Abisko, Sweden, showing the extent of the ‘macro-scale’ study area. Macro-scale measurements of LAI and vegetation type were recorded at each location marked with a black circle. The location of the nine micro-scale plots are indicated by black circles. The coordinates are in UTM (m), with east on the x axis and north on the y-axis. The contours are in m above a local datum.
using minimum values for the last return pulse. Estimated elevation errors were approximately 1 m. Missing data values were interpolated using IDW and standard pit removal procedures were undertaken in ArcInfo.

For both micro-scale and macro-scaled data, a series of topographic indices were generated to describe slope aspects and surface curvature from the DEM. By taking quadratic approximations of the first and second derivatives of the surface (Evans, 1980), the slope was simply the first derivative of the elevation surface, while the curvature was given by the Laplacian of the DEM. Aspect was derived from directional terrain slope using the Shortwave function for each time step, taking into account the instantaneous terrain effects (slope and aspect). Shadows were avoided by extending the DEM beyond the LAI data extent.

### TERRAIN INDICES

The compound topographic index (CTI) was developed to summarize landscape elevation and moisture (Beven, 1977). CTI was calculated using surface drainage characteristics of the DEM, namely the upslope area ($A_u$) and local slope ($β$) (eqn 1). $A_u$ was estimated in ArcInfo and $β$ was set to 45° for most of the region. The process was repeated at a number of increasing time steps, so terrain adjacency issues were avoided by extending the DEM beyond the LAI data extent.

$$\text{CTI} = \ln (\frac{A_u}{\tan(β)})$$  

(eqn 1)

Potential incoming shortwave radiation was calculated over the growing season (mid-May to mid-September), using the Shortwave AML (Kumar et al., 1997) for ArcInfo. The model calculated the solar radiation at each time step (30 min), taking into account instantaneous terrain effects (slope and aspect). Shadows were projected on the surface at each time step, so terrain adjacency issues were also accounted for (Kumar et al., 1998). Higher scores were associated with moist sites.

### DATA TRANSFORMATION AND MODEL TESTING

Prior to analysis, it was ensured that the pooled LAI data approximated normal distribution using Box-Cox transformation (Box & Cox, 1964). The Box-Cox transform ($Y_{bc}$) of a variable $Y$ given by equation 2. The power parameter $λ$ was estimated by maximum likelihood methods.

$$Y_{bc} = \left( \frac{Y}{λ} - 1 \right) / λ$$  

(eqn 2)

Ordinary least squares (OLS) regressions were fitted to the transformed data (LAI) to assess the significance of the derived terrain indices and model goodness of fit.

### ORDINATION METHODS

Because of the large dataset used for the micro-scale analysis, some degree of data thinning was required for practicality and hypothesis testing. Topographic variables were selected based on initial partitioning of the parameter space using regression trees (Breiman, 1984). The regression tree selects variables that are best able to classify the response (LAI) into distinct clusters in parameter space. The process proceeds by forward selection (binary recursive partitioning), splitting the data set using the predictor variable that explains the maximum amount of the remaining deviance in the response variable. The process results in a series of splitting rules, by which parameter space can be partitioned into ordered categories of LAI.

### STATISTICS TO MEASURE SPATIAL DEPENDENCY

To assess the validity of OLS, wetness for auto-correlation in LAI, using Moran’s I test (Moran, 1950). Moran’s tests for significant correlation in neighbouring points controlled for the overall variance in the dataset. Semi-variograms (Cressie, 1989) were used to quantify the spatial auto-correlation of the data. We explored semi-variograms in terms of spatial continuity of the data. The theoretical exponential function, which is known to be perform well, was chosen (Christakos, 1984; Mbratney & Webster, 1986). Spatial variation was characterized by the range ($τ$) parameter at zero separation, indicating noise or variability at smaller scales; while auto-correlation was observed, and a ‘nuget’ ($ρ$) parameter at zero separation, indicating noise or variability at smaller scales; while auto-correlation was observed, and a ‘nuget’ ($ρ$) parameter at zero separation, indicating noise or variability at smaller scales than those observed.

### SPATIAL REGRESSION MODELS

To account for spatial auto-correlation, we implemented spatial lattice modelling using maximum likelihood (ML) methods. Spatial lattice models were designed for data sampled on a grid, and include the effects of spatial auto-correlation by incorporating information on sample adjacency when fitting regressions. Adjacency was quantified using the semi-variogram model, $κ$ and $κ$ was fitted by ML methods. Two additional parameters, $τ$ and $ρ$, describe the spatial correlation structure. The spatial Durbin model was the most complex model fitted, and incorporates the spatially lagged response, along with spatially lagged predictors, i.e. neighborhood effects for all topographic variables tested, and an LAI auto-correlation term. Details of these models can be found in the Appendix.

Lattice models were not feasible for the micro-scale data, due to computational restrictions on the 7625 data points. Instead, we fitted spatial analysis of covariance (ANCOVA) models on a continuous spatial metric. The ANCOVA was fitted by ML methods, with two additional parameters $τ$ and $ρ$, to describe the spatial correlation structure, as defined by the semi-variogram. All statistical analyses were carried out in R version 2.4.1 (R Foundation for Statistical Computing, Vienna, Austria).
Results

The micro-scale LAI data were heavily skewed (skewness = 0.23), with most values between 0–1, but some values up to approximately 3 (Williams et al., 2008). The macro-scaled data were more normally distributed, because of averaging occurring at a resolution of approximately 10 m (Williams et al., 2008). A Box-Cox transformation resulted in a normal distribution for all data, and a constant was added to the transformed LAI data to make them strictly positive. The maximum likelihood estimate of transformation parameter $\lambda$ was 0.4. Unless otherwise stated, all analyses were undertaken using the transformed variable LAI $\tilde{L}$.

**MICRO-SCALE ANALYSIS**

The median transformed LAI of the micro-scale data was 0.9, ranging from 0.1 to 3.6. Elevation ranges from 615 to 618 m, with a mean of 616.6 m. Slopes were generally moderate, with 74% of all observations facing east, 23% facing south, and 32% facing west. Slopes were generally moderate, with 74% of all observations facing east, 23% facing south, and 32% facing west. Slopes were generally moderate, with 74% of all observations facing east, 23% facing south, and 32% facing west.

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| Parameter | Estimate | Standard error | $r$ value | $P(|r|)$ | $r^2$ | Kendall’s $\tau$ |
|-----------|----------|---------------|-----------|---------|------|-----------------|
| Elevation (m) | $-2.06 \times 10^{-1}$ | $1.29 \times 10^{-2}$ | $-16.00$ | $< 0.001$ | 0.05 | $-0.15$ |
| Aspect* | $-2.89 \times 10^{-2}$ | $2.94 \times 10^{-2}$ | $-0.98$ | 0.33 | 0.00 | $-0.01$ |
| Slope (°) | $2.17 \times 10^{-2}$ | $1.48 \times 10^{-3}$ | $14.67$ | $< 0.001$ | 0.04 | 0.13 |
| Curvature | $-3.02 \times 10^{-4}$ | $3.84 \times 10^{-5}$ | $-7.86$ | $< 0.001$ | 0.01 | $-0.08$ |
| CTI | $1.61 \times 10^{-3}$ | $3.14 \times 10^{-4}$ | $5.12$ | $< 0.001$ | 0.00 | 0.01 |
| PI‡ | $-4.30 \times 10^{-2}$ | $5.61 \times 10^{-3}$ | $-7.69$ | $< 0.001$ | 0.01 | $-0.06$ |
| TOPEX‡ | $-1.63 \times 10^{-1}$ | $1.24 \times 10^{-2}$ | $-13.26$ | $< 0.001$ | 0.03 | $-0.13$ |

*Aspect converted to circular score ranging from 0° to 360°.$\pi$/360.
†Compound topographic index.
‡Potential insolation over the growing season (May–September) in MJ m$^{-2}$ d$^{-1}$.
§Topographic exposure index.

Fig. 2. Histograms of DEM derived terrain indices. The upper row summarizes micro-scale data, while the lower row contains macro-scale data. Elevations are in metres, slope and aspect are in degrees. Potential insolation (PI) is measured in MJ m$^{-2}$ d$^{-1}$ for the growing season, while Curvature, Compound Topographic Index (CTI) and Topographic Exposure (TOPEX) are unitless.
In order explicitly to treat the auto-correlation present in the data, the ANOVA was repeated specifying exponentially structured spatial errors and spherically structured spatial errors (Fig. 5). In both cases, the fitted semivariogram models indicated auto-correlation at separation distances below 2.5 m. The models with spatial error structures both outperformed the original model (Table 4), with the additional exponential spatial structure providing the best results (Likelihood ratio = 500.0, \( P < 0.0001 \)). After inclusion of the exponential spatial error term (Table 3) TOPEX remained highly significant \( (F = 66.0, \ P < 0.0001 \) ), but the slope effect became insignificant \( (F = 2.2, \ P = 0.14) \), and a significant effect of elevation was revealed \( (F = 8.1, \ P < 0.01) \). The spatial ANOVA model could explain 16% of the observed variation in micro-scale LAI.

Summarising the LAI data by dominant vascular species for the 81 harvest sites indicated a strong relationship that followed expectation from plant functional types (Fig. 6). Highest LAI values were associated with deciduous shrub dominated communities (B. nana and Salix spp.) and the lowest with dwarf ericaceous shrubs (Fig. 6). The high LAI associated with deciduous species is related to their thin leaves (Van Wijk et al. 2005) compared to ericaceous shrubs. Thus, deciduous shrubs can produce a larger leaf area than can evergreen shrubs for the same investment of C in foliage.

When grouped by dominant species, there were close links between LAI values and elevation within the micro-scale site, with lower LAI values occurring at higher elevations. We grouped the dominant species data into the 10 m × 10 m plots \( (n = 9) \), and found that the mean number of ‘micro-scale’ dominant species per 10 m × 10 m ‘macro-scale’ plot was 3.2, with a range from 2–5.

**MACRO-SCALE ANALYSIS**

The mean LAI at the macro-scale was 0.8 with a standard deviation of 0.3 (Williams et al. 2008) and a range from 0.1–1.6. The smaller range of LAI at the macro-scale reflects

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Fig. 3. Regression tree for micro-scale LAI observations. Terminal points in the tree indicate clusters in parameter space associated with high or low LAI values (mean LAI of the cluster is displayed at the terminus).

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Fig. 4. Ordination matrix from principal components (PC) analysis of the micro-scale data. The matrix illustrates the relationship between the first three principal components of the data set, which capture 62% of the total variation. For all plots, the 95% quantiles of LAI, are indicated in white and the 5% quantiles in dark grey. The boxplots on the diagonal show the distribution of the PC scores for the 95% and 5% LAI quantiles, labelled High and Low respectively. Notches indicate the non-parametric 95% confidence interval of the median. The scatter plots in the top right of the matrix show the pairwise relationship between components. The plots on the lower left of the matrix illustrate the loading of the factors for each PC. Abbreviated factor names are: LAI = transformed LAI, E = elevation, SI = slope, A = aspect, CV = curvature, T = topographic exposure index, CTI = compound topographic index, PI = potential insolation over the growing season.
the spatial auto-correlation of LAI of approximately 0.5–
1.0 observed at the site (Williams et al. 2008). The elevation
range sampled was 604–640 m, with a mean of 621 m. The site
was on a north-facing slope, with 51% of all observations on
a northerly aspect. Slopes were moderate on the macro-scale,
with 91% of all observations < 10°, while the steepest slope
recorded was 18°. Most of the valley was concave, with
curvature and TOPEX scores below zero. The mean curvature

Table 2. Principal components (PC) analysis results for the micro-scale LAI dataset

<table>
<thead>
<tr>
<th>Factor</th>
<th>Loadings by component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
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<tr>
<td>LAI</td>
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<tr>
<td>Elevation (m)</td>
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<tr>
<td>Aspect*</td>
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<tr>
<td>Slope (°)</td>
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<tr>
<td>Curvature</td>
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<td>PI‡</td>
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<td>TOPEXS§</td>
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<td>variance</td>
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<tr>
<td>Cumulative variance</td>
<td>0.25</td>
</tr>
</tbody>
</table>

Factor loadings for each component indicate the direction and magnitude of the loadings of each variable onto the component. Data capture is indicated by the cumulative variance.

*Aspect converted to circular score ranging from 0–1 via sin(Aspect* π/360).
†Compound topographic index.
‡Potential Insolation over the growing season (May–September) in MJ m$^{-2}$ d$^{-1}$.
§Topographic exposure index.

Table 3. Data summary of digital elevation map derived topographic indices for the micro-scale spatial clusters LAI values from a tundra site near Abisko, Sweden

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High clusters</th>
<th>Low clusters</th>
<th>ANCOVA</th>
<th>Spatial ANCOVA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>LAI*</td>
<td>1.51</td>
<td>0.22</td>
<td>0.20</td>
<td>0.22</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1.45</td>
<td>0.65</td>
<td>1.85</td>
<td>0.50</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>8.99</td>
<td>6.29</td>
<td>5.84</td>
<td>4.05</td>
</tr>
<tr>
<td>TOPEXS†</td>
<td>−7.21</td>
<td>76.82</td>
<td>22.65</td>
<td>54.66</td>
</tr>
</tbody>
</table>

Fig. 5. Semivariogram of the residuals of the micro-scale ANCOVA. Semivariance ($\gamma$) measures the statistical difference between points separated by a distance vector ($h$). Two models were fitted to describe the spatial structure of the residuals: The solid line is an exponential model with intercept ($\tau$) = 0.2, and range ($\phi$) = 2.4 m. The broken line denotes a spherical model with $\tau$ = 0.3, $\phi$ = 2.3 m. In both cases, a contribution parameter ($c$) was used to scale the model. For separation distances greater than the spherical model takes a value equal to the sill variance ($\tau + c$).
was −0.3, while the mean TOPEX was −4. TOPEX scores were generally close to zero, indicating the macro-scale DEM with 4-m resolution was flatter than the micro-scale observations (Fig. 2). CTI scores ranged from 2 to 14, with a median of 6. PI ranged from 15–22 MJ m⁻² day⁻¹, with a median of 20 MJ m⁻² day⁻¹. A summary of the DEM derived topographic indices is presented in Fig. 2.

Initial exploratory analysis of the macro-scale data by univariate linear regression indicated that only a small proportion of variation in LAI could be explained by topographic factors. However, there were significant relationships for elevation \((P < 0.001, r^2 = 0.12)\), TOPEX \((P < 0.001, r^2 = 0.08)\), aspect \((P < 0.001, r^2 = 0.06)\) and potential insolation \((P < 0.01, r^2 = 0.03)\) (Table 5).

Just as at the micro-scale, there was also a significant correlation between dominant vegetation type and LAI, \((P < 0.001, r^2 = 0.14)\). Summarizing topographic variables by dominant vegetation indicated a strong interaction between landscape level community structure and topographic position. In particular, a toposequence of community types became apparent, with a corresponding downward shift in LAI with increasing elevation (Fig. 6).

We fitted a linear mixed effects model to the macro-scale data to predict LAI, from the full set of topographic indices and physical models, but analysis of the residuals of the fitted model showed that significant auto-correlation was present in the error term (Moran’s \(I = 0.14, P < 0.001\)), indicating that OLS fitting methods were inappropriate. Residuals were found to be auto-correlated below a distance of 116 m, when an exponential auto-correlation structure was imposed upon the error term of the model. To incorporate the spatial auto-correlation structure, a series of simultaneous auto-regressive linear models were fitted to the data. Lagrange multiplier tests (Anselin 1988; Anselin & Rey 1991) indicated that fitting spatial auto-regressive models were appropriate; diagnostics for lagged-response, lagged-errors and Durbin models were all highly significant \((P < 0.0001)\).

Clear improvements to the spatial regression model fit over OLS were observed for increasingly complex ML models (Table 6). The best choice of model for macro-scale LAI, as indicated by the Akaikes information criterion (Akaikes 1974), was the spatial Durbin model (pseudo \(r^2 = 0.32\)). An examination of the terms of the Durbin model (Table 7) indicated that the only significant local topographic term was elevation \((P < 0.001)\); however, significant adjacency effects were indicated for elevation \((P < 0.01)\) and PI \((P < 0.05)\). Significant residual variation was also indicated by the auto-correlation parameter \(\rho\) \((P < 0.001)\). The residuals of the Durbin model were not auto-correlated (Moran’s \(I = -0.002, P = 0.47\)), indicating robust estimation of model parameters.

### Discussion

The analyses at the macro- and micro-scales demonstrated that explicit treatments for the effects of spatial auto-correlation

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**Table 4.** Analysis of covariance (ANCOVA) model selection criteria for micro-scale transformed leaf area index (LAI) data

<table>
<thead>
<tr>
<th>Model</th>
<th>Log likelihood</th>
<th>AIC</th>
<th>Pseudo (r^2)</th>
<th>DF</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANCOVA</td>
<td>−576</td>
<td>1565</td>
<td>18</td>
<td>6</td>
</tr>
<tr>
<td>Spatial ANCOVA</td>
<td>−526</td>
<td>1069</td>
<td>16</td>
<td>8</td>
</tr>
<tr>
<td>Spatial ANCOVA</td>
<td>−528</td>
<td>1071</td>
<td>16</td>
<td>8</td>
</tr>
</tbody>
</table>

The first model is a non-spatial analysis of covariance, fitted by maximum likelihood methods. The two spatial models add a spatially auto-correlated error function to the model, requiring an extra two degrees of freedom for the nugget \((\tau)\) and \((\phi)\) range parameters. AIC is Akaikes information criterion. DF is degrees of freedom.
Topographic exposure index. Parameter in the macro-scale analysis, an erroneously high pseudo parameter, until auto-correlation was accounted for. Similarly analysis, in which slope appeared to be a highly significant significance of effects, most clearly illustrated in the micro-scale auto-correlation in the data led to false inferences on the of LAI under our sampling strategy. Failure to treat for the were required to make valid inferences regarding the distribution of LAI under our sampling strategy. Failure to treat for the auto-correlation in the data led to false inferences on the significance of effects, most clearly illustrated in the micro-scale analysis, in which slope appeared to be a highly significant parameter, until auto-correlation was accounted for. Similarly in the macro-scale analysis, an erroneously high pseudo $r$ was arrived at before treating the analysis for spatial effects. Problems arose because of the inflation of the probability for committing Type I errors in the presence of spatial auto-correlation, because of the bias towards artificially lowering the estimate of sample variance (Haining 2003; Kuhn 2007). For this reason, the most useful and valid statistical outputs of the were the spatial Durbin model, the most complex, adding spatial interactions for all predictors, and LAI, $\text{AIC} = \text{Akaike information criterion.}$ $\text{DF}$ is degrees of freedom. RMSE is root-mean-square-error of the model predictions.  

* Lagged response and lagged predictors. 

were required to make valid inferences regarding the distribution of LAI under our sampling strategy. Failure to treat for the auto-correlation in the data led to false inferences on the significance of effects, most clearly illustrated in the micro-scale analysis, in which slope appeared to be a highly significant parameter, until auto-correlation was accounted for. Similarly in the macro-scale analysis, an erroneously high pseudo $r$ was arrived at before treating the analysis for spatial effects. Problems arose because of the inflation of the probability for committing Type I errors in the presence of spatial auto-correlation, because of the bias towards artificially lowering the estimate of sample variance (Haining 2003; Kuhn 2007). For this reason, the most useful and valid statistical outputs of the study were the spatial ANCOVA and the spatial Durbin model (Table 8). 

The statistical tests suggested we cannot accept $H_1$, that elevation was a significant determinant of LAI at both the macro- and micro-scales ($P < 0.001$, $P < 0.01$ respectively, although the variance explained was low). The elevation change at the macro-scale was an order of magnitude greater than at the micro-scale. For most other terrain indices there were clear and even striking similarities between the scales (Fig. 2). 

The elevation response was most clearly observed at the macro-scale, and decreased in influence and significance at the micro-scale. 

Increased elevation is linked with lower temperatures through diabatic lapse rates (approximately 0.6 °C per 100 m). The elevation change at the macro-scale study was $\leq 40 m$, corresponding to 0.2 °C expected drop in mean temperature. The direct effect of a 0.2 °C change in mean temperature on LAI distribution is unclear, but likely to be small even in a montane sub-Arctic ecosystem with short growing season. 

At the micro-scale, elevation change of 2–3 m, the adiabatic effect on temperature would be trivial. The regression tree analysis, PCA, and spatial ANCOVA confirmed the combined importance of elevation and exposure in explaining LAI variation at the micro-scale (Table 3, Figs 3 and 4) – both factors are likely to influence snow distribution. Thus a more likely explanation for the elevation effect is through its interaction with exposure in determining distribution of snow and the acedetic and thermal stress substrate that accumulates when the land surface is exposed to the atmosphere in winter.

There was no significant relationship between CTI and LAI at either the macro-scale or the micro-scale, and hence we rejected $H_2$, that the primary constraint on LAI distribution was through landscape soil moisture. We observed that drainage at the site was complicated by the steep nature of the substrate, a result of the intense glacial activity in the late Pleistocene. CTI may be a poor predictor of water transport through this complex substrate.

There was no evidence to support $H_3$, that exposure was the dominant control on LAI ($P = 0.0001$), where it was observed to be the most significant factor measured, but with exploratory power ($r^2 = 0.03$). However, there was no supporting evidence for exposure effects at the macro-scale, where calculated TOPEX values were generally $$\text{Table 5. Linear association between an indexed leaf area index (LAI) and individual macro-scale terrain properties derived from a digital elevation model from a study site in eastern Abisko, Sweden}$$

| Parameter     | Estimate | Std. error | t-value | Pr(>|t|) | $\tau^2$ | Kendall’s $\tau$ |
|---------------|----------|------------|---------|---------|---------|------------------|
| Elevation(m)  | $-1.7 \times 10^{-02}$ | $3.2 \times 10^{-03}$ | $-5.30$ | <0.001 | 0.12 | -0.28 |
| Aspect*       | $-3.7 \times 10^{-01}$ | $9.7 \times 10^{-02}$ | $-3.82$ | <0.001 | 0.06 | -0.17 |
| Slope(°)      | $8.2 \times 10^{-03}$ | $4.9 \times 10^{-03}$ | 0.97 | 0.35 | 0.00 | 0.07 |
| Curvature     | $-1.3 \times 10^{-02}$ | $9.7 \times 10^{-03}$ | -1.34 | 0.18 | 0.00 | -0.05 |
| CTI†          | $1.5 \times 10^{-02}$ | $1.1 \times 10^{-02}$ | 1.23 | 0.20 | 0.00 | 0.03 |
| PI‡           | $-8.3 \times 10^{-02}$ | $2.9 \times 10^{-02}$ | -2.84 | <0.01 | 0.03 | -0.15 |
| TOPEX§        | $-8.0 \times 10^{-04}$ | $1.9 \times 10^{-04}$ | -4.13 | <0.001 | 0.08 | -0.22 |

*Aspect converted to circular score ranging from 0:1 via sin(Aspect* $\pi$/360). 
†Compound topographic index. 
‡Potential Insolation over the growing season (May-September) in MJ m$^{-2}$ day$^{-1}$. 
§Topographic exposure index.
lower than at the micro-scale. TOPEX is a higher order topographic effect, derived in part from slope curvature, but a better indicator of sheltering than instantaneous curvature because it integrates enclosure over a wide distance, rather than within the narrow confines of DEM pixel adjacency.

The index of exposure is likely to be an indicator of snow accumulation, or lack thereof. The significant result at the micro-scale provides support for the hypothesis that areas with snow accumulation are linked to high LAI.

H4, that short wave radiation budget was the dominant control on LAI, can be rejected; no significant effect was observed. Interestingly, PIwas observed to have a negative spatial interaction with LAI at the macro-scale, indicating that an adjacent site with high solar intercept reduced the LAI at the prediction location. This may be an artefact of the dataset, or not a true outcome of the interaction between topography and LAI.

The model incorporates local effects of topography at the prediction location, along with spatial interactions between these terms and their neighbours. A neighbourhood interaction in the response (ρ) is also included.

*Aspect converted to circular score ranging from 0:1 via sin(Aspect×π/360).
†Potential Insolation over the growing season (May–September) in MJ m⁻² d⁻¹.
‡Topographic exposure index.

Table 7. Spatial Durbin model of macro-scale LAI, against DEM derived terrain variables

| Parameter       | Effect         | Estimate | Likelihood ratio | Pr(>|z|) |
|-----------------|----------------|----------|------------------|---------|
| Intercept       | Intercept      | 9.98     |                  |         |
| Elevation       | Local effect   | -8.07×10⁻⁵ | 11.50             | <0.001  |
| Aspect          | Local effect   | -2.44×10⁻⁵ | 3.58             | 0.06    |
| TOPEX           | Local effect   | -2.32×10⁻⁴ | 1.17             | 0.28    |
| PI              | Local effect   | 1.11×10⁻³ | 0.08             | 0.77    |
| Lagged elevation| Spatial interaction | 7.18×10⁻³ | 8.49             | <0.001  |
| Lagged aspect   | Spatial interaction | 4.43×10⁻³ | 3.41             | 0.06    |
| Lagged TOPEX    | Spatial interaction | -6.42×10⁻³ | 0.03             | 0.87    |
| Lagged PI       | Spatial interaction | -1.69×10⁻³ | 6.31             | <0.05   |
| ρ               | Spatial auto-correlation | 0.33    | 11.44             | <0.001  |

Table 8. A summary of the two key statistical relationships between LAI and topography identified in the study, the method used, the reason for applying the specific method, and the key statistical finding

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Method</th>
<th>Reason</th>
<th>Key finding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topography and LAI at macro-scale</td>
<td>Spatial Durbin model</td>
<td>Interaction of controlling factors</td>
<td>pseudo r²=0.32</td>
</tr>
<tr>
<td>Exposure and elevation effect on LAI at micro-scale</td>
<td>Spatial ANCOVA</td>
<td>Accounts for spatial auto-correlation</td>
<td>r²=0.16</td>
</tr>
</tbody>
</table>

Optical approaches for LAI determination with DEMs generated by LiDAR may result in improved regional attribution of LAI. There were striking similarities in species/PFT-LAI patterns, and their arrangement along elevation gradients at different scales in investigations of this study (Fig. 6). There was a clear toposequence of PFTs at the macro-scale site, related to the correlation of elevation with LAI. On high sites, fell field communities dominated, with associated lower mean vascular LAI values. Down the elevation profile, graminoid and moss-dominated sub-Arctic meadow communities were more common, associated with relatively flat but sheltered topographic positions. Below this were heath communities, with an increasing dominance of *Betula nana* elevation decreased, and an associated increase in mean LAI. *Salix* communities dominated on low elevation sites with steep slopes bordering the drainage channels. There was a similar toposequence of dominant vegetation at the micro-scale (Fig. 6). *Salix* spp. and *B. nana* tended to dominate at lower elevations, with dwarf shrubs as part of alpine-dominated vegetation more common at higher sites. LAI for dominant species matched patterns and values observed at the macro-scale.

The correlation between dominant vascular species and LAI (macro-scale r=0.40) was greater than the correlation between dominant PFT and LAI at the macro-scale (r=0.77). At the macro-scale, LAI was better explained by
topographic parameters and spatial autocorrelation (pseudo \( r^2 = 0.32 \)) than it was at the micro-scale (\( r^2 = 0.16 \)). What determined this switch in the relative importance of topography and dominant species/PTFs with changing scales? The heredity in importance of species/PTFs at coarser scales was probably related to problems in defining single PTFs at 10 m resolutions, because if heterogeneity in species dominance patterns within 10 m × 10 m micro-scale plots were rather 2–5 different dominant species, often in different functional types, as determined from the sub-samples at 0.2 m resolution. Thus the concept of a dominant plant functional type at 10 m resolution may explain why continuous measure like LAI that can integrate vegetation patterns is a more effective means to identify the complex topographic and related environmental filters determining mining vegetation pattern at the coarser scale.

The present study did not incorporate belowground processes and plant community interaction effects, and this may account for the residual variation in the spatial patterns of LAI. Thesoisof Abisk owaholvfertilit (Hinnert et al., 1975; Ratcliffe 2005), but the residual spatial variability has not been well studied. Drainage pattern and the distribution of snowbeds, and the nature of the rocky substrate probably generate a heterogeneous distribution of soil nutrients that may explain the residual variation in LAI. Factors related to site history, reindeer management and disturbance may also play an important role in the distribution of LAI. Further research into below-ground processes and community interactions is therefore likely to improve our understanding of the spatial patterns of Arctic LAI.

There is some evidence that there is a relationship between micro-scale vegetation patterns and LAI variation in tundra ecosystems across the Arctic. We can recognize these patterns described here in tundra elsewhere in the Arctic Walker et al., 1994. These PTFs have the same general evolutionary adaptations, wherever they occur. Thus, although the species, even in low-mesic cases, the genus of plant may differ, different Arctic species, their function is similar. As a result, we can recognize similar plant assemblages of PFTs occurring as similar components of the tundra in response to the varying above- and below-ground conditions arising from topographic variability. Further studies on different Arctic landscapes would be valuable for instance, focusing on older landscapes (i.e., a loam with a podzol) where tundra in this indeterminate has been modified by a longer period of fluvial action, or landscapes overlying permafrost.

Conclusions

Vegetation type, topography and LAI are tightly coupled in tundra ecosystems across broad ranges of scales. Examined at two different resolutions (0.2 m and approximately 10 m) there were striking similarities in LAI, dominant vegetation type and most terrain indices for both domains (40 m × 40 m, and 500 m × 500 m). Topographic variables explained more of the variance in LAI at the micro-scale than at the macro-scale. The explanatory power of dominant species or functional type for LAI variation was weaker at coarser scales, because communities contain more than one functional type at 10 m resolution. Therefore, the explanatory power of the digital elevation maps for LAI suggests that remotely sensed topography combined with remotely sensed optical measurements would be a powerful tool for LAI mapping in Arctic environments.

Acknowledgements

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References


