

OPTICAL INSTRUMENTS FOR MEASURING LEAF AREA INDEX IN LOW VEGETATION: APPLICATION IN ARCTIC ECOSYSTEMS

MARK T. VAN WIJK^{1,2,3} AND MATHEW WILLIAMS¹

¹*School of GeoSciences, University of Edinburgh, Darwin Building, Edinburgh EH9 3JU, UK*

²*The Ecosystems Center, Marine Biology Laboratory, Woods Hole, Massachusetts 02543 USA*

Abstract. Leaf area index (LAI) is a powerful diagnostic of plant productivity. Despite the fact that many methods have been developed to quantify LAI, both directly and indirectly, leaf area index remains difficult to quantify accurately, owing to large spatial and temporal variability. The gap-fraction technique is widely used to estimate the LAI indirectly. However, for low-stature vegetation, the gap-fraction sensor either cannot get totally underneath the plant canopy, thereby missing part of the leaf area present, or is too close to the individual leaves of the canopy, which leads to a large distortion of the LAI estimate. We set out to develop a methodology for easy and accurate nondestructive assessment of the variability of LAI in low-stature vegetation. We developed and tested the methodology in an arctic landscape close to Abisko, Sweden.

The LAI of arctic vegetation could be estimated accurately and rapidly by combining field measurements of canopy reflectance (NDVI) and light penetration through the canopy (gap-fraction analysis using a LI-COR LAI-2000). By combining the two methodologies, the limitations of each could be circumvented, and a significantly increased accuracy of the LAI estimates was obtained. The combination of an NDVI sensor for sparser vegetation and a LAI-2000 for denser vegetation could explain 81% of the variance of LAI measured by destructive harvest. We used the method to quantify the spatial variability and the associated uncertainty of leaf area index in a small catchment area.

Key words: *arctic tundra; LAI; leaf area index; low-stature vegetation; normalized difference vegetation index; optical instruments; Sweden; uncertainty analysis.*

INTRODUCTION

Leaf area index (LAI, measured as square meters per square meter) is a key plant characteristic within ecophysiology research (e.g., Boelman et al. 2003, Breda 2003, Ewert 2004, Van Wijk et al. 2005). Plant biomass production is closely related to light interception, which is mainly determined by leaf area index. Leaf area index drives both the within- and the below-canopy microclimate, determines and controls canopy water interception, radiation extinction, and water and carbon exchange. Despite the fact that many methods have been developed to quantify LAI, both directly and indirectly (Breda 2003, Jonckheere et al. 2004, Weiss et al. 2004), leaf area index remains difficult to quantify accurately, owing to large spatial and temporal variability (Breda 2003).

The Plant Canopy Analyser, LAI-2000 (LI-COR, Lincoln, Nebraska, USA), is one of the most widely used pieces of equipment to estimate the LAI indirectly. By measuring below- and above-canopy radiation, the fraction of transmitted radiation that passes through a

plant canopy can be quantified, which is then used to estimate LAI. The technique is applied in a whole range of (agro-)ecosystems ranging from coniferous and deciduous forests to agricultural crops (e.g., Gower and Norman 1991, Deblonde et al. 1994, Dufrene and Breda 1995, Hicks and Lascano 1995, Cutini et al. 1998, Le Dantec et al. 2000). The main problems with using this fast and easy-to-apply LAI-2000 tool for low-stature vegetation are that the sensor either cannot get totally underneath the plant canopy, thereby missing part of the leaf area present, or that the sensor is too close to the individual leaves of the canopy, which leads to a large distortion of the LAI estimate (LI-COR 1992). The LAI-2000 is therefore limited in its applicability for low-stature vegetation, which is typically at the low ranges of LAI.

Spectral reflectance indices, derived from optical remote sensing equipment, also have been used widely to estimate LAI (Tucker 1979, Boelman et al. 2003). The standard index that is used is the normalized difference vegetation index (NDVI), developed originally by Rouse et al. (1974). Recent developments in optical remote sensing equipment have made it possible to use hand-held sets to estimate the reflectance characteristics of vegetation at small spatial scales, ranging from the individual leaf level to the plot size level, up to 4–5 m² (Boelman et al. 2003). NDVI has been shown to be a good proxy for LAI, up to levels at which the

Manuscript received 31 October 2003; revised 1 July 2004; accepted 26 October 2004. Corresponding Editor: M. L. Goulden.

³ Present address: Plant Production Systems, Department of Plant Sciences, Wageningen University, P.O. Box 430, 6700 AK Wageningen, The Netherlands.
E-mail: Mark.vanwijk@wur.nl

plant canopy closes. When the vegetation canopy is closed, the NDVI–LAI curve saturates, and NDVI can no longer be used to detect any differences in LAI (e.g., Pontauiller et al. 2003). NDVI characterization of the vegetation canopy in order to estimate LAI is therefore limited in its applicability at the higher ranges of LAI.

In this study, we first develop and test a new methodology to measure the LAI of different low-stature vegetation types in an easy and relatively quick manner, nondestructively. We combine the LAI-2000 and NDVI methodologies in order to circumvent the weaknesses of both approaches, and to derive a more reliable estimate of the LAI of low-stature vegetation. We develop, test, and apply the method in an arctic landscape. Arctic landscapes are characterized by their heterogeneity, with many different vegetation types located within small areas (Williams and Rastetter 1999, Gould et al. 2002). The distribution of LAI across an arctic landscape is closely related to the underlying variation in vegetation types. Thus, accurate estimation of LAI variation in the field can be used both to estimate distributions of different vegetation types (Myneni et al. 1997), and to derive estimates of the variation of GPP (gross primary productivity) in a certain landscape (Williams et al. 2001). After developing the methodology, we test the workability of the method by quantifying the spatial variability of LAI within a small catchment area.

The measurements were performed in a small catchment area close to Abisko, Sweden. In this relatively sparse arctic vegetation of low stature (height up to ~1.5 m), it is relatively simple to apply optical measurement techniques both above the vegetation and underneath the vegetation, thereby allowing easy application of both radiation reflectance and interception measurements. However, the approach is applicable in any low-stature vegetation type, such as alpine, coastal, marsh, or short grassland vegetation.

METHODS

Measurements

There are several methods for measuring LAI in the field. The direct method involves harvesting vegetation in a certain area and measuring one-sided leaf area of all the vegetation directly. The direct method is time-consuming, but is easier to perform in low-stature systems of the arctic than in tall canopy forests. Indirect methods involve using optical devices. One common approach is to use a fish-eye lens placed beneath the canopy. The images from the lens can be analyzed to determine the gap fraction and estimate the LAI. The LI-COR Plant Canopy Analyzer LAI-2000 (LI-COR, Lincoln, Nebraska, USA) uses such a method and incorporates automated analysis software. By taking two readings, one above and one below the canopy, the LAI-2000 can process a normalized image and thus reduce errors. The short stature of arctic systems is

both an advantage and a problem for the LAI-2000; it is easy to take an above-canopy reading with the LAI-2000 in tundra, but if the tundra is very short, then the below-canopy reading is problematic; is the instrument recording all the foliage near the surface? The height of the sensor is ~3 cm, and sparse arctic vegetation can be of similar height.

Another indirect method is to use canopy reflectance data: NDVI measurements, similar to those obtained from satellites. While the LAI-2000 uses an upward-looking sensor, NDVI data are obtained with a downward-looking sensor. The advantage of the hand-held NDVI sensor is that (1) it can be more directly related and compared to satellite data than the LAI data themselves, and (2) there are no problems in measuring short-stature vegetation. The disadvantage is that reflectance measurements tend to saturate once the canopy closes.

Because the ranges of LAI-values in which each of the methods works well seem to be complementary, we tested whether a combination of the two measurement techniques (using NDVI for the low LAI values and LAI-2000 for the higher LAI values) can lead to better LAI estimates.

Site description

The study was conducted from 10 to 31 July 2002, at a site near Abisko Scientific Research Station (68°21' N, 18°49' E), Sweden, above the tree line at elevation 540 m above sea level. During this period, peak-level plant biomass and LAI were present. The area studied is located within a small catchment. The total area of the catchment is ~1 ha, and the average slope in the catchment is ~5%. The soil is rocky, and is characterized by good drainage (Jonasson et al. 1999, Van Wijk et al. 2005). We laid out nine 10 × 10 m plots along a regular grid covering the main vegetation types in the catchment (Fig. 1). The vegetation types ranged from very low density heath at exposed ridge tops to more dense arctic shrub vegetation close to the stream running through the center of the catchment. To extend the scope of the calibration curve of directly estimated LAI and the indirect measures of the LAI-2000 and NDVI, we also included leaf area samples of a wet sedge vegetation type near the catchment.

Vegetation description

The vegetation types that we investigated in this study differ in the contributions that the several plant types make to the total leaf area of the vascular plant communities (Table 1). 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-idea*, *Empetrum nigrum*) and deciduous shrubs (especially *Betula nana*). In the Swedish peat

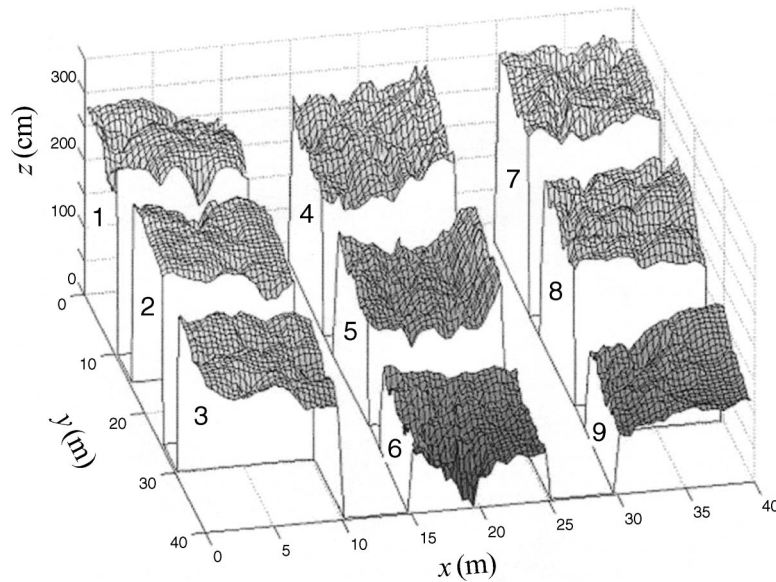


FIG. 1. Elevation map of the nine 10×10 m plots (large numbers are plot numbers).

systems, *Rubus chaemaemorus* is also very important. The peat vegetation type is also characterized by high moss cover, whereas the shrub vegetation type has patches of moss.

Topography

For a general characterization of the nine plots, we measured surface topography by recording the relative elevation of each of the 625 grid points within each of the nine plots (spacing between the grid points was therefore 40 cm). We used standard surveying techniques (a level and survey pole) to record elevation of the surface (the reference level was the soil surface). The lowest point measured in the catchment was taken as the reference point, and was set at zero m (Fig. 1). The digital elevation map of the site is characterized by a large variation in microtopography, with many

small pits present, and by the stream that flows through plots 4, 5, and 6 (Fig. 1). Overall, the elevation of plots 4, 5, and 6 is lower than that of plots 1, 2, 3, 7, 8, and 9. This difference in elevation is also reflected in the vegetation cover measured: plots 4, 5, and 6 are characterized by shrub vegetation.

Indirect measurement

Before harvesting a quadrat, we performed the optical measurements. First, we made an estimate of leaf area index with a LI-COR LAI-2000 Canopy Analyzer (LI-COR, Lincoln, Nebraska, USA), collecting one above- and one below-canopy measurement. We ensured that direct sunlight was never incident on the sensor and that the surrounding vegetation was in the shade. We used a 45° view cap on the lens. We estimated the NDVI for each quadrat by measuring the reflectance of the vegetation with a Skye Instruments 2 Channel Sensor SKR1800 (Skye Instruments, Powys, UK). The Skye sensor has a field-of-view of 8° . The sensor was kept at 0.90 m height, thereby resulting in a measurement area of $\sim 0.2 \times 0.2$ m. The reflectance bandwidths used to calculate NDVI were $0.58\text{--}0.68 \mu\text{m}$ (channel 1) and $0.725\text{--}1.1 \mu\text{m}$ (channel 2). The NDVI was then calculated with

$$\text{NDVI} = \frac{\text{Ch2} - \text{Ch1}}{\text{Ch2} + \text{Ch1}} \quad (1)$$

where Ch1 and Ch2 are respectively channel 1 and 2.

Direct measurements

In each of the nine plots, we collected all above-ground vegetation from nine regularly spaced 0.2×0.2 m quadrats. Two extra 10×10 m plots were situated in the wet sedge vegetation, where in each plot

TABLE 1. Contribution in percentages to total plant community leaf area by the dominant plant types in the vegetation types investigated in this study.

Vegetation type and plant type	Percent cover
Wetland	
Graminoids	85–90
Pteridophytes	0–10
Shrubs	
Deciduous	60–90
Evergreen	10–35
Heath	
Evergreen	45–100
Deciduous	0–50
Peat tundra	
Deciduous	25–70
Graminoids	20–40

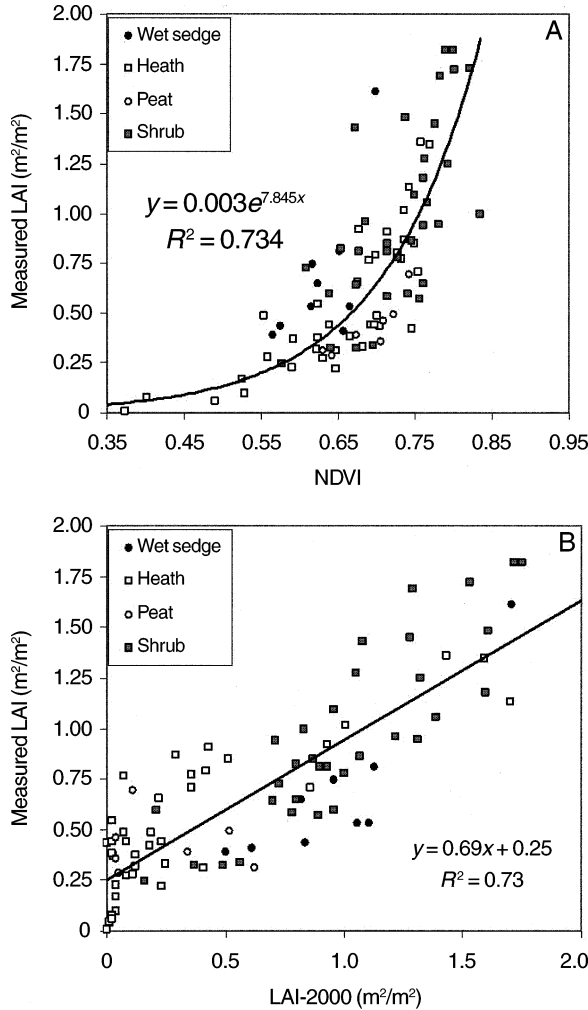


FIG. 2. Empirical relationships between measured LAI and (A) NDVI and (B) LI-COR LAI-2000 measurements.

nine regularly spaced 0.2×0.2 m quadrats also were sampled. In total, therefore, 99 quadrats were sampled. The quadrats were located at a regular 3×3 spacing, 3 m apart, and with each quadrat located at least 2 m from the edge of the plot. Aboveground biomass of each quadrat was harvested and we determined one-sided leaf area of all vascular plants in each quadrat using a camera (JVC TK-S310, Tokyo, Japan) and accompanying software, Delta-T Digital Analysis System, Version 1.1 (Delta-T Software, Cambridge, UK).

Data analysis

We calculated relationships between the harvest LAI of the 0.2×0.2 m quadrats and the LAI-2000 and NDVI measurements. Besides determining the optimal relationships, we also quantified the uncertainty of the parameters of the relationships between harvest LAI, LAI-2000, and NDVI data.

We used the maximum likelihood approach to estimate the different unknown parameters of the rela-

tionships. Maximum likelihood estimators properly represent measurement error, and thus provide a statistically sound basis for evaluating the adequacy of a model fit and for finding the multivariate parameter confidence region (Press et al. 1989, Van Wijk and Bouten 2002). The optimal parameters were found by minimizing the objective function:

$$O(p) = \sum_{i=1}^N \frac{1}{\sigma_{y_i}^2} [y_{i,\text{meas}}(x_i) - y_{i,\text{mod}}(x_i; p)]^2. \quad (2)$$

Here N is the total number of measurements, p is the number of parameters, $y_{i,\text{meas}}(x_i)$ is the measured value of output variable y at the value x_i of driving variable x , $y_{i,\text{mod}}(x_i)$ is the modeled value of output variable y at the value x_i of driving variable x , given the p parameters, and $\sigma_{y_i}^2$ is the measurement error variance for each of the N observations. The minimal sum of squares follows a χ^2 distribution with $N - p$ degrees of freedom.

For nonlinear models, the parameter confidence regions can be found exactly with Monte Carlo simulations. With these simulations, a contour surface in the parameter space of an allowable objective function increment, $\Delta O(p) = O(p) - O(p_{\text{opt}})$, is found. $\Delta O(p)$ follows a χ^2 distribution with $N - p$ degrees of freedom (Press et al. 1989). With this distribution, the appropriate contour value of $\Delta O(p)$ can be determined at a desired confidence level. We varied each of the parameters used in the relationships, and determined the 95% confidence intervals (Van Wijk and Bouten 2002).

Setup

First, we quantified the relationships between directly measured LAI and the indirect optical methodologies, and tested whether combining the LAI-2000

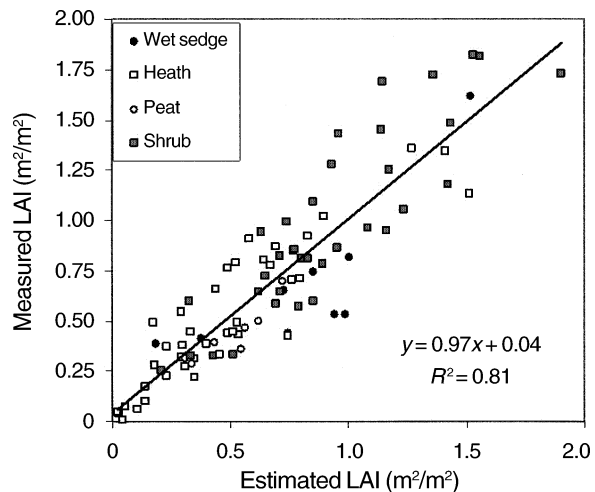


FIG. 3. Scatter plots between directly measured LAI and estimated LAI using a combination of LI-COR LAI-2000 and NDVI measurements ($n = 99$ quadrats). The empirical formulas used are: estimated LAI = $0.0063e^{6.2\text{NDVI}}$ if $L_g < 0.66$; estimated LAI = $0.825L_g$ otherwise. L_g is the LAI derived from the gap fraction estimate of the LAI-2000.

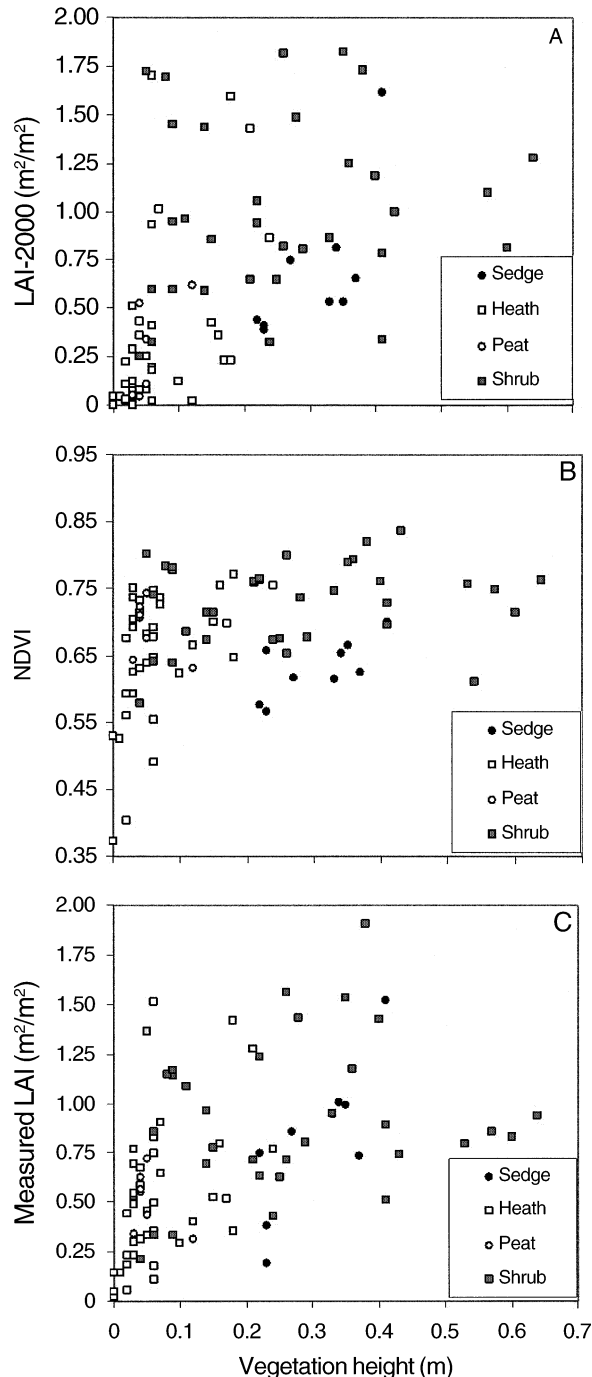


FIG. 4. Scatter plots between (A) LAI-2000, (B) NDVI, and (C) measured LAI and vegetation height ($n = 99$ quadrats).

together with NDVI measurements increased the quality of the estimates of the directly measured LAI. We also quantified the uncertainty of the parameters of the relationships between indirect methods and the directly measured LAI. Second, after we derived these relationships, we applied the methodology to estimate the

spatial variability of LAI in the small catchment, thereby testing whether this approach is applicable for fast and easy characterization of LAI variability. The spatial variability of LAI within the nine plots was determined by performing LAI-2000 and NDVI measurements in each plot in a regular grid at 0.4-m intervals; we collected 625 measurements for each variable in each plot, and thus 5625 measurements in total. Vegetation height was also measured at each of the grid points, by measuring the height difference between the top leaf within a 5 cm radius of the grid point and the moss surface. We furthermore quantified the uncertainty in the estimated LAI variability.

RESULTS

Relationships between direct and indirect measurement techniques

Plotting harvest LAI vs. NDVI of the 0.2×0.2 m quadrats resulted in a highly curved relationship (Fig. 2A). There was a clear saturation of NDVI at LAI values higher than $\sim 1 \text{ m}^2/\text{m}^2$. On the other hand, the empirical relationship between harvest LAI and LAI-2000 readings was linear (Fig. 2B). However, at low LAI values, the LAI-2000 clearly underestimated the harvest LAI values, thereby resulting in an optimal regression line that had a positive intercept and a slope < 1.0 . This underestimation could have been caused by the fact that the LAI-2000 sensor is placed too close to the leaves of these low LAI vegetation types, which also are often small in height. The LAI estimates based just on the LAI-2000 measurements would have an unrealistic zero-offset of $0.25 \text{ m}^2/\text{m}^2$, whereas in the barren heath plots, it was clear that sometimes no leaf area was present at all. For the individual vegetation types, there were no clear systematic errors visible in the two techniques, except for the wet sedge plots. The fitted NDVI-LAI curve underestimated the measured LAI of wet sedge (Fig. 2A), whereas the LAI-2000 relation overestimated the measured LAI of wet sedge (Fig. 2B).

Estimating LAI values using a combination of the two measurement techniques resulted in a much higher explained variance (81%, rather than 72–73%) and no systematic over- or underestimations (Fig. 3). Using the maximum likelihood analysis, there were no statistically acceptable parameter combinations ($P < 0.05$) if we used only the NDVI or the LAI-2000 data. Only when the two measurement techniques were combined (see Eq. 3), were there model parameter combinations that were statistically acceptable ($P < 0.05$). We combined the two empirical relationships used in Fig. 2, and fitted the data by minimizing Eq. 2 to the empirical formula

$$\text{estimated LAI} = \begin{cases} ae^{b \cdot \text{NDVI}} & \text{if } L_g < c \\ d \times L_g & \text{otherwise} \end{cases} \quad (3)$$

where L_g is LAI derived from the gap-fraction estimate

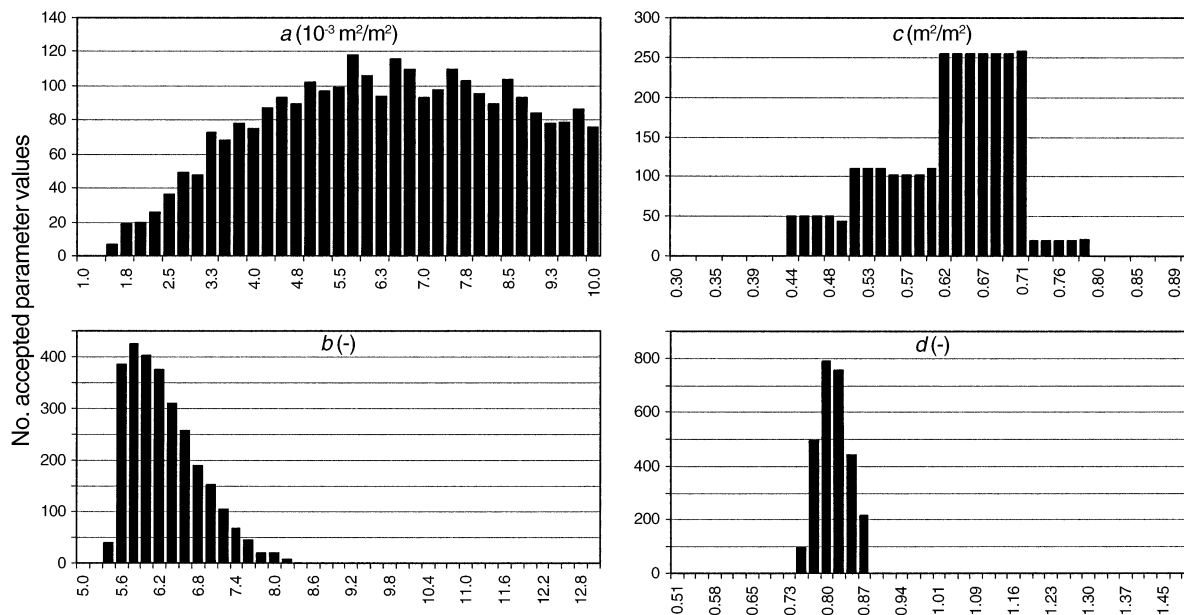


FIG. 5. Histograms of acceptable parameters a – d using the χ^2 test with a confidence interval of 95%. See Results (Eq. 3) for a definition of the parameters.

of the LAI-2000. The optimal parameter values were $a = 0.0063 \text{ m}^2/\text{m}^2$, $b = 6.2$, $c = 0.66 \text{ m}^2/\text{m}^2$ and $d = 0.825$.

The combination of the two methodologies showed no strong systematic deviations for one of the vegetation types. The systematic errors detected earlier for wet sedge (Fig. 2A, B) disappeared because, for part of the wet sedge data points, NDVI measurements were used to estimate the measured LAI, and for the other part, LAI-2000 measurements were used (Fig. 3).

The threshold (parameter c) at an LAI-2000 value of $0.66 \text{ m}^2/\text{m}^2$ seemed to be related to a shift from data points dominated by heath vegetation to data points dominated by shrub vegetation (Fig. 2B). Up to LAI-2000 values of $0.5 \text{ m}^2/\text{m}^2$ no relationship between LAI-2000 values and measured LAI was visible. The threshold value was also related to vegetation height (Fig. 4). The NDVI signal showed a clear correlation with vegetation height up to heights of $\sim 8 \text{ cm}$ (Fig. 4A), which is the maximum height of most of the heath vegetation. The LAI-2000 could not detect any LAI below vegetation heights of 3 cm (Fig. 4B), and then showed a large scatter of values. The results of these two graphs are reflected in Fig. 4C, where there was a clear correlation between vegetation height and measured LAI up to vegetation height values of $\sim 8 \text{ cm}$. The correlation broke down at higher values of vegetation height.

The 95% confidence intervals of the four parameters used in Eq. 3 were surprisingly large, thereby resulting in large acceptable parameter intervals for Eq. 3 (Fig. 5). The a and b parameters showed a strong correlative structure, and almost all values of the a parameter, in

combination with certain values of the other parameters, resulted in a statistically satisfactory model performance.

Spatial maps

Overall, the same major spatial vegetation patterns were visible in the three variables measured (i.e., NDVI, LAI-2000, and vegetation height). The plots with the lowest elevation (4, 5, and 6; see Fig. 1), characterized by shrub vegetation, had relatively high values for LAI-2000, NDVI, and vegetation height. However, there were differences in detection of the low vegetation densities. For example, in plot 9 (the plot at the bottom right) the vegetation cluster in the center, extending both to left, right and above, is much more blurred in the NDVI measurements than in the LAI-2000 measurements, and is barely visible in the height plot (Fig. 6). This difference can be linked to the fact that the LAI-2000 measures light penetration through the vegetation; with low-stature vegetation, this method is not very reliable. This means that low LAI cannot be detected, and that the borders of the vegetation clusters found with the LAI-2000 will occur at higher LAI values. Low-stature vegetation with, in most cases, low LAI can be detected much more easily by NDVI. This increased sensitivity of NDVI for lower LAI is also clear when the NDVI and LAI-2000 measurements are combined to achieve a more reliable estimate of LAI variations of the plots (Fig. 7).

The main relative uncertainty in the estimated LAI values (Fig. 7) occurred around the threshold value used for switching from NDVI measurements to LAI-2000 measurements, the c coefficient of Eq. 3, while

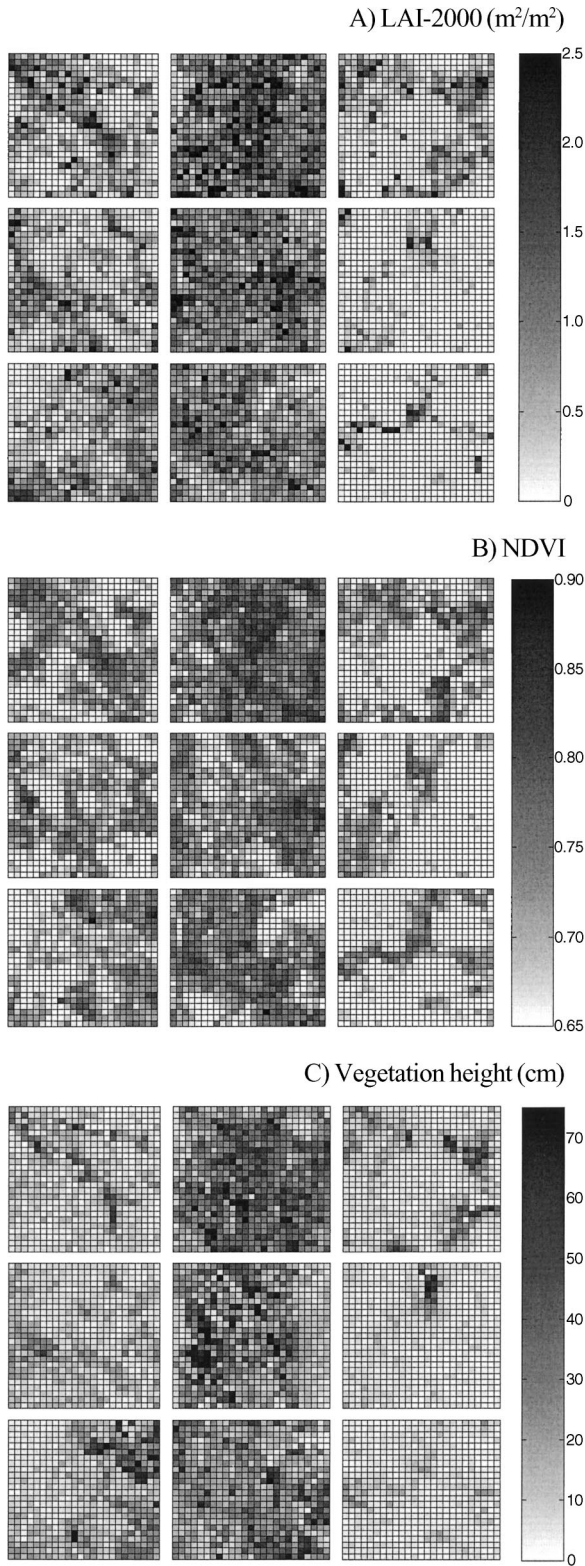


FIG. 6. Spatial maps of measurements of (A) LAI-2000, (B) NDVI, and (C) vegetation height in the nine plots.

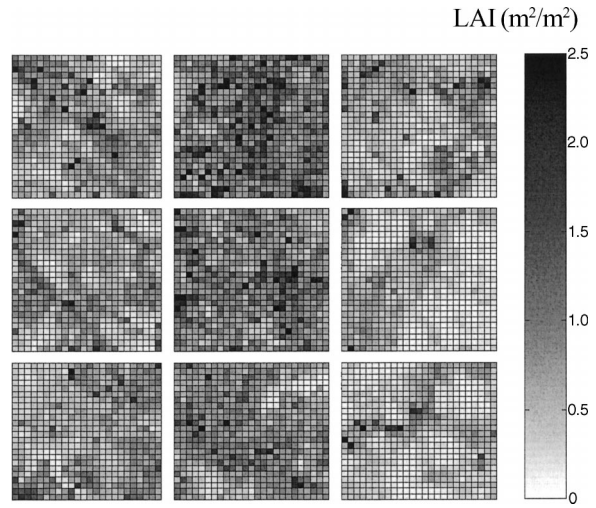


FIG. 7. Spatial map of definitively estimated LAI, using both LAI-2000 and NDVI in Eq. 3.

overall, with increasing LAI values, the absolute uncertainty increased (Fig. 8). The uncertainty intervals were quantified with the 95% confidence intervals of the parameters presented in Fig. 7.

DISCUSSION

Variations in leaf area index in arctic ecosystems can be measured nondestructively, easily, and quickly by combining NDVI measurements with measurements obtained with a LI-COR LAI-2000. With this measurement protocol, we were able to measure the spatial variability of leaf area index within a small catchment area, and to obtain relatively reliable LAI estimates from a total of 5625 measurement points.

A high relative uncertainty in estimated LAI occurred around the threshold value at which the switch

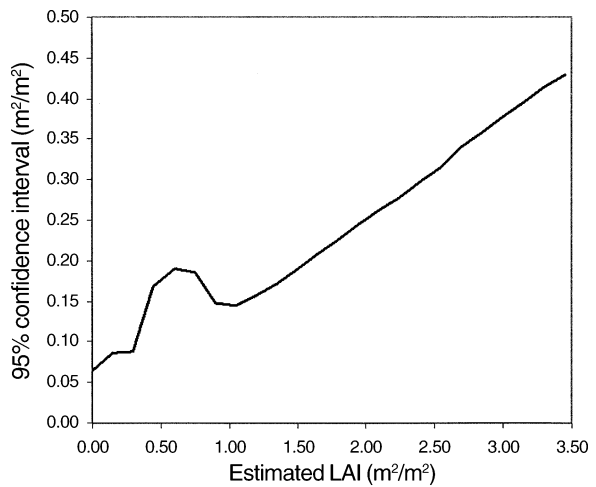


FIG. 8. The 95% uncertainty interval of estimated LAI (as shown in Fig. 7) simulated using the acceptable parameter combinations shown in Fig. 5.

occurred from using NDVI data to using gap-fraction measurements in order to calculate the estimated LAI. The uncertainty of relatively high and low values of estimated LAI was much lower, because of (1) the relatively large range of harvested LAI values that we had available for calibrating the combined NDVI–LAI-2000 response, and (2) the simple linear relationship that existed between LAI-2000 measurements and harvested LAIs. Using either the NDVI or LAI-2000 measurements individually led to a decrease in performance, in the form of a statistically unacceptable model parameterization.

Because of its relative ease and speed, this methodology offers the possibility of accurately quantifying LAI variability of sparse vegetation, such as the arctic vegetation in this study, over much larger areas than is possible by direct measurement. This combination of NDVI and LAI-2000 also can be applied to vegetation types other than arctic, e.g., alpine, marshland, coastal, or grassland vegetation. Potentially, the vegetation characteristics within a certain area can be linked directly to a remotely sensed aggregated measurement. Our methodology provides a means to quantify how vegetation characteristics and their variability determine the aggregated values viewed from space. Thereby, more basic relationships between satellite data and ground truth can be derived. This will allow more accurate quantification of the uncertainty of remotely sensed data that are used as an input of vegetation properties at regional scales for, e.g., GCMs. Williams et al. (2001) used satellite images at a pixel scale of 1 km² to estimate LAI variability at a regional scale. They showed that, in predicting regional primary production, the uncertainty in estimating LAI was the most significant problem. The LAI estimation methodology also can be useful for estimating the temporal development of vegetation, e.g., leaf expansion in spring and leaf senescence in autumn (Oberbauer et al. 1998, Van Wijk et al. 2003). As the method is non-destructive, continuous measurements can be performed and, in an easy manner, the temporal variations can be ascertained.

A limitation of the application of the NDVI sensor in the Arctic could be the distortion that can take place due to the variability in reflectance characteristics of mosses. If these are green, the NDVI values will probably get higher, and an overestimation of the LAI could be the consequence. However, in this study no clear effect of this was apparent. Mosses were present, and especially in one of the wet sedge plots, they were green during the measurement period. However, this did not seem to distort our calibration curve. For the wet sedge, there seemed to be systematic underestimation of the LAI, especially in the harvest LAI vs. NDVI scatter plot (Fig. 2B). This is probably caused by the black background originating from stagnant water in one of the plots. Because a number of wet sedge sites had an LAI higher than 0.7 (the threshold value), this deviation

was corrected for by the LAI-2000 values, where there seemed to be an overestimation of the real LAI. At the heath sites, the white background caused by lichens did not seem to cause a major distortion of our calibration curve. Overall, the LAI-2000–NDVI curve worked surprisingly well along the whole range of LAI values.

The calibration curve, however, will be different for other ecosystems. The shift from heath to shrub systems, while the LAI is increased, clearly affected the threshold point at which the LAI-2000 values are used rather than the NDVI values. This seemed to be mainly triggered by vegetation height (Fig. 4A–C). This can be linked to the way in which the different equipment systems worked: at low vegetation height, the LAI-2000 is severely limited in its applicability. It is clearly shown, in this study, that using an NDVI sensor in such a case can improve the LAI estimates considerably.

ACKNOWLEDGMENTS

This research was funded by U.S. National Science Foundation grant DEB0087046. We thank Terry Callaghan and Gus Shaver for their support during this research and Willem Bouten for the use of the LI-COR LAI-2000. We are grateful to Lorna Street and Sven Rasmussen for field assistance.

LITERATURE CITED

- Boelman, N. T., M. Stieglitz, H. Rueth, M. Sommerkorn, K. L. Griffin, G. R. Shaver, and J. A. Gamon. 2003. Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* **135**:414–421.
- Breda, N. J. J. 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *Journal of Experimental Botany* **54**:2403–2417.
- Cutini, A., G. Matteucci, and G. S. Mugnozza. 1998. Estimating of leaf area index with the LI-COR LAI 2000 in deciduous forests. *Forest Ecology and Management* **105**: 55–65.
- Deblonde, G., M. Penner, and A. Royer. 1994. Measuring leaf area index with LI-COR LAI-2000 in pine stands. *Ecology* **75**:527–511.
- Dufrene, E., and N. Breda. 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. *Oecologia* **104**:156–162.
- Ewert, F. 2004. Modelling plant responses to elevated CO₂: how important is leaf area index? *Annals of Botany* **93**: 619–627.
- Gould, W. A., S. Edlund, S. Zoltai, M. K. Reynolds, D. A. Walker, and H. Maier. 2002. Canadian Arctic vegetation mapping. *International Journal of Remote Sensing* **23**: 4597–4609.
- Gower, S. T., and J. M. Norman. 1991. Rapid estimation of leaf area index in conifer and broad-leaf plantations. *Ecology* **72**:1896–1900.
- Hicks, S., and R. Lascano. 1995. Estimation of leaf area index for cotton canopies using the LI-COR LAI 2000 plant canopy analyser. *Agronomy Journal* **87**:458–464.
- Jonasson, S., A. Michelsen, I. K. Schmidt, and E. V. Nielsen. 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology* **80**:1828–1843.
- Jonckheere, I., S. Fleck, K. Nackaerts, B. Muys, P. Coppin, M. Weiss, and F. Baret. 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.

- Le Dantec, V., E. Dufrene, and B. Saugier. 2000. Interannual and spatial variation in maximum leaf area index of temperate deciduous stands. *Forest Ecology and Management* **134**:71–81.
- LI-COR. 1992. LAI-2000 plant canopy analyzer. Operating manual. LI-COR, Lincoln, Nebraska, USA.
- Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**:698–702.
- Oberbauer, S. F., G. Starr, and E. W. Popp. 1998. Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra in Alaska. *Journal of Geophysical Research* **103**:29,075–29,082.
- Pontauiller, J. Y., G. J. Hymus, and B. G. Drake. 2003. Estimation of leaf area index using ground-based remote sensed NDVI measurements: validation and comparison with two indirect techniques. *Canadian Journal of Remote Sensing* **29**:381–387.
- Press, W., S. A. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1989. *Numerical recipes in FORTRAN: the art of scientific computing*. Cambridge University Press, Cambridge, UK.
- Rouse, J. W., R. H. Haas, J. A. Schell, and D. W. Deering. 1974. Monitoring vegetation systems in the great plains with ERTS. Pages 301–317 *in* Proceedings of the Third Earth Resources Technology Satellite-1 Symposium. NASA, Greenbelt, Maryland, USA.
- Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of the Environment* **8**:127–150.
- Van Wijk, M. T., and W. Bouten. 2002. Simulating daily and half-hourly fluxes of forest carbon dioxide and water vapor exchange with a simple model of light and water use. *Ecosystems* **5**:597–610.
- Van Wijk, M. T., M. Williams, J. A. Laundre, and G. R. Shaver. 2003. Inter-annual variability of plant phenology in tussock tundra: modelling interactions of plant productivity, plant phenology, snowmelt and soil thaw. *Global Change Biology* **9**:743–758.
- Van Wijk, M. T., M. Williams, and G. R. Shaver. 2005. Tight coupling between leaf area index and foliage N content in arctic plant communities. *Oecologia* **142**:421–427.
- Weiss, M., F. Baret, G. J. Smith, I. Jonckheere, and P. Coppin. 2004. Review of methods for in situ leaf area index (LAI) determination. Part II. Estimation of LAI, errors and sampling. *Agricultural and Forest Meteorology* **121**:37–53.
- Williams, M., and E. B. Rastetter. 1999. Vegetation characteristics and primary productivity along an arctic transect: implications for scaling-up. *Journal of Ecology* **87**:885–898.
- Williams, M., E. B. Rastetter, G. R. Shaver, J. E. Hobbie, E. Carpino, and B. L. Kwiatkowsky. 2001. Primary production of an arctic watershed: an uncertainty analysis. *Ecological Applications* **11**:1800–1816.