

PROJECT SUMMARY

Scientific Merit: The proposed research will contribute to the Arctic System Science program by improving understanding of the broad patterns of vegetation function across the Arctic, specifically through research on the relationships among (1) arctic vegetation canopy structure, N allocation, and whole-system CO₂ fluxes, and (2) ecosystem respiration and its main components, plant and soil respiration. The research represents a continuation of a series of NSF-OPP supported research projects, begun in 1995, and designed as a search for the general characteristics of vegetation function, resource allocation, and allometry that can be used to develop large-scale, long-term predictions of vegetation and ecosystem properties and of the role of arctic ecosystems in the Arctic System.

The proposed sites for new and continued research include Toolik Lake and Barrow, Alaska; Cherskii, Siberia; Thule, Greenland; and perhaps other sites in northern Canada. Field research at each site will include measurements of the light response of CO₂ flux in diverse vegetation (Net Ecosystem Exchange, NEE; Gross Primary Production, GPP; Ecosystem Respiration, R_E; Autotrophic Respiration, R_A, Heterotrophic Respiration, R_H). The vegetation and soil variables to be evaluated--canopy photosynthetic area and its N content, NDVI, soil C and N content, and microclimatic variables like canopy air and soil temperatures--are all key components of regulation of the feedbacks and interactions between the terrestrial landscape and the cycles of energy, water, and elements in the Arctic System. The core hypotheses to be tested are:

1. Over the entire Arctic Region, canopy N content will be a better overall predictor of NEE and GPP than leaf area because leaf N concentrations will increase in higher, colder latitudes, leading to higher GPP per unit leaf area with latitude but similar GPP per unit leaf N.
2. In the long term R_E, R_A, and R_H must all be related to GPP and its controls because GPP determines the total C inputs to the ecosystem. In the short term, R_A and R_H will respond differently to environmental variation: R_A will be most closely correlated with relatively rapid changes in air temperature while R_H will change more slowly and in correlation with more slowly-changing variables like soil temperature and moisture

In addition to empirical analysis of results, modeling of NPP, GPP, and R_E will test our ability to extrapolate from one site to another within the Arctic and will help to determine whether a single model parameterization can be developed for the entire Arctic. A key product will be a data base for modeling and extrapolation of vegetation properties and CO₂ fluxes across the Arctic region. Long-running collaborations with other established modeling groups will continue.

Broader Impacts: The potential impacts of this research are much broader than an increase in understanding of arctic vegetation, the controls on its broad patterns of growth and greenhouse gas exchange, and the potential for future change in response to climate. The major issues of broader interest here are (1) the scaling of ecological understanding from single sites and species to larger, regional environmental systems, (2) the effects of individual species or plant "functional types" on overall ecosystem and landscape-level processes, and (3) the role of vegetation in regulating feedbacks between the arctic land surface and the atmosphere, and between the Arctic System and the global environmental system. Resolution of these issues is key to development of sound policies on conservation and management of ecosystems and landscapes everywhere.

The proposed research will also make several contributions to education of future professionals and of the general public, by continuing our long-term involvement with training of undergraduate REU students, postdoctoral fellows, technicians, and science journalists. If appropriate graduate students in the new MBL-Brown Graduate Studies Program are identified, the postdoc and/or research assistant positions currently budgeted will be filled by students.

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INTRODUCTION

This proposal requests renewed support for research on canopy structure and CO₂ exchange of arctic ecosystems. The broad theme of this research is the regulation of the primary production system in arctic landscapes and especially the controls at the whole-vegetation level. This theme is important because vegetation is a key regulator of feedbacks from the arctic land surface to the regional and global systems, and plays a central role in mediating responses of the arctic landscape to disturbance and change of all kinds. Vegetation is central because it controls the surface characteristics of the landscape. Its species composition and physical structure are among the principal determinants of the arctic land surface energy balance, of the terrestrial water budget, of nutrient inputs to aquatic systems, and of the exchanges of carbon dioxide and other trace gases with the atmosphere (ACIA 2005, McGuire et al. 2002). Both the composition and the structure of arctic vegetation are not only highly variable across the landscape; they also can change dramatically over periods of years to decades, the same time scale over which climate is now changing as a result of human activities (Kittell et al. 2000, McGuire et al. 2000, Sturm et al. 2001, Tape et al. 2006). Changes in vegetation composition and structure, over the same time scale as climate change, will change the nature of the feedbacks from the terrestrial landscape to rest of the arctic system (e.g., Hobbie et al. 2002, Chapin et al. 2005, Cornelissen et al. 2007). Through its emphasis on vegetation as a major control over land surface properties and functions, the proposed research is particularly relevant to the emerging "Surface Interactions" Community of Practice within the ARCSS program.

Two general goals have guided the development of this research over the past 12 years:

1. The first goal is to search for general characteristics of arctic vegetation function and allometry that can be used to make broad predictions of the magnitude and trajectory of ecosystem response to climate change across the Arctic.
2. The second goal is to identify the vegetation types and plant species that are most sensitive to climate change, and the mechanisms that make them so.

To meet these goals, the research design is focused on comparative analyses of vegetation growth, allocation, allometry, and surface properties like energy and greenhouse gas exchange in multiple sites, vegetation types, and long-term field experiments. Because the broad aim of the work is to increase our ability to predict change within the arctic system as a whole, major efforts are made to compare vegetation properties and processes among different parts of the Arctic, including Alaska, Scandinavia, Greenland, Canada, and Siberia. The research design builds on a long history of research on species-level adaptations to arctic environments, but attempts to place the work in the context of its implications for larger-scale ecosystem, landscape, and regional processes and feedbacks. The effects of individual species on larger-scale processes are currently a major focus of research in ecology in general, as part of the global effort to understand the importance of "biodiversity" to human domination of the earth (e.g., Schulze and Mooney 1994, Loreau et al. 2001, 2002, Kinzig et al. 2002). Within ARCSS, the International Tundra Experiment (ITEX) has made important contributions to predictions of arctic plant responses to climate across the Arctic (Henry and Molau 1997, Arft et al. 1999, Walker et al. 2006, Oberbauer et al. 2007), and much of Shaver's research over the past 12 years has focused on these issues (e.g., McKane et al. 2002, Bret-Harte et al. 2001, 2002, Hobbie et al. 2005, Shaver et al. 1998, 2001, 2007).

GOALS FOR THE NEXT THREE YEARS

The goals for the next three years are derived directly from recent work in which we described the light response of net CO₂ exchange (Net Ecosystem Exchange, NEE) and its two main components, Gross Primary Production (GPP) and Ecosystem Respiration (R_E) in a range of ecosystems near Toolik Lake, Alaska; Abisko, Sweden; Longyearbyen, Svalbard; and Zackenberg, Greenland. For the two Low Arctic sites (Toolik and Abisko) we developed a model that explains ~80% of the variation in NEE among diverse vegetation types knowing only

leaf area, light intensity and air temperature (Shaver et al. 2007; Street et al. 2007). Toolik Lake and Abisko, however, are at virtually the same latitude (68°30'N), with similar summer climates. The next step is to test this model in High Arctic ecosystems, leading to a truly PanArctic understanding of controls on NEE, GPP, and R_E . We have already begun some of this work, with field surveys at Longyearbyen, Svalbard (78°30' N) and Zackenberg, Greenland (74°30' N) in 2005 and 2006. A key finding of this preliminary work (Shaver et al. unpublished data) is that GPP per unit leaf area at the High Arctic sites is consistently greater than at the Low Arctic sites, leading to consistent underestimation of CO_2 fluxes using the model of Shaver et al. (2007). We also have found that leaf N concentrations at Svalbard are higher than at Toolik or Abisko, so that the High Arctic sites depart from the consistent relationship between canopy leaf area and its N content described for the Low Arctic by Williams and Rastetter (1995) and van Wijk et al. (2005). This leads to our first goal for the next three years, to answer the question:

Goal 1: What is the relationship between canopy N content, canopy photosynthetic area, and canopy photosynthesis (GPP) in arctic vegetation including both Low and High Arctic sites?

- a. Does this relationship change predictably with climate or latitude, or in ecosystems that are changing in species composition and canopy structure?
- b. Can we develop a single parameterization of this relationship that is useful in predicting GPP across the full range of arctic ecosystem types, or must we use different parameterizations to predict GPP at different arctic latitudes or climates?

A second important step is to improve understanding of the respiration component of net CO_2 exchange, including whole-system respiration (R_E) and its two principal components, autotrophic and heterotrophic respiration (R_A and R_H , \approx "vegetation" and "soil" respiration; Randerson et al. 2003, Chapin et al. 2006). We expect R_A and R_H to respond differently to diurnal or to short-term weather changes, for example, because the vegetation component (R_A) is affected directly by the more variable temperatures in the air and upper soil, while the soil environment, affecting R_H , is less variable in the short-term (days to weeks). On longer time scales (years to decades), changes in the soil environment may be more dramatic leading to large changes in R_H that can change the sign of the overall C balance (e.g., Oechel et al. 2000). On very long time scales (decades to centuries), changes in vegetation biomass, productivity, and species composition will determine long-term change in the quantity and chemical quality of organic matter inputs to soils, which will determine changes in R_H along with slower changes in soil microclimate, but again the changes in R_H should lag behind the changes in vegetation composition and R_A on these long time scales. Existing landscape-scale models of partitioning and changes in R_A and R_H in arctic ecosystems are primitive and largely phenomenological rather than mechanistic, including the model of Shaver et al. (2007). Thus, our second goal for the next three years is to answer the question:

Goal 2: What is the relationship between R_E , R_A , and R_H in arctic ecosystems and how does it change in space and time?

- a. In relatively stable arctic ecosystems does this relationship vary predictably with climate, latitude, vegetation composition, and canopy structure?
- b. Can we predict the changes in R_E and its components as weather, climate, and vegetation composition change?

RESULTS OF PRIOR NSF SUPPORT

NSF-OPP-0352897: "*Resource Allocation and Allometry of Plant Growth in the Arctic: Key Constraints on Change and Predictability of the Arctic System*"; 5/1/04-4/30/07; \$870,809 (G.R. Shaver, Principal Investigator). The current project is the third in a series that began with NSF-OPP support in 1995 as part of the International Tundra Experiment (ITEX). The general aim of these projects has been to understand and predict effects of climate change on arctic plant species and plant communities, using PanArctic comparisons of similar observations and experiments at multiple sites (Henry and Molau 1997, Arft et al. 1999, Walker et al. 2006). The series of projects has been exceptionally productive, responsible in whole or in part for over 80

peer reviewed publications with Shaver as author or coauthor, including both multisite syntheses and focused site-specific studies; the 33 publications and manuscripts produced during the current funding period (since April 2004) are identified with asterisks in the REFERENCES section. Data sets are archived in the Arctic LTER data base at <http://ecosystems.mbl.edu/arc/>, and linked to the ARCSS Data Coordination Center at <http://nsidc.org/arcss/>.

Since 1995 these projects have also contributed to the training of 24 summer REU students (13 female/11 male), funded with supplements to these and related NSF grants; about half have gone on to graduate schools (as well as two research assistants). Five postdoctoral fellows have been supported directly by these grants and have gone on to academic jobs. Before 2003 the MBL was not a degree-granting institution; we now have an agreement for joint graduate training with Brown University, and one student (M. Alexander-Ozinskas) completed a Brown University Master's degree in May 2007 with support from the current grant. Finally, as a part of the strong international collaborations developed in this project at least 8 foreign graduate students have been able to complete part of their dissertation research at Toolik Lake and other arctic sites, and Shaver has served on 6 Ph.D. examinations in Sweden, the Netherlands, and the UK.

Since 1995, research on these projects has focused increasingly on PanArctic comparisons of the primary production system in diverse arctic vegetation, leading directly to the proposed research. The starting point for this work was the observation that, despite a 1000-fold range in productivity among arctic ecosystems (Shaver and Jonasson 2001, Jonasson et al. 2001),

production:biomass relationships of arctic vegetation types are similar throughout the Arctic (Shaver et al. 1996). This observation (Figure 1) suggests strongly similar controls on the production process despite the wide range of productivity and the dramatic variation in plant functional types that dominate in diverse arctic ecosystems. A later study by Williams and Rastetter (1999) showed that the total vascular leaf area of tundra vegetation in northern Alaska is very tightly correlated with the total amount of N in the canopy (Figure 2).

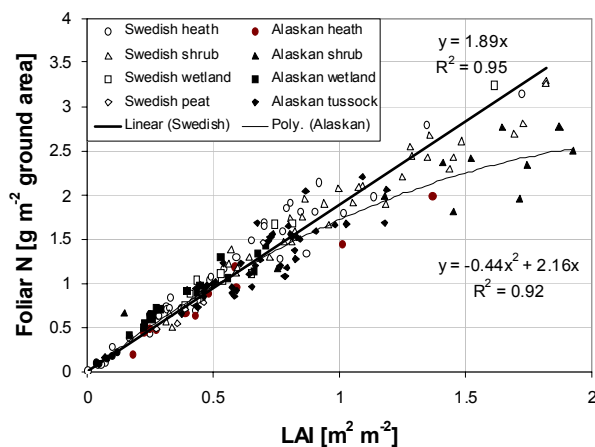


Figure 2. Across a wide range of tundra vegetation in both Alaska and Sweden, leaf area and N content are closely correlated, suggesting tight control over canopy architecture and N use in arctic vegetation (van Wijk et al. 2005). LAI=Leaf area index (m² leaf per m² ground surface).

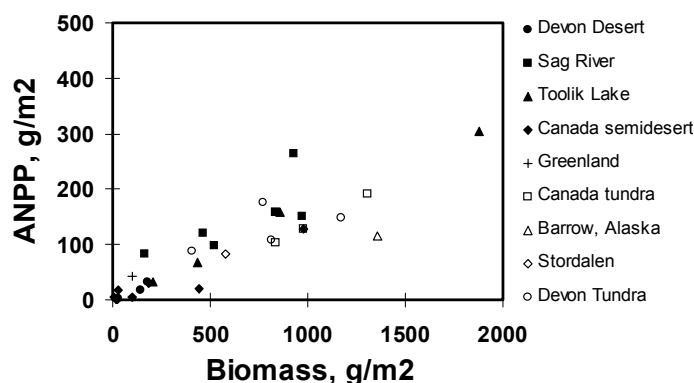


Figure 1. Aboveground net primary production (ANPP) versus vegetation biomass at 28 arctic sites (Original data in Weiglowski et al. 1981, Shaver and Chapin 1991, and Shaver et al. 1996). For the data in this graph, $ANPP = (0.14 * Biomass) + 12.5$; $P < 0.0001$, $r^2 = 0.77$.

This relationship holds across a wide range of tundra types, including wet sedge, moist tussock, deciduous shrub, and dry heath vegetation dominated by very different plant types and covering virtually the entire range of plant production and biomass that occurs in northern Alaska.

Our recent work on arctic plant canopies has greatly strengthened the evidence for a common set of controls over canopy-level CO₂ exchange in diverse arctic ecosystems. In 2002, we completed a survey of LAI-canopy N relationships near Abisko, in northern Sweden. The results were nearly identical to what Williams and Rastetter found

in Alaska, with the two data sets lying nearly on top of each other and the overall correlation between LAI and canopy N content explaining more than 90% of the variance (Figure 2; van Wijk et al. 2005). Below LAI values of about 1, the correlation between the two data sets from Alaska and northern Sweden was particularly tight, with some divergence between the Swedish and Alaskan results above one m^2 leaf per m^2 ground. In both Alaska and Sweden, and indeed over most of the Arctic, the land surface is covered with vegetation that has LAI less than 1.0–1.5 m^2 leaf m^{-2} ground.

In 2003–2005, we pursued the implications of this consistent canopy structure (Figure 2) by measuring the light responses of whole-canopy CO_2 fluxes in diverse arctic plant canopies in Alaska and northern Sweden. In this work we showed that canopy leaf area *alone* is an excellent predictor of whole-canopy photosynthesis, explaining ~80% of the variance in Gross Primary Production (GPP) at constant irradiance ($\text{PPFD}=600 \mu\text{mol m}^{-2} \text{s}^{-1}$) across a wide range of plant canopies (Figure 3; Street et al 2007).

Furthermore, for unfertilized plots the relationship between GPP and leaf area is the same at both Toolik Lake, Alaska and at Abisko, Sweden. This is a key finding suggesting that a single model parameterization can be used to predict CO_2 flux for whole canopies of diverse species composition, at least throughout the Low Arctic region.

How can we use this information to “scale up” our predictions of CO_2 flux from small, homogeneous plots of diverse vegetation to large, heterogeneous landscapes and watersheds? There are two fundamentally different approaches available to us: First, we can view the landscape as a mosaic of large patches with that differ in leaf area among patch types but are homogeneous within patches; we can predict CO_2 flux within each patch; and finally we can sum the fluxes knowing the areas of each patch. Second, we can view the landscape as varying continuously at a fine scale (e.g., 1 m^2 , the scale at which we actually measure canopy-level CO_2 flux); we can estimate leaf area at this fine scale; and we can predict CO_2 flux as a continuous variable over the landscape. In our research since 2003 we have used both of these methods to predict CO_2 flux from the same data set, allowing direct comparisons of the relative accuracy and precision of predictions based on different methods.

Using the first approach (i.e., viewing the arctic landscape as a mosaic of patches), we used a maximum likelihood method to estimate parameters regulating CO_2 flux (both whole-system respiration in the dark, R_E , and canopy photosynthesis, GPP) in relation to light and air temperature in the Imnavait Creek watershed, near Toolik Lake (Figure 4; Williams et al. 2006). The maximum likelihood method allowed estimation of acceptable parameter spaces for each measured CO_2 flux response curve, given a known measurement uncertainty (Root Mean Square Error, RMSE) of $0.42 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ estimated by repeated measurement of fluxes

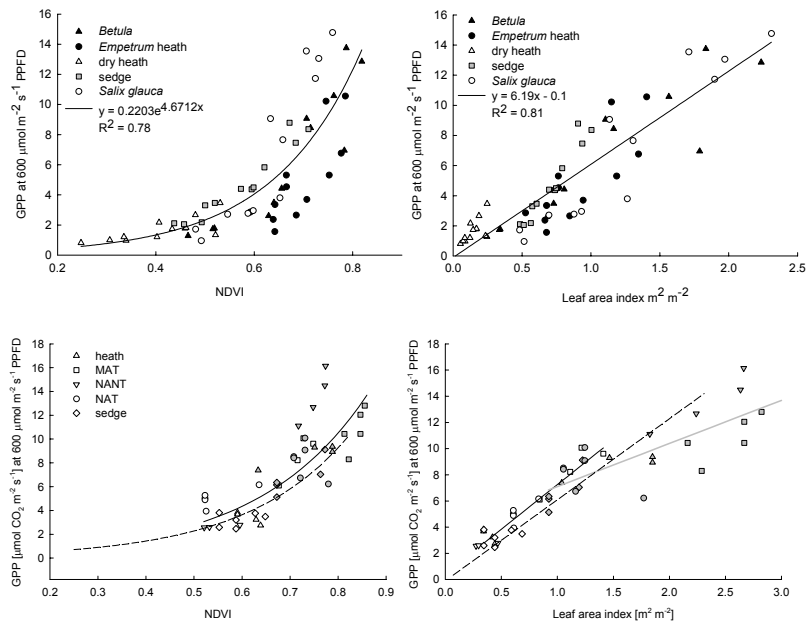
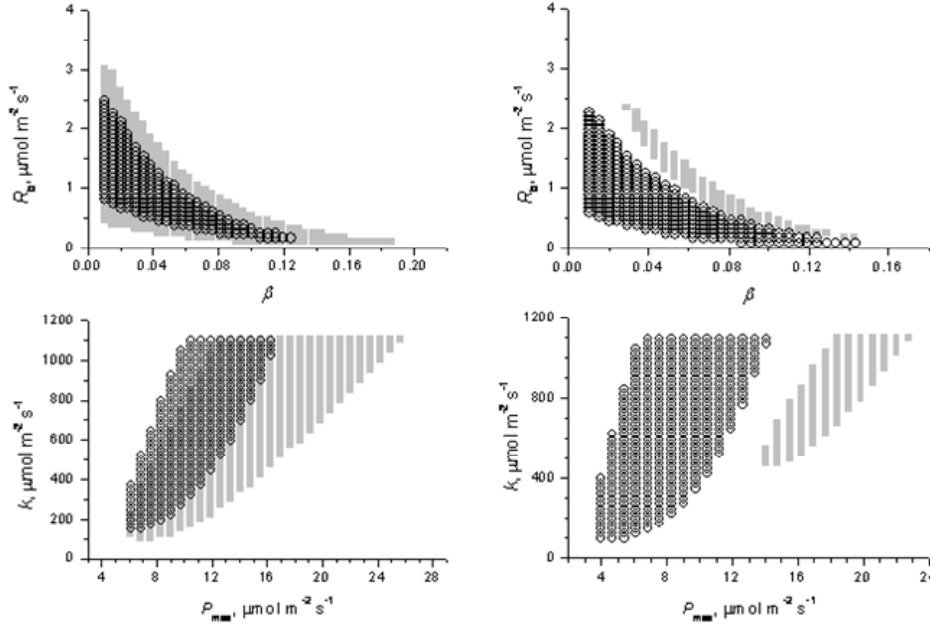


Figure 3. (from Street et al. 2007). Upper panels show the relationship between GPP600 and (A) NDVI and (B) predicted LAI for 5 vegetation types at Abisko, Sweden. Lower panels show the relationship between GPP600 and (C) NDVI or (D) leaf area for control and fertilized plots in 5 vegetation types at Toolik Lake, Alaska. Filled symbols in (C) and (D) are fertilized plots. Gray line in (D) is the best-fit linear regression for fertilized plots only ($R^2 = 0.63$), solid line in (D) is for Toolik 2004 control plots only ($R^2 = 0.89$). Dashed lines in (C) and (D) are regression lines derived using Abisko data in upper panels.

Figure 4. Williams et al. 2006; A comparison of acceptable parameters for the PIRT model applied to paired data sets. The left hand panels compare data collected for plot 1 (wet sedge), in periods 1 (open symbols) and 2 (grey symbols). There is clear parameter overlap for both the photosynthesis and respiration model parameters, indicating similar functional activity. The right hand panels compare data collected in period 1, for Tussock wet (plot 3, open symbols) and Hilltop heath (plot 7, grey symbols). The lack of overlap in the photosynthesis parameters suggests different functional attributes of these sites. 2.56 million parameter combinations were tested for acceptability at the 95 % confidence interval for each dataset.



under similar conditions at the same plots To explain canopy CO₂ fluxes at all sites and time periods required a minimum of 7 distinct, generic parameter sets, but just one of these 7 parameter sets could explain 23 of the measured 43 curves; all 23 were from the most common tundra type in the Imnavait watershed, moist tussock tundra. Using the 7 generic parameter sets resulted in a mean prediction RMSE of 0.70 µmol CO₂ m⁻² s⁻¹. Overall, the conclusion was that

CO₂ flux in the Imnavait Creek watershed could be modeled with acceptable accuracy as a mosaic of 7 different patch types, with most of the area of the watershed as one patch type, moist tussock tundra.

Using the second approach (continuously variable leaf area at fine scale), we developed a new model of Net Ecosystem Exchange (NEE), where:

$$NEE = \left((R_0 * e^{\beta T} * LAI) + R_x \right) - \left(\frac{P_{maxL} * \ln \left(\frac{P_{maxL} + E_0 * I}{P_{maxL} + E_0 * I * e^{-k * LAI}} \right) \right) \quad (\text{Equation 1})$$

In this model (Shaver et al. 2007), the first term describes ecosystem respiration (R_E) as the sum of a constant, basal respiration rate (R_x) and a respiration component (R₀) that increases with both temperature and leaf area. The second term of the model is adapted from Rastetter et al. (1992) and describes canopy photosynthesis (GPP) as a function of a maximum photosynthetic rate per unit leaf area (P_{maxL}), a light extinction coefficient (k), a quantum efficiency (E₀), leaf area (LAI), and photosynthetically active photon flux (I).

To apply the model, we use nonlinear regression to estimate the six parameters (R_x, R₀, β, P_{maxL}, k, and E₀) of Equation 1 (Shaver et al. 2007). We then use the measured values of LAI, air temperature (T), and photon flux (I) to predict NEE, substituting using these estimated parameters into Equation 1. When we use the entire data set to do this we have a measure of the ability of the model to encapsulate the variability in NEE within a single equation. In Figure 5, we used 1410 individual measurements of NEE in 79 plots of 32 different site/vegetation type combinations in Alaska and Sweden to estimate the model parameters and predict NEE. The model explains ~80% of the measured variance in NEE with zero bias (slope =1.000, intercept =0.000) across the full range of measured and modeled values. Only about a dozen of the 1410 data points might be considered outliers (lower left quadrant of lower panel in Figure 5). All but 4 of these outlying data points represent CO₂ fluxes in just 2 individual light response curves, both of them measured in willow communities at Abisko. The willows in these two

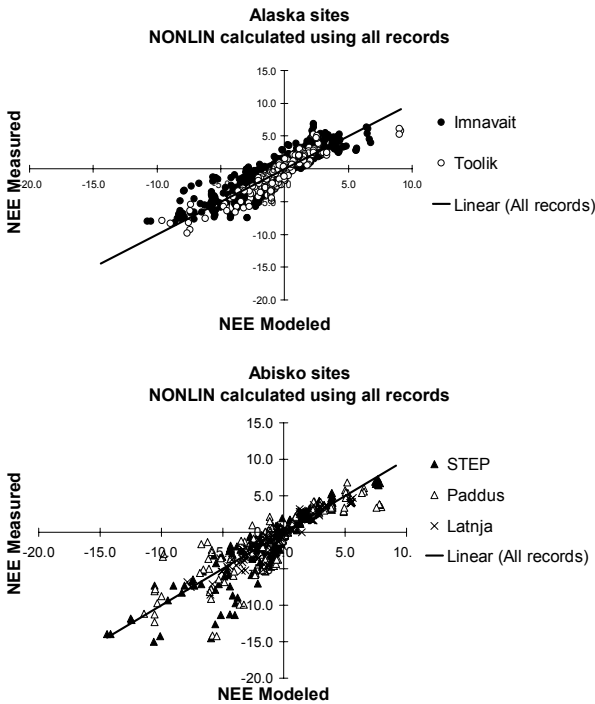


Figure 5. Measured versus modeled NEE, using all available data from 32 site/vegetation type combinations. Predicted and measured values from Alaska and Sweden are on separate panels to facilitate viewing only. Also to facilitate comparison, the same overall regression line is plotted in both panels. Overall r^2 for this parameterization is 0.799, the slope is 1.000, the intercept is 0.000, and the root mean square error (RMSE) is $1.529 \mu\text{mol m}^{-2} \text{s}^{-1}$.

intercept are very close to 1.00 and zero, respectively; and the RMSE varies from 1.0 to $2.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The predictions are most accurate and precise when we use a survey of CO_2 flux in diverse vegetation types within a local region to parameterize the model, as opposed to using measurements from just a single vegetation type to develop parameters that are then used to predict NEE in very different kinds of vegetation.

*Overall, the primary conclusion of the past three years of work on this project is that **all of the Low Arctic tundras that we have examined seem to be following the same rules with respect to regulation of their canopy-level CO_2 exchange.** Because leaf area, and its N content, are tightly constrained across diverse kinds of plant canopies, we can parameterize the model described in Equation 1 using a survey of CO_2 fluxes in one part of the Low Arctic, and we can use that parameterization to predict NEE with acceptable accuracy and precision in other parts of the Low Arctic. To do this we need to know only (1) total canopy leaf area, (2) photosynthetically active photon flux, and (3) air temperature, all of which can be sensed remotely at the site where NEE is to be predicted. This is a major step forward in development of a PanArctic CO_2 flux model, as well as a major step toward confirmation of our overall hypothesis that natural selection places very tight constraints on how plant canopies can develop in arctic vegetation.*

There is considerable room for improvement, however, in our ability to predict NEE and its components, GPP and R_E . We particularly need to know more about how the total photosynthetic area and its N content (in both vascular and nonvascular plants) is regulated at the level of whole canopies, and *how it will change* as the climate changes. We already know, for example, that GPP in fertilized plots at Toolik Lake, where the vegetation composition and

communities have distinctly silver-grey leaves, and we believe the main reason they are outliers in Figure 5 is that the leaf color affects our estimate of NDVI, and thus LAI.

The root mean square error (RMSE) of prediction in Figure 5 is $1.53 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, double the RMSE using the “mosaic” or patch-based maximum likelihood method of Williams et al. (Figure 4). One major advantage, however, of the “continuous variation” approach of Figure 5 is that it uses a single model parameterization applied everywhere, versus the requirement to identify and parameterize separately each of the patch types of interest using the “mosaic” approach.

To evaluate our ability to use data from one site, vegetation type, or region to predict NEE, GPP, or R_E in other places we use different subsets of the data for parameter generation vs. tests of model predictions. For example, we can use the data from all Alaskan sites to develop model parameters (by nonlinear regression on Equation 1), and then use those parameters to predict NEE at all Swedish sites and to compare predicted with measured NEE. In general the model does extremely well at predicting NEE in one place with parameters developed from measurements in another place. The r^2 of predicted vs. measured NEE is almost always >0.75 ; the slope and

canopy structure are still changing, has a different relationship to leaf area (Figure 3D). We also know from our surveys of CO₂ flux at two High Arctic sites, Zackenberg, Greenland, and Svalbard, Norway, that GPP per unit leaf area (at a standard PPFD=600 μmol photons m⁻² s⁻¹) is consistently higher than in the Low Arctic (Figure 6, top panel). We believe that this difference is due to consistently higher overall canopy N concentrations in the High Arctic sites (Figure 6, middle panel; data are available only from Svalbard). Because of the higher leaf N concentrations in the High Arctic, GPP per unit leaf N (at PPFD=600) is quite similar among sites (Figure 6, lower panel). Additional data are needed for a full test of this hypothesis (Goal 1 of the proposed research).

ADDITIONAL BACKGROUND

There isn't room for a comprehensive review of arctic CO₂ fluxes and canopy structure within the constraints of the NSF proposal format. Instead, we emphasize just two key points:

First, arctic vegetation and arctic C balance are both changing. Evidence for change in arctic vegetation comes from analyses of satellite imagery (e.g., Myneni et al. 1997, Stow et al. 2003, Jia et al. 2004, Stow et al. 2004, Hinzman et al. 2005) and from comparison of photographs taken at different times (Sturm et al. 2001, Tape et al. 2006), and is suggested but not yet clear from long-term monitoring programs and other studies (Shaver et al. 2001, Mack et al. 2005). Many of the changes that are occurring (particularly the increases in deciduous shrubs) have been predicted for many years from both field studies and from modeling (Miller et al. 1984, Chapin and Shaver 1985, Chapin et al. 2005).

Changes in arctic vegetation have the potential to cause profound changes in feedbacks between the land surface and the atmosphere. Many of these will be related to species and functional type composition of the vegetation. Changes in the relative abundance of mosses and lichens, for example, may have major impacts on soil thermal regimes, surface water balance, and nutrient cycling in addition to changes in CO₂ exchange (e.g., Cornelissen et al. 2007, Gornal et al. 2007). Changes in species composition may affect litter quality and decomposability, leading to major changes in C and N turnover rates in the soils (e.g., Hobbie et al. 2000, Weintraub and Schimel 2005). Changes in vegetation canopies also have the potential to change the soil thermal regime in both summer and winter, with warmer temperatures in winter due to greater snow accumulation beneath shrubs (Sturm et al. 2001) and cooler temperatures in summer due to interception of solar radiation by a denser, taller canopy (Chapin et al. 1995). Vegetation also affects the timing of snow and ice cover and melt (Sturm et al. 2001, Jia et al. 2004), and a shift to shrub- or tree-dominance is expected to lead to a large increase in sensible heat exchange with the atmosphere (Chapin et al. 2005).

Changes in both climate and vegetation will have major impacts on the regional and global CO₂ exchange with the atmosphere. During the last few decades, the shape of the seasonal cycle of atmospheric CO₂ has changed at CO₂ observation stations north of 55°N (Keeling et al. 1996, Conway et al. 1994, Manning 1993). The peak-to-trough amplitude has substantially increased and the phase has advanced (Zimov et al. 1999). The footprint of these observation stations consists primarily of arctic and boreal vegetation types (Kaminski et al. 1996, Goetz et al. 2005), and top-down atmosphere inversion analyses suggest that within these ecosystems, carbon uptake has increased during the first half of the growing season (Randerson et al. 1999).

Annual estimates of NEE are now available for a growing number of arctic sites (ACIA 2005). It is clear that GPP and RE respond differently to weather and climate changes (e.g., Oechel et al. 1998, Corradi et al. 2005, Oberbauer et al. 2007), and that NEE varies among

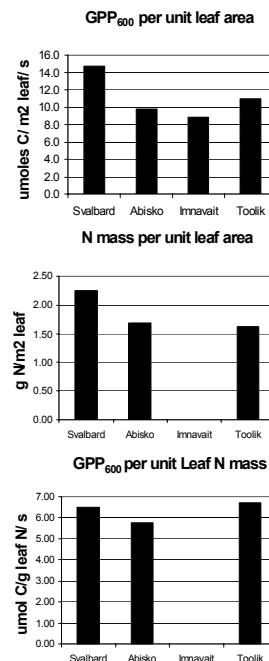


Figure 6. GPP per unit leaf area is higher on Svalbard than at three Low Arctic sites, but the differences disappear when expressed as GPP per unit leaf N mass. (GPP at constant PPFD of 600 μmol photons/m²/s)

years and shows distinct long-term trends (Oechel et al. 2000, ACIA 2005). However, the mechanisms underlying these changes, and their full extent, are not yet known (Hinzman et al. 2005). Intensive observations of carbon, energy, and water fluxes across the PanArctic, combined with experimental manipulations, are necessary in order to characterize how changes on land feed back to regional and global climate, now and in the future.

Second, canopy photosynthetic area and light interception are key predictors of ecosystem photosynthesis and net CO₂ exchange. The dominant species of arctic vegetation are known to differ significantly in their photosynthetic properties, whether expressed per unit leaf area or per unit leaf mass (e.g., Chapin and Shaver 1985, Johnson and Tieszen 1976, Bigger and Oechel 1982, Oberbauer and Oechel 1989, Oberbauer et al. 1996, Baddeley et al. 1994). These species differences often were used in past research as indicators of the relative fitness of arctic plants in different microenvironments, and were key components of most of the well-known models of arctic photosynthesis and C cycling that were developed during the 1970s -1990s (e.g., Miller et al. 1984, Tenhunen et al. 1994, Reynolds et al. 1996, Rastetter et al. 1997, McKane et al. 1997). At the whole-canopy or ecosystem scale, however, many studies have shown that leaf area is both a better predictor and a key unknown in models of C cycling (e.g., Williams and Rastetter 1999, Williams et al. 1997, 2001, 2006). The correlation of CO₂ exchange with NDVI has been explored in several studies at the landscape and regional level in northern Alaska (e.g., Hope et al. 1993, 1995, Vourlitis et al. 2000, 2003), and in satellite studies for the boreal and arctic region (e.g., Goetz et al 2005); our proposed research adds a more explicit and quantitative analysis of the NDVI-LAI relationship than in this past work.

Leaf area and mass, leaf N content, leaf longevity, and leaf-level CO₂ exchange are all related to each other in “The Worldwide Leaf Economics Spectrum” (Wright et al. 2004), and much of our ability to explain CO₂ exchange of diverse mixed-species arctic plant canopies must be related to these fundamental constraints on relationships among leaf traits. Wright et al. (2004) also found only minor effects of climate on leaf trait relationships, suggesting that differences in the individual leaf traits we actually observe in different arctic climates (such as high N concentrations in the High Arctic) are probably due to tradeoffs among these traits both within and among species rather than some specific Arctic-related adaptation.

The usefulness of canopy leaf area and light interception as predictors of landscape-level CO₂ fluxes has been shown in many studies both within and outside the Arctic (e.g., Monteith 1972, Goward et al. 1985, Prince and Goward 1995, Waring and Running 1998, Anderson et al. 2000, Turner et al. 2003, Goetz et al. 2005); these two variables are key components of most of the current global “big leaf” models of GPP and NEE (e.g., Running et al. 2004). These models typically predict CO₂ fluxes as a function of NVDI or the fraction of intercepted PAR (FPAR), multiplied by an efficiency measure (“ ϵ ”) that varies among vegetation types. One implication of our work is that the value of “ ϵ ” should be essentially constant for Low Arctic vegetation (e.g., Figure 3). The most likely reason for this is the generally low LAI in arctic vegetation. “Big leaf” models have been criticized for their unrealistic assumptions about light extinction in dense canopies such as forests (e.g. De Pury and Farquhar 1997). This is much less of a problem in the Arctic where LAI is usually less than 1-1.5; however, we do need to deal with light extinction in canopies with dense moss cover (Tenhunen et al. 1994, 1996, Williams et al. 2001) and this is one of our goals for the next three years. We also need to combine this work with a more extensive analysis of variability in CO₂ fluxes within the “footprint” of flux towers, similar to past work by Oechel and colleagues (e.g., Oechel et al. 2000).

HYPOTHESES AND MAJOR RESEARCH TASKS

Goal 1: What is the relationship between canopy N content, canopy photosynthetic area, and canopy photosynthesis (GPP) in arctic vegetation including both Low and High Arctic sites?

The hypothesis underlying our approach to this question is that **canopy N concentrations should increase in higher latitudes as summer air temperatures and incident PPFD decrease, leading to higher GPP per unit leaf area with latitude but similar GPP per unit leaf N.** This is an extension of the hypothesis first advanced by Chapin (1983; see review by

Chapin and Shaver 1985) as an explanation for the frequently high overall metabolic rates of arctic plants, especially in photosynthesis at low temperatures. Chapin's underlying assumption was that to maintain efficient metabolism at predictably low temperatures significant investments in enzymes such as Rubisco are necessary. In the context of the "Leaf Economics Spectrum" of Wright et al. (2004), an overall high canopy N concentration in colder, higher latitudes would be achieved mainly by correlated shifts in multiple leaf traits, both within and among species, between Low and High Arctic. To test our hypothesis we must:

- a. Extend our survey of the light response of NEE and GPP in both Low and High Arctic vegetation while adding estimates of leaf and whole-canopy N content to the data base. For a full test of the Shaver et al. (2007) model we particularly need to characterize the light response and N content of moss- and lichen-covered surfaces, both with and without vascular canopies (e.g., Douma et al. 2007), and to characterize NEE in systems with large proportions of bare ground or small, isolated vegetation patches.
- b. Characterize the light response of NEE and GPP, canopy leaf area, and canopy N content in vegetation that we know is changing in its species composition and productivity, including the well-documented time series of long-term experimental plots at Toolik Lake.
- c. Substitute measures of canopy N content for canopy leaf area in the model of Shaver et al. (2007), and evaluate the ability of the model to explain these results using the data subsetting methods and sensitivity analyses as in Shaver et al. (2007).

Goal 2: What is the relationship between R_E , R_A , and R_H in arctic ecosystems and how does it change?

Our underlying hypothesis here is that ***in the long term R_E , R_A , and R_H must all be related to GPP and its controls because GPP determines the total C inputs to the ecosystem including litter inputs to soil organic matter. In the short term, R_A and R_H will respond differently to environmental variation; R_A will be most closely correlated with relatively rapid changes in air temperature while R_H will change more slowly and in correlation with more slowly-changing variables like soil temperature and moisture.*** This means that prediction of R_E and its components requires a model that incorporates both long-term controls related to C pool sizes and GPP (and perhaps a measure of C "quality") and shorter-term controls related to microenvironmental variation. The tasks required to test this hypothesis include:

- a. In a wide range of vegetation types in Low Arctic and High Arctic landscapes, make separate measurements of R_E and R_H , and estimate R_A as the difference between these two variables, using the method of Johnson et al. (2000). This should be done as part of the continuing survey of the light response of NEE in Low and High Arctic systems, including descriptions of canopy structure, N content, species composition and cover, and air and soil microenvironmental variables (Shaver et al. 2007). Additional data required include estimates of the total soil C and N pools within the annually-thawed active layer of soil (Mack et al. 2004).
- b. In conjunction with the survey of canopy structure, NPP, and GPP in disturbed and manipulated ecosystems, also measure R_E and its components and describe total C and N pools and microenvironmental variation.
- c. Evaluate alternative formulations of the respiration term of the Shaver et al. (2007) model including new, separate temperature and moisture responses and explicit separation of R_A and R_H .

RESEARCH SITES AND SCHEDULE

Field research sites (Figure 7) will be at Toolik Field Station and nearby Imnavait Creek in northern Alaska (<http://www.uaf.edu/toolik/>), at the Barrow Arctic Science Consortium in Barrow, Alaska (<http://www.arcticsscience.org/>), at the Northeast Science Station, Cherskii, Russia (<http://www.faculty.uaf.edu/fffsc/station.html>), and at Thule, Greenland (<http://www.thule.af.mil/>). If our Canadian colleague Greg Henry (University of British Columbia)



Figure 7. Past and proposed research sites.

is successful in obtaining Canadian IPY funding to establish CO₂ flux sites at Alexandra Fjord and Lake Hazen, we will also try to visit these extreme High Arctic sites (Svoboda and Freedman 1994) as well. At all sites a primary goal will be to expand the range of vegetation types included in our data base on canopy structure (especially LAI and N content), CO₂ fluxes, and production-biomass relationships, by surveying a wide range of systems dominated by different plant forms. At Toolik Lake we will focus on trajectories of change, working in long-term experimental plots of the Arctic LTER project based there (e.g., Shaver et al. 1998, 2001, Hobbie et al. 2005, Mack et al. 2004). At Imnavait Creek, Cherskii, and Barrow we will also work on upscaling our results, by systematic sampling of different patches of vegetation in the footprints of established eddy covariance flux towers

As in the past several summers, we will work at Toolik Lake and nearby Imnavait Creek all summer long for all three years, taking a smaller crew on 3-6 week expeditions to the other sites in mid-summer (to Barrow in year 1, to Cherskii in Year 2, and to Thule and/or northern Canada in Year 3). Modern laboratories with electric power are available at all of these sites, as well as long histories of published research and climatic and other data (described in web sites cited above). Although travel to Cherskii and Thule is logistically difficult, communications are excellent; we will work with the OPP Arctic Logistics provider, VECO Incorporated, to make these arrangements. All sites have well-established, well-described research areas in diverse vegetation types within walking or driving distance of the labs. Shaver has long experience working at Toolik Lake and Imnavait Creek. He completed his Ph.D. research at Barrow in the 1970s and has revisited there three times in the last 10 years. Shaver is also Principal Investigator of a new IPY project to create flux observatories at Imnavait Creek and Cherskii.

Past experience has also given us a good feel for the data requirements of our proposed work. Reliable analysis using nonlinear regression in 3-7 parameter models will require at least 250-400 individual flux measurements in light response curves from each site, ideally from 10-15 different plots per site representing 5-8 contrasting vegetation types. These light response curves will include ~40-50 “full dark” measurements of R_E. To meet our R_E/R_A/ R_H modeling needs we will make additional measurements of R_H in vegetation-free soil cores (Johnson et al. 2000) and make diurnal flux measurements of NEE, R_E, and R_H (Johnson et al. 2000, Oberbauer et al 2007). All of this can be done in ~3-4 weeks by 2-3 people in our High Arctic campaigns at Barrow, Thule, and Cherskii, including sampling of vegetation for NDVI-LAI relationships (van Wijk and Williams 2005, Street et al. 2007) and collection of leaf samples for N analysis. At Toolik Lake we will extend these data sets by measuring fluxes through the summer including the early leaf expansion period in late May and June, and leaf senescence in August. In Year 1 of the work we will extend the field season through October to document changes in respiration components at low temperatures.

MEASUREMENTS AND MODELING

Light response curves and related data: Description of the light response of NEE and GPP and relating them to LAI, N content, and microclimate requires a series of steps. The first step is a *measurement of the light response of CO₂ flux* in whole vegetation and soils (Williams et al. 2006, Street et al. 2007, Shaver et al. 2007, Douma et al. 2007). To do this we place a square metal frame above the plot of interest, with the frame supported by metal rods at the corners. A plastic sheet hangs vertically down from the frame and is sealed to the ground by weighting the plastic down with a heavy chain. A clear acrylic cuvette is placed over the frame, attached to a LiCor 6400 photosynthesis system. The initial measurement of CO₂ flux is made in full sunlight, followed by a series of measurements under increasing shade, with the shading caused by using 1-4 thicknesses of mosquito netting (the cuvette is lifted from the frame and ventilated

between each measurement). A final, dark measurement is made by covering the cuvette with an opaque tarp. Following the flux measurements we then estimate cover by species within the plot, and measure thaw depth, soil temperature and moisture, and the volume enclosed beneath the frame. We have used this method in a wide range of tundras and find that it gives highly repeatable, useful results, with a typical root square mean error (RMSE) of measurement of $\sim 0.49 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, well within the bounds needed for useful modeling and direct comparison (Williams et al. 2006). We consider these measurements direct measurements of NEE, and estimate GPP by subtracting the dark measurement (R_E) from NEE.

The second step is *measurement of surface reflectance (including NDVI) of the flux plot*, accomplished by scanning the plot with a Unispec Spectral reflectance system (Boelman et al, 2003, 2005, Street et al. 2007). We can use the NDVI measurement directly as a correlate of NEE, GPP, and R_E , or we can convert NDVI to LAI knowing the NDVI-LAI relationship (e.g., Figure 3; van Wijk and Williams 2005, Street et al. 2007).

The third step is *measurement of NDVI, LAI, and canopy N content*. We do this by measuring spectral reflectance (including NDVI) of a smaller, separate plot (usually a 20 cm-diameter circle) with the Unispec instrument (Boelman et al. 2003, 2005) and then by harvesting all leaf area within the field of view of the Unispec. Leaves are sorted to species, run through a scanner to determine leaf area by species, and then dried for later weighing and for analysis of N content. One addition to this routine for the next three years is to estimate cover of nonvascular plants and bare ground, and to sample mosses and lichens for N content, so that we can add nonvascular cover and N content to vascular LAI and its N content for a more complete accounting of photosynthetic area in relation to NDVI. Again, we have already done this in many different tundra types and feel that it gives us an excellent measure of leaf area (van Wijk and Williams 2005, Street et al. 2007, Shaver et al. 2007).

In selected plots where NEE and GPP of the whole system are measured, we will follow these measurements with an additional *description of the light response of GPP of the moss and lichen cover only*. Immediately after the whole-system measurements are completed, we remove all the aboveground vascular vegetation by clipping and complete another light response curve on the exposed moss and lichen cover (Douma et al. 2007). We finish with a new measurement of dark respiration from the clipped surface, which we subtract from net CO_2 flux at various light levels to obtain moss/lichen GPP. In 2005 and 2006 we experimented with this method in a wide range of vegetation at Abisko, Svalbard, and Zackenberg, including the use of a range of cuvette sizes and wetting treatments (i.e., measuring the short-term response of dry moss surfaces to water addition) and feel that it gives consistent, interpretable results (Douma et al. 2007, van Wijk et al. 2007).

R_E , R_A , and R_H : We will estimate R_E and its components by measuring whole-system CO_2 flux in the dark (R_E) as described above and by removing all or part of the vegetation biomass and measuring respiration of the remainder. We define R_H as the respiration of the system from which the vegetation biomass has been removed (following a period of 24-48 hours to allow initial, disturbance-related respiration to subside). R_A is then the difference between R_E and R_H . In the past we have used this approach successfully by pairing measurement of R_E in undisturbed plots with vegetation-free soil cores collected from adjacent to the plots and incubated in the same holes from which the cores were collected (Johnson et al. 2000).

In the proposed research these respiration measurements will be made in close association with the measurement of the light response of NEE and GPP described above. In most instances R_E data will actually be collected as part of the light response curves and each R_H core will be linked to a single light response plot. Because the two sets of measurements are linked, we can use all of the associated measurements of vegetation species composition and cover, NDVI, LAI, PPFD, air and soil temperature, and soil moisture to help explain variation in R_E , R_A , and R_H . To measure respiration over a wider range of temperatures and other conditions within the same plot or core, we will occasionally complete diurnal measurements in these plots and cores (measurements every 4 hours for 36-40 hours), and we will make repeated measurements in the same plots and cores over the summer season.

A key assumption that underlies our approach to separating the components of R_E is that respiration of recently-fixed C that goes into plant exudates below ground is included (implicitly) in our estimate of R_A . The reason for this is that, by measuring respiration of plant-free soil and calling it R_H we are excluding the microbial respiration of labile plant C that is exuded into the soil by roots, as well as the respiration of C translocated from roots to mycorrhizal fungi (Hobbie and Hobbie 2006). Thus when we subtract this measure of R_H from R_E , the resulting estimate of R_A includes the respiration of labile plant C that is actually converted to CO_2 by bacteria and fungi. In moist tussock tundra and wet sedge tundra at Toolik Lake, recent research using ^{14}C isotopic tracers of the fate of GPP suggests that this “exudation” of C accounts for about 15-25% of GPP (G. Kling, K. Nadelhoffer, and M. Sommerkorn, unpublished data). The problem of accounting for C exudation in partitioning of ecosystem respiration across the Arctic is still not completely resolved, and it probably explains, for example, why our own laboratory soil incubations (Shaver et al. 2006) failed to predict the large net soil C losses with fertilization that we have observed in the field (Mack et al. 2004). Nonetheless it is clear that respiration of recently-fixed plant exudates is closely associated with vegetation and its GPP, and in this sense it is appropriate to include “exudate” respiration in our estimate of R_A as “plant-associated” respiration that can be predicted from our measures of vegetation structure, composition, and GPP. We may also be able to estimate the size of this labile C pool by monitoring the initial decline in respiration in plant-free soil cores until a stable rate is reached and integrating the CO_2 -C losses over this time (after subtracting estimated R_H).

Most of our measurements of R_E and its components will be focused on the summer season because this is when most of the annual respiration occurs. Respiration during the winter, however, probably accounts for at least 20% of annual R_E although there is great variability among estimates (3-50%; Hobbie et al. 2000). One reason for the great variability in “winter” respiration estimates is variation in the definition of when the “winter” starts and ends. It is clear, though, that respiration rates (mostly R_H) during the coldest parts of the winter are extremely low, with most of the cold-season respiration actually occurring during the autumn (late September through December) and a smaller portion during the spring (May and early June; Schimel et al. 2006). Although R_A has apparently not been measured through the arctic winter, there is little reason to expect that R_A is significant except in the same fall and spring periods as R_H ; in fact it is likely that the aboveground component of R_A is very low through most of the autumn as air temperatures are colder than soil temperatures in autumn, winter, and spring. For the purposes of this research, we will focus on the estimating R_E , R_A , and R_H during the autumn period in Year 2 of this research, when we will extend our survey of respiration at Toolik Lake through at least the end of October.

Modeling NEE and GPP: The first modeling task is the substitution of canopy N mass ($g\ N\ m^{-2}$ ground) for LAI ($m^2\ leaf\ m^{-2}$ ground) in the NEE model of Equation 1. This requires a change in units of the terms k , P_{maxL} , and R_0 ($k=m^2\ ground\ g^{-1}\ canopy\ N$, $P_{maxL}=\mu mol\ CO_2\ g^{-1}\ canopy\ N\ s^{-1}$, $R_0=\mu mol\ CO_2\ g^{-1}\ canopy\ N\ s^{-1}$). The leaf N data then must be scaled appropriately to provide measures of whole-canopy N mass (including green portions of moss and lichen mass). This is done knowing the N concentrations in leaves of the 5-8 most abundant species and each species’ leaf mass and area per m^2 ground, from the data collected as part of the light response curve measurements described above (we assume that less abundant species have the same N concentration as the mean for abundant species). We can also develop predictions of canopy N content from NDVI measurements at individual sites, using the same regression approaches described by Street et al. (2006; e.g., Figure 3) and van Wijk and Williams (2005).

The second modeling task is to complete a series of analyses similar to Shaver et al. (2007), in which various subsets of the data are used to develop model parameters by nonlinear regression. These parameters are then used to predict NEE and GPP in the same sites or vegetation types where the data were collected, and also to predict NEE and GPP in *different* sites or vegetation types. The Root Mean Square Error (RMSE) of prediction is used as the measure of the model’s accuracy of prediction, and the slope and intercept of predicted versus measured values as measures of model bias. We consider the predictions useful if the model

consistently predicts NEE with an RMSE of no more than about twice the known measurement error, and less than 10% of the range of observed NEE. If NEE in any particular subset of the data is predicted equally well using parameters generated from different data subsets, we conclude that the model has captured the essential controls over NEE and that all sites and vegetation types are following essentially the same “rules” with respect to canopy-level CO₂ exchange.

Finally, we must compare the performance of the LAI-based model (Shaver et al. 2007) with the leaf N-based model to be developed in the proposed research. If the LAI-based model requires separate parameterizations for accurate prediction of Low Arctic versus High Arctic NEE and GPP, but the N-based model requires only a single parameterization for all sites, we can conclude that canopy N is a better predictor of CO₂ flux than leaf area for the Arctic region as a whole. We will use the same approach to determine whether the control over CO₂ fluxes by leaf area-canopy N relationships changes in vegetation that is changing in species composition and canopy structure. We can also use the maximum-likelihood-based method of Williams et al. (2006; Fig 4) to evaluate the relative accuracy and precision of using single versus multiple parameterizations of the models.

Modeling R_E, R_A, and R_H: To evaluate short and long-term controls on R_E, we first need to evaluate alternative model structures. In developing the current NEE model (Equation 1), for example, we evaluated three different formulations of the R_E term:

$$R_{E1} = R_0 * e^{\beta T} * LAI \quad (\text{Equation 2})$$

$$R_{E2} = (R_0 * e^{\beta T} * LAI) + R_x \quad (\text{Equation 3})$$

$$R_{E3} = (R_0 * LAI + R_x) * e^{\beta T} \quad (\text{Equation 4})$$

Equation 2 can be thought of as representing an ecosystem in which a single there is a single source of respiration (containing both vegetation and soils), in which both R_A and R_H respond identically to temperature and leaf area. Equation 3, on the other hand, implicitly assumes that there are two sources of respiration in the ecosystem, one (R₀) responsive to both air temperature and leaf area and the other (R_x) that simply respire at a constant rate. Equation 4 also assumes that there are two sources of respiration, but in this case R₀ is related to LAI while both R₀ and R_x respond identically to temperature. Note that LAI and e^{βT} are both dimensionless here (m²m⁻² and T⁻¹*T), so the units of the R parameters are all μmol CO₂ m⁻² s⁻¹.

Shaver et al. (2007) used Equation 3 in the overall NEP model (Equation 1) because it gave the best fit to the data for Alaska and Sweden, but it is unsatisfactory as a mechanistic explanation for variation in R_E throughout the Arctic including High Arctic sites with much lower soil C accumulations and large areas of bare ground. In the proposed research we will start with an equation that identifies R_A and R_H explicitly and that makes each responsive to both vegetation abundance (LAI or canopy N in this case) and temperature:

$$R_E = (R_A * \alpha_1 LAI * e^{\beta_1 T_1}) + (R_H * \alpha_2 LAI * e^{\beta_2 T_2}) \quad (\text{Equation 5})$$

In this equation the α and β parameters (α₁, α₂, β₁, β₂) account for different relationships to LAI and to temperature in controlling R_A versus R_H, and T₁ might represent air temperature while T₂ represents a soil temperature.

We will evaluate this Equation 5 using the respiration and other data described above and the same nonlinear regression and data subsetting and sensitivity approaches as for the NEE and GPP modeling described above. Equation 5 is only a starting point, however. We will also substitute canopy N content and perhaps other measures of vegetation for the LAI variable (with appropriate changes in units of α₁ and α₂) and evaluate these variables as predictors of our field measurements of R_E, R_A, and R_H. Additional parameters and variables that may be evaluated include soil moisture and total soil C and N content. Of course, the overall goal of this exercise is to come up a simple equation with as few parameters and measured variables as possible that gives us a reliable prediction of R_E anywhere within the terrestrial Arctic System.

DATA BASE DEVELOPMENT, APPLICATIONS, AND SYNTHESIS

The data to be collected as part of this research, particularly when combined with existing data sets, will provide a rich suite of opportunities for analysis of CO₂ flux in relation to canopy composition and structure across the Arctic, and for evaluation of scaling relationships that can be used for prediction of CO₂ flux across vegetation types dominated by a wide range of plant species and functional groups, and across a 1000-fold range of productivity (Figure 1). Our recent research has laid a strong foundation for meeting these goals, indicating high likelihood of success. The main need now is to expand the scope of the analysis to make it more useful to the needs of the central ARCSS program themes of predictability, feedbacks, and sustainability *at the regional scale*, and to the aims of the SEARCH program and the International Polar Year to understand the Arctic as a distinct regional environmental system.

Full exploitation of the data base will also require extensive interactions with existing models and future model development. Based on previous, extensive experience with development and testing of several models of arctic ecosystems and biogeochemistry, we feel comfortable with the basic formats and organization now used in the Arctic LTER data base (<http://ecosystems.mbl.edu/ARC/>)--our data have been widely used by others, with an increasing number of requests over the past several years. The main need is to improve the data sorting, merging, filtering, and transformation capabilities. These improvements are already underway as part of the development of the next generation network-level LTER data base (EML: Ecological Metadata Language). Another need is to ensure access to the data by ARCSS researchers specifically, through the ARCSS Data Coordination Center at <http://nsidc.org/arcss/>; this is done through a hot link to the Arctic LTER data base. Typically our major data sets are freely available within 12-24 months of field collection (or within 6-12 months after chemical analyses are completed) and can be downloaded directly by anyone, with the only request being that investigators notify the Arctic LTER data manager of their interest and that use of the data be acknowledged formally in publications.

Collaborations: An important part of this work is continuation of long-term collaborations with Ed Rastetter (MBL), Mathew Williams (University of Edinburgh), and Mark van Wijk (Wageningen Agricultural University, Netherlands), including field data collection, modeling, and exchanges of visits to field sites by students and postdocs. Shaver has a long record of data sharing, model development, and publication with these first-rate ecologists. With support from NSF-OPP and European agencies, all of us are currently involved in the development of long-term carbon/water/energy flux observatories at Toolik Lake and Cherskii, and with development of a PanArctic carbon/water/energy flux data base including data from Abisko, Zackenberg, and other arctic sites as part of the International Polar Year (IPY). Rastetter is also developing a improved model of canopy N allocation for arctic vegetation including light extinction in denser canopies (LAI ≥ 2.0), and we expect to work particularly closely with Rastetter in both field data collection and model development. In general, the role of the Shaver project in these collaborations is to provide a common data base on canopy-level C and water fluxes, and canopy structure and canopy N content, that includes a broad survey of local and PanArctic variation. The Shaver project will also be distinguished from these others in 2008-2010 in its focus on (1) vascular versus non-vascular C exchange in whole vegetation, (2) describing the long-term trajectory of change in C fluxes in relation to species changes in experimental plots, and (3) upscaling from 1 m² plots to the footprint of eddy covariance towers.

For the past 12 years this project has also supported Shaver's participation in a broad range of synthesis and planning activities that will continue with renewed funding. These activities include the ITEX syntheses of species and community responses to experimental warming (e.g., Walker et al. 2006), the Arctic Climate Impacts Assessment (Callaghan et al. 2005 and 10 other papers), the International Conference on Arctic Research Planning (ICARP), and the EU CAT-B project on effects of biodiversity on arctic ecosystem function (Wookey et al. in prep.). Since 2002 Shaver has served on the steering committee of SEARCH. All of these activities will continue with renewed funding, with the addition of service on the International Study of Arctic Change (ISAC) Council beginning in 2008.

SIGNIFICANCE AND BROADER IMPACTS

Predictability, feedbacks, and sustainability of the Arctic System are three central themes of the NSF Arctic System Science program. The proposed research will contribute significantly to development of these themes by improving our understanding of the broad patterns of vegetation/soil function and vegetation change across the Arctic, with a specific focus on vegetation canopies and ecosystem CO₂ fluxes. The underlying assumption is that adaptation to the arctic environment places major constraints on the growth rates, allocation patterns, and physiology of arctic plants and that these adaptations in turn play an important role in regulating change and resilience in arctic vegetation and its feedbacks to the arctic system. The proposed research is designed essentially as a search for the general characteristics of plant growth, resource allocation, and physiology that can be used to develop large-scale, long-term predictions of ecosystem processes and of the role of arctic vegetation in the Arctic System. By comparing a wide range of vegetation types in widely-separated sites, the research will also help to identify the relative vulnerability of different vegetation types, plant functional types, and species to climate change and other forms of disturbance. The variables to be evaluated—net and gross C fluxes, primary production, N allocation, canopy structure, and NDVI—are all key components of the feedbacks and interactions between the terrestrial landscape and the cycles of energy, water, and elements in the Arctic System.

In a broader scientific context, the proposed research is both significant and timely because it will contribute to understanding of several issues that are of great current interest and research activity in Ecology and Environmental Science. These include:

- 1.) The role of vegetation in determining surface properties of the arctic landscape. *How do the structural and functional characteristics of arctic vegetation determine the feedbacks and interactions between the land surface and other components of the Arctic System?*
- 2.) The effects of individual species or plant "functional types" on overall ecosystem and landscape-level processes: *When and where must we consider the actual species composition of the vegetation, and when can we ignore variability in responses among species and plant functional types?*
- 3.) The general issue of scaling ecological understanding from single sites and species to larger, regional environmental systems: *How can we make predictions of regional change when most of our process-level information on a key component of the system, the vegetation, comes from fine-scale measurements at a small number of sites?*

The proposed research will also make several contributions to education of both future professionals and the general public. Current plans call for a postdoc and RA support. Over the past 20 years, all of our postdocs and most of our RAs have moved on to full-time jobs in ecology teaching and/or research. At the Ecosystems Center, RA positions are generally filled by recent undergraduate or M.S. students who are encouraged to view their time at the Center as an opportunity to gain experience and training so as to make informed decisions about future careers. We also provide excellent opportunities for REU students, supporting one or two each year through annual supplemental requests. Usually, REU students are selected through a nationally-advertised search but more recently about half of our REU students have come from a new undergraduate program at the Ecosystems Center called the Semester in Environmental Science (SES). Increasingly, our teaching in the SES course is integrated with results from our field research. Finally, every summer the Arctic LTER project supports at least two science journalists to come to Toolik Lake for several weeks. These internships have exposed about 30 journalists over the past 12 years to the details of how ecological research actually gets done, leading to numerous newspaper and magazine articles, books, and radio stories. Over 75% of our postdocs, RAs, REU students, and journalists over the past 10 years have been women.

In 2004, the MBL joined with Brown University to create a joint graduate program in Ecology and Evolutionary Biology, which currently includes 5 students and is growing rapidly. If appropriate graduate students are found, either or both of the postdoc and RA positions may be filled by graduate students.

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