

SCALING UNCERTAINTIES IN ESTIMATING CANOPY FOLIAR MAINTENANCE RESPIRATION FOR BLACK SPRUCE ECOSYSTEMS IN ALASKA

XINXIAN ZHANG¹, A. DAVID MCGUIRE^{2,*} and ROGER W. RUESS³
¹*Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK;*
²*U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit,*
University of Alaska Fairbanks, Fairbanks, AK; ³*Institute of Arctic Biology,*
University of Alaska Fairbanks, Fairbanks, AK
(*Author for correspondence: Tel: +1-907-474-6242, Fax: +1-907-474-6716;
E-mail: fjadm@uaf.edu)

(Received 10 August 2003; accepted in final form 19 May 2004)

Abstract. A major challenge confronting the scientific community is to understand both patterns of and controls over spatial and temporal variability of carbon exchange between boreal forest ecosystems and the atmosphere. An understanding of the sources of variability of carbon processes at fine scales and how these contribute to uncertainties in estimating carbon fluxes is relevant to representing these processes at coarse scales. To explore some of the challenges and uncertainties in estimating carbon fluxes at fine to coarse scales, we conducted a modeling analysis of canopy foliar maintenance respiration for black spruce ecosystems of Alaska by scaling empirical hourly models of foliar maintenance respiration (R_m) to estimate canopy foliar R_m for individual stands. We used variation in foliar N concentration among stands to develop hourly stand-specific models and then developed an hourly pooled model. An uncertainty analysis identified that the most important parameter affecting estimates of canopy foliar R_m was one that describes R_m at 0 °C per g N, which explained more than 55% of variance in annual estimates of canopy foliar R_m . The comparison of simulated annual canopy foliar R_m identified significant differences between stand-specific and pooled models for each stand. This result indicates that control over foliar N concentration should be considered in models that estimate canopy foliar R_m of black spruce stands across the landscape. In this study, we also temporally scaled the hourly stand-level models to estimate canopy foliar R_m of black spruce stands using mean monthly temperature data. Comparisons of monthly R_m between the hourly and monthly versions of the models indicated that there was very little difference between the estimates of hourly and monthly models, suggesting that hourly models can be aggregated to use monthly input data with little loss of precision. We conclude that uncertainties in the use of a coarse-scale model for estimating canopy foliar R_m at regional scales depend on uncertainties in representing needle-level respiration and on uncertainties in representing the spatial variability of canopy foliar N across a region. The development of spatial data sets of canopy foliar N represents a major challenge in estimating canopy foliar maintenance respiration at regional scales.

Keywords: black spruce, boreal forests, canopy, ecosystems, maintenance respiration, modeling, spatial scaling, temporal scaling

Introduction

The boreal forest biome occupies an area of 18.5 million km², which is approximately 14% of the vegetated cover of the Earth's surface (McGuire et al. 1995a).

Boreal forests have been estimated to contain 27% of the world's vegetation carbon (C) inventory and 28% of the world's soil C inventory (McGuire et al. 1997). There is evidence that warming is occurring in some high latitude areas (Beltrami and Mareschal 1991; Chapman and Walsh 1993; Osterkamp and Romanovsky 1999; Serreze et al. 2000), and that the warming may be impacting both ecosystem function and structure (Oechel et al. 1993, 1995, 2000; Chapin et al. 1995; Kurz and Apps 1999; McGuire et al. 2003; Myneni et al. 1997, 2001; Zhou et al. 2001). Because of the large stores of C in the boreal forest biome, the response of C storage in boreal ecosystems to climate change has the potential to influence concentrations of radiatively active gases in the atmosphere (McGuire and Chapin 2003). A major challenge confronting the scientific community is to understand both patterns of and controls over spatial and temporal variability of C exchange between boreal forest ecosystems and the atmosphere (McGuire et al. 2002; Dargaville et al. 2002).

There are a variety of methods for estimating changes in terrestrial C storage at large scales. Atmospheric methods generally use data on the atmospheric concentration of CO₂ to estimate the location and timing of sources and sinks (Prentice et al. 2001; Schimel et al. 2001; Dargaville et al. 2002). Inventory methods rely on periodic measurements of forest biomass to estimate changes in C storage (Kurz and Apps 1999; Kurz et al. 2002; Goodale et al. 2002). In contrast to atmospheric- and inventory-based methods, which are primarily useful for detecting changes in terrestrial C storage at large spatial scales, analyses based on ecological process-based models have the potential to provide information on mechanisms responsible for changes in C storage. It has been possible to quantify uncertainties in atmospheric and inventory methods of estimating changes in C storage (Schimel et al. 2001; Dargaville et al. 2002; Goodale et al. 2002). Although process-based models have been evaluated in the context of these uncertainties based on atmospheric and inventory methods (McGuire et al. 2001; Dargaville et al. 2003; Zhuang et al. 2003), the uncertainties are so large that evaluations have only provided general confidence in the models and have not been very successful in identifying process-based uncertainties within and among models. The identification of process-based uncertainties in ecological analyses of terrestrial C dynamics is difficult because process-based models that are used at large spatial scales are generally based on fine-scale understanding of controls over C dynamics. Methods for scaling understanding of fine-scale processes to model processes at a coarser scale often require accounting for the variability in variables that drive the process (Rastetter et al. 1992). Thus, an understanding of the sources of variability of C processes at fine scales and how these contribute to uncertainties in estimating C fluxes is relevant to representing these processes at coarse scales.

Whether a forest stand will be a source or sink for atmospheric CO₂ is controlled by the balance between gross primary production (GPP, i.e., gross assimilation of C captured through photosynthesis) and ecosystem respiration, which includes autotrophic respiration and decomposition (heterotrophic respiration). While eddy covariance techniques have become a popular method for estimating net C exchange

between boreal forest ecosystems and the atmosphere (Sellers et al. 1997; Hall et al. 1999; Hall et al. 2001), true understanding of controls over net C exchange requires estimation of the component fluxes. In eddy covariance studies, GPP is generally estimated by developing an empirical model between ecosystem respiration and air temperature and then subtracting estimates of ecosystem respiration from net C exchange estimates. Comparisons of the performance of nine ecosystem models for the northern study area black spruce site of the Boreal Ecosystem Atmosphere Study (BOREAS; Amthor et al. 2001; Potter et al. 2001) illustrate the difficulties of evaluating ecosystem models to gain insights on controls over net C exchange. While the median model estimates of net C exchange were similar to observations (Amthor et al. 2001), the responses to changes in driving variables like temperature were quite variable among the models (Potter et al. 2001). Part of the difficulty in evaluating model performance in the model comparisons of Amthor et al. (2001) and Potter et al. (2001) was that there was an incomplete understanding of the component fluxes of ecosystem respiration for the stand, i.e., autotrophic and heterotrophic respiration. Estimating these fluxes at the stand level is difficult because the sources of variation in controlling respiration within a stand are incompletely understood. Furthermore, the application of stand-level models of respiration to different stands requires some understanding of sources of variation in controlling respiration among stands. To explore some of the challenges and uncertainties in estimating respiration within and among stands we conducted a modeling analysis of canopy foliar maintenance respiration for black spruce ecosystems of Alaska.

Background

Black spruce is an important, widespread species in northern North America and occurs in a variety of environmental settings. In interior Alaska, black spruce ecosystems cover 44% of the landscape (Viereck and Dyrness 1986). Thus, black spruce forests have the potential to play an important role in determining whether boreal forests in North America will become sources or sinks for atmospheric CO₂ in the context of climate warming (Goulden et al. 1998). In black spruce forests, autotrophic respiration can be responsible for nearly 80% of the CO₂ fixed in photosynthesis, which is a higher percentage than in other mature boreal forest ecosystems (Ryan et al. 1997). Autotrophic respiration may play a role in regulating productivity and C storage in boreal forest ecosystems (Ryan et al. 1997). In black spruce forests, foliar respiration has been documented to be 1.6 times as high as wood respiration (calculated from Ryan et al. 1997), and thus, represents an important part of the C budget of black spruce forests.

The functional model of autotrophic respiration typically includes components of both growth respiration (R_g) and maintenance respiration (R_m) (Ryan 1991; Lavigne and Ryan 1997; Thornley and Cannell 2000; Lusk and Reich 2000). Traditionally, R_m has been estimated as a function of plant biomass and ambient

temperature with the assumption that maintenance respiration increases logarithmically with a conservative Q_{10} (between 2.0 and 2.3) (Raich et al. 1991). A number of studies have documented that R_m also depends on tissue nitrogen (N) content (Ryan 1995; Lavigne and Ryan 1997; Reich et al. 1998; Burton et al. 2002). This relationship exists because most plant N is in protein that is linked with metabolic activity, including protein repair and replacement. Burton et al. (2002) found root respiration was highly correlated with root N concentration when standardized at a given temperature across eight forest types in North American biomes. Ryan (1995) developed a zero-intercept linear regression model between R_m and foliar N concentration at 10 °C for different boreal forest vegetation types. Foliar R_m of boreal forest stands varies with temperature as well as with foliar N content (Ryan 1997). Thus, models of foliar autotrophic respiration should consider both temperature and N content.

In this study, we first evaluate issues involved in scaling an hourly needle-level model to estimate canopy foliar R_m of individual black spruce stands in interior Alaska, and then evaluate issues involved in scaling a stand-level model to estimate canopy foliar R_m of different black spruce stands using mean monthly air temperature data. To accomplish these goals, we first developed a needle-level model of R_m for black spruce stands based on foliar N concentration and ambient temperature. To evaluate spatial scaling issues, we assessed factors responsible for variation in foliar N concentration to scale the needle-level model of R_m to estimate stand-level canopy foliar R_m and compared the estimates of both stand-specific and stand-independent models. We then conducted uncertainty analyses to identify parameters that exerted a strong influence on simulation results. Finally, we scaled hourly stand-level models of canopy foliar R_m driven by monthly temperature values to evaluate whether the models could be applied with temperature inputs at monthly temporal resolution.

Methods

RELATIONSHIP AMONG FOLIAR R_m , FOLIAR N AND AIR TEMPERATURE

In order to establish the relationship between foliar R_m , N content, and air temperature, we measured foliar R_m , foliar N concentration, and air temperature in three stands. The study sites (designated here as S1, S2, and S3) were located in Fairbanks (64°40'N, 148°15'W), Alaska (S1: 64°52.164'N, 147°51.462'W; S2: 64°52.058'N, 147°51.378'W; S3: 64°51.603'N, 147°52.789'W). Black spruce is the only over-story species in all the stands, but the stand age, tree density (Figure 1) and diameter at breast height (Figure 2) differed among stands. In contrast, soil temperature did not vary among stands (Figure 3). In 1998 we conducted a pilot study at one stand (S1) to evaluate potential sources of variation in foliar N concentration. The factors evaluated included trees (ten trees), height (three levels in the canopy), aspect (north

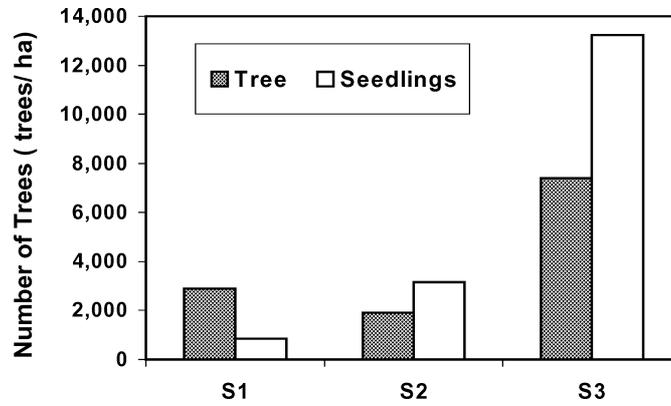


Figure 1. The densities of trees and seedlings in stands S1, S2, and S3.

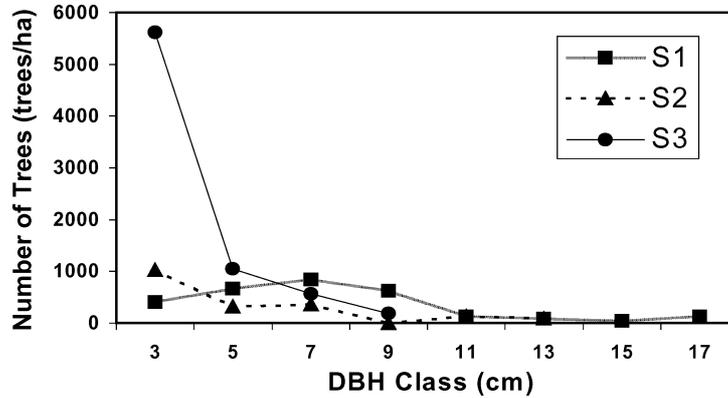


Figure 2. The distributions of diameter at breast height (DBH) in stands S1, S2, and S3. Labeled values for the DBH class axis identify the middle of the DBH categories.

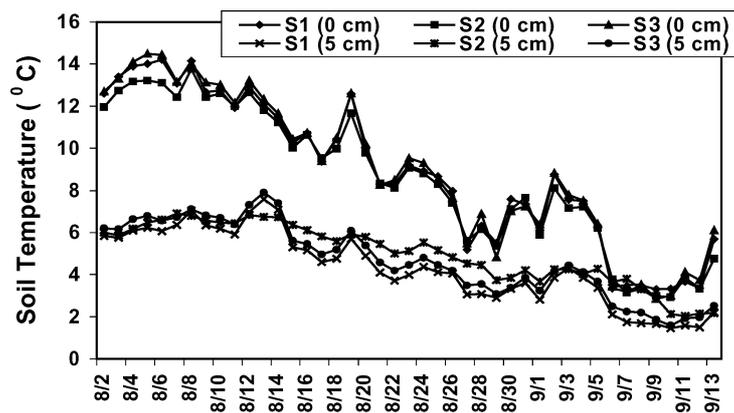


Figure 3. Soil temperatures at depths of 0 cm and 5 cm in stands S1, S2, and S3 from August 2, 1999 through September 14, 1999.

vs. south), branches (three branches for each tree-height-aspect combination) and needle age (ages 0, 1, 4, 9, and 19 on each branch). Data analysis indicated that canopy aspect and height did not significantly influence needle concentration, but needle age ($F = 555$, $P < 0.0001$) and individual trees within a stand ($F = 108$, $P < 0.0001$) combined to explain over 90% of the variation in foliar N.

Based on these results, we measured needle respiration in stands S1, S2, and S3 between 13 and 25 August 1999, concentrating on variation among individuals and needle age cohorts. We assumed that because respiration was measured on fully expanded foliage, it represented foliar R_m only, because growth (and growth respiration) had ceased. At each of the three stands, we randomly selected one branch of each of three randomly selected trees. For each branch we randomly selected one current-year, 1-year-old, 4-year-old, and 9-year-old shoot. Measurements were made on detached shoots with attached needles, which were placed within a XL conifer chamber linked to a LICOR 6400 portable photosynthesis system (LICOR Inc., Lincoln, Nebraska) and expressed as $\mu\text{mol CO}_2 \text{ shoot}^{-1} \text{ s}^{-1}$. We assumed that relative to needle respiration, respiration from the stem within a shoot was negligible. Measurements were made by enclosing detached shoots within the chamber and covering the chamber with a black cloth to prevent photosynthesis from occurring. We used a LICOR 6200 to evaluate whether R_m measurements on intact shoots differed from measurements on detached shoots, but no significant differences were found. Reich et al. (1998) also reported no difference in respiration rates for intact and detached foliage of species from four functional groups in six biomes traversing the Americas. Chamber temperature was maintained at ambient temperature and shoot respiration rate was allowed to stabilize before measurements were logged. This typically occurred within 30 minutes. After respiration measurements, samples were oven dried at 50°C for three to five days, and needles were removed from shoots, weighed, ground through a $20 \mu\text{m}$ mesh screen, and analyzed for total N on a LECO 2000 CNS Autoanalyzer (St. Joseph, Michigan).

Respiration measurements were used to estimate parameters in a nonlinear regression model that relates needle R_m to N content and temperature:

$$\frac{R_{mn}}{N} = A_r e^{R_r T} \quad (1)$$

where R_{mn} is foliar maintenance respiration of the shoot (g C s^{-1}), N is the mass of nitrogen for the needles on the shoot (g), T is air temperature ($^\circ\text{C}$), A_r is R_{mn} at 0°C per gram N per second ($\text{g C g N}^{-1} \text{ s}^{-1}$), and R_r is a parameter that defines the exponential sensitivity of R_{mn} to temperature over all temperatures. For the regression that was fitted using data from all three stands, A_r and R_r are among-stand parameters for the model. Based on the needle-level model, we developed three stand-specific models for S1, S2, and S3 that considered variation in foliar N concentration among stands, and one pooled model for the three stands to estimate

hourly stand-level canopy foliar maintenance respiration (R_{mc} ; $g\ C\ m^{-2}\ hr^{-1}$):

$$R_{mc} = (3600A_r e^{R_r T_h}) \sum_{i=1} N_i \quad (2)$$

where T_h is mean hourly temperature and $\sum N_i$ is needle $N\ m^{-2}$ in a stand, which is determined by summing over each component i (e.g., foliar age within a tree, trees within a stand) that contributes significantly to variability in foliar N within the canopy (see below). Monthly and yearly estimates of canopy foliar R_m were obtained by summing hourly canopy foliar respiration over the month or year with respect to variation in hourly temperature.

ASSESSMENT OF IMPORTANT COMPONENTS OF CANOPY FOLIAR N VARIATION

Because our intensive study of stand S1 in 1998 indicated that needle age and individual trees within a stand explained over 90% of the variation of foliar N , we focused field work on determining how needle N varied with needle age, with trees in a stand, and among stands. In addition to the three stands (S1, S2, S3) in which we measured needle respiration, we included two additional black spruce stands (S4, S5) in Delta, Alaska ($64^{\circ}10'N$, $145^{\circ}30'W$) to assess variation in these components of canopy foliar N . In each stand, 30 trees were randomly selected for sampling. Within each tree, five shoots were collected from the southern aspect of the mid-canopy height from each of the following age classes: 0-, 1-, 4-, 9-, and 19-years old. In two of the Fairbanks stands (S2, S3), 19-year old needles were not present. A total of 690 samples over the five stands include 150 samples per stand in three stands (S1, S4, S5) and 120 samples per stand in the other two stands (S2, S3). We used the methods described earlier to determine needle N concentration.

We used a three-factor nested analysis of variance (ANOVA) to evaluate differences in needle N concentration among the ages of needles on a tree, among trees nested within a stand, and among stands. Ages and stands were treated as fixed factors and tree was treated as a random factor. The ANOVA and means testing for these differences used Proc GLM in the SAS statistical package with needle N content as the dependent variable and needle age, tree, and stand as independent variables. The GLM procedure handled the problem of missing treatment combinations within the ANOVA. Type III sum of squares was used to test the effects of factors without interactions.

DEVELOPMENT AND EVALUATION OF THE HOURLY MODELS OF CANOPY FOLIAR R_m

We developed an hourly stand-specific model of canopy foliar R_m for each stand in Fairbanks (S1, S2, S3) by combining the needle-level empirical model with assumptions about the needle-age distribution and with stand-specific equations that related N concentration to needle age and with stand-independent equations that related canopy foliar biomass to the diameter of trees in a stand. The model

used air temperature measured at the Bonanza Creek Experimental Forest located near Fairbanks to simulate canopy foliar R_m for each of the black spruce forest stands.

We developed allometric equations that related canopy foliar biomass (kg C) to the diameter of trees from the three stands in Fairbanks. In September 1999, five trees in each of the three stands were selected from outside the plots for destructive sampling. All branches with needles were divided into shoots with current-year foliage and shoots with older foliage and weighed separately. We selected 200-g sub-samples from foliage-bearing shoots from the current year and older samples to calculate needle water content of new and old age classes. The sub-samples were dried at 70 °C for 48 hrs and then reweighed. The dry weight of new or old needles (including both stem and needle tissue of the shoots) was then calculated for each tree sampled, and converted to C units assuming that C content was 50% of dry weight.

From these data, we developed two equations for canopy foliar biomass (kg C):

$$L_n = b_{n0} + b_{n1}(\log_{10}(d_i)) \quad (3)$$

$$L_o = b_{o0} + b_{o1}(\log_{10}(d_i)) \quad (4)$$

to relate new- (i.e., current-) year needle mass (L_n) and older needle mass (L_o) of a tree to diameter at breast height (d_i) of the tree. We established one 15 × 15 m plot in each of the three stands (S1, S2, and S3) and recorded DBH of all trees greater than 2cm DBH. We used the allometric equations above to calculate L_n and L_o , and then used the sum of L_n and L_o to calculate the total needle mass of trees within the plots.

We partitioned canopy foliar biomass of needles by needle age, and assumed that needles do not survive for more than 20 years in black spruce. The range of needle age was distributed between current year ($i = 0$) and 19 years ($i = 19$). We expressed the proportion of needles in each age class (P_i) as

$$P_i = \frac{e^{-k*i}}{\sum_{i=0}^{19} e^{-k*i}} \quad (5)$$

where k is needle turnover in yr^{-1} , which we estimated as 0.05582 from the ratio of needle litter fall and canopy foliar biomass from Tables VI and VII of Gower et al. (1997). This estimate of k was similar to estimates of k based on Van Cleve et al. (1981).

Because foliar N concentration decreased with increasing needle age, we fitted a nonlinear regression model for each stand and for the pooled data from the five stands, expressed as

$$[N]_i = A_n e^{(R_n i)} \quad (6)$$

where i is needle age (from 0 to 19 yr), $[N]_i$ is needle N concentration for i -year old needles (%) and A_n and R_n are regression coefficients. Thus, we had three

stand-specific N concentration models for each of three stands in Fairbanks (S1, S2, and S3) and one pooled model developed from data pooled across the five stands.

We combined Equations 3–6 to estimate total needle N ($\sum N_i$) of all trees (T) in a stand by summing up individual trees (t), expressed as follows:

$$\sum N_i = \sum_{i=0}^{19} \left\{ A_n e^{(R_n i)} \sum_{t=1}^T \left[\frac{e^{-k*i}}{\sum_{i=0}^{19} e^{-k*i}} (b_{n0} + b_{n1} \log_{10}(d_t) + b_{o0} + b_{o1} \log_{10}(d_t)) \right] \right\} \quad (7)$$

For each stand, we calculated two estimates of canopy foliar R_m (Equation 2) by combining Equations 1 and 7 based on stand-specific estimates and pooled estimates for parameters A_n and R_n . These models used pooled estimates for the other parameters (A_r , R_r , k , b_{n0} , b_{n1} , b_{o0} , and b_{o1}). For each stand, we also conducted an uncertainty analysis for annual canopy foliar R_m between 1990 and 1997 by performing independent sets of 100 Monte Carlo iterations applied to nine parameters in applications of the models that used hourly air temperature from Bonanza Creek Experiment Forest as input data. These uncertainty analyses were performed to relate the variability among model predictions to variation in parameters of interest, for which we specified a normal distribution centered on a mean defined by our initial estimate of the parameter. The standard deviation of the normal distribution in the uncertainty analyses was specified as the standard error of the initial parameter estimate. The variability of predictions was used to identify parameters that exerted a strong influence on simulation results. Simple Pearson correlation coefficients (r) were calculated between each of the parameters and the model predictions. Similar to Turner et al. (1994), we used the squared Pearson correlation coefficient (r^2) as a measure of the percentage of the total variance in the model prediction that was explained by the variability of each of the parameters.

DEVELOPMENT AND EVALUATION OF MONTHLY STAND-LEVEL MODELS OF CANOPY FOLIAR R_m

We re-estimated parameters with respect to the relationship between R_m , N content and temperature to develop monthly models of canopy foliar R_m and evaluated the performance of these models for each stand. We ran hourly stand-level models of canopy foliar R_m from 1990 through 1997 to simulate hourly R_m , which was then aggregated to estimate monthly R_m . Monthly R_m was divided by N content within stands to determine monthly R_m per unit N. To estimate the monthly-scale values of A_r and R_r in Equation 2, we used nonlinear regression to determine the relationship between monthly R_m per unit of N and mean monthly air temperature. We developed monthly stand-specific models for each of the three stands in Fairbanks and a monthly pooled model for application to all stands. These models used the new estimates of parameters A_r and R_r and monthly temperature as input data to simulate

canopy foliar R_m at monthly resolution for each stand. Finally we compared monthly estimates from the monthly model simulation to monthly estimates from the hourly model simulation aggregated to monthly resolution, and calculated an index of temporal aggregation error (E_a):

$$E_a = \frac{\sqrt{\sum_{i=1}^{96} (M_i - H_i)^2}}{96}$$

where M_i and H_i are monthly canopy foliar R_m estimates of the corresponding monthly and hourly models, respectively, and i is the month starting in January 1990 and ending in December 1997.

Results

NEEDLE-LEVEL MODELS OF R_m

For each of the three stands in Fairbanks (S1, S2, S3), the nonlinear relationship (not shown) between air temperature T , foliar N and R_m significantly explained variation in R_m ($P < 0.001$, $P < 0.009$, and $P < 0.001$ for S1, S2, and S3 respectively). Models that depended on T and foliar C explained similar amounts of variation in R_{mn} because of correlations between foliar C and N . However, the models of needle R_m for the three stands were not significantly different from each other because the standard errors of the coefficients of fitted models for each of three stands were large (the 95% confidence intervals of A_r are $[-0.032, 0.342]$, $[-0.029, 0.233]$, and $[-0.288, 0.542]$ for S1, S2, S3, respectively; the 95% confidence intervals of R_r are $[-0.0319, 0.0871]$, $[0.014, 0.126]$, and $[-0.120, 0.210]$ for S1, S2, S3, respectively). The pooled model significantly explained variation in R_m ($P < 0.001$) (see Figure 4), and the coefficients of the regression were significantly different from 0 ($P = 0.046$ and $P < 0.001$ for A_r and R_r , respectively). Also, 95% confidence intervals for A_r $[0.001, 0.089]$ and R_r $[0.051, 0.141]$ were substantially smaller than the confidence intervals for the stand-specific relationships. Thus, we used the pooled model for needle R_{mn} to develop stand-level models of canopy foliar R_m .

ESTIMATION OF FOLIAR N WITHIN STANDS

Although there were significant differences in foliar N concentration among stands ($F = 263.6$, $df = 4$, $P = 0.0001$), trees ($F = 5.0$, $df = 145$, $P = 0.0001$) and needle-age classes ($F = 432.5$, $df = 4$, $P = 0.0001$), the contributions of these factors to variation of foliar N concentration were different. Needle age and stand explained 35.9% and 40.2% of variation in foliar N concentration, respectively, while trees within a stand explained only 6.4%.

Among the five stands, needle N concentration ($[N]$) decreased with increasing needle age in a non-linear fashion (Figure 5). We fitted a nonlinear equation

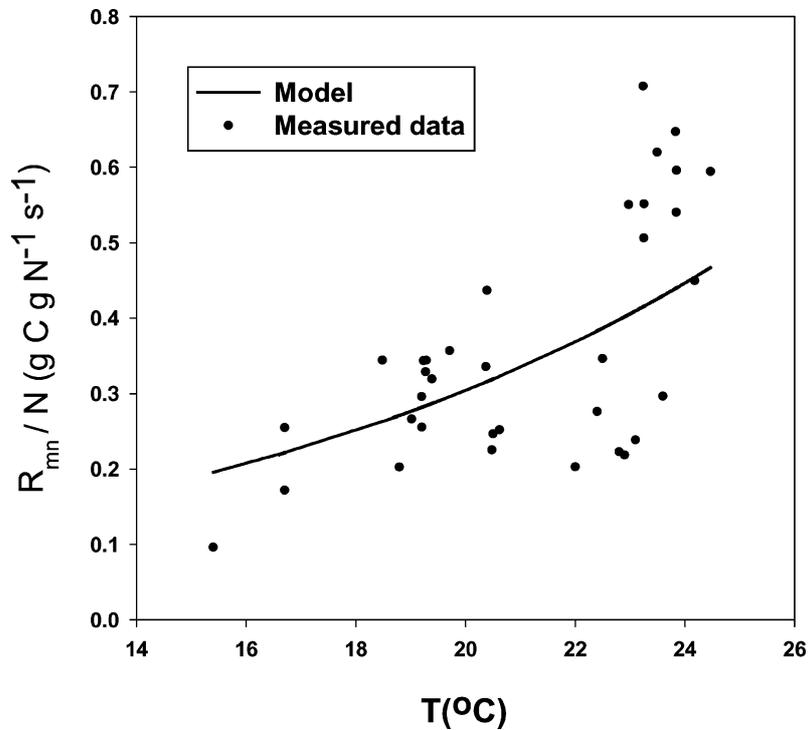


Figure 4. Needle-level model of $R_{mn}/N = A_r e^{R_r T}$, where R_{mn} is CO_2 efflux from needle maintenance respiration (g C s^{-1}), T is air temperature ($^{\circ}\text{C}$), and N is foliar nitrogen content (g N). For the pooled data from the three stands (S1, S2, S3): $R_{mn}/N = 0.0447 e^{0.0959T}$ ($r^2 = 0.480$, $P = 0.046$ for A_r and $P < 0.001$ for R_r , $n = 36$).

(Equation 6: $[N] = A_n e^{R_n i}$) to determine relationships between $[N]$ and needle age i for each of the three stands (S1, S2, and S3) and for data pooled across the five stands (S1, S2, S3, S4, and S5). The fitted models were all significant ($P < 0.001$ for S1, S2, S3, and the pooled data). For S1, S2, and S3, the relationship explained 63.5%, 37.8%, and 52.8%, respectively, of variation in foliar N concentration associated with needle age. The pooled model explained 26.1% of the variation in foliar N concentration associated with needle age. Because the three stand-specific relationships were significantly different from each other, we used the stand-specific relationships in developing the stand-specific models of canopy foliar R_m for each of three stands in Fairbanks (S1, S2, and S3).

The relationships in Figure 5 suggest that foliar N concentrations are primarily controlled by stand-specific factors. To identify stand-level control over foliar N concentration, we examined stand-specific factors that we hypothesized might be important. These factors included tree density, distribution of tree diameter, soil temperature, the depth of thaw, and the community composition of understory species. None of the factors we examined explained variation in foliar N concentration among stands.

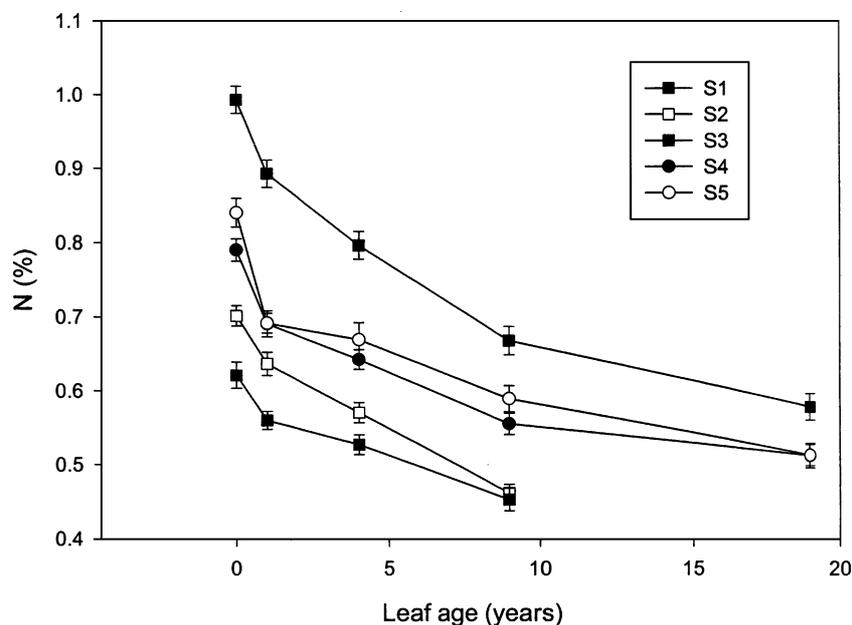


Figure 5. Relationships between N concentration and needle age for five stands (S1–S5). The error bars indicate standard errors. Pooled and stand-specific nonlinear models, $[N] = A_n e^{R_n i}$, were fit to the data, where $[N]$ is foliar N concentration (%), i is needle age (yr). For the pooled data from the five stands (S1–S5): $[N] = 0.732 e^{-0.0232i}$ ($r^2 = 0.261$, $P < 0.001$ for A_n and $P < 0.001$ for R_n , $n = 684$). For the data from S1: $[N] = 0.935 e^{-0.0295i}$ ($r^2 = 0.635$, $P < 0.001$ for A_r and $P < 0.001$ for R_n , $n = 149$). For the data from S2: $[N] = 0.602 e^{-0.0325i}$ ($r^2 = 0.378$, $P < 0.001$ for A_r and $P < 0.001$ for R_n , $n = 119$). For the data from S3: $[N] = 0.684 e^{-0.0437i}$ ($r^2 = 0.528$, $P < 0.001$ for A_r and $P < 0.001$ for R_n , $n = 118$).

For data pooled across stands, needle mass was related to DBH (d_t) in a logarithmic fashion ($P < 0.001$; Table I). We used these allometric equations to predict needle mass given the distribution of DBH for each of the three stands. Based on our assumptions about the distribution of needle age, we combined Equations 3–6

TABLE I

Sample size ($n =$ trees), regression coefficients, r^2 (coefficient of determination), and mean square error (MSE) for logarithmic relationships between needle carbon (kg) and diameter at breast height (d_t) of new foliage (NF) and old foliage (OF)

d_t range	Tissue	n	a	b	r^2	MSE
2–12	NF	15	–0.181	0.484	0.655	0.006
2–12	OF	15	–0.734	2.252	0.692	0.115

Relationships were determined from data pooled across the three stands. Both relationships were described by the equations $Y = a + b (\log_{10} X)$, where X is stem diameter (cm) at breast height (1.37 m) and Y is carbon mass of needles (kg C).

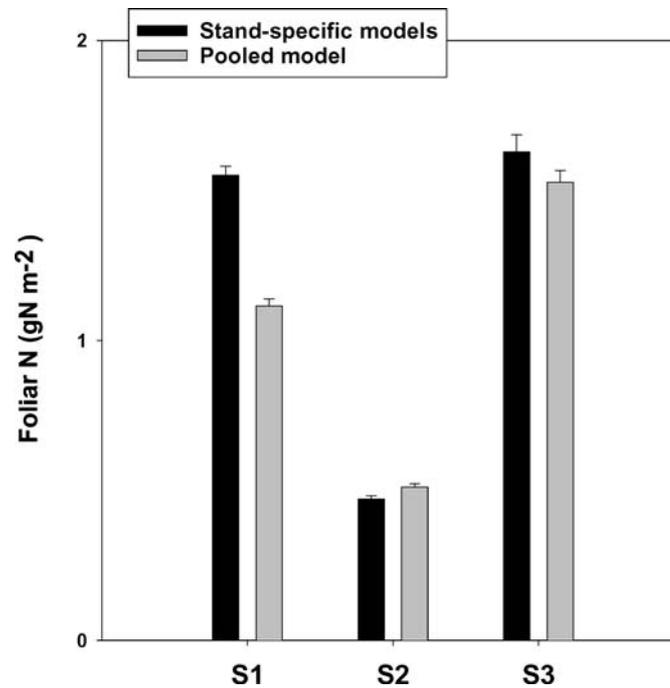


Figure 6. Comparison of simulated foliar N between stand-specific and pooled models for each of three stands (S1, S2, and S3). Error bar indicates standard error from uncertainty analysis based on 100 Monte Carlo simulations.

to calculate the foliar N for each stand with Equation 7 (Figure 6). For the stand-specific Equations of S1, S2, and S3, foliar N of S1, S2, and S3 was estimated to be 1.6, 0.4, and 1.7 g N m⁻², respectively. For the pooled equation, foliar N of S1, S2, and S3 was estimated to be 1.1, 0.5, and 1.5 g N m⁻², respectively.

EVALUATION OF THE HOURLY STAND-LEVEL MODELS OF CANOPY FOLIAR R_m

Based on the relationships for R_{mn} with temperature and needle N content, needle N concentration with needle age, and canopy needle mass with tree diameter, we developed stand-level hourly models of canopy foliar R_m . The models were developed using stand-specific estimates and pooled estimates for parameters A_n and R_n in the relationship between foliar N concentration and needle age, and pooled estimates for other parameters. We evaluated the stand-specific models based on the parameters we estimated for each model. By comparing the simulation of the stand-specific and pooled models, we were able to examine issues involved in scaling stand-level models to estimate canopy foliar R_m .

We conducted uncertainty analyses on annual estimates of canopy foliar R_m by performing independent sets of 100 Monte Carlo iterations applied to nine

TABLE II

Mean and standard deviation of normal distributions for stand-independent parameters used in the uncertainty analyses (see methods)

Parameter symbol	Description	Mean	Standard deviation
A_r	Coefficient in needle R_m model	0.045	0.022
R_r	Exponential coefficient in needle R_m model	0.096	0.022
K	Needle turnover	0.059	0.005
b_{n0}	Intercept of allometric equation for needle mass of new foliage	-0.181	0.062
b_{n1}	Slope of allometric equation for needle mass of new foliage	0.484	0.101
b_{o0}	Intercept of allometric equation for needle mass of old foliage	-0.734	0.266
b_{o1}	Slope of allometric equation for needle mass of old foliage	2.252	0.434

Foliar R_m per unit N = $A_r e^{R_r T}$; current needle quantity $L_n = b_{n0} + b_{n1} (\log_{10} (\text{dbh}))$; old needle quantity: $L_o = b_{o0} + b_{o1} (\log_{10} (\text{dbh}))$. The parameters were determined from the data pooled across stands. Mean and standard deviation were obtained from regression analyses for each of empirical models, where the standard deviation is equal to the standard error of the parameter estimate. The parameter k was estimated using data from Gower et al. (1997) and its standard deviation was assumed to be 10% of its value.

TABLE III

Mean and standard deviation of normal distributions for stand-specific parameters used in the uncertainty analyses (see Methods)

Parameter Symbol	Description	Mean (stand-specific models)			Standard deviation (stand-specific models)			Mean (pooled model)	Standard deviation (pooled model)
		S1	S2	S3	S1	S2	S3		
A_n	Coefficient in N concentration model	0.963,	0.621,	0.685	0.041,	0.019,	0.013	0.742	0.042
R_n	Exponential coefficient in N concentration model	-0.030,	-0.032,	-0.005	0.006,	0.006,	0.005	-0.021	0.007

Age (i)-specific foliar N concentration = $A_n e^{(R_n i)}$. In stand-specific models the values of parameters A_n and R_n in the table were determined from data from each of three stands S1, S2 and S3, respectively. In the pooled model, data from three stands were determined from the data pooled across stands. Mean and standard deviation were obtained from regression analyses for each of empirical models, where the standard deviation is equal to the standard error of the parameter estimate.

parameters (Tables II and III). The comparison of simulated annual canopy foliar R_m from 1990 through 1997 identified differences between stand-specific models and the pooled model for each of the three stands showing little inter-annual variance among the eight years (see Figure 7 for 1997 estimates). For S1 and S3, estimated

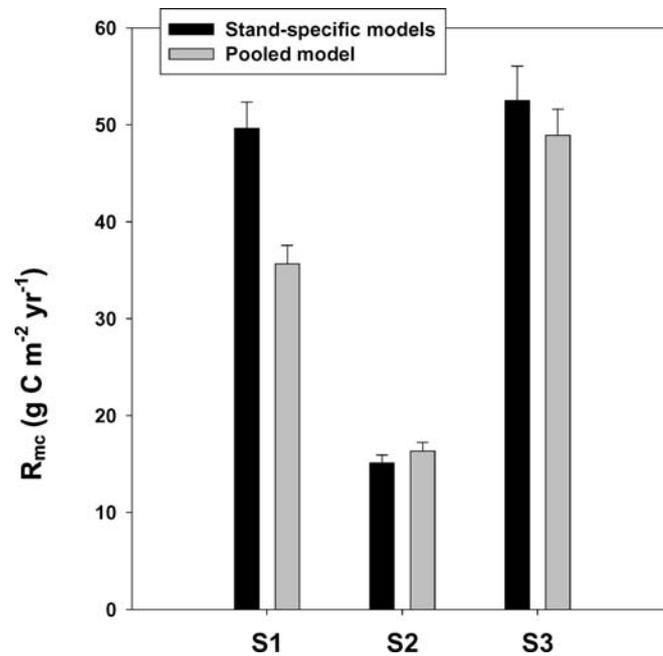


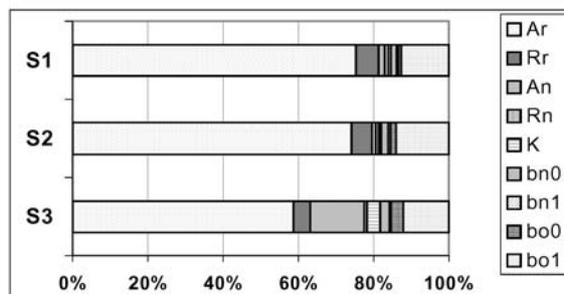
Figure 7. Comparison of simulated annual canopy foliar R_m in 1997 between stand-specific and pooled models for each of three stands (S1, S2, and S3). Error bar indicates standard error from uncertainty analysis based on 100 Monte Carlo simulations.

canopy foliar R_m is higher using stand-specific models than using the pooled model (for S1: t -test, $T = 39.0$, $P < 0.001$, $df = 198$; for S3: $T = 3.6$, $P < 0.001$, $df = 198$). On average, the pooled model estimate was 28% and 7% lower than the stand-specific model for S1 and S3, respectively. For S2, however, R_m estimated by the pooled model was 8% higher than the estimate by the stand-specific model (t -test, $T = 22.6$, $P < 0.001$, $df = 198$). The comparison of foliar N estimates between stand-specific models and the pooled model for each of the three stands (Figure 6) explained differences in canopy foliar R_m estimates between the stand-specific and pooled models.

For each model, variance in annual canopy foliar R_m was associated primarily with A_r , which explained over 55% of the variance in each of the three stands for the stand-specific models and for the pooled model (Figure 8). The uncertainty analyses indicated that the differences in the estimates of A_r had large effects on estimates of canopy foliar R_m . For both stand-specific and pooled models, b_{o1} was the second most important parameter, explaining between 12% and 18% of the variance. Among the stand-specific models, A_n , a parameter in the N concentration relationship, was an important factor for S3, which had the lowest canopy foliar N among the three stands.

To evaluate whether the sample size across the three stands was adequate, we decreased sample size from 36 to 30, 25, 20, 15 and 10 by randomly selecting

(a) Stand-specific models



(b) Pooled model

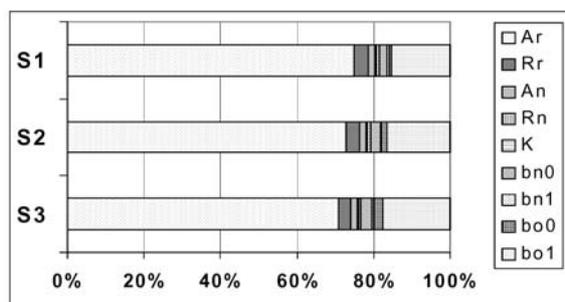


Figure 8. Comparison of variance explained by parameters in uncertainty analyses of annual R_{mc} in 1997 between applications of stand-specific (a) and pooled models (b) to the three stands (S1, S2 and S3). Percentage identifies variation explained by an individual parameter relative to variation explained by all parameters. The variation explained by all parameters was greater than 95% of the variance in all cases. There was little variability in these patterns among the different years. See Tables II and III for parameter definitions and values.

samples from the original data each time to evaluate how the standard error (SE) of A_r varied with sample size (n). This analysis indicated that when $n < 20$, SE of A_r decreased rapidly with an increase in n . In contrast, SE didn't change substantially with increasing n when $n > 20$. Thus, it appeared that the SE in A_r would not be substantially reduced by increasing the size of the pooled sample.

EVALUATION OF THE MONTHLY STAND-LEVEL MODELS OF CANOPY FOLIAR R_m

We re-estimated parameters A_r and R_r in Equation 1 to estimate stand-level canopy foliar R_m at monthly temporal resolution so that stand-specific and pooled models simulated canopy foliar R_m with mean monthly temperature data. The values estimated for A_r and R_r were, respectively, 0.0202 and 0.0254 for S1; 0.0149 and 0.0681 for S2; 0.387 and 0.0425 for S3; and 0.00693 and 0.0961 for the pooled model. Comparisons of monthly R_m between the hourly and monthly versions of

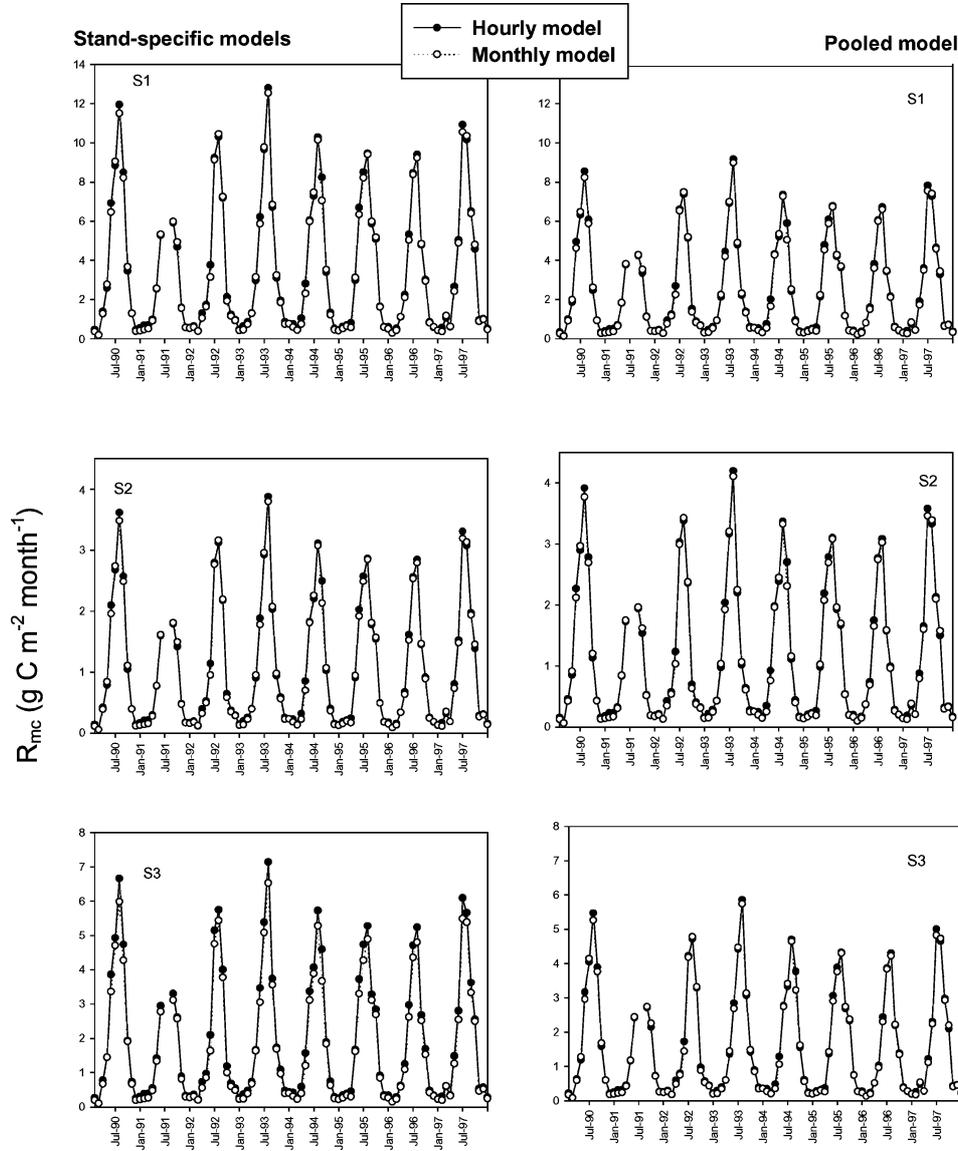


Figure 9. Comparison of monthly canopy foliar maintenance respiration (R_{mc}) between hourly and monthly models for stands S1, S2 and S3, respectively from January 1990 through December 1997. The estimates of the hourly models were aggregated to monthly temporal resolution.

the models indicated that there was very little difference between the estimates of corresponding hourly and monthly models (Figure 9). For the application of the stand-specific models to each of the three stands, S1, S2, and S3, the index of temporal aggregation error (E_a) was 0.046, 0.019, and 0.004 $\text{g C m}^{-2} \text{ month}^{-1}$, which was only 0.5–0.7% of the mean monthly canopy foliar R_m between January 1990

and December 1997. For the applications of pooled model to S1, S2, and S3, the index was 0.016, 0.010, 0.007 g C m⁻²month⁻¹, or 0.6% of mean monthly canopy foliar R_m for all three stands. The agreement between hourly and monthly models suggests that the hourly models can be aggregated to use monthly input data with little loss of precision.

Discussion

While much progress has been made in estimating the timing and location of C sources and sinks for the terrestrial biosphere at large spatial scales (Schimel et al. 2001; Goodale et al. 2002), process-based controls over source and sink activity are incompletely understood (McGuire et al. 2001). In the boreal forest region, it is important to understand process-based controls over source and sink activity because warming of the region has the potential to affect ecosystem processes in a manner that may affect source and sink activity. Analyses based on satellite data suggest that both production and vegetation C storage have generally been enhanced across the boreal forest in recent decades (Myneni et al. 1997, 2001; Randerson et al. 1999; Zhou et al. 2001). One hypothesis for the mechanism of increased production is that warming increases decomposition of soil organic matter to release N in forms that can be taken up by plants. It has been well documented that production in boreal forests is often limited by plant N supply (Van Cleve and Zasada, 1976; Van Cleve et al. 1981; Chapin et al. 1986; Vitousek and Howarth, 1991), and that an increase in N availability to plants should increase production. Several boreal warming experiments and modeling studies have provided support for the mechanism that an increase in N availability to plants should increase production (Van Cleve et al. 1990; Bonan and Van Cleve, 1992; Bergh et al. 1998; Stromgren and Linder, 2002; Clein et al. 2002).

As production is the difference between photosynthesis and autotrophic respiration, it is important to understand controls over both of these processes. Nitrogen concentration in boreal forest species plays an important role in controlling production (Yarie, 1997), photosynthesis (McGuire et al. 1995b; Hom and Oechel, 1983), and both shoot (Ryan, 1995; Lavigne and Ryan, 1997; Reich et al. 1998) and root (Burton et al. 2002; Ruess et al. 2003) respiration. To better understand spatial and temporal uncertainties in estimating canopy foliar C fluxes of boreal forest species, we conducted a modeling analysis in this study to evaluate how sources of variation associated with foliar N concentration influence estimates of canopy foliar R_m within and among black spruce ecosystems of interior Alaska. Spatial uncertainties evaluated in this study included variation associated with (1) the dependence of needle respiration on foliar N concentration and temperature, and (2) the distribution of foliar N within and among stands. Our evaluation of temporal uncertainties focused on scaling an hourly canopy foliar R_m model so that it was driven with monthly temperature data.

UNCERTAINTIES ASSOCIATED WITH NEEDLE RESPIRATION

In many species, R_m generally increases linearly with tissue N content (Kawahara et al. 1976; Jones et al. 1978; Merino et al. 1982; McCree 1983; Waring et al. 1985; Irving and Silsby 1987; Burton et al. 2002). Based on the observation that R_m increases linearly with tissue N content, Ryan (1995) proposed a N-based foliar R_m model for boreal forests. Reich (1998) also found highly positive relationships between R_m and foliar N from four functional groups (forbs, broad-leaf trees and shrubs, and needle-leaf conifers) in six biomes across the Americas. In agreement with these studies, we also found that needle respiration depends on N concentration.

Our uncertainty analyses indicated that the parameter A_r , which describes needle R_m rate at 0 °C per g N, had a profound effect on estimates of annual canopy foliar R_m for each of the three stands. This suggests that increasing the accuracy of A_r would be the most effective way to improve annual estimates of canopy foliar R_m . Because we developed a relationship for the dependence of needle respiration on N concentration and temperature from only 36 data points, we were concerned about whether the accuracy of A_r was associated with small sample size. Our evaluation of the effects of sample size on A_r indicates that the standard error of A_r may be difficult to reduce when sample size is greater than 20 measurements. Shoot respiration, which we assumed was negligible, may be a factor affecting the variability in measured R_{mn} and may inflate the SE of A_r .

Two other concerns about the relationship for needle respiration that we developed include the methodology for measuring needle respiration, and the temperature range over which we measured needle respiration. Some studies have suggested that estimates of needle respiration may be biased high when relying on the shading technique we used in this study (Hubbard et al. 1995). If this were an issue in our study, then it would likely manifest itself as an overestimate of A_r . The other concern is that the measurements of needle respiration in this study were representative of the upper tail (15 to 24 °C) in the distribution of hourly temperature that ranged from -41.2 to 33.2 °C in Fairbanks from 1990 through 1997. One solution to this would be to measure needle respiration throughout the year and to more precisely and accurately estimate A_r by measuring respiration near 0 °C. Alternatively, we took a modeling approach to evaluate whether A_r was biased by comparing simulated canopy foliar R_m with field-based estimates of winter ecosystem respiration for a black spruce stand (Goulden et al. 1998; Clein et al. 2002) that was part of the Boreal Ecosystem Atmosphere Study (BOREAS; Sellers et al. 1997). Because ecosystem respiration is the sum of autotrophic and heterotrophic respiration, simulated winter canopy foliar R_m should be considerably less than winter respiration for the entire ecosystem. For the winter season (December, January, and February), the average simulated canopy foliar R_m of the stands in our study (0.6, 0.2, 0.3 g C m⁻² month⁻¹ for S1, S2, and S3 using stand-specific models) was substantially less than field-based estimates of ecosystem respiration for the BOREAS black spruce stand (7.0 g C m⁻² month⁻¹; Clein et al. 2002). Thus, the winter estimates

of canopy foliar R_m by the models in this study appear to be reasonable, which suggests that the estimate of A_r is also reasonable.

UNCERTAINTIES IN THE DISTRIBUTION OF FOLIAR N WITHIN AND AMONG STANDS

Compared to other factors measured, needle age was the most important factor to influence foliar N concentration within a stand, and foliar N concentration covaried with needle age in a similar fashion among stands. Although variation among trees was also a significant factor influencing N variation within a stand, it explained only 6% of the variation within a stand. We found no dependence of N concentration with either aspect or height in the canopy.

It has been shown that N concentration of black spruce canopies in interior Alaska is sensitive to soil warming (Van Cleve et al. 1990). Presumably, the warming of soil enhances decomposition to increase the availability and uptake of N by trees, which results in a greater concentration of foliar N in the canopy. Because we saw little difference in soil temperature among the stands, we were not able to directly link soil temperature to differences in N concentration among stands. We were also unsuccessful in relating differences in needle N concentration among stands to other structural features that differed among stands. Although we were not able to identify the factors that explain variability in foliar N concentration among stands, the comparison of simulated annual canopy foliar R_m identified significant differences between stand-specific and pooled models for each of the stands, suggesting that stand-level controls over foliar N concentration should be considered in models that estimate canopy foliar R_m of black spruce stands across the landscape.

ESTIMATING CANOPY FOLIAR R_m AT COARSE TEMPORAL AND SPATIAL SCALES

We were interested in whether the canopy foliar R_m model we developed in this study would be useful for incorporation into large-scale ecosystem models. Large-scale ecosystem models are often driven with monthly climate inputs (Heimann et al. 1998; Cramer et al. 1999; Kicklighter et al. 1999; McGuire et al. 2001). For a fine-scale model to be useful at the coarse scale, it needs to be scaled so that it produces accurate estimates when driven by coarse-scale data (Rastetter et al. 1992). To evaluate this issue, we scaled the hourly model so that it was driven by monthly temperature data. Our strategy in scaling was to use a calibration technique of scaling in which we re-estimated parameters in a relationship of needle R_m with N content and mean monthly temperature. In comparison to other scaling techniques, Rastetter et al. (1992) found that the calibration technique was superior to other scaling techniques. The agreement between the hourly and monthly models in our study suggests that the hourly models can be aggregated to use monthly input data with little loss of precision. Uncertainties in the use of the coarse-scale model for estimating R_m at regional scales depend on previous uncertainties we've discussed

about the needle-level model of respiration and how well the large-scale ecosystem model estimates spatial variability in canopy foliar N across the region. Thus, the development of data sets for testing the ability of large-scale models to simulate spatial variability in canopy foliar N at large scales represents a major challenge in estimating component regional canopy C fluxes like GPP and foliar R_m .

Acknowledgments

This research was supported by the Taiga Long Term Ecological Research Program with funding from the National Science Foundation. First, we would like to thank Dr. Terry Chapin, for his valuable suggestions on the project. We thank Kathleen Doran for her help with the LICOR 6200 and 6400. We also thank Lola Oliver at the UAF Forest Soils Lab for assistance with the analysis of needle samples. We appreciate the help of Dr. Rich Boone, Dr. Dave Verbyla, Rich Brenner, and Jonathan Massheder in providing advice concerning fieldwork. Finally we thank Dr. Les Viereck and Dr. Phyllis Adams for providing unpublished air temperature data for a black spruce stand at the Bonanza Creek Experimental Forest.

References

- Amthor, J.S., Chen, J.M., Clein, J.S., Frolking, S.E., Goulden, M.L., Grant, R.F., Kimball, J.S., King, A.W., McGuire, A.D., Nikolov, N.T., Potter, C.S., Wang, S. and Wofsy, S.C.: 2001, 'Boreal forest CO₂ exchange and evapotranspiration predicted by nine ecosystem process models: Intermodel comparisons and relationships to field measurements', *Journal of Geophysical Research – Atmospheres* **106**, 33,623–33,648.
- Beltrami, H. and Mareschal, J.C.: 1991, 'Recent warming in eastern Canada inferred from geothermal measurements', *Geophys. Res. Lett.* **18**, 605–608.
- Bergh, J., Linder, S., Lundmark, T. et al.: 1999, 'The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden', *Forest Ecology and Management* **119**, 51–62.
- Bonan, G.B., and Van Cleve, K.: 1992, 'Soil temperature, nitrogen mineralization, and carbon source-sink relationships in boreal forest', *Can. J. For. Res.* **22**, 629–639.
- Burton, A.J., Pregitzer, K.S., Ruess, R.W., Hendrick, R.L. and Allen, M.F.: 2002, 'Fine root respiration rates in North American forests: Effects of nitrogen concentration and temperature across biomes', *Oecologia* **131**, 559–568.
- Chapman, W.L. and Walsh, J.E.: 1993, 'Recent variations of sea ice and air temperatures in high latitudes', *Bull. Am. Meteor. Soc.* **74**, 33–47.
- Chapin, F.S., III, Vitousek, P.M. and Van Cleve, K.: 1986, 'The nature of nutrient limitation in plant communities', *American Naturalist* **127**, 48–58.
- Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. and Laundre, J.A.: 1995, 'Responses of arctic tundra to experimental and observed changes in climate', *Ecology* **76**, 694–711.
- Clein, J.S., McGuire, A.D., Zhuang, X., Kicklighter, D.W., Melillo, J.M., Wofsy, S.C., Jarvis, P.G. and Massheder, J.M.: 2002, 'Historical and projected carbon balances of mature black spruce ecosystems across North America: The role of carbon-nitrogen interactions', *Plant and Soil* **242**, 15–32.

- Cramer, W., Kicklighter, D.W., Bondeau, A., Moore, B. III, Churkina, G., Nemry, B., Ruimy, A. and Schloss, A.L.: 1999, 'The participates of the postdam NPP model intercomparison, Comparing global models of terrestrial net primary productivity (NPP) overview and key results', *Global Change Biology* **5**(Suppl. 1), 1–15.
- Dargaville, R., McGuire, A.D. and Rayner, P.: 2002, 'Estimates of large-scale fluxes in high latitudes from terrestrial biosphere models and an inversion of atmospheric CO₂ measurements', *Climatic Change* **55**, 273–285.
- Dargaville, R.J., Heimann, M., McGuire, A.D., Prentice, I.C., Kicklighter, D.W., Joos, F., Clein, J.S., Esser, G., Foley, J., Kaplan, J., Meier, R.A., Melillo, J.M., Moore, B. III, Ramankutty, N., Reichenau, T., Schloss, A., Sitch, S., Tian, H., Williams, L.J. and Wittenberg, U.: 2002, 'Evaluation of terrestrial carbon cycle models with atmospheric CO₂ measurements: Results from transient simulations considering increasing CO₂, climate and land-use effects', *Global Biogeochemical Cycles* **16**, 1092, doi:10.1029/2001GB001426.
- Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S., Nabuurs, G., Nilsson, S. and Shvidenko, A.Z.: 2002, 'Forest carbon sinks in the Northern Hemisphere', *Ecological Applications* **12**, 891–899.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A. and Munger, W.: 1998, 'Sensitivity of boreal forest carbon balance to soil thaw', *Science* **279**, 241–247.
- Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. and Stow, T.K.: 1997, 'Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada', *Journal of Geophysical Research – Atmospheres* **102**, 29,029–29,041.
- Hall, F.G.: 1999, 'Introduction to special section: BOREAS in 1999: Experimental and science perspective', *Journal of Geophysical Research – Atmospheres* **104** (D22), 27,627–27,639.
- Hall, F.G.: 2001, 'Introduction to special section: BOREAS III', *Journal of Geophysical Research – Atmospheres* **106**(D24), 33,511–33,516.
- Heimann, M., Esser, G.A., Haxeltine, J., Kaduk, D.W., Kicklighter, W., Knorr, G.H., McGuire, A.D., Melillo, J.M., Moore, B. III, Otto, R.D., Prentice, I.C., Sauf, W., Schloss, A., Sitch, S., Wittenberg, U. and Wurth, G.: 1998, 'Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO₂: First results of a model intercomparison study', *Global Biogeochemical Cycles* **12**, 1–24.
- Hom, J.L. and Oechel, W.C.: 1983, 'The photosynthetic capacity, nutrient content, and nutrient use efficiency of different needle age-classes of black spruce (*Picea mariana*) found in interior Alaska', *Can. J. For. Res.* **13**, 834–839.
- Hubbard, R.M., Ryan, M.G. and Lukens, D.L.: 1995, 'A simple, battery operated, temperature-controlled cuvette for respiration measurements', *Tree Physiology* **15**, 175–179.
- Irving, D.E. and Silsbury, J.H.: 1987, 'A comparison of the rate of maintenance respiration in some crop legumes and tobacco determined by three methods', *Annals of Botany* **59**, 257–264.
- Jones, M.B., Leafy, E.L., Stiles, W. and Collett, B.: 1978, 'Pattern of respiration of a perennial ryegrass crop in the field', *Annals of Botany* **42**, 693–703.
- Kawahara, T., Hatiya, K., Takeuti, I. and Sato, A.: 1976, 'Relationship between respiration rate and nitrogen concentration of trees', *Japanese Journal of Ecology* **26**, 165–170.
- Kicklighter, D.W., Bruno, M., Doenges, S., Esser, G. and Heimann, M.: 1999, 'A first-order analysis of the potential role of CO₂ fertilization to affect the global carbon budget: A comparison of four terrestrial biosphere models', *Tellus* **51B**, 343–366.
- Kurz, W.A. and Apps, M.J.: 1999, 'A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector', *Ecol. Appl.* **9**, 526–547.
- Kurz, W.A., Apps, M., Banfield, E. and Stinson, G.: 2002, 'Forest carbon accounting at the operational scale', *The Forestry Chronicle* **78**, 672–679.

- Lavigne, M.B. and Ryan, M.G.: 1997, 'Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites', *Tree Physiology* **17**, 543–551.
- Lusk, C.H. and Reich, P.B.: 2000, 'Relationships of leaf dark respiration with light environment and tissue nitrogen in juveniles of 11 cold-temperate tree species', *Oecologia* **123**, 318–329.
- McCree, K.J.: 1983, 'Carbon balance as a function of plant size in sorghum plants', *Crop Science* **23**, 1173–1177.
- McGuire, A.D., Melillo, J.M. and Joyce, L.A.: 1995a, 'The role of nitrogen in the response of forest net primary production to elevated atmospheric carbon dioxide', *Annual Review of Ecology and Systematics* **26**, 473–503.
- McGuire, A.D., Melillo, J.M., Kicklighter, D.W. and Joyce, L.A.: 1995b, 'Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates', *Journal of Biogeography* **22**, 785–796.
- McGuire, A.D., Melillo, J.M., Kicklighter, D.W., Pan, Y., Xiao, X., Helfrich, J., Moore, B. III, Vorosmarty, C.J. and Schloss, A.L.: 1997, 'Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to changes in vegetation nitrogen concentration', *Global Biogeochemical Cycles* **11**, 173–189.
- McGuire, A.D., Sitch, S., Clein, J.S., Dargaville, R., Esser, G., Foley, J., Heimann, M., Joos, F., Kaplan, J., Kicklighter, D.W., Meier, R.A., Melillo, J.M., Moore, B. III, Prentice, I.C., Ramankutty, N., Reichenau, T., Schloss, A., Tian, H., Williams, L.J. and Wittenberg, U.: 2001, 'Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO₂, climate and land-use effects with four process-based ecosystem models', *Global Biogeochemical Cycles* **15**, 183–206.
- McGuire, A.D., Wirth, C., Apps, M., Beringer, J., Clein, J., Epstein, H., Kicklighter, D.W., Bhatti, J., Chapin, F.S., III, de Groot, B., Efremov, D., Eugster, W., Fukuda, M., Gower, T., Hinzman, L., Huntley, B., Jia, G.J., Kasischke, E., Melillo, J., Romanovsky, V., Shvidenko, A., Vaganov, E. and Walker, D.: 2002, 'Environmental variation, vegetation distribution, carbon dynamics, and water/energy exchange in high latitudes', *J. Vegetation Sci.* **13**, 301–314.
- McGuire, A.D., Sturm, M. and Chapin, F.S., III: 2003, 'Arctic Transitions in the Land-Atmosphere System (ATLAS): Background, objectives, results, and future directions', *Journal of Geophysical Research – Atmospheres* **108**(D2), 8166, doi:10.1029/2002JD002367.
- Merino, J., Field, C. and Mooney, H.A.: 1982, 'Construction and maintenance costs of Mediterranean-climate evergreen and deciduous leaves. I. Growth and CO₂ exchange analysis', *Oecologia* **53**, 208–213.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and Nemani, R.R.: 1997, 'Increased plant growth in the northern high latitudes from 1981 to 1991', *Nature* **386**, 698–702.
- Myneni, R.B., Dong, J., Tucker, C.J., Kaufmann, R.K., Kauppi, P.E., Liski, J., Zhou, L., Alexeyev, V. and Hughes, M.K.: 2001, 'A large carbon sink in the woody biomass of northern forests', *Proc. Natl. Acad. Sci. USA* **98**, 14784–14789.
- Oechel, W.C., Hastings, S.J., Vourlitis, G.L., Jenkins, M., Reichers, G. and Grulke, N.: 1993, 'Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source', *Nature* **361**, 520–523.
- Oechel, W.C., Vourlitis, G.L., Hastings, S.J., and Bochkarev, S.A.: 1995, 'Change in arctic CO₂ flux over two decades: Effects of climate change at Barrow, Alaska', *Ecol. Appl.* **5**, 846–855.
- Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zuleta, R.C., Hinzman, L., Kane, D.: 2000, 'Acclimation of ecosystem CO₂ exchange in Alaskan Arctic in response to decadal climate warming', *Nature* **406**, 978–981.
- Osterkamp, T.E. and Romanovsky, V.E.: 1999, 'Evidence for warming and thawing of discontinuous permafrost in Alaska', *Permafrost and Periglacial Processes* **10**, 17–37.
- Potter, C., Wang, S., Nikolov, N.T., McGuire, A.D., Liu, J., King, A.W., Kimball, J.S., Grant, R.F., Frolking, S.E., Clein, J.S., Chen, J.M. and Amthor, J.S.: 2001, 'Comparison of boreal ecosystem

- model sensitivity to variability in climate and forest site parameters', *Journal of Geophysical Research – Atmospheres* **106**, 33,671–33,688.
- Prentice, I.C., Farquhar, G.D., Fasham, M.J.R., Goulden, M.L., Heimann, M., Jaramillo, V.J., Kheshgi, H.S., Le Quere, C., Scholes, R.J. and Wallace, D.W.R.: 2001, 'The carbon cycle and atmospheric carbon dioxide, in J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. Van der Linden, X. Dai, K. Maskell and C.A. Johnson (eds.), *Climate Change 2001: The Scientific Basis*, Cambridge, Cambridge University Press, pp. 183–237.
- Raich, J.W., Rastetter, E.B., Mellillo, J.M., Kicklighter, D.W., Steudler, P.A. and Peterson, B.J.: 1991, 'Potential net primary productivity in South America: Application of a global model', *Ecological Applications* **1**, 399–429.
- Randerson, J.T., Field, C.B., Fung, I.Y. and Tans, P.P.: 1999, 'Increases in early season net ecosystem uptake explain changes in the seasonal cycle of atmospheric CO₂ at high northern latitudes', *Geophysical Research Letters* **26**, 2765–2768.
- Rastetter, E.B., King, A.W., Cosby, B.J., Hornberger, G.M., O'Neill, R.V. and Hobbie, J.E.: 1992, 'Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems', *Ecological Applications* **2**, 55–70.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C., Bowman, W.D.: 1998, 'Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: A test across biomes and functional groups', *Oecologia* **114**, 471–482.
- Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F. and Maurer, G.E.: 2003, 'Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska', *Ecological Monographs* **73**, 643–662.
- Ryan, M.G.: 1991, 'The effect of climate change on plant respiration', *Ecological Applications* **1**, 157–167.
- Ryan, M.G.: 1995, 'Foliar maintenance respiration of subalpine and boreal trees and shrubs in relation to nitrogen content', *Plant, Cell and Environment* **18**, 765–772.
- Ryan, M.G., Lavigne, M.B. and Gower, S.T.: 1997, 'Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate', *Journal of Geophysical Research – Atmospheres* **102**(D24), 28,871–28,883.
- Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Moore, B. III, Murdiyarso, D., Noble, I., Pacala, S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L. and Wirth, C.: 2001, 'Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems', *Nature* **414**, 169–172.
- Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Jon Ranson, K., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E. and Guertin, F.E.: 1997, 'BOREAS in 1997: Experiment overview, scientific results, and future directions', *Journal of Geophysical Research – Atmospheres* **102**(D24), 28,731–28,769.
- Serreze, M.C., Walsh, J.E., Chapin, F.S., III, Osterkamp, T., Dyrgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T. and Barry, R.G.: 2000, 'Observational evidence of recent change in the northern high-latitude environment', *Climatic Change* **46**, 159–207.
- Stromgren, M. and Linder, S.: 2002, 'Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand', *Global Change Biology* **8**, 1195–1204.
- Thornley, F.H. and Cannell, M.G.R.: 2000, 'Modelling the components of plant respiration: Representation and realism', *Annals of Botany* **85**, 55–67.
- Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H. and Brenkert, A.: 1994, 'Simulating winter interactions among ungulates vegetation and fire in northern Yellowstone Park', *Ecological Applications* **4**, 472–496.

- Van Cleve, K. and Zasada, J.: 1976, 'Response of 70-year-old white spruce to thinning and fertilization in interior Alaska', *Can. J. For. Res.* **6**, 145–152.
- Van Cleve, K., Barney, R. and Schlentner, R.: 1981, 'Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems', *Canadian Journal Forest Research* **11**, 259–273.
- Van Cleve, K., Oechel, W.C. and Hom, J.L.: 1990, 'Response of black spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska', *Can. J. For. Res.* **20**, 1530–1535.
- Viereck, L.A. and Dyrness, C.T.: 1986, 'Forest ecosystem distribution in the taiga environment', in K. Van Cleve, F.S. Chapin, III, P.W. Flanagan, L.A. Viereck and C.T. Dyrness (eds.), *Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function*, New York, Springer-Verlag, pp. 22–43.
- Vitousek, P.M. and Howarth, R.W.: 1991, 'Nitrogen limitation on land and in the seas: How can it occur?', *Biogeochemistry* **13**, 87–115.
- Waring, R.H., McDonald, A.J., Larsson, S., Ericsson, T., Win Arwidsson, E., Ericsson, A. and Lohammar, T.: 1985, 'Different chemical composition of plants grown at constant relative growth rates with stable mineral nutrition', *Oecologia* **66**, 157–160.
- Yarie, J.: 1997, 'Nitrogen productivity of Alaskan tree species at an individual tree and landscape level', *Ecology* **78**, 2351–2358.
- Zhou, L., Tucker, C.J., Kaufmann, R.K., Slayback, D., Shabanov, N.V. and Myneni, R.B.: 2001, 'Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999', *Journal of Geophysical Research – Atmospheres* **106**, 20,069–20,083.
- Zhuang, Q., McGuire, A.D., Melillo, J.M., Clein, J.S., Dargaville, R.J., Kicklighter, D.W., Myneni, R.B., Dong, J., Romanovsky, V.E., Harden, J. and Hobbie, J.E.: 2003, 'Carbon cycling in extratropical ecosystems of the Northern Hemisphere during the 20th Century: A modeling analysis of the influences of soil thermal dynamics', *Tellus* **55B**, 751–776.