

Carbon cycling in the Kuparuk basin: Plant production, carbon storage, and sensitivity to future changes

J.E. Hobbie, B.L. Kwiatkowski, and E.B. Rastetter

The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts

D.A. Walker

Institute for Arctic and Alpine Research, University of Colorado, Boulder

R.B. McKane

U.S. Environmental Protection Agency, Corvallis, Oregon

Abstract. The Marine Biological Laboratory General Ecosystem Model was calibrated for an arctic tussock tundra system using data from long-term observations and experiments at Toolik Lake, Alaska. These experiments include the effects of changes in temperature, light, CO₂, and nutrients, so the model could be applied to five regions comprising the entire Kuparuk River basin. Net primary production, averaged for the entire basin, was 92 g C m⁻² yr⁻¹. A 150 year simulation of carbon storage under a doubling of CO₂ (slow ramp-up) and a temperature increase of 3.5°C gave an estimate of +400 g C m⁻² when soil moisture increased and +500 g C m⁻² when soil moisture decreased. Drier soils stimulated decomposition producing an increase in nitrogen availability; the increased N led to increased net primary production. If this result is applicable to other arctic ecosystems, then it is unlikely that warming will enhance carbon loss to the atmosphere to further enhance warming.

1. Introduction

Global warming is predicted to produce a warming in northern lands several times greater than the global mean of 1.5°–4.5°C [*Intergovernmental Panel on Climate Change*, 1992]. One possible outcome of such warming is the stimulation of decomposition and subsequent release as CO₂ of a substantial portion of the 455 Gt (455 × 10¹⁵ g) carbon stored in northern ecosystems; some 50 Gt of this is stored in soils of wet and moist arctic tundras [*Oechel et al.*, 1993]. Another possible outcome of future warming in the Arctic is that the increase in soil decomposition will produce an increase in available nitrogen in the soil with a subsequent increase in net primary production and storage of carbon. This latter scenario would be enhanced by a doubling of the CO₂ in the atmosphere. Depending on whether the stimulation of decomposition or the stimulation of productivity dominates, the tundra will either lose or gain carbon.

To predict which of these opposing series of processes will dominate, the interactions of the carbon and nitrogen cycle must be understood [*Billings et al.*, 1984; *Shaver et al.*, 1992]. There are three main types of interactions between the carbon and the nitrogen cycles that impact the source versus sink question. As explained in detail by *Rastetter et al.* [1997] and summarized here, they present a conceptual description of carbon and nitrogen cycling in the tundra.

1. Nitrogen availability is the key to predicting carbon storage. In tundra systems, most of the nitrogen is stored in organic matter in the soil. Each year a small amount of nitrogen is added to the system through rainfall, dry deposition, and nitrogen fixation, but this amount is small compared to the large internal recycling rates, i.e., the rates of decomposition and uptake. The small rates of nitrogen addition are nearly balanced by a trickle of losses resulting from leaching and export of gases. Changes in carbon storage depend in part upon the ability of plants and soils to scavenge nitrogen from this trickle passing through the ecosystem. One way the scavenging can increase is through an increase in plant capture-efficiency for nitrogen. This could occur if the increase in CO₂ concentration increases photosynthesis and thus allows plants to allocate more resources to growing roots supporting mycorrhizae and producing N-uptake enzymes. This increase in N-uptake effort will make plants more efficient at removing nitrogen from the environment. It should also be noted that the increase in photosynthesis might have an opposite effect; that is, in the presence of higher levels of CO₂ the plant material formed will have a high C:N ratio [e.g., *Bazzaz*, 1990]. To decompose this larger amount of low-nitrogen litter, the microbes need to take up nitrogen and thus compete with the plants. The result could be that nitrogen becomes less available to the plants.

2. Carbon storage is also strongly influenced by changing ratios of C:N in vegetation and soils. For vegetation, a shift to woody plants and tissues will raise the C:N ratio, and more carbon will be stored for each unit of nitrogen. Long-term fertilization experiments [*Chapin et al.*, 1995] suggest that increased nutrient availability will favor woody tundra species and a high allocation of carbon to woody tissues in

Copyright 1998 by the American Geophysical Union.

Paper number 98JD00804.
0148-0227/98/98JD-00804\$09.00

some species. The ratio of C:N in vegetation is also increased by high concentrations of CO₂ [Bazzaz, 1990]. For soils, there is a high potential for decreasing the C:N ratio. During decomposition the C:N ratio of organic matter decreases from that of fresh litter (~40) to that of humus (~12). The same type of shift will take place during the decomposition that occurs when wet and cold tundra soils with well-preserved remnants of vegetation dry out and warm. The decrease in the C:N ratio results in less carbon storage in the soils.

3. Ecosystem carbon storage is strongly influenced by the redistribution of nitrogen between soils and vegetation. Tundra soils have much lower C:N ratios (~18) than vegetation (~40), so much more carbon can be stored per unit of nitrogen in vegetation than in soils. Redistribution can occur when the organic matter in soils decomposes, releasing N, and the nitrogen is used in plant growth. One way this can occur is when warmer conditions stimulate decomposition which results in release of CO₂ and nitrogen. If vegetation takes up this available nitrogen and incorporates it into plant tissues, then there will be about twice as much carbon tied to that nitrogen than there was in the soil. In contrast, if the released nitrogen is leached from the system, then there will be a net loss of carbon.

In a series of papers, *Rastetter et al.* [1997] and *McKane et al.* [1997a, b] have used the Marine Biological Laboratory General Ecosystem Model (MBL GEM) to investigate changes in the amount of carbon stored in the tundra in response to increases in CO₂, temperature, and nitrogen throughput in the ecosystem as well as in response to an increase and a decrease in soil moisture. The response of a single type of vegetation, tussock tundra, was analyzed in these papers; the model was applied to the Toolik Lake site where a long-term experiment provided data for a calibration.

In 1994 the National Science Foundation Arctic System Science program titled the Arctic Flux Study began collecting data over the entire Kuparuk River basin, which includes the Toolik Lake site. This basin in northern Alaska extends from the Brooks Range in the south to the Arctic Ocean in the north. Over the basin there are gradients of growing season temperatures, soil moisture, and irradiance. As a result, there are differences in vegetation with the largest difference being the dominance by tussock tundra in the south and wet sedge tundra in the north.

The goal of the Arctic Flux Study is to understand the variables and processes controlling the fluxes of gases, water, and water-transported material from an arctic river basin to the atmosphere and ocean and to predict future changes in these fluxes [Weller *et al.*, 1995]. We have taken this opportunity to use MBL GEM to estimate plant productivity throughout the entire Kuparuk River basin and plant carbon cycling at one site, Toolik Lake, for historical and future climate. These are the first steps in the extension of the modeling of the carbon cycle to a regional level and eventually to the entire circumpolar region.

2. Background

2.1 Site Description

The study area consists of the 9200 km² Kuparuk River watershed located on the North Slope of Alaska. The Kuparuk watershed extends from the Brooks Range, north through the foothills and coastal wet tundra to the Arctic

Ocean. Extensive research has been conducted at several sites within the Kuparuk basin, including Prudhoe Bay (US IBP), Imnavait Creek (DOE R4D), and Toolik Lake (NSF LTER).

The vegetation in the northern section of the basin, including Prudhoe Bay, Alaska, is dominated by tussock and wet sedge tundra. The southern section, including Imnavait Creek and Toolik Lake, is dominated by tussock and shrubland tundra. In general, the northern part of the basin is underlain by nonacidic soils, whereas the southern part is underlain by acidic soils. The mean summer temperature ranges from 5.8°C at Prudhoe Bay to 9.7°C at Toolik Lake [Haugen, 1982].

2.2. Model Description, MBL GEM

The Marine Biological Laboratory General Ecosystem Model (MBL GEM) is a process-based, lumped-parameter model of the interactions of carbon and nitrogen in terrestrial ecosystems (see *Rastetter et al.*, [1991] for a detailed description). The model calculates ecosystem responses to changes in atmospheric CO₂ concentration, temperature, soil moisture, inorganic nitrogen inputs from outside the ecosystem, and irradiance. It simulates stand-level photosynthesis and nitrogen uptake by plants, allocation of carbon and nitrogen to foliage, stems, and fine roots, respiration in these tissues, turnover of biomass through litterfall, and decomposition of that litter in soils. The only losses from the ecosystem are CO₂ losses through plant and soil respiration and inorganic nitrogen losses, which are assumed to be proportional to inorganic nitrogen concentrations in the soils. MBL GEM models only the active growing season and operates on an annual time step.

A major feature of this model is the acclimation of vegetation to maintain a nutritional balance between carbon and nitrogen as the environment changes. Changes that stimulate photosynthesis, for example, an increase in the concentration of CO₂, result in an increase in allocation of carbon and nitrogen to fine roots, which eventually stimulates nitrogen uptake. In a similar manner an increase in the levels of inorganic nitrogen will increase allocation of carbon and nitrogen to foliage, which stimulates carbon uptake.

For the application of MBL GEM to tundra ecosystems, we use the implementation described in several publications [McKane *et al.*, 1997a, b; Rastetter *et al.*, 1997]. Briefly, the model was calibrated to biomass and productivity of acidic tussock tundra based on a 9 year study reported by *Chapin et al.* [1995] in which vegetation plots at Toolik Lake, Alaska, were experimentally manipulated with fertilizer, greenhouses, and shade houses. Data from a 2 times ambient CO₂ experiment at the same site by *Oechel et al.* [1986] were also used. The calibration procedure resulted in a single parameter set that is consistent with all these experimental manipulations.

On the basis of this calibration, *McKane et al.* [1997a] were able to analyze the differential controls of various climatic factors on decomposition and production for the tussock tundra at Toolik Lake. In brief, their results indicate that climatic changes that result in carbon losses from the soil (e.g., warmer temperatures) also release inorganic nitrogen, which stimulates production and can compensate for these losses. An analysis by *Rastetter et al.* [1997] indicates that the stimulation of productivity under a 5°C increase and a

drying of the soil can be sustained for about 30 years before the canopy closes and further stimulation by increased nitrogen availability becomes negligible.

There are several important qualifications that must be understood about the application of MBL GEM. These are explained in detail by *Rastetter et al.* [1997] and summarized here.

1. Species composition is not explicitly simulated. Instead, the modeled results are for the biomass and nutrient composition of the entire tussock tundra, which includes grasses and sedges, forbs, evergreen shrubs, and deciduous shrubs. However, the model structure and the calibration include biogeochemical consequences of a species change. For example, in the 9 year experiment used as the calibration [*Chapin et al.*, 1995] the fertilizer treatment resulted in a tripling of deciduous woody shrub biomass. This result is simulated by the model and appears as a large increase in the C:N ratio. It also appears that the model and calibration are robust in that although the calibration was based entirely upon data from Toolik Lake, the model works well for other arctic sites such as Prudhoe Bay and Barrow on the arctic coast where both climate and species composition are different. Nevertheless, we do not know how extreme these changes in species composition can be and still be accommodated in this calibration.

2. Only vascular plants are represented. The acclimation concept in MBL GEM is based on *Thornley's* [1972] root-shoot partitioning model, which does not apply to nonvascular plants. Yet, mosses and lichens at the Toolik site can make up 30% of the biomass, so a significant component of the ecosystem is omitted. On the other hand, the experimental evidence [*Chapin et al.*, 1995] showed a strong shading-out of the mosses and lichens when the leaf area of vascular plants increased, so there may be a compensatory shift that will reduce possible errors.

3. The possible climate-changed depth of thaw of the soil is not explicitly treated. These changes will affect the volume of soil and amount of nutrients and organic matter available to plant roots. In addition, there may be changes in drainage of the upper layers with accompanying changes in soil moisture and decomposition.

4. The long-term validation of the model is difficult [*Rastetter*, 1996]. Our experience with the model suggests that the slow turnover of soil organic matter leads to a very long response time of tundra to changes in climate and CO₂. Validation at the appropriate timescale will have to wait for either the long-term data set of the future or for accurate reconstructions of past soil moisture, temperature, nitrogen deposition, and cloudiness. *Rastetter et al.* [1997] point out (p. 441) that "Intercomparisons among models, developed

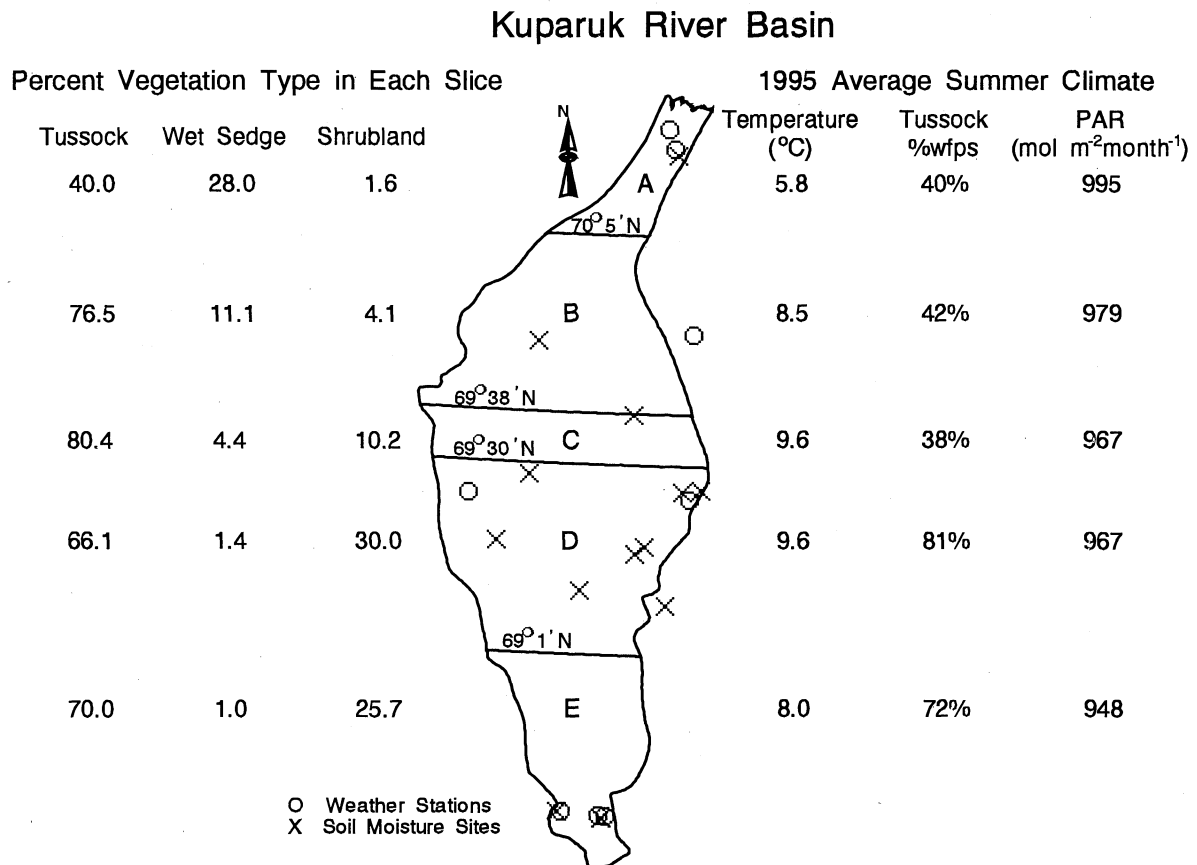


Figure 1. Kuparuk River basin in northern Alaska. Slices A-E are delimited by degrees of north latitude. Temperature data on the 1995 summer climate are from L. Hinzman (ARCSS data set on WWW) and Hobbie (Toolik Lake data on Arctic LTER WWW). Soil moisture measurement sites are indicated by crosses and are reported as percent water-filled pore space (% wfps) (data are from F. Nelson, personal communication, 1995 soil survey). Photosynthetically active radiation (PAR) data are from G. Vourlitis (personal communication, 1997) and from Toolik Lake data (on Arctic LTER WWW). The percent vegetation type in each slice came from the database of D. Walker.

from a variety of perspectives, is the only short-term way to evaluate long-term predictions and is the best short-term substitute for long-term validation.”

2.3. Simulations and Data Sources

In this paper we use MBL GEM to examine 1995 net primary productivity throughout the Kuparuk basin and to examine the response of one site, Toolik Lake, within the basin to reconstructed historical changes and predicted future changes in CO₂, temperature, soil moisture, and light. Net primary productivity (NPP) is the gross primary production minus plant respiration. All simulations use the tussock tundra calibration developed by *McKane et al.* [1997a] for Toolik Lake, Alaska.

2.3.1. Kuparuk net primary productivity. We estimate the 1995 net primary productivity throughout the Kuparuk River basin based on the steady state response of tussock tundra to 1995 mean summer values for temperature, soil moisture, irradiance, CO₂ concentration, and nitrogen input. Changes in temperature, soil moisture, and irradiance across the basin were represented by dividing the Kuparuk River basin into five regions or slices and modeling each slice under the assumption that the climate was constant across the slice. CO₂ concentration (365 ppm) (G. Kling, personal communication, 1996) and nitrogen input (0.06 g N m⁻² yr⁻¹) [*McKane et al.*, 1997a] are assumed constant across the basin.

Values for the 1995 mean summer climate drivers are shown in Figure 1, along with the location of the weather stations and soil moisture sites used to calculate the means. The mean summer temperature for each slice was calculated using the measurements at the Prudhoe Bay, Betty Pingo, Franklin Bluffs, Sagwon Hill, West Kuparuk, Imnavait Creek, Toolik Lake, and Upper Kuparuk weather stations (all sites except Toolik Lake: L. Hinzman, ARCSS data set on the WWW, Toolik Lake: Hobbie, LTER data set on the Arctic LTER WWW). Tussock tundra soil moisture, represented as percent water-filled pore space (% wfps) in MBL GEM, is derived from the 1995 soil survey conducted by F. Nelson (personal communication, 1996). This survey consisted of single measurements at numerous sites throughout the basin. Photosynthetically active radiation (PAR) (400-700 nm) was measured at the Toolik Lake, Happy Valley, and Prudhoe Bay

sites in 1995 (Toolik Lake: Hobbie, LTER data set on the Arctic LTER WWW, Happy Valley and Prudhoe Bay: G. Vourlitis personal communication, 1997). PAR for other sites was estimated using a linear regression between PAR and site latitude. The total area of each vegetation type in a slice was calculated using the Kuparuk River vegetation map developed by D. Walker and N. Auerbach (personal communication, 1997).

The model was calibrated for the acidic tussock tundra at Toolik Lake. Yet, there are also two other types of vegetation (Figure 2), shrubland tundra and wet sedge as defined by D. Walker. To calculate the NPP for these two types, we used the ratio between the NPP of tussock tundra and the NPP of wet sedge and low shrub tundra in Table 1 of *Oechel and Billings* [1992]. This ratio was 0.83 for wet sedge tundra and 0.67 for shrubland tundra; that is, both of these types of tundra are more productive than tussock tundra. While this method of calculation gives a rough estimate of steady state NPP in these types of tundra, the result cannot be used to infer the response of wet sedge and shrubland tundra to a changing climate. In the next stage of modeling we would need calibrations for each tundra type to predict the effects of a changing climate.

Another complication is that there are two forms of moist tussock tundra, the acidic and the nonacidic. Most of the detailed research and experiments have been carried out on acidic tundra. Nonacidic tundra predominates in the three northernmost sections of the basin (Figures 1 and 2, slices A, B, C) where its distribution may be associated with loess. Unfortunately, we do not yet have enough data to separate these two tundra types in the model, but preliminary information indicates that the nonacidic tussock tundra is drier, less productive, and contains less carbon than the acidic tundra. The modeled NPP for tussock tundra lumps together both acidic and nonacidic tundra assuming that these different tundra types are adequately represented in MBL GEM by soil moisture differences alone.

To estimate the 1995 net primary production (NPP) for each slice, the steady state estimates for all of the variables in the model must first be calculated on the basis of the climate for that slice. However, because the model equations are difficult to invert, these steady state estimates had to be

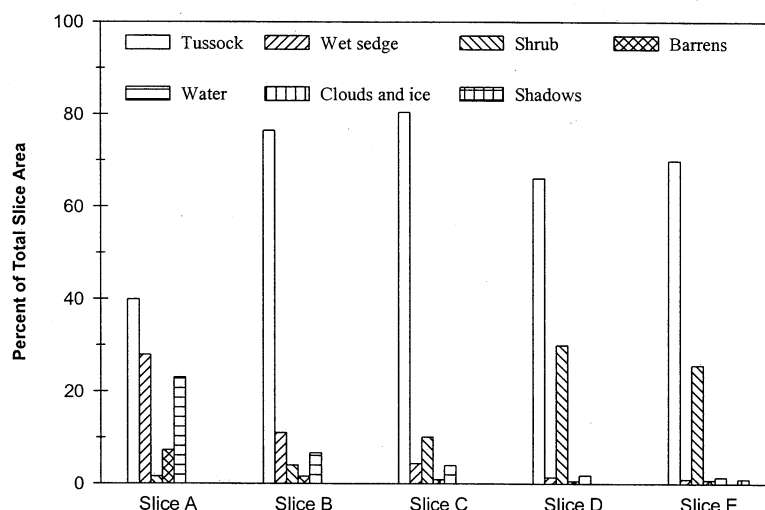


Figure 2. Percent of the total area of a slice in each vegetation class. Data provided by D. Walker.

Table 1. 1995 Net Primary Production in Each Slice of the Kuparuk River Basin Reported as Grams (g) and Million Grams (10^6 g).

Region	Tussock NPP Mg C slice ⁻¹ yr ⁻¹	Wet Sedge NPP Mg C slice ⁻¹ yr ⁻¹	Shrub NPP Mg C slice ⁻¹ yr ⁻¹	Total NPP Slice ⁻¹ Mg C slice ⁻¹ yr ⁻¹	NPP Slice ⁻¹ Unit Area ⁻¹ g C m ⁻² yr ⁻¹	NPP Slice ⁻¹ Unit Area ⁻¹ * g C m ⁻² yr ⁻¹
Slice A	14,855	12,468	908	28,231	64	78*
Slice B	168,639	29,403	13,428	211,471	89	105*
Slice C	49,607	3,284	9,430	62,320	60	92*
Slice D	213,595	5,374	145,532	364,501	116	103*
Slice E	117,246	1,997	64,659	183,901	116	105*

*For the NPP reported in column 7, soil moisture was increased by 4% wfps.

estimated by running the model to steady state. Each of these simulations began at the steady state calibration for conditions at Toolik Lake (8.3°C, 71% wfps, 344 ppm CO₂, and PAR of 1273 mol m⁻² month⁻¹). Beginning in year 3, each climate driver was then individually ramped to the 1995 measured value for that slice (Figure 1). The simulation was then run until a new steady state was reached and the steady state estimate of NPP could be made.

2.3.2. Slice E net ecosystem productivity. The NEP is the net primary productivity minus the respiration of the soil. At steady state, NEP is zero and the ecosystem is in balance with no gain or loss of total carbon over the year. When NEP is positive the ecosystem is storing carbon in the biomass of plants and in soil carbon. McKane [1997b] gives the soil carbon as 15,737 g m⁻² and the plant carbon as 471 g m⁻² at Toolik Lake.

To investigate the long-term response of tussock tundra to a changing climate, we simulated the response of NEP in slice E to historical climate and to a predicted future climate. We decided to focus on slice E and not on the whole basin because we are most confident in the dynamic response of our calibration for tussock tundra in that region [see McKane *et al.*, 1997a, b]. This simulation is made up of two parts. The first part or historical portion is based on a reconstruction of historical climate drivers from 1921 to 1995. In this study we only analyze NEP in 1994, 1995, and 1996, the years of intensive field studies throughout the Kuparuk River basin. The second part or future portion is based on a doubling of CO₂ and the concurrent changes in temperature, soil moisture, and irradiance over the next 100 years. Since future ecosystem response depends on both historical and future conditions the combination of these two parts provides a long-term (1921-2095) simulation of tussock tundra response to a changing climate.

The reconstruction of the historical climate is based primarily on the long-term temperature record at Barrow, Alaska (NOAA Global Historical Climate Network data on the CDROM titled ARCSS/LAI Data Series Volume 1: Alaska North Slope Data Sampler). The Slice E summer temperature for 1921-1995 was calculated using the linear regression between slice E and Barrow 1976-1995 summer temperatures. PAR was estimated using the linear regression between PAR and temperature at Toolik Lake for 1994 and 1995. There are two scenarios for changes in soil moisture. Scenario 1 represents an inverse relationship between soil moisture and temperature and scenario 2 represents a direct relationship. In both cases the average historical soil moisture is equal to the 1995 value plus yearly fluctuations.

These fluctuations are correlated (inversely or directly) to the magnitude and direction of the temperature fluctuations. We use these two soil moisture regimes to investigate the effects of two opposing climate change scenarios: warmer and drier (inverse relationship) and warmer and wetter (direct relationship). Although the inverse temperature % wfps scenario appears similar to scenario 2 in the work of McKane *et al.* [1997b], the magnitude of the % wfps fluctuations in McKane *et al.* is about 60% wfps, while the magnitude of the % wfps fluctuations in the simulation presented here is 7% wfps. In addition, the scenarios presented here include changes in PAR, while those of McKane *et al.* [1997b] did not. For atmospheric CO₂ concentrations we use the reconstruction developed by McKane *et al.* [1997b] based on

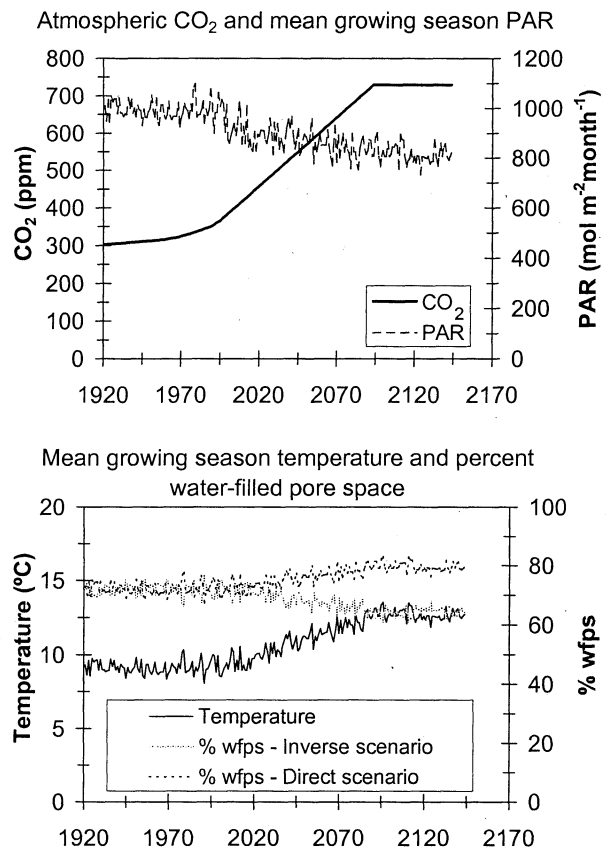


Figure 3. Reconstructed and predicted climate drivers for slice E of the Kuparuk basin net ecosystem productivity simulations.

the Siple ice core from the Antarctic [Neftel *et al.*, 1985] and Mauna Loa [Keeling *et al.*, 1982] records. Throughout the historical reconstruction, calculated climate drivers were supplemented with measured values whenever possible.

The predicted future climate is based on an assumed doubling of CO₂ over 100 years and the concurrent changes in temperature, soil moisture, and irradiance. This part of the simulation involves a doubling of CO₂, a 3.5°C increase in air temperature [Maxwell, 1992], a 15% decrease in PAR, and either a 10% increase or a 10% decrease in the average soil moisture. The changes in soil moisture and PAR are estimates based on the projections of four general circulation models (GCMs) for increased summer precipitation in northern Alaska under greenhouse warming [Maxwell, 1992]. We simulate both an increase and a decrease in soil moisture because GCM projections for changes in soil moisture are uncertain [Maxwell, 1992]. In one scenario, the first part, which is the historical part, has the direct temperature % wfps relationship; the second part, which is the future part, has the increased soil moisture. The other scenario has the inverse temperature % wfps relationship in the historical part and decreased soil moisture in the future part. Note that the future part of the simulations does not use the temperature-based regressions described for the historical reconstruction. All climate drivers were varied linearly over 100 years from the initial value (a long-term average) to the final value with random fluctuations added to all drivers except CO₂. The combined climate scenarios, the reconstructed historical climate plus the predicted future climate, are shown in Figure 3.

The model simulation of tussock tundra carbon storage began in steady state with the calibration climate (8.3°C, 71 % wfps, 344 ppm CO₂, and PAR of 1273 mol m⁻² month⁻¹). The climate drivers were then ramped up to the reconstructed 1921 slice E climate and allowed to reach a steady state. When steady state was reached, climate drivers were varied yearly (1921-1995) based on the historical reconstruction and from 1995-2095 based on the predicted future climate. The simulations were run an additional 50 years, 2095-2145, with the climate drivers held at the 2095 values plus small yearly variations.

3. Results and Discussion

3.1. Net Primary Production in the Kuparuk River Basin

The Kuparuk basin is dominated by moist tussock tundra, made up chiefly of grasses and sedges (Figure 2). In general, the wet sedge tundra is an important part of the total vegetation only in the northern two sections of the basin (Figure 2, slices A, B). In contrast, the shrublands become important only in the southern section of the basin (Figure 2, slices C, D, E). Obviously, the moist tussock tundra dominates in all sections.

The net primary production (NPP) is affected by plant type because shrublands are more productive than tussock tundra, by temperature because warmer areas are more productive than cooler areas, by soil moisture, which can both increase and decrease decomposition rates and the subsequent release of nitrogen, and by light because higher light levels lead to higher productivity. The 1995 NPP in each slice was estimated using simulated tussock NPP in steady state with

the climate drivers shown in Figure 1. For 1995, the estimated net plant productivity was lowest in the north section of the Kuparuk basin (64 g C m⁻² yr⁻¹) and highest (116 g C m⁻² yr⁻¹) in the southern section (Table 1). Within each section, the proportion attributed to shrubland, wet sedge, or tussock tundra was roughly equivalent to the area covered (Table 1), although shrubland vegetation was more productive per unit area than the other types. The average NPP for the entire basin was 92 g C m⁻² yr⁻¹.

While the NPP is affected by a number of factors, we are able to assess the importance of the distribution of the three vegetation types. To do this, we estimated the NPP for the Kuparuk basin using the slice E proportion of each vegetation type across the whole basin. Under this assumption, the average NPP for the Kuparuk basin was 94 g C m⁻² yr⁻¹ compared to our estimate of 92 g C m⁻² yr⁻¹ using the true vegetation distribution shown in Figure 2. The difference in these two estimates illustrates that NPP in the Kuparuk basin is insensitive to climate changes in the range found across the Kuparuk basin. Conversely, NPP in the Kuparuk basin using

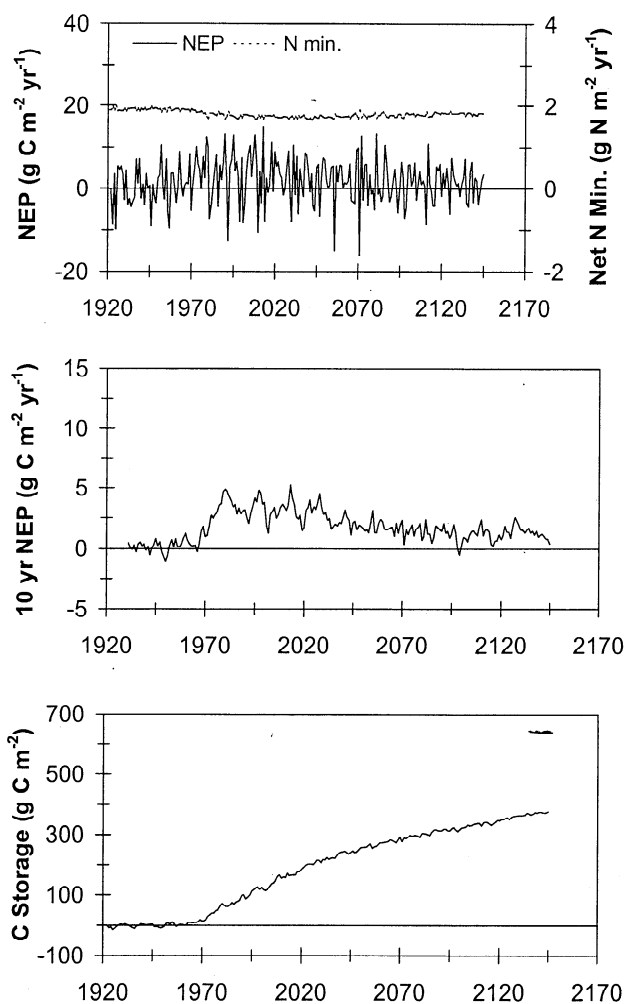


Figure 4. Historical and future simulations of carbon storage for tussock tundra in slice E (location of Toolik Lake). Data are presented as net ecosystem productivity (NEP) and cumulative carbon storage. The NEP data are given as yearly data and as 10 year running means. For this simulation the percent water-filled pore space varied directly with the temperature changes.

the slice E climate for all slices, and the true vegetation distribution is $106 \text{ g C m}^{-2} \text{ yr}^{-1}$. This shows that NPP in the Kuparuk basin is more sensitive to changes in climate than changes in vegetation under the conditions of these simulations. Our simulations for the future do not incorporate any changes in the distribution of vegetation, but it is obvious that these changes will have to be made a part of any future assessment of changes in NPP.

The effect of soil moisture on NPP deserves special notice because of its importance in controlling the decomposition process. To test this for each slice, we made an additional calculation of NPP in which the percent water-filled pore space (soil moisture) was increased by 4%. In slice C, for example, this increase of only 4% increased the NPP from 60 to $92 \text{ g C m}^{-2} \text{ yr}^{-1}$. At least for these ranges, the model output was very sensitive to soil moisture. An examination of the model run for slice C revealed that the rate of mineralization of N was increased from 1.22 to 1.77 by the increase in soil moisture. Because this N was originally in soil organic matter with a relatively low C:N ratio and was transformed into plant organic matter with a relatively high C:N ratio, there was a resulting strong increase in the NPP. However, this large increase in NPP would be unlikely when changes are made in the full suite of climatic variables because the increase in soil moisture would be correlated with colder temperatures and lower light, both of which would limit productivity. For example, the range of soil moisture in the whole basin is greater than the 4% increase simulated for slice C, yet the variation in NPP is only 30%.

It is also evident from Table 1 that the effect of a change in soil moisture on NPP depends on just how wet the soils are. For the wetter soils, slices D and E in Figure 1, NPP actually decreases when the soil moisture increases. This result agrees with the results of *McKane et al.* [1997b] who used the same model calibration for Toolik Lake tussock tundra. As shown by *McKane et al.* [1997b, Figure A1], the modeled response of decomposition to soil moisture ramps up to a single peak with a gradual tail-off as soil moisture increases from 0% to saturation. *McKane's* soil moisture and those for slices D and E were on the tail-off part of the curve, while slices A, B, and C are on the ramp-up part of the curve.

3.2. An Estimate of the Net Ecosystem Productivity at Toolik Lake, 1994, 1995, and 1996

We have restricted the estimates of NEP to the tussock tundra near Toolik Lake where a careful calibration of the model has been carried out. Moreover, we have chosen to use the scenario in which the soil moisture (% wfps) was inversely related to temperature. This was the scenario that appears to be most similar to the actual conditions. In addition, the drivers of temperature and PAR were a combination of actual measured and derived values in 1994 and 1995 but were all derived numbers for 1996. The % wfps driver was based on measurements for 1995 but was derived for 1994 and 1996.

For the three years of 1994, 1995, and 1996 the estimated NEP values were 0.1, 1.2, and $-8.1 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively. While 1994 and 1995 estimates are very similar, there was a negative NEP or a loss of carbon from the tundra in 1996. What caused this modeled result? If the climate drivers for 1995 and 1996 are compared, the 1996 season was slightly cooler, the soil moisture was increased by about 4%, and the

PAR was reduced. The NPP's were identical for the two years, but the year with more soil moisture had an increase in the soil respiration. Evidently, the increased nitrogen availability associated with the increased respiration maintained the rate of photosynthesis, even though both PAR and temperature decreased.

Relatively small shifts in climate will cause the NEP to shift from positive to negative. This is understandable and should be recognized as typical for this tussock ecosystem.

3.3. Analysis of the Sensitivity of the Net Ecosystem Productivity to Future Changes

When the annual NEP is estimated for the next 150 years, the same type of year-to-year shifts from positive to negative NEP are seen. Although this type of variation undoubtedly will occur in the future, they occur in the simulation because we have introduced a small random variability into the climatic drivers. The variability has the same amplitude as the natural variability observed in the field. Our experience with the model indicates that the simulation is more sensitive

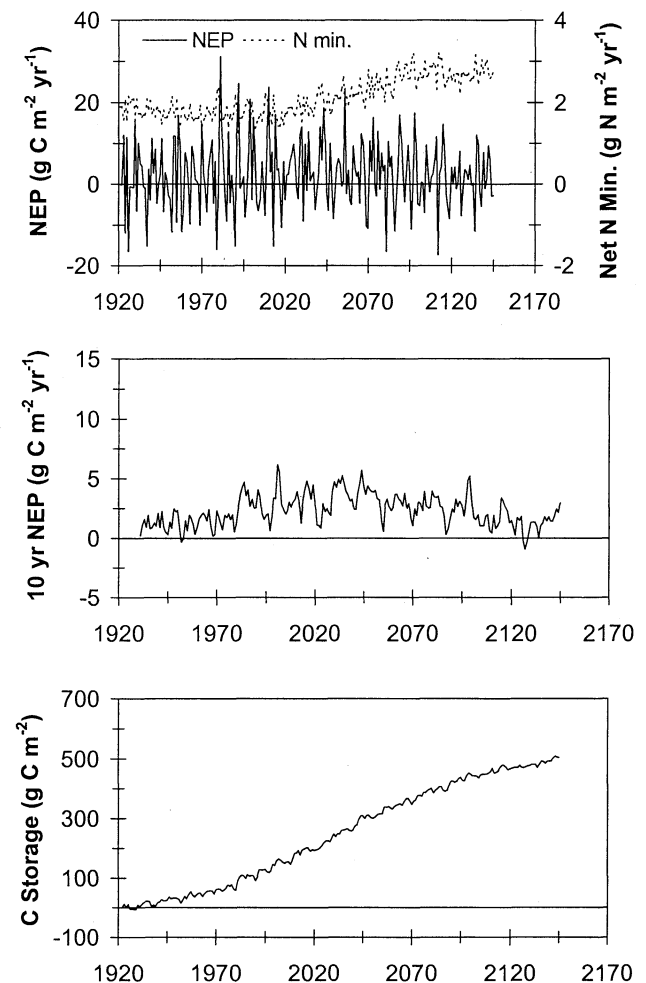


Figure 5. Historical and future simulations of carbon storage for tussock tundra in slice E (location of Toolik Lake). Data are presented as net ecosystem productivity (NEP) and cumulative carbon storage. The NEP data are given as yearly data and as 10 year running means. For this simulation the percent water-filled pore space varied inversely with the temperature changes.

to small changes in soil moisture than to small changes in temperature or light.

The NEP is equal to the amount of carbon stored each year in the tundra plants and soils. In both the warmer and wetter scenario (Figure 4) and the warmer and drier scenario (Figure 5), the NEP and net N mineralization of tussock tundra at Toolik Lake varies from year to year as the environmental conditions shift slightly. Even when the NEP data are plotted as a 10-year moving average, the trends are difficult to distinguish. It is clear, however, from the plots of cumulative carbon storage, that after about year 2045 there was a slower rate of storage in the wetter soil than in the simulation with drier soil (Figure 4, 5). By 2140 the amount of carbon storage was 50% higher in the drier scenario than in the wetter scenario. The most likely explanation for these results is that the increased photosynthesis caused by higher levels of CO₂ and higher temperature coupled with increased available nitrogen was enough to compensate for the increased soil respiration found at the lower levels of soil moisture.

The only other analysis of the interactions of temperature and soil moisture on ecosystem carbon [Rastetter *et al.*, 1997] employed a constant CO₂ concentration and the combination of a 5° C increase in temperature with a 10% decrease in soil moisture. The drivers were changed in a single step at the beginning of the run. Their simulation, showing a decrease over 50 years in ecosystem C, was caused in part by a decoupling of the N mineralization and N uptake rates after 20 years. Nitrogen loss from the ecosystem increased dramatically during the last 20 years. In the GEM model, N losses are strictly proportional to the concentration of inorganic N in the soil. Nitrogen losses are clearly more complex in natural ecosystems and this complexity should be incorporated in future modifications to the model. However, tussock tundra ecosystems on the North Slope of Alaska are severely N limited [Chapin *et al.*, 1995] and strongly retain any N that becomes available. Thus we believe that increased CO₂ concentration and the slow change in all the climate drivers in our simulation allowed plants to add biomass and take up the N as it became available.

For MBL GEM, Rastetter *et al.* [1992] developed equations for calculating how much of the change in carbon storage is associated with various factors: (1) changes in the total amount of N in the ecosystem, (2) changes in the C:N ratios of vegetation and soil, (3) redistribution of N between soil and vegetation, and (4) the interaction of factors 1, 2, and 3. We have used these equations to partition the cumulative carbon storage over the period 1921 to 2145 into these four parts (Figure 6).

The cumulative carbon storage in the warmer-wetter scenario (Figure 6a) was caused almost completely by changes in the C:N ratio in the plants and soils. This can be safely attributed to a strong effect of higher CO₂ concentrations that result in a high C:N ratio in the new plant matter [Melillo *et al.*, 1993]. In the warmer-drier scenario analyzed in Figure 6b, the change in C:N ratio was also the most important factor influencing cumulative carbon storage. However, in this scenario the redistribution of N (N shift) and the interaction of all factors also became important, beginning in about year 2030.

In conclusion, we have described a modeling method of analyzing experimental data on the effects of changes in temperature, soil moisture, CO₂, and light on the carbon

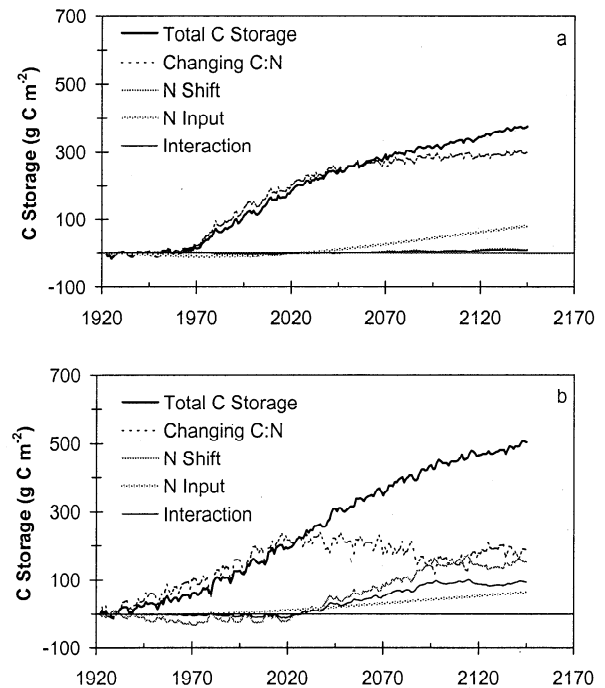


Figure 6. Cumulative changes in carbon storage for tussock tundra in slice E (location of Toolik Lake). The changes are given as the total and also partitioned into changes caused by a change in the ratio of C:N in plants and soils, by a shift in N from low C:N organic matter to high C:N organic matter, by a change in the retention of N added in input, and by the interactions of all three of these changes. Figure 6a is carbon storage for the GEM simulation in which percent water-filled pore space varied directly with the temperature changes. Figure 6b is carbon storage for the GEM simulation in which percent water-filled pore space varied inversely with the temperature changes.

cycling of arctic terrestrial ecosystems. Further, the method allows extrapolation of terrestrial primary productivity results to larger regions, here the entire Kuparuk River basin. These ecosystems are strongly nitrogen limited and their carbon cycling will likely be able to respond only slowly to global change. If other arctic ecosystems respond to global change in a manner similar to the simulated tussock tundra ecosystem, then they will not be a major contributor to the control of atmospheric CO₂. Even with 200-300 g C m⁻² accumulation over a century, this is only about 1% change in the nearly 16,000 g C m⁻² now found in these tundra soils. This rate translates to a cumulative storage rate of a few Tg C yr⁻¹ for the pan-arctic plants and soils. In comparison, global fossil fuel combustion is some 5 Pg C yr⁻¹. If this result is applicable to other arctic ecosystems, then there is little chance that warming will enhance carbon loss to the atmosphere to further enhance warming. These results are consistent with the global-scale analysis of Schimel *et al.* [1994] and McGuire *et al.* [1995] which indicate that steady state responses of soil carbon to warming is minimal in high latitudes.

The next field effort needed to improve the modeling of carbon cycling in the Kuparuk River basin, and eventually in the entire Arctic, is a better measurement of soil moisture. Remote sensing techniques are urgently needed. Experiments are also needed in which nonacidic tussock tundra and

shrubland tundra are manipulated by changing temperature, light, nutrients, and CO₂. The resulting data will allow a calibration of the model for these important types of tundra.

Acknowledgments. This research was supported by funds from the ARCSS program of NSF (OPP 9318529 to JEH, OPP 9614038 to EBR, and OPP 9318530 to DAW), NSF-Ecosystems (DEB 9307888 to EBR), and from NSF-LTER (DEB 9211775). We wish to thank Nancy Auerbach, Larry Hinzman, Fritz Nelson, and George Vourlitis for data.

References

- Bazzaz, F.A., The response of natural ecosystems to the rising global CO₂ levels, *Annu. Rev. Ecol. Syst.*, *21*, 167-196, 1990.
- Billings, W.D., K.M. Peterson, O.J. Luken, and D.A. Mortensen, Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms, *Oecologia*, *65*, 26-29, 1984.
- Chapin, F.S., G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, and J.A. Laundre, Responses of arctic tundra to experimental and observed changes in climate, *Ecology*, *76*, 694-711, 1995.
- Haugen, R.K., Climate of remote areas in north central Alaska, *Rep. 82-35*, 110 pp., U.S. Army Cold Regions Res. Eng. Lab., Hanover, N. H., 1982.
- Intergovernmental Panel on Climate Change, (IPCC), *Climate Change 1992*, supplementary report, IPCC Sci. Ass., Cambridge Univ. Press, New York, 1992.
- Keeling, C.D., R.B. Bacastow, and T.P. Whorf, Measurements of the concentration of carbon dioxide at Mauna Loa Observatory, Hawaii, in *Carbon Dioxide Review: 1982*, edited by W.C. Clark, pp. 377-385, Oxford Univ. Press, New York, 1982.
- Maxwell, B., Arctic climate: Potential for change under global warming, in *Arctic Ecosystems in a Changing Climate*, edited by F.S. Chapin, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda, pp. 11-34, Academic, San Diego, CA, 1992.
- McGuire, A.D., J.M. Melillo, D.W. Kicklighter, and L.A. Joyce, Equilibrium responses of soil carbon to climate change: Empirical and process-based estimates, *J. Biogeogr.*, *22*, 785-796, 1995.
- McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin, Effects of experimental changes in CO₂ and climate on carbon storage in arctic tundra, *Ecology*, *78*, 1170-1187, 1997a.
- McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin, Reconstruction and analysis of historical changes in carbon storage in arctic tundra, *Ecology*, *78*, 1188-1198, 1997b.
- Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore III, C.J. Vorosmarty, and A.L. Schloss, Global climate change and terrestrial net primary production, *Nature*, *363*, 234-240, 1993.
- Neftel, A., E. Moor, H. Oeschger, and B. Stauffer, Evidence from polar ice cores for the increase in atmospheric CO₂ in the past two centuries, *Nature*, *315*, 45-47, 1985.
- Oechel, W.C., and W.D. Billings, Effects of global change on the carbon balance of arctic plants and ecosystems, in *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, edited by F.S. Chapin, R.L. Jefferies, J.E. Reynolds, G.R. Shaver, and J. Svoboda, pp. 139-168, Academic, San Diego, CA, 1992.
- Oechel, W.C., G. Riechers, J. Beyers, S. Cowles, N. Grulke S.J. Hastings, S. Oberbauer, T. Prudhomme, and N. Sionit, Response of tundra ecosystems to elevated carbon dioxide, *Progr. Rep. 037*, U.S. Dep. of Energy, Carbon Dioxide Res. Div., Oak Ridge, Tenn., 1986.
- Oechel, W.C., S.J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Gruelke, Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source, *Nature*, *361*, 520-533, 1993.
- Rastetter, E.B., Validating models of ecosystem response to global change, *Bioscience*, *46*, 190-198, 1996.
- Rastetter, E.B., M.G. Ryan, G.R. Shaver, J.M. Melillo, K.J. Nadelhoffer, J.E. Hobbie, and J.D. Aber, A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate, and N deposition, *Tree Physiol.*, *9*, 101-126, 1991.
- Rastetter, E.B., R.B. McKane, G.R. Shaver, and J.M. Melillo, Changes in C storage by terrestrial ecosystems: How C-N interactions restrict responses to CO₂ and temperature, *Water Air Soil Pollut.*, *64*, 327-344, 1992.
- Rastetter, E.B., R.B. McKane, G.R. Shaver, K.J. Nadelhoffer, and A.E. Giblin, Analysis of CO₂, temperature, and moisture effect on carbon storage in Alaskan arctic tundra using a general ecosystem model, in *Global Change and Arctic Terrestrial Ecosystems*, edited by W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, O. Molau, and B. Sveinbjörnsson, pp. 437-451, Springer-Verlag, New York, 1997.
- Schimel, D.S., B.H. Braswell, E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter, W.J. Parton, and A.R. Townsend, Climatic, edaphic and biotic controls over storage and turnover of carbon in the soils, *Global Biogeochem. Cycles*, *8*, 279-293, 1994.
- Shaver, G.R., W.D. Billings, F.S. Chapin, A.E. Giblin, K.J. Nadelhoffer, W.C. Oechel, and E.B. Rastetter, Global change and the carbon balance of arctic ecosystems, *Bioscience*, *42*, 433-441, 1992.
- Thornley, J.H.M., A model to describe the partitioning of photosynthate during vegetative growth, *Ann. Bot.*, *36*, 419-430, 1972.
- Weller, G., F.S. Chapin, K.R. Everett, J.E. Hobbie, D. Kane, W.C. Oechel, C.L. Ping, W.S. Reeburgh, D. Walker, and J. Walsh, The Arctic Flux Study: A regional view of trace gas release, *J. Biogeogr.*, *33*, 365-374, 1995.
- J.E. Hobbie, B.L. Kwiatkowski, and E.B. Rastetter, The Ecosystems Center, Marine Biological Laboratory, 7 MBL St., Woods Hole, MA 02543. (e-mail: jhobbie@lupine.mbl.edu; bonniek@lupine.mbl.edu; erastett@lupine.mbl.edu)
- D.A. Walker, Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO 80309.
- R.B. McKane, U.S. Environmental Protection Agency, 200 S.W. 35th St., Corvallis, OR 97333. (e-mail: bmckane@mail.cor.epa.gov)

(Received August 8, 1997; revised February 3, 1998; accepted March 4, 1998.)