

## A simple model for analyzing climatic effects on terrestrial carbon and nitrogen dynamics: An arctic case study

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[1] We developed a simplified plant-soil model (PSM) composed of four coupled differential equations that simulate the effects of climate change on major stocks and fluxes of carbon (C) and nitrogen (N) in terrestrial ecosystems. Here we use the model to examine past, present, and future changes in C storage in arctic Alaska, a region undergoing rapid climate change. Model parameters were initialized to simulate the buildup of C and N stocks from the beginning of the current postglacial period (~10,000 years BP) to present-day levels for tussock tundra at Toolik Lake, Alaska. For projected rates of warming during the next century, the model predicts an increase in aboveground plant biomass and a net loss of soil carbon, resulting in almost no net change in total ecosystem C. The simplified model structure serves to clarify several important issues that have not been adequately addressed in previous studies. These issues include altered residence times of C and N in soils and plants, decreased synchrony of above and belowground processes, and the relationship between a model's initial conditions and the ecosystem's trajectory at the point of initialization.

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### 1. Introduction

[2] The magnitude and spatial extent of high-latitude warming during the past century is well documented [Chapman and Walsh, 1993; Intergovernmental Panel on Climate Change, 2001; Overpeck *et al.*, 1997; Serreze *et al.*, 2000] and is expected to continue into the next century (ACIA, Arctic Climate Impact Assessment Report, 2004, available at <http://www.acia.uaf.edu/>). In many arctic regions this warming is associated with increased precipitation [Dai *et al.*, 1997; Groisman and Easterling, 1994; Ye *et al.*, 1998] and river discharge [Peterson *et al.*, 2002], a longer growing season [Foster, 1989; Foster *et al.*, 1992; Stone *et al.*, 2002], a change in the distribution of plant species [Sturm *et al.*, 2001], an increase in the spatial extent of woody species, and higher aboveground photosynthetic rates [Myneni *et al.*, 1997; Nemani *et al.*, 2003]. Borehole temperature measurements also indicate strong subsurface warming [Lachenbruch and Marshall, 1986; Oberman and Mazhitova, 2001; Osterkamp and Romanovsky, 1999; Pavlov, 1994; Romanovsky *et al.*, 2002; Stieglitz *et al.*, 2003].

[3] Northern soils hold ~30% of the world's 1500 gigatons of soil organic carbon [Post *et al.*, 1982]. Between 43

and 200 gigatons of this is in tundra soils [Post *et al.*, 1982; Shaver *et al.*, 1992] and 200–500 gigatons in boreal forests [Dixon *et al.*, 1994; Gorham, 1991; Schlesinger, 1997; Whittaker, 1975]. Although the arctic climate may have been favorable for carbon sequestration during the past 10,000 years [Billings, 1987; Gorham, 1991; Mann *et al.*, 2002; Oechel and Billings, 1992], this may no longer be the case. If soils become warmer in this extremely nitrogen limited ecosystem [Shaver *et al.*, 1986], increased microbial activity may release nitrogen and carbon currently stored in the soil, especially deep soil C frozen in permafrost, below the seasonal active layer. Mack *et al.* [2004] examined intensively fertilized tussock tundra plots in arctic Alaska [Hobbie, 1996; Shaver *et al.*, 1992] to quantify the effect of increased nutrient availability on ecosystem carbon dynamics. For the 20-year period of fertilization, they reported a shift in species dominance away from graminoids and toward woody species (especially *Betula nana*) and a large net loss of ecosystem C, primarily a loss of deep soil C. Mack *et al.* [2004] concluded "Our study suggests that projected release of soil nutrients associated with high-latitude warming may further amplify carbon release from soils, causing a net loss of ecosystem carbon and a positive feedback to climate warming." At the same time, increased temperatures may augment the sequestering of atmospheric CO<sub>2</sub>, increase plant growth and alter species composition. Which process dominates, soil decomposition or plant growth, will determine whether tundra biomes are a net source or net sink of atmospheric CO<sub>2</sub> in a climate-changed world.

[4] Questions such as these have been addressed through experiments [Chapin *et al.*, 1995; Shaver *et al.*, 2001] and

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model simulations [McKane et al., 1997a, 1997b; Rastetter et al., 2004; Stieglitz et al., 2000; Williams et al., 2001]. However, while both approaches indicate a future arctic dominated by shrubs, the interpretation of either is not straightforward. To make the study of climate change feasible, experimental treatments generally have been fertilized or warmed at high levels over short periods of time. However, it is unclear how the results of such experiments relate to effects of much more gradual and less intense climate change. In addition, it is difficult to separate the effects of temperature and nutrient availability. Simulation studies that aim to do this have their own difficulties. Model predictions depend on model structure and complexity (processes included or excluded), assumptions concerning initial conditions, the data and methods by which parameter values are specified or calculated (e.g., top-down versus bottom-up parameterization [Jarvis 1993]), and other factors. Although complex models have reproduced arctic ecosystem responses to interacting disturbances [McKane et al., 1997a], it can be difficult to ascertain whether a modeling solution is unique. That is, does the model accurately represent the processes and interactions that underlie an observed system response?

[5] Given these difficulties, we sought to identify the simplest possible model structure that provides a parsimonious description of experimental and observational evidence concerning past, present and future tundra carbon and nitrogen dynamics. Our intent is not to replace complex models, but rather to establish a heuristic framework that, in its simplicity, may elucidate underlying controls on ecosystem response to warming. We use the model to explore the effects of warming in tundra regions, specifically for tussock tundra at the Toolik Lake Long Term Ecologic Research (LTER) Station, located in the northern foothills of the Brooks Range, Alaska (68°38'N, 149°43'W, elevation 720 m). The research site was last deglaciated 60,000–100,000 years BP [Hamilton, 1986; Walker et al., 1989]. The temperature regime for this region has been relatively stable for the last 10,000 years [Kaufman et al., 2004], and favorable for peat growth [Billings, 1987; Gorham, 1991; Mann et al., 2002; Oechel and Billings, 1992]. Prior to 10,000 yr BP conditions were much colder and drier and not favorable to peat accumulation [Kaufman et al., 2004]. Appendix A presents a more detailed description of the research site.

[6] We calibrated the model based on long-term (1980–2000) measures of soil and plant C and N stocks and fluxes for control (unmanipulated) plots at the Toolik Lake site. We then ran the calibrated model for two types of scenarios: (1) an arctic “buildup” that simulates the accumulation of ecosystem C and N stocks from the beginning of the current postglacial period to the present, and (2) several climate warming scenarios for the period 2000–2100 to explore potential future states of arctic tundra. We use the simulation results for both scenarios to examine several important issues related to modeling the effects of warming on arctic ecosystems, specifically, altered residence times of soil and plant carbon, decreased synchrony of above and below-ground processes, and the relationship between a model’s initial conditions and the system’s trajectory at the point of

initialization. Although the specific focus is on high-latitude processes, our modeling approach and the issues discussed are generally applicable to terrestrial ecosystems.

## 2. Plant-Soil Model (PSM)

[7] The PSM simulates the effects of climate warming on ecosystem C storage and the cycling of C and N between plants and a shallow active soil pool. The model includes four coupled differential equations: aboveground vegetation biomass ( $P$ ); soil carbon including humus and detritus ( $D$ ) (excluding deep “noninteractive” carbon); plant-available soil nitrogen ( $N$ ) including dissolved inorganic and organic forms; and leaching losses of dissolved organic carbon (DOC). DOC is lost at a rate  $l_c \times \text{DOC}$ . Dissolved inorganic nitrogen (DIN) is lost at a rate  $l_n \times N$ . In addition, recalcitrant dissolved organic nitrogen (DON) is lost at a rate  $q \times D \times \nu(T)$ , where  $D \times \nu(T)$  represents first-order detritus decomposition and  $T$  is the near-surface ground temperature. Although DON loss has been ignored in most modeling applications (but see Rastetter et al. [2005]), field studies indicate the importance of DON loss in maintaining N limitation and stability in ecosystems [Hedin et al., 1995; Perakis and Hedin, 2001, 2002; Peterson et al., 1992]. We treat atmospheric inputs of wet and dry deposition of N as a constant,  $n_{in}$ . Uptake of N by plants is simulated using a Type II Michaelis-Menton function. Plant biomass is lost only through density-independent mortality at a rate  $m \times P$ . While our model does not explicitly simulate respiratory losses of C by plants or soil microbes, it is implicitly accounted for in the model framework (see below). Plants and soils are assumed to have a single C:N [Gough et al., 2002; Schmidt et al., 2002; Shaver et al., 2001; Shaver and Chapin, 1991], defined as  $\alpha$ . For these simulations, C:N is held constant at 26 [Mack et al., 2004].

[8] The equations representing these processes are

$$\frac{\partial P}{\partial t} = \mu(T) \times f(N) \times P - m \times P, \quad (1)$$

$$\frac{\partial D}{\partial t} = m \times P - D \times \nu(T), \quad (2)$$

$$\frac{\partial N}{\partial t} = n_{in} - l_n \times N - \mu(T) \times f(N) \times P + (1 - q) \times D \times \nu(T), \quad (3)$$

$$\frac{\partial \text{DOC}}{\partial t} = \alpha \times D \times \nu(T) - l_c \times \text{DOC}, \quad (4)$$

where

$$f(N) = N / (N + k_n).$$

Parameter values and references for the values used are given in Table 1. In this model framework, soil respiration and lateral DOC loss are modeled implicitly within the

**Table 1.** Parameter Values Used to Simulate the Postglacial Buildup of Ecosystem C and N Stocks in Tussock Tundra at Toolik Lake, Alaska

Parameter	Value	Reference
$n_{in}$	0.1 g N m <sup>-2</sup> yr <sup>-1</sup>	Everett <i>et al.</i> [1996]
$l_n$	0.015 g N m <sup>-2</sup> yr <sup>-1</sup>	back-calculated
$\mu$	0.33 yr <sup>-1</sup>	Chapin <i>et al.</i> [1995], Shaver <i>et al.</i> [2001], Shaver and Chapin [1991]
$\nu$	0.0002 yr <sup>-1</sup>	back-calculated
$m$	0.01 yr <sup>-1</sup>	Mark <i>et al.</i> [1985], D. Bret-Harte, unpublished data, 2005
$\alpha$ (C:N)	26	Gough <i>et al.</i> [2002], Schmidt <i>et al.</i> [2002]
$l_c$	1 yr <sup>-1</sup>	back-calculated
$k_n$	10 g N m <sup>-2</sup>	back-calculated
$q$	.5	back-calculated

general first-order decomposition function. Plant respiration is modeled implicitly through a calibrated function of N uptake.

### 3. Model Simulations

[9] Current trends in arctic ecosystem carbon stocks are uncertain [Oechel *et al.*, 2000]. Nonetheless, most models used to simulate the effects of arctic warming have been initialized assuming that present-day arctic C stocks are at equilibrium, potentially biasing predictions about past and future trends [e.g., McKane *et al.*, 1997b; Rastetter *et al.*, 1997; Stieglitz *et al.*, 2000]. We present two simulations that demonstrate the utility of the PSM for addressing this assumption and exploring its implications: (1) an arctic “buildup” that simulates the accumulation of ecosystem C and N stocks from the beginning of the current postglacial period to the present, and (2) warming scenarios for the period 2000–2100 to explore potential future states of arctic tundra. Model calibration was based on long-term (1980–2000) measures of soil and plant C and N stocks and fluxes for control (not manipulated) plots at the Toolik Lake site.

#### 3.1. Postglacial “Buildup” of Ecosystem Carbon and Nitrogen Stocks

[10] We assume that rates of change in the contemporary ecosystem (prior to the current warming trend) reflect the trajectory of accumulation in soil and plant C and N stocks following the most recent glacial retreat. This trajectory was inferred through an arctic ecosystem “buildup” that simulates the accumulation of ecosystem C and N stocks from 10,000 yr BP to the present. Temperature for this simulation was held constant at a “combined” air and soil annual growing season temperature of 1°C [Kaufman *et al.*, 2004]. We adjusted the parameters to achieve a buildup trajectory that passed through present control plot measurements, thereby initializing the model for the future climate warming scenarios (Table 1). Control plot targets included mean values for the period 1980–2000 for soil and aboveground plant C and N stocks, and rates of nitrogen uptake and loss. For conditions at 10,000 yr BP we set initial plant available N and soil C stocks at zero and 100 g C m<sup>-2</sup>,

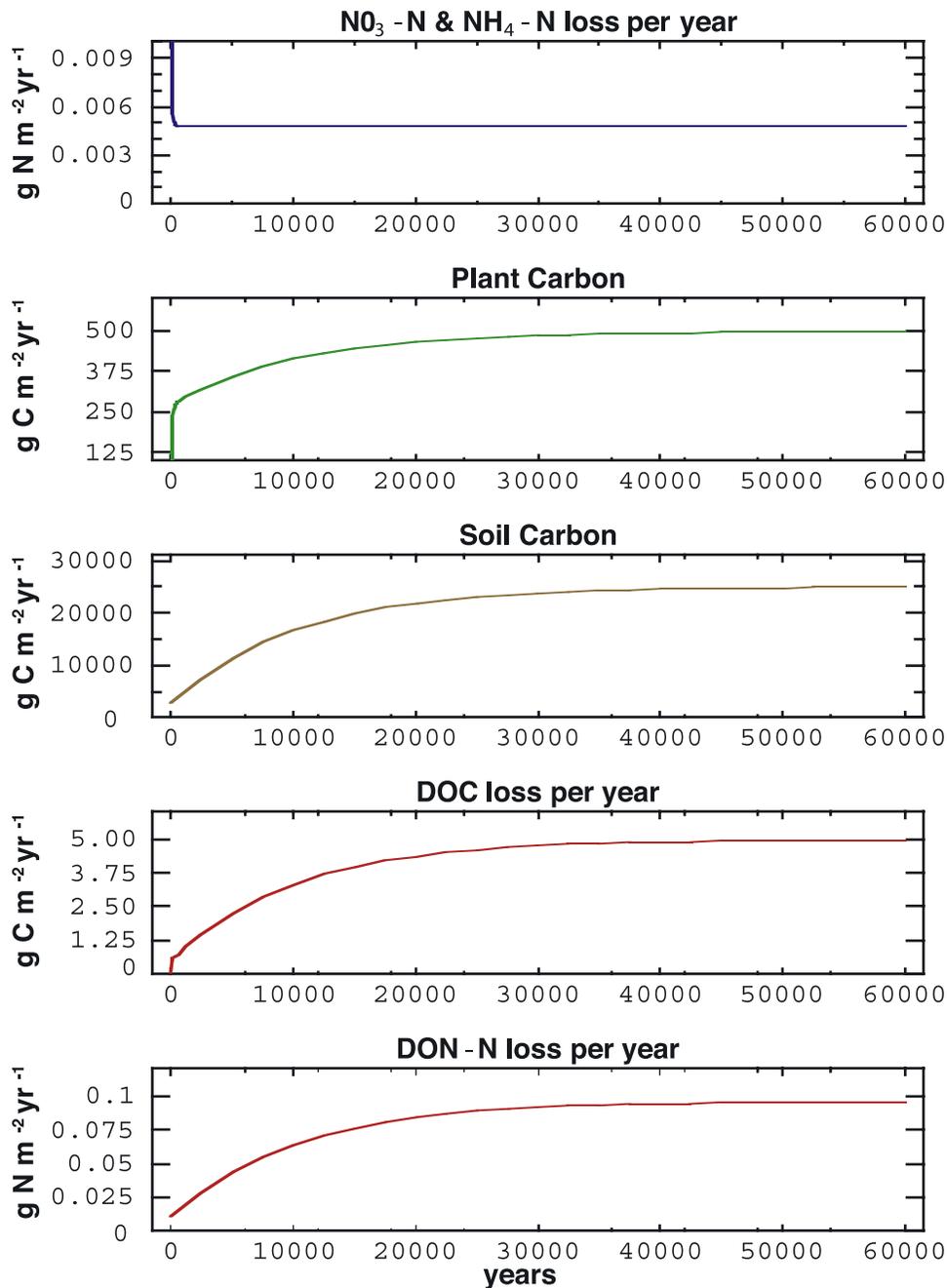
respectively. Overall mortality of tussock forming plants was set at 100 years [Mark *et al.*, 1985; D. Bret-Harte, unpublished data, 2005]. Deposition of atmospheric N was set at 0.1 g m<sup>-2</sup> yr<sup>-1</sup> [Everett *et al.*, 1996], a level consistent with other studies [Peterson *et al.*, 1992; Rastetter *et al.*, 2004], if one assumes that wintertime deposition is not flushed during the spring melt.

[11] Simulated plant and soil carbon stocks increased asymptotically from the beginning of the postglacial period. Carbon stocks after 10,000 yr (i.e., present day) represented ~3/4 of the maximum stocks attainable after 30,000 yr (Figure 1). At the beginning of the simulation, very little DON was lost from the system, as ~90% of total atmospheric N deposition ( $n_{in}$ ) was immobilized in the accumulating pool of soil organic matter (Figure 1). DON losses subsequently increased until after about 30,000 years when losses balanced atmospheric inputs of N to the system. In contrast, plant-available N quickly stabilized after 50 years. After 10,000 years of ecosystem buildup at a constant temperature [Kaufman *et al.*, 2004], plant and soil carbon and nitrogen stocks were near observed values for control plots, and system losses of dissolved carbon and nitrogen closely approximated watershed-scale export to streams [Gough *et al.*, 2002; Kling *et al.*, 1996; Oswood *et al.*, 1996; Peterson *et al.*, 1992; Shaver *et al.*, 2001]. Losses of DOC, DIN and DON were approximately 4 g C m<sup>-2</sup> yr<sup>-1</sup>, 0.005 g N m<sup>-2</sup> yr<sup>-1</sup>, and 0.1 g N m<sup>-2</sup> yr<sup>-1</sup>, respectively. At 10,000 years, aboveground stocks of plant and soil C were approximately 400 and 16,000 g C m<sup>-2</sup>, respectively. It should be noted that whether we initialized soil C at 100 g C m<sup>-2</sup> or 1000 g C m<sup>-2</sup>, the system as a whole still took approximately 30,000 years to equilibrate, and the resulting pool sizes or constituent losses were nearly identical.

#### 3.2. Warming Scenarios

[12] To examine the effects of global warming on arctic tundra, we applied a 5°C warming scenario (ACIA, Arctic Climate Impact Assessment Report, 2004, available at <http://www.acia.uaf.edu>) to the model for the period 2000–2100. We used the simulated results for year 10,000 of the postglacial buildup to establish initial conditions and trajectories for the present-day ecosystem. The effects of temperature on soil and plant processes are simulated directly through equations (1)–(4). However, the effect of temperature on the decomposition of soil C required additional consideration. At this arctic site, for a baseline air temperature of 1°C and warming of 5°C, soil respiration in the PSM is assumed to increase by a factor of 4 [Kirschbaum, 2000; Mack *et al.*, 2004; Mikan *et al.*, 2002]. For simplicity, this was modeled by linearly incrementing  $\nu$  over the 100-year warming period. Because it is reasonable to assume that plant uptake in nutrient-limited systems will keep up with decomposition-driven nutrient mineralization, the parameter  $\mu$  was incremented in a likewise fashion, i.e., by a factor of 4 over the 100-year warming. In section 5 we examine simulation results that are based on a more moderate increase in the rates of soil respiration and nutrient uptake.

[13] We present three warming scenarios that explore the extent to which initial conditions influence future responses

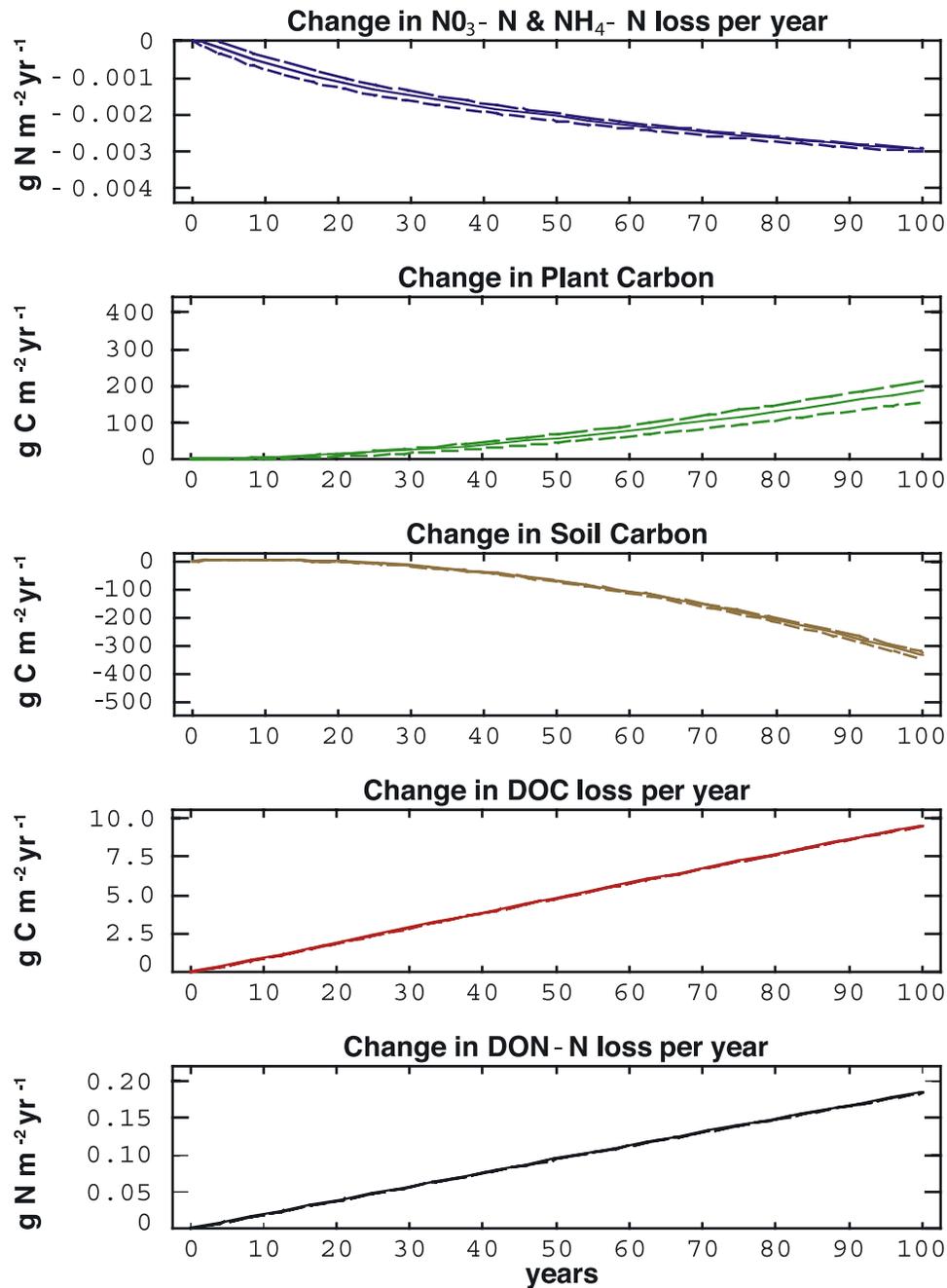


**Figure 1.** Simulated postglacial “buildup” of soil and plant C and N stocks, and losses of recalcitrant DON and DOC, since 10,000 yr BP.

to warming. These scenarios start with initial conditions taken from the built-up, present-day conditions (the non-equilibrium case) or conditions at 20,000 years into the future (equilibrium conditions), and different assumptions about nitrogen loss rates and mortality: (1) Initial C and N stocks represent the 10,000-year built-up values shown in Figure 1, and the DON loss rate is altered by  $\pm 10\%$  around the value used in the buildup simulation (see Figure 2), (2) initial C and N stocks represent the 10,000-year built-up values shown in Figure 1, the DON loss rate is altered by

$\pm 10\%$ , and plant mortality is decreased by 50% (Figure 3), and (3) initial C and N stocks represent the 30,000-year built-up values shown in Figure 1, the DON loss rate is altered by  $\pm 10\%$ , and plant mortality is decreased by 50%, (see Figure 4).

[14] All warming simulations show the same general trends (Figures 2–4). From the onset of warming, plant C increased while soil C decreased, thus reversing the simulated postglacial trend of increasing soil C stocks. After 100 years of warming, losses of soil C slightly exceeded

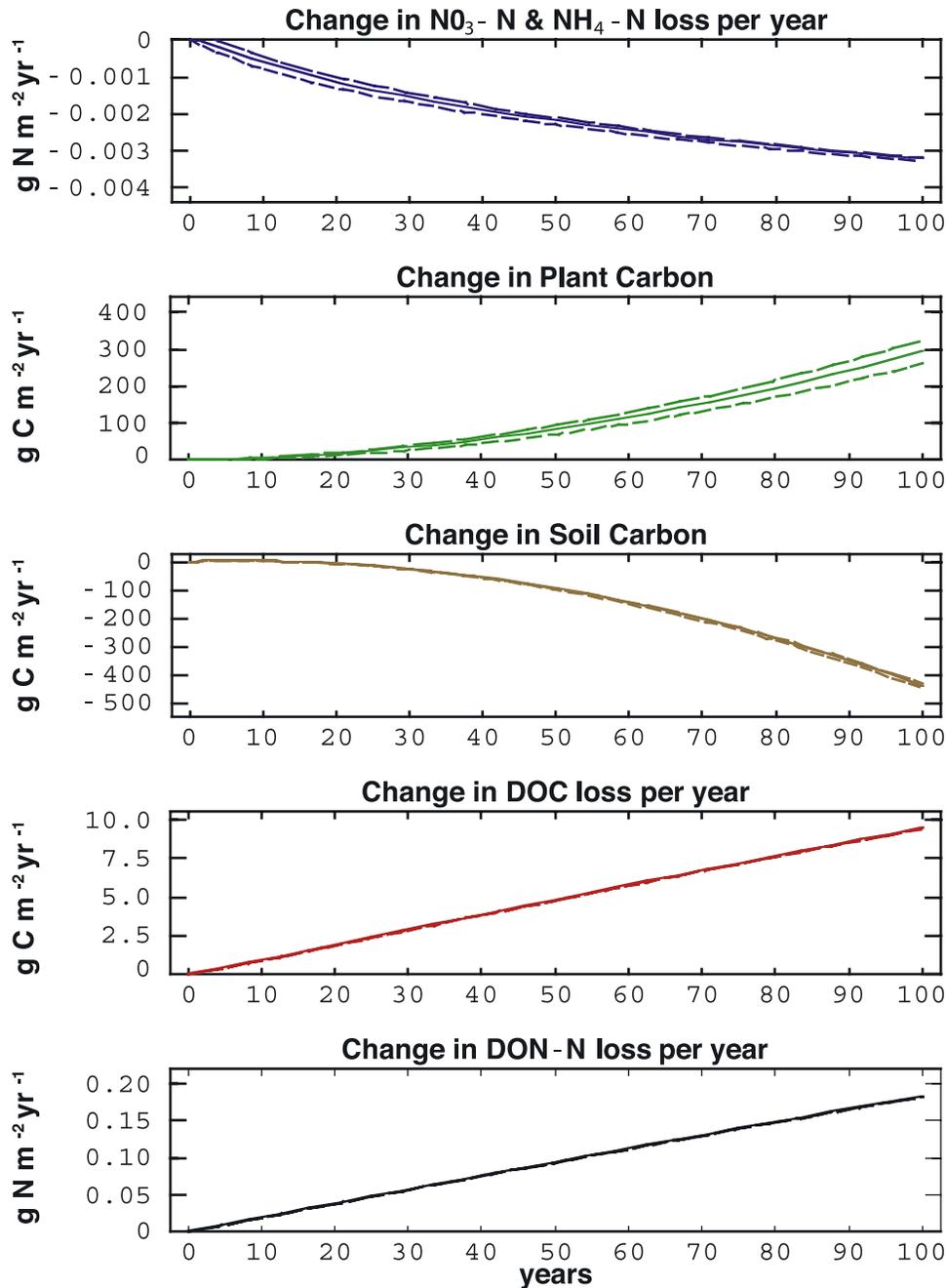


**Figure 2.** Simulated effects of a  $5^\circ\text{C}$  warming for the period 2000–2100. Initial C and N stocks represent the 10,000-year built-up values shown in Figure 1, and the DON loss rate is altered by  $-10\%$  (long-dashed line) or  $+10\%$  (short-dashed line) around the value used in the buildup simulation. Simulated values are changes in C and N stocks ( $\Delta\text{g}/\text{m}^2$ ) and fluxes ( $\Delta\text{g m}^{-2} \text{yr}^{-1}$ ) relative to initial totals.

gains in plant C, resulting in a net decrease in total ecosystem C stocks of  $\sim 1$ – $3$  percent. Warming increased the loss rates of DOC and DON by a factor of  $\sim 2$  to  $4$ . Note that we do not model the loss of C from deeper soils, i.e., the permafrost layer. This would require a more sophisticated treatment of temperature evolution within the active

soil layer. However, loss of C from the large pool of deep soil C could significantly accentuate the overall net loss of ecosystem C in response to the warming.

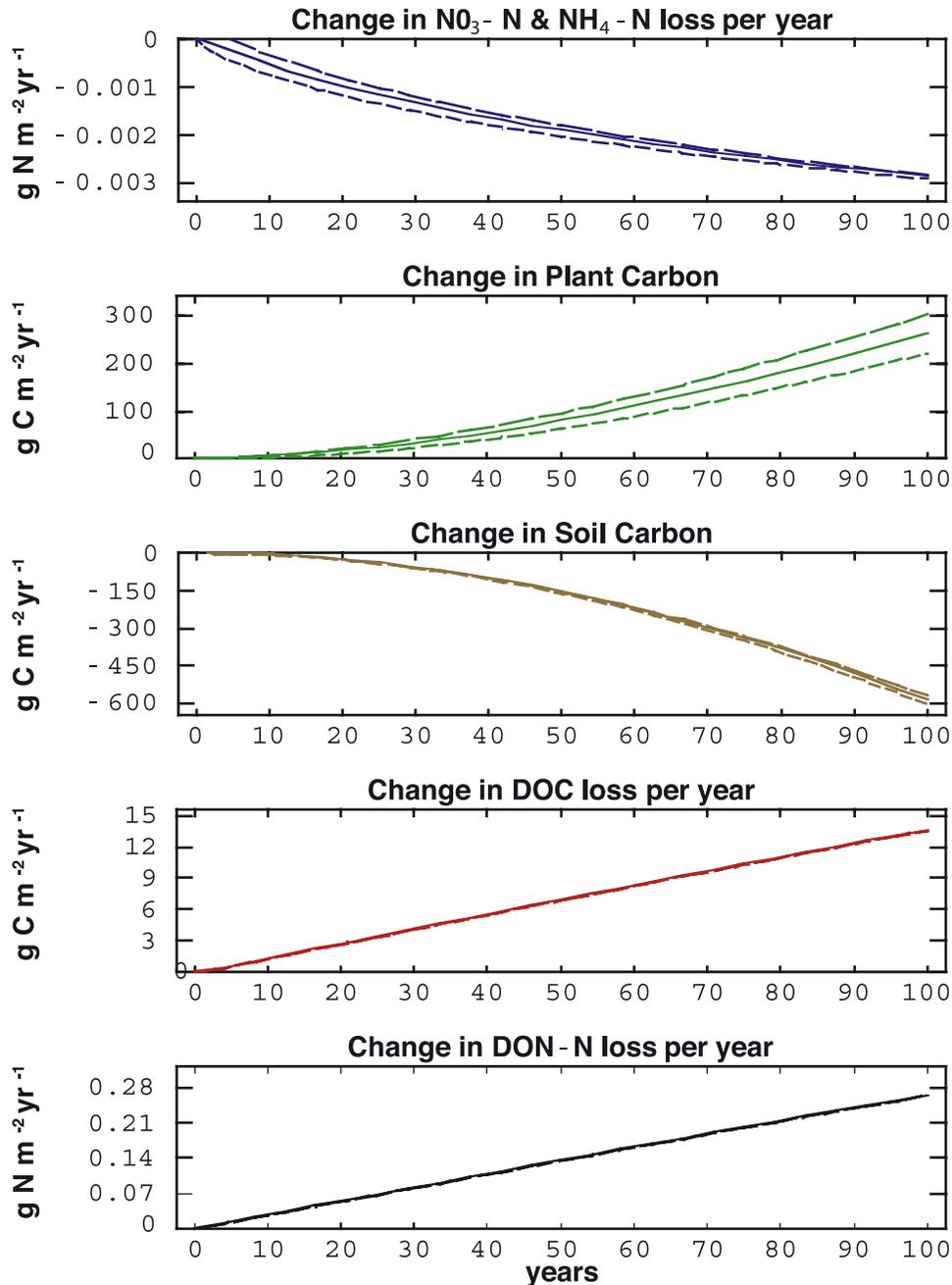
[15] The simulated increase in plant biomass is consistent with observed increases in plant biomass in experimentally warmed and fertilized plots at Toolik Lake [Chapin *et al.*,



**Figure 3.** Simulated effects of 5°C warming for the period 2000–2100. Initial C and N stocks represent the 10,000-year built-up values shown in Figure 1, the DON loss rate is altered by –10% (long-dashed line) or +10% (short-dashed line) around the value used in the buildup simulation, and plant mortality is decreased by 50%. Simulated values are changes in C and N stocks ( $\Delta\text{g}/\text{m}^2$ ) and fluxes ( $\Delta\text{g m}^{-2} \text{yr}^{-1}$ ) relative to initial totals.

1995]. The experimental manipulations of temperature and nutrient availability were intended to simulate anticipated changes in the arctic environment. The increases in plant biomass within these plots were driven in part by a shift in species composition toward shrubby species, especially *Betula nana*. Considering that the overall C:N of tussock

tundra is only marginally less than that of *Betula nana* [Shaver *et al.*, 2001], the near equality of C:N ratios for aboveground plants and soil organic matter should remain essentially unchanged after a shift in species composition. This suggests that our assumption of a constant  $\alpha$  is a

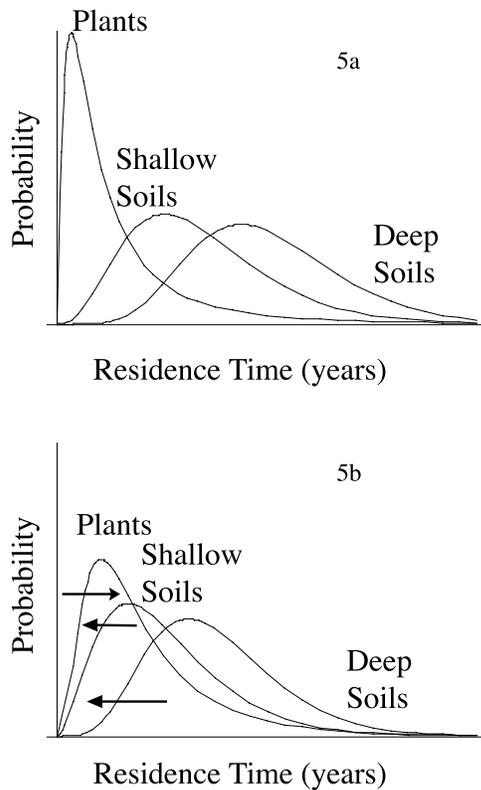


**Figure 4.** Simulated effects of a  $5^\circ\text{C}$  warming for the period 2000–2100. Initial C and N stocks represent the 30,000-year built-up values shown in Figure 1. The DON loss rate is altered by  $-10\%$  (long-dashed line) or  $+10\%$  (short-dashed line) around the value used in the buildup simulation, and plant mortality is decreased by  $50\%$ . Simulated values are changes in C and N stocks ( $\Delta\text{g m}^{-2}$ ) and fluxes ( $\Delta\text{g m}^{-2} \text{yr}^{-1}$ ) relative to initial totals.

reasonable approximation for modeling the effects of warming in this particular ecosystem.

[16] We hypothesized that a shift in species composition toward shrubby species would result in a  $50\%$  decrease in the rate of plant mortality [Mark *et al.*, 1985; D. Bret-Harte, unpublished data, 2005]. This was implemented for the simulations shown in Figure 3 by linearly decreasing

the mortality rate used for Figure 2 over 100 years. The decrease in mortality rate primarily accentuated gains in plant C, by about  $100 \text{ g C m}^{-2}$  or  $50\%$  more than the gains shown in Figure 2. By decreasing inputs of detritus to soil, the lower plant mortality rate increased the loss of soil C to about  $420 \text{ g C m}^{-2}$ , or about  $100 \text{ g m}^{-2}$  more than the loss shown in Figure 2. However, compared to



**Figure 5.** Hypothesized effects of warming on the residence times of C and N in three pools: the plant pool, the shallow (active) soil pool, and the deep soil pool. (a) Assuming current climate conditions. (b) Assuming a warming climate.

initial (present day) stocks shown in Figure 1, the net decrease in soil and ecosystem C stocks was less than 2% and 0.5%, respectively.

[17] Figure 4 also illustrates the effect of a 50% decrease in plant mortality, but with the additional effect of initializing the simulation with modeled values for year 30,000 of the postglacial buildup (Figure 1). Thus, at the onset of warming, initial soil and plant C stocks were about 50% and 20% greater, respectively, than the year 10,000 values used to initialize the simulations for Figures 2 and 3. As a percentage of initial stocks, gains in plant C and losses of soil C are very similar to the results shown in Figures 2 and 3. The only notable differences between the results in Figure 4 and those in Figures 2 and 3 are the >50% increase in the loss rates of DON and DOC.

[18] The above simulations indicate that the current observed “greening” is not a short-term transient due to the warming, but rather the beginning of a more protracted response. Even so, given a warming trend similar to that used in our simulations, net ecosystem C storage is likely to remain within ~1 percent of current values. However, experimental evidence suggests this may be a “best case” scenario, as thawing of permafrost may release significant amounts of deep soil C [Mack *et al.*, 2004]. In addition, as

other models have also predicted [Rastetter *et al.*, 2005], increased leakage of DON will progressively constrain plant growth in this N-limited system, and ultimately constrain the buildup of plant biomass in response to warming. After 100 years of warming, simulated losses of DON were approximately  $0.3 \text{ g N m}^{-2} \text{ yr}^{-1}$ , or 4 times greater than present-day losses.

[19] Our simplified model makes many assumptions. The very nature of choosing a set of parameters and coefficients for decomposition of soil C, loss rates of dissolved organic C and N, etc., determines the residence times of C and N in the ecosystem. Allowing decomposition to vary with temperature renders this residence dynamic. Allowing soil decomposition to increase with increases in air temperature, while at the same time assuming a shift in species composition toward a community having a lower mortality rate, begins to decouple plant and soil C pools. Finally, two fundamentally different warming simulations are conducted, one using initial conditions established after 10,000 and 30,000 years of postglacial buildup, respectively. These two sets of simulations attempt to elucidate the effect of the ecosystem’s initial state and trajectory on the response to warming. We discuss these issues in turn, below, to explore their implications for our modeling exercise and modeling in general.

## 4. Key Issues for Modeling Arctic Plant-Soil Biogeochemical Processes

### 4.1. Plant-Soil System Residence Times

[20] Here we develop a conceptual framework for understanding the dynamics of the plant-soil system in response to climate change. The probability density functions (pdfs) in Figure 5a depict hypothetical residence times of C or N in three distinct pools: a plant pool, a seasonally active (seasonally thawed) soil pool that cycles C and N within itself and the plant pool, and a deep soil pool that is located below the active layer and essentially isolated from the other pools. For each pool, the pdfs show the continuum of residence times, reflecting a wide range of substrates (labile to recalcitrant) and micro-site conditions (e.g., aerobic to anaerobic) that affect turnover rates. For example, within the seasonally active soil layer, decomposition and mineralization rates are fastest near the surface where temperatures are warmest and labile substrates are abundant. Likewise, along a hillslope toposquence, well-drained soils near ridge and midslope locations will experience faster, aerobic decomposition compared to waterlogged, anaerobic soils within the riparian zone. The important point is that for arctic soils, whether one thinks “vertically” or “horizontally,” a continuum of C and N residence times exists. Unfortunately, determining the residence time for arctic soils is not easily quantifiable. If we only include near-surface soils that interact with the plant system, then a soil distribution for residence can be ascertained. However, the inclusion of a noninteractive deeper C pool complicates matters. Much of this soil C is located where temperatures are less than  $0^{\circ}\text{C}$ , and the overall soil residence time is long, but how long? If the active layer deepens in a warmer world, deep C will decompose faster, shortening the overall

soil residence time, but to what extent? The addition of a deep C pool with a very long residence time complicates the issue of defining an overall residence time distribution for the soil system. These and similar uncertainties may best be resolved through a combination of experimental and modeling studies.

#### 4.2. Plant-Soil Synchronicity

[21] The relationship between the residence times of the pools and interaction timescales between pools is an indication of how tightly C and N are retained within the ecosystem. To illustrate, the soil and plant residence times shown in Figure 5a are redrawn in Figure 5b. The arrows in Figure 5b depict opposing shifts in plant and soil residence times in response to warming and suggest a decrease in the synchronicity between plant and soil processes. First and foremost, warmer soil temperatures will increase decomposition and N mineralization, and probably the production of DOC, DON, and DIN, as well. Assuming the soil loss rates of DOC, DON, and DIN are proportional to their respective concentrations, there will be a net loss of soil C and N, unless plant uptake of C and N and production of litter in a warmer world can keep up. If plant uptake of labile N cannot keep up with soil N production, the plant and soil pools will slowly decouple as depicted, perhaps leading to a “leakier” and ultimately, over hundreds of years, a less productive system. This is certainly the case with respect to the deep soil C pool, which may yield the greatest ecosystem loss of C and N when permafrost soils are thawed, decomposed and, in relative isolation from plants, effectively leached from the system. Other aboveground changes may accentuate these effects. If observed trends continue, further arctic warming will be accompanied by an increase in shrubbiness and a lower rate of plant mortality [Mark *et al.*, 1985; D. Bret-Harte, unpublished data, 2005]. Consequent accumulation of C in woody plant tissues and decreased inputs of high-quality litter to soils should promote the decoupling of the plant and soil pools, at least until the system reaches a new equilibrium.

#### 4.3. System Trajectory

[22] Assumptions concerning the initial state of a system influence the calibration of simulation models and, consequently, the accuracy and interpretation of model output. As an example, numerous different ecosystem models have been calibrated for tussock tundra [McKane *et al.*, 1997a, 1997b; Hobbie *et al.*, 1998; Stieglitz *et al.*, 2000; Rastetter *et al.*, 2004]. All of the above were run for tussock tundra at the Toolik Lake Long Term Ecological Research (LTER) Station. Common to all three simulations was the assumption that existing, “present-day” control plots were in equilibrium. That is, on average, net primary production balanced soil heterotrophic respiration. In other words, the models were initialized using a flat trajectory of total ecosystem C. This choice was not made purely for convenience. If the current trajectory of the system is unknown or possibly unknowable, the simplest starting point was chosen, i.e., equilibrium. The problem that this assumption entails is shown in Figure 1. The simulation shows that it takes approximately 30,000 postglacial years for ecosystem

C to reach equilibrium. Assuming that conditions from 10,000 yr BP to the present have been favorable for peat accumulation and net C sequestration [Mann *et al.*, 2002], a model initialized for equilibrium conditions may be starting from an incorrect state. For example, for a historical simulation of change in arctic C storage from the early 1800s to the present, McKane *et al.* [1997b] assumed an ecosystem initially at equilibrium. Their simulation predicted an average net accumulation of  $\sim 2\text{ g C m}^{-2}\text{ yr}^{-1}$  during this period, a rate of C accumulation that is similar in magnitude to our modeled present-day trajectory of ecosystem C storage ( $\sim 0.5\text{ g C m}^{-2}\text{ yr}^{-1}$ ) (Figure 1). Although we do not claim to know what the present-day rate of C storage actually is, this comparison suggests that the choice of an initial condition for a model may produce an error that is within the range of values that the model is being used to address.

### 5. Conclusions

[23] A simple model is developed to explore the impacts of climate warming in tundra regions. Simulations are broadly consistent with (1) previous simulations focusing on tundra plant-soil interaction in a warmer world [McKane *et al.*, 1997b; Rastetter *et al.*, 2004; Stieglitz *et al.*, 2000], (2) a shrubbier future [Sturm *et al.*, 2001], (3) recent findings of Mack *et al.* [2004], and (4) modeling results [Rastetter *et al.*, 2005] that show significant sensitivity of the system to DON loss. However, while the overall result is no significant net loss of ecosystem C, the timing of this is uncertain as we do not fully understand where the system is with respect to its current trajectory. At a minimum, we have attempted to constrain this uncertainty via our sensitivity simulations. One could imagine that this loss of soil C could be ameliorated if nitrogen fixing organisms become more active, but this seems unlikely given that warmer tundra regions dominated by shrubs store considerably less ecosystem C. Further, it should be kept in mind that as the soils warm, the C loss from the deep pool may swamp the combined effects of C-N cycling between the plant and shallow soil system, leading to a combined “greening” of the arctic as well as a significant net loss of soil C. Concerning the model coefficients used in this study, an exhaustive set of sensitivity analyses was not conducted. Altering DON by  $\pm 10\%$  yielded little change in the system trajectory. Varying  $l_n$  by  $\pm 10\%$  (not shown) also had little impact on results. As the model structure does not consider DOC degradable, varying  $l_c$  alters only the catchment retention of DOC, not the trajectory of the plant-soil C storage. For the three warming simulations conducted (Figures 2–4), plant C storage over the 100-year period increased by 200–300  $\text{g C m}^{-2}$  and soil C decreased by 200–600  $\text{g C m}^{-2}$ .

[24] What separates this modeling exercise from others is that we find no need to explicitly model the details of autotrophic respiration or photosynthesis. Assuming a constant ecosystem C/N, we are able to accumulate soil organic carbon and plant biomass with time, as well as account for system losses of DON, DIN, and DOC. We do assume that the primary controlling factor on decomposition is temper-

ature. The next logical progression in this work is to account for the importance of landscape drying on soil decomposition and the subsequent impact this has on soil and plant C and N changes. As yet, however, there is little indication of landscape tundra drying, and only now are large-scale, in situ, experiments being conducted to examine the importance of moisture on decomposition. We acknowledge that while we employed a constant temperature for the initial model spin-up, there were periods such as the Medieval warming anomaly that violate this assumption. However, as it is not clear how the magnitude of this warming translates to arctic regions, and that this spin-up covers a period much longer than the 400 years of warming, we have currently ignored it. Climate scenarios that include such warming and cooling periods could in principle be constructed to explore these potential effects. We have also not considered how the processes of weathering and soil development impact ecosystem carbon storage over long time-scales. Genesis and accumulation of clay particles have a stabilizing effect on soil organic matter, leading to greater retention of C and N [Schimel et al., 1994]. Consequent changes in soil texture and bulk density also affect soil thermal and hydrologic properties. However, the long-term effects of soil development on arctic hydrology and biogeochemical cycling are beyond the scope of the present work. Finally, the simulations conducted here for control plots in tussock tundra at the Toolik Lake LTER should be generally representative of much of the North Slope of Alaska. To simulate pan Arctic responses, however, we would need to consider that the C:N of soil and plant pools differ and that during periods of vegetation change C:N will be variable. We propose that this does not necessitate a more explicit treatment of these effects. Instead, changes in vegetation could be implicitly addressed by allowing for a variable value of  $\alpha$  based on data obtained from harvests of the chronosequence of sites that have shown a shift to shrub dominance.

## Appendix A

[25] The Toolik Lake Long Term Ecologic Research (LTER) Station is located in the northern foothills of the Brooks Range, Alaska (68°38'N, 149°43'W, elevation 720 m). The research site was deglaciated 60,000–100,000 yr BP, following the Iktikik I glaciation [Hamilton, 1986; Walker et al., 1989]. Soils are always moist and vegetation is underlain by a silty mineral soil with a maximum thaw depth of 30–50 cm. Vegetation at the tussock site is dominated by approximately equal biomass of low stature (10–30 cm) rhizomatous sedges (mainly *Eriophorum vaginatum*), deciduous shrubs (mainly *Betula nana*), evergreens (mainly *Ledum palustre. decumbens* and *Vaccinium vitis-idaea*), and mosses (mainly *Sphagnum* spp., *Hylocomium splendens*, and *Aulacomnium* spp.) [Shaver and Chapin, 1991]. Experimental treatments were applied to wet sedge tundra annually, in late May or early June, beginning in 1981: N fertilization; P fertilization; N+P fertilization; warming with field greenhouses; warming and N+P fertilization; and light reduction (50% ambient photon flux density) via shade cloths. Control plots were

also maintained. For each experimental treatment, as well as control plots, aboveground plant biomass measurements were conducted regularly [Bret-Harte et al., 2001; Shaver et al., 2001]. Belowground plant biomass measurements were conducted in 2000 [Mack et al., 2004].

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