

Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks

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Abstract. Assessing potential future changes in arctic and boreal plant species productivity, ecosystem composition, and canopy complexity is essential for understanding environmental responses under expected altered climate forcing. We examined potential changes in the dominant plant functional types (PFTs) of the sedge tundra, shrub tundra, and boreal forest ecosystems in ecotonal northern Alaska, USA, for the years 2003–2100. We compared energy feedbacks associated with increases in biomass to energy feedbacks associated with changes in the duration of the snow-free season. We based our simulations on nine input climate scenarios from the Intergovernmental Panel on Climate Change (IPCC) and a new version of the Terrestrial Ecosystem Model (TEM) that incorporates biogeochemistry, vegetation dynamics for multiple PFTs (e.g., trees, shrubs, grasses, sedges, mosses), multiple vegetation pools, and soil thermal regimes. We found mean increases in net primary productivity (NPP) in all PFTs. Most notably, birch (*Betula* spp.) in the shrub tundra showed increases that were at least three times larger than any other PFT. Increases in NPP were positively related to increases in growing-season length in the sedge tundra, but PFTs in boreal forest and shrub tundra showed a significant response to changes in light availability as well as growing-season length. Significant NPP responses to changes in vegetation uptake of nitrogen by PFT indicated that some PFTs were better competitors for nitrogen than other PFTs. While NPP increased, heterotrophic respiration (R_H) also increased, resulting in decreases or no change in net ecosystem carbon uptake. Greater aboveground biomass from increased NPP produced a decrease in summer albedo, greater regional heat absorption ($0.34 \pm 0.23 \text{ W} \cdot \text{m}^{-2} \cdot 10 \text{ yr}^{-1}$ [mean $\pm$ SD]), and a positive feedback to climate warming. However, the decrease in albedo due to a shorter snow season ($-5.1 \pm 1.6 \text{ d}/10 \text{ yr}$) resulted in much greater regional heat absorption ($3.3 \pm 1.24 \text{ W} \cdot \text{m}^{-2} \cdot 10 \text{ yr}^{-1}$) than that associated with increases in vegetation. Through quantifying feedbacks associated with changes in vegetation and those associated with changes in the snow season length, we can reach a more integrated understanding of the manner in which climate change may impact interactions between high-latitude ecosystems and the climate system.

Key Words: arctic; biogeochemistry model; boreal; climate feedbacks; dynamic vegetation model; future climate; plant functional type; soil thermal model; terrestrial ecosystems.

INTRODUCTION

The Arctic has experienced significant warming in the past three decades, with warming expected to continue through the 21st century (Serreze et al. 2000, Overland et al. 2004). In particular, northern Alaska, USA, has experienced warming by $\sim 0.5^\circ\text{--}1.0^\circ\text{C}/10 \text{ yr}$ during recent years (Serreze et al. 2000). Documented environmental responses to this warming include a decrease in snow cover duration and extent (Dye 2002, Stone et al. 2002, Euskirchen et al. 2006, 2007), a decrease in permafrost stability (Osterkamp and Romanovsky 1999, Jorgenson et al. 2001), and a lengthening of the growing season (Myneni et al. 1997, Smith et al. 2004).

These environmental responses alter the carbon (C) and nitrogen (N) cycling in terrestrial arctic ecosystems, with concurrent shifts in plant species abundance, ecosystem composition, and canopy complexity. These shifts in the overall structure and function of an ecosystem may influence ecosystem energy balance, resulting in feedbacks to the climate system (McFadden et al. 1998, Chapin et al. 2000, 2005, Beringer et al. 2005). While the changes in ecosystem structure may result in feedbacks to climate, changes in snow cover duration and extent may also result in climate feedbacks. The relative responses of climate to future changes in vegetation vs. changes in the snow season in the arctic and boreal ecosystems of northern Alaska remain largely unknown (Chapin et al. 2005, Sturm et al. 2005).

Changes in net primary production (NPP), biomass, and plant species abundance in the vegetation in northern Alaska in response to warming have been

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observed with repeat aerial photography (Tape et al. 2006), satellite studies (Hope et al. 2003, Jia et al. 2003, Stow et al. 2003), and warming experiments (Bret-Harte et al. 2001, van Wijk et al. 2004, Hollister et al. 2005). Repeat aerial photography and remote-sensing studies have documented an expansion of deciduous shrubs in tundra areas in northern Alaska (Hope et al. 2003, Jia et al. 2003, Stow et al. 2003, Tape et al. 2006). Field studies have documented changes in the growth of trees at the tree line and the expansion of the tree line on the Seward Peninsula of Alaska (Lloyd and Fastie 2002, Lloyd et al. 2003). Warming experiments in northern Alaska and other Arctic locations have found differential responses of species to warming. These responses include increases in deciduous shrubs and decreases in lichen and moss (Chapin et al. 1995, Hobbie and Chapin 1998, Bret-Harte et al. 2001, Cornelissen et al. 2001, van Wijk et al. 2004, Hollister et al. 2005, Walker et al. 2006). While some evidence suggests an advance in tree line with warming (Kaplan et al. 2003), other studies have found a decrease in tree growth in response to warming due to temperature-induced drought stress (Barber et al. 2000, Wilkening et al. 2004). These studies point to a complexity of plant responses to climate change, with large uncertainty surrounding the response of vegetation to potential future change in the next century.

Changes in NPP under climate change may be due, in part, to N dynamics and interactions between the C and N cycles. Nitrogen is a limiting nutrient in the Arctic (Shaver and Chapin 1986, Chapin 1991), but greater N mineralization rates may occur with increases in temperature (Binkley et al. 1994, Hobbie 1996), which leads to greater N availability, stimulating plant growth (Shaver and Chapin 1986). Likewise, increases in the growing-season length (Myneni et al. 1997, Euskirchen et al. 2006) may also induce increases in plant growth (e.g., NPP). Increases in plant growth due to greater N availability and a longer growing season may lead to changes in community composition (Chapin et al. 1995, Hobbie and Chapin 1998) and structure. For example, if tall-statured species have greater positive responses to the combined effects of increases in N availability and an increased growing-season length, then they may ultimately exert a large shading effect on the shorter-statured species in an ecosystem. On the whole, future climate changes may then generate dramatic changes in the structure and function of arctic terrestrial ecosystems and therefore also changes in the terrestrial C and N cycles.

The overall change in net ecosystem productivity (NEP) is determined by the difference between NPP and heterotrophic respiration (R_H ; e.g., $NEP = NPP - R_H$). Heterotrophic respiration releases CO_2 to the atmosphere through the decomposition of organic matter. If more CO_2 is released to the atmosphere through R_H than is taken up in NPP, then NEP is negative. Northern soils contain large amounts of organic matter, and soil heterotrophs are generally more responsive to warm temperatures. Consequently, increases in soil tempera-

ture are associated with an increase in soil organic matter decomposition and increased available nutrient supplies, thereby stimulating plant growth (Bonan and Van Cleve 1992, Oechel and Billings 1992). However, it is also possible that increases in N may stimulate decomposition, leading to greater carbon losses (Mack et al. 2004).

Changes in climate have recently impacted, and continue to impact, terrestrial ecosystems in northern Alaska. In this study, we examine future (2003-2100) change in the plant communities in this region. We introduce a new version of a biogeochemistry model, the Terrestrial Ecosystem Model (TEM; version 7.0), that includes soil thermal dynamics, multiple vegetation pools (leaf, wood, and roots), and a dynamic vegetation component (TEM-DVM) that includes competition for light and nitrogen among the plant functional types (PFTs) in an ecosystem (Fig. 1). It is the first time that a dynamic vegetation model has been linked to TEM to incorporate the responses of major PFTs to climate change. Furthermore, this model is unique because it has been developed specifically to take into account terrestrial high-latitude (e.g., arctic and boreal ecosystems) C and N cycling, including feedback between the C and N cycles, permafrost dynamics, and a large number of high-latitude PFTs (a total of 26 in the application presented herein). Our study focuses on the area in northern Alaska extending from the Arctic Ocean to the tundra-boreal forest ecotone, which is dominated by sedge tundra, shrub tundra, and boreal evergreen forests. There is a wealth of field-based data collected from this region, and consequently we are able to explicitly parameterize our model with data for the region's dominant PFTs, including a variety of mosses, sedges, grasses, shrubs, and trees within the three modeled ecosystem types.

In addition to assessing changes in the dominant plant functional types in this region, TEM can also be used to assess potential changes in albedo (reflectance) due to changes in the aboveground biomass of these PFTs. Absorbed energy depends on the albedo of individual leaves. Albedo has been shown to decrease dramatically along the vegetation gradient from tundra to forest due to increasing canopy complexity (Thompson et al. 2004). Decreases in albedo due to increases in vegetation complexity may act as a positive feedback to radiative forcing and amplify atmospheric warming. However, at the same time that decreases in albedo due to increases in biomass may amplify climate warming, climate warming may also be amplified by changes in albedo due to a shorter snow season (Groisman et al. 1994, Euskirchen et al. 2007). This study compares the relative importance of albedo change due to vegetation changes with albedo change due to changes in the length of the snow season in order to gain a better understanding of the possible future feedbacks associated with changes in the land surface cover. Because of the inherent uncertainty in future climate projection, we take a robust

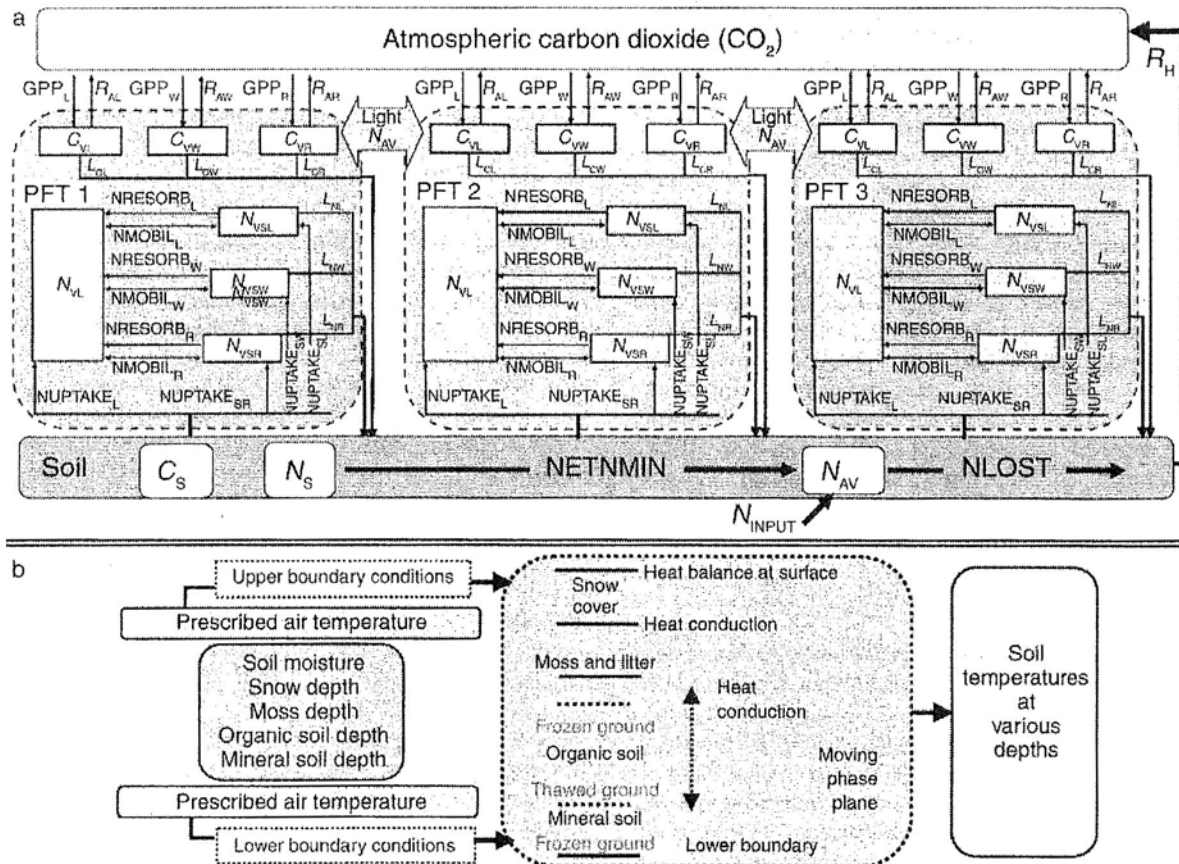


FIG. 1. (a) Conceptual diagram of the dynamic vegetation model (DVM) of the terrestrial ecosystem model (TEM-DVM) with multiple vegetation pools, including the leaf, wood, and root pools. The model in panel (a) is coupled to the soil thermal model (STM) in panel (b). The example in panel (a) shows three plant functional types (PFTs) in a given ecosystem, although the number of PFTs in an ecosystem may be either more or less in model applications. The arrows with "light" and "N" between the PFTs illustrate that competition occurs between the PFTs, as described in *Methods: Description of the model components*. . . Abbreviations are: R_H , heterotrophic respiration; GPP_L , GPP_W , GPP_R , gross primary productivity of the leaves, wood, and roots, respectively; R_{AL} , R_{AW} , R_{AR} , autotrophic respiration from the leaves, wood, and roots, respectively; C_{VL} , C_{VW} , C_{VR} , carbon in living vegetation in the leaves, wood, and roots, respectively; L_{CL} , L_{CW} , L_{CR} , litterfall carbon from the leaves, wood, and roots, respectively; N_{VL} , nitrogen in living vegetation of the leaves; N_{VSL} , N_{VSW} , N_{VSR} , structural nitrogen in living vegetation of the leaves, wood, and roots, respectively; $NRESORB_L$, $NRESORB_W$, $NRESORB_R$, nitrogen resorption by the leaves, wood, and roots, respectively; $NMOBIL_L$, $NMOBIL_W$, $NMOBIL_R$, mobile nitrogen in the leaves, wood, and roots, respectively; $NUPTAKE_L$, total nitrogen uptake by the leaves; $NUPTAKE_{SL}$, $NUPTAKE_{SW}$, $NUPTAKE_{SR}$, structural nitrogen uptake by the leaves, wood, and roots, respectively; L_{NL} , L_{NW} , L_{NR} , litterfall nitrogen in the leaves, wood, and roots, respectively; C_S , soil carbon; N_S , soil nitrogen; NETNMIN, net nitrogen mineralization; N_{AV} , total available nitrogen; NLOST, nitrogen lost from the ecosystem; N_{INPUT} , nitrogen inputs into the ecosystem.

approach to the issue of future change by driving our simulations with the output of three global climate models under three different climate change scenarios (nine total climate scenarios; Fig. 2) into our analyses. We ask the following questions, based on arctic and boreal ecosystems in northern Alaska between the years 2003–2100: (1) How does NPP change across the dominant PFTs under changes in climate (e.g., changes in growing season length) and competition for nitrogen and light? (2) Given these changes in NPP, do we also see changes in R_H , NEP, and the pools of vegetation C and soil C? (3) Finally, what are the relative effects of changes in vegetation structure and changes in snow cover on atmospheric heating?

METHODS

Overview

We evaluated how changes in atmospheric CO_2 concentrations and climate may alter terrestrial ecosystem net carbon uptake (e.g., NEP), ecosystem structure, and the snow season in northern Alaska using a new version of the Terrestrial Ecosystem Model (TEM, version 7.0; Fig. 1) with a dynamic vegetation component (TEM-DVM). Unlike previous versions of the model, this version of TEM takes into account multiple vegetation pools, soil thermal regimes, and plant functional types that compete for nitrogen and light. Following model calibration, we performed nine model

simulations for the years 1901–2100 and analyzed the data between 2003 and 2100. While each model simulation used the same input climate data for the historical period, 1901–2002, nine different flume climates were used for the years 2003–2100. We then examined changes in regional C dynamics including stratifications by PFT and ecosystem type. We calculated summer changes in albedo, radiation, and the fractions of latent heat and sensible heat to net radiation based on changes in aboveground biomass. We also determined the day of snowmelt and snow return. Using our calculations of changes in the latent heat fraction, sensible heat fraction, net radiation fraction from changes in biomass, and the changes in the snow season, we were able to compute the relative climate feedbacks from both changes in vegetation and changes in snow cover.

Description of the model components: the Terrestrial Ecosystem Model with dynamic vegetation and multiple vegetation pools

A complete description of the TEM-DYM and the model parameters is provided in Appendix A. Here we briefly describe the conceptual design of the model, including the underlying equation for gross primary productivity (GPP) and interactions among PFTs for light and N. An ecosystem is assumed to be composed of several PFTs that obtain nitrogen from a single soil-available nitrogen pool and contribute carbon and nitrogen to a single soil organic carbon and nitrogen pool, respectively (Fig. 1a). The PFTs and the number of PFTs may vary among ecosystem types. The biogeochemistry component of the model simulates the monthly fluxes and pools of C and N for the wood, leaf, and root components of each PFT in an ecosystem (Fig. 1a). Carbon assimilation of a PFT is represented by the flux of gross primary productivity, which is allocated to the leaf (L), wood (W), and root (R) tissues of the PFT. The gross primary productivity of a PFT (GPP_{PFT}) is a function of the maximum rate of C assimilation (C_{max}), moderated by several scalars:

$$GPP_{PFT} = C_{max} f(CO_2) f(PAR) f(T) f(G_v) f(LEAF) \times f(FOLIAGE) f(THAWPCT) f(FPC) f(N_{AV}) \quad (1)$$

where $f(CO_2)$ is a function of the atmospheric CO_2 concentration, $f(PAR)$ is a function of photosynthetically active radiation, and $f(T)$ is a function of the monthly mean air temperature. The effects of elevated atmospheric CO_2 directly affect $f(G_v)$, where G_v is relative canopy conductance, by altering the intercellular CO_2 of the canopy (McGuire et al. 1997). Precipitation also influences $f(G_v)$ through the effects on estimated evapotranspiration. The function $f(LEAF)$ is monthly leaf area relative to leaf area during the month of maximum leaf area. This depends on monthly estimated evapotranspiration, air temperature, and the previous month's photosynthetic capacity to describe the seasonal

changes in the vegetation's capacity to assimilate C (Raich et al. 1991). The scalar function (FOLIAGE) ranges from 0.0 to 1.0 and represents the ratio of canopy leaf biomass relative to maximum leaf biomass (Zhuang et al. 2002). The function $f(THAWPCT)$ is a freeze/thaw index that calculates the proportion of the month that the soil is either frozen or thawed using simulated soil temperatures at 10-cm depth (Euskirchen et al. 2006). The 10-cm depth is used since previous analyses with TEM showed that the timing of thaw at this depth agreed well with the onset of photosynthesis for ecosystems above 30°N. Growing-season length is calculated from $f(THAWPCT)$ based on the combination of the frozen and nonfrozen months (Euskirchen et al. 2006). The function $f(FPC)$ represents the effect of competition among PFTs for light based on foliar projected cover (FPC). In TEM, $f(N_{AV})$ is dynamically calculated to model the limiting effects of plant N status on GPP based on a comparison of N availability and N demand (McGuire et al. 1992, Pan et al. 1998). Additional details about the calculation of GPP can be found in Tian et al. (1999), Zhuang et al. (2003), and Euskirchen et al. (2006).

A key limiting factor in the growth of arctic vegetation is N availability, i.e., inorganic N in the soil solution (Shaver and Chapin 1986, Chapin 1991), while light availability is also a key component of PFT interactions in canopied vegetation (Hart and Chen 2006). In TEM-DVM, we have implemented GPP_{PFT} to first consider interactions among PFTs for light and then to consider how interactions among PFTs for N availability limit GPP_{PFT}. In the TEM-DVM, shorter stature vegetation competes with the taller stature vegetation for light. This is modeled with an implementation of Beer's Law based on foliar projected cover (FPC; Haxeltine and Prentice 1996, Pan et al. 2002). The FPC is a conversion of leaf area index and describes the effect of foliage on NPP. While large plants may decrease the growth of smaller plants, the competition may also result in mutual inhibition of growth by plants of the same stature. The total FPC is constrained to be less than or equal to one. If FPC is less than one, then there is no competition for light. If FPC is calculated to be greater than one, then the taller stature PFTs (e.g., trees in the boreal forest, shrubs in the tundra) have a competitive advantage over the shorter stature PFTs (e.g., grasses and sedges). Consequently, the FPC is reduced in equal proportions among the shorter stature PFTs such that the total FPC does not exceed one (see Appendix A for details). When light competition occurs among vegetation with the same stature (e.g., grasses and sedges), the equivalent proportion of FPC is reduced to meet the total FPC constraint (Sitch 2000).

The gross primary productivity of each PFT in TEM is limited by N availability by downregulating GPP_{PFT} of all PFTs based on a comparison of N demand and N supply in the ecosystem. Nitrogen demand in the ecosystem is the amount of N required to build new

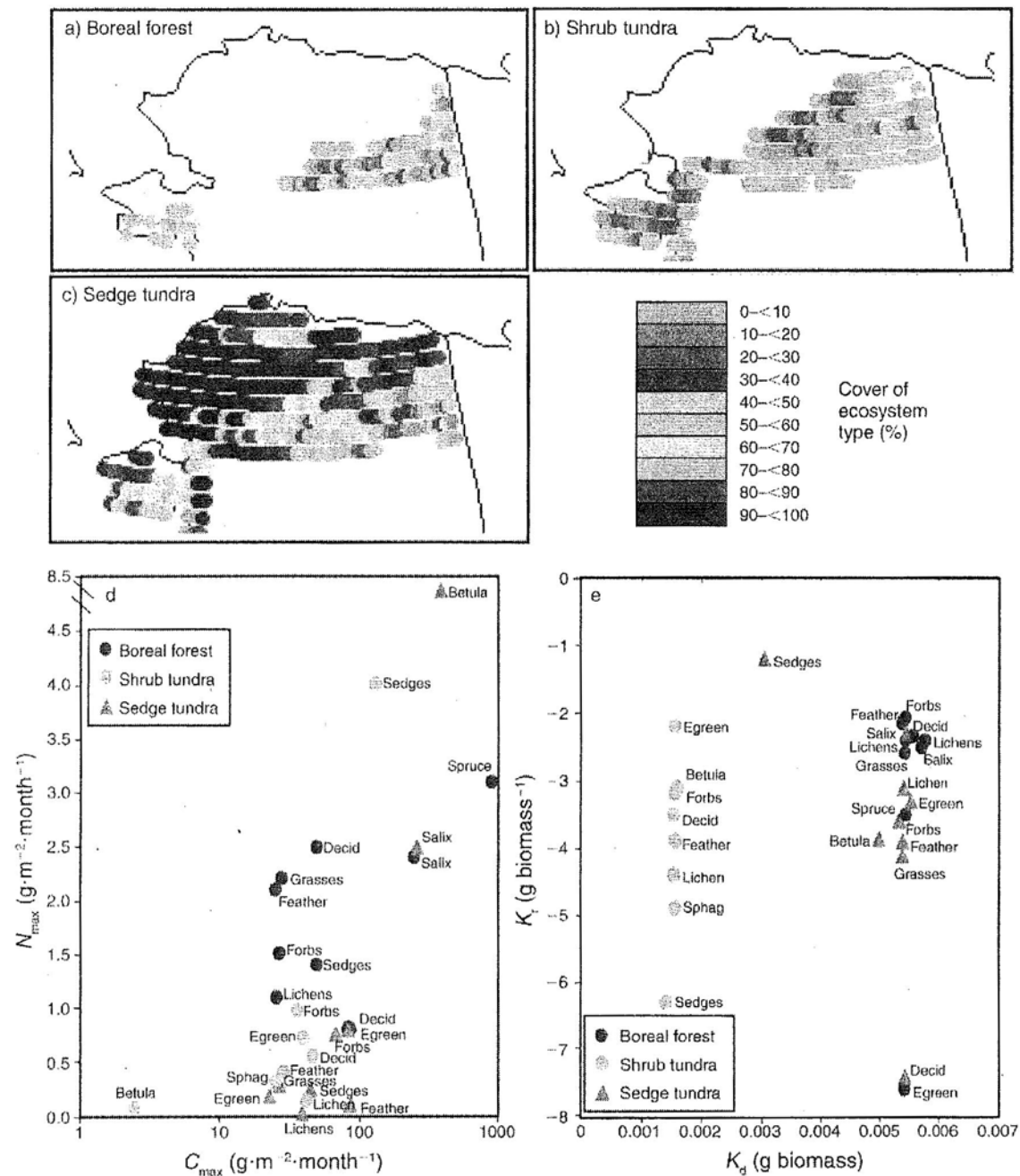


FIG. 2. (a-c) Map of the study region in northern Alaska, USA, and the corresponding percent cover of each of the three ecosystem types. (d, e) Each ecosystem contains eight to nine plant functional types that are parameterized according to the ecosystem in which they are located. Abbreviations are: $C_{\max}$, maximum rate of photosynthesis; $N_{\max}$, maximum rate of N uptake; K_t , heterotrophic respiration rate at 0°C; K_g , the per-gram-biomass autotrophic respiration rate of the vegetation at 0°C; Decid, deciduous shrubs; Egreen, evergreen shrubs; Spagh, Sphagnum moss; Feather, Feathermoss.

tissue based on the sum of GPP_{PFT} for $f(\text{NAV}) = 1$, i.e., no N limitation to C assimilation, across all PFTs in the ecosystem. The amount of N required to build new tissue in a PPT depends on production C:N ratios for leaf, wood, and roots of the PFT that are estimated from field data (see Appendix A: Tables A2-A4). Nitrogen

supply in the ecosystem is the sum of N uptake ($\text{NUPTAKE}_{\text{PFT}}$) across all PFTs plus the sum of N in the vegetation labile nitrogen pool (NVL in Fig. 1a) across all PFTs. Nitrogen uptake across all PFTs is a function of soil moisture (MOIST), air temperature (T), NAV , the maximum rate of N uptake by the vegetation

($N_{\max}$), a parameter accounting for the influence of soil moisture conditions on N movement through the soil (K_s), a half-saturation constant for N uptake (k_n), normalized leaf phenology (LEAF), fine-root biomass (N_{Vsr}), and the Q10 value of root respiration (RESPQ_{10R}):

$$\text{NUPTAKE}_{\text{PFT}} = f(\text{MOIST})f(T)f(N_{\text{AV}})f(N_{\max}) \\ \times f(K_s)f(k_n)f(\text{LEAF})f(N_{\text{Vsr}})f(\text{RESPQ}_{10R}). \quad (2)$$

If the sum of $\text{NUPTAKE}_{\text{PFT}}$ across all PFTs exceeds N_{AV} , the $\text{NUPTAKE}_{\text{PFT}}$ of each PFT is downregulated by the same proportion so that N_{AV} is not depleted. If N demand is greater than N supply, then GPP_{PFT} is decreased in equal proportions for each PFT.

Soil thermal dynamics

The TEM is coupled to a soil thermal model (STM; Zhuang et al. 2001) that is based on the Goodrich model (Goodrich 1976) and uses a finite element approach to determining heat flow in soils (Fig. 1b). The model is appropriate for both permafrost and non-permafrost soils. The STM receives monthly, gridded estimates of air temperature, soil moisture, and snowpack from the water balance model in TEM. These estimates of snowpack are a function of elevation as well as monthly precipitation and have an influence on the soil moisture in the water balance model of TEM. Snowpack accumulates whenever mean monthly temperature is below -1°C , and snowmelt occurs at or above -1°C . At elevations above 500 m, the melting process requires two months above -1°C , with half of the first month's snowpack retained to melt during the second month (Vorosmarty et al. 1989).

Snow cover

The model includes an algorithm to estimate the date of snowmelt (or snow return) from the monthly estimates of snowpack. We incorporated an algorithm that uses a "ramp" between monthly temperatures (Euskirchen et al. 2007). Linear interpolations of data for monthly air temperature and the month(s) preceding snowmelt (or snow return), the month of snowmelt (or snow return), and the month following snowmelt (or snow return) are performed. For example, to calculate the date of snowmelt when all snow has disappeared by April, approximately 30 points are interpolated between mean monthly March and April air temperature to determine the 15 points for the first half of April and approximately 30 points are interpolated between mean monthly air temperature in April and May to determine the 15 points for the second half of April. The length of the snow-free season is calculated by subtracting the Julian date of snowmelt from the Julian date of snow return. As discussed in Euskirchen et al. (2006, 2007), the model estimates of the spatial extent and the temporal dynamics of snow cover are in agreement with those of Dye (2002).

Model parameterizations

The model is parameterized with both field-collected data and those obtained through a calibration process for the three dominant ecosystem types (sedge tundra, shrub tundra, and boreal forest; Fig. 2a-c) found in northern Alaska. Each ecosystem type is assumed to be comprised of eight to nine PFTs: *Betula* spp., deciduous shrubs other than *Betula*, evergreen shrubs, sedges, forbs, lichen, feathermoss, and Sphagnum moss for sedge tundra; *Salix* spp., *Betula* spp., deciduous shrubs other than *Betula* and *Salix*, evergreen shrubs, sedges, forbs, lichen, and feathermoss for shrub tundra; and spruce, *Salix* spp., deciduous shrubs (which includes *Betula* spp., but not *Saxifraga*, since the maximum number of PFTs that can be included in the model is nine per ecosystem type), evergreen shrubs not including spruce, sedges, forbs, lichen, and feathermoss for boreal forest. While the ecosystems may contain the same type of PFT, the PFTs are parameterized differently depending on the ecosystem in which it is located so that northern Alaska is assumed to be covered by a total of 26 PFTs in our simulations.

The field-collected data used in this study were collected at representative sites in northern Alaska. The sedge tundra parameterization is based on data collected in Ivotuk Alaska (68.5°N , 155.5°W), and the shrub and boreal forest parameterizations were based on data collected at field sites near Council, Alaska (64.5°N , 163.41°W). Each of these sites and the data collection methodology are described further in Thompson et al. (2004, 2006). Generally, the vegetation productivity data were based on measurements performed during the midsummer months, with harvests of the vegetation performed during late summer and later analyzed for concentration of C and N. Soil C and N data were sampled at the same sites (Michaelson and Ping 2003). Grouping of the PFTs were chosen based on the dominant vegetation classes in the region (Thompson et al. 2004). For these TEM simulations, we used the same vegetation and soil parameterizations as those used in the retrospective analysis of Thompson et al. (2006). However, while Thompson et al. (2006) estimated plant C and N fluxes and pools for each plant tissue (leaf, wood, and roots) for each PFT and then modeled variations in the aggregated sum of these components (i.e., vegetation carbon) for their simulations, here we explicitly model the leaf, wood, and root fluxes and pools of C and N for each PFT (Fig. 1a; Appendix A).

While most of the model parameters are assigned from the field-collected data, some of the parameters are calibrated to the C and N pools from the field-based studies (Appendix A; Tables A2–A4). In the calibration process (Raich et al. 1991, McGuire et al. 1992), rate-limiting parameters for GPP ($C_{\max}$ in Eq. 1), autotrophic respiration (R_a), heterotrophic respiration (R_h), maximum plant N uptake ($N_{\max}$), N in litter production, and soil C and N immobilization are adjusted until model values match the field-based estimates of GPP,

NPP, N uptake, and vegetation and soil C and N pools (Fig. 2d, c; Appendix A: Tables A2-A4). These adjusted rate-limiting parameters and field-based estimates of GPP, NPP, N uptake, and vegetation and soil C and N pools are then used to initialize the model simulations. In this version of the model, the PFTs are calibrated relative to one another in terms of monthly N uptake.

Input data sets

The application of the model requires input data sets of vegetation distribution, soil texture, elevation, atmospheric CO₂ concentration, and climate. In this study, we drove the model with input data sets gridded at half-degree resolution (0.5° latitude X 0.5° longitude). The input vegetation map used in this study is the same as that used in Thompson et al. (2006), with each of the 418 half-degree grid cells in this region classified as a certain percentage of sedge tundra, shrub tundra, and forest. This vegetation map combines several 1-km resolution maps for the North Slope (Muller et al. 1999), Seward Peninsula (available online)⁵ and areas not considered in these two maps (available online)⁶. Each 1-km pixel was reclassified as tundra, shrub, or forest (Thompson et al. 2006). The northern Alaska region is classified as approximately 79% sedge tundra, 13% shrub tundra, and 8% boreal coniferous forest (Fig. 2a-c). The input soil texture and elevation data sets are also the same as those used in Thompson et al. (2006). We drove the model with observed CO₂ data for the historical period of our simulations (1901-2002) based on Keeling et al. (1995, updated); which reached 372 parts per million by volume (ppmv) in 2002. Each future scenario included projections of atmospheric CO₂ starting from 372 ppmv in 2003 and increasing to the magnitude of warming in year 2100 for the given scenario: to ~800 ppmv in the warmest climate (A2 scenario), to ~555 ppmv in the coolest climate (B1 scenario), and to ~600 ppmv in the "intermediate" climate (B2 scenario). Each scenario is available from the International Panel on Climate Change (IPCC) Data Distribution Center (available online⁷ see also Nakicenovic and Swart 2000).

We chose three future climate scenarios described in Nakicenovic and Swart (2000) and three of the modeled global climate model (GCM) outputs for use as input climate data. The scenarios we chose were the A2, B1, and B2. Of these three scenarios, the A2 scenario includes the greatest accumulated radiative forcing and exhibits the fastest rate of warming. The B2 scenario exhibits less accumulated radiative forcing than the A2 and a slightly slower rate of warming, while the B1 scenario exhibits the least amount of radiative forcing and the slowest rate of warming (IPCC 2000, Nakicenovic and Swart 2000). We chose three GCMs (Commonwealth Scientific and Research Organization

general circulation model version 2 [CSIRO2], The Hadley Centre for Climate Prediction and Research general circulation model version 3 [HadCM3], and a parallel climate model [PCM]) that represented a range of sensitivity to greenhouse gas forcing (Fig. 3). Generally, within each scenario, the CSIRO2 corresponded to a relatively high estimate in temperature increase, the HadCM3 represented a medium estimate, and the PCM represented a low estimate for each scenario (Fig. 3a). Thus, the combination of scenarios and models permits a robust analysis of potential future response of terrestrial ecosystems to climate change.

We downloaded the monthly data for air temperature, precipitation, and cloudiness from the IPCC Data Distribution Center (see footnote 7). Since the outputs from the GCMs are not matched directly to historical climate, we matched the projections to the historical climate record to ensure that there was continuity in the time series using baseline observational data. We overlaid the projected changes in climate on the mean historical climate based on the period 1961-1990 using the database of historical climate obtained from the Climate Research Unit (CRU), which includes precipitation, air temperature, and cloudiness data for the years 1901-2002 (New et al. 2002, Mitchell and Jones 2005). The absolute differences in mean monthly temperatures and the ratios in monthly precipitation and monthly mean cloudiness for 1961-1990 were then calculated, with the baseline values corresponding to the simulated climate from the GCMs.

Since this procedure resulted in "smooth curves" of changes in temperature, cloudiness, and precipitation for the future scenarios, we then added interannual variability to the future climate. We did this by randomly picking a sequence of years within the 1901-2002 CRU period, using the same seed for all half-degree grid cells so each cell used the same sequence of years. We calculated the mean value for the CRU period for each of the grid cells and then computed scenario change for each GCM scenario as: (GCM scenario value for location)/(mean value for location). Finally, the forecasted value for each grid cell was calculated as (value from random base year) X (scenario change). The modeling results from the "smoothed data" and those with interannual variability added both show the same amount of change for all three of the climate variables, air temperature, precipitation, and cloudiness, by the end of 2100. To determine significant differences ($P < 0.0001$) between the climate data sets, we performed least-squares linear regression of seasonal and annual means of air temperature, precipitation, and cloudiness by year (Fig. 3).

Climate trend,

The mean annual air temperature between 2003 and 2100 over the domain significantly ($P < 0.0001$) increased in all scenarios, with a maximum change of +0.12°C/yr in the A2 CSIRO2 climate and a minimum

⁵ <http://www.arcticatlas.org/atlas/aatvm/aatvmvg/g42>

⁶ <http://agdc.usgs.gov/data/projects/hlct/hlct.html#K>

⁷ <http://www.ipcc-data.org/>

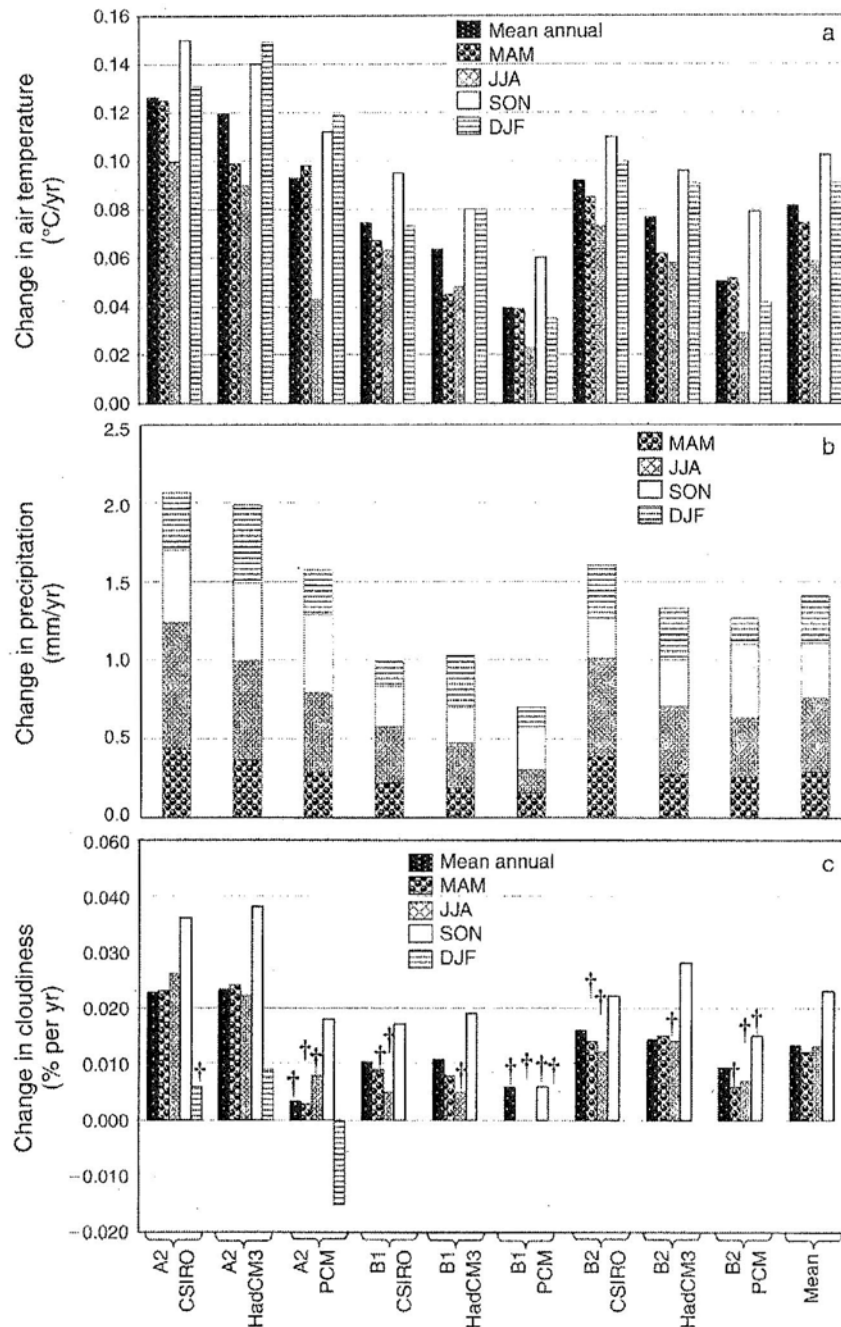


FIG. 3. Trends in air temperature, precipitation, and cloudiness in northern Alaska during 2003–2100 based on three climate models (CSIRO2, HadCM3, and PCM) and scenarios (A2, B1, and B2). See *Methods: Input data sets* for an explanation of the climate models and scenarios. Trends are based on the slopes of least-squares linear regression. All trends in air temperature and precipitation were statistically significant at $P < 0.0001$. Cloudiness trends marked with a dagger were not statistically significant at $P < 0.0001$. “Mean” refers to the mean across all scenarios and climate models. Abbreviations are: MAM, March, April, and May; JJA, June, July, and August; SON, September, October, and November; DJF, December, January, and February.

change of $+0.04^{\circ}\text{C/yr}$ in the B1 PCM climate (Fig. 3a). Across all climates, air temperature increases were greater in the fall (September, October, November; SON) and the winter (December, January, February; DJF) than in other seasons. Precipitation also significantly ($P < 0.0001$) increased across all climates, with

the greatest increases (~ 2.0 mm/yr) occurring in the A2 CSIRO2 and A2 HadCM3 climates and the smallest increases (0.75 mm/yr) occurring in the B1 PCM climate (Fig. 3b). Across all climates, precipitation increases were greatest in the summer (mean of 0.48 mm/yr occurring as rain in June, July, August: JJA) and

smallest in the spring (0.29 mm/yr occurring as either rain or snow in March, April, May; MAM) and winter (0.30 mm/yr occurring as snow in DJF). Mean percentage of cloudiness also increased across all climates, although this increase was not always statistically significant ($P > 0.01$). Changes in cloudiness were near zero during DJF in all of the B1 and B2 climates. Cloudiness increases were greatest during SON for all climates.

Vegetation albedo and climate feedbacks

We also assessed potential changes in albedo due to changes in vegetation biomass and feedbacks to climate. Strong predictive relationships between albedo and vegetation biomass have been developed for this region in northern Alaska based on summer vegetation biomass (Thompson et al. 2004). The relationship is nonlinear, with albedo and the heat fluxes showing the greatest sensitivity to lower levels of biomass:

Summer albedo

$$= [1 \times 2^{-9} (\text{above ground biomass})^2] - [1 \times 3^{-5} (\text{above ground biomass})] + 0.21$$

$$(R^2 = 0.99, P < 0.0001). \quad (3)$$

Decreases in albedo due to changes in vegetation may act as a positive feedback to radiative forcing and amplify atmospheric warming. To quantify this change in atmospheric heating due to changes in vegetation, we used predictive equations based on the data of Thompson et al. (2004) to determine changes in the partitioning of energy fluxes based on changes in biomass. These included the ratio of net radiation (R_N) to incoming solar radiation (R_s), the ratio of latent energy (LE) to R_N , and the ratio of sensible heat (H) to R_N . These equations also show greater sensitivity at lower levels of biomass. From the tundra to the forest, R_N , LE, and H fractions increase:

Summer net radiation fraction (R_N/R_s)

$$= [1 \times 2^{-6} (\text{aboveground biomass})^2] + [0.0194 (\text{aboveground biomass})] + 78.628$$

$$(R^2 = 0.84, P < 0.0001) \quad (4)$$

Summer latent heat fraction (LE/R_N)

$$= [1 \times 4^{-7} (\text{aboveground biomass})^2] + [0.0043 (\text{aboveground biomass})] + 39.966$$

$$(R^2 = 0.89, P < 0.0001) \quad (5)$$

Summer sensible heat fraction (H/R_N)

$$= [1 \times 9^{-7} (\text{aboveground biomass})^2] + [0.0099 (\text{aboveground biomass})] + 34.048$$

$$(R^2 = 0.93, P < 0.0001) \quad (6)$$

We converted the estimates of aboveground vegetation C into biomass by summing the leaf and wood pools for each PFT and then multiplying by two to obtain aboveground biomass (in grams per square meter), assuming a conversion factor of two between vegetation C and biomass.

We also calculated R_s in TEM for each half-degree grid cell. These estimates are based on the methodology of Turton (1986) and are attenuated by the input cloud cover with a correction based on that described in Chang (1968). Following methodology similar to that of Chapin et al. (2005) and Euskirchen et al. (2007), we estimated seasonal atmospheric heating for each vegetation type in each half-degree grid cell by multiplying R_s by the proportion of incoming R_s that is absorbed by the land surface (R_N/R_s) times the proportion of R_N that is transferred to the atmosphere ($(H + LE)/R_N$).

Changes in albedo and atmospheric heating due to changes in the snow season

We also estimated changes in atmospheric heating due to changes in the length of the snow season, in terms of both snowmelt in the spring and snow return in the fall. Our estimates of changes in heating due to changes in snow cover follow the methodology outlined in Euskirchen et al. (2007). We use TEM-derived values of R_s and literature-derived values of heat fluxes, with the literature-derived values of the heat fluxes being the same as those in Table 1 in Euskirchen et al. (2007) for the sedge tundra, shrub tundra, and boreal evergreen needleleaf forest. As above, we multiply R_s by the proportion of incoming R_s that is absorbed by the land surface (R_N/R_s) times the proportion of R_N that is transferred to the atmosphere ($(H + LE)/R_N$). We then compare pre- and post-snowmelt and pre- and post-return energy budgets to estimate the changes in snowmelt and snow return on atmospheric heating: {[daily atmospheric heating post-snowmelt (or pre-snow return)] -- [daily atmospheric heating pre-snowmelt (or post-snow return)]} $\times$ [change in snow cover duration], where the daily atmospheric heating is in units of megajoules per square meter per day and the change in snow cover duration is in days per year. The estimates of heating are then averaged over the length of the snow-free season, as calculated in the water balance model. Estimates of heating are presented at the decadal time scale in watts per square meter based on the mean annual changes in the surface energy flux.

Model simulations and post-processing of data

We performed model simulations with transient climate data for the years 1901-2100 and analyzed the output data from the period 2003-2100. To initialize the simulation, we ran TEM to equilibrium for all grid cells following the protocol of Zhuang et al. (2003), which consisted of using the mean climate from the period 1901-1930 as the equilibrium climate in 1900.

TABLE 1. Coefficients of significant variables and model intercept and R^2 values used in predicting percentage of change in net primary productivity (NPP), based on a stepwise linear regression by ecosystem type in northern Alaska, USA.

Plant functional type	Intercept	Change in GSL (d/yr)	Change in FPC (%)	Change in vegetation N (%)	Model R^2
Forest					
<i>Salix</i>	0.99	...	5.60	...	0.85
Deciduous shrubs	-12.24	...	7.18	...	0.85
Evergreen shrubs	39.99	-35.04	...	...	0.55
Sedge	26.99	10.63	15.49	-20.11	0.96
Forb	27.25	...	14.93	...	0.89
Grass	27.16	...	14.92	...	0.88
Lichen	72.23	...	-33.75	-155.82	0.89
Feathermoss	73.72	-30.37	...	-81.22	0.85
Shrub tundra					
<i>Betula</i>	28.47	...	...	2.56	0.78
Deciduous shrubs	-70.92	...	5.86	9.62	0.87
Evergreen shrubs	19.44	25.59	...	19.75	0.91
Sedge	-330.66	35.72	21.27	...	0.93
Forb	23.97	40.65	...	...	0.84
Lichen	25.39	...	...	-49.88	0.39
Feathermoss	18.48	35.76	...	...	0.87
Sedge tundra					
<i>Betula</i>	29.29	10.77	...	59.20	0.71
Deciduous shrubs	23.03	25.10	...	5.52	0.77
Evergreen shrubs	19.71	37.68	...	9.09	0.91
Sedge	19.37	36.58	...	5.06	0.89
Forb	18.53	35.78	...	23.51	0.81
Lichen	17.05	30.89	...	10.66	0.87
Feathermoss	20.16	32.37	...	10.75	0.85
Sphagnum moss	19.57	35.16	...	6.16	0.93

Notes: Ellipses indicate that the variable did not meet the significance level of 0.15 for entry into the model. For *Salix* in the shrub tundra, no variable met the 0.15 significance level for model entry. For spruce in the forest and grass in the shrub tundra the trends in NPP were not statistically significant under the various climates (see Appendix B). Abbreviations are: GSL, growing-season length; FPC, foliar projected cover.

We calculated temporal trends (overall and for each PFT) of NPP, R_H , and NEP simulated by the model from the slopes obtained in least-squares linear regression of the fluxes with years between 2003 and 2100. We also calculated a percentage of change in mean NPP for each PFT (NPP_{PFT}) based on mean decadal NPP between 2091–2100 and 2003–2012 as

$$\frac{[100 \times \text{NPP}_{\text{PFT}}(2091-2100)]}{\text{NPP}_{\text{PFT}}(2003-2012)} - 100 \quad (7)$$

where the mean is computed across the grid cells in which the PFT was present.

In order to better understand the various responses of the PFTs to changes in climate and their relative ability to compete for light and nitrogen, we examined the relationships between the percentage of change in NPP for each PFT with changes in: (1) growing season, (2) shading (in terms of changes in foliar projected cover of the PFT in the ecosystem), and (3) vegetation N of each PFT in the ecosystem. We calculated the change in growing season length using methodology described in Euskirchen et al. (2006). The effect of shading was determined based on the percentage of change in FPC of each PFT between the years 2003 and 2100. Changes in vegetation N were based on the percentage of change in

vegetation N for each PFT between the years 2003 and 2100. We performed these stepwise regressions for the regional means of these values for each climate scenario.

RESULTS

Changes in NPP by plant functional type

The NPP of most PFTs increased during the study period, with the only decreases occurring in the lichens in the shrub tundra (Fig. 4a, Appendix B). The largest gains were simulated for *Betula* in the shrub tundra, with a mean gain across the climates of $\sim 175 \text{ g C/m}^2$ (Fig. 4a). This gain was more than three times the gain in the spruce in the forest, which had the second largest increase ($\sim 50 \text{ g C/m}^2$ between 2003 and 2100). However, while the spruce showed large gains, these gains were not statistically significant since the initial parameterized value of the spruce NPP (e.g., the parameterized value) was large. Another deciduous shrub in the shrub tundra, *Salix*, also showed statistically significant increases in NPP and the third largest gains in NPP, $\sim 30 \text{ g C/m}^2$ between 2003 and 2100. Based on the percentage of change in NPP, the sedges, forbs, and grasses in the forest showed the greatest gains in NPP, where NPP for these PFTs was ~ 1.5 times greater from 2091 to 2100 in comparison to 2003–2012 (Fig. 4b).

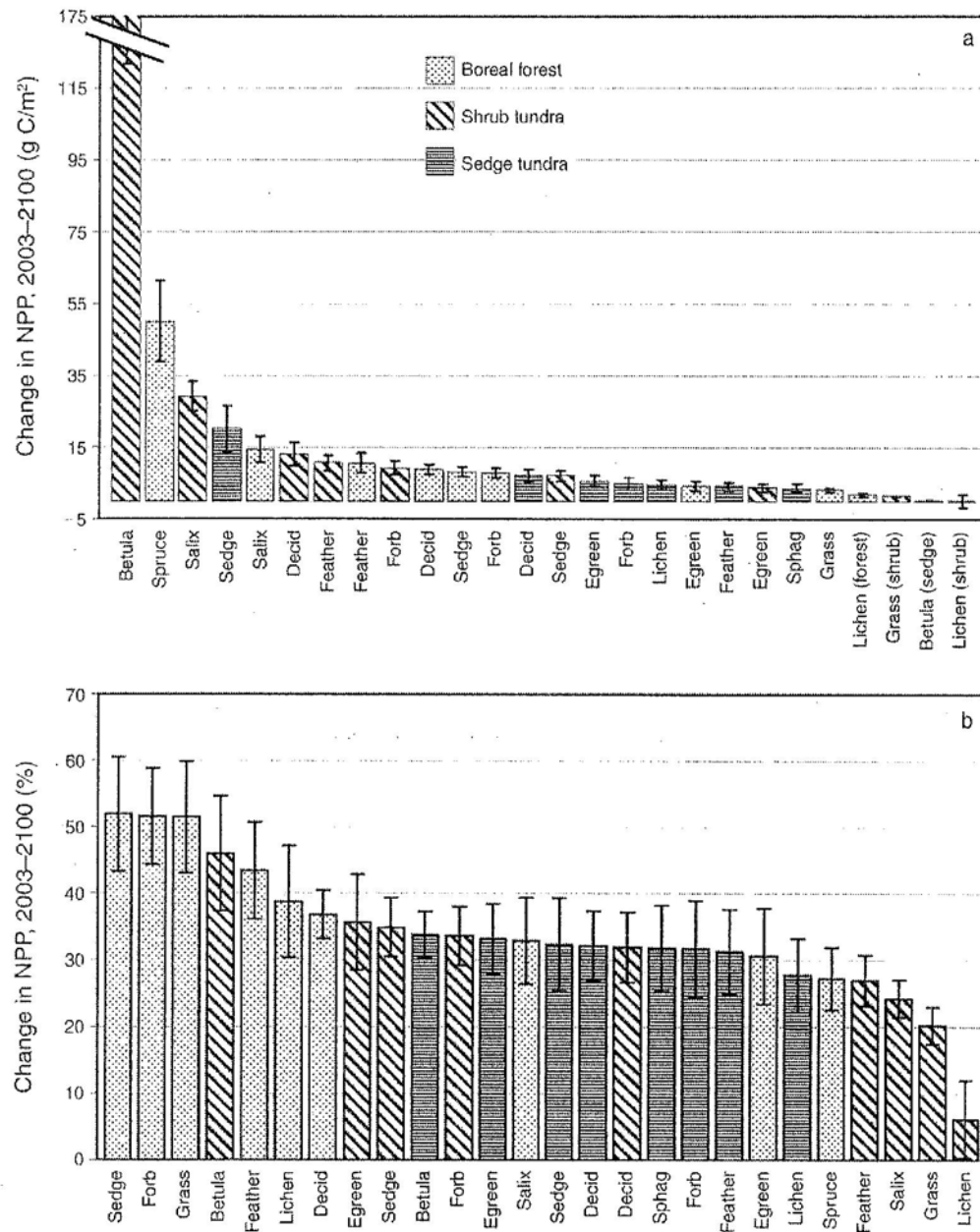


FIG. 4. (a) Actual amount of change and (b) percentage of change (mean $\pm$ SD) in net primary production (NPP) for the plant functional types (PFTs) in the forest, shrub, and tundra ecosystems across various climate scenarios, arranged in descending order by PFT. Trends in NPP were linear increases or decreases (Appendix B). See Fig. 2 legend for an explanation of PFT abbreviations.

The stepwise regressions of change in NPP of a PFT (Table 1) vs. changes in growing-season length (Table 2), changes in FPC (Table 2), and changes in vegetation N (Appendix B Table B1) revealed that each of these factors could act as a significant predictor of NPP, depending on the ecosystem type and PFT. Generally, in the forest, changes in NPP were best predicted by changes in FPC (Table 1), illustrating a PFTs ability to compete for light. In the shrub tundra, changes in NPP were predicted by a combination of changes in growing-season length, FPC, and vegetation nitrogen. In

particular, in the shrub tundra, based on the significant vegetation N regression coefficients, the *Betula*, deciduous shrub, and evergreen shrub PFTs appeared to act as the best competitors for N. In the sedge tundra, changes in NPP were best predicted by both growing-season length and vegetation N, with all PFTs showing significant relationships to both variables. Overall, these regression analyses revealed that NPP was not consistently predicted by a single factor across the ecosystem types and PFTs, due in large part because some PFTs were either good or poor competitors for light and N.

TABLE 2. Changes in indicators of plant productivity (foliar percent cover [FPC] and growing season length [GSL]) and snow cover duration (snowmelt, snow return, and the total number of snow-free days by the year 2100) by vegetation type, climate scenario, and climate model in northern Alaska, USA.

Global climate model	Change in FPC, 2003–2100 (%)	Increase in GSL, 2003–2100 (d/yr)	Change in snow cover duration (d/yr)			Length of snow-free season at 2100 (d)
			Snowmelt	Snow return	Total	
Forest						
A2						
CSIRO2	3.21	0.49	−0.33	0.40	−0.73	169
HadCM3	2.77	0.45	−0.31	0.37	−0.68	171
PCM	3.75	0.45	−0.33	0.28	−0.61	167
B1						
CSIRO2	3.64	0.35	−0.17	0.28	−0.45	173
HadCM3	3.61	0.22	−0.12	0.21	−0.33	165
PCM	3.53	0.16	−0.09	0.14	−0.23	156
B2						
CSIRO2	2.55	0.39	−0.25	0.30	−0.55	176
HadCM3	3.32	0.27	−0.18	0.26	−0.44	167
PCM	3.51	0.22	−0.33	0.28	−0.61	167
Mean	3.32	0.33	−0.23	0.28	−0.51	168
Shrub tundra						
A2						
CSIRO2	15.73	0.41	−0.32	0.38	−0.70	164
HadCM3	15.70	0.33	−0.29	0.35	−0.64	163
PCM	15.67	0.30	−0.31	0.27	−0.58	161
B1						
CSIRO2	15.42	0.22	−0.17	0.27	−0.44	166
HadCM3	15.39	0.14	−0.12	0.22	−0.34	158
PCM	15.50	0.11	−0.08	0.13	−0.21	150
B2						
CSIRO2	15.54	0.28	−0.24	0.28	−0.52	169
HadCM3	15.56	0.19	−0.17	0.25	−0.42	160
PCM	15.58	0.16	−0.31	0.27	−0.58	161
Mean	15.57	0.24	−0.22	0.27	−0.49	161
Sedge tundra						
A2						
CSIRO2	0.36	0.55	−0.31	0.41	−0.72	164
HadCM3	0.34	0.35	−0.28	0.39	−0.67	158
PCM	0.33	0.33	−0.28	0.31	−0.59	155
B1						
CSIRO2	0.34	0.24	−0.16	0.29	−0.45	162
HadCM3	0.34	0.16	−0.11	0.24	−0.35	153
PCM	0.32	0.05	−0.08	0.15	−0.23	145
B2						
CSIRO2	0.32	0.38	−0.22	0.31	−0.53	164
HadCM3	0.32	0.22	−0.16	0.28	−0.44	155
PCM	0.32	0.12	−0.28	0.31	−0.59	155
Mean	0.33	0.27	−0.21	0.30	−0.51	157
Region						
A2						
CSIRO2	0.96	0.53	−0.31	0.41	−0.72	164
HadCM3	0.85	0.35	−0.28	0.38	−0.66	158
PCM	1.05	0.33	−0.28	0.31	−0.59	155
B1						
CSIRO2	1.03	0.24	−0.16	0.29	−0.45	161
HadCM3	1.03	0.16	−0.11	0.24	−0.35	153
PCM	0.99	0.06	−0.08	0.15	−0.23	145
B2						
CSIRO2	0.79	0.37	−0.22	0.31	−0.53	164
HadCM3	0.95	0.22	−0.16	0.28	−0.44	155
PCM	0.99	0.13	−0.28	0.31	−0.59	155
Mean	0.96	0.27	−0.21	0.30	−0.51	157

Notes: A minus sign indicates earlier melt or a shorter snow season. The changes are determined based on the slope of least-squares linear regression, with all values statistically significant ($P < 0.0001$). Data are given by ecosystem type and regionally for each scenario (A2, B1, and B2) and climate model (CSIRO2, HadCM3, and PCM), as well as the overall means across all scenarios and climate models. See *Methods: Input data sets* for an explanation of the climate models and scenarios.

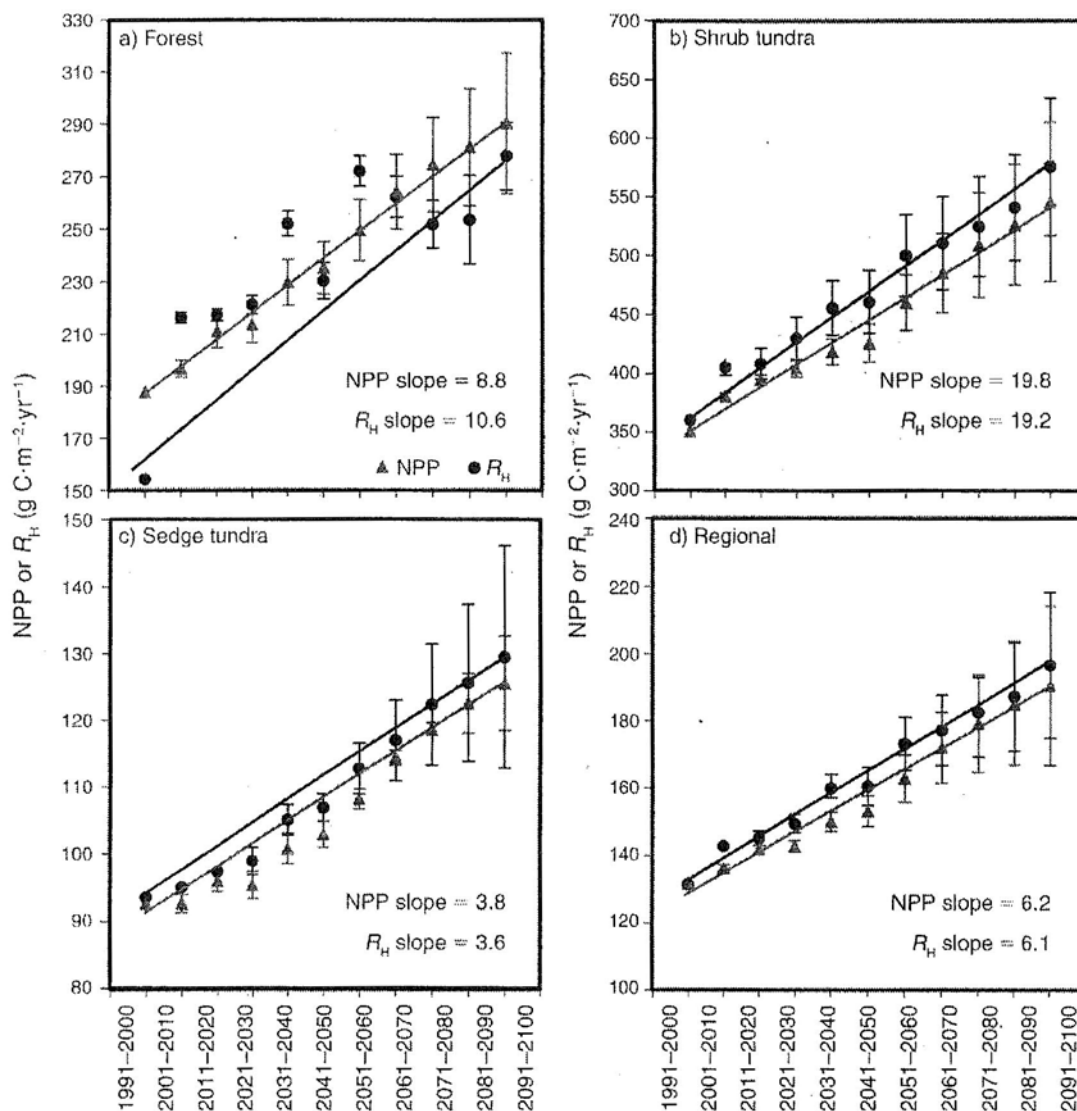


FIG. 5. Decadal net primary productivity (NPP) and heterotrophic respiration (R_H) (mean $\pm$ SD) across the nine climate scenarios for the (a) boreal forest, (b) shrub tundra, (c) sedge tundra, and (d) regionally. Also shown are the slopes of the least-squares regression line, with all trends significant ($P < 0.0001$).

*Ch[Il]ges in C[Il]xes and pools regionall
and by ecosystem type*

Across all climates and ecosystems, trends in NEP were usually not statistically significant ($P > 0.0001$) because increases in R_H were slightly larger than or nearly equal to increases in NPP (Fig. 5, Table 3). Increases in R_H were statistically significant ($P < 0.0001$) in all climates and ecosystems. In the shrub and sedge tundra increases in NPP were also statistically significant, but this was not always the case for forest, for which NPP did not show significant trends in four of the climates (A2 CSIRO2, A2 PCM, B1 PCM, B2 CSIRO2; Table 3). However, in the forest, across all scenarios, changes in R_H were large enough (Fig. 5) such that NEP became negative (e.g., net C loss) by the end of the

simulation. Initially, R_H was $\sim 150 \text{ g C/m}^2$ in the forest between 1991 and 2000, but increased to $\sim 215 \text{ g C/m}^2$ between 2001 and 2100 (Fig. 5a).

Vegetation C increased for all climates and all ecosystem types. The soil C pool increased under all climates in the sedge tundra and shrub tundra ecosystems, but decreased in the forest for four of the nine climates that had the largest differences between trends in R_H and trends in NPP (Table 3). Decreases in total ecosystem C occurred only in the forest ecosystem for the four climates that experienced decreases in the soil C (Table 3).

Changes in vegetation C were strongly predicted by both changes in R_H and NPP for the shrub tundra, sedge tundra, and regionally, and by changes in NPP for boreal forests. In the shrub tundra, the removal of one

TABLE 3. Trends by cover types for carbon fluxes (net ecosystem productivity [NEP], heterotrophic respiration [R_H], and net primary productivity [NPP]) and change in carbon pools by vegetation type, climate scenario, and climate model.

Climate model	Carbon trend ($\text{g C m}^{-2} \text{yr}^{-1}$)			Carbon pool (g/m^2)		
	NEP	R_H	NPP	Vegetation C	Soil C	Ecosystem C
Forest						
A2						
CSIRO2	-1.14	1.56	0.42 NS	580.45	-2584.38	-2003.94
HadCM3	-0.72 NS	1.43	0.71	694.11	-1086.03	-391.92
PCM	-0.28 NS	1.11	0.83 NS	723.18	671.02	1294.19
B1						
CSIRO2	-0.45 NS	0.82	0.36	539.91	-1562.89	-1022.98
HadCM3	-0.16 NS	0.82	0.66	674.13	1099.41	425.28
PCM	0.04 NS	0.58	0.61 NS	613.70	1508.78	2122.48
B2						
CSIRO2	-0.70	1.05	0.35 NS	530.79	-2016.79	-1486.00
HadCM3	-0.23	0.97	0.74	742.47	972.98	972.98
PCM	-0.02 NS	0.71	0.68	656.53	1276.02	1932.55
Shrub tundra						
A2						
CSIRO2	-0.64	3.18	2.54	695.16	1061.90	1757.06
HadCM3	0.21 NS	2.49	2.70	725.16	1919.93	2645.09
PCM	0.26 NS	1.62	1.88	553.18	1343.13	1896.31
B1						
CSIRO2	-0.17 NS	2.14	1.97	141.70	759.70	901.40
HadCM3	0.10 NS	1.56	1.66	493.92	2331.60	2825.51
PCM	0.10 NS	0.89	0.98	287.00	1252.13	1539.13
B2						
CSIRO2	-0.32 NS	2.54	2.22	631.31	2728.85	2097.53
HadCM3	0.12 NS	1.86	1.73	544.87	1983.55	2528.42
PCM	0.11 NS	1.21	1.10	355.62	1329.64	1685.26
Sedge tundra						
A2						
CSIRO2	-0.11 NS	0.94	0.83	242.37	6.89	249.27
HadCM3	-0.01 NS	0.79	0.77	213.78	104.62	318.41
PCM	0.01 NS	0.53	0.54	137.84	128.61	266.45
B1						
CSIRO2	-0.02 NS	0.60	0.58	170.13	289.70	459.83
HadCM3	0.01 NS	0.47	0.47	130.53	301.73	432.27
PCM	0.02 NS	0.27	0.29	70.27	228.35	298.62
B2						
CSIRO2	-0.05 NS	0.71	0.66	194.25	1967.00	391.25
HadCM3	0.00 NS	0.53	0.53	148.99	213.58	362.57
PCM	0.02 NS	0.34	0.36	91.36	220.12	311.48
Region						
A2						
CSIRO2	-0.26 NS	1.28	1.02	328.28	-63.26	265.03
HadCM3	-0.04 NS	1.06	1.02	318.69	245.36	564.05
PCM	0.02 NS	0.72	0.74	238.66	329.89	560.55
B1						
CSIRO2	-0.07 NS	0.82	0.74	196.02	202.59	398.61
HadCM3	0.01 NS	0.64	0.64	221.26	629.43	742.83
PCM	0.03	0.38	0.41	141.92	463.88	605.80
B2						
CSIRO2	-0.14 NS	0.98	0.84	277.99	1747.34	462.89
HadCM3	0.00 NS	0.74	0.70	247.93	485.99	692.96
PCM	0.03 NS	0.48	0.48	170.93	448.83	619.76

Notes: The changes in the pools are obtained by subtracting pool value in the last year from that in the first year. Trends marked with "NS" are not significant at $P < 0.001$. Trends for vegetation C, soil C, and ecosystem C are for the period 2003–2100. See *Methods: Input data sets* for an explanation of the climate models and scenarios.

outlier from the B1 CSIRO2 climate (Fig. 6a, b) changed the R^2 value to 0.95 for both linear regression equations of R_H and NPP vs. vegetation C in the shrub tundra. Changes in soil C were strongly correlated with both R_H and NPP in the forest and more strongly correlated with NPP in the shrub tundra. In the shrub tundra, sedge tundra, and regionally, changes in soil C were not

correlated with either changes in R_H or NPP. In the case of the sedge tundra and regionally, this was due to the presence of outliers based on the B2 CSIRO2 climate. Removal of the outliers in the regressions for the sedge tundra and regionally resulted in R^2 values of 0.51 ($P < 0.0001$) for both regression equations of R_H and NPP vs. soil C (Fig. 6c, d). It is not clear what factors may be

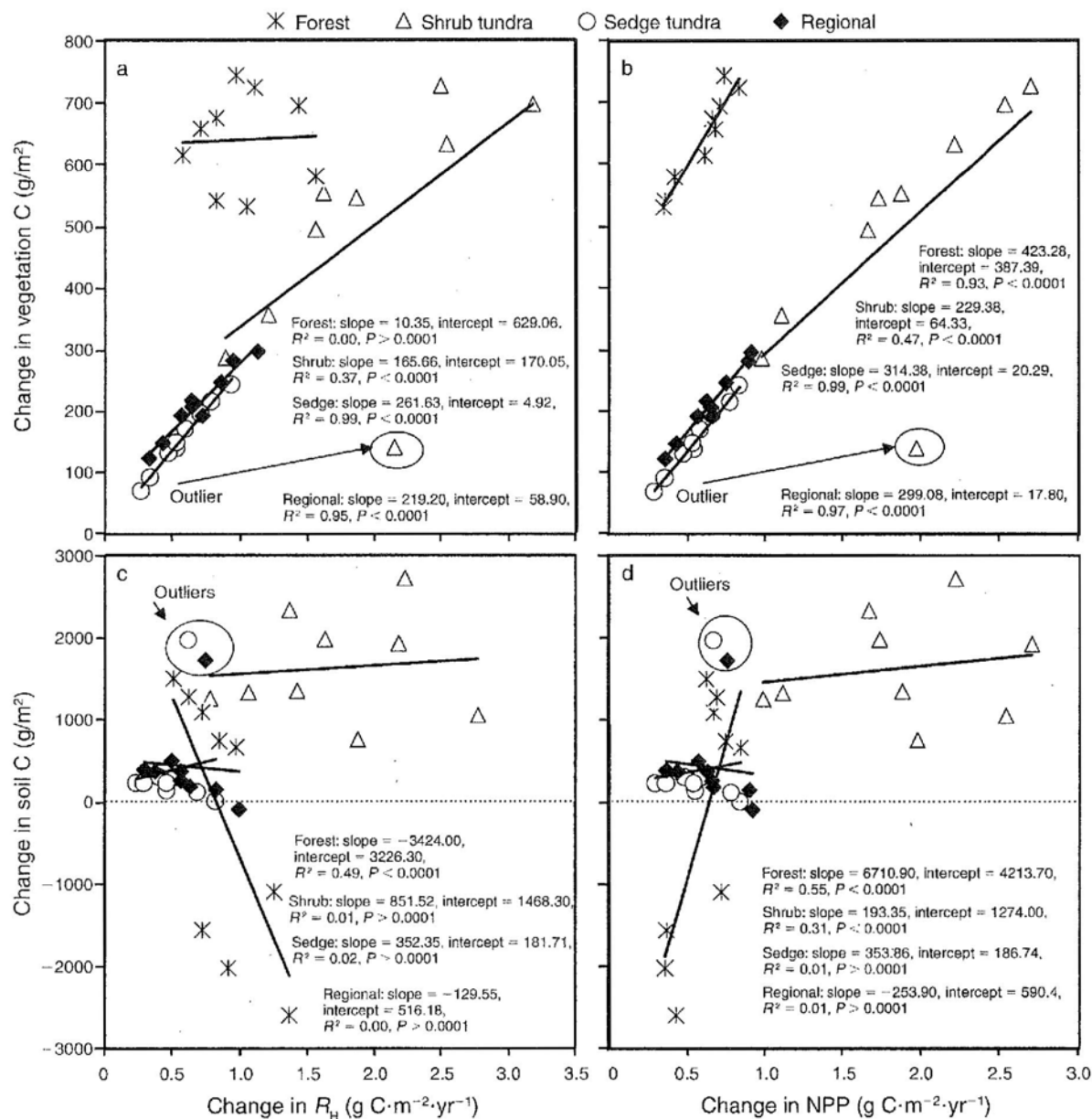


FIG. 6. Relationship between selected carbon pools and fluxes for 2003–2100. Each point represents the mean based on one climate scenario and vegetation type, as well as the regional means. Also shown are the slopes, intercepts, R^2 , and P values for each relationship: (a) change in heterotrophic respiration (R_H) vs. change in vegetation C, (b) change in net primary production (NPP) vs. change in soil C, (c) change in R_H vs. change in soil C, and (d) change in NPP vs. change in soil C.

causing the outliers described above. A principal component analysis (PCA) based on the three climate variables for each of the ecosystem types did not lead to a separation on the first axis of outlying climates that would have matched the outliers in Fig. 6.

Changes in albedo, snow cover and surface heating

Our estimates of summer albedo based on Eq. 3 indicated that between 2003 and 2100 all of the ecosystems experienced decreases in summer albedo due to increases in biomass (Fig. 7). The shrub tundra

experienced the greatest decline in summer albedo (0.01–0.021, mean of 0.017; Fig. 7b, d) due to the large increases in NPP in the *Betula* PFT (Fig. 4a) and was approaching the summer albedo of the forest by the year 2100 (Fig. 7d). The sedge tundra, with the overall smallest amount of aboveground biomass (e.g., Appendix A: Table A4) showed the smallest decreases in summer albedo (0.003–0.010, mean of 0.007; Fig. 7c). Regionally, the changes in summer albedo most closely resembled those of the sedge tundra due to the

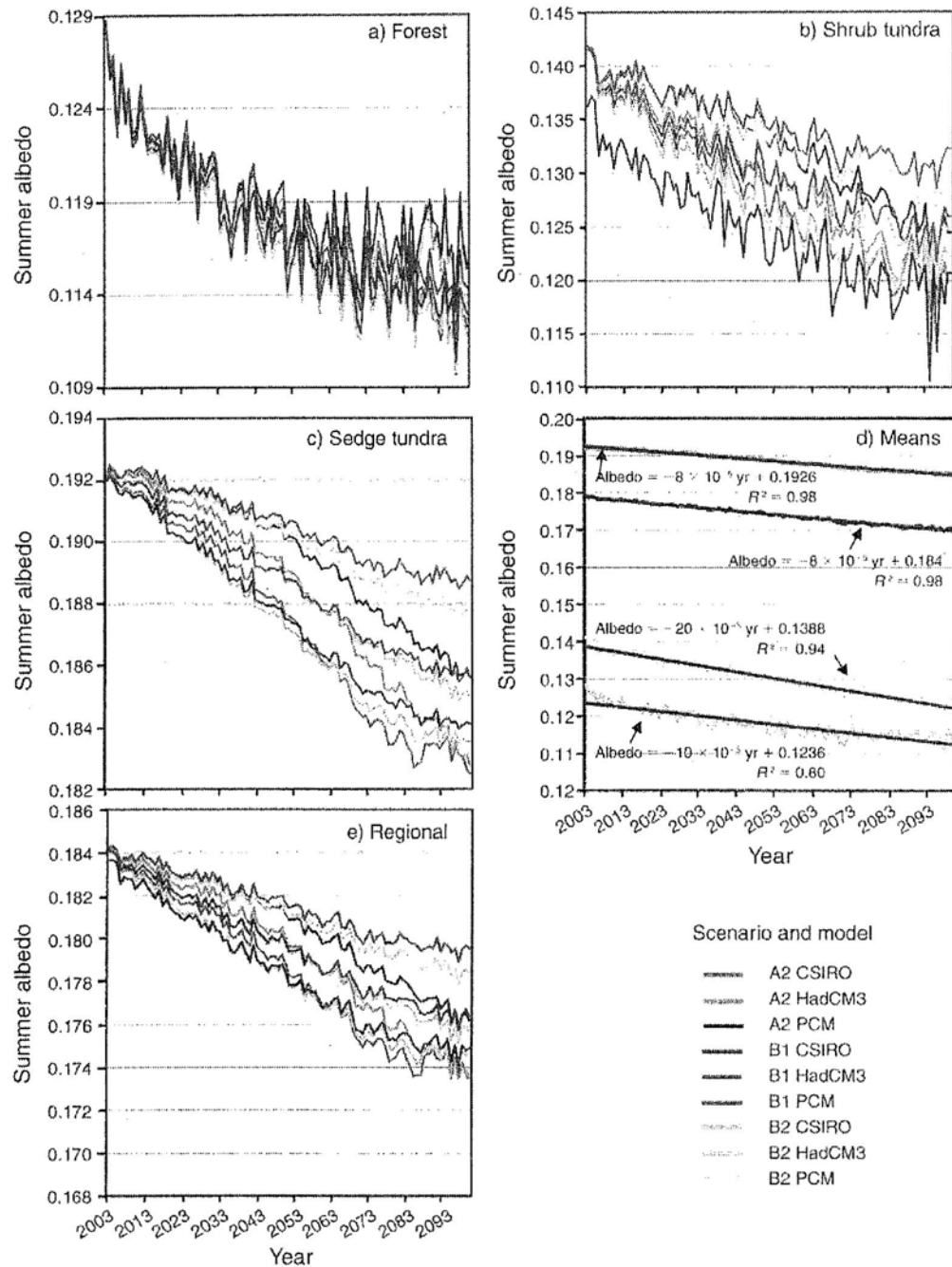


FIG. 7. Change in summer albedo by climate scenario for (a) boreal forest, (b) shrub tundra, and (c) sedge tundra. The figure also presents (d) means across the climate scenarios for each ecosystem type and (e) regional means across all ecosystem types. In panel (d) the regression lines from top to bottom are: sedge tundra, regional, shrub tundra, and forest ($P < 0.0001$ for all types). Albedo is calculated based on Eq. 3. See *Methods: Input data sets* for an explanation of the climate models and scenarios.

dominance of the sedge tundra in the study region (Fig. 7c,d).

The ecosystem types showed similar changes in snowmelt (0.08–0.33 d earlier/yr, Table 2) and snow return (0.13–0.41 d later/yr), with the strongest trends occurring under the warmer climate scenarios (e.g., A2 CSIRO2, A2 HadCM3; Fig. 3a). Across all climates, the

change in the snow season was due more to a later return of snow in the fall than to an earlier melt in the spring, a result that attributable to the greater temperature increases during the SON months than during the MAM months under all climates (Fig. 3(1). By year 2100, the mean number of snow-free days across the region was ~ 157 , which is ~ 50 more snow-free days

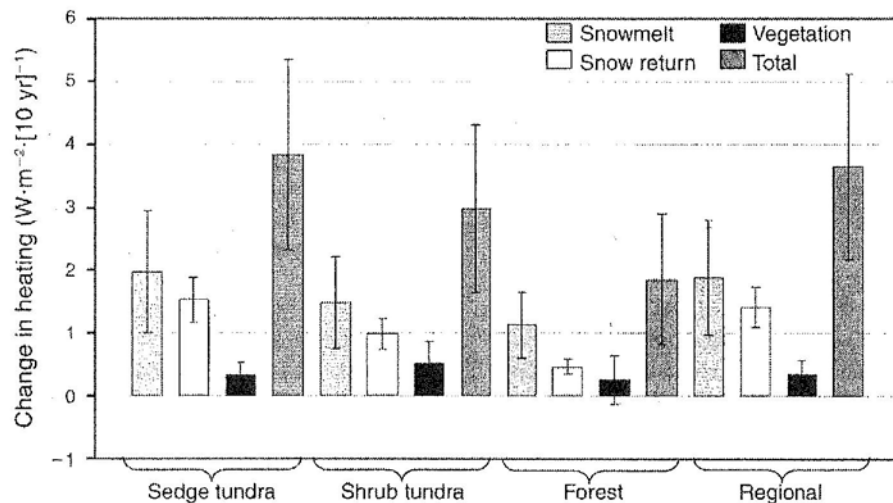


FIG. 8. Changes in atmospheric heating across all nine input climate scenarios (mean $\pm$ SD) due to changes in snowmelt, snow return, and vegetation, and combined for the years 2003–2100. “Regional” refers to the regional average, weighted by vegetation type years 2003–2100. We also examined climate feedbacks to

compared to the beginning of the simulation in 2003 (Table 2).

The changes in the land surface due to increases in biomass and decreases in the period of snow-covered ground resulted in an increase in atmospheric heating (Fig. R). Across all vegetation types, the change in the timing of snowmelt resulted in the largest increase in atmospheric heating, and the increase in biomass resulted in the smallest increase in atmospheric heating. Even though the change in the length of the snow-free season was due more to the later snow return than to earlier melt (Table 2), the increase in atmospheric heating during the time of melt was magnified. This is because changes in the atmospheric heating of snow-covered and snow-free ground are greater in spring than in autumn (Euskirchen et al. 2007). Large differences in atmospheric heating were also noted between the vegetation types with large seasonal-albedo contrast (e.g., tundra) compared to low seasonal-albedo contrast (e.g., forests) even if they exhibited similar changes in snow cover duration. For example, although the sedge tundra and boreal forests displayed comparable decreases in snow cover duration (~ 0.50 d/yr; Table 2), the increase in atmospheric heating due to changes in snow cover was larger for the sedge tundra (~ 3.7 W·m $^{-2}$ ·10 yr $^{-1}$) than boreal forests (1.7 W·m $^{-2}$ ·10 yr $^{-1}$) due to the high contrast in albedo between snow-covered and snow-free ground in the tundra.

DISCUSSION Overview

This study used a new version of the TEM, which includes a dynamic vegetation component with multiple vegetation pools coupled to a soil thermal model, to assess how possible future changes in climate impacted the productivity of PFTs in sedge and shrub tundra and boreal conifer ecosystems in northern Alaska over the

atmospheric heating based on changes in vegetation and changes in the length of the snow season. We found overall increases in NPP across all PFTs. However, large increases in RH resulted in little overall increase and even decreases in NEP under the various climate scenarios. Increases in NPP in this study, particularly in the shrub tundra, agree with other empirical and model-based studies (Epstein et al. 2000, Jia et al. 2003, Sturm et al. 2005, Walker et al. 2006, Wolf et al. 2008). In our comparisons of changes in atmospheric heating due to changes in snow cover vs. vegetation structure, changes in snow cover accounted for 90% of the changes in atmospheric heating. In the discussion below, we evaluate (1) the results of the simulations we conducted in this study, (2) the implications of our results for issues related to biodiversity, (3) the implications of our results for C storage, and (4) the implications of our results for atmospheric heating.

Evaluation of model simulations

To evaluate our results, it is useful to examine how the future climates used in this study compare with climate trends observed in recent decades in this region. Data from the Climate Research Unit (New et al. 2002, Mitchell and Jones 2005), used as input data for TEM simulations over this same region in Thompson et al. (2006), showed that between 1981 and 2000, annual air temperature in northern Alaska increased by 0.86°C ($0.04^{\circ}\text{C}/\text{yr}$), with JJA air temperature increasing by $\sim 1.0^{\circ}\text{C}$ ($0.05^{\circ}\text{C}/\text{yr}$). These historical increases are similar to the lower-end estimates of temperature increases, as seen in the climates for the B1 scenario (Fig. 3a). According to the CRU data, precipitation for the region decreased by 1.5 mm between 1981 and 2000, with growing-season (JJA) precipitation decreasing by ~ 1.2 mm during this same time period (Thompson et al.

2006). In contrast, all of the future climate scenarios showed increases in precipitation (Fig. 3b). Other research suggests that these estimates of future changes in climate may be thought of as somewhat conservative in light of the recent observation that the IPCC scenarios published in 2001 are basically independent from the observed climate data since 1990 (Rahmstorf et al. 2007). Nevertheless, the results from the model simulations presented here illustrate that it is important to monitor climate change indicators, such as air temperature, cloudiness, precipitation, and atmospheric CO₂, to assess which climate scenario we are most closely following.

Other recent research in arctic and boreal ecosystems has also documented changes in vegetation composition and productivity under a changing climate. Remote-sensing studies have found that vegetation greenness, as measured with the normalized difference vegetation index (NDVI), has increased in northern Alaska with increasing temperatures between 1981 and 2000, corresponding to an increase in plant biomass of ~171 g/m² (Jia et al. 2003). Repeat aerial photography at dozens of sites in northern Alaska shows an increase in shrub abundance on both hill slopes and valley bottoms over the past 50 years (Tape et al. 2006). Using a point-based dynamic vegetation model to simulate arctic vegetation, Epstein et al. (2000) found increases in shrub biomass and reductions in moss biomass under 3°C of warming. Another dynamic vegetation model simulated over the tundra and boreal forest of the Barents Region detailed a complex array of responses of vegetation to future climate change, including an advancement of treeline that resulted in a decrease in shrublands and an expansion of tundra in the far north due to a replacement of open ground with vegetation (Wolf et al. 2008). Cumulatively, results from these studies, well the present work, highlight recent changes in the composition and function of arctic and boreal vegetation, with trends expected to continue into the future.

The dynamic vegetation component of the TEM that we implemented in this study is unique because it has been developed specifically for the arctic and boreal ecosystems, taking into account soil thermal regimes (including permafrost), nitrogen limitation and competition, and specific parameterizations of dominant arctic and boreal PFTs. To our knowledge, other arctic DVMs take into account one or two of the attributes mentioned above but not all three (e.g., Epstein et al. 2000, Kaplan et al. 2003, Beer et al. 2007, Wolf et al. 2008). Other DVMs have been developed for simulations over the global scale (Cramer et al. 2001, Sitch et al. 2003), with coarse groupings of vegetation and a limited representation of nitrogen and soil thermal dynamics. This coarse-scale approach is useful for some applications, but it may not properly represent vegetation dynamics in this region. For example, C3 grasses are mistakenly used to model arctic tundra, and permafrost and nitrogen dynamics are generally not taken into account (Cramer

et al. 2001). Furthermore, our approach of taking into account numerous high-latitude PFTs permits us to consider biodiversity issues (see *Implications for issues related to vegetation structure* below). The permafrost dynamics we considered in this study influence the seasonality of C exchange in high-latitude ecosystems via the effects of freeze-thaw dynamics on C uptake and decomposition (Zhuang et al. 2003, Euskirchen et al. 2006).

In contrast to DVMs that define bioclimatic types and model migration (e.g., Kaplan et al. 2003, Wolf et al. 2008), the goal of the model used in this study was not to include the movement of one vegetation type to another grid cell (e.g., to model the advancement of treeline). Except for the spruce PFT, all of the ecosystem types in this study share the same PFTs, so there is no reason to consider migration of those PFTs. With respect to the migration of the spruce PFT, a number of analyses suggest that these migrations could take centuries to occur (MacDonald et al. 1993, Chapin and Starfield 1997, Rupp et al. 2001, Nielson et al. 2005), a time scale that is much longer than that presented in this analysis. Furthermore, for our study region, the Brooks Range presents a significant topographic barrier to migration of trees in northern Alaska (Rupp et al. 2001).

Implications for issues related to vegetation structure

The various responses of the PFTs to the climate scenarios have implications for issues related to vegetation structure. The large increase in *Betula* in the shrub tundra may impact the function and structure of the terrestrial ecosystems in northern Alaska because of negative responses of the highly diverse ground cover of mosses and lichens to increases in *Betula*. While some studies suggest that latent heating may currently be controlled by mosses through their surface evaporation, this may change as the vertical complexity of the canopy increases, thereby shading the mosses and reducing the ground surface evaporation (Thompson et al. 2004, Gornall et al. 2007). Likewise, changes in moss biomass may be important because of their role in changing heating effects during the summer and winter. During the summer, they may reduce heat input to soils because their high porosity allows air to act as an insulator. However, during winter, ice conducts heat effectively through mosses from the soil to the atmosphere (Thompson et al. 2004). The small increases or decreases in the lichen NPP, which are also generally attributable to shading and a negative response to nitrogen fertilization, agree with empirical studies conducted in the Arctic (Cornelissen et al. 2001). Since lichens are a primary food source for grazers such as caribou and reindeer in the Arctic, these potential losses of lichen may affect subsistence resources. While none of the PFTs in this study became extinct or disappeared from a grid cell, there is the potential that they can due to decreases in NPP that may eventually result in no remaining vegetation C or biomass.

Implications for C storage

Ecosystem responses that generate losses of C to the atmosphere under a changing climate could further amplify climate warming. This issue is particularly relevant in high-latitude arctic and boreal ecosystems because they contain more than one-third of the world's soil carbon (Schuur et al. 2008). In general, under the warmer, wetter trends in our simulations, trends in RH were greater than trends in NPP, and trends in NEP were either negative or not significant. However, our simulations resulted in increases in ecosystem C in all of the ecosystem types, except for four of the nine climates in the forest. This general increase in ecosystem C occurred because NEP was slightly positive at the end of the historical simulation and negative trends in NEP were not strong enough to cause NEP to become significantly negative except for three of the nine climates in the forest ecosystem (Fig. 5, Table 3). That is, even though the model continued to simulate positive NEP (i.e., ecosystem accumulation of C), there was a reduced capability of the system to sequester carbon. Previous research (Thompson et al. 2006) on the historical changes in the carbon balance in this region simulated a slight gain in net carbon storage for the last two decades of the 20th century, but there was large spatial variability that depended on the climate trends (e.g., for different combinations of warmer/cooler and wetter/drier). Based on CO₂ flux measurements from a limited number of sites between 1960 and 1998 in northern Alaska, Oechel et al. (2002) hypothesized that NEP in the arctic coastal and inland tussock tundra ecosystems under increases in temperature and decreases in precipitation had acclimated to climate warming, after initially acting as a source due to drying of the soils that caused increased RH. Cumulatively, these results suggest that a slight change in temperature and precipitation regimes can bring about changes in the net carbon uptake of these ecosystems and their ability to sequester carbon.

Implications for atmospheric heating

Other studies have examined the implications of transition between northern Alaska vegetation types during the growing season (McFadden et al. 1998, Chapin et al. 2000, 2005, Beringer et al. 2005, Sturm et al. 2005). These studies have found changes in atmospheric heating due to changes in albedo from vegetation transitions. In measuring the transition from tundra to tall shrub and then to forest, Beringer et al. (2005) found an increase in sensible heat flux of 7 to 13 W/m², respectively. Chapin et al. (2000) modeled the tundra-to-shrub transition feedbacks in relation to changes in air temperature for northern Alaska and found a 1.0°–4.0°C increase, depending on the area of northern Alaska. In a synthesis of field data from northern Alaska, Chapin et al. (2005) found that past increases in northern Alaska vegetation from 1950 to the present accounted for an increase in atmospheric heating of ~0.20 W·m⁻²·10 yr⁻¹,

while the increase in atmospheric heating due to snowmelt advance accounted for ~3.3 W·m⁻²·10 yr⁻¹. However, in the future, under a complete conversion to shrubland or forest, the increase in summer atmospheric heating was estimated as ~6.4 W/m² due to shrubland conversion and 24.5 W/m² due to forest conversion, with a smaller increase under the effect of snowmelt advance, 2.5 W·m⁻²·10 yr⁻¹ in the tundra and ~1.4 W·m⁻²·10 yr⁻¹ in the forest (Chapin et al. 2005). The simulations in this study build upon this research by providing a transient analysis of how changes in vegetation and snow cover of northern Alaska are likely to influence atmospheric heating during the 21st century. Our results indicate that vegetation change would increase regional summer heat absorption by 0.34 ± 0.23 W·m⁻²·10 yr⁻¹ during the 21st century and that regional heat absorption associated with changes in snow cover would be similar to $(3.3 \pm 1.24$ W·m⁻²·10 yr⁻¹) that of Chapin et al. (2005). As the vegetation change we simulated was most consistent with the conversion to shrubland, our analysis suggests that the degree of conversion to shrubland in the 21st century would only affect summer atmospheric heating ~5% of the complete conversion to shrubland. It is important to note that if northward tree migration in Alaska were substantial in the 21st century, then summer atmospheric heating would be substantially larger. However, as noted earlier, previous analyses suggest that northward tree migration into our study region would likely take centuries to occur (Chapin and Starfield 1997, Rupp et al. 2001).

Our estimates of atmospheric heating in the winter do not currently take into account the increasing shrubiness of the sedge tundra, and we are of the opinion that shrub increases will not substantially influence atmospheric heating during winter. The winter albedo of the shrub tundra has the potential to approach that of a deciduous forest as the reflective snow is replaced by protruding shrub branches with a lower albedo. While this may, in theory, seem to have a large impact on atmospheric heating, the effect may be small for two reasons: (1) in early and mid-winter, when there is little or no sunlight, the difference in atmospheric heating between the forest and shrub tundra is very small and (2) the shrubs may not be exposed above the snow surface until most of the snow has melted in the late spring as they may lay down under a snow load (Sturm et al. 2005). Thus, we feel that our conclusion that the effects of vegetation change on atmospheric heating are likely to be an order of magnitude lower than the effects of snow cover change during the 21st century is a robust conclusion.

CONCLUSIONS

The results from this study and other research emphasize the importance of continued monitoring of changes in arctic and boreal climate and vegetation, particularly with respect to the increases in deciduous shrubs in the tundra. These changes in shrubs, as well as

those in snow cover, will alter both local and global carbon budgets and feedback to atmospheric heating. Taking into account these terrestrial feedbacks to atmospheric heating in concert with those from a diminishing sea ice (Perovich et al. 2007) suggests amplification of atmospheric heating due to changes in the Arctic. Even small changes in global temperatures could result in imbalanced responses in arctic and boreal regions, with feedbacks that may alter such processes as photosynthesis and decomposition. As results from this study show, the difference between net ecosystem carbon losses vs. net carbon gains depends on a fine balance between R_H and NPP. Shifting this balance in either direction has implications for the structure of these plant communities, and the animal habitat and subsistence resources that they provide. Future progress in assessing the entire suite of the effects of climate change on these tundra and boreal ecosystems requires an integrated approach, incorporating field-based studies, remotely sensed data, dynamic vegetation, biogeochemical, and sea ice models. This will then provide information on changes in vegetation that influence not only the climate system, but also the ecosystem services related to animal habitat and subsistence resources and thus provide a scientific basis for management and policy making.

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APPENDIX A

Model description and logic (*Ecological Archives* A019-041-A1).

APPENDIX B

Trends in net primary productivity, vegetation carbon, and vegetation nitrogen by plant functional type and climate scenario (*Ecological Archives* A019-041-A2).