NET CARBON EXCHANGE ACROSS THE ARCTIC TUNDRA-BOREAL FOREST TRANSITION IN ALASKA 1981–2000

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Abstract. Shifts in the carbon balance of high-latitude ecosystems could result from differential responses of vegetation and soil processes to changing moisture and temperature regimes and to a lengthening of the growing season. Although shrub expansion and northward movement of treeline should increase carbon inputs, the effects of these vegetation changes on net carbon exchange have not been evaluated. We selected low shrub, tall shrub, and forest tundra sites near treeline in northwestern Alaska, representing the major structural transitions expected in response to warming. In these sites, we measured aboveground net primary production (ANPP) and vegetation and soil carbon and nitrogen pools, and used these data to parameterize the Terrestrial Ecosystem Model. We simulated the response of carbon balance components to air temperature and precipitation trends during 1981–2000. In areas experiencing warmer and dryer conditions, Net Primary Production (NPP) decreased and heterotrophic respiration (R_H) increased, leading to a decrease in Net Ecosystem Production (NEP). In warmer and wetter conditions NPP increased, but the response was exceeded by an increase in R_H; therefore, NEP also decreased. Lastly, in colder and wetter regions, the increase in NPP exceeded a small decline in R_H, leading to an increase in NEP. The net effect for the region was a slight gain in ecosystem carbon storage over the 20 year period. This research highlights the potential importance of spatial variability in ecosystem responses to climate change in assessing the response of carbon storage in northern Alaska over the last two decades.

Keywords: net carbon exchange, net primary productivity, Alaskan Arctic, tundra

Introduction

High-latitude ecosystems play an important role in the earth's climate system (Bonan et al. 1995). The direction and magnitude of shifts in their carbon balance, in response to environmental change, are particularly important because high latitude systems contain nearly 40% of the world's soil carbon (McGuire et al. 1995; Melillo et al. 1995). Future changes in net carbon storage are presently difficult to predict because of the interactions between ecosystem processes such as primary production, decomposition, nitrogen mineralization; ecosystem controls such as temperature and moisture; and other dynamic ecosystem components such as

active layer depth, and permafrost distribution. Temporal and spatial variability in the coupled climate-land system contributes considerably to the complexity of predicting the long-term carbon balance in these systems.

Net carbon storage in terrestrial ecosystems is primarily determined by the balance between net primary production (NPP) and decomposition. Changes in the sink strength of ecosystems in response to climate change are controlled in part by plant uptake of carbon through responses of NPP. Changes in NPP can occur through growth responses, changes in relative abundance of existing species, or additions or losses of new species to or from the community. For example, the woody deciduous shrub *Betula nana* can significantly increase its production in response to experimental fertilization and warming (Bret-Harte et al. 2001). The growth response by this shrub has likely contributed to shrub expansion during the last several decades that has been detected using aerial photographs (Sturm et al. 2001) and remote sensing (Stow et al. 2003). Shifts in tundra carbon balance might be more rapid at the southern extent of tundra near treeline where greater vegetation biomass and greater occurrence of shrub tundra maximize the potential for increases in net primary production. Although forests are generally expected to expand in response to warming (Prentice et al. 1992), temperature-induced drought stress can limit the growth of individual trees at treeline (Lloyd and Fastie 2002) and within the boreal forest (Barber et al. 2000). These examples of differential species responses to recent warming highlight key uncertainties regarding the role of species in determining net carbon exchange over time.

Heterotrophic respiration (R_H) releases CO_2 to the atmosphere, primarily through decomposition of organic matter. The response of net carbon exchange (net ecosystem production- NEP) to warming therefore depends on whether the response of R_H is greater or less than the response of NPP. Decomposition rates are expected to increase in response to warming temperatures (Oechel et al. 1993). Temperature changes act in concert with precipitation changes to affect below-ground processes. Cold wet soils have low decomposition rates, resulting in long-term storage of carbon in high-latitude soils (Gorham 1991). Decreases in soil moisture would be expected to enhance R_H. Changes in soil moisture may have a stronger effect than changes in temperature on decomposition and therefore may influence the trajectory of net carbon exchange over time depending on climatic conditions (Oechel et al. 2000).

Because of the strong nutrient (primarily N) limitation of growth in Arctic regions (Shaver and Chapin 1986), the net balance between NPP and R_H is likely to be influenced by interactions between the carbon and nitrogen cycles in these ecosystems. Decomposition rates are indirectly affected by increases in nutrient availability (Mack et al. 2004), which in turn is tightly coupled to rates of nitrogen (N) mineralization (Nadelhoffer et al. 1991; Shaver et al. 1992). Over time, losses of C from the soil are accompanied by a redistribution of N in the ecosystem. Losses of N from the soil can also occur if the active layer deepens (Waelbroeck et al. 1997),

which enhances soil drainage and results in transfers of N to aquatic and marine systems (but see Rastetter et al. 2004). Soil N can also be transferred to the vegetation, which has a higher C:N ratio. Increasing the litter C:N ratio, which can occur through shifts in species composition or within species allocation changes (Hobbie 1996) could provide a mechanism by which increased plant growth could be a negative feedback to R_H.

Net carbon exchange varies spatially because of temporal variation in climate and because of landscape-scale vegetation patterns. Variability in the broad scale patterns of temperature and precipitation have been documented for the Alaskan Arctic (Fleming et al. 2000). Recent changes in climate have not been uniform across the region, creating new gradients of temperature and precipitation, and driving temporal patterns.

Landscape scale vegetation heterogeneity is a complex combination of topography, climate, soil resources and other factors. Vegetation responses to changes in these factors are determined by genetics, physiology, and inter-specific competition. Spatial heterogeneity is potentially greater in transitional areas that span a gradient of vegetation complexity such as the area in this study, which spans treeline (Thompson et al. 2004). Small (landscape-scale) spatial heterogeneity has explained variation in short-term measurements of net summer carbon fluxes (McFadden et al. 2003) and was important to consider in modeling net carbon exchange at the scale of the Kuparuk River basin in Alaska (Le Dizes et al. 2003). The high degree of landscape heterogeneity in the Alaskan Arctic could result in high levels of the spatial variability in the ecosystem carbon response, as patterns are evaluated across broader spatial scales. However, landscape heterogeneity could also lead to dampened responses at a coarser scale, if the responses are non-linear (Rastetter et al. 1992).

In this study we evaluated the temporal and spatial patterns of net carbon exchange in Alaskan ecosystems that span the transition from arctic tundra to boreal forest. We specifically addressed the following questions: (1) What is the influence of climate variability on the net ecosystem carbon exchange during the last two decades?; and (2) do the major community types in the Alaskan Arctic at treeline respond in a similar fashion to decadal climate trends? To address these questions, we measured net primary production (NPP), vegetation and soil carbon and nitrogen pools in tundra, shrub tundra and treeline evergreen conifer forest ecosystems. We used these field data to parameterize a biogeochemical model that simulates changes in vegetation and soil carbon storage in northern Alaska across the transition from arctic tundra to boreal forest. In this study we evaluate the trends in the two major components of net carbon exchange (NEP): (1) carbon into the vegetation, NPP; (2) carbon out of the soil, R_H. We assess the controls over the net carbon exchange in response to climate during the past two decades, and discuss the interactions between regional climate variability and vegetation composition and function in controlling net carbon exchange in the Alaskan Arctic.

Methods

OVERVIEW

We measured growing season Aboveground Net Primary Productivity (ANPP), biomass, and soil C and N in a tundra site located at Ivotuk on the north slope of Alaska and in tall shrub tundra and forest at treeline near Council, Alaska on the Seward Peninsula in western Alaska. We used these data to develop parameterizations for a version of the Terrestrial Ecosystem Model (TEM 5.0) that simulates interactions between ecosystem processes and thermal dynamics of soils with permafrost (Zhuang et al. 2003). We extrapolated the model spatially over the Alaskan Arctic to boreal treeline, to simulate changes in vegetation and soil carbon storage from 1981–2000.

STUDY SITES

We developed a tundra parameterization using field data from a moist acidic tundra (MAT) site in Ivotuk, Alaska (68.5°N 155.5°W). Tall shrub and forest parameterizations were based on field sites in Council (64.5°N 163.41°W) on the Seward Peninsula, in northwestern Alaska. The Ivotuk MAT site had equal biomass of deciduous and evergreen shrubs and sedges (*Eriophorum vaginatum*). The tall shrub site featured 2 m tall deciduous shrubs *Betula glandulosa* and *Salix spp.* with smaller deciduous shrubs, forbs and mosses in the understory. The forest site canopy was comprised of white spruce (*Picea glauca*) with an understory of tall *Salix spp.* shrubs. Low shrubs, forbs and feather mosses formed a near-continuous ground cover (Thompson et al. 2004).

MODEL DESCRIPTION

In this study we used TEM 5.0, which couples the Terrestrial Ecosystem Model (TEM) with a soil thermal model (Zhuang et al. 2003). As in preceding versions of TEM, this version uses spatially referenced information on climate, elevation, soils and vegetation to simulate carbon and nitrogen dynamics. The soil temperatures and freeze-thaw dynamics simulated by the model drive soil processes such as R_H and net nitrogen mineralization. Snow characteristics also influence the soil thermal regime. Freeze-thaw dynamics influence the seasonal onset and cessation of Gross Primary Productivity (GPP) by scaling GPP based on the fraction of a month during which the soil is thawed (Zhuang et al. 2003). In TEM 5.0, as in previous work with TEM focused on tundra carbon balance (Clein et al. 2000), we used a relationship between moisture and plant litter decomposition developed by Flanagan and Veum (1974) to scale decomposition relative to the moisture values. In this relationship, decomposition is zero at low soil moistures, reaches optimal values at field capacity

and returns to zero at saturated conditions. TEM 5.0 assumes that the response of decomposition to temperature and moisture is similar for plant litter and organic soil.

MODEL PARAMETERIZATION -NPP, GPP AND VEGETATION AND SOIL CARBON AND NITROGEN

Information from the field sites was used to estimate the values of parameters that determine the quantities of C and N in the vegetation and soil and the rates of the C and N fluxes for each vegetation type. Many parameters in the model are defined from published information; however, some of the vegetation-specific parameters are determined by calibrating the model to the fluxes and pools sizes at the representative field sites. In the calibration process, parameters controlling the rate of C assimilation, tissue respiration, heterotrophic respiration, maximum N uptake by the vegetation, N in litter production, and nitrogen mineralization were adjusted until model values match field-based estimates of NPP, GPP, nitrogen uptake, and soil carbon and nitrogen pools (McGuire et al. 1992).

At each study site, we measured plant biomass and production (new leaves and stems) in 10–12 randomly selected 20×50 cm quadrats in the understory and 1×1 m quadrats of the tall shrub overstory in the tall shrub and forest sites. All sampling occurred at the time of peak aboveground biomass, between mid July and mid August. Aboveground vascular plant biomass was harvested to the top of the moss or lichen layers, which were collected separately. Plant biomass was oven-dried at $60\,^{\circ}$C for at least 48 hr and weighed. Carbon (C) and nitrogen (N) concentrations were measured on a Carlo-Erba CHN analyzer. We combined data for individual species because TEM 5.0 does not consider species or plant functional types explicitly (Table I). Assumptions used to determine values for NPP and NPPn in Table I are described below.

For the components of plant production that were not directly measured we made estimates based on several assumptions. We estimated wood production based on measured secondary growth rates of 16% for *Betula nana.*, 18% for *Salix pulchra* and 8% for *Ledum palustre* (Bret-Harte et al. 2002). We multiplied these relative growth rates by the old stem biomass pool. We also used the *Ledum* rate for the deciduous species because the deciduous shrubs other than *Betula* and *Salix* had stem diameters and growth rates more similar to *Ledum*. *Sphagnum* spp and feather moss production was estimated from Oechel and Van Cleve (1986) (8% and 21% of standing pool, respectively). Root production was estimated for the functional types based on field data from several sources (e.g., Hobbie and Chapin 1998). Lichen production (2% of pool) was based on Wielgolaski et al. (1981). For the tundra and shrub sites, we estimated that GPP was twice NPP, similar to assumptions for tundra in McGuire et al. (1992). Nitrogen uptake

TABLE I

Annual Net Primary Production (NPP), the nitrogen content in NPP (NPPn), vegetation carbon (VegC) and nitrogen (VegN) in the major plant functional groups and species at the calibration sites

Functional group	Tundra				Shrub				Forest			
	NPP	NPPn	VegC	VegN	NPP	NPPn	VegC	VegN	NPP	NPPn	VegC	VegN
Spruce	–	–	–	–	–	–	–	–	134	1.3	2052	7.3
Salix spp.	–	–	–	–	72	2.4	224	3.2	41	1.2	147	3.6
Betula spp.	–	–	–	–	144	4.7	579	8.1	1	0.0	3	0.1
Deciduous Shrubs	28	0.8	95	1.2	21	0.9	48	1.4	14	0.5	89	3.5
Evergreen Shrubs	26	0.4	73	0.9	5	0.1	11	0.2	11	0.3	20	0.4
Sedges	66	1.3	66	1.4	10	0.3	10	0.3	15	0.4	15	0.4
Forbs	18	0.3	10	0.2	14	0.4	14	0.4	14	0.4	14	0.4
Grasses	–	–	–	–	6	0.2	6	0.2	6	0.2	6	0.2
Lichens	0.2	0.02	12	0.2	8	0.0	19	0.7	4	0.0	35	1.0
Feather Moss	8	0.1	39	0.4	19	0.5	89	2.6	21	0.5	100	2.3
Sphagnum spp.	3	0.1	34	0.4	–	–	–	–	–	–	–	–
All	148	3.1	328	4.6	298	9.5	999	17.1	260	5.0	2482	19.3

Dashes indicate functional group not present at site. Units g C m^{-2} or g N m^{-2}.

was estimated to be correlated to the nitrogen content in new tissues and was calculated as a fixed percent (50% for evergreen and non-vascular plant functional types and 75% for deciduous, herbaceous and graminoid plant functional types).

We used an allometric equation developed for *Picea glauca* in Alaska (J. Yarie, unpublished data) to estimate the total spruce biomass. Estimates for spruce production based on white spruce biomass are from Yarie and Van Cleve (1983) and J. Yarie (unpublished data). For the white spruce functional type, we estimated GPP to be slightly more than twice NPP, based on relationships for Jack pine (Ryan et al. 1997).

Soil chemical and physical properties were sampled in the same sites (Michaelson and Ping 2003) that were used to develop the vegetation parameterizations. We used the total organic carbon (TOC) stocks reported for the top 30 cm, which generally included the organic (Oi, Oe and Oa) layer. In the shrub site this depth also included the A/B soil layer. Total soil N pools were determined using the LECO CHN analyzer. Plant available nitrogen (NH_4 and NO_3) were extracted from the soil with 2M KCl and determined colorimetrically (Michaelson and Ping, unpublished data).

MODEL EXTRAPOLATION

TEM 5.0 requires gridded input data sets for monthly climate (air temperature, precipitation, mean cloudiness), soil texture (percent sand, silt, clay), elevation and vegetation type. Input data sets were as in Zhuang et al. (2003) except for air temperature, precipitation and vegetation. We used monthly air temperature and precipitation data from a global data sets developed from thousands of station observations for the period 1901–2000 (Mitchell and Jones 2005; see also New et al. 2000). This climate data set was developed using an anomaly approach in which grids of anomalies relative to a standard normal period (1961–1990) were combined with high-resolution mean monthly climatology. Data were interpolated using an angular distance weighting function based on data from the eight nearest climate stations. At grid points beyond the influence of any stations, the anomaly fields were forced towards zero, the result of which is that the monthly climate relaxes toward the (warmer) 1961–1990 mean climatology. One additional consequence of the sparse coverage of climate stations in Alaska is an underestimation of the inter-annual variation in precipitation (New et al. 2000).

The vegetation data used for the model simulation combines several 1 km resolution vegetation maps for the North Slope (Muller et al. 1999), Seward Peninsula (http://www.geobotany.uaf.edu/arcticgeobot/spscs.html), and areas not covered in those two maps (http://agdc.usgs.gov/data/projects/hlct/hlct.html#K). We re-classified each 1-km vegetation pixel as tundra, shrub tundra or forest. The spatial domain (described below) consisted of 79% tundra, 13% shrub and 8% forest.

MODEL APPLICATION

We ran the model for the area of northern Alaska that extends from the Arctic Ocean to the tundra-boreal forest ecotone. This model domain encompasses 418 0.5 × 0.5 (latitude × longitude) degree grid cells. We ran the model for each vegetation type within each grid cell and then weighted the results in each grid cell by the percentage of each vegetation type in order to derive a spatial estimate. We present the results for the sum of the weighted results for each grid cell ("All") as well as the fraction contributed by each vegetation type (Tundra, Shrub, Forest).

The simulation began in 1900 and ran through 2000. In this study we only evaluate the results from 1981–2000, a time period when climate has warmed dramatically (Serreze et al. 2000). Changes in vegetation and soil carbon pools were calculated as the difference between the 2000 and 1980 December pool values. The fluxes were totaled for the entire year and the growing season (June, July, August-JJA). Trends for the climate responses and carbon fluxes were calculated as the regression of climate or flux variable from each grid cell on year, and the slope of the regression relationship is reported as the trend.

Results

FIELD BASED ESTIMATES USED TO CALIBRATE THE MODEL

Field-based measurements of total annual NPP across the sites ranged from 148 g C m^{-2} yr^{-1} in the tundra, to 298 g C m^{-2} yr^{-1} in the shrub and 260 g C m^{-2} yr^{-1} in the forest (Table I). Contributions to NPP in the tundra were from multiple functional types: sedges, evergreen and deciduous shrubs. In the tall shrub site, *Betula glandulosa* and *Salix spp.* dominated NPP. In the forest site, *Picea glauca* comprised the majority of NPP followed by *Salix spp* and feather moss (mainly *Pleurozium schreiberi*) (Table I). Vegetation carbon, which was estimated based on total biomass, increased 8-fold across the sites. Vegetation nitrogen also increased across the sites, leading to a higher vegetation C:N ratio in the forest than in the sites with less woody vegetation. Soil carbon was greatest in the forest site followed by the tundra, and lowest in the shrub sites. Soil nitrogen was highest in the forest site, but because of the large carbon stores the C:N ratio (16:1) was low and was similar to the shrub site (15:1), with the tundra having the highest ratio (28:1) (Table II).

CLIMATE TRENDS

Average annual air temperature over the domain increased by 0.86 °C from 1981 to 2000 ($F_{1,19} = 84.65$, $p < 0.001$). Growing season (June, July, August- JJA) air temperature increased by slightly less than 1.0 °C from 1981 to 2000 ($F_{1,19} = 119$, $p < 0.001$). Precipitation decreased 1.5 mm yr^{-1} (6% of the annual precipitation), with a total decrease of around 30 mm over the two decades ($F_{1,19} = 60.22$, $p < 0.001$). Growing season precipitation decreased an average of 0.6 mm yr^{-1}

TABLE II

Ecosystem pools and fluxes based on field data and estimates used in model calibration. Fluxes (g m^{-2} yr^{-1}): net primary production, nitrogen in net primary production, estimated gross primary production, nitrogen uptake. Pools (g m^{-2}): vegetation carbon, vegetation nitrogen, soil carbon and soil nitrogen.

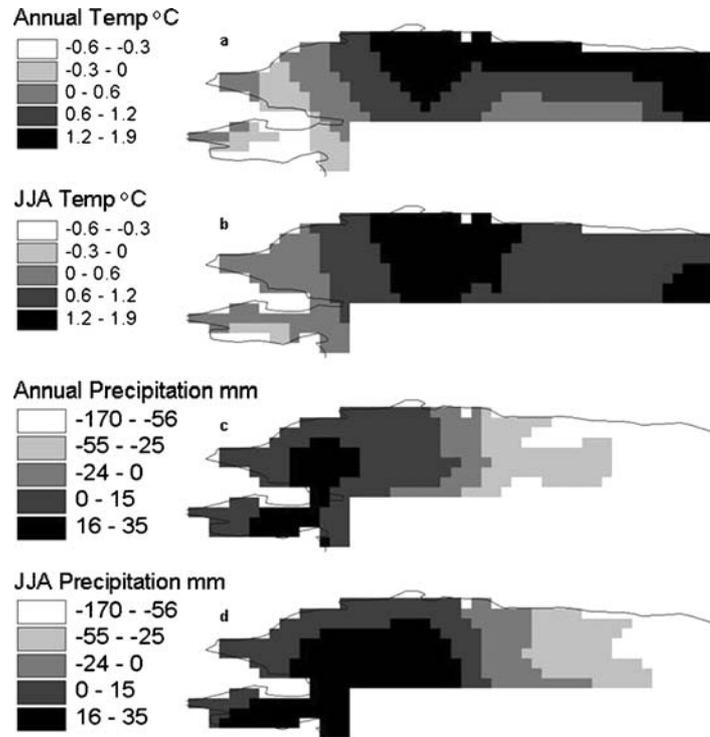|	Tundra	Shrub	Forest
Net primary production	148.37	298.43	260
Nitrogen in net primary production	3.11	9.51	4.98
Gross primary production	296.75	596.86	721.56
Nitrogen uptake	1.76	3.43	2.49
Vegetation carbon	328.04	999.02	2481.63
Vegetation nitrogen	4.55	17.1	19.26
Soil carbon	14200	12800	22500
Soil nitrogen	500	800	1500

Figure 1. Climate trends 1981–2000: annual and growing season (June July August JJA) temperature and precipitation changes. Data from Mitchell et al. (submitted).

(9% of the summer precipitation) for the 20 years resulting in a decrease of about 12 mm over the two decades ($F_{1,19} = 644.26$, $p < 0.001$). The statistical analyses indicate that the relationship between year and each climate variable (i.e., trend with time) is statistically significant, but that there is substantial variability about the trend line.

We calculated the trend in the temperature and precipitation data by regressing each of the annual average climate parameters in each grid cell with year. Changes in air temperature and precipitation have distinct spatial patterns over the domain of our study (Figure 1). Annual temperatures generally increased over the entire region, with the greatest warming in the central north, near Barrow (Figure 1a). Western Alaska, especially the Seward Peninsula appears to experience cooling of less than $1.0\,^\circ$C. Most of the domain showed increases in growing season air temperatures (Figure 1b). The annual precipitation trends show a strong west to east gradient, with the greatest increases in precipitation centered over the northwestern portion of the domain, including the Seward Peninsula (Figure 1c). Precipitation decreases across in the eastern half of the domain, with the greatest decreases at Alaska's eastern border. This pattern is maintained in the growing season (JJA)

data but is shifted to the east (Figure 1d). Thus the gradients in continentality of precipitation have steepened in the last 20 years.

When the combined temperature and precipitation trends are considered, most grid cells (53%) experienced warmer and dryer conditions over the 20 years, 28% experienced warmer and wetter conditions, and 18% became colder and wetter; the climate data did not indicate colder and drier conditions over the duration of this study. During the growing season, 44% of cells warmed and dried, 53% became warmer and wetter and only 3% of grid cells became colder and wetter, indicating that the shift to warm wet conditions was more widespread and the shift to cold wet conditions was less widespread in summer than annually.

REGIONAL CHANGES IN ECOSYSTEM CO_2 FLUXES

Modeled annual NPP, when averaged over the entire domain for the combined vegetation, showed a slight but non-significant increase over the two decades (Figure 2a). Of the three vegetation types, tundra was the only type with a significant positive NPP response to changing climate in the period 1981–2000. In contrast, shrub and forest NPP decreased over this time period. Annual R_H increased across the domain (Figure 2b). The tundra response dominated the overall R_H response. For the shrub and forest types, the change in annual R_H was close to zero and the relationships with year were non-significant. NEP was positive during the beginning of the period but decreased with year for the overall domain and in each vegetation type with year (Figure 2c). The overall NEP in the region switched from net sink to net source in the mid 1990s, NEP declined in tundra because the strong positive R_H response in the tundra type outpaced the slight increases in NPP. NEP decreased in the shrub type because the slight decreases in NPP exceeded the near flat R_H response; however the trend for the shrub NEP is close to zero. The forest NEP appears to switch to a net source in the early 1980s and NEP in the forest vegetation type decreases on the same order of magnitude as the tundra type. Although the R_H response outpaces NPP, NPP exceeds R_H for a majority of the time period of the analysis, therefore the dominant cumulative effect is due to the NPP rather than R_H (Figure 2c).

Across the entire domain the mean vegetation carbon pools increased slightly during the period, despite the decreases in NEP (Table III, Figure 3a). The tundra type showed small losses (Table III, Figure 3b), while the shrub and forest types increased (Table III, Figure 3c,d). Of the three vegetation types, the forest had the greatest range in vegetation carbon change across the domain. Soil carbon for the entire domain showed negligible change over the two decades (Table III, Figure 4a). This resulted from substantial gains in soil C in tundra balanced by large losses in shrub and slight losses in the forest (Figure 4b–d). The shrub ecosystems had the greatest variability in soil carbon losses and gains across the domain (Table III, Figure 4c).

TABLE III

Change in vegetation, soil and ecosystem carbon pools from 1980 to 2000. Area weighted means and standard deviations shown. Units for carbon pools g C m^{-2}

	All	Tundra	Shrub	Forest
Vegetation Carbon	20.1 ± 111	-1.2 ± 53	17.3 ± 101	41.1 ± 106
Soil Carbon	9.6 ± 483	106.6 ± 234	-149.1 ± 513	-9.9 ± 45
Ecosystem Carbon	29.7 ± 507	105.0 ± 261	-132.0 ± 522	31.1 ± 104
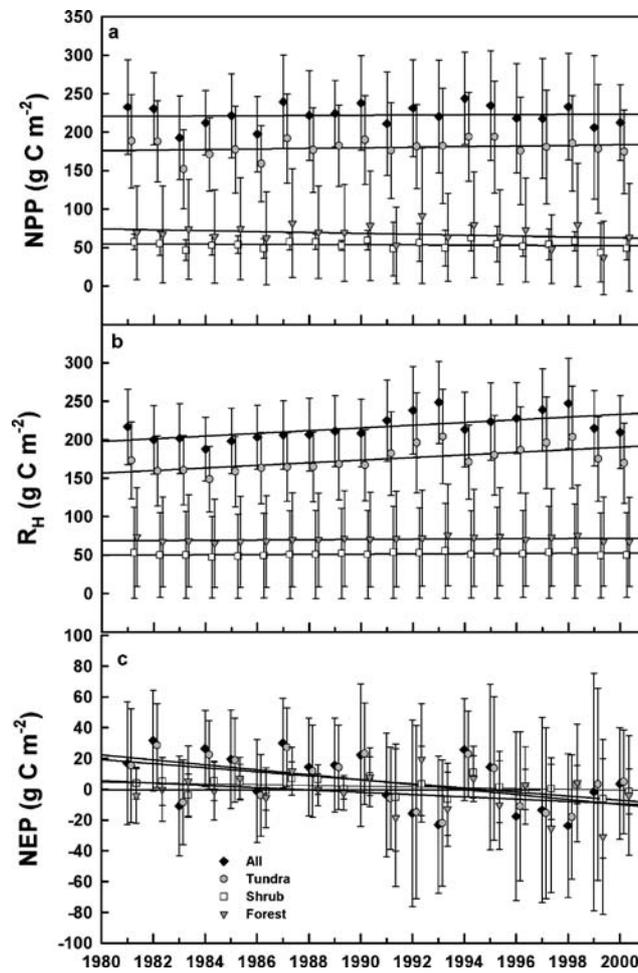
Figure 2. NPP, R_H and NEP fluxes for the domain. Mean and standard deviation shown for combined vegetation and tundra, shrub and forest results separately. Graphic appears offset by year for easier viewing.
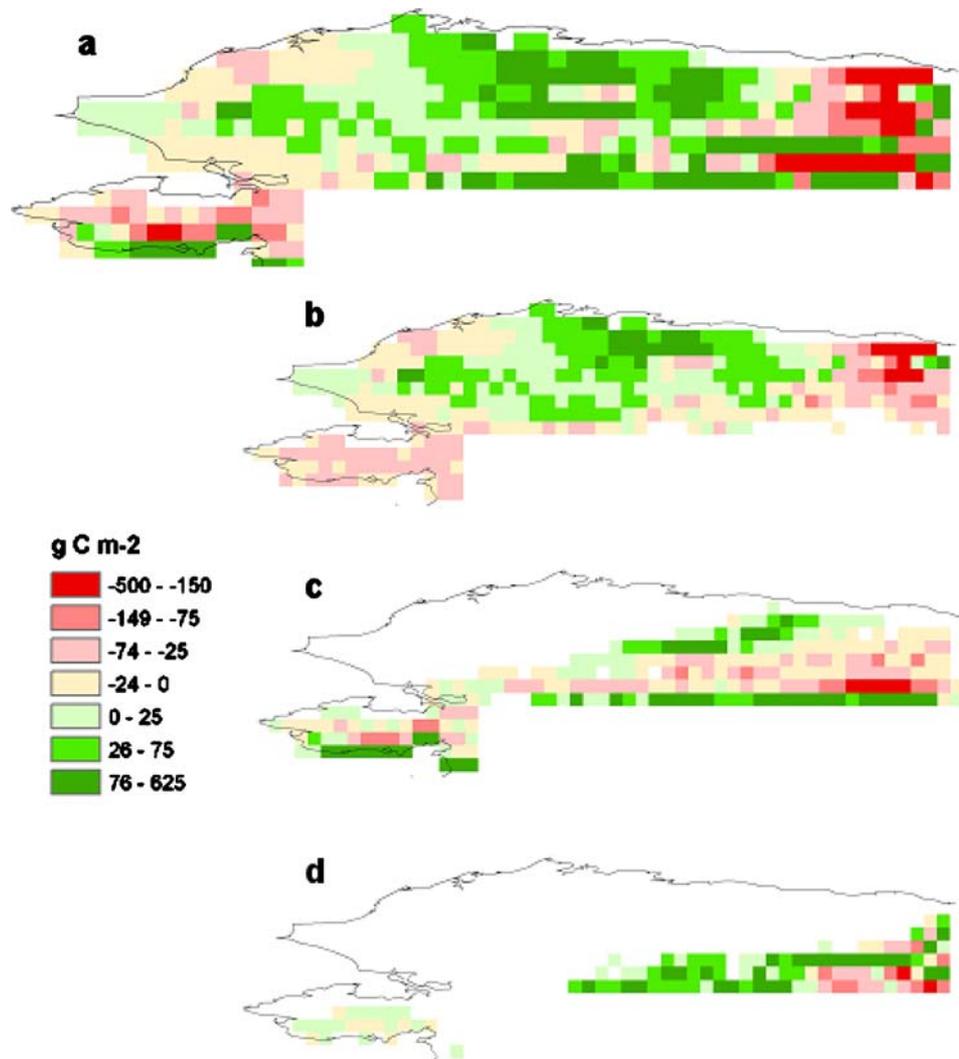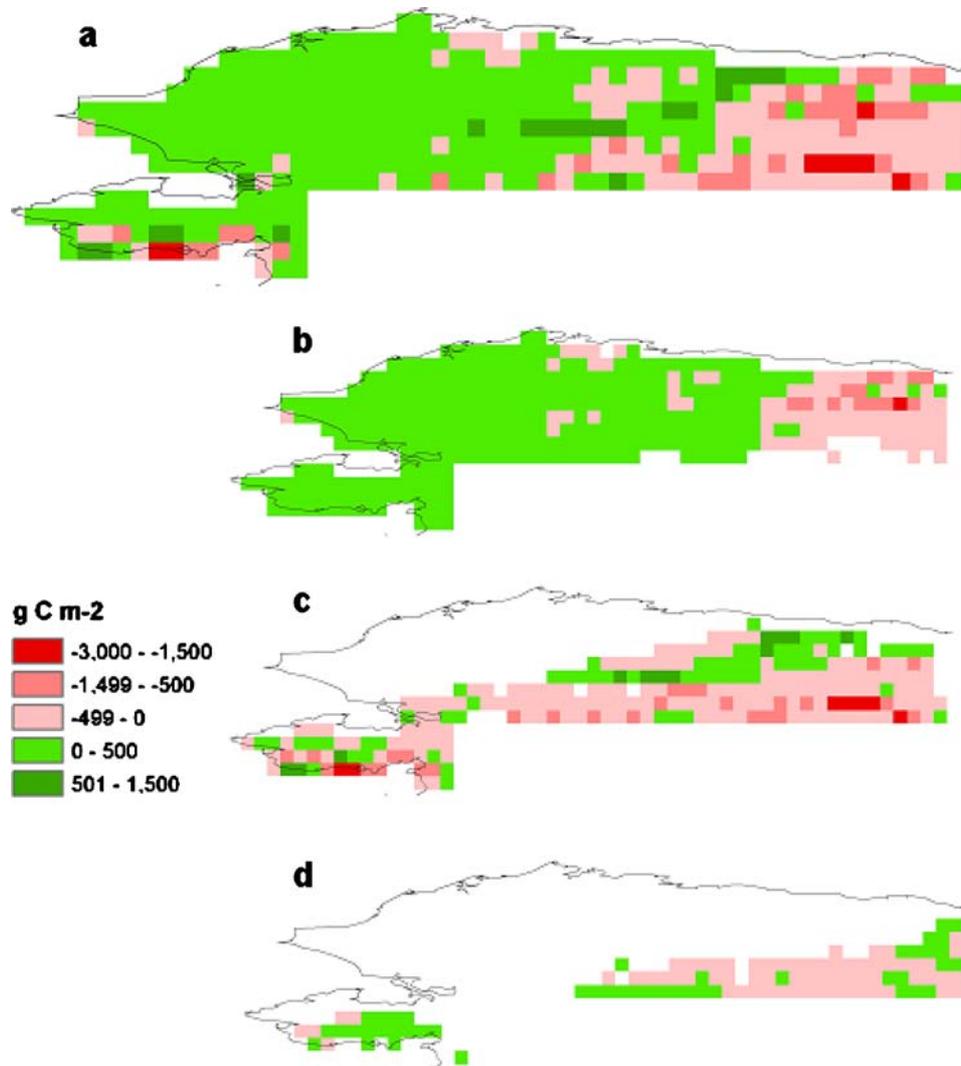
Figure 3. Changes in vegetation carbon (g C m^{-2}) for the time period 1981–2000. (a) combined vegetation types, (b) tundra, (c) shrub, (d) forest vegetation types.

RELATIONSHIP OF TRENDS IN CARBON POOLS AND FLUXES TO SPATIAL
VARIABILITY IN CLIMATE TRENDS

Spatial variation in climate trends was a strong driver of the spatial variation in the trends of carbon fluxes. We used stepwise linear regressions of trends in carbon fluxes on air temperature and precipitation trends to evaluate the spatial component of the regional patterns presented in the previous section. For all three fluxes modeled, the most significant regression model contained both the

Figure 4. Changes in soil carbon (g C m^{-2}) for the time period 1981–2000. (a) combined vegetation types, (b) tundra, (c) shrub, (d) forest vegetation types.

trends in air temperature and precipitation. However, the relative importance of the driving climate variable, varied among the fluxes. In all vegetation types NPP was positively correlated with both air temperature and precipitation (Figure 5a). Although the overall correlation of trends in NPP with trends in temperature were positive, there were many cases in which temperature increases coincided with large decreases in NPP (Figure 5a), suggesting an interaction between temperature and precipitation effects on NPP. NPP trends responded nonlinearly to precipitation trends in all vegetation types, with the largest increases in NPP at a precipitation
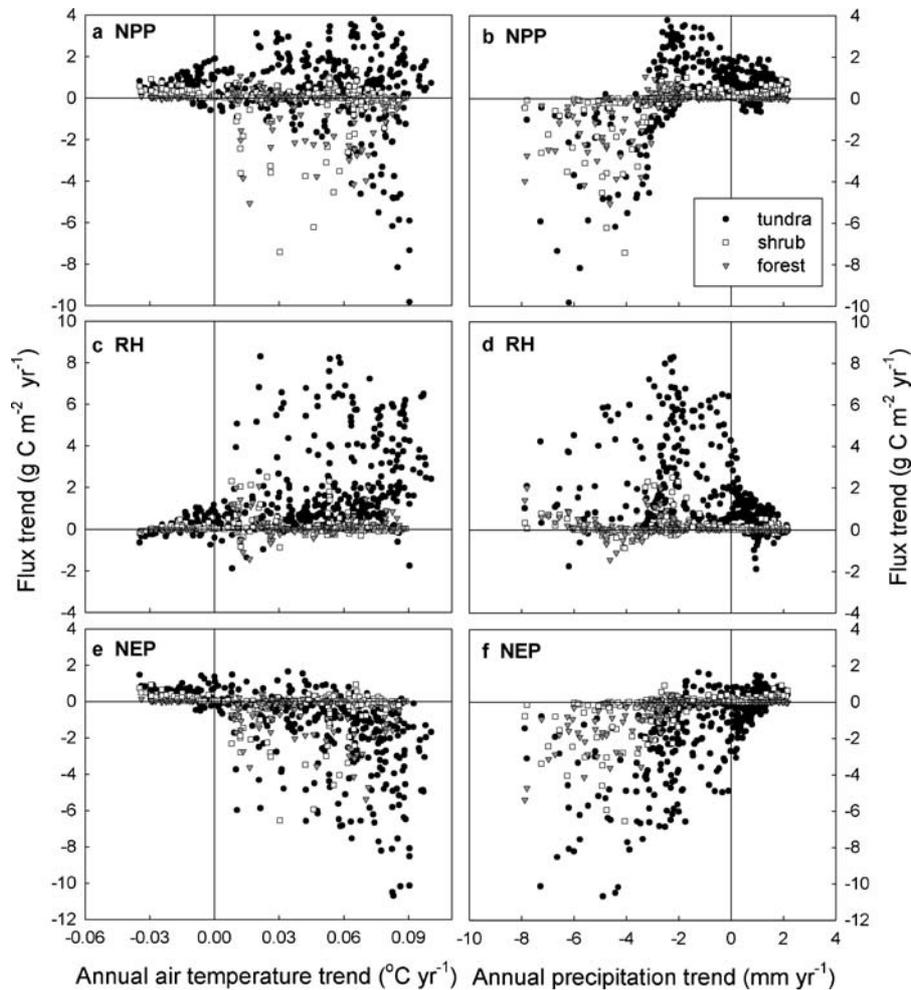
Figure 5. Response of fluxes (NPP, R_H and NEP) to annual air temperature and precipitation trends.

decrease of about 3 mm yr^{-1}. In this range the shrub and forest types showed much less variability than the response of tundra NPP to precipitation changes. At larger decreases in precipitation, NPP trends declined precipitously, especially in tundra. Across this range in precipitation trends, all vegetation types showed large variability (Figure 5b), especially in tundra. Results from the stepwise regressions showed that the variation in the NPP trends for the combined types was largely explained by the precipitation trends. Changes in vegetation carbon pools across the domain were correlated with the trends in NPP (Figure 6a) ($R^2 = 0.11$). Changes in vegetation carbon pools were not well correlated with R_H trends (Figure 6b) ($R^2 = 0.02$).
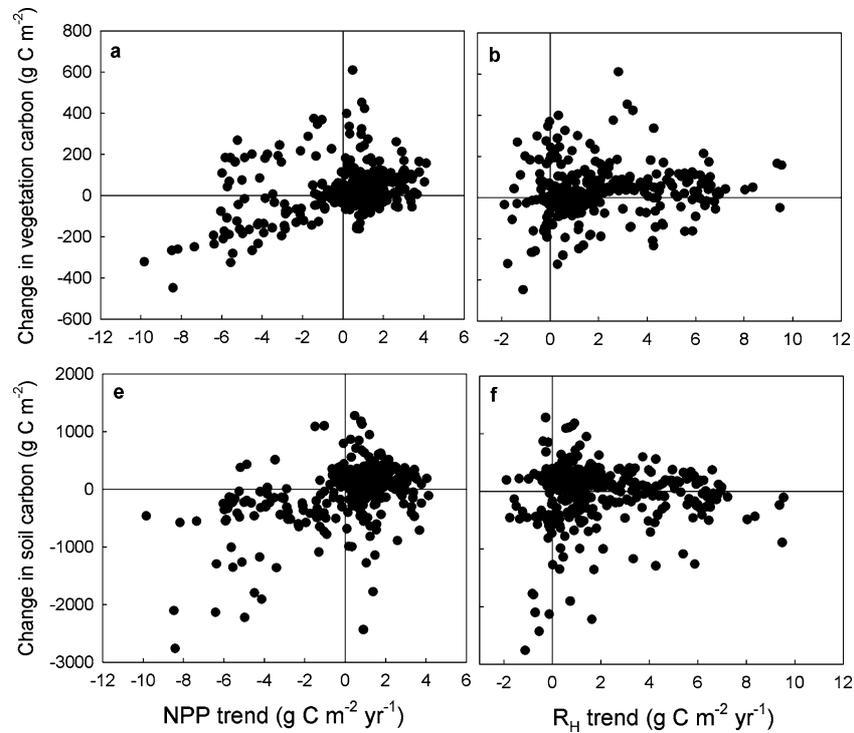
Figure 6. Relationship between selected pools and fluxes: (a) changes in vegetation carbon vs. NPP, (b) changes in vegetation carbon vs. R_H, (c) changes in soil carbon vs. NPP (d) changes in soil carbon vs. R_H.

Trends in R_H were positively correlated with temperature trends (Figure 5c) but negatively correlated with changes in precipitation (Figure 5d). These climatic sensitivities were most pronounced in tundra. The range in the tundra flux response was high at all ranges of temperature increases (Figure 5c). The negative correlation of the R_H trends with precipitation explained less variability than the relationship with temperature (Figure 5d). The R_H trends in both shrub and forest types were not significantly correlated with either of the climate trends. However, the shrub type had a greater range in response to the climate trends than the forest and both were much less varied than the tundra. Changes in soil carbon were more strongly correlated with NPP trends than they were with R_H trends (Figure 6c and d). NPP correlated positively with soil C ($R^2 = 0.21$), so that the areas where net primary production increased also accumulated soil carbon. Changes in the soil carbon pools were not well correlated with the trends in R_H ($R^2 = 0.00$).

NEP trends correlated negatively with temperature trends in combined vegetation and tundra and positively with temperature trends in shrub and in forest. All vegetation types showed a strong positive linear correlation between NEP trends

and precipitation trends (Figure 5f). These analyses indicate that non-linear responses of NPP and R_H with temperature and moisture caused NPP and R_H to essentially cancel each other under scenarios where temperature and precipitation were both increasing.

INTERACTION BETWEEN CARBON FLUXES AND CLIMATE

The relationships described above illustrate the complex responses of carbon pools and fluxes to changes in climate. This is further complicated by the spatial variation of climate and a possible spatial correlation of vegetation type to climate. To separate these interacting effects, we used ANOVA to compare climate responses in the three climate states; warm/dry, warm/wet and cold/wet. We performed ANOVAs using these climate states as the independent variable, to look specifically at the range of responses to these combined temperature and precipitation effects. Overall, NPP decreased where climate trends were toward warm and dry conditions and increased where trends were toward warm/wet or cold/wet conditions (Figure 7a). The means for the two trends with increasing moisture were not significantly different. This suggests that trends toward drier conditions had a stronger negative effect on NPP than did trends in temperature. Unlike the other vegetation types, tundra NPP response increased in all climate combinations (Figure 7b–d).

R_H increased overall with all three categories of climate states (Figure 7a). The mean increase was greatest where conditions became warmer and drier and least where conditions became colder and wetter, suggesting that increased moisture dampened the R_H response to increased temperature. Tundra R_H trends followed this overall response. In contrast to the tundra response, shrub R_H trends did not differ significantly among climate trends. Forest R_H responded more to warming and drying trends than wetter conditions.

Trends in overall NEP differed significantly among categories of climate states (Figure 7). Warmer-drier (223 grid cells) and warmer-wetter (118 grid cells) areas had the greatest decreases in NEP, resulting in decreases in their carbon storage capacity. In contrast, in colder/wetter areas (77 grid cells) NEP responded positively, which would lead to increases in carbon storage under this climate condition. The NEP response parallels the R_H, response for the warmer/dryer climate trends but follows the NPP response where conditions became colder and wetter. The NEP response was significantly different among climate trends for the tundra and forest types but not for the shrub.

In summary, results from the ANOVA provide insights into the interactions between temperature and precipitation trends. Under warmer and drier conditions, NPP responded negatively and R_H responded positively, leading to net release of carbon to the atmosphere. This climate combination drove the greatest negative NEP trends. In warmer and wetter conditions NPP responded positively, however, the negative R_H response outpaced the NPP response so that the net response of NEP was negative, also resulting in net release of carbon. Lastly, in colder and
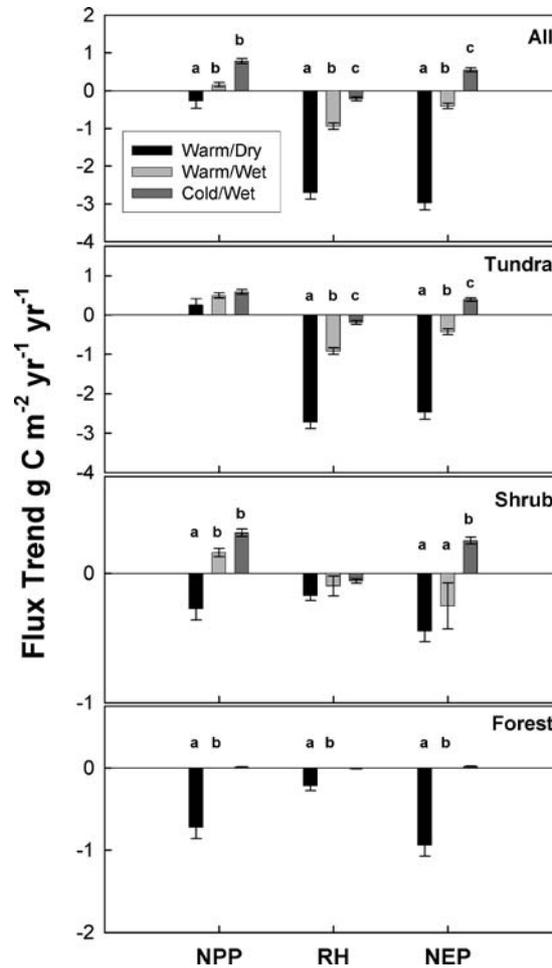
Figure 7. ANOVA analysis of means for NPP, R_H and NEP responses in different climate states. Letters represent significant differences in means at the $p < 0.05$ level. Note scale change for shrub and forest vegetation type fluxes.

wetter regions, NPP increased, and R_H decreased. This is the only climate state which resulted in positive NEP trends, or net storage of carbon.

Discussion/Conclusion

Our research highlights the potential importance of spatial variability in Alaskan Arctic carbon balance. Our results, which show a slight overall increase in vegetation carbon over the last two decades follow expectations that high-latitude

ecosystems would show an increase in NPP as climate warms (Oechel et al. 2000; Shaver et al. 2000; Shaver et al. 2001).

In an Alaskan moist acidic tundra ecosystem, long-term experimental warming has led to increases in vegetation carbon (Shaver et al. 2001). Our model results show the same direction of change. We compared a subset of the domain, which included predominately tundra cells, to the area used by Jia et al. (2003) in an analysis of NDVI changes and correlated biomass change. The modeled change in total vegetation C in this area between 1980 and 2000 was 27.6 ± 75 g C m^{-2}, less than the C increases of about 81 ± 38.5 g C m^{-2} (increase in biomass was 171.5 ± 81 g m^{-2}) reported by Jia et al. (2003) for the same time period but still within the range of their estimates. These independent estimates of changes in vegetation carbon both show a similar trend towards increases in the Alaskan tundra region.

Modeled shrub vegetation carbon increased, although there was considerable spatial variability in the changes in shrub carbon pools over the last twenty years. In long-term warming experiments, particularly in combination with N fertilization, moist acidic tundra has shifted to tall shrub-dominated tundra (Shaver et al. 2001). There have been few experiments on the responses of tall shrub tundra to warming. Expansion and infilling of existing patchy tall shrub tundra has been documented in the Alaskan Arctic using repeat photography (Sturm et al. 2001). Regions in our study area that did show increases in shrub vegetation carbon were located near these aerial photograph transects. Shrub vegetation also increased on the Seward Peninsula, where shrub growth during the last two decades was documented using remote sensing (Silapaswan et al. 2001). Shrub change detection has not been conducted in the areas of our study near treeline area in the Brooks Range where modeled shrub carbon decreased. It is possible that existing shrubs may become drought-stressed at treeline. Warming experiments over taller shrub canopies or measurement of ring widths in treeline shrubs would increase our understanding of the shrub responses to changing climate conditions along the transition from tundra to boreal forest.

Modeled forest vegetation carbon also responded positively to the climate trends over the last 20 years. The relatively small increases in forest biomass are not surprising given the increasing evidence that warming conditions combine with decreasing moisture to create drought stress for trees close to treeline (Wilmking et al. 2005). A possible compensatory response over time would occur between decreases in NPP for mature trees and increases in NPP for seedling recruitment and survival. These demographic responses are not likely to have had a strong positive effect on vegetation carbon pools over the last two decades, and are not included in the model that we used.

Soil carbon pools might also be expected to decrease with warming conditions, as heterotrophic respiration increases in response to more favorable temperature conditions. Warming in combination with moisture decreases would also be expected to lead to even greater increases in R_H, which was the case in this

study. Across the domain soil carbon decreased although there were significant differences among the vegetation types. Tundra was the only vegetation type in which soil carbon increased, in spite of increases in R_H. As NPP increases in tundra areas, litter inputs to the soil also increase. In contrast with the tundra, shrub soil carbon decreased significantly. This result agrees with results from a long term fertilization of moist acidic tundra, where soil carbon losses were associated with the development of a shrub canopy, and in conjunction with this change, soil carbon losses averaged 200 g Cm^{-2} yr^{-1}(Mack et al. 2004). In that study, the carbon loss occurred in the deep soil layers, perhaps as a result of increased decomposition in response to increased nutrient availability in old litter, decomposition of labile SOC in deep soil layer, and losses through mineralization or leaching of DOC or less inputs from deep-rooted species (Mack et al. 2004). This scale of soil carbon loss is an order of magnitude greater than the average changes we saw in modeled shrub tundra; however, our results do include grid cells in which shrub tundra soil carbon changes were of this order of magnitude.

The observed climate changes over the 20-year period of this study resulted in non-significant increases in NPP. However, R_H did increase slightly across the domain. The net result of these flux responses is a decreasing trend in NEP during the 1981–2000 period, including a switch from net sink of C to net source in the region during the mid-1990s. However, the dominant cumulative effect is due to the NPP rather than R$_H$. The region-wide results were characterized by significant variability, which prompted a further comparison of spatial variability in the trends in carbon fluxes with the trends in air temperature and precipitation.

Our analysis by grouped climate states showed that domain-averaged NPP responded positively to wetter conditions, and negatively to drier conditions, leading to net storage of vegetation carbon in areas where climate was warmer and wetter. R_H increased where temperatures increased or precipitation decreased, or where NPP had increased. NEP decreased with temperature increases, and also with precipitation decreases, so that regions experiencing warmer, drier conditions had decreases in net carbon storage when evaluated on an annual basis. In our study, modeled plant community types responded differently to the climate trends, which also contributed to the spatial variability in the net carbon fluxes. NPP increased only in tundra areas regardless of the climate trend, and negative responses were seen in the shrub and forest ecosystems under drier conditions. Changes in NPP significantly affected the R_H fluxes and therefore the net storage of carbon. These results are similar to the results of a modeling study of carbon balance in the Kuparuk river basin (Les Dizes et al. 2003) in which spatial patterns of tundra C responses differed greatly and depended on whether the future climate conditions were wet or dry. Although both scenarios were under warmer temperatures, in contrast to our results, the dry scenario in the Les Dizes et al (2003) study led to more C storage than a wet scenario. The sensitivity of both modeling approaches to precipitation changes highlights the need for accurate climate data sets for use in historical and projected change. The low density of weather stations in this region has made the

uncertainty regarding the input climate data sets a common problem for models applied to northern regions.

The variability in our results also point to the difficulties in extrapolating plot or landscape-scale carbon budget studies in Alaska because the responses of single studies may not apply to all climate states, and the extrapolation of different sets of plot based studies may lead to different conclusions about future net carbon balance in the region. For example, based on CO_2 flux measurements from a limited number of sites, Oechel et al. (2000) hypothesized that net ecosystem CO_2 flux in the Alaskan arctic coastal and inland tussock tundra ecosystems had acclimated to climate warming. Temperature increases documented in that study were similar to those in our climate data set; however the summer precipitation showed no significant trend, whereas the precipitation trends in our study, which extends further east and south, were towards drier conditions. In contrast with the results of Oechel et al. (2000), in our study the warmer wetter climate states were associated with decreases in carbon storage, rather than increases. Our results parallel those of Stieglitz et al. (2000) which evaluated mechanisms governing carbon dynamics using a combined hydrologic, canopy and soil model. The results from Stieglitz et al. (2000) indicated that over short time scales, dry conditions led to increased soil decomposition and a net loss of ecosystem carbon while cool moist conditions led to decreased soil decomposition and a net gain in ecosystem carbon.

While we caution against the simple extrapolation of field studies that do not span all climate states, it is important to recognize that the parameterizations we used in this modeling study are based on studies that have been conducted at a limited number of sites. Because of the limited data we used in our parameterizations, it is not clear how well the parameters in the model are constrained. There are also substantial uncertainties in the climate data sets we used to drive the model because of the sparse data coverage of climate stations in northern Alaska. We must therefore also caution against accepting the accuracy of the results of this model exercise as better than the accuracy of simple extrapolations of field studies that have limited spatial coverage. The value of this study is that it identifies the potential complexity of ecosystem carbon responses over a region in which climate variability may be heterogeneous. Clearly, what is needed in assessing the effects of climate change on regional carbon storage is a more rigorous assimilation by ecosystem models of all available data on ecosystem carbon responses in the region (e.g., see Braswell et al. 2005; Williams et al. 2005). Such studies have the potential to better quantify uncertainties in simulated carbon responses given the model and the available data on ecosystem carbon dynamics.

In summary, our research highlights the potential importance of interactions between spatial/temporal variability in climate trends and the major arctic/treeline vegetation types in controlling net carbon exchange across the arctic tundra-boreal forest transition zone. This modeling study suggests that the spatial variation in the magnitude and direction of observed climate change, in combination with landscape-scale vegetation heterogeneity is likely to have a significant influence

on the regional carbon budgets. Future progress in assessing the effects of climate change on regional carbon storage will require a more rigorous assimilation of data on ecosystem carbon responses by ecosystem models.

Acknowledgements

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