VEGETATION-CLIMATE INTERACTIONS ALONG A TRANSITION FROM TUNDRA TO BOREAL FOREST IN ALASKA

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A

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ABSTRACT

The climate of the Alaskan Arctic is warming more rapidly than at any time in the last 400 years. Climate changes of the magnitude occurring in high latitudes have the potential to alter both the structure and function of arctic ecosystems. Structural responses reflect changes in community composition, which may also influence ecosystem function. Functional responses change the biogeochemical cycling of carbon and nutrients. We examined the structural and functional interactions between vegetation and climate across a gradient of vegetation types from arctic tundra to boreal forest.

Canopy complexity combines vegetation structural properties such as biomass, cover, height, leaf area index (LAI) and stem area index (SAI). Canopy complexity determines the amount of the energy that will be available in an ecosystem and will also greatly influence the partitioning of that energy into different land surface processes such as heating the air, evaporating water and warming the ground. Across a gradient of sites in Western Alaska, we found that increasing canopy complexity was linked to increased sensible heating. Thus, vegetation structural changes could represent an important positive feedback to warming.

Structural changes in ecosystems are linked to changes in ecosystem function. High latitude ecosystems play an important role in the earth's climate system because they contain nearly 40% of the world's reactive soil carbon. We examined Net Ecosystem Production (NEP) in major community types of Northern Alaska using a combination of field-based measurements and modeling. Modeled NEP decreased in both warmer and drier and warmer and wetter conditions. However, in colder and wetter conditions, NEP increased. The net effect for the region was a slight gain in ecosystem carbon; however, our research highlights the importance of climate variability in the carbon balance of the study region during the last two decades.

The next step forward with this research will be to incorporate these results into coupled models of the land-atmosphere system. Improved representations of ecosystem structure and function will improve our ability to predict future responses of vegetation composition, carbon storage, and climate and will allow us to better examine the interactions between vegetation and the atmosphere in the context of a changing climate.

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In memory of Taryn Hoover

CHAPTER 1: INTRODUCTION

Introduction

Atmospheric concentrations of greenhouse gases have increased steadily since the pre-industrial era. The Intergovernmental Panel on Climate Change (IPCC) has concluded that the buildup of these gases is likely to lead to increases in the annual global surface temperature of 1.0 to 3.0 °C by the end of the 21st century (IPCC 2001). The climate of the Alaskan Arctic is currently warming more rapidly than at any time in the last 400 years (Overpeck et al. 1997, Serreze et al. 2000, Hinzman et al. In press). Climate changes of the magnitude predicted to occur in high latitudes could significantly alter both the structure and function of arctic ecosystems. Structural responses reflect changes in community composition at a species level, which may also influence ecosystem function (Melillo et al. 1995). Functional responses are defined as changes in the biogeochemical cycling of carbon, nutrients and water (McGuire et al. 1995) (Fig. 1.1).

The recent warming in high latitude regions has triggered structural changes, including increases in plant growth observed from satellites (Myneni et al. 1997, Hope et al. 1999, Zhou et al. 2001) and expansion of trees and shrubs (Silapaswan et al. 2001, Sturm et al. 2001). These vegetation structural changes may have consequences for climate by modifying land-surface characteristics such as albedo, roughness length, and canopy resistance. These changes could affect the climate system through alterations in surface energy balance (Chapin et al. 2000, Kittel et al. 2000, McGuire et al. 2002) by affecting the quantity of energy absorbed and the pathways by which energy is transferred to the atmosphere and soil (Bonan 2002).

Canopy complexity summarizes the combination of vegetation properties such as biomass, cover, height, leaf area index (LAI) and stem area index (SAI). Canopy complexity can be broken into a horizontal component i.e., the spatial variability in vegetation distribution, and a vertical component, i.e., the vertical distribution of leaf and stem biomass. Canopy complexity will determine the amount of the sun's energy that will be available in an ecosystem and will also greatly influence the partitioning of that energy into different land surface processes, such as heating the air, evaporating water and warming the ground. In Chapter 2, we describe the structural differences in the major ecosystem types that characterize the transition from arctic tundra to boreal forest in western Alaska and evaluate the relationship between canopy complexity and the partitioning of net radiation budget in the context of arctic ecosystem responses to a changing climate. This chapter is the first explicit analysis of the impact of ecosystem structure on climate feedbacks.

Structural changes in ecosystems are linked to changes in ecosystem function. As distributions of plant communities in an ecosystem change, so does their capacity to store carbon. Because high latitude ecosystems contain nearly 40% of the world's reactive soil carbon (McGuire et al. 1995), they play an important role in the earth's climate system (Bonan et al. 1995). The direction and magnitude of shifts in ecosystem function in response to environmental change, specifically shifts in net carbon storage, are particularly important. Future changes in net carbon storage are presently difficult to predict because of interactions among ecosystem processes, such as primary production, decomposition, nitrogen mineralization and other dynamic ecosystem components, such as soil moisture and temperature, 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 arctic ecosystems.

Net carbon storage in terrestrial ecosystems is primarily determined by the balance between net primary production (NPP) and heterotrophic respiration (R_H). 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 species in the community. Heterotrophic respiration releases CO_2 to the atmosphere, primarily through decomposition of organic matter. The response of net carbon exchange, i.e., net ecosystem production (NEP), to climate change, therefore depends on whether the response of R_H is greater or less than the response of NPP. Ecosystem processes respond differently to changes in temperature and moisture. R_H is expected to increase in response to warming temperatures (Oechel et al. 1993). NPP has increased in response to warming in some ecosystems (Chapin et al. 1995), but has also been shown to be limited by moisture in others (Barber et al. 2000). Because of the differential responses of NEP to climate changes, understanding the relative effects of changes in climate are important to predicting the trajectory of net carbon exchange over time (Oechel et al. 2000).

In Chapter 3, we evaluate the temporal and spatial patterns of changes in ecosystem function, specifically net carbon exchange, in Alaskan ecosystems that span the transition from arctic tundra to boreal forest. We examine the influence of climate variability on net ecosystem carbon exchange during the last two decades and the differential response of major community types to decadal temperature and precipitation trends. We use field-based measurements of NPP, vegetation, and soil carbon and nitrogen pools in tundra, shrub tundra, and treeline evergreen conifer forest ecosystems 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. We use this approach of combining field measurements with modeling to assess the controls over the net carbon exchange in response to climate during the past two decades. This work represents the first analysis of interactions between regional climate variability and vegetation composition and function in controlling net carbon exchange in the Alaskan Arctic. The work presented in this dissertation adds to our understanding of the structural and functional interactions of vegetation with climate in the Arctic. Incorporating the results presented in this dissertation into coupled models of the land-atmosphere system will improve our ability to predict the responses of arctic and boreal ecosystems to a changing climate and the influence of vegetation changes on climate.

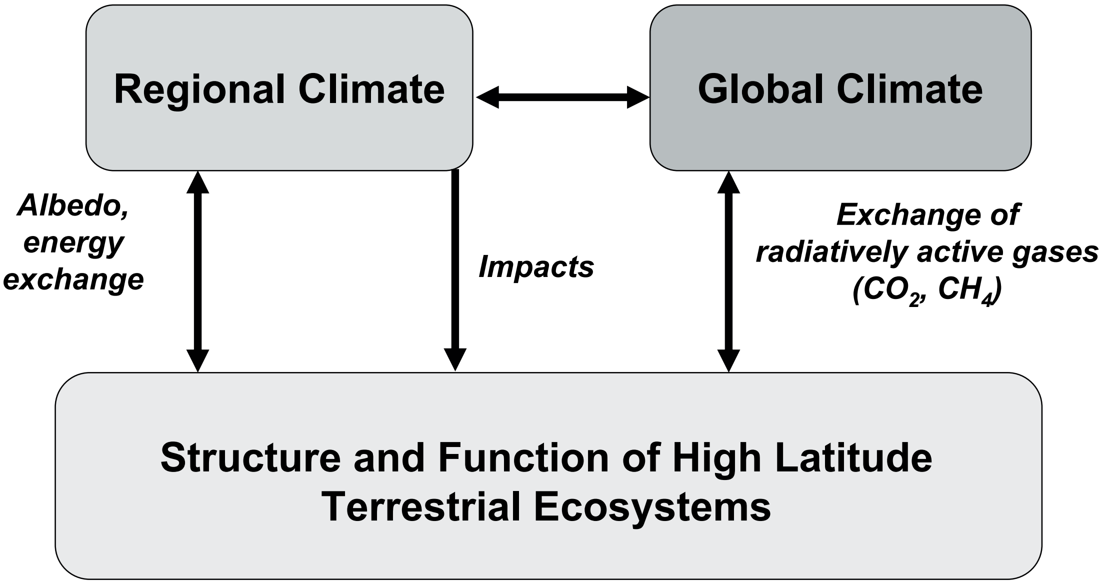

Figure 1.1 The interactions of ecosystem structure and function with regional and global climate via albedo and energy exchange and the exchange of radiatively active gases.

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CHAPTER 2: STRUCTURAL FEEDBACKS TO CLIMATE*

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Abstract

Current climate changes in the Alaskan Arctic, which are characterized by increases in temperature and length of growing season, could alter vegetation structure, especially through increases in shrub cover or the movement of treeline. As these changes in vegetation structure have consequences for the climate system, we investigated the relationship between structural complexity and partitioning of surface energy in five ecosystems that span the transition from tundra through shrub tundra to closed canopy forest. Along this gradient of increasing canopy complexity, we measured key vegetation characteristics, including community composition, biomass, cover, height, leaf area index and stem area index. In this study we relate these vegetation characteristics to albedo and the partitioning of net radiation into ground, latent, and sensible heating fluxes. Canopy complexity increased along the sequence from tundra to forest due to the addition of new plant functional types. This led to non-linear changes in biomass, cover, and height in the understory. The increased canopy complexity resulted in reduced ground heat fluxes, relatively conserved latent heat fluxes and increased sensible heat fluxes. The localized warming associated with increased sensible heating over more complex canopies may amplify regional warming, causing further vegetation change in the Alaskan Arctic.

Introduction

The climate of the Alaskan Arctic is currently warming more rapidly than at any time in the last 400 years (Overpeck et al. 1997; Serreze et al. 2000). This warming appears to have triggered vegetation changes that include general increases in plant growth observed from satellites (Myneni et al. 1997; Zhou et al. 2001) and expansion of trees and shrubs (Silapaswan et al. 2001; Sturm et al. 2001). Indigenous observations suggest that this shrub expansion is widespread in the North American Arctic (Thorpe et al. 2002). These observations are consistent with warming experiments in which some species or groups of species (plant functional types), especially key deciduous shrub species, have been particularly responsive to recent warming in Alaska (Chapin et al. 1995; Hobbie & Chapin 1998; Bret-Harte et al. 2001) and other arctic sites (Graglia et al. 1997; Shevtsova et al. 1997; Hartley et al. 1999). If species respond differentially to warming, the relative abundances of plant growth forms will likely change through changes in the biomass of existing plants or immigration of new species. In either case, these vegetation changes will alter the structure of an ecosystem and may have consequences for climate by modifying surface characteristics such as albedo, roughness length, and canopy resistance. These changes could feed back to the climate system through alterations in surface energy balance and carbon storage (McGuire et al. 2002; Kittel et al. 2000).

Community differences in biomass and vegetation structure strongly influence surface energy exchange by determining the quantity of energy absorbed and the pathways by which energy is transferred to the atmosphere and soil (Bonan 2002). The energy absorbed depends on the quantity of absorbing surfaces (approximated by leaf area), the albedo (reflectance) of individual leaves, and the complexity of the canopy, which influences the efficiency with which the canopy traps incoming solar radiation (Oke 1987). Canopy complexity also influences the efficiency and pathway by which absorbed energy is transferred to the atmosphere. The height and density of roughness elements and their structure govern mechanical turbulence and efficiency of convective exchange between leaf and soil surfaces and the atmosphere. The canopy properties also influence, through shading, the partitioning of energy to the ground and the atmosphere.

Despite several key roles of canopy complexity in controlling important aspects of land-atmosphere energy exchange, canopy complexity has rarely been quantified and has never been related to differences in energy exchange among arctic ecosystems. In this paper, we consider canopy complexity to be the combination of vegetation properties such as biomass, cover, height, leaf area index (LAI) and stem area index (SAI). We examined the horizontal component of complexity by looking at the variability in vegetation distribution and the vertical component of canopy complexity by measuring the vertical distribution of leaf and stem biomass. In this paper we describe the compositional and structural differences in the major ecosystem types that characterize the transition from arctic tundra to boreal forest in western Alaska. We then describe several measures of complexity and analyze their relationship to land-atmosphere exchange of water and energy.

Study Sites

We studied the transition from arctic tundra to boreal forest near Council (64.50˚N 163.41˚W) on the Seward Peninsula, in northwestern Alaska. The climate of the region is warmer and wetter than Alaska's North Slope (Fleming et al. 2000). Monthly mean air temperatures in Nome (the climate station closest to the study site) range from –15^{o}C in January to 11^{o}C in July (mean 1950-1999; Western Regional Climate Center). Average annual precipitation is 406 mm, including 1549 mm of snowfall. Shrubs (Silapaswan et al. 2001) and trees (Lloyd & Fastie 2002) are currently expanding into tundra on the Seward Peninsula in apparent response to regional warming in the area during the last

40 years (Barber et al. 1998; Keyser et al. 2000). The sequence of five sites in Council was selected to represent a structural transition from tundra through low shrub, tall shrub and woodland tundras to closed-canopy *Picea glauca* forest, analogous to vegetation transitions that might occur through time in response to warming. The sites were located within 5 km of each other (Fig. 2.1) and therefore were influenced by the same local climate. Site differences in vegetation reflected variation in topography, soil moisture, soil temperature, and disturbances associated with the 1898 discovery of gold in the region. Human disturbance of these sites appears to have been negligible during the last 80 years.

The tundra site was located on the floodplain of the Niukluk River (Fig. 2.1) with permafrost near the surface. Active thermokarst development in the site is leading to sparse moist depressions with sedges (*Eriophorum angustifolium*). The site featured large patches of lichens (*Cladina mitis* and *Cladina rangiferina*) and *Sphagnum* spp. hummocks. Sedges and low evergreen shrubs comprised most of the vascular biomass (Table 2.1). The low shrub site was located on a moderate (9º) SSW-facing slope (Fig. 2.1). Lichens and low evergreen shrubs dominated microsites with a thin organic layer, whereas taller deciduous shrubs and sedges dominated stripes with deeper organic and mineral soils (Table 2.1). The tall shrub site was located on a well-drained (6º) S-facing slope (Fig. 2.1). Tall (>2 m) *Betula glandulosa* and *Salix spp.* shrubs dominated the canopy with smaller deciduous shrubs, forbs and mosses in the understory (Table 2.1). The disturbance history of this site is unknown, but it is close to an area mined for gold around 1900, and ditches and pipes used in mining were found near the site. The woodland site was located in a moderately drained (5º) ESE-facing broad creek valley and featured tall (>2 m) *Betula glandulosa* and *Salix spp.* shrubs with a low density of *Picea glauca* (Table 2.1). Permafrost was found underlying the site. The site was located close to the town of Council, but historic photographs from the height of the gold-mining era indicated vegetation on the site that was similar to that which occurs presently. The forest site was flat (3º) and faced ESE (Fig. 2.1). The forest canopy species was *Picea glauca* with an understory of tall *Salix* shrubs. Low shrubs, forbs and mosses formed a near-continuous ground cover (Table 2.1). A 1901 photograph showed that a majority of the site had been cut in about that year, and tree cores indicate that the forest is approximately 100 years old (A. Lloyd & C. Fastie, pers. comm.).

Methods

Biomass and Horizontal /Vertical Complexity

Within each site, we selected a large homogeneous area of vegetation that met eddy covariance requirements of fetch and slope (Baldocchi & Meyers 1998). In 100 m x 100 m sampling grids centered on an eddy covariance tower, we measured a variety of vegetation characteristics such as cover, height, biomass, leaf and stem area index in 10-12 randomly selected 20 x 50 cm quadrats of the understory and 1 x 1 m quadrats of the tall shrub overstory, where present. All sampling occurred at the time of peak aboveground biomass, between mid July and mid August. Tall shrub, understory and ground cover were measured using a point frame. In this study, cover is the uppermost leaf hit of each species at each point, which is a variation on point-framing methods used in other tundra studies (Arft et al. 1999; Shaver et al. 2001) (Table 2.1). The coefficient of variation (COV) of canopy cover provides an estimate of the *horizontal* complexity in the ecosystem. Horizontal complexity is greatest in sites with a discontinuous canopy or patchy distribution of cover or biomass. *Picea* density was measured in the woodland and forest sites by counting stems in a subsample of 10 x10 m plots in the grid (42 in the woodland site and 25 in the forest).

For the canopy plant functional types (PFTs), we measured *Picea* heights using an inclinometer and recorded the height the top leaf for the tall shrubs. For the understory species, height was recorded at the uppermost height where the vertical pin of the point frame intercepted the plant; therefore, the height represents the average height of individuals in the quadrat. We measured the depth of live biomass for the ground cover PFTs.

Aboveground vascular plant biomass was harvested down to the top of the moss or lichen layers, which were collected separately. We used an allometric equation (386 * DBH^2 * 0.001) developed for *Picea* in interior Alaska (J. Yarie, pers. comm.) to estimate the total spruce biomass. Mosses and lichens were harvested to the level of the depth measurements. Plant biomass was oven-dried at 60º C for at least 48 hr and weighed.

Leaf and Stem Area Index

We made site-wide measurements of LAI using a Licor 2000 Optical Plant Canopy Analyzer by sampling every 10 meters within the grid (n=121 points). For the tall shrub layer, we measured stem area index (SAI), i.e., the number of stems intersected by a pin dropped from the top of the canopy to the ground surface, as our measure of stem density. Our measure of SAI therefore represents the *vertical* complexity of the tall shrubs.

Surface energy and moisture exchange measurements

In the center of each vegetation grid we measured water and energy exchange by eddy covariance. These data and methods are described in detail in Beringer et al. (submitted). The absolute magnitude of the fluxes at each site is affected by seasonal variation in incoming radiation and variability in the climate drivers. The sites were measured at different times; therefore, in order to compare the sites we normalized all values to a reference site (the tundra site), which was measured continuously during summer. We then constructed ratios to examine the relative partitioning to ground, latent and sensible heating fluxes among sites.

Results

Total aboveground biomass ranged 9-fold from tundra site to forest (Table 2.2). The dominant plant functional type shifted across the sites. Biomass was dominated by lichens and mosses in the tundra site, by low deciduous shrubs in the low shrub site, by tall shrubs in the tall shrub site and in the woodland site, and by trees (*Picea*) in the forest.

Canopy and Shrub Overstory Biomass

Picea accounted for 85% of the aboveground biomass in the spruce forest, with tall shrubs (mainly *Salix*) contributing another 7% of aboveground biomass (Table 2.2). In contrast, the deciduous shrub canopy contributed less than 1% of total biomass in the tundra site. At intermediate sites there was a more even distribution of biomass among overstory PFTs. At the woodland site, for example, the overstory canopy still accounted for most (65%) of total biomass, and the aboveground biomass was shared among the three canopy groups (*Picea, Betula* and *Salix*). At the tall shrub site, the canopy PFTs contributed 80% of the aboveground biomass, with *Betula* accounting for 68% of canopy biomass and *Salix* the remainder. At the low shrub site, the canopy (primarily *Betula*) accounted for 39% of aboveground biomass.

Understory Biomass

Understory biomass differed less strongly than canopy biomass across sites and was distributed across sites in a greater diversity of plant functional types. Understory biomass was greatest in the low shrub site but remained substantial in all sites (Table 2.2). Deciduous and evergreen shrubs co-dominated the understory in all sites except the tall shrub and woodland, where deciduous shrub biomass exceeded evergreen biomass. Sedges accounted for a substantial proportion (19%) of understory biomass in the tundra, and grasses and forbs both accounted for a similar proportion (16-19%) of understory biomass in the woodland site.

Groundcover Biomass

The biomass of groundcover, which consisted of non-vascular plants, was greatest in the tundra site and least in the woodland site (Table 2.2). Lichens and non-*Sphagnum* mosses were important in all sites except the woodland, where lichens were negligible. *Sphagnum* biomass, which was very high at the tundra site, comprised little or none of the groundcover in the other sites. Lichens and non-*Sphagnum* mosses showed complex patterns of distribution across sites, and were not clearly correlated with canopy biomass.

Canopy Height

Canopy height is often used as a surrogate of canopy complexity in studies of energy exchange because height correlates closely with roughness length, the aerodynamic property that partly determines the efficiency of convective exchange between the canopy and the atmosphere (Oke 1987). Canopy height ranged from 0.10 m in tundra to 7.3 m in the woodland site (Table 2.3). Average *Picea* height was 15% less (6.2 m) in the forest than in the woodland (7.3 m). Average height of *Betula* shrubs was very similar between the shrub and woodland sites (0.83 and 0.85 m, respectively). Average height for *Salix* increased from 0.82 m in the tall shrub site to 0.98 m and 1.2 m in the woodland and forest sites, respectively (Table 2.3).

A MANOVA test at the alpha = 0.05 level followed by a Ryan-Einot-Gabriel-Welsch multiple range test was used to evaluate height differences among sites. For most functional types, heights were similar across sites (Table 2.3). The heights of the low deciduous and evergreen shrubs did not vary significantly across the gradient of sites ($F_{4, 37} = 2.28$, $p > .0794$; $F_{4, 38} = 0.97$, $p > 0.4350$, respectively), suggesting that low shrub morphology was relatively insensitive to shading. Sedges and grasses, with their vertical leaf structure and low stem allocation were at the top of the canopy, deciduous shrubs were intermediate, and the more shade-tolerant evergreen shrubs were at the bottom of the canopy. Forbs were variable in their canopy position, due to site differences in species composition.

Canopy Cover

Detailed measurements of canopy cover showed a different pattern of canopy complexity than would be inferred from site differences in canopy height. The forest had more continuous tree cover than the woodland (see density measurements below). The tall shrub layer had a nearly continuous cover of leaves that was identical (92%) between the tall shrub and woodland site (Fig. 2.2). However, the lower coefficient of variation (COV) in the woodland site than in the tall shrub site (32% and 38%, respectively) suggests a more uniform canopy in the woodland site. In the tall shrub site, *Betula* accounted for 56% of the tall shrub cover and *Salix* accounted for the remainder. In the woodland site the proportional contribution of tall shrub species to total cover was the reverse (43% *Betula*, 57% *Salix*) (Fig. 2.2). The canopy cover of tall shrubs in the forest site was much lower (39%) and had a higher COV (77%) than in the shrub-dominated sites, reflecting a sparser distribution and greater horizontal complexity of tall shrubs in that site. *Salix* accounted for almost all (94%) of the tall-shrub cover in this site (Fig. 2.2).

Understory Density

Total understory density, which is approximated by measurements of cover, tended (non-significantly) to increase along the gradient from tundra to forest (Fig. 2.3, Table 2.1). The coefficient of variation for total density was also similar among sites.

The low shrub site had the greatest variability (COV 52%), indicating greater horizontal heterogeneity, and the tundra site had the lowest (COV 32%). These patterns are roughly similar to those described above for biomass and could reflect restriction of understory deciduous shrubs to the least shaded sites (tundra, low shrub, and tall shrub) and the concentration of forbs and grasses in the more productive sites (tall shrub, woodland, and forest).

Ground cover

Non-vascular plants covered 87% of the ground surface in the tundra and forest sites, 50% - 60% of the ground surface in the low-shrub and tall shrub sites and less than 20% in the woodland site (Table 2.1). The variability among sites was much greater among sites in ground cover than in the understory cover (Fig. 2.3). The woodland site had the greatest COV (84%), reflecting its sparse distribution of mosses and lichens. The low shrub site also had a highly variable distribution of ground cover (COV 57%). The ground cover distribution was less variable in the tall shrub, forest and tundra sites, reflecting their more continuous distribution of mosses and lichens.

Ground cover was deepest in the tundra site, and slightly shallower in the low shrub site and forest site. Lichens were deepest in the woodland site. Neither moss functional group varied significantly in depth between the tundra and low shrub site (Table 2.3).

Leaf and Stem Area Index

LAI increased across the vegetation gradient from tundra to forest (Table 2.4). The pattern of increase was different from that of biomass, with the greatest increase from tundra to tall shrub and relatively minor increases from the tall shrub to forest, where biomass increased most dramatically.

Stem density or SAI provides a measure of the density of roughness elements, another structural attribute of vegetation that influences convective exchange with the atmosphere. The density of *Picea* trees increased 20-fold from the woodland site (54.8 trees ha^{-1}) to the forest (1090 trees ha^{-1}). In the tall shrub layer, combined SAI of *Betula* and *Salix* decreased along the vegetation gradient from tall shrub to woodland to forest (3.2, 2.8, and 0.94, respectively) (Table 2.4). The forest showed the greatest coefficient of variation of SAI among plots (COV 87%), the woodland showed the least (COV 39%), and the tall shrub site was intermediate (COV 54%). *Salix* accounted for 38%, 44%, and 96% of the SAI in the shrub, woodland, and forest sites, respectively (Fig. 2.4). The contribution of *Salix* to total SAI was less than its proportional contribution to canopy cover because of its greater leaf allocation than *Betula* (Fig 2.3).

Discussion

Energy Absorption

The patterns of biomass and canopy complexity that we documented had important consequences for land-surface energy exchange characteristics measured by Beringer et al. (submitted) in the same sites. Albedo (the proportion of incoming shortwave radiation reflected by the ecosystem) decreased dramatically along the vegetation gradient from tundra to forest (Table 2.4). Site differences in albedo correlated closely with total aboveground biomass (Fig. 2.5a) and with LAI (Fig. 2.5b).

Albedo responded most sensitively to changes in biomass at low levels of biomass (Fig. 2.5a), although the relationship is only slightly different than linear. This suggests that masking of the reflective groundcover of lichens and of standing dead leaves of sedges contributes strongly to site differences in albedo in open communities (tundra to low shrub site to shrub sites). Albedo decreased with increasing LAI (Fig 2.5b). This relationship is expected from theory because increments in biomass and leaf area increase the probability that radiation reflected from one canopy element will be absorbed by another rather than being reflected back to space (Oke 1987). The greater diversity of functional types and associated vertical canopy complexity at sites with high LAI could also contribute to their low albedo. Our data suggest that both masking of the ground surface and canopy complexity contribute to site differences in albedo, and that the relative importance of these mechanisms depends on canopy biomass and LAI. Patterns of albedo across the Council sites were similar to those in other tundra and boreal sites (Table 2.4) (Betts & Ball 1997; McFadden et al. 1998; Baldocchi et al. 2000).

Site differences in vegetation composition, vertical and horizontal complexity, and albedo drive site differences in net radiation (the energy absorbed by the ecosystem). Sites with high aboveground biomass, high LAI, and low albedo absorb more solar energy than sites with low values of these vegetation parameters (Table 2.4). These site differences in net radiation are important because they determine the energy available for transfer to the atmosphere and soil (Oke 1987; Beringer et al. submitted). Available net radiation was very similar in all sites with the exception of the forest site, which had a 20% greater net radiation. The greater amount of net radiative energy available at the surface at the forest site will likely amplify differences in energy partitioning in this site.

Energy Partitioning

Site differences in energy balance depend on the partitioning of energy between ground heat flux and convective fluxes to the atmosphere (latent and sensible heat fluxes). The fraction of net radiation partitioned into ground heat flux is controlled by canopy shading, the insulative properties of the groundcover, and the temperature gradient within the soil, which is strongly influenced by presence or absence of permafrost. No single vegetation characteristic that we measured (canopy biomass, canopy cover, moss biomass, moss cover, LAI) showed a significant regression relationship with ground heat flux, indicating that no single vegetation property that we examined accounted for site differences in ground heat flux (Fig. 2.5c,d). It seems likely that ground heat flux responds to some combination of factors. Among our five sites, shading and/or the thermal gradient created by presence of permafrost appeared more important than moss biomass or moss type in controlling ground heat flux. We conclude this based on the following observations. First, ground heat fluxes were high in the two sites with permafrost (the tundra and woodland sites), which suggests that the presence of permafrost contributed substantially to ground heat flux in sites where it was present. Second, the site with the most radiation reaching the moss surface (tundra) had intermediate partitioning to ground heat flux whereas the site with the least radiation reaching the moss surface (the forest) had the lowest ground heat flux, indicating that shading does not, by itself, control ground heat flux but could be a contributing factor. Finally, contrary to our expectation that moss biomass would reduce ground heat fluxes, the tundra site, which had the most insulative groundcover (*Sphagnum*; (Beringer et al. 2001a)) and greatest moss biomass, did not have the lowest ground heat flux (Fig. 2.5d). The presence of permafrost in this site appeared more important than moss biomass or moss type in controlling summer ground heat flux. Over the longer term, mosses may be an important factor contributing to the presence of permafrost because they are more effective in reducing heat input to soils in summer (due to abundant air spaces) than in winter (when ice conducts heat effectively through mosses from the soil to the atmosphere).

Our ground heat flux values were generally within the range reported by Eugster et al. (2000) (Table 2.4). Previous studies (summarized in Eugster et al. (2000)) concluded that partitioning to ground heat fluxes is generally negatively correlated with LAI. However the correlation among the Council sites was not as strong as suggested by the literature, perhaps because the Council sites varied in presence/absence of permafrost, which was not the case in previous comparisons. It should be noted that ground heat flux, which is measured at several single points, is not strictly comparable to net radiation measured across a broad footprint (Mayocchi & Bristow 1995).

Latent heating should be controlled by both the surface evaporation from mosses and soil and evapotranspiration from the vascular canopy. Across the Council sites, the evaporative fraction was nearly constant. Contrary to our expectations, the fraction of net radiation partitioned to latent heat flux (the evaporative fraction) showed only a weak relationship with moss cover (Fig. 2.5e) and decreased slightly along the gradient of increasing biomass (Fig. 2.5f). Mosses evaporate freely as long as they are moist, and their contribution to latent heating is determined by the net radiation they receive. As the vertical complexity of the canopy increases, the mosses at the ground surface are increasingly shaded, reducing ground surface evaporation. On the other hand, total vascular transpiration increases as canopy leaf area increases. The combined effect of decreasing ground evaporation and increasing transpiration is that the evaporative fraction appears nearly constant across the sites. However, under conditions of moisture stress, increasing stomatal resistance results in decreased transpiration from the vascular canopy. In the Council sites, drying of the surface and air in summer during the measurement period decreased partitioning into latent heating in the forest site. However, the absolute value of the latent heat flux was greater due to greater available energy (net radiation minus the ground heat flux). The partitioning of net radiation into latent heat fluxes that we observed in the Council sites was lower for shrub tundra and higher for the forest sites compared to values reported for similar vegetation types in other arctic and boreal ecosystems (Eugster et al. 2000) (Table 2.4), probably because the forest at Council had a denser canopy than those studied in other forest-tundra comparisons (Rouse 1984; McFadden et al. 2003).

The fraction of net radiation partitioned into sensible heat flux correlated very strongly with total plant biomass (Fig. 2.5g). Decreasing ground heat fluxes, combined with the little variation in latent fluxes, meant that along the gradient from tundra to forest an increased proportion of net radiation was available for sensible heating. The greatest increase in sensible heating occurred between the woodland and forest sites, which suggests that development of a full *Picea* canopy was important in enhancing convective efficiency, because a well-developed canopy has more turbulence and more efficient turbulent transport.

Conclusions

In conclusion, our measurements of vegetation characteristics (biomass, density, height, LAI, and SAI) show that there are multiple dimensions to the variation among sites in canopy complexity. The changes in canopy complexity across the vegetation gradient resulted from both the addition of the new functional types (tall deciduous shrubs and *Picea*) across the gradient and interactions among the functional types. The addition of a full spruce canopy had the greatest effect on the tall shrubs, leading to a 60% reduction in total shrub biomass. This effect was strongest on the *Betula* shrubs, which were virtually absent from the forest site. In the groundcover layer, the addition of tall shrubs and *Picea* reduced the *Sphagnum* mosses; however total ground cover was fairly similar across the sites. Even in the understory, where total biomass and cover were relatively similar across the sites, there was a complex pattern of change in abundances within and among functional types. This suggests that the functional types are responding to site characteristics other than to just canopy development, e.g., differences in nutrient cycling. For example, forbs and grasses had higher biomass and cover in the high-biomass sites (tall shrub, woodland, and forest), where nutrients were presumably more available than in the low shrub and tundra sites.

The changes in canopy complexity along this gradient affected the net radiation at each site and its partitioning into ground and convective fluxes. Albedo decreased and net radiation increased along the gradient from tundra to forest. It was difficult to determine the relative influence of moss biomass and canopy cover on ground heat fluxes due to the confounding effect of permafrost presence and absence in the sites. Latent heat fluxes appeared to be better correlated with the development of a leafy canopy than the presence of mosses. Increasing canopy complexity, particularly increasing biomass, had a strong positive relationship with sensible heat fluxes.

The warming associated with the increased sensible heating over more complex canopies could have local effects, including feedbacks to biogeochemical processes such as enhanced decomposition and production. Accelerated nutrient cycling could favor deciduous shrubs over functional types with slower nutrient turnover. Other regional effects of changes in energy partitioning could include changes to the disturbance regime such as increased fire frequency, due to warmer, drier air and more flammable vegetation types, as well as more frequent insect outbreaks (Lloyd et al. 2003). Localized warming above ecosystems with a tall, complex canopy may feed back to regional climate by warming the boundary layer (Beringer et al. 2001b). Our results lend further evidence to the complexity of the interactions between vegetation changes due to an increasing canopy complexity and other ecosystem characteristics, such as the presence of a moss layer or permafrost, in determining the changes to surface energy and moisture balance.

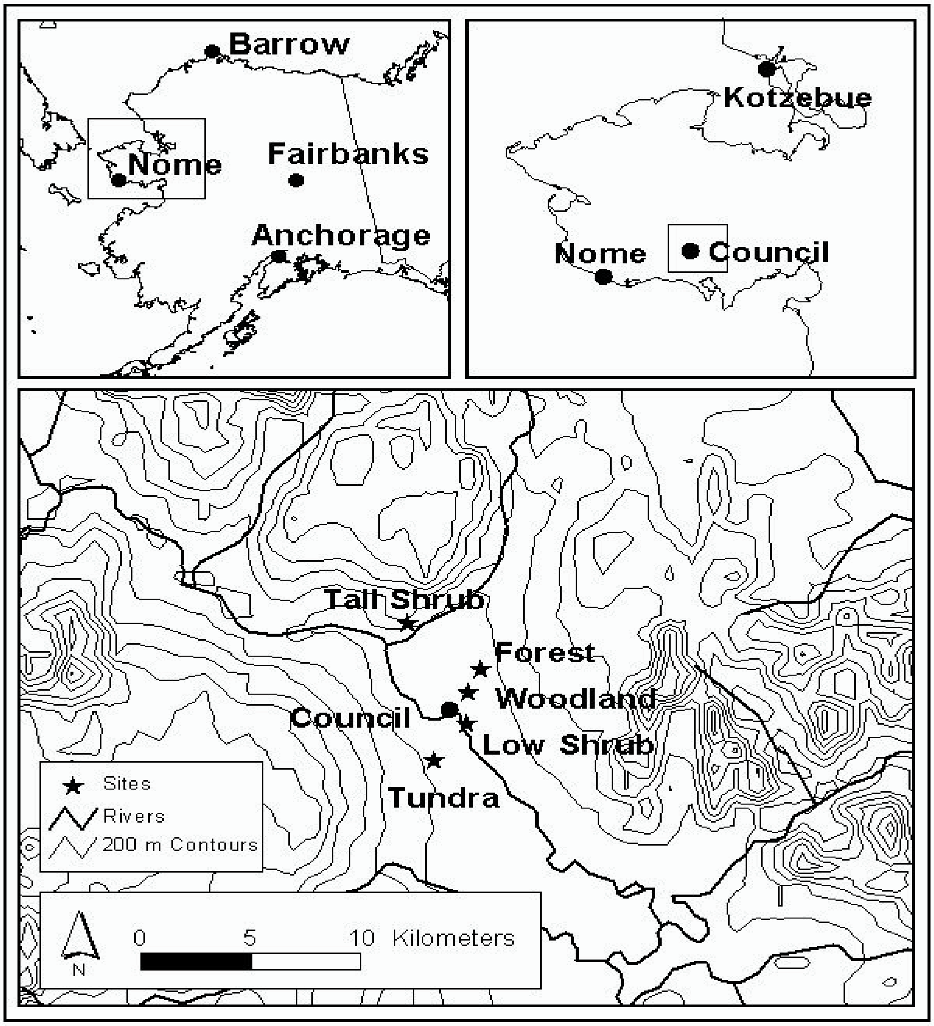

Figure 2.1: Location of Council and Council Sites

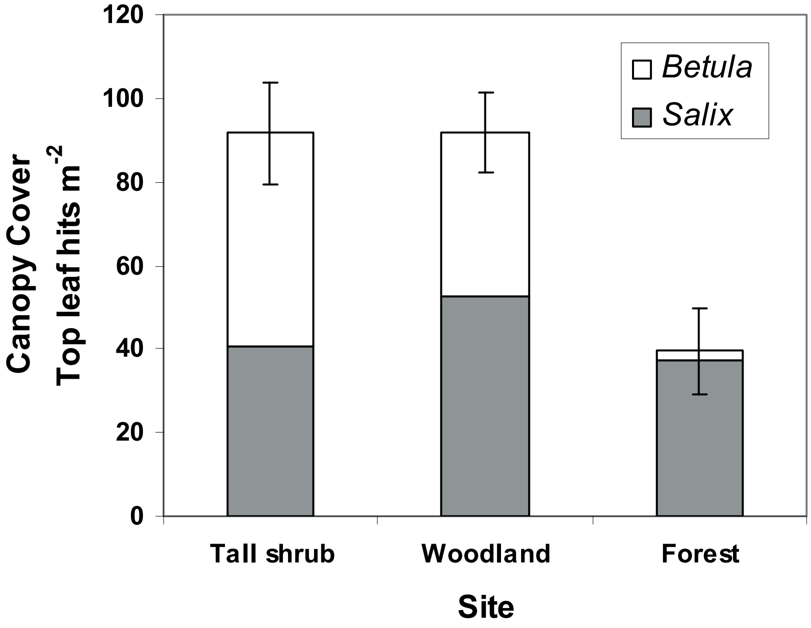

Figure 2.2: Canopy cover of *Betula* and *Salix* shrubs measured with a point frame. Hits on the top leaf of each species determine canopy cover. Data shown are mean and standard error.

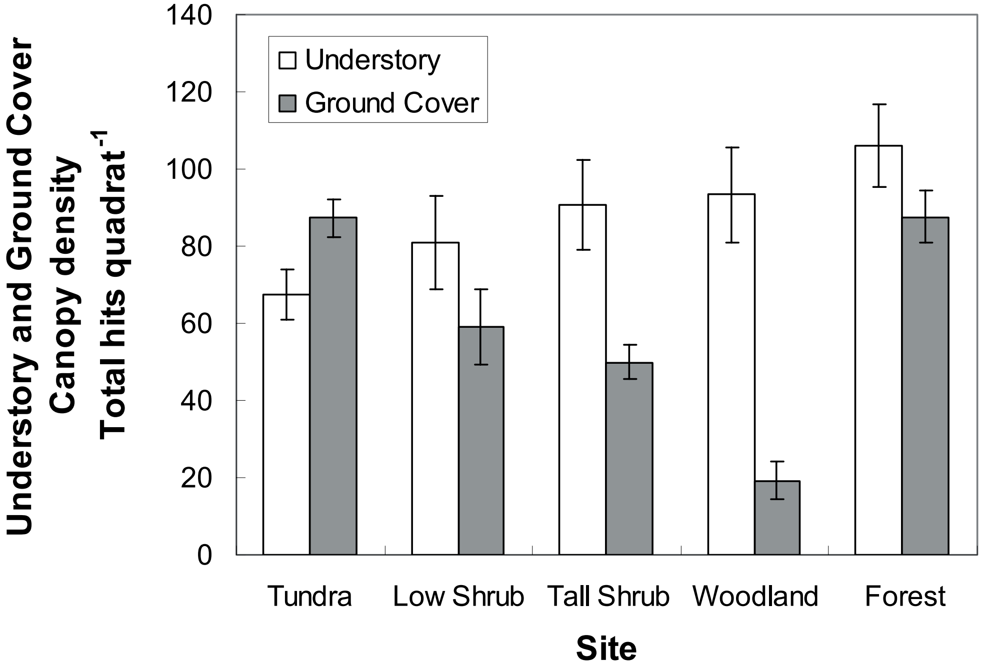

Figure 2.3: Understory and ground cover canopy density for all sites with mean and standard error bars shown.

Figure 2.4: *Betula* and *Salix* Stem Area Index (SAI) for the sites with a tall shrub component to the canopy. Mean and standard error shown. Units for SAI are m^2/m^2.

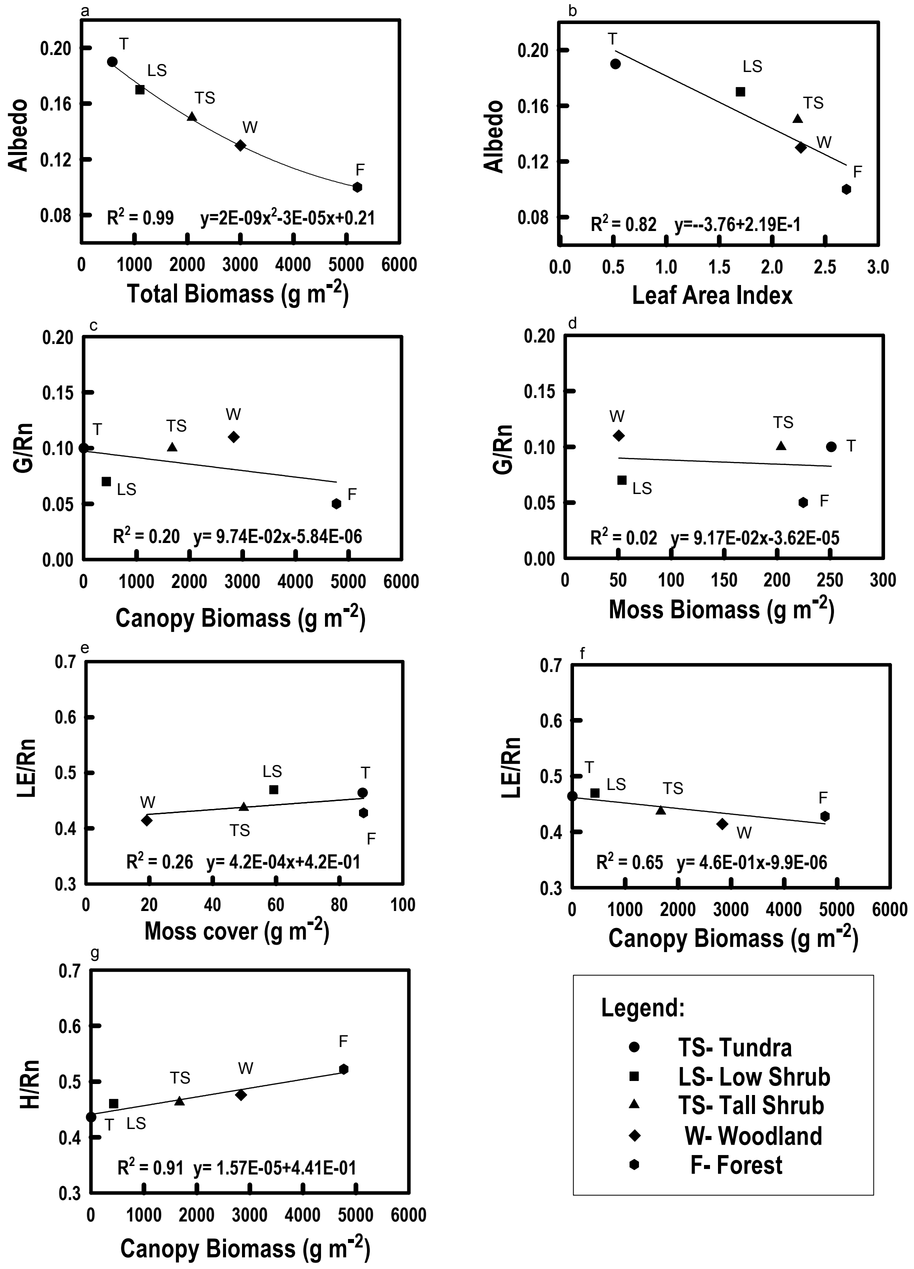

Figure 2.5: Regression of key land-surface varibles on vegetation varibles (a) Regression of albedo on total biomass (b) Albedo regressed on LAI (c) Fraction of net radiation (Rn) partitioned to ground heat flux (G) regressed on moss biomass (d) Regression of ground heat fraction and canopy biomass (e) Relationship of latent heat flux fraction (LE) and moss biomass (f) Latent heat flux fraction regressed on canopy biomass (g) Sensible heat flux (S) regressed on total biomass. Units for flux ratios are W m^{-2}/W m^{-2}.

Table 2.1: Cover of uppermost leaves in the understory class and cover of non vascular plants in ground classes organized by canopy class and plant functional type (PFT). Data are means ± standard error (n=10-12). Letters signify a significant difference between sites at the alpha = 0.05 level based on a significant MANOVA followed by a Ryan-Einot-Gabriel-Ilsch multiple range test. nd = PFT absent from site. The cover of canopy shrubs and trees (tall shrub, woodland, and forest sites) is not included.

	Cover (hits quadrat^{-1})				
Canopy Class/PFT	**Tundra**	**Low Shrub**	**Tall Shrub**	**Woodland**	**Forest**
Understory					
Deciduous shrubs	14.3 ± *3.5*	24.8 ± *5.8*	26.5 ± *5.1*	10.0 ± *4.0*	16.5 ± *5.2*
Evergreen shrubs	28.3 ± *4.7 a,b*	33.9 ± *5.5 a*	12.7 ± *5.7 b,c*	3.1 ± *1.8 c*	19.0 ± *4.6 a,b,c*
Forb	1.2 ± *0.5 c*	2.6 ± *0.8 c*	15.7 ± *4.2 b,c*	33.7 ± *7.2 a*	29.5 ± *6.0 a,b*
Grass	*nd*	2.0 ± *1.6*	15.1 ± *2.9*	33.1 ± *8.5 a*	13.9 ± *3.0*
Sedge	23.7 ± *4.0*	11.5 ± *3.2*	23.0 ± *4.0*	13.4 ± *4.5*	27.7 ± *3.1*
Total	67.5 ± *6.5*	81.1 ± *12.1*	90.8 ±*11.5*	93.27 ± *12.3*	105.9 ±*10.6*
Ground Cover					
Lichen	38.5 ± *10.2 a*	41.6 ± *10.6 a*	6.6 ± *3.3 b*	0.2 ± *0.1 b*	11.6 ± *4.2 b*
Non-*Sphagnum* moss	26.9 ± *7.4 b,c*	17.2 ± *5.2 c*	43.2 ± *5.1 b*	19.0 ± *5.0 c*	76.0 ± *5.6 a*
Sphagnum	24.0 ± *4.6 a*	1.3 ± *0.7*	*nd*	*nd*	*nd*
Total	87.3 ± *5.01 a*	59.3 ± *9.8 b*	49.8 ± *4.4 b*	19.2 ± *4.9 c*	87.6 ± *6.6 a*

Table 2.2: Total aboveground biomass of major plant functional types (PFT) in five ecosystems ranging from tundra to forest. Data are means ± SE (n=10-12). Statistics and abbreviations as in Table 2.1.

	Aboveground Biomass (g m^{-2})				
Canopy Class/ PFT	**Tundra**	**Low Shrub**	**Tall Shrub**	**Woodland**	**Forest**
Canopy					
Picea	*nd*	*nd*	*nd*	882.0 ± *162.7*	4454.0 ± *194.3*
Betula	3.8 ± *2.6*	428.2 ± *141.7 a,b*	1142.8 ± *383.8 a*	1069.0 ± *407.2 a*	6.1 ± *4.4 b*
Salix	*nd*	2.5 ± *2.3*	529.2 ± *199.0 a,b*	884.5 ± *298.3*	312.0 ± *143.2 a,b*
Understory					
Deciduous shrubs	42.8 ± *15.1*	276.7 ± *75.8 a*	101.5 ± *25.1*	59.3 ± *31.7*	42.1 ± *14.0*
Evergreen shrubs	55.2 ± *13.2*	159.7 ± *24.8 a*	38.7 ± *19.2*	5.5 ± *3.6*	56.2 ± *19.5*
Forb	6.5 ± *3.2*	6.2 ± *2.8*	13.2 ± *4.0*	19.0 ± *4.7*	13.2 ± *2.4*
Grass	*nd*	1.5 ± *0.8*	4.5 ± *1.1*	21.2 ± *8.2 a*	5.1 ± *1.4*
Sedge	24.5 ± *4.2 a*	12.9 ± 3.5 *a,b*	8.6 ± *3.0 b*	7.5 ± *3.1 b*	13.1 ± *3.5 a,b*
Ground Cover					
Lichen	197.7 ± *84.7*	162.4 ± *52.6*	42.7 ± *20.9*	1.9 ± *1.3*	81.2 ± *62.2*

Table 2.3: Canopy and understory heights and ground cover depths. Data are means ± SE (n =10-12). Statistics and abbreviations as in Table 2.1.

	Vegetation Height and Ground Cover Depth (cm)				
Canopy class/PFT	**Tundra**	**Low Shrub**	**Tall Shrub**	**Woodland**	**Forest**
Canopy					
Picea	*nd*	*nd*	*nd*	730 ± *0*	620 ± *80*
Betula	9.9 ± *4.6*	34.75 ± *5.99*	82.8 ± *12.0*	85.0 ± *14.5*	15.4 ± *17.4*
Salix	*nd*	*nd*	81.7 ± *15.9*	97.7 ± *13.2*	119.5 ±*2.5*
Understory					
Deciduous shrubs	8.4 ± *0.9*	15.5 ± *4.6*	11.1 ± *1.5*	15.6 ± *2.2*	7.0 ± *1.2*
Evergreen shrubs	5.7 ± *0.8*	7.2 ± 9.8	5.4 ± *0.9*	6.85 ± *1.1*	5.74 ± *0.7*
Forb	4.2 ± *0.9*	8.07 ± *0.68*	22.3 ± *4.9 a*	10.1 ± *1.2*	5.49 ± *0.5*
Grass	*nd*	44.4 ± *4.4 a*	6.6 ± *1.4 c*	31.2 ± *2.1 b*	6.64 ± *0.3 c*
Sedge	25.4 ± *0.2 b*	33.3 ± *3.5 a*	5.8 ± *0.7 b*	28.2 ± *1.5 a,b*	8.1 ± *1.2 c*
Ground Cover					
Lichen	4.6 ± *0.8 a,b*	1.7 ± *0.4 c*	1.7 ± *0.7 c*	6.0 ± *0.0 a*	1.78 ± *0.4 c*
Non-*Sphagnum* moss	2.1 ± *0.3 a*	0.9 ± *0.8 b*	1.4 ± *0.3 a,b*	2.1 ± *0.4 a*	0.74 ± *0.3 b*

Table 2.4: Leaf Area Index (LAI), shrub Stem Area Index (SAI) albedo, net radiation, and fraction of net radiation partitioned into sensible, latent, and ground heat fluxes. Flux and LAI values from Beringer et al. (submitted). Numbers in brackets are values reported by Eugster et al. (2000) for comparable arctic and subarctic ecosystems. nd= parameter not measured in those sites. Units for flux fractions are W m-2/W m-2.

Site	**LAI**	**SAI**	**Albedo (midday mean)**	**Net radiation (W m^{-2})**	**Ground heat flux fraction**	**Latent heat flux fraction**	**Sensible heat flux fraction**
Tundra	0.52	*nd*	0.19 [0.16]	94.2	0.10 [0.11-0.24]	0.46 [0.40-0.55]	0.44 [0.22-0.42]
Low Shrub	1.70	*nd*	0.17 [0.16]	92.1	0.07 [0.11, 0.13]	0.47 [0.38, 0.44]	0.46 [0.46, 0.55]
Tall Shrub	2.24	3.22	0.15 [0.16]	104.1	0.10 [0.10, 0.21]	0.44 [0.33, 0.48]	0.46 [0.48, 0.51]
Wood land	2.27	2.82	0.13 [0.13]	123.8	0.11 [0.06, 0.12]	0.41 [0.28, 0.45]	0.48 [0.49, 0.60]
Forest	2.70	0.94	0.10 [0.11]	118.5	0.05 [0.09]	0.43 [0.58, 0.38]	0.52 [0.38, 0.47]

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CHAPTER 3: FUNCTIONAL FEEDBACKS TO CLIMATE*

**Manuscript title: Net carbon exchange across the arctic tundra-boreal forest transition in Alaska 1981-2000. Authors: C. C. Thompson, A. D. McGuire, J. S. Clein, F. S. Chapin, III, and J. Beringer. Submitted to Ecological Applications.*

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 annual 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 responded positively, but the response was exceeded by the negative R_H response; therefore, the net response was also negative. Lastly, in colder and wetter regions, positive NPP response exceeded the relatively small declines in R_H, resulting in a positive NEP response. The net effect for the region was a slight gain in ecosystem carbon, however our research highlights the importance of spatial variability over the region in the carbon balance during the last two decades.

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 reactive soil carbon (McGuire et al. 1995). Future changes in net carbon storage are presently difficult to predict because of the feedbacks between ecosystem processes, such as primary production, decomposition, nitrogen mineralization, and other dynamic ecosystem components, such as soil moisture and temperature, active layer depth, and permafrost distribution. Temporal and spatial variability in the coupled climate-land system contributes considerably to the difficulty of predicting the long-term carbon balance in these systems.

Net carbon storage in terrestrial ecosystems is determined primarily 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* significantly increases its production in response to experimental fertilization and warming (Bret-Harte et al. 2001). The growth response by this shrub has likely contributed to expansion of shrubs 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 limit 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 the precipitation regime may have a stronger effect than changes in temperature on decomposition and therefore may influence the trajectory of net carbon exchange over time (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 also can 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 changes in allocation within species (Hobbie 1996) could provide a mechanism by which increased plant growth could be a negative feedback to R_H.

Net carbon exchange varies because of spatial and 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 spatial patterns of temperature and precipitation.

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. 2003). Small (landscape-scale) spatial heterogeneity accounts for 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 and Shaver 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 was 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 on the North Slope and in tall shrub tundra and forest at treeline near Council, Alaska on the Seward Peninsula. 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 based on representative 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

2m 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. 2003).

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 pool sizes at the field sites used in this study. 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 matched field-based estimates of NPP, GPP, nitrogen uptake, and soil carbon and nitrogen pools (McGuire et al. 1992).

At each study site, we measured production (new leaves and stems) and plant biomass (old leaves and stems) in 10-12 randomly selected 20 x 50 cm quadrats in the understory and 1x 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 (Thompson et al. 2004). Aboveground vascular plant biomass was harvested to the top of the moss or lichen layers, which were collected separately in the same quadrats. Plant biomass was oven-dried at 60º 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 most species because TEM 5.0 does not consider species or plant functional types explicitly (Table 3.1). Assumptions used to determine values for NPP and NPPn in Table 3.1 are described below.

For the components of plant production that were not directly measured, we made estimates based on several assumptions. We estimated annual 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 (mainly *Hylocomium splendens* and *Pleurozium schreiberi*) production was estimated from Oechel and Van Cleve (1986) (8% and 21% of standing pool, respectively). 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).

We used an allometric equation developed for *Picea glauca* in Alaska (J. Yarie, unpublished data) to estimate the total white 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 all organic (Oi, Oe and Oa) layers. 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) was 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 (mean air temperature, precipitation, and 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 developed from station observations by New et al. (2000) for the period 1901-1990 and extended to 2000 using data developed by Mitchell et al. (submitted). 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 spatial variation in annual 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 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 x 0.5 (latitude x 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 estimated 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 3.1). 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 3.1). 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, intermediate in 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 3.2).

Climate trends

Average annual air temperature in the region increased by 0.86 deg C from 1981 to 2000 ($F_{1, 19}$= 84.65, $p < 0.001$, R^2= 0.01). Growing season (June, July, August- JJA) air temperature increased by slightly less than 1.0 ˚C . ($F_{1, 19}$=119, $p < 0.001$, R^2= 0.01). Precipitation decreased 1.5 mm yr^{-1} (6% of the annual precipitation), with a total decrease of about 30 mm over the two decades ($F_{1, 19}$=60.22, $p < 0.001$, R^2= 0.01). Growing season precipitation decreased an average of 0.6 mm yr^{-1} (9 % of the summer precipitation), resulting in a decrease of about 12 mm over the two decades ($F_{1, 19}$=644.26, $p < 0.001$, R^2=0.01).

We calculated the trends 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 (Fig. 3.1). Annual temperatures generally increased over the entire region, with the greatest warming in the central north, near Barrow (Fig. 3.1a). Western Alaska, especially the Seward Peninsula appeared to experience cooling of less than 1.0 °C. Most of the domain showed increased growing season air temperatures (Fig. 3.1b). The annual precipitation trends showed a strong west to east gradient, with the greatest increases in precipitation centered over the northwestern portion of the domain, including the Seward Peninsula (Fig. 3.1c). Precipitation decreased 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) but is shifted to the east (Fig. 3.1d). 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 for any gtrid cell 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 (Fig. 3.2a). 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 throughout the domain (Fig. 3.2b). 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 (Fig. 3.2c). The overall NEP in the region switched from net sink to net source in the mid 1990s. In tundra, NEP declined because the strong positive R_H response outpaced the slight increases in NPP. In shrub, NEP decreased because the slight decreases in NPP exceeded the nearly flat R_H response; however the trend for the shrub NEP was close to zero. The forest NEP appeared to switch to a net source in the early 1980s and NEP decreased on the same order of magnitude as in tundra.

Across the entire domain the mean vegetation carbon pools increased slightly during the period, despite the decreases in NEP (Table 3.3, Fig. 3.3a). The tundra type showed small losses (Table 3.3, Fig. 3.3b), while carbon pools in the shrub and forest types increased (Table 3.3, Fig. 3.3c,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 3.3, Fig. 3.4a). This resulted from substantial gains in soil C in tundra, balanced by large losses in shrub and slight losses in the forest (Fig. 3.4b-d). The shrub ecosystems had the greatest variability in soil carbon losses and gains across the domain (Table 3.3, Fig. 3.4c).

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 trends in air temperature and precipitation. However, the relative importance of the driving climate variable varied among the fluxes. In all vegetation types, trends in NPP were positively correlated with both air temperature and precipitation (Fig. 3.5a, b). 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 (Fig. 3.5a), 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 decrease of about 3 mm yr^{-1}. In this range the shrub and forest types showed much less variability than tundra NPP in response 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 high variability (Fig. 3.5b), 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 (Fig. 3.6a) ($R^2 = 0.11$). Changes in vegetation carbon pools were not well correlated with R_H trends (Fig. 3.6b; $R^2 = 0.02$).

Trends in R_H were positively correlated with temperature trends (Fig. 3.5c) but negatively correlated with changes in precipitation (Fig. 3.5d). These climatic sensitivities were most pronounced in tundra. The range in the tundra flux response was high at all ranges of temperature increases (Fig. 3.5c). The negative correlation of the R_H

trends with precipitation explained less variability than the relationship with temperature (Fig. 3.5d). 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 (Fig 3.6c,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 trends in NEP and with precipitation trends (Table 3.4, Fig. 3.5f). These analyses indicate that non-linear responses of NPP and R_H to 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 classes; warm/dry, warm/wet and cold/wet. We performed ANOVAs using these climate states as the independent class 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 (Fig 3.7a). 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 (Fig 3.7b-d).

R_H increased overall with all three categories of climate states (Fig. 3.7a). 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, R_H trends in shrub types did not differ significantly among climate classes. Forest R_H responded more to warming and drying trends than wetter conditions.

Trends in overall NEP differed significantly among categories of climate states (Fig. 3.7). Warmer/drier regions had the greatest decreases in NEP, resulting in decreases in their carbon storage capacity. In contrast, in colder/wetter regions 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 classes 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 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 and Conclusion

Our research highlights the importance of spatial variability in Alaskan Arctic carbon balance. In past research this variability has not been adequately captured because of the limited spatial and temporal coverage of the field-based measurements in this region. 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 historical and recent photographs (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). No examination of changes in shrub cover has been conducted 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. submitted). 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 study 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 (Hobbie 1996) . One possible hypothesis for this result, which was not tested in this study, is that a greater C:N ratio of litter resulted in inputs of material that is less decomposable (Hobbie 1996) that were not readily decomposed during the relatively short duration of this modeling study (also see (McGuire et al. 1997)). In contrast with the tundra, soil carbon in the shrub type decreased significantly. This result agrees with results from a long-term fertilization experiment in 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 no increase 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 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 (Le 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 points 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. 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 increased, whereas the precipitation trends in our study, which extends farther 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.

In summary, our research highlights the importance of interactions between spatial and temporal variability in climate trends and the major arctic and 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 (and probably predicted) climate change, in combination with landscape-scale vegetation heterogeneity, is likely to have a significant influence on the regional carbon budgets.

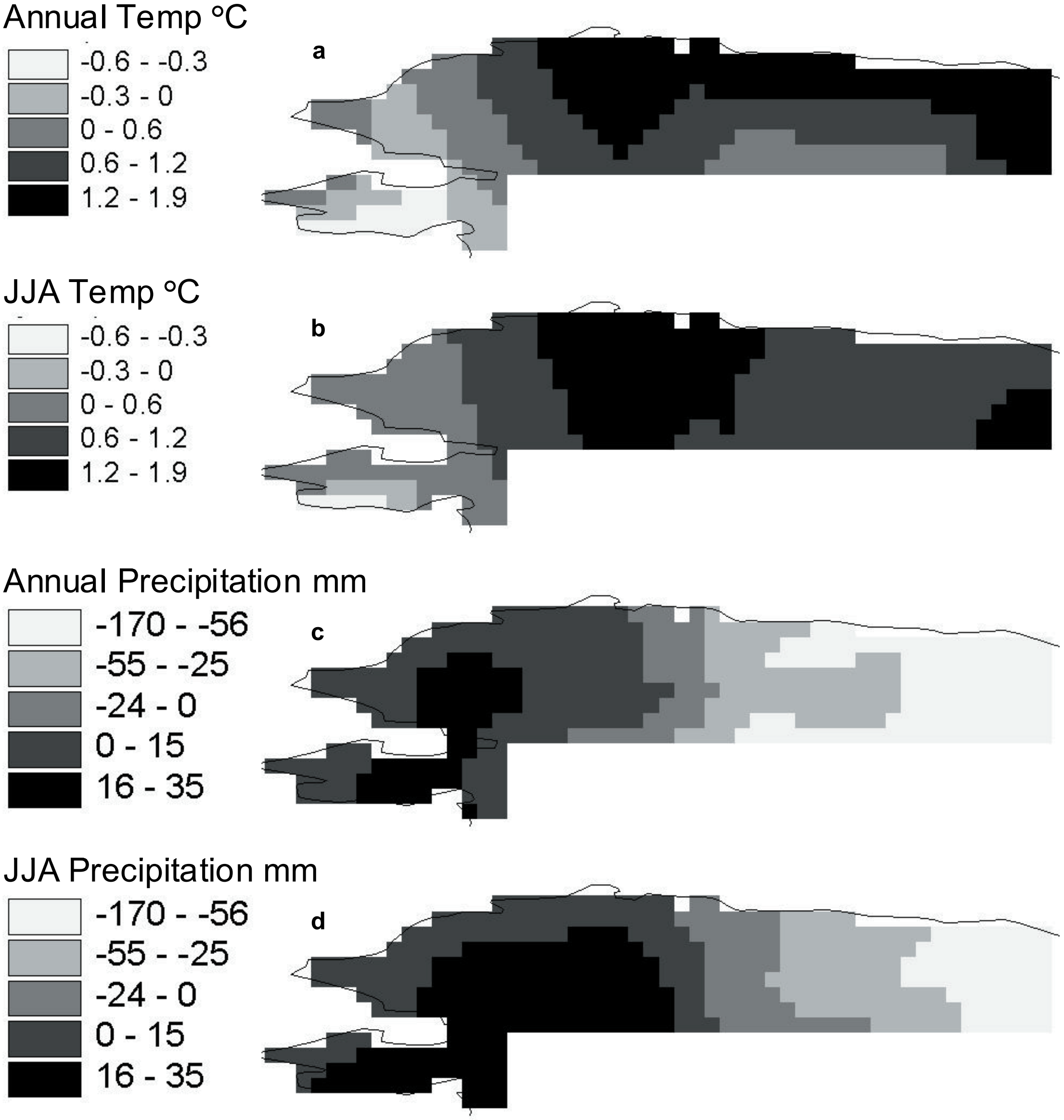

Figure 3.1: Climate trends 1981-2000: annual and growing season (June July August - JJA) temperature and precipitation changes. Data from Mitchell et al. (submitted).

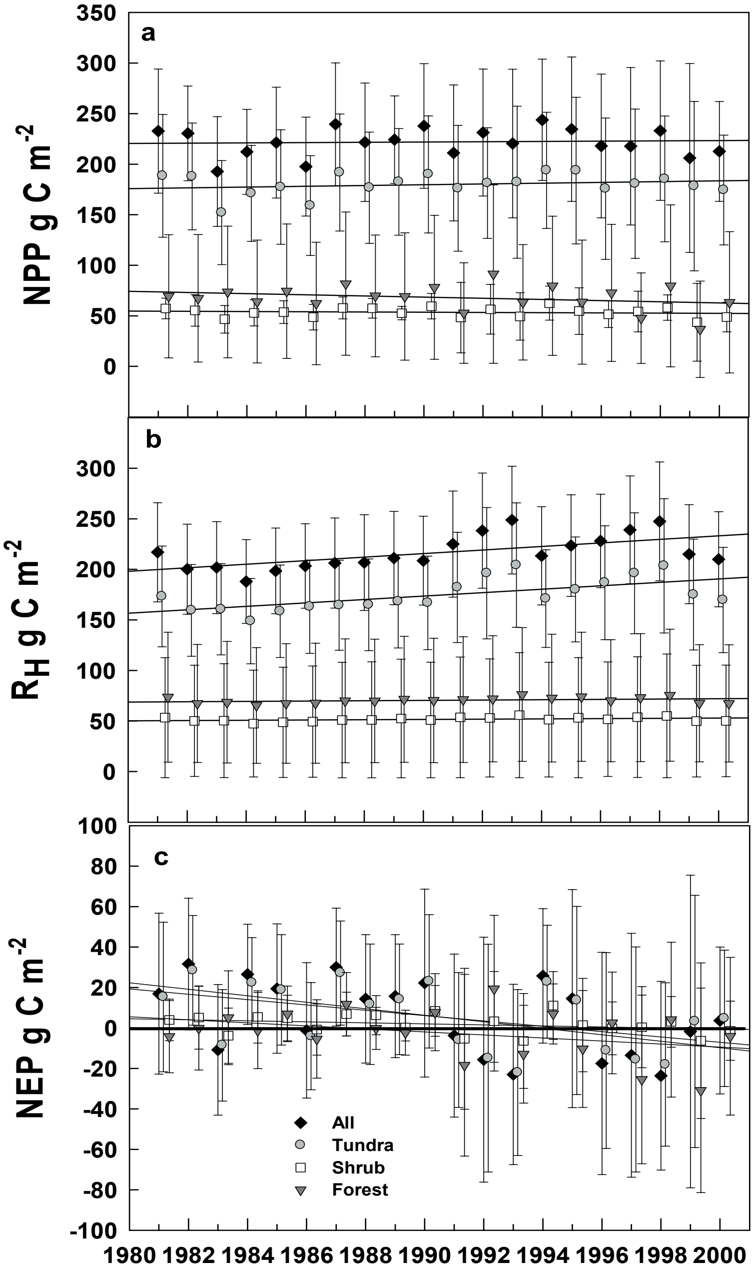

Figure 3.2: NPP, RH and NEP fluxes for the domain. Mean and standard deviation shown for combined vegetation and tundra, shrub and forest results separately.

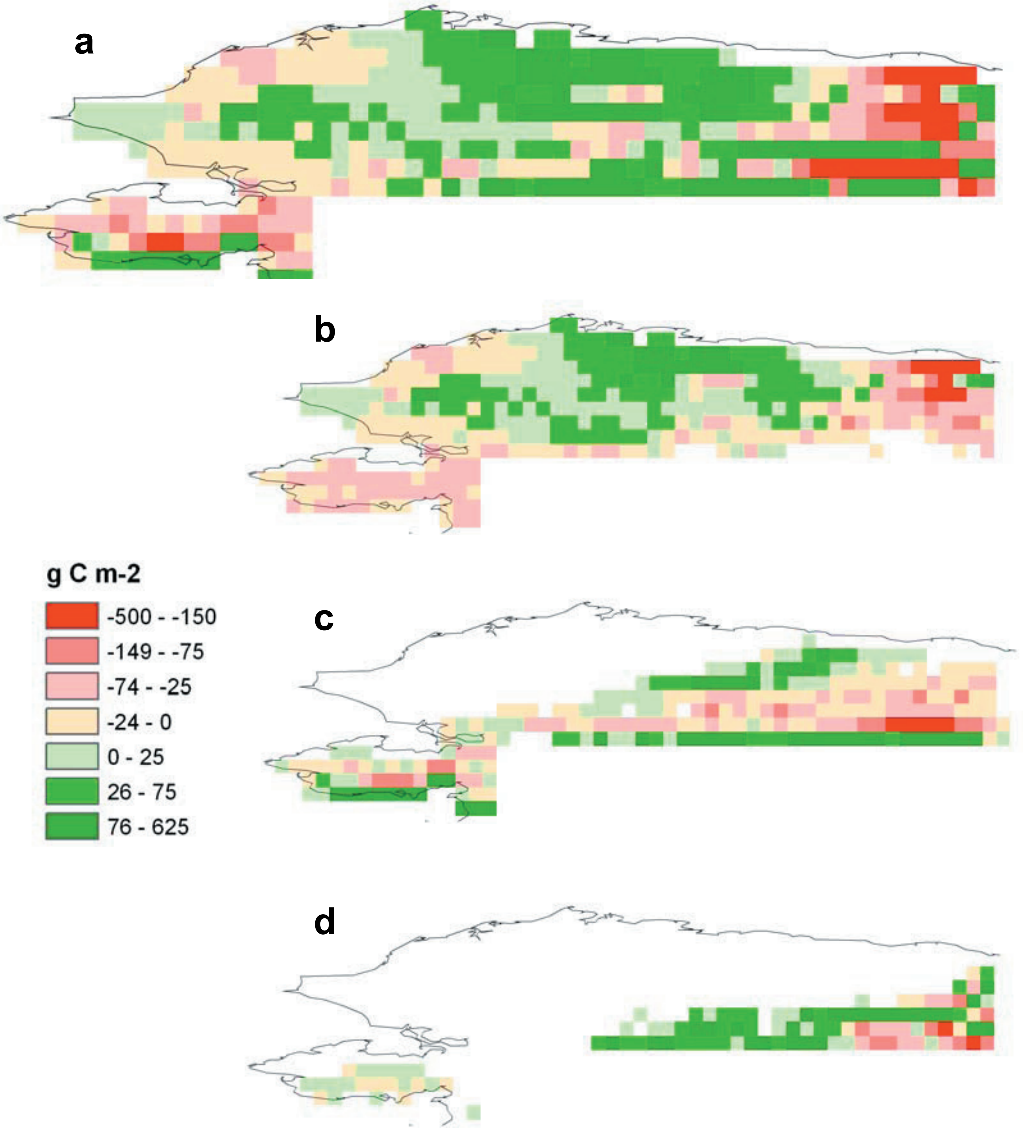

Figure 3.3: Changes in vegetation carbon (g C m^2) for the time period 1981-2000. a) combined vegetation types, b) tundra, c) shrub, d) forest vegetation types.

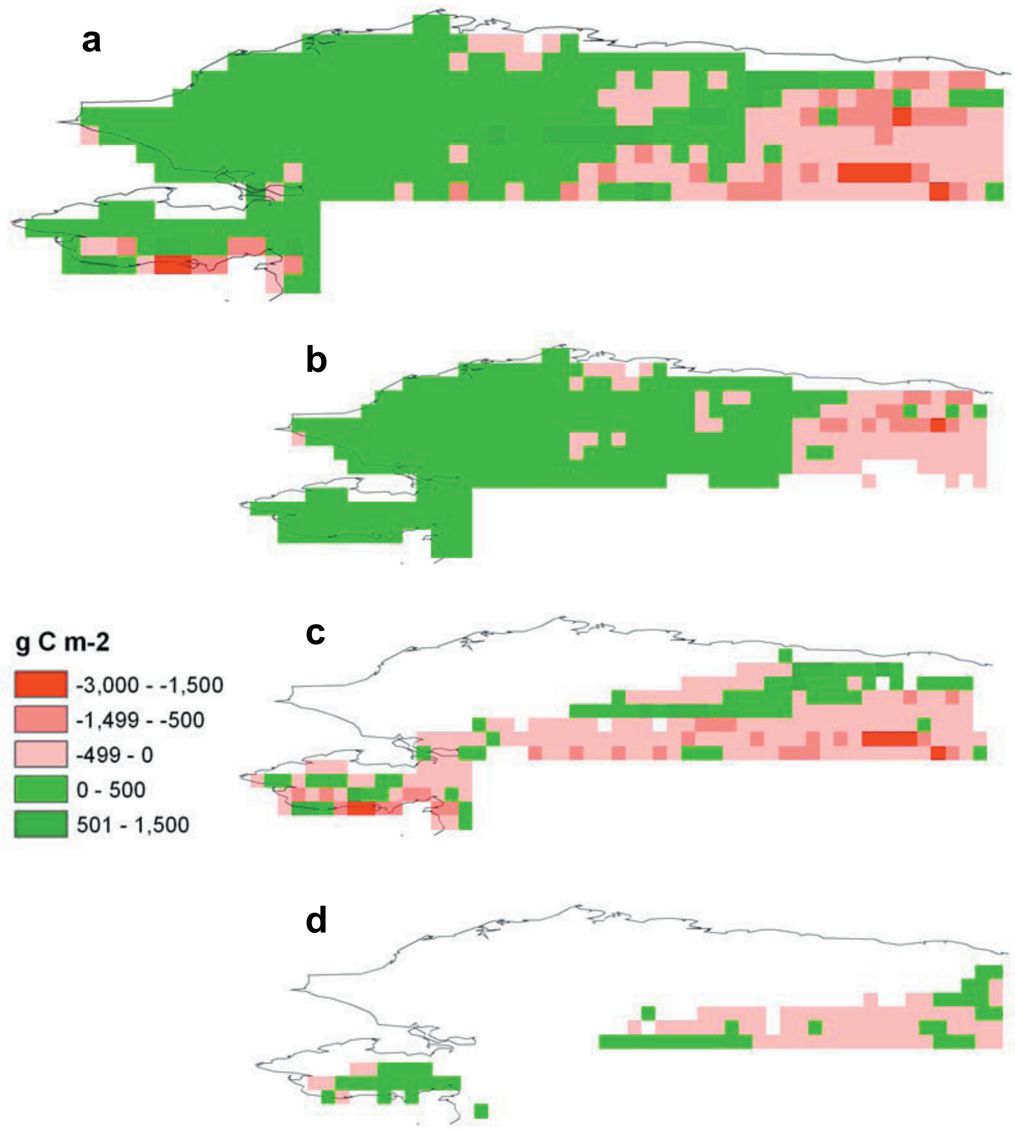

Figure 3.4: Changes in soil carbon (g C m^2) for the time period 1981-2000. a) combined vegetation types, b) tundra, c) shrub, d) forest vegetation types.

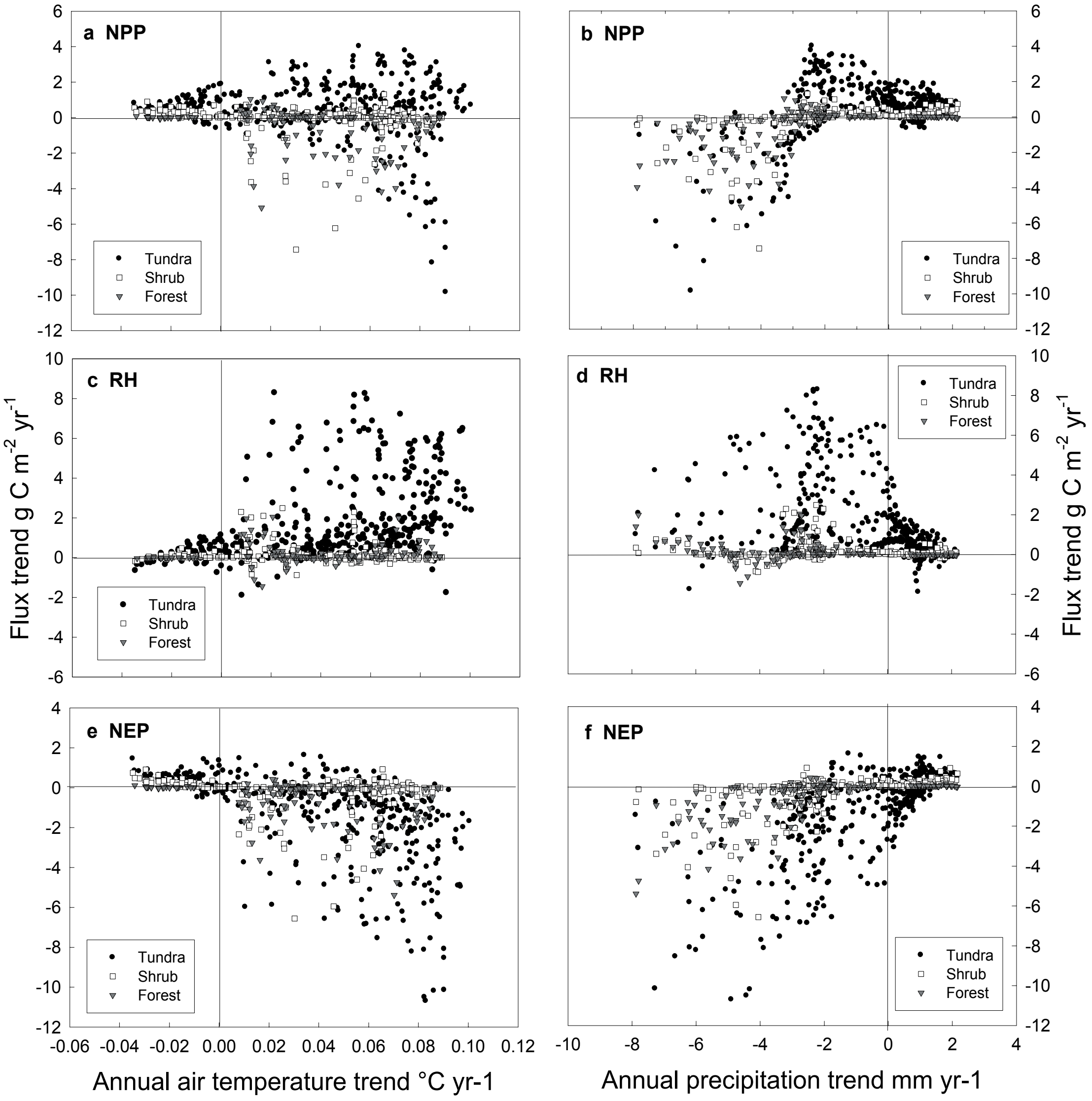

Figure 3.5: Spatial variability in response of fluxes (NPP, RH and NEP) to annual air temperature and precipitation trends.

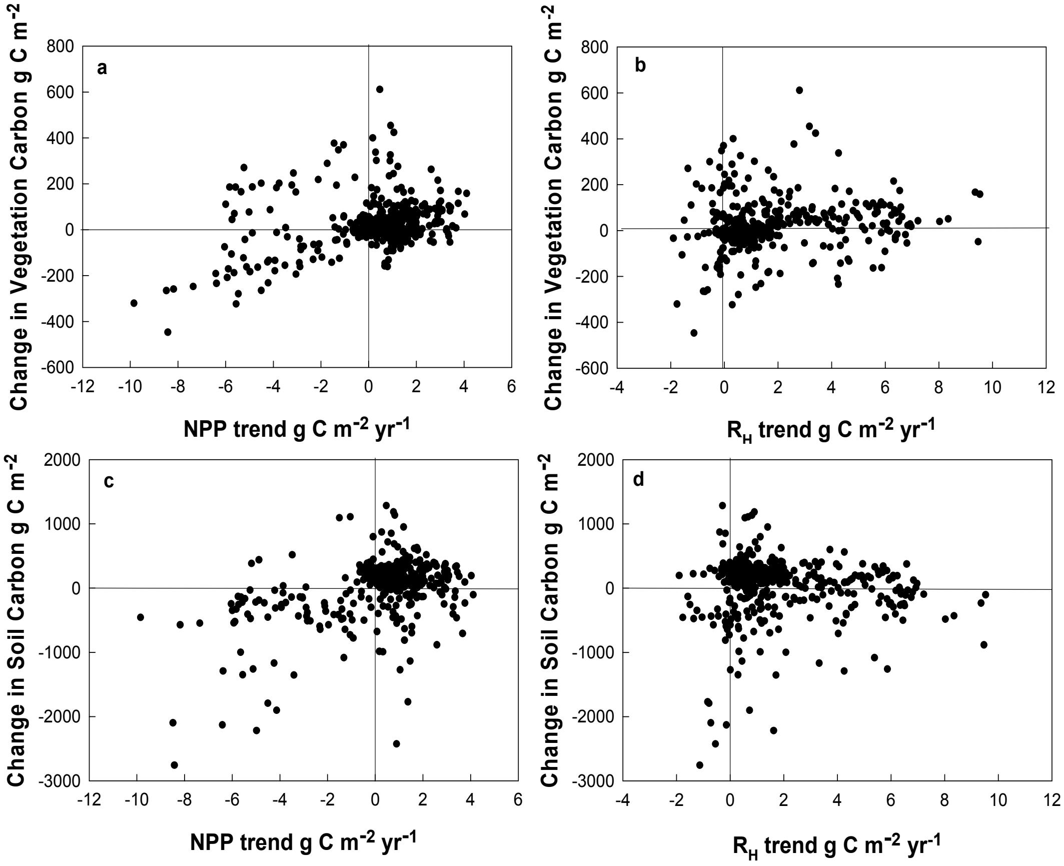

Figure 3.6: Relationship between selected pools and fluxes: a) changes in vegetation carbon vs. change in NPP, b) changes in vegetation carbon vs. change in RH, c) changes in soil carbon vs. change in NPP, d) changes in soil carbon vs. change in RH.

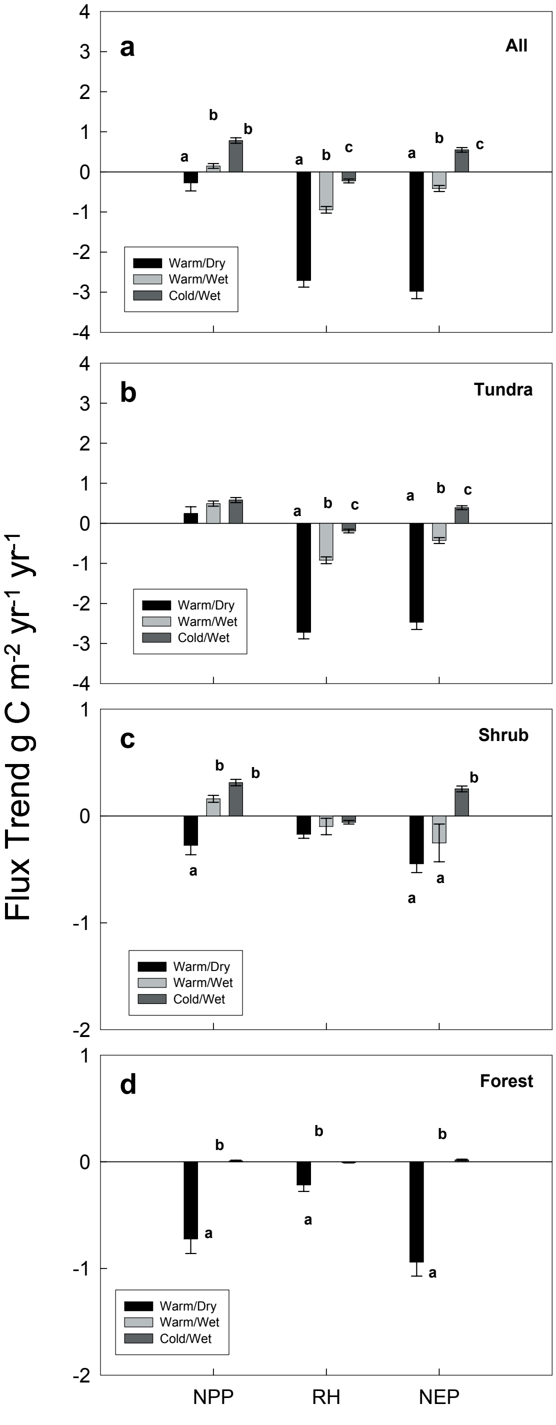

Figure 3.7: ANOVA analysis for NPP, RH and NEP responses in different climate classes. Letters represent significant differences in means at the $p < 0.05$ level. Note scale change for shrub and forest vegetation type fluxes.

Table 3.1: 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. Units g C m^{-2} or g N m^{-2}.

	Tundra				Shrub				Forest			
Functional Group	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

Table 3.2: Ecosystem fluxes and pools based on field data and estimates used in model calibration. Fluxes (g m^{-2} yr^{-1}): net primary productivity (NPP), nitrogen in net primary productivity (NPPn), estimated gross primary productivity (GPP), nitrogen uptake (Nup). Pools (g m^{-2}): vegetation carbon (VegC), vegetation nitrogen (VegN), soil carbon (Soil C), and soil nitrogen (Soil N).

	Tundra	Shrub	Forest
NPP	148	298	260
NPPn	3.1	9.5	5.0
GPP	297	597	722
Nup	1.8	3.4	2.5
Veg C	328	999	2482
Veg N	4.6	17.1	19.3
Soil C	14200	12800	22500
Soil N	500	800	1500

Table 3.3: Modelled change in vegetation, soil, and ecosystem carbon pools from 1980 to 2000. Area weighted means and standard deviations shown. Units for carbon pools are g C m^{-2}

	All		Tundra		Shrub		Forest	
Vegetation Carbon	20.1	*110.9*	-1.2	*53.0*	17.3	*100.9*	41.1	*106.1*
Soil Carbon	9.6	*483.4*	106.6	*234.1*	-149.1	*512.8*	-9.9	*44.8*
Ecosystem Carbon	29.7	*507.0*	105.0	*261.0*	-132.0	*522.0*	31.1	*104.0*

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CHAPTER 4: CONCLUSIONS

High-latitude ecosystems are an important component of the global climate system (Bonan et al. 1995). Improving our understanding of the structural and functional responses of these ecosystems to changing climate helps reduce uncertainty associated with predicting potential trajectories of the coupled land-atmosphere system in response to changing climate. The previous two chapters in this dissertation presented several structural and functional links between vegetation and climate in high latitude ecosystems. In this chapter, we summarize the major findings from this work and suggest possible future directions.

Chapter 2 described mechanistic links between vegetation structure and climate. The research summarized in Chapter 2 described how canopy complexity increased in conjunction with increases in shrub cover and the addition of an evergreen conifer canopy. Net radiation increased along this gradient of canopy complexity and the differences in complexity drove differences in the partitioning of net radiation into its major components: latent, ground, and sensible heating. In summary, greater heating of the air occurred over taller, more complex canopies. The warming associated with the increased sensible heating over more complex canopies could result in local effects, including feedbacks to biogeochemical processes such as enhanced decomposition and production. Localized warming above ecosystems may also affect regional climate by warming the boundary layer (Beringer et al. 2001) leading to more broad-scale heating over parts of the Arctic. This result suggests that the increasing vegetation complexity seen in the Arctic in response to recent warming (Silapaswan et al. 2001, Sturm et al. 2001) could represent an important positive feedback to warming.

Chapter 3 presented a modeling study that evaluates the responses of net ecosystem productivity in important high latitude vegetation types (tundra, shrub-tundra, and forest) to climate trends from 1981-2000. In this simulation, the net storage of carbon (C) decreased during this period; and the region switched from a net sink of C to a net source during the mid-1990s. The modeled plant community types responded differently to the climate trends, which contributed to spatial variability in the net carbon fluxes. Under warmer and drier conditions, NPP decreased and R_H increased, leading to net release of carbon to the atmosphere. This climate combination drove the greatest negative NEP trends. In warmer and wetter conditions NPP increased; 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 wetter regions, NPP increased, and R_H decreased. This was the only climate state which resulted in positive NEP trends, or net storage of carbon.

The research presented in this dissertation has added to our understanding of the structural and functional mechanisms by which arctic vegetation can influence the climate system. Currently, biogeochemical models, such as the Terrestrial Ecosystem Model used in Chapter 3, represent the important arctic vegetation types, and can reasonably simulate the carbon dynamics of high-latitude ecosystems (McGuire et al. 2000, McGuire et al. 2002). Land-surface models, which model the structural components of ecosystems and are usually included in regional and global climate models, have two major shortcomings: 1) they do not adequately represent carbon dynamics, and/or 2) their representation of arctic vegetation is limited.

The next step in this research will be to incorporate these results into coupled models of the land-atmosphere system to improve our ability to predict future vegetation, carbon storage, and climate. This modeling effort will incorporate our new understanding of important vegetation canopy characteristics that control structural properties, such as albedo and energy partitioning, and will be able to combine these structural characteristics with the vegetation properties that influence ecosystem function, particularly carbon storage. Thus, the research presented in this thesis is an important contribution towards developing models that represent both the structural and functional characteristics of arctic vegetation and allow us to better examine the interactions between vegetation and the atmosphere in the context of a changing climate.

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