Journal of Vegetation Science 13: 301-314, 2002
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Environmental variation, vegetation distribution, carbon dynamics and water/energy exchange at high latitudes

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Abstract. The responses of high latitude ecosystems to global change involve complex interactions among environmental variables, vegetation distribution, carbon dynamics, and water and energy exchange. These responses may have important consequences for the earth system. In this study, we evaluated how vegetation distribution, carbon stocks and turnover, and water and energy exchange are related to environmental variation spanned by the network of the IGBP high latitude transects. While the most notable feature of the high latitude transects is that they generally span temperature gradients from southern to northern latitudes, there are substantial differences in temperature among the transects. Also, along each transect temperature co-varies with precipitation and photosynthetically active radiation, which are also variable among the transects. Both climate and disturbance interact to influence latitudinal patterns of vegetation and soil carbon storage among the transects, and vegetation distribution appears to interact with climate to determine exchanges of heat and moisture in high latitudes. Despite limitations imposed by the data we assembled, the analyses in this study have taken an important step toward clarifying the complexity of interactions among environmental variables, vegetation distribution, carbon stocks and turnover, and water and energy exchange in high latitude regions. This study reveals the need to conduct coordinated global change studies in high latitudes to further elucidate how interactions among climate, disturbance, and vegetation distribution influence carbon dynamics and water and energy exchange in high latitudes.

Keywords: Boreal; Climate; Disturbance; Energy; Gradient; Tundra.

Introduction

As high latitude ecosystems contain ca. 40% of the world's soil carbon inventory that is potentially reactive in response to near-term climate change (McGuire et al. 1995), functional and structural changes in high latitude ecosystems have the potential to influence carbon exchange with the atmosphere (Smith & Shugart 1993; McGuire & Hobbie 1997; McGuire et al. 2000). Regions affected by permafrost are especially vulnerable to climate change because of altered drainage. Thermakarst lakes and wetlands may become large sources of methane (Reeburgh & Whalen 1992; Zimov et al. 1997). Reductions in the water table of tundra ecosystems substantially enhance the release of carbon from high latitude soils (Christensen et al. 1998). In contrast, earlier, longer and warmer growing seasons may increase production in tundra and boreal forest to increase carbon sequestration (Chapin et al. 1995; Frolking et al. 1996; Oechel et al. 2000; McGuire et al. 2000). The replacement of tundra with boreal forest might initially decrease but eventually increase carbon storage in high latitudes (Smith & Shugart 1993). Disturbance in the boreal forest region may substantially influence regional carbon exchange with the atmosphere (Kasischke et al. 1995; Kurz & Apps 1999; Schulze et al. 1999; Shvidenko & Nilsson 2000; Wirth et al. in press). The functional and structural responses of carbon storage in high latitude ecosystems have important implications for the rate of CO_2 accumulation in the atmosphere and international efforts to stabilize the atmospheric concentration of CO_2 (Smith & Shugart 1993; McGuire & Hobbie 1997; McGuire et al. 2000).

Responses of high latitude ecosystems to global change have the potential to influence water and energy exchange with the atmosphere in several ways. Sharp discontinuities in ecosystem structure, such as the forest-tundra boundary, are hypothesized to strongly influence temperature (Eugster et al. 2000). In comparison to boreal forest, snow-covered tundra and boreal wetlands have a much higher albedo, absorb less radiation, and warm the atmosphere less than boreal forest (Betts & Ball 1997; Chapin et al. 2000). Spatial variation in vegetation within arctic tundra may have climatic effects that extend beyond arctic tundra (e.g., see Lynch et al. 1999). The open woodlands of boreal Eurasia that result from repeated surface fires may have a ratio of sensible to latent heat that is a factor of 8 higher than closed stands (Schulze et al. 1999; Rebmann et al. in press). During the growing season, deciduous stands have twice the albedo, i.e., reflect twice the short-wave radiation, and have 50% to 80% higher evapotranspiration than coniferous forests (Baldocchi et al. 2000). An expansion of boreal forest into regions now occupied by tundra has the potential to reduce albedo and increase spring energy absorption to enhance atmospheric warming (Chapin et al. 2000). Other effects that may enhance atmospheric warming include earlier snow melt, which is likely to decrease springtime albedo, and expansion of shrub tundra, which in summer is likely to decrease evaporation losses because of lower evaporation from mosses (Chapin et al. 2000) and in winter is likely to accumulate more drifting snow during the winter and delay snow melt in spring (Liston et al. 2002; Sturm et al. 2001). In contrast, responses of the disturbance regime that increase the proportion of non-forested lands and deciduous forests have the potential to reduce spring energy absorption and work against atmospheric warming (Chapin et al. 2000; Eugster et al. 2000).

It is clear that the responses of high latitude ecosystems to global change involve complex interactions among environmental variables, vegetation distribution, carbon dynamics, and water and energy exchange. In addition, it is also clear that these responses may have important consequences for the earth system. As our understanding of controls over these responses is incomplete, it is important to improve our understanding of how environmental variation will affect carbon, water, and energy exchange with the atmosphere. The high latitude transects of the International Geosphere-Biosphere Programme (IGBP) span significant variation and co-variation of several environmental variables. Together, these transects provide a network for improving our understanding of controls over vegetation dynamics, carbon dynamics, and water and energy exchange in high latitudes. In this paper, we take a step toward clarifying the complexity of these interactions by evaluating how vegetation distribution, carbon stocks and turnover, and water and energy exchange are related to environmental variation spanned by the network of the IGBP high latitude transects. We first briefly describe the high latitude transects in the network and describe the sources of data used in our analyses. We then examine the environmental variation spanned by the transects and document how the environmental variation relates to vegetation distributed along each of the transects. Next, we compare patterns of carbon storage, net primary production (NPP), and carbon turnover among the transects in relation to environmental variation, vegetation distribution, and disturbance. We then evaluate how water and energy exchange relates to environmental variation and vegetation distribution.

General description of the High Latitude Transects

The Far East Siberia Transect

The Far East Siberia Transect (FEST) (also known as the 'Northeast Eurasian transect' and the 'Yakutsk transect') is a north-south transect centred on ca. 135° E that has been designed with respect to temperature variability between 52° and 70° N (Fig. 1). We have identified 36 study sites in this transect between 120° and 145° E where numerous studies have estimated carbon stocks of vegetation and the upper soil layers, to understand energy, water, and carbon dynamics and to reconstruct palaeo-environmental conditions (Hollinger et al. 1995, 1998; Schulze et al. 1995; Kobak et al. 1996; Vygodskaya et al. 1997). In addition, atmospheric carbon dioxide and methane concentrations have been monitored within this transect by aircraft sampling (Izumi et al. 1993; Machida et al. 1995). Vegetation within this transect includes alpine tundra, forest tundra, boreal forest and extra-boreal vegetation types. We define extra-boreal vegetation types as vegetation types that are located in transitional regions between boreal forest and temperate ecosystems or that are not characteristic of vegetation located in arctic and boreal regions.

The East Siberian Transect

The East Siberia Transect (EST) (also referred to as the 'Central Siberian transect' and the 'Yenisei transect') is a north-south transect centred on 90° E that has been designed with respect to temperature variability between the latitudes of 59° and 69° N (Fig. 1). Along the Yenisei there are several ecological field stations with numerous sites mainly organized by the Sukachev Institute of Forest in Krasnoyarsk. In addition, we identified 52 sites in this transect between the longitudes of 85° and 95° E where a variety of studies have been conducted primarily as part of the Eurosiberian Carbon Flux Project to estimate carbon stocks of vegetation and the upper soil layers, and to understand energy, water, and carbon dynamics with convective boundary layer measurements and ancillary process-based studies (Anon. 1996; Kelliher et al. 1999; Schulze et al. 1999; Wirth et al. 1999, in press; Valentini et al. 2000; Zimmerman et al. 2000; Lloyd et al. 2001; Rebmann et al. in press). Vegetation within this transect includes alpine tundra, forest tundra, boreal forest and extra-boreal vegetation types, but does not include tundra.

The Scandanavian Transect (ScanTran)

ScanTran is a new IGBP high latitude transect located in northern Europe. The primary ScanTran transect is arranged with respect to temperature variability and extends from around 55° N in Denmark to just over 80° N in Svalbard, Norway from ca. 9° E in the south to 18° E in the north (Fig. 1). The secondary transects, which are oriented east to west, are arranged with respect to maritime to continental environmental variation, extend at their extreme from approximately 30° W in eastern Greenland to 60° E in western Siberia and Franz Josef Land for the most northern transect, and from ca. 5° W in Scotland to 30° E in Finland for the most southern transect. Because data related to carbon dynamics has not been organized for the primary ScanTran transect, we report carbon data that have been organized for a north-south transect in Finland (Fig. 1). The Finland transect stretches over 1500 km from the forest-tundra transition zone in the north to the southern boreal forest biome in the south of the country (Liski et al. 1999). Vegetation within the ScanTran transect includes polar desert, alpine tundra, tundra, forest tundra, boreal forest, and extra-boreal vegetation types.

The Boreal Forest Transect Case Study (BFTCS)

The Boreal Forest Transect Case Study (BFTCS) is 1000 km by 100 km with generally flat topography and is oriented southwest-northeast in central Canada. The transect extends from 53.5° N, 107.167° W to 52.583° N, 106.25° W in the south, and 57.25° N, 94.833° W to 56.333° N, 94.25° W in the north. This orientation is along an ecoclimatic gradient characterized by co-variation in temperature and moisture with vegetation ranging from agricultural grasslands in southern

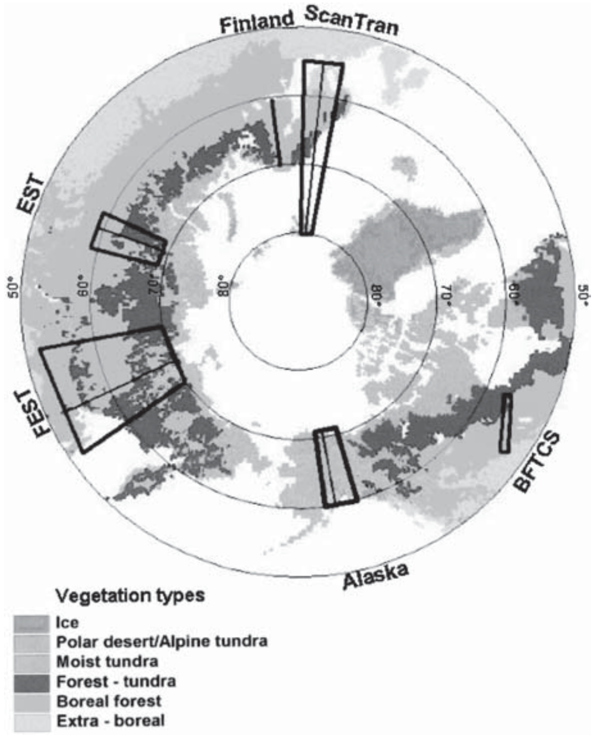

Fig. 1. Polar projection vegetation map indicating the location of high latitude transects.

Saskatchewan, through the boreal forest in the central portion, to forest tundra in northern Manitoba (Price & Apps 1995). The BFTCS transect and the southern part of the transect is dominated by chernozemic soils, while the northern part of the transect is dominated by shallow less fertile podsols and fibrosols overlaying the Canadian Shield bedrock. Within this transect, we identified 99 sites (Halliwell & Apps 1997a, b) which include sites associated with both the northern and southern study areas of the Boreal Ecosystem Atmosphere Study (BOREAS; Sellers et al. 1997; Hall 1999).

The Alaska Transect

The Alaska transect, which is a north-south transect that roughly follows the 150° W meridian between the latitudes of 60° and 71° N (Fig. 1), is characterized by complex environmental gradients between the Arctic Front, which in summer is often located near the northern coast of Alaska, and the Aleutian Low, which is located in the northern Pacific near the southern coast of Alaska. These climatic features interact with the east-west orientation of the Brooks Range in northern Alaska, the Alaska Range in central Alaska, and the mountains along the coast of southern Alaska to produce maritime to continental gradients that seasonally influence north-south temperature gradients along the transect. We have identified 34 sites in this transect between the longitudes of 153° and 145° W where a variety of ecological studies have been conducted. A number of these sites are associated with the Toolik Lake and Bonanza Creek Long Term Ecological Research (LTER) programs, which are conducting intensive studies to elucidate controls over the structure and function of tundra and boreal forest ecosystems in Alaska. The Alaska transect also includes a number of sites from two research campaigns in Alaska: (1) the ARCSS-LAII Flux Study (Kane & Reeburgh 1998; Walker et al. 1998) and (2) the Arctic Transitions in the Land-Atmosphere System Study (ATLAS; McGuire et al. in press). Vegetation within the Alaska transect includes alpine tundra, tundra, and boreal forest, but does not include forest tundra or extra-boreal vegetation types. In comparison to some of the other transects, the forest-tundra area in Alaska is less pronounced because interaction of the Arctic Front with the east-west orientation of the Brooks Range results in tundra north of the Brooks Range, boreal forest south of the Brooks Range, with a mosaic of forest tundra and alpine tundra in between tundra and boreal forest (Fig. 1).

Data sources

In this study, we focus on the presentation of means for purposes of comparing and contrasting patterns among the transects. While this strategy primarily limits us to evaluating macro-scale patterns, it is also an important step towards evaluating meso-scale and micro-scale variability in the context of regional-scale climatic gradients.

Climate and vegetation data

For comparison of environmental variation spanned we used the Cramer-Leemans CLIMATE database, which is a major update of the database assembled by Leemans & Cramer (1991). The CLIMATE database provides global coverage of long-term mean monthly temperature, precipitation, and sunshine duration at 0.5° (latitude × longitude) spatial resolution. For our analyses we extracted these variables for 0.5° transects through approximately the center of each of the IGBP transects (see Fig. 1). We used data on sunshine duration as an input to the Terrestrial Ecosystem Model (TEM; Raich et al. 1991) to calculate photosynthetically active radiation (PAR) for each of the 0.5° transects; the calculation of PAR by TEM considers cloudiness. The monthly climate values for June, July, and August were averaged, or totaled in the case of precipitation, to represent 'summer' climate. Similarly, 'winter' climate variables are integrated for September through May. For comparing the environmental variation with vegetation distribution among the transects, we used a vegetation distribution for high latitudes (Fig. 1) that was based on the global potential vegetation described in Melillo et al. (1993). From the vegetation categories of Melillo et al. (1993), we aggregated temperate forest, temperate grasslands and temperate savannas into an extra-boreal category to indicate vegetation types that are located in transitional regions between boreal forest and temperate ecosystems or that are not characteristic arctic and boreal regions. For evaluating patterns of canopy development along each of the transects, we used mid-summer NDVI estimates derived from a 1-km resolution, Advanced Very High Resolution Radiometer (AVHRR) data set for 1995 (Eidenshink & Faundeen, USGS EROS Data Center, Distributed Active Archive Center, http://edcdaac.usgs.gov/1KM/1kmhomepage.html).

Carbon data

For the FEST and EST transects, the estimates of vegetation and soil carbon of more than 700 sites were extrapolated to a 300 km width along the transect by the methods described in Shvidenko et al. (2000). It is important to note that the estimates for FEST and EST do not include peatlands, and that the transects considered in this study do not represent the vast low-lying areas of western Siberia that are rich in peatlands. For the Finland Transect, estimates of vegetation carbon are based on Kauppi et al. (1995), while estimates of organic and mineral soil carbon are based on Liski & Westman (1997) and Liski (unpubl.). For the BFTCS, estimates of vegetation and soil carbon are based on data reported in a number of studies that participated in BOREAS (see Sellers et al. 1997; Hall 1999). For the Alaska transect, vegetation carbon for tundra were based on a number of studies (Shaver & Chapin 1991; Chapin et al. 1980, 1995; Walker et al. 1998; Gilmanov 1997; Shaver et al. 1996; Epstein et al. 2000) and for boreal regions in Alaska were based on inventory estimates of Yarie & Billings (2002). The estimates for organic and mineral soil carbon along the Alaska transect are also from several studies (Michaelson et al. 1996; Ping et al. 1997, 1998; Michaelson & Ping unpubl.; Zimmermann unpubl.). When possible, we developed estimates to 1 m depth in the mineral soil. Because of some interesting patterns in carbon stocks between southern boreal forest and more northern boreal forest along the transects, we decided to analyze data on carbon stocks separately for these subregions of boreal forest along the transect. For convenience, we refer to these regions as 'boreal' and 'southern-boreal' forest.

Because there are very few estimates of total NPP, i.e., above-ground plus below-ground NPP, we evaluated whether it would be useful to compare modeled estimates of total NPP among the transects. We used version 4.2 of TEM (McGuire et al. 2001), which considers spatial variation in temperature, precipitation, and cloudiness, to simulate total NPP along each transect and compared these estimates with estimates aggregated for several vegetation types located along the FEST (Shvidenko unpubl.), EST (Shvidenko unpubl.), and BFTCS (Peng & Apps 1998) transects; we did not compare the TEM estimates to estimates available for the Alaska transect, as TEM is already parameterized for NPP measurements in Alaska. This comparison indicated that the TEM estimates were highly correlated with the estimates for FEST, EST, and BFTCS (Table 1; $r^2 = 0.96$, $P < 0.001$, $N = 10$). Based on the strong correlation between the TEM estimates and transect-based estimates for different vegetation types, we aggregated the TEM estimates of NPP for different vegetation types along each transect to compare vegetation-specific NPP patterns among the transects. For our analysis of NPP, we do not distinguish between 'boreal' and 'southern' boreal forest.

As fire can be an important factor in the carbon dynamics of high latitude regions (Kasischke et al. 1995; Kasischke & Stocks 2000), we also compare the mean percentage of area burned annually among the transects for different vegetation types. For this comparison, we obtained fire data from a variety of sources. For both the FEST and EST transects, estimates were determined for a transect width of 300 km following the approach suggested by Shvindenko & Nilsson (2000). As fire statistics in Russia only exist for protected areas, and are subject to substantial uncertainties even in those areas, some assumptions had to be made based on expert judgement because a significant part of both Siberian transects cross unprotected areas. A model-based correction factor was applied for periods prior to 1988 to account for biased fire statistics (Shvidenko & Goldammer 2001). The estimates for extra-boreal vegetation in the southern part of the EST transect are derived from fire data for the Tuva mountain forest steppe ecoregion. For the Finland transect, data were for the time period from 1970 through 1998 (Finnish statistical year book of forestry 1999). For the BFTCS, the fire statistics were based on analyses from provincial data for Manitoba and Saskatchewan (Stocks et al. unpubl.). For the Alaska transect, data were obtained from the Alaska Fire Service for the time period from 1950 through 1997 (see Murphy et al. 2000). Additional information that contributed to our analyses can be located at http://www.uni-freiburg.de/fireglobe/.

Other data

We obtained additional data for our analyses from studies that have been conducted along the different transects. These data include information on permafrost depth (Fukuda, unpubl.; Vaseliev unpubl.; Hinzman, Crow & Lachenbrach, Osterkamp & Romanovsky at http://sts.gsc.nrcan.gc.ca/gtnp/english/bhinventory/us.htm), snowfree days (Vaganov unpubl.), active layer depth (Romanovsky & Osterkamp 1997; http://www.geography.uc.edu/~kenhinke/CALM/, Vaseliev unpubl.). Note that for the comparisons of snow-free days and active layer depth with mean annual temperature (MAT), MAT represents temperature at the measurement sites for these variables. This contrasts with other analyses in this study involving comparisons with MAT in which MAT was determined from the CLIMATE database. Our evaluation of water and energy exchange patterns focuses on the ratio of sensible to latent heat, also known as the Bowen ratio, and on the maximum canopy conductance as determined at eddy covariance towers that have been operated in the transects. For the EST, Bowen ratio data were obtained from Schulze et al. (1999), Valentini et al. (2000), and Rebmann et al. (in press). The data on Bowen ratio and maximum canopy conductance for the BFCTS were primarily obtained as part of BOREAS and for the Alaska transect were obtained as part of the ARCSS-LAII Flux Study as reported in Eugster et al. (2000). For the Alaska transect, some of the Bowen ratio data were also obtained from eddy covariance towers operating as part of ATLAS (Beringer unpubl.).

Environmental variation spanned by the transects

The most notable feature of the IGBP high latitude transects is that they span decreasing temperature gradients from southern to northern latitudes (Fig. 2). The MAT of the FEST transect, which spans the largest range in latitude among the transects (45° to 70° N),

Table 1. Estimates of annual net primary production (g C m^{-2} yr^{-1}) for the Boreal Forest Transect Case Study (BFTCS), the East Siberian Transect (EST), and the Far East Siberian Transect (FEST). See text for data sources used to develop the estimates.

	BFTCS	EST	FEST
Extra-boreal	284	340	
Southern-boreal	384	296	357
Boreal	191	242	204
Forest-tundra	192	165	124
Tundra		124	82
Polar desert		8	6

ranges from just above freezing at the southern end of the transect to −15 °C at the northern end of the transect (Fig. 2a). The gradient of MAT with latitude is not likely responsible for the relationship between total permafrost depth and latitude along the FEST (Fig. 3a), as permafrost depth drops off suddenly at the southern end of the transect. In comparison to the same latitudes of the FEST, MAT of the other transects is higher. Differences in MAT between the FEST and Alaska transects may explain differences in permafrost depths between the transects (Fig. 3a). Among the transects, the BFTCS transect, which is oriented from southwest to northeast between the warm and cold poles of the region, has the steepest gradient of MAT with latitude. For the same latitudes, MATs along the ScanTran and Finland transects are substantially higher in comparison with the other transects. From data on snow-free days from the Alaska and the Siberia transects, the relationship between length of the growing season and MAT suggests that the length of the growing season may be coupled to MAT for areas where the snow-free season exceeds ca. 100 days (Fig. 3b). This arises because the number of snow-free days is dominantly controlled by energy input, which generally varies with latitude (but see Vaganov et al. 1999). Although vegetation type may also play a role in the number of snow-free days by influencing the albedo of the surface and hence the amount of energy absorbed, this effect is small compared to the control of MAT which can affect the number of snow-free days by up to 100 days (Fig. 3b).

In comparison to the MAT-latitude relationships among the transects, the relationships between mean monthly summer temperature and latitude are qualitatively different (Fig. 2b). While south of 60° N, summer temperature of the FEST transect is lower in comparison with the other transects, north of 60° N the Alaska and ScanTran transects are lower than the other transects, which have similar relationships between mean summer temperature and latitude north of 60° N. The effects of lower summer temperatures in Alaska are likely responsible for the shallower active layer depths observed in Alaska in comparison to the other transects (Fig. 4a) as there is little relationship between MAT and active layer depth among the transects in Alaska and Russia (Fig. 4b) because the active layer depth depends on the thermal conditions at the surface and the thermal state and properties of the vegetation and soil.

While temperature is the most notable environmental gradient common to the high latitude transects, there is other environmental variation both within and among transects that is of importance (Figs. 5 and 6). South of 60° N, BFTCS has the lowest winter and summer precipitation in comparison with the other transects (Fig. 5a). For latitudes north of 60° N, there tends to be a decrease in both summer and winter precipitation for all transects

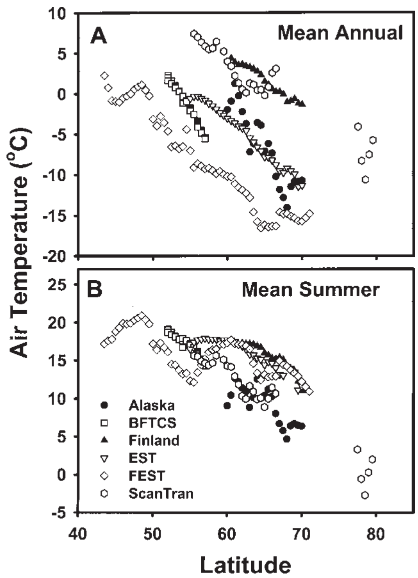

Fig. 2. Relationships of **(a)** mean annual temperature and **(b)** mean July temperature with latitude along each of the transects.

south to north (Fig. 5a, b), except for ScanTran where winter precipitation increases between 60° and 70° N because of the special influence of the Gulf Stream on this transect. In comparison to the FEST, BFCTS and Alaska transects, the EST, ScanTran and Finland transects are wetter in both summer (Fig. 5a) and winter (Fig. 5b), with the differences in winter more disparate. The cloudiness associated with summer precipitation south of 60° N is reflected in summer PAR differences among the transects south of 60° N (Fig. 6a), as the FEST has higher precipitation and lower PAR in comparison to the BFCTS.

Environmental variation and vegetation distribution

For evaluating how environmental variation spanned by the transects relates to vegetation distributed along each of the transects, we consider five general vegetation categories: alpine tundra, tundra, forest tundra, boreal forest, and extra-boreal vegetation. We do not explicitly consider polar desert, which we define as the cushion-forb tundra and prostrate dwarf-tundra zones of Walker (2000), in this study because ScanTran is the only transect that contains polar desert. While there are vast biotic and environmental differences between polar desert and alpine tundra, we present data for polar desert along the ScanTran transect under that category of alpine tundra for purposes of this study as there are physiognomic similarities between the two vegetation types with respect to low stature that is associated with wind-scoured environments during the winter. Our definition of tundra in this study is generally consistent with the

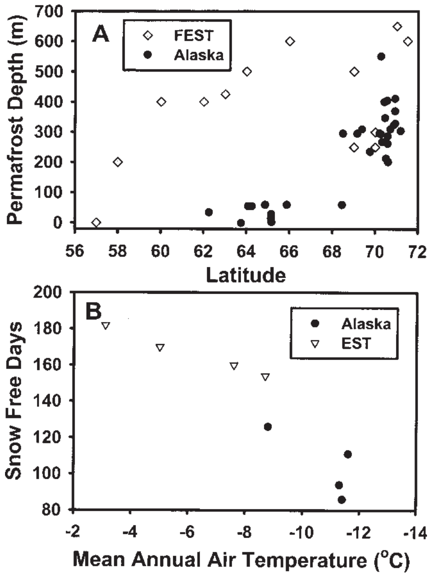

Fig. 3. Relationships of **(a)** permafrost depth with latitude and **(b)** snow-free days with mean annual temperature from data collected along the Alaskan and Siberian transects.

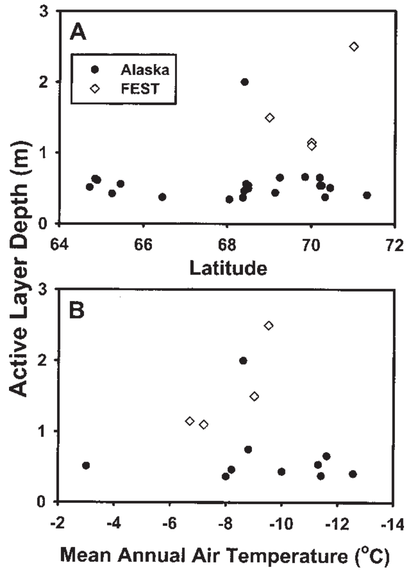

Fig. 4. Relationships of active layer depth with **(a)** latitude and **(b)** mean annual temperature along the Alaskan and Siberian transects.

erect dwarf-shrub and low-shrub zones of Walker (2000). In our analyses, the location of the vegetation types are as defined in Fig. 1.

While MAT generally decreases as vegetation changes from extra-boreal to alpine tundra vegetation types for all the transects, the relationships are separated by approximately 10 °C among the transects (Fig. 7a). The lower winter temperatures of the FEST are likely an important factor in the dominance of the boreal forest of this transect by deciduous conifers *Larix gmelinii* and *Larix cajanderi*. In comparison to the other transects, the relationship between mean monthly summer temperature and vegetation type is lower for the Alaska and ScanTran transects (Fig. 7b), which are the transects where summer temperature is most affected by maritime influences. In comparison to the other transects, the Alaska transect generally has the lowest summer and winter precipitation in boreal forest and tundra, as can be inferred from comparison of winter and summer precipitation between the Alaska and other transects from 60º to 70º N (Fig. 5). In comparison to the other transects, the ScanTran transect has the largest winter precipitation in forest tundra as the increasing winter precipitation between 60° and 70° N along the ScanTran transect (Fig. 5) occurs predominantly in forest tundra. It is notable that summer PAR is highest for forest tundra, boreal forest, and extra-boreal vegetation for BFCTS in comparison with the other transects (Fig. 6b). Also, the Alaska transect tends to have higher PAR in alpine tundra and tundra vegetation types in comparison with the other transects (Fig. 6b).

Environmental variation, vegetation distribution and carbon dynamics

The relationship of midsummer NDVI with latitude was similar among the transects, with values of between ca. 0.5 and 0.6 north of 65° N and then dropping linearly to ca. 0.2 between 65° and 75° N (Fig. 8a). South of 65° N, the BFCTS tends to have lower NDVI than the other transects, a pattern which may reflect effects of moisture limitation on canopy development in comparison to the other transects. The transition from high to low NDVI between 65° and 75° N reflects the general transition from boreal forest to forest tundra to tundra among the transects in this latitudinal zone.

Although vegetation carbon tends to decrease as the vegetation changes from temperate to tundra regions among the transects (Fig. 8b), the similarity in NDVI among the transects is not necessarily reflected in the patterns of vegetation carbon. Except for the EST, vegetation carbon shows a concave upward decrease from southern boreal forest through tundra. The large decrease in vegetation carbon from the southern boreal forest to the boreal forest for the BFCTS transect is associated with a soil fertility transition from chernozemic soils in the south to less fertile shallow podzols and fibrosols overlaying the Canadian Shield bedrock to the north. Thus, while the increase in vegetation carbon from tundra to southern boreal regions is likely primarily driven by climate factors among the transects, differences in soil fertility and disturbance regimes among the transects are likely responsible for variability in the

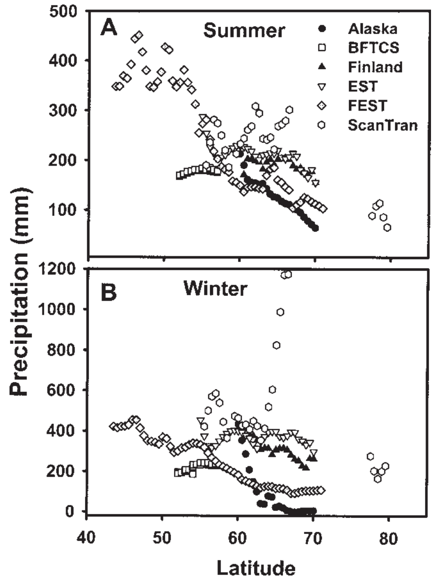

Fig. 5. Relationships of **(a)** summer (June-August) and **(b)** winter (September-May) precipitation along each transect.

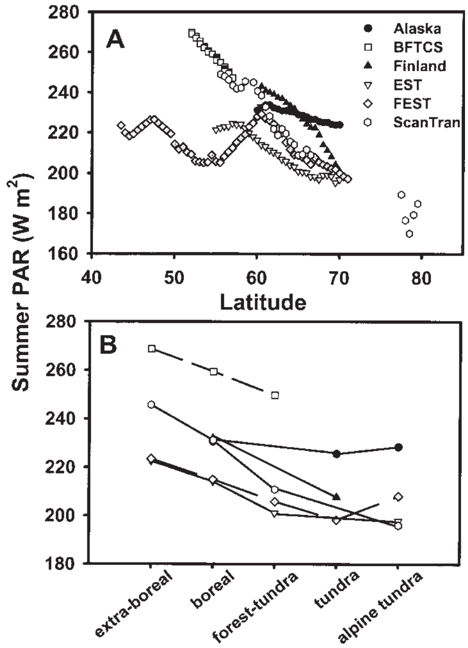

Fig. 6. Relationships of summer (June-August) photosynthetically active radiation (PAR) with **(a)** latitude and **(b)** vegetation along each of the transects.

relationship of vegetation carbon with vegetation distribution among the transects.

For all the transects, mean carbon stocks of the organic soil layer in upland areas excluding peatlands are < 10 kg C m^{-2} (Fig. 9a). Within the EST, FEST and Finland transects there is little pattern along the sequence of vegetation types from southern boreal forest to forest tundra with stocks between 1 and 2 kg C m^{-2}. In contrast, organic layer carbon stocks were above 4 kg C m^{-2} in the southern boreal and boreal forest of BFTCS. Large differences in organic carbon stocks among the transects occurred in tundra, for which organic layer carbon stocks were between 6 and 9 kg C m^{-2} in the BFCTS and Alaska transects compared to less than 1 kg C m^{-2} in the EST and FEST transects. There was an interesting pattern

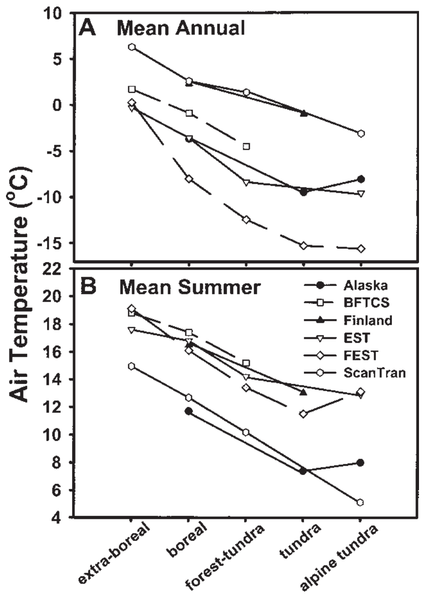

Fig. 7. Relationships of **(a)** mean annual temperature and **(b)** mean summer temperature with vegetation distribution along each of the transects.

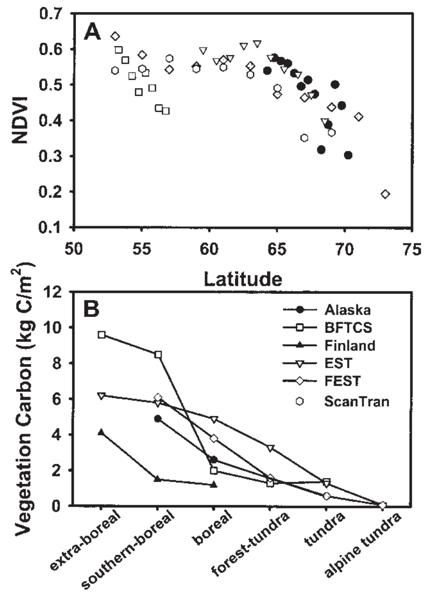

Fig. 8. The relationship of **(a)** NDVI with latitude along each of the transects and the pattern of **(b)** vegetation carbon with vegetation distribution along each of the transects.

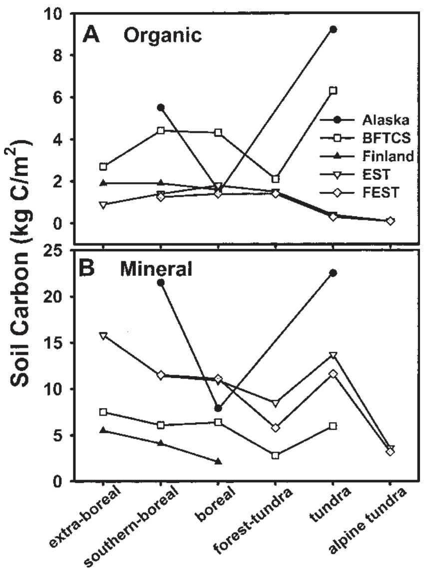

Fig. 9. Patterns of **(a)** soil organic carbon and **(b)** soil mineral carbon with vegetation distribution along each of the transects.

for Alaska, in which organic layer carbon stocks were larger than other transects in tundra and southern boreal forest, but were similar to other transects in boreal forest.

In comparison to the Finland and BFTCS transects, which were glaciated during the Wisconsin glaciation, it is interesting to note that patterns of mineral soil carbon stocks are higher in the EST, FEST, and Alaska transects, which were unglaciated (see Fig. 9b). Patterns of mineral soil carbon to 1 m with vegetation distribution are quite similar between the FEST and EST transects, with gradual decreases from extra-boreal systems to forest tundra, increases from forest tundra to tundra, and then decreases from tundra to alpine tundra. In comparison to other transects, mineral soil carbon for boreal forest and southern boreal forest is lowest along the Finland and BFTCS transects, and is highest for tundra and southern boreal forest along the Alaska transect. Similar to organic layer carbon stocks, Alaska had a pattern where mineral soil carbon stocks were greater than other transects in southern boreal forest and tundra, but were similar to other transects in boreal forest.

For the FEST, EST, and BFTCS transects, total ecosystem carbon stocks decrease in a similar fashion as vegetation changes from extra-boreal ecosystems to tundra (Fig. 10a). In contrast, total ecosystem C stocks are substantially higher for tundra and southern boreal forest along the Alaska transect because of high mineral carbon stocks in southern boreal forest between the Alaska and coast ranges. In comparison to the other transects, the Finland transect has lower total ecosystem carbon in forest tundra and boreal forest because of both low vegetation and mineral soil carbon stocks.

In general, patterns of NPP simulated by TEM show similar decreases among the transects for vegetation changes from extra-boreal ecosystems through alpine tundra (Fig. 10b). In comparison to the other transects, simulated NPP tends to be highest in forest-tundra and boreal forest for BFTCS. This may be caused by high summer temperatures and high summer PAR for the BFTCS transect in comparison with the other transects (Fig. 6b). In contrast, simulated NPP does not decrease from extra-boreal to boreal forest as it does for the EST and ScanTran transects despite higher PAR. The limitation in simulated NPP for extra-boreal ecosystems of the BFTCS transect is likely caused by an interaction between lower summer precipitation (Fig. 5a) and higher radiation that leads to greater moisture stress in comparison with the other transects.

By combining simulated NPP (Fig. 10b) with vegetation carbon estimates (Fig. 8b), we observed that the estimated number of years for the turnover of vegetation carbon (Fig. 11a) is substantially higher in boreal forest for the FEST (15.9 yr) and EST (21.0 years) transects than it is for the Finland (4.7 yr), BFCTS (7.1 yr), and Alaska (10.8 yr) transects. The nature of fire disturbance may explain differences in turnover of vegetation carbon. While historically the annual area burned is greatest for the EST transect (Fig. 11b), which would suggest that vegetation carbon should turnover more quickly in comparison with the other transects, fires in east Siberia and western parts of far east Siberia tend to be surface fires in which the trees survive because

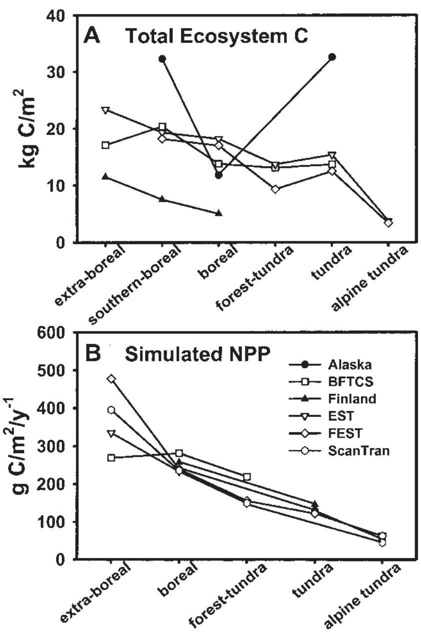

Fig. 10. Patterns of **(a)** total ecosystem carbon and **(b)** net primary production (NPP) with vegetation distribution along each of the transects.

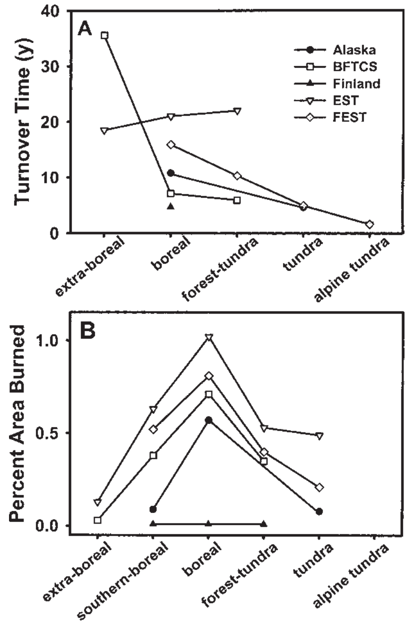

Fig. 11. (a) Estimates of the number of years for vegetation carbon to turnover based on the ratio of vegetation carbon from Fig. 8b and net primary production from Fig. 10b and **(b)** Patterns of historical annual area burned with vegetation distribution.

of thick bark in *Pinus* and *Larix* species. In contrast, fires in North America tend to be stand-replacing crown fires, and vegetation carbon appears to turnover much faster for boreal forest of the BFTCS transect than for the FEST transect (Fig. 11a), which have similar historical fire regimes (Fig. 11b). In comparison to the other transects, the pattern that soil carbon stocks along the Alaska transect are higher in tundra and southern boreal forest and similar in boreal forest (Fig. 9) may be explained by the pattern of percentage area burned, which is low for the Alaska transect in southern boreal forest and tundra, but similar in boreal forest (Fig. 11b). Although fires have effectively been suppressed in Finland (Fig. 11b), the similar turnover rate of vegetation carbon in boreal forest of the Finland, BFTCS, and Alaska transects (Fig. 11a) suggests that other disturbances like timber harvest influence the dynamics of vegetation carbon in Finland.

The relationship between disturbance regimes, vegetation carbon and the turnover of vegetation carbon is further supported by the fact that the average age of boreal forest stands is higher in Siberia as compared to Canada and Alaska. In the boreal forest of Canada only 11% of the stands are older than 90 years (Rapalee et al. 1998) and in Alaska 35% are older than 100 years (Yarie & Billings 2002). In contrast, for total Siberia nearly 50% of the forested area is classified as being covered by mature and over-mature stands. Repeated surface fires in Siberia are probably also responsible for the low soil organic layer carbon stocks.

Environmental variation, vegetation distribution and water/energy exchange

The partitioning of available energy at the surface into turbulent fluxes, defined by the Bowen ratio (sensible heat/latent energy flux, H/LE), is characterized by high variability across the latitudinal transects (Fig. 12a). There is far more variability in the Bowen ratio at any one latitude than across the entire range of latitudes that span the transect. The lack of a definitive relationship with latitude occurs because energy partitioning is strongly controlled by vegetation type, the spatial distribution of which is influenced at the macro-scale by environmental variability that is associated with the zonal climate and at meso- and micro-scales with other factors such as slope, elevation, soil type, and nutrient availability. There are, however, three significant effects that arise from an examination of these data, and these are all controlled by vegetation type and structure rather than directly by climate or latitude. Within tundra a change in functional group dominance along a climatic transect from south to north with changing non-vascular and woody vascular components (e.g., see Fig. 13) can influence energy partitioning. As non-vascular plants (mosses and lichens) have little control over their water loss, they tend to lose water more readily when wet than vascular plants. An increase in non-vascular components in conjunction with a decrease in woody plants that have a much higher resistance to water vapour loss leads to increases in maximum canopy conductance as is seen to increase with lower temperatures in the summer for tundra in Alaska (Fig. 12b). A second effect is associated with the decrease in canopy biomass north of 65° N as inferred by decreasing NDVI (Fig. 8a), which influences energy partitioning (Fig. 12a) as the ground becomes more open and the ground heat fluxes become a higher proportion of net radiation (Table 2). The third effect is associated with the decrease in leaf area and an increase in canopy conductance in moving from coniferous forest to tundra, which causes a decrease in the fraction of energy that is used in heating the atmosphere (sensible heat flux, Table 2). This effect is also observed in transitions from coniferous to deciduous forest (Table 2) and from closed forest stands to open woodlands that result from disturbance (Schulze et al. 1999). Although the partitioning of energy fluxes may not be greatly different across the latitudinal transects, the absolute magnitude of daily fluxes across a transect will however be strongly determined by the total solar irradiance, which varies with latitude. In addition, the total magnitude of fluxes summed across the season depends on the length of the growing season that also varies with latitude.

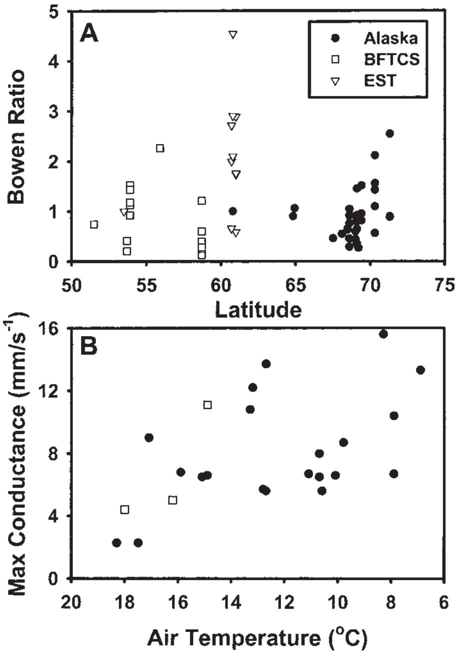

Fig. 12. Patterns of **(a)** Bowen ratio (sensible heat / latent heat) with latitude and **(b)** maximum canopy conductance with summer temperature measured for the BFTCS, the EST, and the Alaska transect. Note that summer temperature ranges from high to low temperature to facilitate interpretation of how maximum canopy conductance changes from southern boreal forest to tundra.

Discussion

There are several difficulties inherent in attempting a comparison of available data on environmental variation, vegetation distribution, carbon dynamics and surface energy exchanges across such wide geographic ranges that encompass the IGBP high latitude transects. Much of the data that we used in this analysis were collected in different years and in different parts of the growing season. There were different methodologies employed in data collection and data processing, and the data encompass micro- and meso-scale differences associated with physical attributes such as slope, aspect and soil in additional to macro-scale environmental variation. Also, data availability was greater for some transects than for others and there were very little data available for polar deserts in the high Arctic. Despite these complexities in assembling data for making comparisons among the high latitude transects, our analysis has provided some general insights on interactions among environmental variation, vegetation distribution, carbon stocks and turnover, and surface energy exchange.

Our analyses of carbon stocks and turnover indicate that both climate and disturbance interact to influence

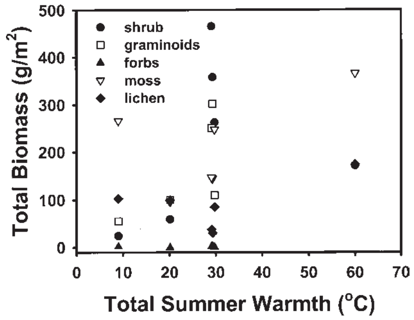

Fig. 13. Patterns of total biomass and total summer warmth for different plant functional types along a north-south latitudinal transect in tundra of northwest Alaska. Summer warmth is defined as the sum of mean monthly temperature for all months in which mean monthly temperature is greater than 0 °C.

latitudinal patterns of vegetation and soil carbon storage among the transects. Also, there is evidence that history of glaciation and edaphic factors such as those associated with the Canadian Shield bedrock play a role. In particular, the insights that our analyses provided concerning controls of the fire regime over carbon storage point at the need for better information on the nature of the fire regimes throughout high latitudes. Clearly, data on the extent and severity of fire are important for understanding influences of the fire regime on regional carbon dynamics at high latitudes. In addition, analyses of disturbance regimes need to be combined with forest inventory analyses to provide insight in how disturbance influences plant demography and ecosystem carbon storage in high latitudes.

Our analyses indicate that vegetation distribution is an important factor in determining the exchanges of heat and moisture in high latitudes, a conclusion that is

Table 2. Heat flux ratios (energy partitioning values, derived from daily flux averages) for different vegetation types across all transects. Le is latent energy flux, H is sensible heat flux, and G is ground heat flux. Bowen ratio is defined as the ratio of sensible heat to latent energy flux. Numbers are mean values determined from various sources described in Eugster et al. (2000), Beringer (unpubl.), and sites in Siberia (Schulze et al. 1999; Wirth et al. 1999, 2001; Valentini et al. 2000; Rebmann et al. 2001). Heath includes 9 sites in Alaska, Canada, Greenland and Norway; tundra includes 14 sites in Alaska only; shrub includes 8 sites in Alaska and Siberia; aspen includes 2 sites in Canada; spruce includes 7 sites in Canada and Sweden; and pine includes 7 sites in Canada and Siberia.

	Le/Rn	H/Rn	G/Rn	Bowen ratio
Heath	0.50	0.40	0.20	1.00
Tundra	0.43	0.37	0.15	0.95
Shrub	0.47	0.33	0.11	0.88
Aspen	0.65	0.20	0.11	0.31
Spruce	0.50	0.50	0.10	1.40
Pine	0.37	0.57	0.03	1.93

consistent with other analyses (Schulze et al. 1999; Chapin et al. 2000). Climate also interacts with vegetation distribution to influence surface energy exchanges. Hence, it is important to understand controls over the distribution of vegetation, which can then potentially be used for generalization and circumpolar extrapolation that is of great value to climate and vegetation modelers. There are many uncertainties about the role of high latitude ecosystems in the earth system (e.g., see Chapin et al. 2000). As biophysical responses of high latitudes to global change may have important consequences for the earth system, it is important to continue to improve our understanding of how environmental variation in high latitudes will affect carbon, water, and energy exchange with the atmosphere. Despite limitations imposed by the data we assembled to make comparisons among the high latitude transects, the analyses in this study have taken an important step toward clarifying the complexity of interactions among environmental variables, vegetation distribution, carbon stocks and turnover, and water and energy exchange in high latitude regions. This study reveals the need to conduct coordinated global change studies in high latitudes to further elucidate how interactions among climate, disturbance, and vegetation distribution influence carbon dynamics and water and energy exchange in high latitudes.

Acknowledgements. We thank J. Liski for providing us with biome-level soil carbon estimates for Finland and R. Zimmermann for providing a wealth of unpublished field data collected during an expedition to Alaska in 1999. We also acknowledge T. Osterkamp, E.A. Vasiliev, and F.I. Pleshikov for providing data on permafrost and G. Michaelson and C. Ping for providing data on soil carbon. We thank C. Silapaswan for assistance with graphics. This study was supported by the Arctic System Science Program and the Bonanza Creek LTER Program with funding from the National Science Foundation and by the Land Cover and Land Use Program with funding from the National Aeronautics and Space Administration.

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Received 9 February 2001;
Revision received 20 January 2002;
Accepted 4 April 2002.
Coordinating Editors: J. Canadell & P.S. White.