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Recent Climate-Driven Increases in Vegetation Productivity for the Western Arctic: Evidence of an Acceleration of the Northern Terrestrial Carbon Cycle

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ABSTRACT: Northern ecosystems contain much of the global reservoir of terrestrial carbon that is potentially reactive in the context of near-term climate change. Annual variability and recent trends in vegetation productivity across Alaska and northwest Canada were assessed using a satellite remote sensing–based production efficiency model and prognostic simulations of the terrestrial carbon cycle from the Terrestrial Ecosystem Model (TEM) and BIOME–BGC (BioGeoChemical Cycles) model. Evidence of a small, but widespread, positive trend in vegetation gross and net primary production (GPP and NPP) is found for the region from 1982 to 2000, coinciding with summer warming of more than 1.8°C and subsequent relaxation of cold temperature constraints to plant growth. Prognostic model simulation results were generally consistent with the remote sensing record and also indicated that an increase in soil decomposition and plant-available nitrogen with regional warming was partially responsible for the positive productivity response. Despite a positive trend in litter inputs to the soil organic carbon pool, the model results showed evidence of a decline in less labile soil organic carbon, which represents approximately 75% of total carbon storage for the region. These results indicate that the regional carbon cycle may accelerate under a warming climate by increasing the fraction of total carbon storage in vegetation biomass and more rapid turnover of the terrestrial carbon reservoir.

KEYWORDS: Boreal forest; Arctic tundra; Vegetation productivity; GPP; NPP; Carbon cycle; AVHRR; BIOME–BGC; TEM; WALE

1. Introduction

Boreal forest and arctic tundra biomes of the northern high latitudes ($>40^{\circ}\text{N}$) are currently undergoing significant changes coinciding with recent and persistent climatic warming (Serreze et al. 2000; Comiso 2003). Terrestrial ecosystem responses to the warming trend include thawing permafrost and deepening soil active layer depths (Oelke et al. 2004), advances in the timing and length of seasonal growing seasons (Myneni et al. 1997a; McDonald et al. 2004), changes in vegetation growth, and alteration of land–atmosphere CO_2 exchange (Rander-son et al. 1997; Nemani et al. 2003; Angert et al. 2005).

Net primary production (NPP) represents the sequestration of atmospheric CO_2 through plant photosynthesis or gross primary production (GPP), and carbon storage in vegetation biomass and soils. Net ecosystem production (NEP) is the residual difference between NPP and CO_2 losses from soil heterotrophic respiration and defines the net ecosystem–atmosphere exchange of CO_2 in the absence of disturbance. Boreal and arctic NPP is characteristically low compared to temperate forests because of reduced solar radiation, colder temperatures, and shorter growing seasons at higher latitudes. Seasonal cold temperatures, permafrost, and wet soils also inhibit soil decomposition and heterotrophic respiration, and provide an additional, indirect constraint to NPP through soil nutrient (primarily nitrogen, N) limitations to vegetation growth (Bonan and Van Cleve 1992; Schimel et al. 1996; Shaver and Jonasson 2001). These environmental conditions have historically favored net annual uptake of atmospheric CO_2 (positive NEP) and relatively stable soil organic carbon (SOC) accumulations throughout the Holocene, despite large interannual variability in NEP and periodic carbon losses from regional disturbances, including fire and insect defoliations.

Previous investigations of northern vegetation activity derived from visible and near-infrared wavelength satellite remote sensing records indicate advances in the onset of vegetation greening and increasing productivity during much of the 1980s and 1990s (Myneni et al. 1997a; Nemani et al. 2003), followed by a recent widespread decline in photosynthetic activity for much of the region (Goetz et al. 2005). However, the validity of these trends has been questioned because of the coarse spatial and temporal compositing of the data required to mitigate cloud cover and atmospheric aerosol effects, problems with sensor and navigational drift, intercalibration of successive instruments, and data contamination from volcanic eruptions and bidirectional effects (Cihlar et al. 1998). While time series remote sensing data are capable of detecting changes in photosynthetic biomass and NPP, more detailed assessment of underlying mechanisms driving observed trends and below-ground processes is limited. Alternatively, prognostic ecosystem process model simulations can be used with these methods to evaluate regional patterns and trends from the remote sensing record in the context of more comprehensive simulations of the terrestrial carbon cycle.

The Western Arctic Linkage Experiment (WALE) was initiated to investigate the role of northern terrestrial ecosystems in the larger Arctic system response to global change through model and satellite remote sensing analyses of regional carbon, water, and energy cycles (McGuire et al., see WALE Special Theme). The objectives of the current investigation are to assess annual variability and regional trends in vegetation productivity for the WALE domain, and the primary mecha-

nisms driving observed changes over the 19-yr (1982–2000) study period. To accomplish these objectives, we apply a biome-specific Production Efficiency Model (PEM) driven by daily surface meteorology and satellite remote sensing observations of photosynthetic leaf area. We also conduct prognostic regional simulations of terrestrial carbon budgets for the same period using two ecosystem process models, BIOME–BGC (BioGeoChemical Cycles) and the Terrestrial Ecosystem Model (TEM); these model simulations are used for independent assessment of satellite remote sensing–derived results and to elucidate underlying mechanisms driving changes in vegetation productivity and the terrestrial carbon cycle.

2. Methods

The WALE domain for this investigation encompasses boreal forest and tundra biomes of Alaska and northwest Canada (Figure 1) and represents approximately 11% of the global aerial extent of these biomes (Saugier et al. 2001). We defined this area in terms of nodes of the National Snow and Ice Data Center (NSIDC) north polar Equal-Area Scalable Earth (EASE) grid (Armstrong and Brodzik 1995). The domain spans a latitudinal range from 56.19° to 71.24°N, while land areas within the region comprise 3511 grid cells with nominal 25 km × 25 km resolution and a total representative area of approximately 2.2 million km². We used a National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR)-based global land cover classification to define major biomes for PEM calculations within the study region (Myneni et al. 1997b; DeFries et al. 1998). Boreal forests and tundra are the major biomes within the region and represent approximately 52% and 30% of the region, respectively. The rest of the domain is composed of permanent ice and snow, barren land, and inland water bodies. These nonvegetated areas were masked from further analysis to isolate relationships between PEM results and environmental parameters.

We applied the PEM described below (see section 2.1.) to assess spatial and temporal variability in annual vegetation productivity for the study region over a 19-yr period from 1982 to 2000. The PEM requires spatially explicit and temporally contiguous inputs of daily surface meteorology, leaf area index (LAI), and fraction of canopy absorbed photosynthetically active radiation (FPAR) to compute GPP and NPP. Monthly LAI and FPAR data were obtained from the NOAA AVHRR Pathfinder dataset, which has an approximate 16 km × 16 km spatial resolution and extends over the entire domain from 1982 to 2000 (Myneni et al. 1997b). The LAI and FPAR data are based on a monthly maximum value compositing of AVHRR spectral reflectance data to mitigate cloud cover, smoke, and other atmospheric aerosol contamination effects. These data were reprojected to the 25-km polar EASE-grid format using a nearest-neighbor resampling scheme. The LAI and FPAR data were then resampled to a daily time step by temporal linear interpolation of adjacent monthly values. Surface air temperature, incident solar radiation, and vapor pressure deficit (VPD) inputs were provided by daily reanalysis data from the National Centers for Environmental Prediction (Kistler et al. 2001). The NCEP meteorological data are available globally at approximately 1.875° (~208 km) spatial resolution and were reprojected into the 25-km resolution polar EASE-grid format using a bi-Lagrange interpolation approach (Serreze et al.

Figure 1. The study domain spans a latitudinal range from 56.19° to 71.24°N, with a total representative area of approximately 2.2 million km²; boreal forest and arctic tundra biomes represent 52% and 30% of the domain, while areas in gray represent permanent ice and snow, barren land, and inland water bodies that were not included in this analysis.

2002). PEM calculations were conducted for vegetated cells within the study region from 1982 to 2000, and spatial patterns and annual variability in LAI and NPP were evaluated accordingly. We conducted statistical time series and correlation analyses to assess regional trends and correspondence between annual productivity calculations, LAI, and meteorological parameters from the NCEP reanalysis. We first tested the time series data for first-order serial correlation using the Durbin–Watson (D) statistic for autocorrelation of the regression residuals. Where D indicated first-order autocorrelation, we performed a simple transformation of the variables following the Cochrane–Orcutt approach for mitigating autocorrelation (Neter et al. 1989). The statistical significance of these relationships was assessed at a 90% confidence level.

We also conducted regional simulations of terrestrial carbon cycle dynamics using two prognostic ecosystem process models, BIOME–BGC and TEM, to assess relative agreement among the different model approaches, underlying pro-

cesses driving PEM-based vegetation productivity, and linkages to other carbon cycle components. The BIOME-BGC and TEM models are described in greater detail below (see section 2.2.). These simulations were conducted for each grid cell within the domain using the NCEP reanalysis daily surface meteorology (Kistler et al. 2001). The BIOME-BGC model runs at a daily time step using daily meteorological inputs of minimum and maximum air temperature, VPD, precipitation, and incident solar shortwave radiation. The TEM is a monthly time step model and was driven by aggregated monthly meteorological inputs from the NCEP reanalysis. Model outputs of LAI, GPP, NPP, and NEP were produced at monthly and annual time scales for major vegetation types identified from a 25-km resolution, NOAA AVHRR land cover classification of the study domain; the map was derived from a 1-km resolution land cover classification and retains subgrid-scale information on the relative proportions of dominant and subdominant land cover types within each 25-km grid cell (McGuire et al., see WALE Special Theme). Ecosystem process model simulations were conducted over the entire domain for arctic tundra and boreal evergreen and deciduous forest classes. Model outputs were then spatially aggregated according to the relative proportions of individual land cover classes identified within each 25-km grid cell. Spatial aggregation of model outputs within each grid cell was based on linear weighting of dominant and subdominant land cover classes, with no lateral transfers of mass or energy within a specified grid cell or between adjacent grid cells. We then aggregated the estimated fluxes across all grid cells in the study region to produce regional estimates.

2.1. Production Efficiency Model calculations

A biome-specific PEM was used to calculate GPP and NPP for unmasked grid cells within the 25-km resolution EASE-grid domain. The PEM logic is described and verified in detail elsewhere (Nemani et al. 2003; Running et al. 2000; Running et al. 2004), and summarized below. GPP (g C m^{-2}) was derived on a daily basis as

$$\text{GPP} = \varepsilon \times \text{FPAR} \times \text{PAR} \quad (1)$$

$$\varepsilon = \varepsilon_{\max} \times T_f \times \text{VPD}_f, \quad (2)$$

where ε is a light use efficiency parameter (g C MJ^{-1}) for the conversion of photosynthetically active radiation (PAR; MJ m^{-2}) to GPP, where PAR is assumed to represent 45% of incident solar radiation; FPAR is the fraction of absorbed PAR; $\varepsilon_{\max}$ is the potential maximum ε under optimal conditions (i.e., no environmental stress); T_f is a scalar that defines reductions in photosynthesis under low temperature conditions; and VPD_f is a scalar that defines similar reductions under suboptimal surface air vapor pressure deficit and associated daytime water stress conditions. Both T_f and VPD_f are dimensionless parameters ranging from 1 for optimal conditions to 0 under complete canopy stomatal closure and minimal photosynthetic activity. Both T_f and VPD_f are defined from daily air temperature ($T_{\min}$) and VPD using simple photosynthetic response curves. These response curves and $\varepsilon_{\max}$ are prescribed for different biome types defined from the global land cover classification.

Net primary production (g C m^{-2}) is derived on an annual basis as the difference

between the annual summation of daily net photosynthesis and autotrophic growth and maintenance respiration:

$$\text{NPP} = \sum_1^{365} (\text{GPP} - R_{m_lr}) - (R_{m_w} + R_g), \quad (3)$$

where R_{m_lr} is the daily maintenance respiration of leaves and fine roots as derived from allometric relationships to canopy LAI and an exponential relationship between respiration and temperature. The R_{m_w} parameter represents the annual maintenance respiration from live wood, while R_g represents the annual growth respiration; both R_{m_w} and R_g are derived from allometric relationships between vegetation biomass and maximum annual LAI, and exponential respiration response curves to air temperature. The characteristic response curves for these calculations vary according to major biomes as defined by a Biome Properties Lookup Table (BPLUT) and the global land cover classification. The BPLUT defines response characteristics for 11 major biomes including evergreen needle-leaf and broadleaf deciduous forests, mixed deciduous and evergreen forests, grasslands, shrublands, and croplands. The PEM used for this investigation is currently being used for operational global assessment and monitoring of GPP and NPP using LAI and FPAR data from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board the National Aeronautics and Space Administration (NASA) Earth Observing System (EOS) *Terra* satellite from 2000 onward (Running et al. 2004; Zhao et al. 2005). A detailed description of these algorithms and associated BPLUT properties can be found in the MODIS MOD17 User's Guide (Heinsch et al. 2003).

2.2. Ecosystem process model simulations

2.2.1. BIOME-BGC

BIOME-BGC is a general ecosystem process model designed to simulate fluxes and storage of carbon, water, and nitrogen for terrestrial biomes ranging from individual plots to global scales. The model has been successfully applied over a range of diverse biomes, spatial scales, and climate regimes including boreal forests of Alaska and Canada (Keyser et al. 2000; Kimball et al. 1997; Kimball et al. 2000; Amthor et al. 2001). Details of the model are presented elsewhere and include applications for multiple biome types and spatial scales (e.g., Thornton et al. 2002; White et al. 2000), while a summary of model components pertaining to this investigation is provided below.

The BIOME-BGC model is designed to realistically simulate soil-plant carbon (C) and nitrogen (N) cycling, but with simplifying assumptions to facilitate application at regional scales using a limited number (34) of biome-specific physiological constants. All plant, litter, and soil carbon; nitrogen; and water pools and fluxes are entirely prognostic. The plant/ecosystem surface is represented by single, homogenous canopy, snow (when present), and soil layers, where understory vegetation is not distinguished from the aggregate canopy layer. The model operates on a daily time step, with daily maximum and minimum air temperature, incident solar shortwave (direct and diffuse) radiation, and precipitation as the primary inputs from which mean daily net radiation, vapor pressure deficit, and

day/night average temperatures are estimated. Biophysical processes represented by the model include photosynthetic C fixation from atmospheric CO₂; N uptake from the atmosphere and soil; C/N allocation to growing plant parts; seasonal phenology, decomposition of fresh plant litter and soil organic matter; plant mortality, growth, litterfall, decomposition, and disturbance (i.e., fire and management); solar radiation interception and partitioning into sunlit and shaded leaf fractions; rainfall routing to leaves and soil; snow accumulation and melting; drainage and runoff of soil water; evaporation of water from soil and wet leaves; and evapotranspiration (ET) partitioning into transpiration, snow, soil, and canopy evaporation components.

Net primary production is determined as the daily difference between net photosynthesis, or GPP, and respiration from autotrophic maintenance (R_m) and growth (R_g) processes. Photosynthesis, including both C₃ and C₄ pathways, is calculated separately for sunlit and shaded canopy components using a modified form of the Farquhar biochemical model (Farquhar and von Caemmerer 1982). Photosynthetic response is regulated by canopy conductance to CO₂, leaf maintenance respiration, and daily meteorological conditions including air pressure, air temperature, and solar irradiance. Canopy CO₂ conductance is calculated as a proportion of the canopy conductance to water vapor (g_c), which is derived from a prescribed maximum rate modulated for suboptimal air temperature, VPD, solar irradiance, or soil water potential conditions (Jarvis and Morison 1981; White et al. 2000). The R_m term represents total C losses from day and night foliar, sapwood, and coarse and fine root respiration components of living tissue. The R_m term is calculated from a base respiration rate adjusted for tissue N concentration and an empirical exponential relationship to estimated daily air and soil temperatures (Ryan 1991). The R_g term is calculated as a constant proportion of new tissue carbon construction for woody and nonwoody tissue types.

NEP is calculated on a daily basis as the difference between NPP and soil heterotrophic respiration (R_h). The R_h term is estimated as a daily rate defined from soil and litter C pools. Soil and litter decomposition and R_h are defined as the aggregate result of characteristic exponential decay functions for a series of cascading soil and litter C pools of decreasing substrate quality. Daily R_h within each C pool is calculated from an empirical decomposition rate modulated by daily soil water potential, soil temperature, and soil N conditions.

The relative proportions of C and N within soil, litter, and vegetation compartments are tightly coupled; plant growth and allocation, soil decomposition, respiration and N mineralization, and immobilization are strongly regulated by C and N availability defined from prescribed C:N ratios for individual compartments and environmental conditions. Vegetation canopy and fine root phenology determines the seasonal pattern of canopy photosynthesis, growth, senescence, and dormancy and is calculated for both evergreen and deciduous vegetation from an empirical phenology model and deviations of current air temperature, soil moisture, and incident solar radiation conditions from the long-term climatology of the site (White et al. 1997; Thornton et al. 2002). Atmospheric N deposition occurs at a constant daily rate applied directly to a soil mineral N pool; N leaching and removal from the system occurs as a constant fraction of soil water outflow. Whole-plant mortality is calculated, in addition to seasonal canopy and fine root losses, as a prescribed annual fraction of plant biomass scaled to a daily loss rate,

which is then transferred to soil litter pools. Annual fire mortality is also specified as a biome-specific physiological parameter scaled to a constant daily rate of consumption for above-ground biomass, and root and soil litter C and N pools (Thornton et al. 2002).

BIOME-BGC model simulations of vegetation and soil carbon stocks across the domain were initialized by “spinning up” the model to steady-state conditions through continuous cycling of the 20-yr NCEP reanalysis daily climatology and model assumptions of constant annual fire disturbance and mortality rates within individual biomes, constant atmospheric N deposition, and constant atmospheric CO₂ levels. Model simulations were then conducted on a daily basis over the 20-yr NCEP daily reanalysis period under a constant rate of atmospheric N deposition, constant annual fire disturbance rates, and historical atmospheric CO₂ concentrations (Thoning et al. 1989).

2.2.2. TEM

The TEM is a process-based, global-scale ecosystem model that incorporates spatially explicit data pertaining to climate, vegetation, soil, and elevation to estimate monthly pools and fluxes of C and N in the terrestrial biosphere. The underlying equations and parameters have been extensively documented (Raich et al. 1991; McGuire et al. 1992; Tian et al. 1999), and the model has been applied to a number of studies in high-latitude regions (Clein et al. 2000; Clein et al. 2002; McGuire et al. 2000a; McGuire et al. 2000b; McGuire et al. 2002; Zhuang et al. 2002; Zhuang et al. 2003; Zhuang et al. 2004). In this study, we used TEM version 5.1, which is revised from TEM version 5.0 (Zhuang et al. 2003), with an updated freeze–thaw algorithm (Euskirchen et al. 2006).

TEM 5.1 is coupled to a soil thermal model (STM; Zhuang et al. 2001) that is based on the Goodrich model (Goodrich 1976) and takes a finite-element approach to determining heat flow in soils. This model is appropriate for both permafrost and nonpermafrost soils. The STM receives monthly gridded estimates of air temperature, soil moisture, and snowpack from TEM. The monthly snowpack estimates are a function of elevation as well as monthly precipitation and monthly air temperature, and have a subsequent influence on soil moisture in the water balance model of TEM (Vörösmarty et al. 1989). The snowpack, air temperature, and soil moisture data are used in the STM to simulate soil temperatures at different depths such that the frozen and thawed boundaries in the soil move up and down during a simulation.

Similar to BIOME-BGC, NPP is calculated as the difference between GPP and autotrophic respiration (R_A). Monthly GPP considers the effects of several factors and is calculated as follows:

$$\text{GPP} = C_{\max} f(\text{PAR}) f(\text{PHENOLOGY}) f(\text{FOLIAGE}) f(T) f(C_a, G_v) f(\text{NA}) f(\text{FT}), \quad (4)$$

where $C_{\max}$ is the maximum rate of C assimilation, PAR is photosynthetically active radiation, and $f(\text{PHENOLOGY})$ is monthly leaf area relative to a maximum monthly leaf area (Raich et al. 1991). The function $f(\text{FOLIAGE})$ is a scalar function that ranges from 0.0 to 1.0 and represents the ratio of canopy leaf biomass to a maximum leaf biomass (Zhuang et al. 2002), T is monthly air temperature,

C_a is atmospheric CO_2 concentration, G_v is relative canopy conductance, and NA is nitrogen availability. The effects of elevated atmospheric CO_2 directly affect $f(C_a, G_v)$ by altering the intercellular CO_2 of the canopy, while the function $f(\text{NA})$ models the limiting effects of plant N status on GPP (McGuire et al. 1992; Pan et al. 1998). The function $f(\text{FT})$ is an index of submonthly freeze–thaw, which represents the proportion of a specific month in which the ground is thawed based on soil temperatures at 10-cm depth as calculated by the STM. This index influences the ability of the vegetation to take up atmospheric CO_2 and is used as a multiplier in the calculation of GPP.

Monthly autotrophic respiration (R_A) in TEM represents total respiration (excluding photorespiration) of living vegetation, including all CO_2 production from various processes including plant respiration, nutrient uptake, and biomass construction. The R_A term is determined as the sum of R_m and R_g , where autotrophic growth respiration is derived as 20% of the difference between GPP and R_m . While R_m is a direct function of plant biomass (C_v) as follows:

$$R_m = K_r(C_v)e^{raT}, \quad (5)$$

where K_r is the per-gram-biomass respiration rate of the vegetation at 0°C , C_v is the vegetation carbon pool, T is the mean monthly air temperature, and ra is the instantaneous rate of change in autotrophic respiration with the change in temperature.

NEP is calculated on a monthly basis as the difference between NPP and R_h . The R_h term represents the decomposition of all organic matter and is calculated as follows:

$$R_h = K_d(C_s)e^{rsT}f(M), \quad (6)$$

where K_d is the per-gram-biomass respiration rate of soil organic matter at 0°C , C_s is soil carbon pool, T is the mean monthly soil temperature calculated at 5-cm depth in the STM, rs is the instantaneous rate of change in decomposition with the change in temperature, and $f(M)$ is a scalar between 0 and 1 of volumetric soil moisture (M) effects on decomposition. The per-gram-biomass respiration rate of the soil is affected by the nitrogen concentration of litter that enters the soil.

Although many of the parameters used in TEM are defined from published information, the rate-limiting parameters in the model (e.g., C_{max} in GPP, K_r in R_m , and K_d in R_h) are determined by calibrating the model to fluxes and pools of intensively studied field sites. For the application of TEM to the study region, we created a parameterization for moist tundra to fluxes and pools measured at the Toolik Lake study site in Alaska (see Table A1 in McGuire et al. 1992). We also created parameterizations for wet coniferous boreal forest, dry coniferous boreal forest, and boreal deciduous forest based on fluxes and pools measured at the Bonanza Creek study site in Alaska and from studies associated with the Boreal Ecosystem–Atmosphere Study (BOREAS). The parameterization for maritime coniferous forest was based on fluxes and pools measured at the H. J. Andrews study site in Oregon (see <http://www.lternet.edu/sites/and/>). Calibration requires the use of climate data. We used the average climate from 1961 to 1990 from the CRU dataset for the parameterizations, since this is the dataset normally used as input

for retrospective simulations with TEM. An atmospheric CO₂ concentration of 280 ppmv was the level of CO₂ that was used to calibrate the model in this study.

The TEM simulations were initialized by spinning up each grid cell to steady-state conditions using the mean monthly climate from 1980 to 2001 and a historical atmospheric CO₂ concentration appropriate for the year 1891. After reaching equilibrium, the cell was then run through five cycles of the 22-yr NCEP reanalysis climate data using historical CO₂ concentrations appropriate for the period 1892–2001. This procedure was used to condition the model to transient climate by the end of the twentieth century. Model outputs from the final cycle and 1982–2000 period were then compared with BIOME–BGC and PEM results.

3. Results and discussion

3.1. Regional climate patterns

Average seasonal air temperatures for the domain ranged from -17.6°C in winter to 8.3°C in summer, with a mean annual temperature of -6.0°C . Mean summer air temperatures warmed by 1.85°C ($P = 0.0008$) from 1982 to 2000 (see Figure 2), while no significant regional trends were observed for spring, fall, winter, or mean annual conditions. Year-to-year variations in average seasonal and annual air temperatures were approximately $\pm 1.6^{\circ}\text{C}$ (s) and were relatively large compared to the long-term (19 yr) trend. Precipitation averaged $565 \text{ kg m}^{-2} \text{ yr}^{-1}$ with the majority falling between June and December. There was no significant trend in mean annual precipitation for the domain, and interannual variability was approximately 18% [$\pm 102 \text{ kg m}^{-2}$ (s)] of the long-term annual average. Environmental conditions from 1982 to 1984 were relatively cool and dry, while 1985 was

Figure 2. Climate analysis showing spatially averaged trends in summer air temperatures and annual precipitation for the study domain as depicted by the NCEP climate reanalysis (Kistler et al. 2001); annual anomalies are determined as the difference from the long-term (1982–2000) mean.

cool and wet; 1989 and 1990 were anomalously warm, while 1991 was cool and wet relative to average conditions. Conditions in 1995 and from 1997 to 1999 were anomalously warm and dry, while 2000 was comparatively cool relative to the long-term regional average.

3.2. PEM assessment of vegetation productivity

A summary of satellite remote sensing–based PEM results is presented in Table 1, while a map of the estimated mean annual NPP for the domain is shown in Figure 3. Estimated annual NPP and autotrophic respiration for the study domain averaged $288 [\pm 105.6 \text{ (s)}]$ and $287 [\pm 78.8 \text{ (s)}]$ g C m^{-2} , respectively, and represented approximately half of annual GPP. Spatial variability in vegetation productivity for the domain was largely stratified by land cover type. Boreal forest annual NPP averaged $320 [\pm 112.4 \text{ (s)}]$ g C m^{-2} and was approximately 28% greater than NPP for arctic tundra. Within a given biome, annual productivity was generally inversely proportional to latitude and elevation, consistent with environmental gradients in seasonal air temperatures and solar irradiance.

Spatial variability in PEM-derived NPP results shows distinctions among major regions and vegetation classes that are generally consistent with other boreal and arctic NPP estimates derived from in situ measurements and stand inventory–based approaches. Annual NPP for arctic tundra has been reported to range from approximately 70 g C m^{-2} for low tundra shrub communities of the high Arctic up to 500 g C m^{-2} for tall shrub communities of the low Arctic (Shaver and Jonasson 2001). Boreal annual NPP for mature spruce forests in central Alaska has been reported to be approximately 225 g C m^{-2} (Ruess et al. 1996), while values reported for boreal forests in central Canada range from 226 to 478 g C m^{-2} and are generally higher for broadleaf deciduous forests relative to needleleaf evergreen forests (Gower et al. 1997). Direct measurements of GPP and R_{aut} are difficult to obtain and are not well represented in the literature relative to NPP. However, annual GPP estimates derived from net CO_2 flux and respiration measurements within mature black spruce forests of central Canada range from 800 to 930 g C m^{-2} (Goulden et al. 1998; Jarvis et al. 2001). Similar studies for Alaskan arctic tundra show a range in annual GPP from 43 to 296 g C m^{-2} (Oechel et al. 1995; Harazono et al. 2003). Annual autotrophic respiration has been found to be approximately 511 g C m^{-2} for mature boreal black spruce forest (Jarvis et al. 2001) and also represents a relatively consistent (40%–70%) proportion of GPP across a range of global ecosystems (Waring et al. 1998; Landsberg and Gower

Table 1. Summary of PEM results for the vegetated study domain; mean standard deviations of spatial means are shown in parentheses.

Classification region	Area* (%)	GPP _{av} ($\text{g C m}^{-2} \text{ yr}^{-1}$)**	NPP _{av} ($\text{g C m}^{-2} \text{ yr}^{-1}$)	NPP/GPP (%)	$R_{\text{aut}}/\text{GPP}$ (%)
Total domain	100	575 (172)	288 (106)	50.1	49.9
Tundra	30	448 (117)	232 (61)	51.8	48.2
Boreal forest	52	649 (154)	320 (112)	49.3	50.7

* Proportional area represented within the entire 2.2 million km^2 study domain.

** Mean annual GPP and NPP (standard deviations in parentheses) from 1982 to 2000.

Figure 3. Mean annual NPP (g C m⁻² yr⁻¹) derived from PEM calculations over the pan-Arctic domain and 19-yr (1982–2000) study period; masked areas are shown in gray and include permanent ice and snow, open water, and barren land.

1997; Gifford 2003). Spatial and temporal variations in these values largely reflect seasonal temperature, light availability, soil moisture, and soil nutrient limitations to vegetation growth and respiration processes at high latitudes and upper elevations (Bonan and Shugart 1989; Churkina and Running, 1998; McGuire et al. 2003).

A map of long-term (1982–2000) trends in PEM-derived annual NPP for the study domain is presented in Figure 4. Long-term NPP patterns showed increasing and decreasing trends across 90.3% and 9.7% of the vegetated study region, respectively. Boreal forest and arctic tundra biomes showed predominantly positive decadal trends in NPP of 9.1% (+33.0 g C m⁻²; $P = 0.037$) and 7.6% (+21.1 g C m⁻²; $P = 0.078$), respectively. The largest and most extensive positive trends occur in boreal northwest Canada and eastern Alaska, while trends were compara-

Figure 4. Map of multiyear (1982–2000) linear trends in annual NPP ($\text{g C m}^{-2} \text{ decade}^{-1}$) as derived from PEM simulations for the study domain, excluding permanent ice and snow, open water, and barren land areas (indicated in gray).

tively small in the western and northern portions of the domain. A map of the statistical significance of these trends is presented in Figure 5 and indicates that trends with a minimum 90% probability level occurred over approximately 37.8% ($737\,023 \text{ km}^2$) of the vegetated study region. NPP trends that were significant at higher 95% and 99% minimum probability levels occurred over approximately 29.5% ($575\,863 \text{ km}^2$) and 14.7% ($287\,931 \text{ km}^2$) of the vegetated region. Areas with significant increasing NPP trends had a mean rate of $+53.7 \text{ g C m}^{-2} \text{ decade}^{-1}$, while there were no areas with significant decreasing NPP trends.

To isolate the relative contribution of climate from other mechanisms influencing regional GPP and NPP trends, we conducted alternate PEM simulations over the 19-yr study period by 1) holding daily meteorological inputs to 1982 condi-

Figure 5. Map of the statistical significance of PEM-derived 19-yr trends in annual NPP across the study domain. Levels of significance of the least squares linear regression relationships between annual NPP and year (independent variable) for the 1982–2000 time series were determined for each 25-km grid cell. Excluding the masked areas (in gray), 15% of the region showed significance levels above 99% (in blue); 15% with levels between 95% and 99% (yellow); and 8% between 90% and 95% (red). Regions shown in dark green make up 62% of the study domain and are those areas for which trends had less than 90% significance.

tions while allowing satellite remote sensing–based LAI and FPAR inputs to vary, and 2) holding LAI and FPAR inputs to 1982 conditions while allowing daily meteorological inputs to vary. We then evaluated differences in regional productivity trends for these scenarios to distinguish the direct effect of recent climate change from other potential impacts to NPP trends, including atmospheric N deposition and CO₂ fertilization, disturbance and forest succession, and sensor calibration and atmospheric aerosol impacts on LAI and FPAR data. The results of

this analysis showed that changes in climate and vegetation contributed approximately 70% and 30% of the positive trend in vegetation productivity, respectively. Also, changes in vegetation structure alone did not produce a significant regional trend in vegetation productivity without the direct contribution of recent climate change. These findings seemingly contrast with global analyses of the NOAA AVHRR time series that indicate a greater contribution of vegetation structural changes to global NPP trends (Nemani et al. 2003). This discrepancy reflects the substantial influence of forest clearing and biomass burning in tropical forests, as well as land-use changes in more heavily populated tropical and temperate regions of the globe. In contrast, boreal and arctic regions are sparsely populated, with comparatively small direct anthropogenic impacts to land cover and NPP. Plant biophysical processes in these regions are also strongly limited by seasonal frozen temperatures, while weather conditions show large interannual variability with an accelerated warming trend over the past several decades relative to the rest of the globe (Serreze et al. 2000; Chapin et al. 2005). However, fire mortality and insect defoliations are major disturbances and drivers of forest succession in boreal regions (McGuire et al. 2004). These factors are represented in the PEM results by their influence on LAI magnitude and temporal variability, though the use of a temporally constant land cover classification and coarse resolution AVHRR LAI time series may not adequately represent spatially heterogeneous disturbance and succession processes (Goetz et al. 2006).

Significant long-term regional trends were observed in the NOAA AVHRR record for LAI, as well as PEM-based NPP and GPP calculations as summarized in Figure 6. Both GPP and NPP showed positive decadal trends of 8.3% ($+42.4 \text{ g C m}^{-2}$; $P = 0.037$) and 9.5% ($+24.6 \text{ g C m}^{-2}$; $P = 0.054$), respectively. NOAA AVHRR-derived observations of maximum annual average leaf area index (LAI_{mx}) for the region also showed a significant positive decadal trend of 2.1% ($+0.11 \text{ m}^2 \text{ m}^{-2}$; $P = 0.094$). Interannual variability in vegetation productivity was also substantial relative to long-term trends. Absolute annual variability in LAI_{mx} , GPP, and NPP was approximately 2.4% [$\pm 0.13 \text{ m}^2 \text{ m}^{-2} \text{ (s)}$], 6.0% [$\pm 34.8 \text{ g C m}^{-2} \text{ (s)}$], and 7.1% [$\pm 21.0 \text{ g C m}^{-2} \text{ (s)}$], respectively. Year-to-year variability in these parameters coincided with changes in regional weather patterns and vegetation structure. Annual anomalies in NOAA AVHRR-derived LAI_{mx} accounted for 55.8% ($P = 0.0002$) and 50.7% ($P = 0.0006$) of variability in annual GPP and NPP, respectively. Years with relatively high vegetation productivity coincided with greater photosynthetic leaf area, while lower productivity years coincided with reduced canopy cover. Annual NPP in 1992 was approximately 7% below average conditions for the 19-yr period and followed an anomalously cool and wet year in 1991 (e.g., see Figure 2). This negative anomaly has also been linked to a 1–2-yr cooling of the northern high latitudes following the June 1991 volcanic eruption of Mt. Pinatubo; previous studies have also documented the apparent short-term effects of the Pinatubo eruption in reducing LAI, NPP, and the growth rate of atmospheric CO_2 concentrations at high latitudes (Lucht et al. 2002; Nemani et al. 2003). Large positive NPP anomalies in 1995, 1997, and 1998 coincided with relatively warm summer conditions, while the large negative NPP anomaly in 2000 coincided with relatively cool summer temperatures across Canada and Alaska (Houghton et al. 2001).

Mean summer air temperatures from the regional daily NCEP reanalysis showed

Figure 6. Trends in spatially averaged maximum annual leaf area index (LAI_{mx}; A), GPP (B), and NPP (C) as derived from NOAA AVHRR Pathfinder mean monthly observations and PEM calculations for the vegetated study domain; annual anomalies represent differences from average (1982–2000) annual conditions.

a significant warming trend over the 19-yr study period (e.g., see Figure 2). Average summer air temperatures were positively correlated with annual anomalies of LAI_{mx} ($r = 0.384$; $P = 0.10$), GPP ($r = 0.662$; $P = 0.003$), and NPP ($r = 0.660$; $P = 0.003$). These results indicate that on average, warmer temperatures during the summer growing season enhanced photosynthesis to a greater degree than autotrophic respiration, leading to a positive response in vegetation productivity. No significant relationships were observed between mean annual air temperature and GPP, NPP, or LAI_{mx}, because temperatures outside the growing

season reflected in mean annual values have little direct impact on vegetation productivity. Similarly, no significant relationships were found between these variables and precipitation, indicating that water availability was not a major constraint to regional vegetation productivity during the study period. These findings are consistent with other global assessments indicating that low temperatures are the primary constraint to vegetation growth at high latitudes (Churkina and Running 1998; Nemani et al. 2003). However, the lack of a significant relationship with precipitation may also be due to regional bias in the NCEP reanalysis surface meteorology (see Drobot et al. 2006).

3.3. Ecosystem model simulations of carbon cycle trends

Ecosystem model simulations differed markedly in terms of the magnitudes of estimated annual C fluxes. A summary of these results for the study domain is presented in Table 2. The BIOME-BGC model produced much larger annual fluxes than TEM. Mean absolute differences (MAE) between ecosystem model simulations of annual C fluxes ranged from 71% for GPP, NPP, and R_h to 123% for NEP. Differences in model results primarily reflect differences in model structure, biophysical parameterizations, and initialization protocols. Both models were initialized using biophysical constants from the literature for individual boreal forest and arctic tundra biomes. However, physical parameters describing biophysical responses to temperature, light, and moisture vary strongly, even within individual biomes, while subtle variations in these parameters can produce substantial differences in model outputs (White et al. 2000). Model initialization protocols also vary widely depending on model structure and application and have been shown to have a major impact on carbon flux simulations even under otherwise consistent model scenarios (Amthor et al. 2001). Despite the large model differences in simulated annual C fluxes, these results are consistent with observed regional heterogeneity within boreal forest and arctic tundra biomes (e.g., Houghton and Skole 1990; Saugier et al. 2001).

The ecosystem models were generally consistent in characterizing interannual variability in GPP, NPP, and R_h ($0.624 \leq r \leq 0.881$; $P \leq 0.0043$), but not for smaller, residual NEP fluxes. Both TEM and BIOME-BGC simulations showed respective positive decadal trends in annual GPP of approximately 3.9% ($+9.53 \text{ g C m}^{-2}$; $P = 0.062$) and 5.4% ($+34.46 \text{ g C m}^{-2}$; $P = 0.038$). Model results also showed positive decadal trends in NPP of 4.7% ($+4.25 \text{ g C m}^{-2}$; $P = 0.100$) and 5.2% ($+17.81 \text{ g C m}^{-2}$; $P = 0.082$), while BIOME-BGC results showed a positive

Table 2. Summary of ecosystem process model results for the study domain; standard deviations of mean annual values are shown in parentheses.

C variables ($\text{g C m}^{-2} \text{ yr}^{-1}$)	BIOME-BGC	TEM	MAE* (%)	<i>r</i> value	<i>P</i> value
GPP	676 (45.0)	242 (13.7)	64.2	0.881	<0.0001
NPP	358 (27.2)	90 (7.0)	74.7	0.794	<0.0001
R_h	340 (20.6)	88 (2.3)	74.0	0.624	0.0043
NEP	18.3 (12.5)	2.5 (5.8)	123.4	0.238	>0.1

* $(\Sigma|(\text{BIOME-BGC} - \text{TEM})/\text{BIOME-BGC}|/\text{No. of measurements}) \times 100.0$.

decadal trend of 3.6% ($+0.15 \text{ m}^2 \text{ m}^{-2}$; $P = 0.10$) in LAI_{mx} . Simulated soil heterotrophic respiration rates also showed positive temporal trends, though TEM showed a relatively small and statistically insignificant ($P > 0.1$) R_h trend of less than 1% decade^{-1} , while BIOME-BGC showed a larger positive decadal trend of 5.0% ($+16.15 \text{ g C m}^{-2}$; $P = 0.033$). The model simulations also showed positive but statistically insignificant NEP trends from $+1.67$ to $+3.66 \text{ g C m}^{-2} \text{ decade}^{-1}$, indicating a general increase in the annual terrestrial sink strength for atmospheric CO_2 .

Model simulations, summarized in Figure 7, indicate that vegetation productivity is a major driver of land-atmosphere CO_2 exchange for the domain, where NPP accounted for more than half of the annual variability in NEP ($P \leq 0.0004$). Relatively productive years (i.e., positive NPP anomalies) appear to enhance the terrestrial sink strength for atmospheric CO_2 , while unproductive years (negative

Figure 7. Statistical correspondence between spatially averaged NPP annual anomalies and NEP ($\text{g C m}^{-2} \text{ yr}^{-1}$) for the study domain as derived from BIOME-BGC and TEM simulations; NPP anomalies are depicted as annual differences from the time series linear least squares regression line.

NPP anomalies) correspond with reduced NEP. BIOME-BGC and TEM simulations of annual NEP also correlated positively with mean air temperatures in spring ($r = 0.60$; $P = 0.007$) and summer ($r = 0.70$; $P = 0.001$), respectively. These findings are consistent with PEM results indicating that the positive temperature trend generally enhanced carbon sequestration over respiration processes, resulting in a small, positive impact on NEP and the relative sink strength of the region for atmospheric CO_2 . Model results showing positive, though variable trends in R_h , also imply increases in soil decomposition rates and plant available N. This may be an additional mechanism supporting positive trends in NPP, since boreal forest and arctic tundra soils tend to be rich in organic C, but lacking in plant-available N because of cold soil temperatures and water-saturated conditions that inhibit soil microbial decomposition processes (Van Cleve et al. 1990; Chapin et al. 1995).

3.4. Model comparisons and carbon cycle implications of regional productivity trends

BIOME-BGC simulations of temporal anomalies and trends in photosynthetic leaf area were generally consistent with satellite remote sensing observations. Model simulations produced a similar, but slightly larger, decadal trend in LAI_{mx} and accounted for 37.1% ($P = 0.006$) of annual variability in NOAA AVHRR-based results (see Figure 8). Similar agreement has also been reported between the AVHRR record and GCM-based dynamic global vegetation model simulations of LAI for the boreal zone (Lucht et al. 2002). Thus, the positive trend and annual anomalies in LAI_{mx} observed from the NOAA AVHRR Pathfinder record are generally confirmed by prognostic model simulations of regional carbon dynam-

Figure 8. Statistical correspondence between spatially averaged LAI_{mx} annual anomalies for the study domain as derived from NOAA AVHRR Pathfinder observations and BIOME-BGC model simulations; anomalies are depicted as annual differences from time series linear least squares regressions.

Table 3. Correspondence between ecosystem process model and PEM mean annual results.

Variables	BIOME-BGC			TEM		
	MAE* (%)	R^2	P value	MAE* (%)	R^2	P value
LAI _{mx} **	22.3 (1.2 m ² m ⁻²)	0.371	0.0056	—	—	—
GPP	16.3 (93 g C m ⁻²)	0.823	<0.0001	58.3 (340 g C m ⁻²)	0.718	<0.0001
NPP	21.1 (61 g C m ⁻²)	0.842	<0.0001	69.4 (207 g C m ⁻²)	0.622	<0.0001

* $(\sum |(\text{PEM} - \text{ecosystem model}) / \text{PEM}| / \text{No. of measurements}) \times 100.0$.

** Leaf area index results were not computed during TEM simulations.

ics, despite the relatively coarse (16 km) spatial scale and monthly temporal fidelity of the remote sensing data, and uncertainties associated with sensor stability and spectral quality of the NOAA AVHRR time series.

BIOME-BGC, TEM, and PEM results occupied respective upper, lower, and intermediate levels of estimated regional C fluxes. BIOME-BGC simulations of annual vegetation productivity were 16%–21% greater than PEM results and 22% smaller than NOAA AVHRR-based observations of LAI_{mx} (see Table 3). Alternatively, TEM simulations of annual productivity were 58%–69% smaller than PEM results. Model statistical correspondence with PEM results also varied between BIOME-BGC and TEM. Model simulations from TEM accounted for 72% and 62% ($P < 0.0001$) of annual variability in PEM-derived GPP and NPP, respectively, while BIOME-BGC simulations captured more than 82% ($P < 0.0001$) of the variability in these parameters (see Figure 9). The general consistency of these results is largely due to the predominance of air temperature as a major control on photosynthetic and respiration rates. The somewhat lower correspondence between TEM and PEM results reflects differences between mean monthly and daily meteorological inputs used as the major drivers of the biophysical process simulations. PEM and BIOME-BGC simulations reflect the cumulative effects of daily variations in meteorological conditions and discrete events, while TEM primarily reflects seasonal patterns captured by a monthly climatology. Despite these differences, all of the models show similar annual anomalies and positive trends in vegetation productivity for the domain.

The ecosystem model simulations showed positive decadal trends in total mean annual SOC storage for the region of +6.3 g C m⁻² ($P = 0.09$) and +11.2 g C m⁻² ($P = 0.02$) for TEM and BIOME-BGC, respectively (see Figure 10). However, BIOME-BGC model results also indicated that the positive trend in SOC storage is largely due to recent increases in relatively labile litter C, rather than the much larger volume of older and more recalcitrant SOC. Litter C accounted for only 9.7% of total SOC within the rooting zone, while nonlabile soil C represented approximately 75% of the total simulated C reservoir for the region. The model results also showed a negative decadal trend in this larger SOC pool of approximately -4.6 g C m⁻² ($P = 0.019$) over the 19-yr period. This small, but significant, decreasing trend in older and historically stable soil C occurred despite a positive decadal trend in litter C of approximately +15.8 g C m⁻² ($P = 0.0004$). Without the additional SOC inputs from a positive NPP trend, annual soil C losses would have been even larger. These results are consistent with the findings of a recent 20-yr manipulative study of Alaskan arctic tundra, where long-term soil

Figure 9. Statistical correspondence between PEM-derived GPP and NPP anomalies ($\text{g C m}^{-2} \text{yr}^{-1}$) and BIOME-BGC and TEM simulations of these variables; values represent spatially averaged annual anomalies for the study domain and are depicted as annual differences from time series linear least squares regressions.

fertilization resembling a projected release of soil nutrients under high-latitude warming increased both NPP and soil decomposition and resulted in C losses from deep soil layers (Mack et al. 2004). The apparent loss of nonlabile SOC in response to regional warming is also consistent with a recent model synthesis of previous soil decomposition studies spanning a broad range of different biomes (Knorr et al. 2005). The negative response of this larger SOC pool to recent warming is difficult to detect because of the masking effects of larger, positive NPP and litterfall trends. The additional inputs of plant-available N provided by the increased decomposition of SOC also represent an indirect mechanism enhancing regional vegetation productivity in this predominantly N-limited system, where soil decomposition is largely constrained by cold temperatures, permafrost,

Figure 10. Trends in spatially averaged SOC pools ($\text{g C m}^{-2} \text{ decade}^{-1}$) for the study domain as derived from BIOME-BGC and TEM model simulations; anomalies are depicted as annual differences from long-term (1982–2000) average conditions. (top) Regional trends in total estimated SOC pools from both models, and (bottom) trends in labile litter and recalcitrant soil carbon components of the total SOC pool as derived from BIOME-BGC simulations.

and shallow, water-saturated soil active-layer conditions (Hobbie et al. 2000; Jarvis et al. 2001; Mack et al. 2004).

The model simulation results also showed a significant, positive, $+0.095\%$ – 0.25% ($0.001 \geq P \leq 0.007$) decadal trend toward an increasing vegetation fraction of total C storage for the region (see Figure 11). Carbon storage in vegetation represented approximately 19.5% [± 0.08 (s)] and 25.1% [± 0.23 (s)] of soil carbon storage for BIOME-BGC and TEM results, respectively. Both models also produced similar annual variability and positive trends in the fraction of vegetation C storage for the region, though the magnitudes of the respective C pools and their relative proportions vary. The apparent trend toward a greater fraction of terrestrial

Figure 11. Trends in spatially averaged vegetation to soil carbon ratios as derived from (a) BIOME-BGC and (b) TEM simulations for the study domain.

C storage in vegetation biomass for the region is due to a larger positive trend in NPP and vegetation biomass relative to SOC. Carbon storage in vegetation is susceptible to more frequent turnover from plant biophysical processes including respiration, phenology, disturbance, and mortality, with a relatively short residence time compared to SOC. The declining trend in nonlabile SOC and the apparent shift toward greater terrestrial C storage in vegetation indicates that warming conditions during the 1982–2000 period accelerated the terrestrial C cycle by enhancing turnover and transfer rates among the terrestrial C pools. This apparent trend toward greater turnover occurs despite model assumptions of a constant disturbance rate. However, the boreal disturbance regime may also be increasing with regional warming (McGuire et al. 2004). The potential implications of this trend and the role of disturbance in reinforcing or mitigating the effects of climate on regional C cycle dynamics are uncertain and require further study.

3.5. Limitations of regional models and datasets

The model simulations and climate analyses for this investigation were derived using surface meteorological inputs from the NCEP reanalysis, satellite optical-infrared remote sensing-based measures of regional vegetation parameters, and general assumptions of plant structure and physiological responses to environmental processes. The regional land cover classification information used for PEM calculations of vegetation productivity largely reflects dominant, overstory vegetation types and does not explicitly represent forest succession or additional or subdominant vegetation categories within individual grid cells. However, the ecosystem model simulations used to derive these variables represent subgrid-scale land cover conditions within each 25-km grid cell to the extent that heterogeneity is captured by a 1-km resolution land cover map. Despite these scale differences in land cover representation, the PEM and ecosystem model results depict similar temporal anomalies and long-term trends in regional biosphere response to recent

warming trends. Also, differences between TEM- and BIOME-BGC-derived magnitudes of regional fluxes and carbon pools were larger than ecosystem model differences with PEM results, even though these models used the same land cover information. Spatially explicit meteorological datasets for the pan-Arctic region available from relatively coarse spatial resolution reanalysis data can differ substantially depending upon the particular model and methods employed in the simulation. The reliability of these datasets is less certain at high latitudes where regional monitoring networks are extremely sparse and largely confined to coastal areas and lower elevations. Satellite monitoring of high-latitude regions from optical-infrared remote sensing is also problematic due to low solar illumination and image degradation from frequent cloud cover and aerosol impacts, while observational trends from the NOAA AVHRR record are uncertain because of issues related to navigational drift and cross calibration of successive instrument series. All of these factors have the potential to adversely impact the relative accuracy of satellite-based NPP simulations for the region. Nevertheless, satellite remote sensing–derived assessment of a positive response in vegetation productivity to recent warming is generally consistent with an independent assessment of these variables from two ecosystem process models. The results of this study are also consistent with a growing body of evidence indicating large-scale changes in vegetation structure and productivity at high northern latitudes associated with regional warming.

4. Conclusions

From 1982 to 2000, CO₂ concentrations in the atmosphere increased by 8% [342 to 371 ppm (ppm)], while average summer air temperatures for Alaska and northwest Canada warmed by 1.8°C. The biosphere response to these changes, inferred from the global satellite remote sensing record, included a 4% increase in photosynthetic leaf area and an 18% increase in vegetation productivity. Ecosystem process model simulations of regional terrestrial carbon cycle dynamics for the same period confirm these findings, though the magnitudes of the trends and estimated fluxes vary between models. The positive productivity trend appears to be a direct response to summer warming. In boreal and arctic environments, NPP is limited by low temperature constraints to plant metabolic processes and an adequate supply of below-ground resources, including soil N. At annual time scales, plants adjust photosynthetic leaf area and vegetation growth to match available resources and are capable of responding rapidly to changes in environmental conditions. Our findings indicate that the positive vegetation productivity trend is both a direct plant response to more favorable conditions for photosynthesis, and an indirect effect of enhanced soil decomposition and N available to support additional plant growth. The potential for this trend to continue is uncertain and depends on the availability of adequate resources, including soil water and nutrients necessary to sustain increasing vegetation growth.

The results of this study indicate that the regional carbon cycle at high latitudes is accelerating under a warming climate. Vegetation productivity increased at a faster rate than soil organic carbon accumulations, resulting in a positive trend in the more volatile vegetation component of terrestrial carbon storage. While positive trends in NPP and associated inputs of relatively labile litter carbon resulted

in a general increase in the estimated soil organic carbon reservoir for the region, there was also evidence of accelerated decomposition and losses of much larger and more recalcitrant SOC stocks in response to regional warming. Carbon storage in vegetation biomass is on the order of decades or less, while turnover rates in boreal and tundra soils are greatly reduced by cold temperatures, water-saturated soils, and related constraints to microbial decomposition. The overall effect of these changes is an increase in the movement and cycling of carbon through boreal and arctic terrestrial systems. The regional carbon balance may be transitioning from a system dominated by a large, stable soil organic carbon reservoir to a system composed of a greater vegetation biomass component, with an accelerated turnover rate. Greater carbon storage in vegetation biomass increases the likelihood of rapid terrestrial carbon losses from fire disturbance, especially in North American boreal forests dominated by frequent stand replacing fires. Recent long-term studies of North American boreal fire regimes also indicate that the extent and frequency of large fires in Alaska and Canada are increasing with global warming (McGuire et al. 2004). The soil organic carbon pool represents approximately 75% of the estimated total terrestrial carbon reservoir for the region, while boreal and arctic biomes contain up to 40% of the global terrestrial soil carbon inventory that is potentially reactive in the context of near-term climate change (McGuire et al. 1995). While model simulations over the analysis period of this study indicated a small terrestrial carbon sink for atmospheric CO₂, this study does suggest that carbon storage in high-latitude regions like the western Arctic is particularly vulnerable to the loss of carbon to the atmosphere from the response of soil organic matter to warming. Such a response would act as a positive feedback to climatic warming (McGuire et al. 2006a; McGuire et al. 2006b).

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