Modelling impacts of recent warming on seasonal carbon exchange in higher latitudes of North America

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<th>Journal:</th>
<th>Arctic Science</th>
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<td>Manuscript ID</td>
<td>AS-2016-0009.R3</td>
</tr>
<tr>
<td>Manuscript Type:</td>
<td>Article</td>
</tr>
<tr>
<td>Date Submitted by the Author:</td>
<td>12-Dec-2017</td>
</tr>
<tr>
<td>Complete List of Authors:</td>
<td>Mekonnen, Zelalem; University of Alberta, Renewable Resources Grant, Robert; University of Alberta, Renewable Resources Schwalm, Christopher; Woods Hole Research Center</td>
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<tr>
<td>Keyword:</td>
<td>ecosys, climate change, Arctic carbon cycle, thawing permafrost, seasonal carbon dynamics</td>
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<td>Is the invited manuscript for consideration in a Special Issue?:</td>
<td>N/A</td>
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Modelling impacts of recent warming on seasonal carbon exchange in higher latitudes of North America

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Abstract

An ecosystem model, ecosys, has been used to examine the effects of recent warming on carbon exchange in higher latitudes of North America. Model results indicated that gradual warming during the past 30 years has increased net ecosystem productivity (NEP) and leaf area index (LAI). Spring increases in LAI advanced by 2.3 days decade\(^{-1}\) and decreases in autumn were delayed by 5.0 days decade\(^{-1}\) from 1982 to 2006. These advances and delays were corroborated by similar trends observed in the Normalized Difference Vegetation Index. NEP modelled during this period increased at an average rate of 17.6 Tg C decade\(^{-1}\). Increasing carbon losses modelled with soil warming in autumn, when thaw depth was greatest, offset 34% of increasing carbon gains modelled in spring. If autumn warming continues, carbon losses in this season may further offset enhanced carbon sequestration in spring.

Keywords: ecosys, thawing permafrost, climate change, Arctic carbon cycle, seasonal carbon dynamics
1. Introduction

Increases in greenhouse gases have resulted in atmospheric warming by changing the radiative forcing of the atmosphere (Jain et al., 2000, IPCC, 2013). The warming has been amplified in higher latitudes of the northern hemisphere (Polyakov et al., 2002, IPCC, 2013): in the last century the rise in average surface air temperature ($T_a$) for the Arctic region was twice the global average (IPCC, 2007). The enhanced warming has been accompanied by an overall increase in precipitation (Dore, 2005, IPCC, 2013).

Several consequences of this amplified warming have affected carbon exchange across northern ecosystems. Permafrost temperatures have risen and the active layer depth (ALD) has increased (Hinzman et al., 2005, Burn and Kokelj, 2009). These changes in soil conditions may increase microbial decomposition and lead to greater heterotrophic respiration ($R_h$) (Davidson and Janssens, 2006). In Arctic tundra, Schuur et al. (2009) estimated 40% more annual losses of old carbon over the last 15 years from areas with ALD of 0.78 ± 0.05 m than from areas with shallower ALD (0.69 ± 0.02 m).

The effect on net carbon exchange from greater $R_h$ may be offset by that from greater vegetative productivity. Climate warming may be causing increases in the length of growing season (LGS) that have been reported by several studies using the Normalized Difference Vegetation Index (NDVI) (Myneni et al., 1997, Zhang et al., 2008, Zhu et al., 2012). Extension of the thaw season in spring and autumn has resulted in changes in phenology (Piao et al., 2007). Increases in vegetation productivity and northward movement of the tree line have also been reported (Swann et al., 2010, Beck et al., 2011, Van Bogaert et al., 2011).

Recent climate change may have diverse effects on gross primary productivity (GPP) and ecosystem respiration ($R_e$) (Albert et al., 2011, Klady et al., 2011). Warming improves the
kinetics of carboxylation and hence rates of CO$_2$ fixation, particularly at lower temperatures (Sjögersten and Wookey, 2002). However, warming in water-limited regions may have adverse effects on productivity, as a result of increased water stress (Grant et al., 2008). Adverse effects of higher air temperatures ($T_a > 20$ °C) on water status and hence CO$_2$ fixation in Arctic tundra were demonstrated by Grant et al. (2015).

Warming also increases the maintenance component of autotrophic respiration ($R_a$), which rises continuously with temperature and thus may increasingly offset rises in GPP, thereby reducing gains in net primary productivity (NPP). Other indirect effects of warming on GPP occur through hastened decomposition from increasing $R_h$ which raises nitrogen mineralization (Ineson et al., 1998, Hart, 2006) and root and mycorrhizal nitrogen uptake, thereby raising leaf nitrogen concentrations and increasing CO$_2$ fixation rates.

Because of these contrasting effects of warming, the extent to which current climate change is affecting seasonal and interannual net carbon exchange at higher latitudes of North America is uncertain. We used a comprehensive mathematical process model *ecosys* in which these contrasting effects are simulated (Grant, 2001, 2014, 2015), to examine (1) how recent changes in $T_a$ and precipitation have affected LGS and ALD, and (2) how these changes have affected the seasonal and annual carbon cycle across the higher latitudes of North America (north of 60° N) over the last three decades (1979 - 2010).

The effects of warming on biochemical and physical processes that control CO$_2$ fixation are explicitly formulated in *ecosys*. The model captures warming effects on ecosystem productivity well when rigorously tested against measured fluxes across different biomes of northern ecosystems: e.g., polygonal Arctic tundra (Grant et al., 2017a,b); coastal Arctic tundra (Grant et al., 2003); mesic Arctic tundra (Grant et al., 2011a); Arctic mixed tundra and fen.
2. Materials and Methods

2.1 Model description

_Ecosys_ is an hourly time-step model with multiple canopy and soil layers and fully coupled carbon, energy, water, and nutrient cycles (Grant, 2001). The model uses algorithms that represent physical, chemical, and biological processes with diverse plant and microbial populations. It implements fully coupled surface energy and water exchanges that drive soil heat and water transfers to determine soil temperatures and water contents (Grant, 2004). These transfers drive soil freezing and thawing and, hence, ALD, through the general heat flux equation. Atmospheric warming increases surface heat advection, soil heat transfers, and hence ALD.

_Ecosys_ explicitly represents processes that control the direct and indirect effects of warming on carbon fixation and ecosystem respiration. Carbon uptake is controlled by plant water status calculated from convergence solutions that equilibrate total root water uptake with transpiration (Grant _et al._, 1999). Canopy temperatures affect rates of CO$_2$ fixation through Arrhenius functions for light and dark reactions (Grant _et al._, 2007). Soil temperatures affect $R_h$ through the same Arrhenius function as for dark reactions (Grant, 2014).

Carbon uptake is also controlled by plant nitrogen uptake. The model has fully coupled transformations of soil carbon, nitrogen, and phosphorus through microbially driven processes (Grant, 2013). Soil warming enhances GPP by hastening microbial mineralization and root uptake of nitrogen (Grant, 2014). Carbon uptake is affected by phenology with leafout and leafoff (deciduous plants) or dehardening and hardening (coniferous plants) being determined by
accumulated exposure to temperatures above set values while day length is increasing or below set values while day length is decreasing. In ecosys, senescence is driven by excess maintenance respiration and also by phenology in deciduous plant functional types. A detailed description of inputs, parameters and algorithms used in ecosys can be found in, e.g., (Grant, 2001) and (Grant et al., 2011b, 2012).

2.2. Model drivers and simulation design

The simulation spatial domain covered the North American landmass north of 60° N at 0.25° x 0.25° spatial resolution. The model was forced with time-varying weather drivers, equilibrated through 179 years prior to 1979 (1800-1978) by randomly distributing North American Regional Reanalysis (NARR) data for 1979-1993 (Wei et al. 2014). This enabled the model to attain a steady state prior to 1979. Subsequently real-time NARR data were used for 1979 – 2010. The model was initialized with attributes from the soil dataset (Wei et al., 2014), and run under dynamic land use/cover changes, atmospheric CO₂ concentrations, nitrogen deposition, and disturbances as described in the Multi-scale Synthesis and Terrestrial Model Intercomparison Project protocol (Huntzinger et al., 2013, Wei et al., 2014, Mekonnen et al., 2016).

2.4. Model testing and analysis

The effects of warming on modelled CO₂ exchange were tested at site scale by comparing CO₂ fluxes measured at the Daring Lake eddy covariance (EC) flux tower (Lafleur and Humphreys, 2008) with CO₂ fluxes modelled for the grid cell in which the tower was located during a relatively cool year (2005) and a warm year (2006) (Table 1). At regional scale, increases in spatially averaged mid-August leaf area index (LAI) modelled for recent decades
were compared with 15-day composite measurements of mid-August NDVI from Advanced Very High Resolution Radiometer (AVHRR) data.

Advances in spring green-up were determined from differences in days of the year when LAI and NDVI rose above threshold values. Delays in vegetation senescence during autumn were determined from differences in days of the year when LAI and NDVI declined below threshold values. These differences were calculated using five-year spatial averages for 1982 - 1986 and 2002 - 2006. These years were selected because of data availability for AVHRR NDVI. To analyze the long-term (1980 – 2010) temporal trends of regional carbon fluxes, spatially averaged values were computed, weighted for the area of each grid cell. Long-term spatial and temporal changes were computed by subtracting averages of the initial five years of gridded annual values (1980 - 1984) from those of the final five years (2006 - 2010). The initial and final five years were averaged to smooth out inter-annual variability and detect the long-term spatial and temporal changes that have occurred over the last three decades. Differences in absolute values were used to detect long-term changes due to non-linearity of ecosystem responses to climate change across different biomes (Burkett et al., 2005). Pixels with less than 60 years from the last stand-replacing forest fire were excluded from spatial and temporal trend analyses to avoid forest age effects on carbon exchange.

3. Results

3.1. Site-scale model testing of seasonal warming effects on net CO₂ exchange

The effects of seasonal warming on net CO₂ exchange in a tundra ecosystem were investigated at the Daring Lake site. Modelled and measured CO₂ exchanges were calculated for 2005 and 2006 (Table 1; Fig. 1). The NARR MAT was 2 °C higher in 2006 than in 2005 while the site MAT was 1.6 °C higher (Table 1). The mean seasonal temperature (MST) was 3.7
(NARR) and 3.3 (site) °C higher in 2006 than in 2005. Greater heat advection caused ALD to deepen by 4 (modelled) and 5 (measured) cm °C\(^{-1}\) increase in \(T_a\).

The warming had several contrasting effects on ecosystem productivity. Seasonal CO\(_2\) fixation increased by 25 (modelled) and 13 (EC-derived) g C m\(^{-2}\) °C\(^{-1}\) during the growing season in 2006, shown by growing season GPP in Table 1. Similarly, \(R_e\) increased by 26 (modelled) and 10 (EC-derived) g C m\(^{-2}\) °C\(^{-1}\) during the growing season in 2006 (Table 1). The increase in modelled \(R_e\) was driven by higher \(R_h\).

The modelled increases in CO\(_2\) fixation were driven by direct effects of warming, but were partially offset by some indirect effects. The indirect effects were caused by more frequent summer warming events during 2006 (e.g., on day 206) that caused declines in modelled CO\(_2\) fixation when \(T_a\) was above 20 °C (Fig. 1a2, b2). The reductions in CO\(_2\) fixation were modelled through the coupled hydraulic scheme for soil-root-canopy-atmosphere water transfer that lowered canopy conductance, hence reduced CO\(_2\) influxes, as well as through the temperature sensitivity of respiration processes that increased CO\(_2\) effluxes. Consequent declines in modelled net ecosystem productivity (NEP) during high temperature events were corroborated by similar occurrences in EC-measured NEP in 2006. However, the decline in NEP modelled with NARR data in this study was greater than that modelled with site weather data because of higher \(T_a\) and greater warming in NARR (Table 1). This resulted in slightly lower modelled seasonal NEP (from mid-June to end of August) in 2006 (modelled = 41 and EC-derived = 61 g C m\(^{-2}\)) vs. 2005 (modelled = 45 and EC-derived = 51 g C m\(^{-2}\)).

Warming also affected phenology and LGS. Earlier spring warming in 2006 than in 2005 caused an advance of 15 days in modelled net CO\(_2\) uptake (Fig. 1b2 and Fig. 1a2), as was also apparent in the EC-measured NEP. However, sustained autumn warming in 2006 adversely
impacted NEP (Fig. 1 b1, b2). Thus spring gains of 5.2 g C m\(^{-2}\) (days 136 -160) were offset by autumn losses of 9.1 g C m\(^{-2}\) (day 250 - 274) in 2006 relative to 2005. The combined effects of warming on CO\(_2\) fixation, respiration and phenology in the model enabled daily NEP to agree closely with measured values (Fig. 1).

3.2. Annual and seasonal changes in regional \(T_a\) and precipitation 1979 - 2010

The NARR dataset indicated spatial heterogeneity in regional changes in \(T_a\) and precipitation across the higher latitudes of North America (Fig. 2). The north and northeast of the High Arctic had the most rapid warming with a spatially averaged trend of \(\sim +0.6 \degree C\) decade\(^{-1}\) from 1979 – 2010, while some areas in the southwestern Alaska and western Canadian boreal regions experienced a slight cooling. Spatially averaged MAT of the entire region increased from 1979 – 2010, with warming in all seasons (Table 2). Annual precipitation has increased in most areas over the last three decades, as derived by the NARR (Fig. 2b).

3.3. Changes in LGS and ALD 1979 - 2010

Warming in spring and autumn observed during the last three decades has caused earlier leafout to be modelled in spring and has delayed senescence in autumn, apparently from increases in spatially averaged spring and autumn LAI (Fig. 3). Leafout advanced by 2.3 days decade\(^{-1}\) in spring and senescence was delayed by 5.0 days decade\(^{-1}\) in autumn from 1982 to 2006 (Fig. 3a) resulting in an extended growing season of 7.3 days decade\(^{-1}\). The maximum values of modelled LAI during the peak growing season in summer also increased, suggesting increases in productivity (Fig. 3). The modelled changes in phenology and increases in LGS were corroborated by similar changes in spatially averaged 15-day composite NDVI showing earlier leafout (2.2 days decade\(^{-1}\)) and delayed senescence (4.0 days decade\(^{-1}\)), resulting in an increase
of 6.2 days decade\(^{-1}\) in LGS. Spatially averaged MAT and modelled ALD exhibited long-term increases of +0.6 ± 0.5 °C decade\(^{-1}\) and +2.3 ± 2 cm decade\(^{-1}\) respectively (Fig. 4; Fig. 5a).

### 3.4. Annual and seasonal changes in modelled carbon exchange 1979 - 2010

The effects of 30-year changes in \(T_a\) and precipitation on carbon fluxes differed among sub-regions of the study area (Fig. 6), but greater increases in productivity were modelled in most parts of northern forests, taiga, and tundra. In most regions ecosystem GPP, NPP and NEP increased with \(T_a\) and precipitation (Fig. 6). Localized decreases in ecosystem productivity were modelled mainly in the southwest, due to the slight regional cooling presented in the NARR (Fig. 2a).

GPP modelled in Arctic ecosystems increased more from 1979 to 2010 than did \(R_a\) and \(R_h\), resulting in increased NEP (Table 2). More positive anomalies in \(T_a\), GPP and NPP occurred in warm (e.g. 2006) than in cool (e.g. 1999) years indicating greater CO\(_2\) fixation was modelled during warmer conditions (Fig. 5).

However, net carbon gains modelled with warming varied seasonally with differing gains in GPP and \(R_e\). Modelled GPP increased in all seasons, but greater increases occurred in spring and summer than in autumn and winter (Table 2). GPP increased more than \(R_a\) in spring but less in autumn so that gains in spring NPP were partially offset by losses in autumn NPP.

Increases in modelled \(R_e\) (= \(R_a + R_h\)) were greatest in summer and slightly larger in autumn than in spring (Table 2). During summer, increases in GPP were greater than those in \(R_e\) causing increases in NEP. During all other seasons, increases in GPP were smaller than those in \(R_e\) causing decreases in NEP that partially offset increases during summer. A larger decrease in NEP was modelled during autumn than spring, due to greater warming in autumn than spring (Table 2).
4. Discussion

4.1. Impacts of changes in LGS and ALD on carbon exchange

The modelled gains in annual GPP are partly attributed to effects of warming on the duration of CO$_2$ fixation from increased LGS. Although general increases in LGS were modelled with warming (Fig. 3), delays in vegetation senescence during autumn were greater than advances in vegetation green-up during spring (Fig. 3a), which we attributed to greater warming observed in autumn than spring (Table 2). The modelled delay in autumn is consistent with the finding by Piao et al. (2007) that vegetation senescence was delayed by 0.5 days yr$^{-1}$ for 1980 – 2002 in North America north of 50° N. The extended LGS resulted in increases of modelled ecosystem productivity (Fig. 6) across much of the study area, from longer periods of CO$_2$ fixation.

Warming in NARR increased modelled ALD across the Arctic (Fig. 4) despite spatial variation in these increases caused by that in soil properties and climate changes. In ecosys, greater ALD increases biologically active soil volumes, and hence hastens $R_h$, soil nutrient mineralization and plant nutrient uptake (Grant et al., 2015). Greater nutrient uptake with ALD causes gains in modelled GPP and NPP beyond those directly attributed to changes in climate (Fig. 6), consistent with control of carbon exchange by hydrology in permafrost regions (Sturtevant and Oechel, 2013). The correlations of anomalies in NPP (Fig. 5) with those in ALD (Fig. 4) in the model were consistent with the findings of Dafflon et al. (2017) that remotely sensed indices of plant productivity showed significant positive correlations with thaw depth.

4.2. Impacts of warming on carbon exchange
The rate of carbon sequestration modelled with climate warming over the North American Arctic during the last 30 years (Figs. 5 and 6) was similar to those modelled and measured with interannual warming at Daring Lake (Table 1). The gain in GPP modelled at Daring Lake in 2006 over 2005 of $38 \text{ g C m}^{-2} \text{ y}^{-1} \text{ °C}^{-1}$ (Table 1) is similar to one of $25 \text{ g C m}^{-2} \text{ y}^{-1} \text{ °C}^{-1}$ in spatially averaged GPP modelled over the higher latitudes during the past three decades (Table 2). The modelled gains in GPP varied across biomes (Fig. 6), mainly due to spatial and temporal variations in changes of $T_a$ and precipitation (Fig. 2). Rising atmospheric CO$_2$ might have contributed to some of the rise in GPP, but in an earlier study, rising CO$_2$ by itself contributed little to increases in Arctic productivity modelled by ecosys in the absence of warming (Grant et al., 2015).

Ecosystem productivity modelled in most parts of the higher latitudes increased as a result of warming in recent decades (Fig. 6). These increases could be attributed to the effects of warming on plant CO$_2$ fixation and soil nitrogen mineralization (Grant et al., 2011b, Grant, 2014). Northern ecosystems are mainly constrained by temperature, thus warming improves the kinetics of carboxylation and hence rates of CO$_2$ fixation (Bernacchi et al., 2001) due to larger temperature sensitivity of biological processes at lower temperatures as modelled by the Arrhenius functions for light and dark reactions (Bernacchi et al., 2003). These modelled increases in productivity have been corroborated by numerous artificial and natural warming experiments (Oberbauer et al., 2007, Hill and Henry, 2011, Klady et al., 2011) that reported increase in productivity attributed to warming in higher latitudes. Results from long-term (1981 – 2008) experimental plots with open-top chambers in the High Arctic (Hudson and Henry, 2009) have shown that warming over the past 30 – 50 years has resulted in an increase in carbon uptake consistent with modelled increases (Fig. 6). Increases in modelled LAI (Fig. 3a) have been

We attribute slight localized declines in modelled productivity in parts of southern Alaska and northwestern Canada (Fig. 6) to localized declines in precipitation and $T_a$ (Fig. 2). These decreases were similar to those reported by Beck et al. (2011) in which satellite and tree-ring data were used to identify a reduction in productivity in interior Alaska. Although overall increases were modelled in ecosystem productivity, spatial heterogeneity in plant responses to warming was apparent in most northern ecosystems (Fig. 6). These diverse responses were consistent with a meta-analysis by Elmendorf et al. (2012) of 61 tundra sites experimentally warmed for up to 20 years that indicated diverse responses of Arctic carbon exchange to warming depending on soil moisture and plant functional type.

Warming resulted in an increase in modelled annual NEP for northern ecosystems, despite seasonal variations (Table 2). The contrasting responses of carbon exchange to warming in spring and autumn (Table 2) may be an important controller of how northern ecosystems have responded to recent changes in climate. The larger rise in $R_e$ modelled during autumn than in spring may be attributed to greater modelled and measured ALD (Table 1; Fig. 4) in autumn that exposed more organic carbon deeper in the soil to microbial decomposition, and to warmer soils, causing $R_h$ and below-ground $R_a$ to remain higher after plant senescence. Thus, about one third of the NPP gains modelled with warming during spring were offset by NPP losses in autumn (Table 2). The carbon loss during autumn was consistent with aggregated EC results from northern ecosystems in which losses from greater increases in respiration than carbon uptake in
autumn offset gains from greater increases in carbon uptake than respiration in spring (Piao et al. (2008).

5. Conclusions

Observed warming in spring and autumn during the last three decades has caused earlier leaf growth to be modelled in spring and delayed senescence in autumn, resulting in an extended growing season of 7.3 days decade⁻¹. Extended growing seasons and deepening of the active layer increased modelled ecosystem productivity across much of the study area.

Northern ecosystems were modelled to be increasing carbon sinks of 17.6 Tg C decade⁻¹, attributed to an increase in $T_a$ of 0.55 °C decade⁻¹ and to an increase in precipitation in much of Arctic North America. However, the net carbon gains varied seasonally, for spring GPP increased more than $R_a$ resulting in gains in NPP, whereas in autumn GPP increased less than $R_a$ resulting in a particularly large reduction in NPP, which offset 34% of the increase in carbon gains modelled with warming in spring. If this offset were to rise with further warming and the consequent deepening of the active layer, annual future NEP could be adversely affected.

Acknowledgements

The research was supported by an NSERC Discovery Frontiers (DF) grant to the Arctic Development and Adaptation to Permafrost in Transition (ADAPT) program. We would like to thank Peter M. Lafleur and Elyn R. Humphreys for providing the Daring Lake EC site data. We acknowledge the Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP; http://nacp.ornl.gov/MsTMIP.shtml) for providing support in environmental driver data. Funding for MsTMIP activity was provided through NASA ROSES Grant #NNX10AG01A. Data management support for preparing, documenting, and distributing model driver and output data was performed by the Modelling and Synthesis Thematic Data Center at

https://mc06.manuscriptcentral.com/asopen-pubs
Oak Ridge National Laboratory (ORNL; http://nacp.ornl.gov), with funding through NASA ROSES Grant #NNH10AN681. Data products in this study are archived at the ORNL DAAC (http://daac.ornl.gov). Computational facility for ecosys was provided by WestGrid supercomputing infrastructure (https://www.westgrid.ca).

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Table 1. Mean seasonal air temperature (MST), mean annual air temperature (MAT), active layer depth (ALD) and growing season carbon budget of modelled vs. EC-derived values for contrasting years: 2005 (cooler) vs. 2006 (warmer) at Daring Lake Arctic tundra site.

Table 2. Changes in annual and seasonal surface air temperature, $T_a$ (°C decade$^{-1}$) and modelled carbon exchanges (Tg C decade$^{-1}$): gross primary productivity (GPP), autotrophic respiration ($R_a$), net primary productivity (NPP), heterotrophic respiration ($R_h$), ecosystem respiration ($R_e$), and net primary productivity (NEP) for higher latitudes (north of 60° N) of North America modelled from 1979 to 2010. Positive carbon fluxes indicate gains.

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Figure 1. Daring Lake Arctic tundra site: (a1, b1) NARR 3-hourly air temperature, (a2, b2) daily NEP measured at the eddy covariance tower (black closed symbols), gap-filled from EC measurements (red open symbols), modelled NEP (blue lines) for a cooler year 2005 and a warmer year 2006. The shaded part indicated cool vs. warm spring and autumn in 2005 vs. 2006. Measured data were obtained from (Lafleur and Humphreys, 2008).

Figure 2. Long-term (1979 – 2010) spatially averaged changes in NARR data (Wei et al. 2014) between 1979 – 1983 and 2006 – 2010 for (a) mean annual air temperature (b) annual precipitation across higher latitudes of North America landmass.

Figure 3. Spatially averaged (a) modelled total LAI (above + below snowpack surface) and (b) 15-day composite NDVI over five-year intervals from 1982 to 2006, showing increasing spring and summer values.

Figure 4. Increase in spatially averaged active layer depth from the long-term mean for higher latitudes of North America over the last three decades. Increasing values indicate deepening of the active layer.

Figure 5. Anomalies of spatially averaged annual (a) NARR $T_a$ (b) modelled NPP and (c) modelled GPP, from the long-term mean for higher latitudes of North America over the last three decades.

Figure 6. Long-term spatially averaged changes between 1980 – 1984 and 2006 – 2010 for annual (a) GPP (b) NPP (c) $R_h$ and (d) NEP over the last three decades for higher latitudes of North America. Pixels with no value in represents forested stands with less than 60 years from the last stand replacing fire.
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<th>Year</th>
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<th>C budget * - modelled (g C m⁻² growing season⁻¹)/ (g C m⁻² year⁻¹)</th>
<th>Site MST/MAT (°C)</th>
<th>Site ALD (m)</th>
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<td>12.2/-5.4</td>
<td>1.12</td>
<td>245/271           106/124                  98/115           204/239          41/32</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Change °C MST/MAT</td>
<td>3.7/2.0</td>
<td>0.04/0.07</td>
<td>25/38             13/17                    12/23            26/40            -1/-2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Site</th>
<th>MST/MAT (°C)</th>
<th>Site ALD (m)</th>
<th>C balance * - derived from EC measurements (g C m⁻² growing season⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>6.9/-8.9</td>
<td>0.74 ± 2</td>
<td>165 ± 6.9            -                        -               114 ± 7.5         51 ± 2.1</td>
</tr>
<tr>
<td>2006</td>
<td>10.2/-7.3</td>
<td>0.92 ± 4</td>
<td>209 ± 9.6            -                        -               148 ± 10.8       61 ± 3.9</td>
</tr>
<tr>
<td>Change °C MST/MAT</td>
<td>3.3</td>
<td>0.055</td>
<td>13                  -                        -               10               +3</td>
</tr>
</tbody>
</table>

* EC-derived values from (Lafleur and Humphreys, 2008) during days of the year: 137 – 240 for 2005 and 2006
Table 2. Changes in annual and seasonal surface air temperature, $T_a$ (°C decade$^{-1}$) and modelled carbon exchanges (Tg C decade$^{-1}$): gross primary productivity (GPP), autotrophic respiration ($R_a$), net primary productivity (NPP), heterotrophic respiration ($R_h$), ecosystem respiration ($R_e$), and net primary productivity (NEP) for higher latitudes (north of 60° N) of North America modelled from 1979 to 2010. Positive carbon fluxes indicate gains.

<table>
<thead>
<tr>
<th>Season</th>
<th>$\Delta T_a$</th>
<th>$\Delta GPP$</th>
<th>$\Delta R_a$</th>
<th>$\Delta NPP$</th>
<th>$\Delta R_h$</th>
<th>$\Delta R_e$</th>
<th>$\Delta NEP$</th>
</tr>
</thead>
<tbody>
<tr>
<td>winter</td>
<td>0.59</td>
<td>0.02</td>
<td>0.32</td>
<td>-0.30</td>
<td>0.64</td>
<td>0.96</td>
<td>-0.96</td>
</tr>
<tr>
<td>spring</td>
<td>0.39</td>
<td>12.76</td>
<td>7.58</td>
<td>5.18</td>
<td>7.98</td>
<td>15.95</td>
<td>-3.19</td>
</tr>
<tr>
<td>summer</td>
<td>0.31</td>
<td>87.75</td>
<td>34.30</td>
<td>53.45</td>
<td>19.94</td>
<td>54.24</td>
<td>34.30</td>
</tr>
<tr>
<td>autumn</td>
<td>0.89</td>
<td>7.02</td>
<td>8.77</td>
<td>-1.75</td>
<td>7.98</td>
<td>16.75</td>
<td>-7.98</td>
</tr>
<tr>
<td>annual</td>
<td>0.55</td>
<td>107.69</td>
<td>51.85</td>
<td>55.84</td>
<td>38.29</td>
<td>90.14</td>
<td>17.55</td>
</tr>
</tbody>
</table>