



# Contrasting changes in gross primary productivity of different regions of North America as affected by warming in recent decades



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## ABSTRACT

Ecosystem responses to the increasing warming in recent decades across North America (NA) are spatially heterogeneous and partly uncertain. Here we examined the spatial and temporal variability of warming across different eco-regions of NA using long-term (1979–2010) climate data (North America Regional Reanalysis (NARR)) with 3-hourly time-step and  $0.25^\circ \times 0.25^\circ$  spatial resolution and run a comprehensive mathematical process model, *ecosys* to study the impacts of this variability in warming on gross primary productivity (GPP). In a site scale test of model results, annual GPP modeled for pixels which corresponded to the locations of 20 eddy covariance flux towers correlated well ( $R^2 = 0.76$ ) with annual GPP derived from the towers in 2005. At continental scale, long-term annual average modeled GPP correlated well (geographically weighed regression  $R^2 = 0.8$ ) with MODIS GPP. GPP modeled in eastern temperate forests and most areas with lower mean annual air temperature ( $T_a$ ), such as those in northern forests and Taiga, increased due to early spring and late autumn warming observed in NARR and these eco-regions contributed 92% of the increases in NA GPP over the last three decades. However, modeled GPP declined in most southwestern regions of NA (accounting >50% of the ecosystems with declining GPP), due to water stress from rising  $T_a$  and declining precipitation, implying that further warming and projected dryness in this region could further reduce NA carbon uptake. Overall, NA modeled GPP increased by 5.8% in the last 30 years, with a positive trend of  $+0.012 \pm 0.01 \text{ Pg C yr}^{-1}$  and a range of  $-1.16$  to  $+0.87 \text{ Pg C yr}^{-1}$  caused by interannual variability of GPP from the long-term (1980–2010) mean. This variability was the greatest in southwest of US and part of the Great Plains, which could be as a result of frequent El Niño–Southern Oscillation events that led to major droughts.

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## 1. Introduction

There is widespread evidence that ecosystems are responding to warming in recent decades. Increase in the length of growing season has been reported by several studies using the Normalized Difference Vegetation Index (NDVI) in different regions: northern hemisphere (Kim et al., 2012), North America (NA) (White et al., 2009; Zhu et al., 2012), northern higher latitudes (McManus et al., 2012; Myneni et al., 1997; Olthof et al., 2008; Tucker et al., 2001; Verbyla, 2008; Zhang et al., 2008). NDVI values are strongly correlated to photosynthetically active radiation absorbed by vegetation. Increasing NDVI values indicating increasing vegetation density and gross primary productivity (GPP) (Box et al., 1989) over time in northern higher latitudes have been reported in some studies

(Myneni et al., 1997; White et al., 2009). Evidence of increases in vegetation cover and northward movement of the tree line in northern higher latitudes has also been reported in several studies (Beck et al., 2011; Swann et al., 2010; Van Bogaert et al., 2011). In contrast, a study in southwest US reported a decline in productivity as a result of warming (Williams et al., 2010).

Warming affects GPP and ecosystem respiration ( $R_e$ ) which are the major components of carbon exchange between the terrestrial ecosystem and the atmosphere (Albert et al., 2011; Hatfield et al., 2011; Klady et al., 2011). There are direct and indirect effects of elevated air temperature ( $T_a$ ) on ecosystem productivity. The direct effects depend on current  $T_a$ . In areas with lower  $T_a$ , as in boreal climates, warming improves kinetics of carboxylation and hence rates of  $\text{CO}_2$  fixation (Bernacchi et al., 2001) due to larger  $Q_{10}$  at lower temperatures. However, warming also raises Michaelis–Menten constant for carboxylation,  $K_c$  (Bernacchi et al., 2003, 2001) and lowers aqueous  $\text{CO}_2$  concentration in canopy chloroplasts,  $C_c$  with respect to gaseous  $\text{CO}_2$  concentration in canopy leaves,  $C_i$  (Farquhar

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et al., 1980). Consequently, in areas with higher  $T_a$ , as in tropical and subtropical climates, warming with smaller  $Q_{10}$  increases photorespiration relatively more than carboxylation (Jordan and Ogren, 1984), and hence causes smaller increases, or even decreases, in rates of  $CO_2$  fixation.

Warming indirectly affects GPP and  $R_e$  through alteration of the environment (Shaver et al., 2000). It can have an adverse effect on water relations: warming increases vapor pressure deficits ( $D$ ), thereby hastening evaporation, transpiration, and soil drying, particularly in warmer climates (Grant et al., 2008). Consequent declines in canopy water potential ( $\psi_c$ ), induce rises in canopy ( $r_c$ ) and leaf ( $r_l$ ) resistances (Grant et al., 1999) and hence declines in rates of  $CO_2$  diffusion and carboxylation, reducing  $CO_2$  fixation. Warming also increases autotrophic maintenance respiration ( $R_m$ ) which rises continuously with temperature while  $CO_2$  fixation does not, so that rises in  $R_m$  increasingly offset those in GPP on net  $CO_2$  fixation with warming. Other indirect effects of warming on GPP occur through hastened decomposition, hence N mineralization (Hart, 2006; Ineson et al., 1998) and root and mycorrhizal N uptake, thereby raising leaf nitrogen concentrations and so increasing  $CO_2$  fixation rates. Warming may also affect GPP by altering species composition and abundance (Hudson and Henry, 2009; Izaurre et al., 2011; Pieper et al., 2011; Shaver et al., 2000) and may thereby change woody carbon stock.

These direct and indirect effects cause ecosystems to increase GPP relatively more with warming in higher latitudes and cooler regions than in lower latitudes and warmer regions (Shaver et al., 2000). This might be due to greater temperature response of  $CO_2$  fixation and nutrient mineralization when temperature is low and  $Q_{10}$  values are larger (Sjögersten and Wookey, 2002). In drier and warmer regions, however,  $D$  rises more rapidly with warming, hastening declines in soil water potential ( $\psi_s$ ),  $\psi_c$  and stomatal conductance ( $g_c$ ), and hence in GPP.

These direct and indirect responses of GPP to warming may also vary with plant functional types and climatic zones. For instance, warming may reduce seasonal carbon fixation of annual plants by hastening phenological advance thereby reducing length of growing season, but may raise seasonal fixation in perennial plants by increasing length of growing season (Grant et al., 2009; Kim et al., 2012; Myneni et al., 1997; Piao et al., 2007; Tucker et al., 2001; Zhu et al., 2012). The same rise in temperature can have different impacts on ecosystem processes in different biomes (Oberbauer et al., 2007) and the responses over time can be different (Peng et al., 2009; Way and Oren, 2010).

To examine these contrasting responses to warming, in this study we first analyzed the spatial and temporal variability and trends of warming and precipitation over the last three decades (1979–2010) in NA using climate data from the North American Regional Reanalysis (NARR) (Wei et al., 2014). We then used a comprehensive mathematical process model, *ecosys* (Grant, 2001, 2014; Grant et al., 2011b) to examine how this variability affected the spatial and temporal changes in GPP and leaf area index (LAI) across different ecological regions (eco-regions) of NA. *Ecosys* was used because the direct and indirect effects of warming on biochemical and physical processes that control  $CO_2$  fixation, as described above, are explicitly modeled. The skill of the model to capture these warming effects on ecosystem productivity at different time steps (hourly, daily, annual and decadal) were shown to be generally high, when rigorously tested against measured fluxes over a wide range of climates across different biomes: e.g. wheat growth under controlled warming (Grant et al., 2011b), natural warming in coastal Arctic tundra in Alaska (Grant et al., 2003), mesic Arctic tundra in Northwest Territories, Canada (Grant et al., 2011a); diverse temperate and boreal forests (Grant et al., 2009, 2010), dry grassland in Mediterranean climate zones (Grant et al., 2012); semi-arid grassland in Lethbridge, Alberta (Grant and Flanagan, 2007;

Li et al., 2004). In a more recent study (Grant, 2014), the effects of experimental soil warming on nutrient cycling, particularly N mineralization, hence ecosystem productivity in the Harvard forest mixed deciduous stand were tested.

## 2. Materials and methods

### 2.1. Model description

A detailed description of inputs, parameters and algorithms used in *ecosys* can be found (Grant, 2001, 2014) and (Grant et al., 2011b, 2012). However, the general descriptions of the algorithms and parameters that are most relevant to modeling the direct and indirect impacts of warming on GPP as described in the introduction are given below and details of the equations used are given in Appendices A–D of the Supplement.

#### 2.1.1. Direct effects

2.1.1.1. *CO<sub>2</sub> fixation.* Warming affects GPP directly through its effects on carboxylation (Eqs. C6b and C10a), oxygenation (Eqs. C6d and C10b),  $K_c$  (Eqs. C6e, C10d and C10e) and modeled by the Arrhenius functions for light and dark reactions, using parameters developed by Bernacchi et al. (2003) for temperatures from 10 to 40 °C and additional parameters for low and high temperatures inactivation by Kolari et al. (2007) as presented in Grant (2014).  $CO_2$  diffusion is controlled by leaf resistance  $r_l$  (Eq. C4) which is calculated from a minimum value  $r_{lmin}$  (Eq. C5) for each leaf surface that allows a set ratio for intercellular to canopy gaseous  $CO_2$  concentration  $C_i:C_b$  to be maintained at  $CO_2$  fixation rate  $V_c$  under ambient  $CO_2$  concentration ( $C_a$ ), irradiance, canopy temperature ( $T_c$ ), leaf nutrient content and zero  $\psi_c$  (Grant et al., 2007a). In areas with lower  $T_a$ , warming improves kinetics of carboxylation and hence rates of  $CO_2$  fixation (Bernacchi et al., 2001) due to larger  $Q_{10}$  at lower temperatures. However, increasing  $T_a$  also raises  $K_c$  (Bernacchi et al., 2001, 2003) and lowers  $C_c$  with respect to  $C_i$  (Farquhar et al., 1980). In areas with lower  $T_a$  where  $Q_{10}$  is larger, the beneficial effect of warming on carboxylation kinetics is greater than the adverse effects of warming on  $K_c$  and  $C_c$ . But in areas with higher  $T_a$  where  $Q_{10}$  is smaller, the beneficial effect of warming may be less than the adverse effects, thereby slowing  $CO_2$  fixation by hastening oxygenation more than carboxylation.

#### 2.1.2. Indirect effects

2.1.2.1. *Water relations.* Warming affects GPP indirectly by increasing  $D$ , hence transpiration demand that lowers  $\psi_c$  (Eq. B14) and raises  $r_c$  (Eq. B2b), thereby slowing  $CO_2$  diffusion (Eq. C2) (Grant et al., 2008). The impact of  $D$  on transpiration is solved through the first-order closure of the energy balance (net radiation  $R_n$  (Eq. B1a) latent heat flux LE (Eqs. B1b,c), sensible heat flux H (Eq. B1d), and change in heat storage G). Total energy and water exchange between the atmosphere and the ecosystem is the sum of the exchanges with vegetation, snow, residue (coarse woody, fine non-woody) and ground surfaces. Surface energy and water exchanges are coupled with soil heat and water transfers through the surface residue and soil profile (Eq. D12), including freezing and thawing (Eq. D13), surface runoff vs. infiltration (Eq. D1) and subsurface flows through micro- and macropores (Eq. D7), which determine soil temperatures ( $T_s$ ) and water contents ( $\theta$ ) (Grant, 2004).

Canopy transpiration ( $E_c$ ) is coupled with water uptake  $U$  (Grant et al., 1999) through a convergence solution for  $\psi_c$  at which  $E_c$  equals  $U$  + change in plant water storage (Eq. B14). During this solution,  $r_c$  rises from a minimum value  $r_{cmin}$  aggregated by leaf surface area from  $r_{lmin}$  (Eq. B2a) at zero  $\psi_c$  through an exponential function of canopy turgor potential  $\psi_t$  (Eq. B2b) calculated from  $\psi_c$  and osmotic water potential  $\psi_\pi$  (Eq. B4).  $U$  from the soil to the canopy is determined by the potential difference between  $\psi_c$  and  $\psi_s$  across

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