

Model-based analysis of environmental controls over ecosystem primary production in an alpine tundra dry meadow

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Abstract We investigated several key limiting factors that control alpine tundra productivity by developing an ecosystem biogeochemistry model. The model simulates the coupled cycling of carbon (C), nitrogen (N), and phosphorus (P) and their interactions with gross primary production (GPP). It was parameterized with field observations from an

alpine dry meadow ecosystem using a global optimization strategy to estimate the unknown parameters. The model, along with the estimated parameters, was first validated against independent data and then used to examine the environmental controls over plant productivity. Our results show that air temperature is the strongest limiting factor to GPP in the early growing season, N availability becomes important during the middle portion of the growing season, and soil moisture is the strongest limiting factors by late in the growing season. Overall, the controls over GPP during the growing season, from strongest to weakest, are soil moisture content, air temperature, N availability, and P availability. This simulation provides testable predictions of the shifting nature of physical and nutrient limitations on plant growth. The model also indicates that changing environmental conditions in the alpine will likely lead to changes in productivity. For example, warming eliminates the control of P availability on GPP and makes N availability surpass air temperature to become the second strongest limiting factor. In contrast, an increase in atmospheric nutrient deposition eliminates the control of N availability and enhances the importance of P availability. These analyses provide a quantitative and conceptual framework that can be used to test predictions and refine ecological analyses at this long-term ecological research site.

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Introduction

Ongoing and projected environmental change in arctic and alpine ecosystems highlights the need to better understand functional response of these unique ecosystems to perturbations. For example, mean atmospheric temperature in the Western U.S.A. has increased by 0.5–1.5 °C over the past century, leading to a decrease by approximately 73 % in the coverage of area classified as alpine tundra (Diaz and Eischeid 2007). Indeed, the rate and magnitude of climate change projections are greater for arctic and alpine ecosystems (Bradley et al. 2004; Diaz et al. 2014; Gibbard et al. 2005; IPCC 2013), and these ecosystems are particularly vulnerable to climate change (Buytaert et al. 2011). At the same time, these alpine ecosystems are also the site of increasing N (Baron et al. 2009), P (Brahney et al. 2014), and base cation deposition (Brahney et al. 2013), which is likely due to the increasing both anthropogenic dust emissions and wind transport (Brahney et al. 2013). Such changes may disproportionately alter environmental conditions and the ecosystem characteristics (e.g., energy balance, ecosystem production, plant cover) in these regions (Beniston et al. 1997; Gurdak et al. 2007; Lesica and McCune 2004; Soja et al. 2007). These findings underscore the need to develop insight into the basic function and likely ecological response of these ecosystems to environmental change.

A change in the productivity of tundra ecosystems is one likely consequence of perturbations such as climate change or nutrient deposition. In alpine tundra ecosystems, Farrer et al. (2015) suggest that environmental conditions have a much stronger influence on ecosystem production than vegetation dynamics or composition. This is likely because these systems tend to be heavily influenced by climatic factors (short and cool growing seasons) and are developed on shallow rocky soils with relatively low nutrient content (Reich et al. 1997). For these reasons, the alpine tundra is both sensitive to a range of environmental changes and presents an ideal test case for studies of environmental controls on GPP.

The environmental controls over GPP in the alpine tundra ecosystems can be roughly separated into physical (temperature and moisture) and nutrient (N and P) controls (Elmendorf et al. 2012; Ernakovich et al. 2014; Freppaz et al. 2012; Jones et al. 1998). Several nutrient amendment experiments (Bowman et al. 2012,

1993; Nemergut et al. 2008; Soudzilovskaia et al. 2007) illustrate that nutrients play an important and limiting role in plant growth in alpine ecosystems and support the generalized notion that these systems are N limited or N and P co-limited. Similarly, studies show that changes in temperature and/or moisture conditions (e.g., soil warming or snow accumulation manipulation experiments) also cause changes in primary productivity (Freppaz et al. 2012; Natali et al. 2012). Despite these experimental studies and the important insights they provide, it remains very difficult to examine the relative importance of environmental physical versus nutrient controls over primary production in alpine (and other) ecosystems. This is due to both the inherent limitations of field studies and the complicated temporal interactions between physical and biogeochemical control of productivity under field conditions. Such limitations may be overcome with quantitative models that can improve understanding ecosystem function (McKane et al. 1997). Our goal here was to create a quantitative and conceptual framework that can be used to examine shifting control of primary productivity over time in the complex physical setting of alpine tundra ecosystems. In developing this modeling framework, other goals of this study were to create testable hypotheses for field studies in a long-term ecological research (LTER) site and to create a framework for model-data iteration that can be used to refine understanding of ecological processes.

In this study, we developed a relatively simple ecosystem model that can simulate the coupled C, N, and P cycles and their interactions with ecosystem productivity. The model simultaneously considers soil physical [e.g., sorption of dissolved organic carbon (DOC)], chemical (i.e., weathering of primary mineral P), biological (e.g., C decomposition and N mineralization), and hydrological processes (leaching of DOC, N, and P). Using observations from the Niwot Ridge Long Term Ecological Research (NWT-LTER), the model was parameterized with data from an alpine dry meadow and then used to investigate the environmental controls over daily and seasonal GPP.

Materials and methods

Model development

We developed a model to simulate the coupled cycling of ecosystem C, N, and P (Fig. 1). In our modeling

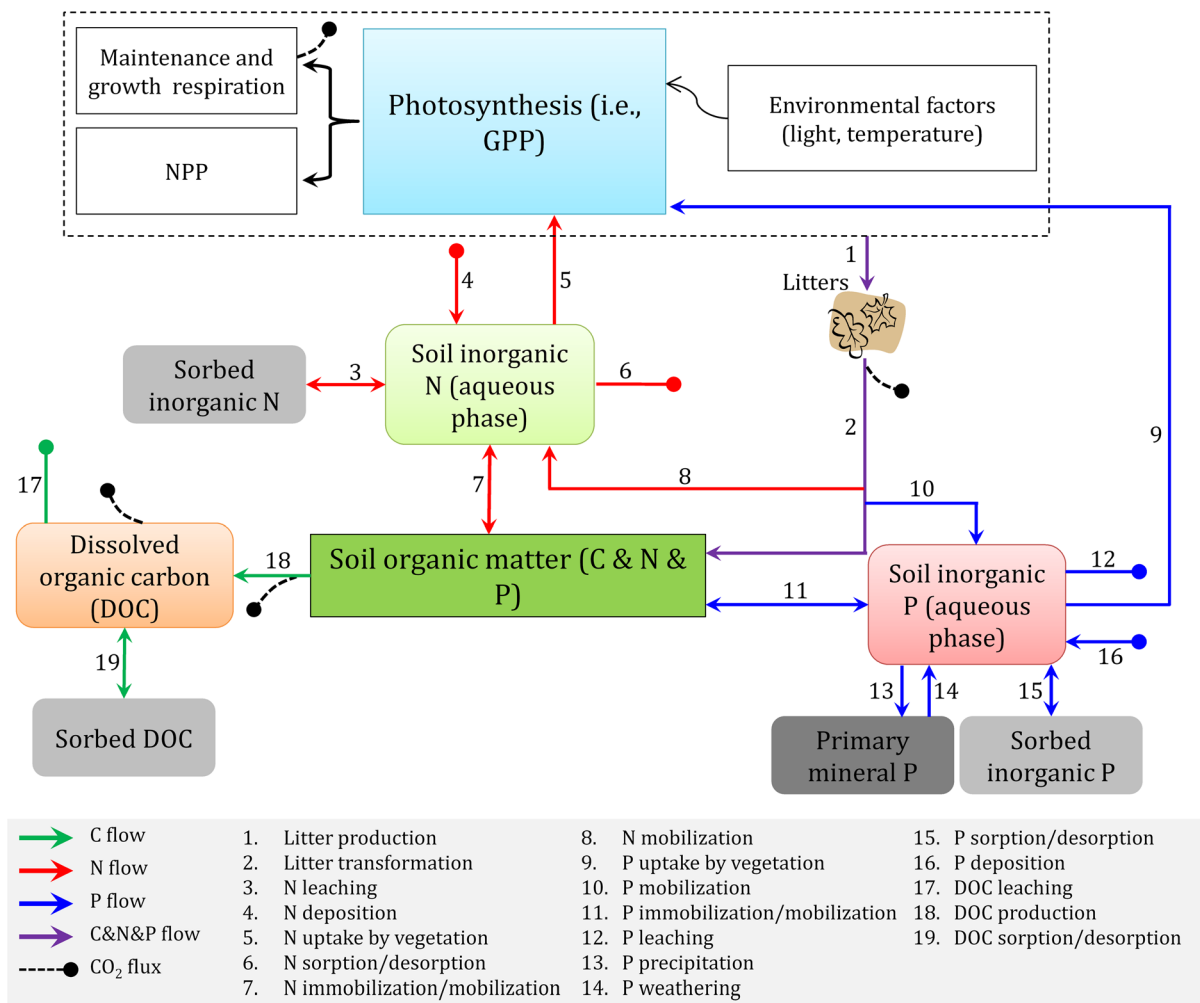


Fig. 1 Model schematic that outlines the coupled cycling of carbon (C), nitrogen (N), phosphorus (P), and their interactions with gross primary production. Boxes indicate geochemical

pools, and arrows indicate fluxes. The equations describing fluxes between pools are described in the supplementary materials

framework, ecosystem C is separated into vegetation (foliage and root), litter, soil, and DOC pools. The model represents parallel organic N and P pools, with additional inorganic pools in aqueous and sorbed phases. Below we provide a brief description of the processes that control each C/N/P pool. Please see the supplementary materials for the detailed mathematical equations.

Gross primary productivity is a function of incoming solar radiation, leaf area index (LAI), photosynthetic efficiency, air temperature, soil moisture content, and soil nutrient conditions (i.e., soil plant-available N and P) (Hilker et al. 2008). NPP is calculated by subtracting autotrophic respiration (sum of vegetation maintenance and growth respiration) from GPP.

Ecosystem C pools depend on inputs and losses from ‘donor’ and ‘receiver’ pools following first-order kinetics. Heterotrophic respiration (R_h) is calculated as the sum of CO₂ released during the turnover of litter C, soil C, and DOC. DOC sorption or desorption is assumed to be instantaneous (Fan et al. 2010). DOC leaching is a function of DOC content and hydrological discharge rate (Cosby et al. 1997).

The organic N and P contents in foliage, root, litter, and soil C pools are calculated based on the C content and the corresponding C:N and C:P stoichiometries for each pool (Cosby et al. 1997; Thornton and Rosenbloom 2005; Yang et al. 2014). Both soil inorganic N and P pools (i.e., plant-available N and P pools)

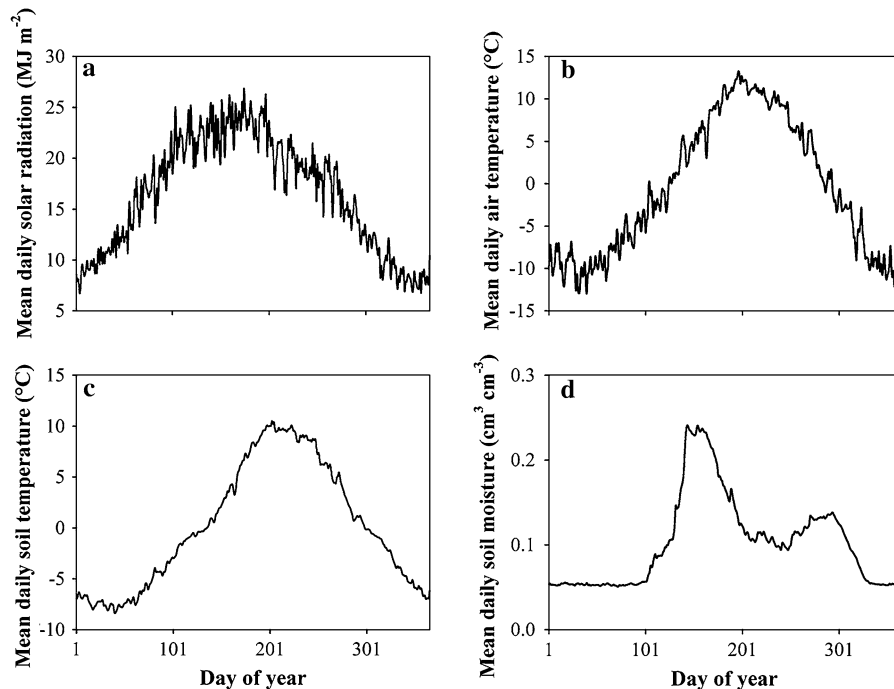


Fig. 2 Climatological mean daily environmental conditions what were used to drive the model including: **a** solar radiation, **b** air temperature, **c** soil temperature, and **d** soil moisture. Data were taken from the NWT-LTER website <http://niwot.colorado.edu>

depend on (1) gain of inorganic N and P due to atmospheric deposition and (2) loss of inorganic N and P due to plant uptake and leaching, respectively. Both soil inorganic N and P pools also depend on either gain or loss due to sorption and *net* N and P mineralization (Raich et al. 1991). The dynamics of organic N in aqueous phase is not included in the model because Hood et al. (2003) indicated that approximately 90 % of dissolved total nitrogen was in inorganic form (i.e., dissolved inorganic nitrogen) in the alpine tundra areas and only approximately 10 % was in organic form (i.e., dissolved organic nitrogen). Additionally, the soil inorganic P pool is also controlled by P gain due to weathering of primary mineral P and P loss due to precipitation (interactions with other elements to form solid minerals) (Yang et al. 2014).

Site description

We applied our model to investigate environmental controls over GPP in a typical alpine dry meadow. The dry meadow is located within the NWT-LTER in the Front Range of the Colorado Rocky Mountains, approximately 35 km west of Boulder, Colorado. At

an elevation of 3500 m, the dry meadow studied here has a mean annual precipitation of approximately 1000 mm (most of precipitation falls as snow) and a mean annual temperature of -3.8°C . The climate at NWT-LTER is characterized by a short-growing season (approximately 2–3 months) and a long cold winter. The thickness of soil above parent materials is approximately 20 cm in the dry meadow. The soil bulk density is approximately 0.8 g cm^{-3} . The dry meadow is mainly covered by *Polygonum viviparum* (L.) Delarbre, *Acomastylis rossii* (R. Br.) Greene, *Kobresia myosuroides* (Vill.) Fiori, and *Trifolium* species. Please refer to Bowman et al. (1993, 1995, 2012), Fisk et al. (1998) and Litaor et al. (2008) for the detailed site and climate descriptions.

Input datasets

The daily mean incoming solar radiation, air temperature, soil temperature, and soil moisture from 2000 to 2010 were obtained from the NWT-LTER website (<http://niwot.colorado.edu>) and used to drive the model (Fig. 2). Key model parameters (e.g., C:N and C:P stoichiometries, and atmospheric N and P deposition

Table 1 The fixed model parameters, values and references

Acronym	Definition	Units	Values	References
Z_S	Length of soil column	m	0.20	http://niwot.colorado.edu
ρ_b	Bulk density	g m^{-3}	8.0×10^5	Litaor et al. (2008)
Vegetation-related parameters				
V_{LAI}	Leaf area index	$\text{m}^2 \text{m}^{-2}$	2.7	Asner et al. (2003)
ε	Photosynthetic efficiency	g C MJ^{-1}	1.7	McCallum et al. (2013)
T_{max}	Maximum air temperature for vegetation growth	$^{\circ}\text{C}$	40.0	Yan and Hunt (1999)
T_{opt}	Optimal air temperature for vegetation growth	$^{\circ}\text{C}$	20.0	Yan and Hunt (1999)
$f_{V,l}$	Fraction of NPP allocated to foliage	Unitless	0.3	Fisk et al. (1998)
$f_{V,r}$	Fraction of NPP allocated to root	Unitless	0.7	Fisk et al. (1998)
$\delta_{V,l}$	C:N ratio of foliage	g g^{-1}	32.0	Fisk et al. (1998) and Cleveland et al. (2004)
$\delta_{V,r}$	C:N ratio of root	g g^{-1}	55.0	Fisk et al. (1998)
δ_L	C:N ratio of litter	g g^{-1}	41.0	Fisk et al. (1998) and Cleveland et al. (2004)
δ_S	C:N ratio of soil	g g^{-1}	13.5	http://niwot.colorado.edu
$\xi_{V,l}$	C:P ratio of foliage	g g^{-1}	416.0	Fisk et al. (1998) and Litaor et al. (2008)
$\xi_{V,r}$	C:P ratio of root	g g^{-1}	715.0	Fisk et al. (1998) and Litaor et al. (2008)
ξ_L	C:P ratio of litter	g g^{-1}	533.0	Fisk et al. (1998) and Litaor et al. (2008)
ξ_S	C:P ratio of soil	g g^{-1}	91.5	http://niwot.colorado.edu
$f_{L,l}$	Fraction of decomposed litter that transfers to soil pool	Unitless	0.5	Thornton and Rosenbloom (2005)
Soil-related parameters				
$\lambda_{d,DOC}$	Linear distribution coefficient of DOC between the sorbed and aqueous phases	$\text{m}^3 \text{g}^{-1}$	7.5×10^{-7}	Kawahigashi et al. (2006)
$\lambda_{d,N}$	Linear distribution coefficient of N between the sorbed and aqueous phases	$\text{m}^3 \text{g}^{-1}$	1.1×10^{-6}	Amin et al. (2014)
$\lambda_{d,P}$	Linear distribution coefficient of P between the sorbed and aqueous phases	$\text{m}^3 \text{g}^{-1}$	2.3×10^{-6}	Hussain et al. (2006)
K_{DOC}	Turnover rate of DOC	d^{-1}	9.6×10^{-4}	Yurova et al. (2008)
N_{ppt}	Atmospheric N deposition rate	$\text{g N m}^{-2} \text{d}^{-1}$	1.2×10^{-3}	Mladenov et al. (2012)
P_{ppt}	Atmospheric P deposition rate	$\text{g P m}^{-2} \text{d}^{-1}$	4.1×10^{-5}	Mladenov et al. (2012)
Q_{lch}	Discharge rate	m year^{-1}	0.03	Hood et al. (2003)

rate as discussed later) are also obtained from the website of NWT-LTER or other similar ecosystems and listed in Table 1.

Parameter estimation

The model pools were initialized with field observations obtained at NWT-LTER (Table 2), leaving eight unknown parameters in the model (Table 3). Due to the

high nonlinearity and large number of unknown parameters, models like our developed model are known to have many local optima. A global optimization strategy, stochastic ranking evolution strategy (SRES), was used to solve this problem and to inversely estimate the unknown parameters (Ji and Xu 2006; Runarsson and Yao 2000, 2005). Several comparison studies (Banga et al. 2003; Moles et al. 2003) have demonstrated that SRES is more computationally

Table 2 The initialized carbon (C), nitrogen (N), and phosphorus (P) pools during model simulations

Acronym	Definition	Units	Initial conditions or target values	Model outputs after 100-year runs	References
$C_{V,l}$	Foliage C pool	g C m^{-2}	105.0	105.0	Fisk et al. (1998)
$C_{V,r}$	Root C pool	g C m^{-2}	245.0	245.0	Fisk et al. (1998)
C_L	Litter C pool	g C m^{-2}	1250.0	1253.0	Fisk et al. (1998)
C_S	Soil C concentration	g C g^{-1}	0.159	0.165	Litaor et al. (2008)
C_{DOC}	DOC concentration	g C m^{-3}	30.0	30.0	Cleveland et al. (2004) and Xu et al. (2009)
$N_{S,avail}$	Plant-available N concentration	g N m^{-3}	1.5	1.5	Xu et al. (2009)
$P_{S,avail}$	Plant-available P concentration	g P m^{-3}	0.2	0.2	Frey et al. (2007)
$R_a:R_h$	Autotrophic: heterotrophic respiration	Unitless	1.0	1.0	

These carbon pools along with C_{NPP} and $R_a:R_h$ are also used as target values during parameter estimates. The parameter estimates are based on the assumption that field observations represent the ecosystem steady states and thus is done by minimizing the differences between target values (initial conditions) with model outputs after 100-year runs. Therefore, the smaller difference between initial conditions and model outputs after 100-year runs, the better performance the parameter estimates

Table 3 The upper and lower parameter estimate bounds and the corresponding parameter estimates

Acronym	Definition	Units	Upper bound	Lower bound	Parameter estimates
$K_{V,m}$	Vegetation maintenance respiration coefficient	$\text{g C m}^{-2} \text{ d}^{-1}$	0.10	1.00×10^{-4}	8.21×10^{-4}
$K_{V,l}$	Turnover rate of foliage	d^{-1}	2.74×10^{-3}	2.74×10^{-4}	9.38×10^{-4}
$K_{V,r}$	Turnover rate of root	d^{-1}	2.74×10^{-3}	2.74×10^{-4}	9.38×10^{-4}
K_L	Turnover rate of litter	d^{-1}	2.74×10^{-3}	1.37×10^{-4}	1.26×10^{-3}
K_S	Turnover rate of soil C	d^{-1}	2.74×10^{-3}	2.74×10^{-6}	2.48×10^{-5}
f_{DOC}	fraction of decomposed SOC that transfers to DOC pool	Unitless	1.00	1.00×10^{-4}	2.43×10^{-3}
$K_{P,p}$	Precipitation rate of P due to P-mineral interaction	d^{-1}	0.001	1.00×10^{-7}	7.31×10^{-4}
$K_{P,w}$	Weathering rate of primary mineral P	d^{-1}	0.001	1.00×10^{-7}	2.04×10^{-6}

efficient and robust than many other global optimization strategies (e.g., differential evolution).

To estimate these eight unknown parameters (Table 3), we made steady-state assumptions that field observations roughly represent the ecosystem steady states. (1) The SRES first randomly generates 200 sets of model parameters (Runarsson and Yao 2000). (2) The model was then run for 100 years with each of the 200 sets of parameters along with the daily mean air temperature, solar radiation, and soil temperature and moisture (Fig. 2). Due to the steady-state assumption, the model outputs after 100-year runs should be the same as, or similar to, the model initial conditions (i.e., initialized pools). Therefore, the model initial conditions in Table 2 can also be used as target values during parameter estimation. One additional target value was considered, that is, the ratio

between autotrophic and heterotrophic respiration was set to one (Pries et al. 2013) (Table 2). (3) The objective functions were then calculated as:

$$Obj = \sum \left(\frac{\theta_t - \theta_m}{W} \right)^2 \quad (1)$$

where Obj is the objective function, θ_t is the target value, θ_m is the model output after 100-year runs, and W is the weighting factor. The weighting factor (W) is set to 100, 250, 1000, 0.1, 20, 1, 1, and 1 for $C_{V,l}$, $C_{V,r}$, C_L , C_S , C_{DOC} , $N_{S,avail}$, $P_{S,avail}$, and $R_a:R_h$ (Table 2), respectively. (4) Based on the calculated objective functions [i.e., Eq. (1)], the SRES selected the best set of parameters from the 200 sets of parameters, and (5) generated another 200 sets of parameters using the selected best set of parameter and evolutionary algorithm (Runarsson and Yao 2000). Procedures 2–5 were

then repeated until the minimum objective function was reached. Upper and lower bounds for the eight unknown parameters were chosen *a priori*, and based on their physical meanings, with large enough bounds to cover ecologically plausible solutions (Table 3).

Modeling exercises

The goal of this modeling exercise was to develop a conceptually robust model that could reasonably be used in a heuristic fashion to examining the controls on GPP in the dry meadow on Niwot Ridge. In this regard, the model served as a framework for testing hypotheses regarding controls on plant production that have emerged over the course of measurements and experiments at this LTER site. Such hypotheses include measurements of the variation in the strength of nutrient limitation across gradients of water availability on Niwot Ridge and anecdotal observations of inter-annual interactions of climate, snowpack, and plant productivity.

To validate model results, we conducted three short-term simulations to check model performance against observations from the NWT-LTER site. The three simulations were with (1) N fertilization (SimNf), (2) P fertilization (SimPf), and (3) N + P fertilization (SimNPf). The fertilization experiments were done by increasing the N and/or P inputs by $25 \text{ g m}^{-2} \text{ year}^{-1}$ to match prior experiments from the LTER site (Bowman et al. 1993). The increased N and/or P inputs were assumed to be evenly distributed to all of days throughout the growing season during model simulation. These three simulations started after the model reaches steady-state (i.e., 100-year run) and were run for 1 year. Additionally, we conducted model simulations (SimD2W) by increasing soil moisture three fold and decreasing soil temperature by 60 % to replicate likely soil conditions in the alpine wet meadow (Knowles et al. 2015), and this simulation (i.e., SimD2W) was run 100 years. We compared the model simulations with field fertilization experiments and observations from the wet meadow site to check the performance of model structure and parameterization. It is important to note that the goal of the modeling in this study was not to perfectly replicate observed field data but rather to general plausible (and testable) evaluations of how limitations change across space and time.

Subsequently, we conducted two long-term simulations to examine how GPP responds to long-term environmental changes. In the first simulation (SimT),

the soil and atmospheric temperatures were increased by 3°C to examine the impacts of warming on GPP. In the second simulation (SimNPd), both N and P loading rates through atmospheric deposition were increased by 5 times (Neff et al. 2008) to $5.89 \times 10^{-3} \text{ g N m}^{-2} \text{ d}^{-1}$ and $2.05 \times 10^{-4} \text{ g P m}^{-2} \text{ d}^{-1}$ to examine the response of GPP to the increasing dust deposition. Both of the two simulations (i.e., SimT and SimNPd) were run 100 years.

Productivity limiting index

A productivity limiting index was calculated to evaluate the relative importance of environmental controls over GPP and defined as:

$$PLI = \frac{\sum_{n=1}^L (DPLI_n \cdot GPP_{n,max})}{\sum_{n=1}^L GPP_{n,max}} \quad (2)$$

where *PLI* and *DPLI* are the growing-season and daily productivity limiting indices of environmental factors over GPP, respectively, *L* is the length of growing season (d), and $GPP_{n,max}$ is the daily theoretical maximum GPP ($\text{g C m}^{-2} \text{ d}^{-1}$). Higher productivity limiting index indicates stronger limiting effect on GPP. The daily productivity limiting index (i.e., *DPLI*) of environmental factors over GPP is defined as:

$$\begin{cases} DPLI_n = 1.0 - F_{GPP,T_A} & \text{for air temperature} \\ DPLI_n = 1.0 - F_{GPP,\theta_s} & \text{for soil moisture content} \\ DPLI_n = 1.0 - F_{GPP,N} & \text{for N availability} \\ DPLI_n = 1.0 - F_{GPP,P} & \text{for P availability} \end{cases} \quad (3)$$

where F_{GPP,T_A} , F_{GPP,θ_s} , $F_{GPP,N}$, and $F_{GPP,P}$ are the daily regulating functions on GPP and defined in the supplementary materials.

Results

Model calibration and validation

The results of parameter estimates are shown in Table 3. The target values and model outputs after 100-year runs with the estimated parameters are shown in Table 2. The simulated daily outputs of key ecosystem variables after 100-year runs are shown in Fig. 3. Annual exports (i.e., leaching) of DOC, DIN, and DIP are 0.15, 0.07, and $0.0008 \text{ g m}^{-2} \text{ year}^{-1}$,

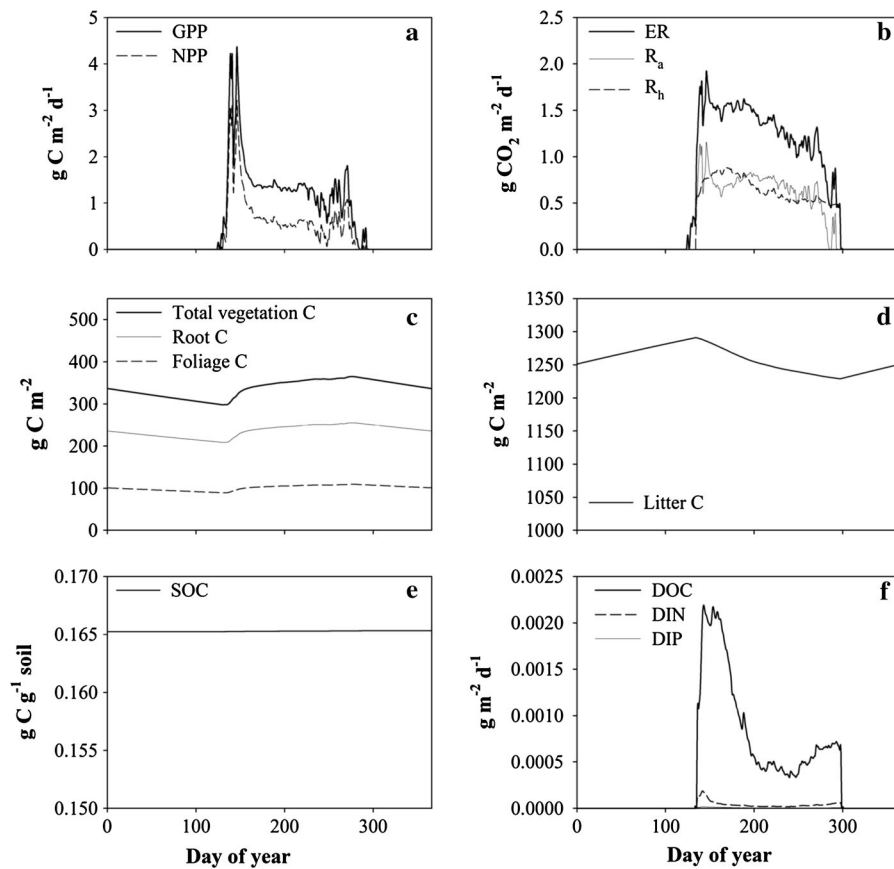


Fig. 3 The simulated key model outputs at the steady state. **a** The simulated gross primary productivity (GPP) and net primary productivity (NPP). **b** The simulated ecosystem respiration (ER), autotrophic respiration (R_a), and heterotrophic respiration (R_h). **c** The

simulated total vegetation C, root C, and foliage C. **d** The simulated litter C. **e** The simulated soil organic carbon (SOC). **f** The simulated dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN), and dissolved inorganic phosphorus (DIP)

respectively. The simulated annual autotrophic, heterotrophic, and ecosystem respiration values are 104, 104, and 209 $\text{g C m}^{-2} \text{ year}^{-1}$, respectively. The simulated GPP and NPP are 216 and 112 $\text{g C m}^{-2} \text{ year}^{-1}$, respectively (Control simulation in Fig. 4; Table 4). The simulated NPP ratios between fertilization and control simulations are 1.2 for N fertilization (i.e., $\text{SimNf}/\text{Control}$), 1.0 for P fertilization (i.e., $\text{SimPf}/\text{Control}$), and 2.4 for combined NP fertilization (i.e., $\text{SimNPf}/\text{Control}$), respectively. Also, the simulated NPP ratio between wet and dry meadows (i.e., $\text{SimD2W}/\text{Control}$ in Table 4) is 1.5.

Environmental controls over ecosystem productivity

The temporal dynamics of the productivity limiting factors indicates that air temperature is the strongest

control over GPP during winter season (Fig. 5). As air temperature increases in spring and early summer, the daily limiting effect of air temperature on GPP gradually decreases. Meanwhile, the limiting effect of N availability gradually increases and becomes the strongest control until the middle of growing season. After that, soil moisture content (or the lack thereof) becomes the strongest control over GPP. With air temperature decreasing in late summer and autumn, air temperature, again, becomes the strongest control over GPP and the limiting effect of soil moisture becomes weak and disappears in winter season. P availability never becomes the strongest control over GPP throughout the year (Fig. 5).

Integrated over the growing-season time-course, the relative importance of environmental and nutrient controls on GPP is as follows: moisture > temperature > nitrogen \gg phosphorus, based on the

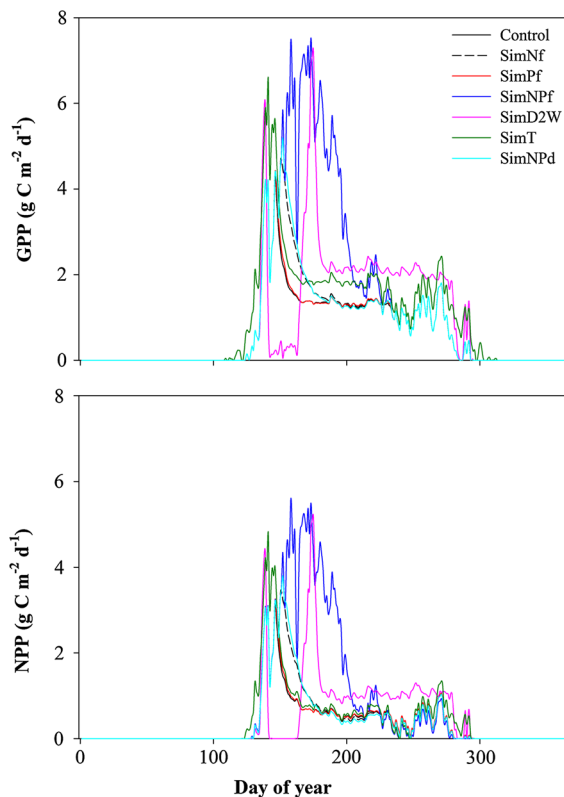


Fig. 4 The simulated seasonality of GPP and NPP with current conditions (Control), N fertilization (SimNf), P fertilization (SimPf), N + P fertilization (SimNPf), soil moisture increased by three fold and soil temperature decreased by 60 % to replicate likely soil conditions in the alpine wet meadow (SimD2W), soil and atmospheric temperatures increased by 3 °C (SimT), and both N and P loading rates (through atmospheric deposition) increased by 5 times (SimNPd)

calculated productivity limiting indices during the growing season (*PLIs*) (i.e., 0.62, 0.42, 0.31, and 0.11 for soil moisture, air temperature, N availability, and P availability, respectively; Table 4).

Long-term response to environmental changes

Warming (SimT) increases the NPP and GPP by ~30 and ~45 %, respectively; and an increase in nutrient deposition (SimNPd) increases the NPP and GPP by ~20 and ~17 %, respectively (Fig. 4; Table 4). Soil moisture is the strongest control over GPP for both warming and under an increase in nutrient deposition. However, warming weakens the control of air temperature to be the third strongest control and causes N availability to become the second strongest control. In comparison, soil temperature is still the second strongest

control after nutrient deposition is increased. Under this scenario, N no longer limits productivity and P availability becomes the third strongest control over GPP (Table 4).

Discussion

Our model provides a means to synthesize long-term data and test ecological theory by heuristically evaluating the relative controls over ecosystem productivity and biogeochemical cycles. Our simulations suggest that GPP in an alpine dry meadow is controlled more by physical environmental conditions than by soil nutrient conditions (N and P availability), but the relative importance of these limitations shifts over the growing season (Fig. 5; Table 4). Moreover, these results generate testable hypotheses on the potential ecosystem response to environmental perturbations and highlight key uncertainties in the understanding of ecological processes that can guide further research. Specifically, the model simulations suggest that long-term shifts in climate and exogenous nutrient deposition could lead to shifts in the timing and magnitude of limitation of productivity by different factors. The model simulations further suggest that many of these shifts will occur via changes in the seasonal patterns of nutrient, water, and temperature limitation with temporal and spatial patterns that can be tested by future monitoring and experimental studies. The development and parameterization of models, however, depend on the availability of appropriate data from well-coordinated LTER. Below we discuss the environmental controls over productivity and important limitations to our biogeochemical model.

Environmental controls over productivity

For the dry meadow, physical conditions (i.e., moisture and temperature) control the plant productivity outside the growing season. In the early and middle growing season, soil moisture content is close to the optimal moisture content for plant growth, resulting in a rapid increase in productivity (i.e., GPP; Fig. 3a), and N is the strongest limiting factor to productivity (due to the highest demand of N for plant growth and relatively slow N mineralization rates). Later in the growing season, soil moisture content falls below the optimal moisture content for plant growth and

Table 4 The sensitivity of NPP and GPP to environmental changes during the growing season

Simulation	NPP (g C m ⁻² year ⁻¹)	GPP (g C m ⁻² year ⁻¹)	Productivity limiting index (PLI) ^a			
			T_a	θ_s	N	P
Control	112	216	0.42	0.62	0.31	0.11
SimNf	135	249	0.42	0.62	0.0	0.27
SimPf	114	219	0.42	0.62	0.31	0.0
SimNPf	266	434	0.42	0.62	0.0	0.0
SimD2W	168	313	0.42	0.25	0.44	0.0
SimT	145	313	0.26	0.62	0.28	0.0
SimNPd	134	253	0.42	0.62	0.0	0.27

The second group of simulations (i.e., SimNf, SimPf, SimNPf, and SimD2W) is used for model validation. The third group of simulations (i.e., SimT and SimNPd) is used to investigate the long-term responses of ecosystem productivity in the dry meadow to environmental changes

Control Simulation with current environmental conditions, *SimNf* simulation with N fertilization, *SimPf* simulation with P fertilization, *SimNPf* simulation with N + P fertilization, *SimD2W* simulation with soil moisture increased by three fold and soil temperature decreased by 60 % to replicate likely soil conditions in the alpine wet meadow, *SimT* simulation with soil and atmospheric temperatures increased by 3 °C, *SimNPd* simulation with both N and P loading rates (through atmospheric deposition) increased by 5 times

^a Greater values denote stronger productivity limiting effects

moisture becomes the strongest limiting factor to productivity, resulting in decrease in productivity (i.e., GPP; Fig. 3a). The reduction in productivity due to moisture limitation is sufficiently large that N is no longer projected to be a limiting factor during this period of time. These results suggest that limitation to productivity in the dry meadow ecosystem can be thought of as a shifting temporal sequence that transitions from temperature to nitrogen, to moisture, and then ultimately back to temperature at the end of the growing season. Such a result is testable and if validated could provide new insights into how these ecosystems would respond to climate changes such as a lengthening of the growing season and/or alternation of nutrient deposition (and deposition timing).

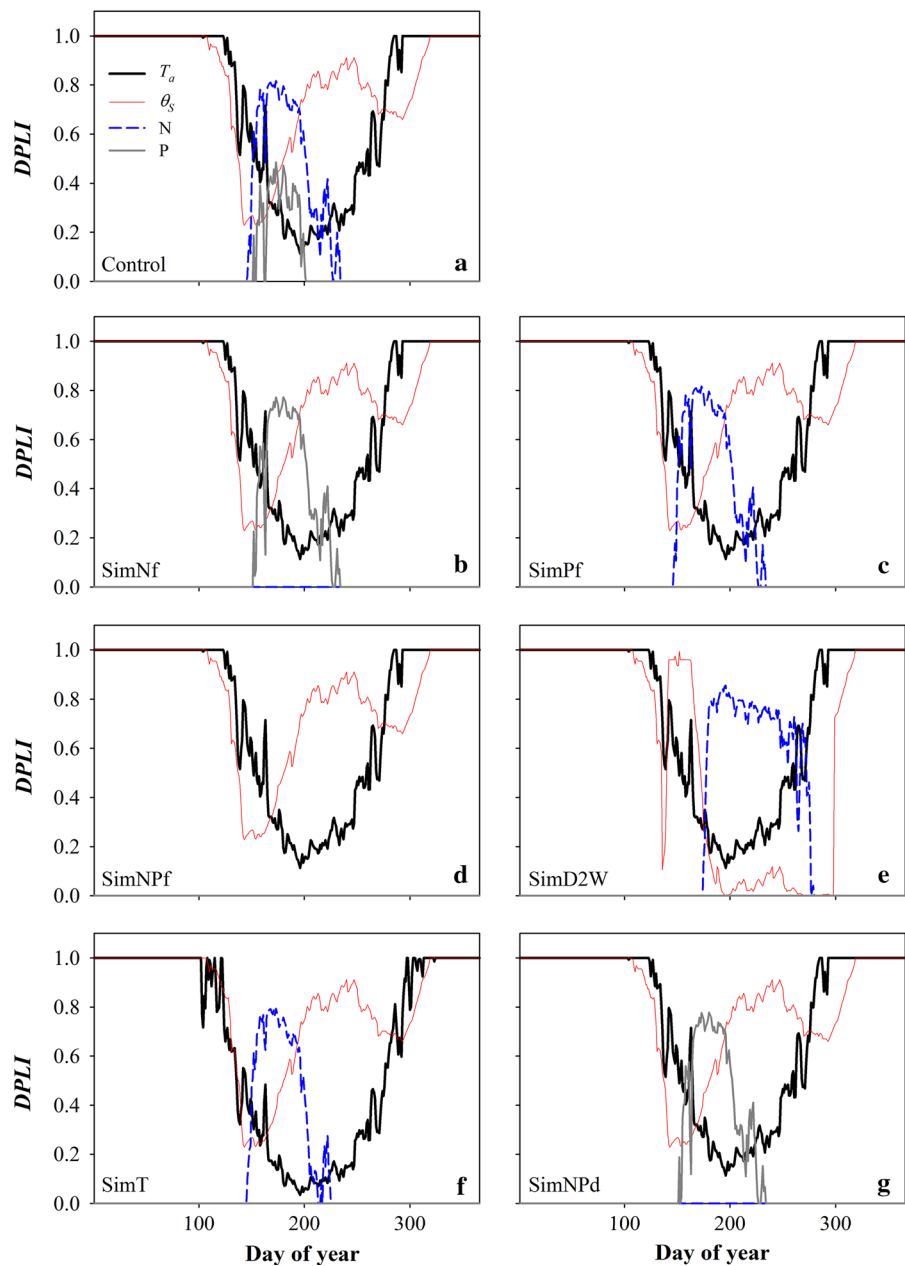
As discussed earlier, nutrients are important in the dry meadow ecosystem, particularly during the peak of the growing season and N availability is a stronger limiting factor on productivity than P availability (Fig. 5a; Control simulation in Table 4). This simulation result is consistent with observations from Bowman et al. (1993) in which fertilization by N increased productivity in the dry meadow ecosystem. The modeling simulations also suggest that climate/decomposition feedbacks play an important role in the nutrient dynamics of these ecosystems. The limiting effects of N and P are strongly dependent of the rate of nutrient supply through decomposition of soil organic

matter, compared to the rate of plant demand for nutrients. Each of these processes (decomposition and productivity) has somewhat different controls by physical processes and so changes in temperature or moisture will have disproportionate effects on decomposition and productivity as has been suggested for other ecosystems (Townsend et al. 1992). Therefore, the simulated N- and P-limitation are the end result of a complex series of controls (over nutrient dynamics and productivity) where temperature and moisture play an important role via regulation of decomposition and nutrient release rates.

Warming could further shift the relative strength of N versus P limitation at the site because of differences in C:N and C:P ratios of organic matter across the ecosystem. For example, the plant C:N ratio is approximately 2.4–4.1 times greater than soil C:N ratio whereas the plant C:P ratio is approximately 4.5–7.8 times greater than soil C:P ratio (Cleveland et al. 2004; Fisk et al. 1998; Litaor et al. 2008). Therefore, warming will have a proportionally larger effect on the supply of N compared to P if warmer temperatures stimulate decomposition of soil organic matter. Further, the increase in the supply of P due to warming is larger than the corresponding increase in plant demand of P, which effectively would diminish or eliminate any P limitation of productivity at this site (SimT in Table 4). In contrast, the warming-induced

Fig. 5 The temporal productivity limiting index (i.e., *DPLI*) of air temperature (T_a), soil moisture (θ_s), nitrogen (N), and phosphorus (P) on gross primary productivity (GPP).

a The simulations with current environmental conditions in the dry meadow. **b, c, d** The simulations with N fertilization (SimNf), P fertilization (SimPf), and N + P fertilization (SimNPf), respectively. **e** The simulations with soil moisture increased by three fold and soil temperature decreased by 60 % to replicate likely soil conditions in the alpine wet meadow (SimD2W). **f** The simulations with soil and atmospheric temperatures increased by 3 °C (SimT). **g** The simulations with both N and P loading rates (through atmospheric deposition) increased by 5 times (SimNPd). A greater value denotes a stronger limiting effect on productivity and zero denotes no limiting effect on productivity [please see Eq. (3)]



increase in the supply of N is similar to the warming-induced increase in the demand of N, resulting in small change in the limiting effect of N (SimT in Table 4) in the context of warming climate.

The N loading rate through atmospheric deposition ($0.43 \text{ g N m}^{-2} \text{ year}^{-1}$) is approximately 29 times greater than the P loading rate ($0.015 \text{ g P m}^{-2} \text{ year}^{-1}$) (Mladenov et al. 2012). This suggests that the greater nitrogen deposition would likely eliminate the limiting

effects of N availability on productivity and thus enhance the productivity limiting effects of P (if nutrient deposition continues with the current deposition rates at NWT-LTER). Given strong N limitation at the site (Bowman et al. 1993) that is captured by our model (Fig. 5), the simulated temporal variations of productivity limiting effects with increased nutrient deposition (SimNPd) are similar to those simulated with N fertilization (SimNf) (Fig. 5; Table 4).

The alpine tundra of Niwot Ridge is diverse and includes distinct vegetation communities. Here again, the modeling analysis presents a series of predictions that may offer improved insights into how limitations shift alongside vegetation composition, and provides some testable hypotheses that maybe useful for future experimental designs. For example, in the wet meadow communities, soil moisture is much higher than optimal moisture content for plant growth during the peak of growing season but is close to optimal moisture content in the late growing season. This results in a pattern of limitation where soil moisture is the strongest limiting factor in the early and middle of summer while N is the strongest limiting factor in the late summer and fall. As with the dry meadow, temperatures provide the ultimate limitation to productivity in the spring and late fall. Based on these simulations, we might hypothesize a different response of the wet meadows to climatic or nutrient deposition changes than those that would occur in the dry meadow. Future field multifactorial experiments (e.g., moisture-manipulation experiments and/or fertilization experiments with different application-timing treatments) would be helpful to test the dramatically different temporal variations of productivity limiting effects between the dry and wet meadows as indicated by the model simulations.

Model calibration and validation

Our results are broadly similar to other ecosystem models of arctic and alpine ecosystems. For example, the estimated vegetation maintenance respiration coefficient ($0.3 \text{ g C m}^{-2} \text{ year}^{-1}$) is similar to the value used for alpine tundra ($0.47 \text{ g C m}^{-2} \text{ year}^{-1}$) in McGuire et al. (1992). The estimated turnover rate of foliage/root (0.342 year^{-1}) is similar to the value (0.313 year^{-1}) estimated for an alpine dry meadow by Fisk et al. (1998). The estimated turnover rates of litter and soil C under field conditions (i.e., the estimated K_L and K_S adjusted by soil temperature and moisture function) during the growing season are 0.004 and 0.204 year^{-1} , respectively, compared to 0.006 and 0.117 year^{-1} estimated during peak productivity season by Fisk et al. (1998).

The estimated annual GPP and NPP (i.e., 216 and $112 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively) are similar to a number of values from nearby research sites and for the purposes of this study, we were not aiming to exactly reproduced productivity values but rather to generate

plausible simulation results that could be used for the goals of this heuristic modeling study. As a comparison to model results, Knowles et al. (2014) estimated mean GPP for a dry alpine fellfield at Niwot Ridge ranged from ~ 105 to $\sim 137 \text{ g C m}^{-2} \text{ year}^{-1}$ based on eddy covariance measurements. Elsewhere, Welker et al. (1999) reported that GPP for arctic and alpine dry tundra ranged from ~ 77 to $\sim 272 \text{ g C m}^{-2} \text{ year}^{-1}$, based on chamber measurements, similar to our GPP estimates (Table 4). Fisk et al. (1998) reported that NPP for dry and wet meadow are ~ 280 and $\sim 600 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively, based on vegetation biomass measurements. Bowman and Seastedt (2001) reported that NPP for dry meadow ranged between ~ 166 and $\sim 181 \text{ g C m}^{-2} \text{ year}^{-1}$ and for wet meadow ranged between ~ 252 and $\sim 332 \text{ g C m}^{-2} \text{ year}^{-1}$; all of these values are higher than the estimated NPP from the dry meadow simulation in this study.

To check model performance, we examined the N and/or P fertilization simulations (SimNf, SimPf, and SimNPf in Fig. 4; Table 4). In this case, we evaluated the proportional treatment responses (in the form of a ratio of fertilized to non-fertilized plots). These ratios provide a sense of the magnitude of vegetation response to changes in nutrients and therefore a more direct evaluation of limitation than absolute GPP or NPP numbers which are highly variable in this tundra site. The simulated NPP ratio numbers (i.e., 1.2 for SimNf/Control, 1.0 for SimPf/Control, and 2.4 for SimNPf/Control) are similar to variation in measured above-ground-biomass ratios (1.6, 1.1, and 2.8 for N, P, and NP fertilization, respectively) based on field fertilization experiments (Bowman et al. 1993). Additionally, the simulated NPP ratio between wet and dry meadows (i.e., 1.5 for SimD2W/Control) is also within the ranges (~ 1.39 – 2.0) reported by Bowman and Seastedt (2001). The broad similarity of model outputs to field observations, although not a formal validation, does serve to build confidence in the utility of the model for the purposes for which it is employed in this study.

Uncertainties and limitations

One of the central tests for this model is the comparison between simulated and observed GPP. GPP in this model is a predicted variable that is not heavily prescribed and depends to a large degree on the physical and nutrient limitations to plant growth at the site. It would seem straightforward to compare

modeled to measured GPP; however, reported GPP and NPP values for alpine tundra vary significantly as presented earlier. The wide range in measured GPP and NPP values and the need to have accurate numbers for the testing of ecosystem models highlights the importance of these measurements for LTER and other ecological observation sites.

Our model simulations suggest that warming increased productivity by approximately 30 % in the dry meadow through directly changing soil temperature (Table 4). However, field observations indicated that warming might also have strong indirect impact on GPP by changing the surface or subsurface hydrological conditions due to permafrost thaw and/or earlier melting of snow and glacial ice (Caine 2011); thus, altering soil moisture regimes (Ababneh and Woolfenden 2010) and ecosystem productivity. Also, warming may cause longer growing season length (Myneni et al. 1997) and thus may significantly affect plant phenology (e.g., canopy properties and LAI) during growing seasons (Smith et al. 2012), which may have great impacts on overall ecosystem productivity (Baptist and Choler 2008; Hu et al. 2010). To develop a more robust projection of changes at this alpine site, it will be important to include more sophisticated representations of hydrological system (including snowpack dynamics) and plant physiological and phenology. Such model improvements could be coupled with additional field experimental studies to investigate how warming-induced changes in soil hydrology, snowpack, and plant phenology (e.g., length of growing season) affect the key processes that control ecosystem productivity.

One important factor that is not considered in our model framework is vegetation community (diversity, richness, and abundance) and its controls over ecosystem production. Such biotic shifts that may accompany climate change would significantly change the C:N:P ratios of soil and vegetation, C/N/P allocations (above-ground vs. belowground), patterns of nutrient uptake and, subsequently, primary production. At this time, it remains difficult to predict how (or why) vegetation may change in the alpine so while this is a limitation of the modeling approach presented here, it is also not an issue that is easily remedied without additional study.

Finally, the model does not consider the microbial response to nutrient enrichment. Microbial decomposition of soil organic matter can affect soil N availability by altering the export of N from soils to river or lake.

For example, Brooks and Williams (1999) indicated an inverse relationship between microbial N immobilization in winter and the leaching loss of N in spring and early summer after snowmelt (e.g., lower microbial activity in winter, higher leaching loss of N in spring after/during snowmelt). Simulating these kinds of temporal dynamics will likely require a greater mechanistic understanding and representation of subsurface biogeochemistry and hydrology in ecosystem models. Moreover, resolving spatial and temporal dynamics of plant and microbial nutrient competition (Kaye and Hart 1997) or a cooperation (via rhizosphere dynamics or mycorrhizae) (Huddleston 2011; Wernet et al. 2014) remains a significant challenge to accurately project biogeochemical responses to global change. For example, changes in soil nutrient conditions have the potential to change microbial community composition that, in turn, affects soil nutrient conditions (Leff et al. 2015; Liu and Greaver 2010; Ramirez et al. 2012). Our model framework could be coupled with the existing microbial models to investigate the microbial controls over soil C and nutrient cycling (Lawrence et al. 2009; Wieder et al. 2015) and the subsequent ecosystem productivity in the future.

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References

- Ababneh L, Woolfenden W (2010) Monitoring for potential effects of climate change on the vegetation of two alpine meadows in the White Mountains of California, USA. *Quat Int* 215:3–14
- Amin MGM, Simunek J, Lægdsmand M (2014) Simulation of the redistribution and fate of contaminants from soil-injected animal slurry. *Agric Water Manag* 131:17–29
- Asner GP, Scurlock JM, Hicke JA (2003) Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Glob Ecol Biogeogr* 12:191–205
- Banga JR, Balsa-Canto E, Moles CG, Alonso AA (2003) Dynamic optimization of bioreactors: a review. *Proc Indian Natl Sci Acad* 69:257–265
- Baptist F, Choler P (2008) A simulation of the importance of length of growing season and canopy functional properties on the seasonal gross primary production of temperate alpine meadows. *Ann Bot* 101:549–559

- Baron JS, Schmidt TM, Hartman MD (2009) Climate-induced changes in high elevation stream nitrate dynamics. *Glob Change Biol* 15:1777–1789
- Beniston M, Diaz HF, Bradley RS (1997) Climatic change at high elevation sites: an overview. *Clim Change* 36:233–251
- Bowman WD, Seastedt TR (2001) Structure and function of an alpine ecosystem: Niwot Ridge, Colorado. Oxford University Press, New York
- Bowman WD, Theodose TA, Schardt JC, Conant RT (1993) Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 74:2085–2097
- Bowman WD, Theodose TA, Fisk MC (1995) Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. *Oecologia* 101:217–227
- Bowman WD, Murgel J, Blett T, Porter E (2012) Nitrogen critical loads for alpine vegetation and soils in Rocky Mountain National Park. *J Environ Manag* 103:165–171
- Bradley RS, Keimig FT, Diaz HF (2004) Projected temperature changes along the American cordillera and the planned GCOS network. *Geophys Res Lett.* doi:[10.1029/2004GL020229](https://doi.org/10.1029/2004GL020229)
- Brahney J, Ballantyne AP, Sievers C, Neff JC (2013) Increasing Ca^{2+} deposition in the western US: the role of mineral aerosols. *Aeolian Res* 10:77–87
- Brahney J, Ballantyne AP, Turner BL, Spaulding SA, Otu M, Neff JC (2014) Separating the influences of diagenesis, productivity and anthropogenic nitrogen deposition on sedimentary $\delta^{15}\text{N}$ variations. *Org Geochem* 75:140–150
- Brooks PD, Williams MW (1999) Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrol Process* 13:2177–2190
- Buytaert W, Cuesta-Camacho F, Tobon C (2011) Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Glob Ecol Biogeogr* 20:19–33
- Caine N (2011) Recent hydrologic change in a Colorado alpine basin: an indicator of permafrost thaw. *Ann Glaciol* 51:130–134
- Cleveland CC, Neff JC, Townsend AR, Hood E (2004) Composition, dynamics, and fate of leached dissolved organic matter in terrestrial ecosystems: results from a decomposition experiment. *Ecosystems* 7:272–285
- Cosby BJ, Ferrier RC, Jenkins A, Emmett BA, Wright RF, Tietema A (1997) Modelling the ecosystem effects of nitrogen deposition: model of ecosystem retention and loss of inorganic nitrogen (MERLIN). *Hydrol Earth Syst Sci* 1:137–158
- Diaz HF, Eiseheid JK (2007) Disappearing “alpine tundra” Köppen climatic type in the western United States. *Geophys Res Lett.* doi:[10.1029/2007GL031253](https://doi.org/10.1029/2007GL031253)
- Diaz HF, Bradley RS, Ning L (2014) Climatic changes in mountain regions of the American cordillera and the tropics: historical changes and future outlook. *Arct Antarct Alp Res* 46:735–743
- Elmendorf SC, Henry GHR, Hollister RD et al (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat Clim Change* 2:453–457
- Ernakovich JG, Hopping KA, Bernadier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD (2014) Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Glob Change Biol* 20:3256–3269
- Fan Z, Neff JC, Wickland KP (2010) Modeling the production, decomposition, and transport of dissolved organic carbon in boreal soils. *Soil Sci* 175:223–232
- Farrer EC, Ashton IW, Spasojevic MJ, Fu S, Gonzalez DJX, Suding KN (2015) Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *J Ecol* 103:351–360
- Fisk MC, Schmidt SK, Seastedt TR (1998) Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology* 79:2253–2266
- Freppaz M, Williams MW, Seastedt TR, Filippa G (2012) Response of soil organic and inorganic nutrients in alpine soils to a 16-year factorial snow and N-fertilization experiment, Colorado Front Range, USA. *Appl Soil Ecol* 62:131–141
- Frey KE, McClelland JW, Holmes RM, Smith LC (2007) Impacts of climate warming and permafrost thaw on the riverine transport of nitrogen and phosphorus to the Kara Sea. *J Geophys Res.* doi:[10.1029/2006JG000369](https://doi.org/10.1029/2006JG000369)
- Gibbard S, Caldeira K, Bala G, Phillips TJ, Wickett M (2005) Climate effects of global land cover change. *Geophys Res Lett.* doi:[10.1029/2005GL024550](https://doi.org/10.1029/2005GL024550)
- Gurdak JJ, Hanson RT, McMahon PB, Bruce BW, McCray JE, Thyne GD, Reedy RC (2007) Climate variability controls on unsaturated water and chemical movement, High Plains Aquifer, USA. *Vadose Zone* 6:533–547
- Hilker T, Coops NC, Wulder MA, Black TA, Guy RD (2008) The use of remote sensing in light use efficiency based models of gross primary production: a review of current status and future requirements. *Sci Total Environ* 404:411–423
- Hood E, McKnight DM, Williams MW (2003) Sources and chemical character of dissolved organic carbon across an alpine/subalpine ecotone, Green Lakes Valley, Colorado Front Range, United States. *Water Resour Res.* doi:[10.1029/2002WR001738](https://doi.org/10.1029/2002WR001738)
- Hu J, Moore DJP, Burns SP, Monson RK (2010) Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Glob Change Biol* 16:771–783
- Huddleston JE (2011) Symbiosis: market economics in plant-fungus relationships. *Nat Rev Microbiol* 9:698–699
- Hussain A, Ghafoor A, Murtaza G (2006) Use of models for phosphorus adsorption on some sodic soils of punjab. *Int J Agric Biol* 8:241–248
- IPCC (2013) Climate change 2013: the physical science basis. Cambridge University Press, Cambridge, UK
- Ji X, Xu Y (2006) libSRES: a C library for stochastic ranking evolution strategy for parameter estimation. *Bioinformatics* 22:124–126
- Jones M, Fahnestock J, Walker D, Walker M, Welker J (1998) Carbon dioxide fluxes in moist and dry arctic tundra during the snow-free season: responses to increases in summer temperature and winter snow accumulation. *Arct Alp Res* 30:373–380
- Kawahigashi M, Kaiser K, Rodionov A, Guggenberger G (2006) Sorption and dissolved organic matter by mineral soils of the Siberian forest tundra. *Glob Change Biol* 12:1868–1877

- Kaye JP, Hart SC (1997) Competition for nitrogen between plants and soil microorganisms. *Trends Ecol Evol* 12:139–143
- Knowles JF, Burns SP, Blanken PD, Monson RK (2014) Fluxes of energy, water, and carbon dioxide from mountain ecosystems at Niwot Ridge, Colorado. *Plant Ecol Divers*. doi:[10.1080/17550874.2014.904950](https://doi.org/10.1080/17550874.2014.904950)
- Knowles JF, Blanken PD, Williams MW (2015) Soil respiration variability across a soil moisture and vegetation community gradient within a snow-scoured alpine meadow. *Biogeochemistry*. doi:[10.1007/s10533-10015-10122-10533](https://doi.org/10.1007/s10533-10015-10122-10533)
- Lawrence CR, Neff JC, Schimel JS (2009) Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. *Soil Biol Biochem* 41:1923–1934
- Leff JW, Jones SE, Prober SM et al (2015) Consistent responses of soil microbial communities to elevated nutrient inputs in grasslands across the globe. *Proc Natl Acad Sci* 112:10967–10972
- Lesica P, McCune B (2004) Decline of arctic alpine plants at the southern margin of their range following a decade of climatic warming. *J Veg Sci* 15:679–690
- Litaor MI, Seastedt TR, Sackett LC (2008) Nutrient status in alpine soils of the Colorado Front Range using the nitrogen/phosphorus ratio index. *Soil Sci Soc Am J* 72:1628–1636
- Liu L, Greaver TL (2010) A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecol Lett* 13:819–828
- McCallum I, Franklin O, Moltchanova E et al (2013) Improved light and temperature responses for light-use-efficiency-based GPP models. *Biogeosciences* 10:6577–6590
- McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, Moore B, Vorosmarty CJ (1992) Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Glob Biogeochem Cycles* 6:101–124
- McKane RB, Rastetter EB, Shaver GR, Nadelhoffer KJ, Giblin AE, Laundre JA, Chapin FS (1997) Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology* 78:1170–1187
- Mladenov N, Williams MW, Schmidt SK, Cawley K (2012) Atmospheric deposition as a source of carbon and nutrients to an alpine catchment of the Colorado Rocky Mountains. *Biogeosciences* 9:3337–3355
- Moles CG, Mendes P, Banga JR (2003) Parameter estimation in biochemical pathways: a comparison of global optimization methods. *Genome Res* 13:2467–2474
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Natali SM, Schuur EAG, Rubin RL (2012) Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *J Ecol* 100:488–498
- Neff JC, Ballantyne AP, Farmer GL et al (2008) Increasing eolian dust deposition in the western United States linked to human activity. *Nat Geosci* 1:189–195
- Nemergut DR, Townsend AR, Sattin SR et al (2008) The effects of chronic nitrogen fertilisation on alpine tundra soil microbial communities: implications for carbon and nitrogen cycling. *Environ Microbiol* 10:3093–3105
- Pries CEH, Schuur EAG, Crummer KG (2013) Thawing permafrost increases old soil and autotrophic respiration in tundra: partitioning ecosystem respiration using $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$. *Glob Change Biol* 19:649–661
- Raich JW, Rastetter EB, Melillo JM et al (1991) Net primary productivity in South America: application of a global model. *Ecol Appl* 1:399–429
- Ramirez KS, Craine JM, Fierer N (2012) Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. *Glob Change Biol* 18:1918–1927
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. *Proc Natl Acad Sci* 94:13730–13734
- Runarsson TP, Yao X (2000) Stochastic ranking for constrained evolutionary optimization. *IEEE Trans Evol Comput* 4:284–294
- Runarsson TP, Yao X (2005) Search biases in constrained evolutionary optimization. *IEEE Trans Syst Man Cybern* 35:233–243
- Smith JG, Sconiers W, Spasojevic JJ, Ashton IW, Suding KN (2012) Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. *Arct Antarct Alp Res* 44:135–142
- Soja AJ, Tchepakova NM, French NHF et al (2007) Climate-induced boreal forest change: predictions versus current observations. *Glob Planet Change* 56:274–296
- Soudzilovskaia NA, Onipchenko VG, Cornelissen JHC, Aerts R (2007) Effects of fertilisation and irrigation on “foliar afterlife” in alpine tundra. *J Veg Sci* 18:755–766
- Thornton PE, Rosenbloom NA (2005) Ecosystem model spin-up: estimating steady state conditions in a coupled terrestrial carbon and nitrogen cycle model. *Ecol Model* 189:25–48
- Townsend AR, Vitousek PM, Holland EA (1992) Tropical soils could dominate the short-term carbon cycle feedbacks to increased global temperatures. *Clim Change* 22:293–303
- Welker JM, Brown KB, Fahnestock JT (1999) CO_2 flux in arctic and alpine dry tundra: comparative field responses under ambient and experimentally warmed conditions. *Arct Antarct Alp Res* 31:272–277
- Wernet GDA, Strassmann JE, Ivens AB et al (2014) Evolution of microbial markets. *Proc Natl Acad Sci* 111:1237–1244
- Wieder WR, Grandy AS, Kallenbach CM, Taylor PG, Bonan GB (2015) Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geosci Model Dev* 8:1789–1808
- Xu C, Guo L, Dou F, Ping C (2009) Potential DOC production from size-fractionated Arctic tundra soils. *Cold Reg Sci Technol* 55:141–150
- Yan W, Hunt LA (1999) An equation for modelling the temperature response of plants using only the cardinal temperatures. *Ann Bot* 84:607–614
- Yang X, Thornton PE, Ricciuto DM, Post WM (2014) The role of phosphorus dynamics in tropical forests—a modeling study using CLM-CNP. *Biogeosciences* 11:1667–1681
- Yurova A, Sirin A, Buffam I, Bishop K, Laudon H (2008) Modeling the dissolved organic carbon output from a boreal mire using the convection-dispersion equation: importance of representing sorption. *Water Resour Res*. doi:[10.1029/2007WR006523](https://doi.org/10.1029/2007WR006523)