Modeling long-term changes in tundra carbon balance following wildfire, climate change and potential nutrient addition

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Abstract

To investigate the underlying mechanisms that control long-term recovery of tundra carbon (C) and nutrients after fire, we employed the Multiple Element Limitation (MEL) model to simulate 200-year post-fire changes in the biogeochemistry of three sites along a burn severity gradient in response to increases in air temperature, CO_2 concentration, nitrogen (N) deposition and phosphorus (P) weathering rates. The simulations were conducted for severely burned, moderately burned, and unburned arctic tundra. Our simulations indicated that recovery of C balance after fire was mainly determined by the internal redistribution of nutrients among ecosystem components (controlled by air temperature), rather than the supply of nutrients from external sources (e.g., nitrogen deposition and fixation, phosphorus weathering). Increases in air temperature and atmospheric CO_2 concentration resulted in 1) a net transfer of nutrient from soil organic matter to vegetation, and 2) higher C:nutrient ratios in vegetation and soil organic matter. These changes led to gains in vegetation biomass C but net losses in soil organic C stocks. Under a warming climate, nutrients lost in wildfire were difficult to recover because the warming-induced acceleration in nutrient cycles caused further net nutrient loss from the system through leaching. In both burned and unburned tundra, the warming-caused acceleration in nutrient cycles and increases in ecosystem C stocks were eventually constrained by increases in soil C:nutrient ratios, which increased microbial retention of plant-available nutrients in the soil. Accelerated nutrient turnover, loss of C, and increasing soil temperatures will likely result in vegetation changes, which further regulate the long-term biogeochemical succession. Our analysis should help in the assessment of tundra C budgets and of the recovery of biogeochemical function following fire, which is in turn necessary for the maintenance of wildlife habitat and tundra vegetation.

INTRODUCTION

In arctic tundra, climate warming (Hinzman et al. 2005, IPCC 2013) accelerates nutrient cycling between soil and vegetation (Mckane et al. 1997, Mack et al. 2004, Sistla et al. 2013), thereby reducing nutrient limitation on plant growth (Shaver and Chapin 1986, Mack et al. 2004) and potentially leading to substantial increases in productivity (e.g., Stow et al. 2004, Goetz et al. 2005, Verbyla 2008, Jiang et al. 2012). Continued increases in productivity might subsequently cause an accumulation of organic carbon (C), while the change in organic nutrient pools (e.g., nitrogen and phosphorus) in soil depends on the litter quality and external inputs (i.e. deposition, weathering, and microbial fixation). Because the external nitrogen (N) and phosphorus (P) sources have much lower input rates than mineralization, N and P supplies to warming-stimulated plant growth depend primarily on the increased N and P mineralization (Shaver et al. 1992). Moreover, both warming experiments (Hudson and Henry 2009, 2010) and long-term photographic monitoring (Sturm et al. 2001, Tape et al. 2006) indicate that warming might cause a shift in community composition toward more woody species in northern Alaska. This shift may alter the C and nutrient dynamics through increases in vegetation C:nutrient ratios and changes in litter production and composition (Hobbie 1996).

Besides climate warming, wildfire is another important disturbance in arctic tundra that greatly reduces C and nutrient stocks (Jiang et al. 2015a). Although combustion of litter and soil organic matter dramatically increase the nutrient availabilities (e.g., NH_4^+, PO_4^{3-}) in surface soil, the total pools (organic and inorganic) of nutrients substantially decrease because of the great nutrient loss (especially N) through volatilization (Mack et al. 2011, Bret-Harte et al. 2013). The 2007 Anaktuvuk River fire burned more than 1,000 km^2 of moist acidic tussock tundra on the North Slope of Alaska (Jones et al. 2009, Bowman et al. 2009), releasing about 2.1 Tg C into the atmosphere and volatilizing an amount of nitrogen (N) equal to about 400 years of N accumulation (assuming steady-state dynamics; Mack et al. 2011). Following fire, the surface greenness in the burned area recovered within three years and was higher than the nearby unburned area thereafter (Figure 1) (https://earthdata.nasa.gov/) (Rocha et al. 2012, Hu et al. 2015). The higher greenness implies higher leaf biomass, probably associated with higher N and P availability at least for a few years after the fire (Jiang et al. 2015a). Although plant growth and net CO_2 exchange have quickly recovered after fire (Rocha and Shaver 2011a, Bret-Harte et al. 2013, Jiang et al. 2015a), the long-term recovery of total ecosystem C stocks might be limited by nutrient availability in burned areas. This limitation is mainly due to the slow recycling of nutrients from the reduced stocks of soil organic matter (SOM) following the fire. However, under a changing climate, stimulation in plant growth associated with CO_2 fertilization and higher mineralization rates might substantially promote the recovery of C stocks after fire.

So far, short-term responses of tundra ecosystems to warming and fire have been well-documented (Schuur et al. 2008, Mack et al. 2011, Sistla et al. 2013) and modeled (Jiang et al. 2015a), while the long-term recovery of tundra C and nutrient stocks from these disturbances is still largely unknown. Uncertainty also remains regarding the effect of future changes in external nutrient inputs (e.g., N deposition and fixation, and P weathering; Hobara et al. 2006, Dentener 2006, Galloway et al. 2004, 2008). Although effects of N and P additions have been examined in field studies, most studies either conducted a single treatment (Shaver and Chapin 1980, Wookey et al. 1995, Robinson et

al. 1998) or put extremely high factorial N and P additions (e.g., Henry et al. 1986, Shaver and Chapin 1995). The rates of these additions are unrealistic compared with any possible nutrient additions via environmentally relevant atmospheric fluxes. To constrain these uncertainties and investigate the underlying mechanisms that control long-term recovery of tundra ecosystems from disturbance, this study employed the Multiple Element Limitation (MEL) model (Rastetter et al. 2013, Pearce et al. 2015, Jiang et al. 2015a) to simulate long-term C and nutrient cycles along a burn severity gradient of the Anaktuvuk River fire scar with varied future climate scenarios. This study builds on our earlier study (Jiang et al. 2015a) in which we analyzed the first five years of recovery from the Anaktuvuk River fire. Our specific objective is to assess the impact of fire-climate interactions on tundra C and nutrient budgets with and without increases in external nutrient inputs over decades to centuries. The results are expected to have important ramifications for tundra fire management and assessments of global change.

MATERIALS AND METHODS
Study area
Our study was conducted at three representative sites (severe burn, moderate burn, and unburned) in the southern portion of the 2007 Anaktuvuk River fire scar on the North Slope of Alaska (Jones et al. 2009). Prior to the 2007 fire, fire had been absent from this landscape for at least 5000 years (Hu et al. 2010). Sites were selected by Rocha and Shaver (2011a, b), based on the two-band enhanced vegetation index (EVI2) (Rocha and Shaver 2009) and the normalized burn ratio (NBR) from the Moderate Resolution Imaging Spectroradiometer (MODIS) (Boelman et al. 2011). These three sites had similar weather and pre-fire surface greenness (i.e. EVI2) but substantially different plant mortality, residual organic matter, and species composition after fire. The average initial NBR in the first post-fire growing season was about -400 in the severely burned site, -200 in the moderately burned site, and 350 in the unburned site, while the average initial EVI2 is about 0.02, 0.06 and 0.27 respectively (Rocha and Shaver 2011a). Before the fire, all three sites were typical moist acidic tussock tundra, dominated by *Eriophorum vaginatum* tussocks, dwarf shrubs (e.g. *Betula nana* and *Ledum palustre*), and *Sphagnum* moss (Walker et al. 2005). The early recovery of surface vegetation in burned tundra mainly consists of regrowth by *Eriophorum* tussocks and herbaceous forbs (e.g., cloudberry; *Rubus chamaemorus* L.), with little moss regrowth.

The severely burned site (68.99^{o}N, 150.28^{o}W) consists of ~1 km^2 area where all of the surface green vegetation was consumed in the fire, and only ~5% of the area was covered by moss immediately following fire. The severely burned site had ~30% mortality of the dominant *Eriophorum vaginatum* tussocks, with ~10% mineral soil exposure due to combustion of the overlying surface organic mat. The moderately burned site (68.95^{o}N, 150.21^{o}W) consisted of a mosaic of completely and partially burned patches scattered across the landscape and varying in size from 1 to 100 m^2. The moderately burned site had ~5% tussock mortality and ~33% remaining moss coverage. The unburned site (68.93^{o}N, 150.27^{o}W) was a large undisturbed area (~10 km^2) dominated by moist acidic tussock tundra. In the unburned site, ~40% of the ground surface was covered by sphagnum and feather mosses, and the remaining was covered by a mixture of tussocks, cloudberry, Labrador tea, cranberry, and dwarf birch [*Betula nana* L.]. All three sites are underlain by permafrost, and the measured pre-fire soil organic

layer depth was 21.5±1.5 cm (Mack et al. 2011). The severely and moderately burned tundra on average lost ~8.7 cm and ~5.0 cm moss and soil organic matter layers, respectively, because of combustion. Details for the 2007-fire sites can be found in Rocha and Shaver (2011a).

Model description

To simulate C, N, and P cycles in the three study sites following fire, we use version IV of the Multiple Element Limitation (MEL) model, which is fully described in Rastetter et al. (2013) and has been applied to tundra by Pearce et al. (2015) and Jiang et al. (2015a). We provide only a brief description here. The model uses a mass-balance approach to simulate the fluxes of C, N, and P through vegetation to debris (standing dead leaves plus any woody litter) and Phase I and Phase II soil organic matter (SOM) (Melillo et al. 1989), and dissolved organic and inorganic pools. The N and P enter the ecosystem through deposition, mineral weathering of P, and biological N fixation and leave the system through leaching and secondary P-mineral formation. Drivers of the MEL model are: daily short wave radiation, maximum and minimum air temperature, precipitation, CO_2 concentration, external apatite input, and deposition of NH_4^+, NO_3^- and PO_4^{3-}.

The major difference between the MEL model and other ecosystem models is that resource acquisition by vegetation in the MEL model is adjusted dynamically by redistributing "uptake effort", which represents an aggregate of all plant assets (e.g. biomass, enzymes, carbohydrate) that can be allocated toward acquiring resources (Rastetter et al. 1997, 2013, Rastetter 2011). The rate at which uptake effort is redistributed among resources is calculated based on the ratio of requirement to current acquisition for each resource; this algorithm drives the vegetation toward a condition where the requirement to acquisition ratio is the same for all resources and, in this sense, toward a condition where all resources are equally limiting (Rastetter et al. 2013). Similarly, rates of N and P immobilization and C, N, and P retention efficiency by soil microbes were dynamically optimized in the model to maintain microbial stoichiometry (Rastetter et al. 2013).

Total vegetation biomass is allometrically partitioned into woody (non-uptake tissues) and active biomass (leaves and roots) using an equation in which the ratio of active to woody biomass decreases as total biomass increases; this equation, with a single parameterization, simultaneously fits the tissue distributions of all major vegetation types on the North Slope (see appendix to Pearce et al. 2015). The active biomass is further partitioned into leaves and roots in proportion to the allocation of uptake effort toward canopy resources (CO_2 and light) versus soil resources (N, P, and water). Following a disturbance (e.g., fire), the reallocation of uptake assets in combination with the changing vegetation allometry reflect both allometric changes in the components of the community as well as shifts in the plant community toward species with characteristics that are better adapted to the changing environmental conditions (Pearce et al. 2015, Jiang et al. 2015).

Leaves, roots, and wood all have prescribed optimal C:N:P ratios from which an optimal C:N:P ratio for the total biomass is calculated. The actual C:N:P ratio is maintained near this optimum through the redistribution of uptake effort among resources. The C:N:P ratios are prescribed for coarse woody debris and phase II SOM, but the C:N:P ratio of phase I SOM varies based on the inputs of litter and the

mineralization and immobilization of nutrients. Phase II SOM mineralizes C and nutrients but does not immobilize nutrients. In MEL, the effect of permafrost thaw on soil C, N, and P in permafrost layers was not explicitly modeled. Nevertheless, an active layer depth is used to calculate infiltration and runoff based on how much of the active layer is thawed not the permafrost. The active layer depth does not affect the internal soil C, N and P cycles.

The model code (MEL, version IV), parameterization, and forcing data used to reproduce the analysis were placed in http://arc-lter.ecosystems.mbl.edu/melarclimfire, doi:10.6073/pasta/3c28308d774de3b01a416bd4cb597067.

Pearce et al. (2015) modified the MEL model by 1) adding a simple calculation of soil temperature that accounts for changes in soil temperature patterns as the insulating organic mat thickens in the recovering soils, to replace the use of soil temperature as input; 2) including labile dissolved organic N (DON) as a source of N supply to plant growth (Schimel and Chapin 1996). They calibrated the MEL model to match annual C, N, P and water cycles on the North Slope of Alaska near Toolik Lake, Alaska, USA (68.63^{o}N, 149.72^{o}W), and then to examine the recovery of tussock tundra from thermal erosion events resulting in downslope displacement of the seasonally thawed surface soil and associated vegetation. Because the tussocks retained dead leaves for several years, we included standing dead litter in the debris pool, which did not decay directly but represented a short-term storage pool that was gradually converted to Phase I material where it began to decompose (Hyvönen and Ågren 2001, Pearce et al. 2015). Because most of the N fixation in these systems occurred via moss- or lichen-associated N-fixers (Hobara et al. 2006), we ignored potential contributions by symbiotic N-fixation associated with vascular plants such as alders (*Alnus* species), which were not abundant in the study area. We also ignore the denitrification process in the model because in arctic tundra the concentration of nitrate in soil is extremely low for two reasons: First, tundra plant growth is highly limited by N availability and the vegetation quickly and efficiently takes up the inorganic N generated from fixation, deposition, and mineralization (Chapin et al. 1980, Dowding et al. 1981, Kling 1995, Brooks and Williams 1999, Hobara et al. 2006); thus nitrate mobility is quite limited. Second, the waterlogged and anoxic conditions in tundra soil constrain the nitrification process (i.e. oxidation of ammonium to nitrate). The small amount of NO_3^- entering the ecosystem through deposition was either taken up by plants or soil microbes or was leached with the soil water. Leaching in MEL includes NH_4^+, NO_3^-, PO_4^{3-}, DOM and DON.

The calibration and spin-up procedures for the model are fully presented in Pearce et al. (2015) and Jiang et al. (2015a). To apply the model to the fire site, Jiang et al. (2015a) simply modified the canopy phenology parameters to fit the length of growing season at the Anaktuvuk River fire sites. These simulations by Jiang et al. (2015a) focused on the first five years following fire and were consistent with the data reported by Mack et al. (2011) and Bret-Harte et al. (2013). In this study we use the same routines and parameterization used by Jiang et al. (2015a) to conduct 200-year simulations in the same three study sites.

Simulation protocols

To assess long-term changes in C and nutrient cycles in burned and unburned tundra, we simulated changes in the biogeochemistry of the three sites in response to increases in

air temperature, CO_2, N deposition and P weathering for the next 200 years. As model inputs, the first year climate data were determined as the average of five years (2008-2012) daily field measurements. Specifically, the growing season radiation and air temperature at the three eddy flux towers were obtained from Rocha and Shaver (2011a) and the non-growing season radiation data were obtained from the ARC LTER experimental site at Toolik Lake (Shaver et al. 1989), about 50 km southeast of the burned sites. The non-growing season air temperature and precipitation were obtained from the Upper Kuparuk Meteorological Station (Kane and Hinzman 2013), which was approximately 48 km southeast of the Anaktuvuk River unburned site. The atmospheric CO_2 concentration was obtained from ice core and the National Oceanic and Atmospheric Administration (NOAA) measurements (Keeling and Whorf 2005).

To develop a future climate data set over the next 199 years, we linearly increased air temperature, CO_2 concentration, N deposition, and P weathering year by year, at rates described below. To cover most projected ranges of warming scenarios by current climate models (IPCC 2013), we increased air temperature so that in the last year of the simulations (year 200) temperature increased by 0, 4, 6, 9, and 12^oC relative to the first year of simulation. Similarly, we increased CO_2 each year so that in the last year CO_2 was 1, 2, 3, 4 and 5 times the value in 2008 (385.6 ppm). The 12^oC increase was used to cover the projected extreme warming condition in arctic tundra over the 21st century (e.g., under RCP8.5, IPCC 2013).

Only limited information is available on deposition of atmospheric N for the North Slope of Alaska. To cover a wide range of uncertainties in N deposition estimated from empirical data and global-scale overview (Jaffe and Zukowski 1993, Woodin 1997, Galloway et al. 2008, Linder et al. 2013) and test the influence of different N deposition rates, we linearly increased annual N deposition rate so that in the 200th year N input was 1, 2, 5, 10, and 20 times their values in 2008 (0.035 g N/m^2/yr); with P weathering rate (1.28×10^{-4} g P/m^2/yr in 2008) increased by the same proportions. However, even at these rates, external nutrient supply was very small relative to plant requirements. In 2008, the N deposition rate was less than 1% of the plant N uptake and the P weathering rate was less than 0.03% of the P uptake rate in the unburned tundra; therefore the plants depended almost exclusively on N and P recycled through the soil. We ran changes in nutrient supply in a factorial combination with 5 sets of N treatments and the 5 sets of P treatments separately, then a total of 5 simulations with both N and P increased by 1, 2, 5, 10, or 20 times their 2008 values. We also ran simulations with the concentrations of NH_4^+, PO_4^{3-}, and DON in the soil held constant at saturating concentrations (1000 times their respective concentrations in the unburned tundra) to show what the post-fire recovery potential was if nutrients were not limiting. In this study, we did not take into account the limitation from secondary nutrients such as calcium (Ca) and magnesium (Mg) because we assumed that they did not play a large role due to the order of magnitude lower C:Ca or C:Mg in arctic plants.

RESULTS
Post-fire recovery under constant climate
Under constant climate and external nutrient inputs, modeled vegetation biomass C accumulated rapidly after fire and exceeded unburned tundra by ~50% within a decade; it then gradually decreased to the level of unburned tundra within ~80 years (Figure 2).

Vegetation biomass N and P had similar recovery patterns but with a lower "overshoot" than C. By the end of the 200-year simulation, vegetation biomass N remained respectively ~2% and 9% lower in the severe and moderate burn than the pre-fire level, while vegetation biomass P almost completely recovered (Table 1). Debris stocks rebuilt and gradually leveled off after 100 years, but remained respectively 5% and 3% lower in the severe and moderate burn than the pre-fire level. The phase I SOM C, N, and P stocks had similar increasing trends (Figure 2) but all remained slightly lower than the pre-fire levels (Table 1). The phase II SOM C, N and P stocks declined throughout the 200 years after fire, and were ~5% lower in the severe burn, and ~3% lower in the moderate burn than the pre-fire levels. Overall, burned tundra gradually approached a quasi-steady state within 200 years following fire (Figure 2), but the total ecosystem C lost in fire combustion was not completely recovered under a constant environment (Table 1).

Recovery with increased external nutrients inputs

The effects of increases in N deposition and P weathering rates on NPP were less than 10 g C/m^2/yr (~5%) even at the highest simulated deposition or weathering rates (Figure 3). For comparison, when available N and P were held at saturating concentrations, both burned and unburned tundra had more than 620 g C /m^2/yr (~284%) higher NPP than the control value (218 g C/m^2/yr in the 1st year unburned tundra) after 200 years. In burned tundra, the net N mineralization and vegetation N uptake both had clear positive responses to the increase in N deposition and P weathering combined. However, in the unburned tundra, the N fluxes had stronger response to the increase in N deposition than P weathering rate. Under an environment with saturating plant available N and P, vegetation N uptake rates were ~19 g N/m^2/yr higher (~410%) than the control value (4.63 g N/m^2/yr), and N mineralization rates were ~17 g N/m^2/yr higher (~359%) than the control value (4.74 g N/m^2/yr), after 200 years. The responses of P uptake and net mineralization rates to the increase in N deposition and P weathering rates combined were both less than 0.04 g P/m^2/yr (~7%). With saturating N and P sources, vegetation P uptake rates were ~1.0 g P/m^2/yr higher (~185%) than the control value (0.54 g P/m^2/yr), and P mineralization rates were ~1.3 g P/m^2/yr higher (~241%) than the control value (0.54g P/m^2/yr), after 200 years.

Recovery with a warming climate

The C, N, and P fluxes also responded to increases in CO_2 concentration and air temperature, but the responses to temperature were much stronger (Figure 3). Increases in CO_2 concentration enhanced nutrient fluxes (i.e. N and P uptake and net mineralization) by about the same magnitude as those caused by the N and P addition treatments. For each 3°C warming, net nutrient mineralization from SOM increased on average by ~1.5 g N/m^2/yr (~32%) and by ~0.2 g P/m^2/yr (~37%) by the end of the 200-year simulation. Thus a 3°C warming resulted in a larger increase in nutrient supply to plants than even a 20-fold increase in N deposition or P weathering. Increases in nutrient availability from increased N and P mineralization raised the plant nutrient uptake by a similar magnitude, which further stimulated NPP (Figure 3). On average, each 3°C warming increased NPP by ~100 g C/m^2/yr (~45%), which was about an order of magnitude higher than the increases caused by the increases in CO_2 concentration, N deposition, or P weathering.

By the end of the 200-year simulation, differences in C, N, and P fluxes between burned and unburned tundra were small compared with the changes caused by warming.

Because warming had a much stronger effect on nutrient availability, uptake, NPP and vegetation biomass accumulation in these ecosystems than any manipulated increases in external nutrient inputs did, we limited our analysis of the responses of ecosystem C stocks to the factorial interactions between warming and elevated CO_2 (Figure 4). Both warming and elevated CO_2 increased vegetation biomass C stocks and fire-caused C loss in vegetation biomass recovered within decades. Stronger warming led to faster post-fire recovery of vegetation biomass C stock. As the vegetation biomass C recovered, the differences among sites associated with different burn severity became smaller. Compared with elevated CO_2, warming had a much stronger effect on tundra vegetation biomass accumulation. With ambient CO_2, a $3^{o}C$ warming increased vegetation biomass by 200 g C/m^2 by year 200 and a $12^{o}C$ warming increased it by 1400 g C/m^2. By contrast, even the highest level of elevated CO_2 by itself increased vegetation biomass by less than 100 g C/m^2. However warming and CO_2 interacted synergistically such that the highest CO_2 increased the response to a $12^{o}C$ warming by an additional 500 g C/m^2 (Figure 4). Warming resulted in a long-term reduction in SOM C stocks in unburned tundra, with stronger warming corresponding to greater loss. Elevated CO_2, through its stimulation of photosynthesis, exacerbated this warming-induced SOM C loss by increasing nutrient transfer to vegetation and thereby decreasing the C-storage potential in the soil (high C:nutrient ratios and lower microbial efficiency).

Despite the effects of warming and increased CO_2 on NPP and vegetation biomass, SOM C in the burned tundra did not recover to pre-burn levels within 200 years under any combination of warming and elevated CO_2 because the increase in litter fall was not sufficient to compensate the increase in soil respiration (Figure 4). However, because the net gain in vegetation biomass C was greater than the net loss in SOM C, both the burned and unburned tundra ecosystems accumulated C, especially under strong warming conditions (Figure 4). Only very strong warming can completely recover fire C losses within 200 years. The MEL simulations indicated that a $12^{o}C$ warming over 200 years was required to offset initial losses due to combustion of ~2300 g C/m^2 in the severe burn; the ~1900 g C/m^2 losses in the moderate burn were offset by the gains from a $9^{o}C$ or $12^{o}C$ warming.

In these scenarios, accelerated N cycling rates exposed N to higher leaching losses and the increases in vegetation biomass N were not sufficient to compensate for the decreases in SOM N stock, therefore leading to a net reduction in ecosystem N stock. In contrast, high P demand by vegetation was more than enough to retain P in the ecosystem, so gains in vegetation biomass P were higher than the P loss from soil, therefore resulting in a net increase in ecosystem P stocks.

Through the first 100 years of simulation, N and P stocks approached a stoichiometric balance with C, so that the vegetation biomass and SOM C:nutrient ratios approached a new steady state (Figure 5). Warming increased vegetation C:N because the stimulated productivity resulted in a larger vegetation biomass with a higher proportion of woody tissues and SOM C:N increased because of faster litter inputs with a higher C:N. The increased SOM C:N ratio also indicates a decrease in immobilization of phase I SOM pool. Warming also increased vegetation and SOM C:P, but the effect was less pronounced. Elevated CO_2 had only a small effect on C:N and C:P ratios relative to the

effects of warming. Overall, the residual differences in C:nutrient ratios after 200 years of recovery from fire were much smaller than those caused by climatic change (Figure 5).

DISCUSSION

Our simulations indicate that air temperature is the most important factor controlling long term recovery of C and nutrient cycles in arctic tundra following fire disturbance. Although climate warming increases soil respiration, MEL predicts that the greater increase in photosynthesis drives the arctic tundra ecosystem to become a strong C sink. Stronger warming leads to an even stronger C sink. MEL also indicates stronger stimulation of mineralization rates with warmer temperature. For example, increased warming from +3 ^{o}C to +6 ^{o}C increases the net N mineralization rate by only 33%, but warming from +6 ^{o}C to +12 ^{o}C will further increase the N mineralization by 87% (Figure 3). This pattern is consistent with the findings of Nadelhoffer et al. (1991), who found that N mineralization is less sensitive to temperature changes between 3 ^{o}C and 9 ^{o}C, but can double as the temperature increases from 9 ^{o}C to 15 ^{o}C. We acknowledge that the sensitivity of N mineralization to warming is influenced by the model parameterization, and the parameters ranges are relatively broad for biogeochemical models. Using the MEL model, Pearce et al. (2015) conducted a sensitivity analysis for a wide range of nutrient supply and initial soil properties. Response to these conditions was very broad and would likely swamp out variations in parameterizations consistent with the tight constraints imposed by the experimental manipulations to which the model was calibrated. After 100 years, recovery of vegetation biomass varied by over a factor of two across the range of these factors (Pearce et al. 2015). These differences in recovery associated with variability in soils and nutrient supply across the arctic landscape need to be factored into the interpretation of the results we present here.

The nutrient demand for plant growth is fulfilled mainly by soil organic nutrient stocks when the tundra ecosystem confronts climate warming and/or fire disturbance, not by external nutrient sources. Field fertilization experiments (e.g., Shaver and Chapin, 1980, 1995) emphasized the strong effect of nutrient fertilization on plant growth and the interaction between N and P. With our model, simulations of responses to similarly high fertilization rates produce similar stimulation of plant growth (Pearce et al. 2015). After fire, the almost unlimited nutrient condition has a strong fertilizing effect, which results in enhanced plant growth in the burned tundra. A great amount of the "fertilizing" nutrients during the early succession are from the burned soil organic matter. The enhanced plant growth is reflected by measurements from eddy flux tower (Rocha et al. 2011) and field harvest data (Bret-Harte et al. 2013). However, our simulations with much lower levels of fertilization show that combined N and P additions (i.e. increases in N deposition and P weathering) only slightly increase net N mineralization and N uptake, with minor effects on NPP, net P mineralization and P uptake. Our factorial additions of N and P, up to 20-fold increases in the current N deposition and P weathering rates, is very far from a nutrient saturation condition, and the plant growth remains strongly limited by N and P availability.

How do increases in air temperature, CO$_2$ concentration, N deposition and P weathering affect tundra C and nutrient cycles?

Based on our simulations, we predict that future changes in arctic tundra

biogeochemistry are likely to be strongly driven by changes in air temperature. Gains in ecosystem C will likely be maintained under long-term warming because (1) the rate of nutrient cycling increases, which results in a net transfer of nutrients from low C:nutrient ratio soil to high C:nutrient ratio vegetation, (2) the increase in vegetation biomass is predominantly in stem tissue with high C:nutrient ratios, and (3) both increased litter inputs rates and litter C:nutrient ratios increase soil C:nutrient ratios. The increase in vegetation biomass with warming is predicted to be greater than the loss of SOM from increased decomposition because the warming-caused increase in nutrient cycling has a stronger effect on productivity than the warming-caused increase in heterotrophic soil respiration. However, permafrost thaw might lead to a great amount of labile C in previously frozen soil layers in a warming climate (Schuur et al. 2008). C releases associated with permafrost thaw can compensate C gain due to warming-enhanced plant growth. Continued warming in the Arctic (Hinzman et al. 2005, IPCC 2013) should therefore increase C stocks of arctic ecosystems and accelerate the C recovery in fire-disturbed tundra (Figure 4). However, because the nutrient turnover is very slow, the large N loss through volatilization during the combustion of organic matter requires at least centuries to recover.

Elevated CO_2 is projected to further stimulate the acquisition of nutrients into vegetation biomass by increasing photosynthetic efficiency and allowing the vegetation to allocate more uptake effort below ground. This reallocation of uptake effort thereby accelerates nutrient transfer from soil to vegetation, and retains nutrients in the ecosystem that would otherwise be lost through leaching, denitrification, and secondary mineral formation (Rastetter et al. 2013). Compared with warming, elevated CO_2 concentration has a smaller effect on plant productivity (Figure 3) because of 1) nutrient limitation and 2) increase in litter C:nutrient ratio, which increases the nutrient immobilization in soil and slows net mineralization rates.

Compared with warming, the manipulated increases in N deposition and P weathering rates have only minor effects on the C cycle (Figure 3), mainly because, even at 20 times the current rates, their magnitudes are still much smaller than the ambient and warming-enhanced mineralization rates. This pattern indicates that the long-term change in the C cycle in arctic tundra depends strongly on the internal turnover of the N and P and on the distribution of total N and P between vegetation and soil. Moreover, the great differences between warming-induced changes in NPP and those with un-limited nutrient availability (Figure 3), indicates that the concentration of plant available nutrients is nowhere near its potential to fully remove the limitation on tundra plant productivity, even under strong warming climates.

As C and nutrient stocks approach a new steady state (Figure 4), the stabilized vegetation biomass and SOM C:nutrient ratios (Figure 5) imply a new equilibrium state for the tundra ecosystem, in which the vegetation is more woody and therefore has higher C:nutrient ratios than the current tundra. This new steady state arises because warming accelerates the release of nutrients from soils and stimulates plant growth. As vegetation biomass increases and the canopy closes, a higher fraction of the vegetation biomass is allocated to wood; the allometric equation in the model imposes this increase in wood allocation as the vegetation biomass increases. The predicted increase in woody biomass is consistent with both warming experiments (Shaver and Jonasson 1999, Walker et al. 2006, Hudson and Henry 2010, Elmendorf et al. 2012) and remotely sensed observations

(Tape et al. 2006), which indicate that a shift to a more shrubby tundra might already be occurring. Because increased woody abundance might also promote flammability, the new steady state is predicted to represent a more fire-prone system (Hu et al. 2010). Meanwhile, the increased C:nutrient ratio of SOM under warming climate indicates that the plant-available nutrients might become more strongly retained by microbes, thereby constraining further increases in vegetation biomass.

We did not assess changes in precipitation in our simulations. However, high soil moisture is thought to constrain decomposition and nutrient mineralization (Nadelhoffer et al. 1992, Oberbauer et al. 2007, Arndal et al. 2009, Dagg and Lafleur 2011, Jensen et al. 2014, Kim et al. 2014). Thus, if precipitation does not increase enough to compensate for elevated evapotranspiration associated with warming and more leaf area, then the drier soil will further accelerate nutrient cycling and associated increases in production and vegetation biomass. If precipitation does increase enough to result in wetter soils it would constrain increases in nutrient cycling.

What is the possible species change and its consequences?

As discussed in Bret-Harte et al. (2013), the low nutrient availability will help retain the pre-fire vegetation composition (i.e. mixed shrub–sedge tussock tundra) and constrain the shift to another trajectory of post-fire succession (e.g., large deciduous shrubs), as long as there is no substantial nutrient release from permafrost thaw. However, under the current soil warming trend, permafrost thaw is likely over wide regions of tundra and previously frozen organic matter can function as new nutrient source (Jiang et al. 2012, 2015b, Liu et al. 2014, Jones et al. 2015). Deepening active layer can lead to high nutrient availability, and drive the vegetation dominance from graminoids to deciduous shrubs (Schuur et al. 2007). Fires may promote this shift, which has been observed in burned sites 2-3 decades after fire (Landhausser and Wein 1993, Racine et al. 2004). Although our model did not explicitly simulate species change, the model does impose allometric changes in vegetation as biomass increases reflecting a shift toward dominance by shrubs as indicated in previous studies (Myers-Smith et al. 2011, Tape et al. 2006, Swanson et al. 2013). However, the expansion of tall shrubs may shade out lichens and other N_2-fixing associations (Joly et al. 2009), which are important to the N budget in this nutrient-poor environment (Hobara et al. 2006, Stewart et al. 2011). Consequently, these relative changes among different species may increase the C uptake, but decrease the N fixation by arctic tundra. As this change continues, the arctic tundra might lose N but gain C in the long-term.

The early vegetation recovery after the Anaktuvuk River fire is consistent with those observed in other burned arctic tundra sites with similar pre-fire surface cover (Bret-Harte et al. 2013). Therefore, continuous monitoring on the Anaktuvuk River fire sites provide a unique chance to identify the influence of potential climate warming on long-term successional trajectory of tundra communities following fire.

What will be the impact of a future warming-intensified fire regime?

Based on our simulations, fire-induced nutrient losses are long-lived because external nutrient inputs (i.e. N deposition and P weathering) are insufficient to both replace the nutrient losses in combustion and compensate for continuing nutrient losses by leaching within the 200-year time frame of our simulations. Even with a 20-fold increase in N and

P inputs, burned tundra still cannot completely recover to its initial nutrient stocks within 200 years. Because the C:nutrient ratios in vegetation and SOM have a constrained maximum, the reduced total nutrient pools is predicted to limit the total ecosystem C stock. The effects of fire-induced nutrient losses on C stocks may be offset by an increase in nutrient turnover induced by a 9-12°C warming over 200 years. However, even though wildfires are still rare in arctic tundra (Higuera et al. 2008, Rocha et al. 2012), the occasional large fire may cause large C and nutrient losses that require a long time to recover. As air temperature increases, the frequency and burned area of fires are predicted to increase (Hu et al. 2010), and the C loss from a warming-intensified fire regime might therefore be too large to be compensated by a long-time C gain associated with warming.

CONCLUSION

Internal redistribution of N and P within the ecosystem plays a major role in regulating nutrient cycles when tundra ecosystems confront climate change and fire disturbance. Our simulations indicate that the long-term recovery of C balance and organic matter stocks in burned tundra are likely to be primarily driven by the warming climate and the resultant acceleration in the N and P cycles, rather than by N deposition or P weathering. Increased air temperature and CO_2 concentration accelerate the nutrient transfer from SOM to vegetation and changes toward vegetation with higher C:nutrient ratios lead to larger vegetation biomass C stocks. Nutrients lost in wildfire are difficult to recover even under substantial increases in N and P input rates because current input rates are very low and the warming causes further net nutrient loss from the system through leaching. Consequently, the recovery of SOM C is delayed and the recovery of total ecosystem C depends mainly on the redistributions of nutrients from soil (low C:nutrient) to vegetation (high C:nutrient) and therefore large increases in the vegetation biomass C pool with smaller losses of soil C.

Under the predicted changing climate in the Arctic, both burned and unburned tundra cycle nutrients faster, resulting in the redistribution of nutrients from soils to vegetation. Eventually the higher soil C:nutrient ratios limit further acceleration of nutrient cycles and increases in C stocks because plant-available nutrients may be more strongly retained by the microbes in the soil. The new equilibrium represents tundra less resilient to future fire disturbances, because 1) there is less nutrients in the system; 2) more nutrients are stored in vegetation, which is subject to combustion in wildfires; and 3) more woody vegetation can be more susceptible to fire. Our study provides insight on the underlying mechanisms that control the resilience of tundra C and nutrient stocks to changing climate and climate-related disturbances such as wildfire.

References

Arndal, M. F., L. Illeris, A. Michelsen, K. Albert, M. P. Tamstorf, and B. U. Hansen. 2009. Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. Arctic, Antarctic, and Alpine Research 41:164-173.

Boelman, N. T., L. Gough, J. R. McLaren, and H. Greaves. 2011. Does NDVI reflect variation in the structural attributes associated with increasing shrub dominance in arctic tundra? Environmental Research Letter 6:035501.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. Bond, J. Carlson, M. Cochrane, C. D'Antonia, R. DeFries, J. Doyle, S. Harrison, F. Johnston, J. Keeley, M. Krawchuk, C. Kull, J. Marston, M. Moritz, I. Prentice, C. Ross, A. Scott, T. Swetnam, G. vader Werf, and S. Pyne. 2009. Fire in the earth system. Science 324:481–484.

Bret-Harte, M. S., M. C. Mack, G. R. Shaver, D. C. Huebner, M. Johnston, C. Mojica, C. Pizano, and J. A. Reiskind. 2013. The response of Arctic vegetation and soils following an unusually severe tundra fire. Philos. Trans. R. Soc. B 368:20120490.

Brooks, P. D., and M. W. Williams. 1999. Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. Hydrol. Process. 13:2177–2190.

Chapin, F. S. III, P. C. Miller, W. D. Billings, and P. I. Coyne. 1980. Carbon and nutrient budgets and their control in coastal tundra. In: Brown, J., Miller, P.C., Tieszen, L.L., and Bunnel, F.L. (eds.), An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska. US/IBP Synthesis Series 12:458–482. Stroudsburg, PA: Dowden, Hutchinson and Ross.

Dagg, J., and P. Lafleur. 2011. Vegetation community, foliar nitrogen, and temperature effects on tundra CO_2 exchange across a soil moisture gradient. Arctic, Antarctic, and Alpine Research 43(2):189-197.

Dentener, F., J. Drevet, and J. F. Lamarque et al. 2006. Nitrogen and sulfur deposition on regional and global scales: A multimodel evaluation. Global Biogeochemical Cycles 20:GB4003.

Dowding, P., F. S. Chapin III, F. E. Wielgolaski, and P. Kilfeather. 1981. Nutrients in tundra ecosystems. 647-684 in Bliss, L.C., O.W. Heal, and J.J. Moore, editors. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge, England.

Elmendorf, S. C., G. H. R. Henry, and R. D. Hollister et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecology Letters 15:164–175.

Galloway, J. N., F. J. Dentener, and D. G Capone et al. 2004. Nitrogen cycles: past, present and future. Biogeochemistry 70:153–226.

Galloway, J. N., A. R. Townsend, J. W. Erisman, M. Bekunda, Z. Cai, and J. R. Freney et al. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. Science 320:889–892.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proceedings of the National Academy of Sciences of the United States of America 102:13521–13525.

Henry, G. H. R., B. Freedman, and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Can. J. Bot. 64:2502–2507.

Hobbie, S. E. 1996. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. Ecological Monographs 66(4):503–522.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, T. A. Brown, A. T. Kennedy, and F. S. Hu. 2008. Frequent fires in ancient shrub tundra: implications of paleorecords for arctic environmental change. PloS ONE 3:e0001744.

Hinzman, L. D., N. D. Bettez, and W. R. Bolton et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. Climatic Change 72:251–298.

Hobara, S., C. McCalley, K. Koba, A. E. Giblin, M. S. Weiss, G. M. Gettel, and G. R. Shaver. 2006. Nitrogen fixation in an arctic tundra watershed: a key atmospheric N source. Arctic, Antarctic, and Alpine Research 38:363-372.

Hobbie, S. E. 1996. Temperature and Plant Species Control Over Litter Decomposition in Alaskan Tundra. Ecological Monographs 66:503–522.

Hu, F. S., P. E. Higuera, J. E. Walsh, W. L. Chapman, P. A. Duffy, L. B. Brubaker, and M. L. Chipman. 2010. Tundra burning in Alaska: linkages to climatic change and sea ice retreat. Journal of Geophysical Research 115:G004002.

Hu, F. S., P. E. Higuera, P. Duffy, M. L. Chipman, A. V. Rocha, A. M. Young, R. Kelly, and M. C. Dietze. 2015. Tundra fires in the Arctic: Natural Variability and Responses to Climate Change. Frontiers in Ecology and the Environment 13(7):369-377.

Hudson, J. M. G., and G. H. R. Henry. 2009. Increased plant biomass in a high Arctic heath community from 1981 to 2008. Ecology 90:2657–2663.

Hudson, J. M. G., and G. H. R. Henry. 2010. High Arctic plant community resists 15 years of experimental warming. J. Ecol. 98:1035–1041.

Hyvönen, R., and G. I. Ågren. 2001. Decomposer invasion rate, decomposer growth rate, and substrate chemical quality: how they influence soil organic matter turnover. Canadian Journal of Forest Research 31:1594–1601.

IPCC. 2013. Climate Change 2013. The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. WMO/UNEP, Cambridge University Press.

Jaffe, D. A., and M. D. Zukowski. 1993. Nitrate Deposition to the Alaskan Snowpack. Atmospheric Environment. Part A. General Topics, 27(17-18):2935-2941.

Jensen, A. E., K. A. Lohse, B. T. Crosby, and C. I. Mora. 2014. Variations in soil carbon dioxide efflux across a thaw slump chronosequence in northwestern Alaska. Environ. Res. Lett. 9:025001.

Jiang, Y., Q. Zhuang, S. Schaphoff, S. Sitch, A. Sokolov, D. Kicklighter, and J. Melillo. 2012. Uncertainty analysis of vegetation distribution in the northern high latitudes during the 21st century with a dynamic vegetation model. Ecology and Evolution 2:593–614.

Jiang, Y., E. B. Rastetter, A. V. Rocha, A. R. Pearce, B. L. Kwiatkowski, and G. R. Shaver. 2015a. Modeling Carbon-Nutrient interactions during the early recovery of tundra after fire. Ecological Applications 25(6):1640-1652.

Jiang, Y., A. V. Rocha, J. A. O'Donnell, J. A. Drysdale, E. B. Rastetter, G. R. Shaver, and Q. Zhuang. 2015b. Contrasting soil thermal responses to fire in Alaskan tundra and boreal forest. Journal of Geophysical Research: Earth Surface 120(2):363-378.

Joly, K., R. R. Jandt, and D. R. Klein. 2009. Decrease of Lichens in Arctic Ecosystems: The Role of Wildfire, Caribou, Reindeer, Competition and Climate in North-Western

Alaska. Polar Research 28(3):433-442.

Jones, B. M., C. A. Kolden, R. Jandt, J. T. Abatzoglou, F. Urban, and C. D. Arp. 2009. Fire behavior, weather, and burn severity of the 2007 Anaktuvuk River Tundra Fire, North Slope, Alaska. Arct Antarct Alp Res. 41:309–316.

Jones, B. M., G. Grosse, C. D. Arp, E. Miller, L. Liu, D. J. Hayes, and C. F. Larsen. 2015. Recent Arctic tundra fire initiates widespread thermokarst development. Nature Scientific Reports 5: 15865.

Kane, D. L., and L. D. Hinzman. 2013. Climate data from the North Slope Hydrology Research project. University of Alaska, Fairbanks, Water and Environmental Research Center, Fairbanks, Alaska, USA.

Keeling, C. D., and T. P. Whorf. 2005. Atmospheric carbon dioxide record from Mauna Loa, in Trends: A Compendium of Data on Global Change. Carbon Dioxide Information Analysis Center, pp. 1–6, Oak Ridge Natl. Lab., Oak Ridge, Tenn.

Kim, Y., K. Nishina, N. Chae, S. J. Park, Y. J. Yoon, and B. Y. Lee. 2014. Constraint of soil moisture on CO_2 efflux from tundra lichen, moss, and tussock in Council, Alaska, using a hierarchical Bayesian model. Biogeosciences 11(19):5567-5579.

Kling, G. W. 1995. Land-water interactions: the influence of terrestrial diversity on aquatic ecosystems. In Chapin, T. and Korner, C. (eds.), Arctic and Alpine Biodiversity. Berlin: Springer-Verlag, 296-308.

Landhausser, S. M., and R. W. Wein. 1993. Postfire vegetation recovery and treeline establishment at the Arctic treeline: climate-change–vegetation-response hypotheses. J. Ecol. 81:665–672.

Linder, G., W. Brumbaugh, P. Neitlich, and E. Little. 2013. Atmospheric deposition and critical loads for nitrogen and metals in Arctic Alaska: review and current status. Open J Air Poll 2(4):76–99.

Liu, L., E. E. Jafarov, K. M. Schaefer, B. M. Jones, H. A. Zebker, C. A. Williams, J. Rogan, and T. Zhang. 2014. InSAR detects increase in surface subsidence caused by an Arctic tundra fire. Geophysical Research Letters 3906-3913.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin III. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431:440-443.

Mack, M. C., M. S. Bret-Harte, T. N. Hollingsworth, R. R. Jandt, E. A. G. Schuur, G. R. Shaver, and D. L. Verbyla. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. Nature 475:489–492.

McKane, R. B., E. B. Rastetter, G. R. Shaver, K. J. Nadelhoffer, A. E. Giblin, J. A. Laundre, F. S. Chapin III. 1997. Reconstruction and analysis of historical changes in carbon storage in arctic tundra. Ecology 78:1188–1198.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant and Soil 115:189-198.

Myers-Smith, I. H., B. C. Forbes, M. Wilmking et al. 2011. Shrub Expansion in Tundra Ecosystems: Dynamics, Impacts and Research Priorities. Environmental Research Letters 6(4):045509.

Nadelhoffer, K. J., A. E. Giblin, G. R. Shaver, and J. A. Laundre. 1991. Effects of temperature and organic matter quality on C, N, and P mineralization in soils from six arctic ecosystems. Ecology 72:242-253.

Nadelhoffer, K. J., A. Giblin, G. R. Shaver, and A. Linkins. 1992. Microbial processes and plant nutrient availability in arctic soils. In Chapin, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., Svoboda, J., and Chu, E. W. (eds.), Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective. San Diego: Academic Press, 281-300.

Oberbauer, S. F., C. E. Tweedie, J. M. Welker, J. T. Fahnestock, G. H. R. Henry, P. J. Webber, R. D. Hillister, M. D. Waler, A. Kuchy, E. Elmore, and G. Starr. 2007. Tundra CO_2 fluxes in response to experimental warming across latitudinal and moisture gradients. Ecol. Monogr. 72:221–238.

Pearce, A. R., E. B. Rastetter, B. L. Kwiatkowski, W. B. Bowden, M. C. Mack, Y. Jiang. 2015. Recovery of arctic tundra from thermal erosion disturbance is constrained by nutrient accumulation: a modeling analysis. Ecological Applications 25:1271–1289.

Racine, C., R. Jandt, C. Meyers, and J. Dennis. 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, USA. Arctic, Antarctic and Alpine Research 36:1–10.

Rastetter, E. B., R. D. Yanai, R. Q. Thomas, M. A. Vadeboncoeur, T. J. Fahey, M. C. Fisk, B. L. Kwiatkowski, and S. P. Hamburg. 2013. Recovery from Disturbance Requires Resynchronization of Ecosystem Nutrient Cycles. Ecological Applications 23:621-642.

Rastetter, E. B. 2011. Modeling coupled biogeochemical cycles. Frontiers in Ecology and the Environment 9:68–73.

Rastetter, E. B., G. I. Ågren, and G. R. Shaver. 1997. Responses of N-limited ecosystems to increased CO_2: A balanced-nutrition, coupled-element-cycles model. Ecological Applications 7:444-460.

Robinson, C. H., P. A. Wookey, J. A. Lee, T. V. Callaghan, and M. C. Press. 1998. Plant community responses to simulated environmental change at a high arctic polar semi-desert. Ecology 79:856–866.

Rocha, A. V., and G. R. Shaver. 2009. Advantages of a two band EVI calculated from solar and photosynthetically active radiation fluxes. Agricultural and Forest Meteorology 149:1560–1563.

Rocha, A. V., and G. R. Shaver. 2011a. Burn severity influences post-fire CO_2 exchange in arctic tundra. Ecological Applications. 21(2):477-489.

Rocha, A. V., and G. R. Shaver. 2011b. Post-fire energy exchange in arctic tundra: the importance and climatic implications of burn severity. Global Change Biology 17(9):2831-2841.

Rocha, A. V., M. M. Loranty, P. E. Higuera, M. C. Mack, F. Hu, B. M. Jones, A. L. Breen, E. B. Rastetter, S. J. Goetz, and G. R. Shaver. 2012. The footprint of Alaskan tundra fires during the past half-century: implications for surface properties and radiative forcing. Environmental Research Letters 7:044039.

Schimel, J. P., and F. S. Chapin III. 1996. Tundra plant uptake of amino acid nitrogen in situ: plants compete well for amino acid N relative to NH_4^+. Ecology 77:2142-2147.

Schuur, E. A. G. et al. 2008. Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. Bioscience 58:701–714.

Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack. 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems 10:280–292.

Shaver, G. R., W. D. Billings, and F. S. Chapin III. et al. 1992. Global change and the carbon balance of arctic ecosystems. Bioscience 61:415–435.

Shaver, G. R., and F. S. Chapin III. 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. Arctic and Alpine Research 18:261-268.

Shaver, G. R., and F. S. Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61(3):662-675.

Shaver, G. R., and F. S. Chapin III. 1995. Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. Ecography 18:259-275.

Shaver, G., T. Chapin, J. Laundre, M. S. Bret-Harte, and M. Mack. 1989. Above ground biomass in mesic acidic tussock tundra experimental site from 1982 to 2000 Arctic LTER, Toolik, Alaska. Arctic LTER, Marine Biological Lab, Woods Hole, Massachusetts, USA.

Shaver, G. R., and S. Jonasson. 1999. Response of arctic ecosystems to climate change: Results of long-term field experiments in Sweden and Alaska. Polar Biology 18:245-252.

Sistla, S. A., J. C. Moore, R. T. Simpson, L. Gough, G. R. Shaver, and J. P. Schimel. 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497:615-618.

Stewart, K. J., D. Coxson, and P. Grogan. 2011. Nitrogen inputs by associative cyanobacteria across a low Arctic tundra landscape. Arctic, Antarctic, and Alpine Research 43:267–278.

Sturm, M., C. Racine, and K. Tape. 2001. Climate change-increasing shrub abundance in the Arctic. Nature 411:546-547.

Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, S. Houston, C. Racine, M. Sturm, K. Tape, L. Hinzman, K. Yoshikawa, C. Tweedie, B. Noyle, C. Silapaswan, D. Douglas, B. Griffith, G. Jia, H. Epstein, D. Walker, S. Daeschner, A. Petersen, L. M. Zhou, and R. Myneni. 2004. Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. Remote Sensing of Environment 89:281–308.

Swanson, D. K. 2013. Three Decades of Landscape Change in Alaska's Arctic National Parks: Analysis of Aerial Photographs, C. 1980-2010," In: N. P. Service, Ed., Fort Collins.

Tape, K., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob. Change Biol. 12:686–702.

Verbyla, D. 2008. The greening and browning of Alaska based on 1982–2003 satellite data. Global Ecol. Biogeogr. 17:547–555.

Walker, M. D., C. H. Wahren, and R. D. Hollister et al. 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103:1342–1346.

Walker, D. A., M. K. Raynolds, F. J. A. Daniëls, E. Einarsson, A. Elvebakk, W. A. Gould, A. E. Katenin, S. S. Kholod, C. J. Markon, E. S. Melnikov, N. G. Moskalenko, S. S. Talbot, B. A. Yurtsev, and CAVM Team. 2005. The Circumpolar Arctic Vegetation Map. Journal of Vegetation Science 16(3):267-282.

Woodin, S. J. 1997. Effects of Acid Deposition on Arctic Vegetation. In: S. J. Woodin and M. Mick, Eds., Ecology of Arctic Environments, Blackwell Science, Oxford, pp. 21-

240.

Wookey, P. A., C. H. Robinson, A. N. Parsons, J. M. Welker, M. C. Press, T. V. Callaghan, and J. A. Lee. 1995. Environmental constraints on the growth, photosynthesis and reproductive development of Dryas octopetala at a high Arctic polar semi-desert, Svalbard. Oecologia 102(4):478-489.

Table 1: The MEL modeled recoveries (percentage of the prefire amount) of carbon, nitrogen and phosphorus stocks after 200 years following fire under constant climate and external nutrient inputs.

|	Severe burn	Moderate burn
Carbon (g C/m^2)		
Vegetation	100.8	100.2
Debris	95.0	96.5
Phase I SOM	94.8	96.3
Phase II SOM	95.2	96.7
Total ecosystem	95.3	96.7
Nitrogen (g N/m^2)		
Vegetation	97.5	91.4
Debris	95.0	96.5
Phase I SOM	94.4	95.2
Phase II SOM	95.2	96.7
Total ecosystem	95.1	96.4
Phosphorus (g P/m^2)		
Vegetation	99.6	99.9
Debris	95.0	96.5
Phase I SOM	94.8	96.6
Phase II SOM	95.2	96.7
Total ecosystem	95.2	96.7

Note: SOM = soil organic matter.
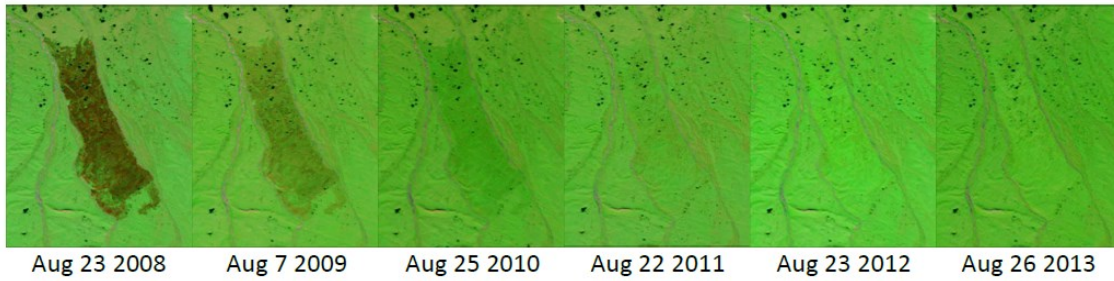
Figure 1: MODIS summer 7-2-1 image for the 2007 Anaktuvuk River fire region from 2008 to 2013. All images are Rapid Response imagery from the Land Atmosphere Near-real time Capability for EOS (LANCE) system operated by the NASA/GSFC/Earth Science Data and Information System (ESDIS) with funding provided by NASA/HQ.
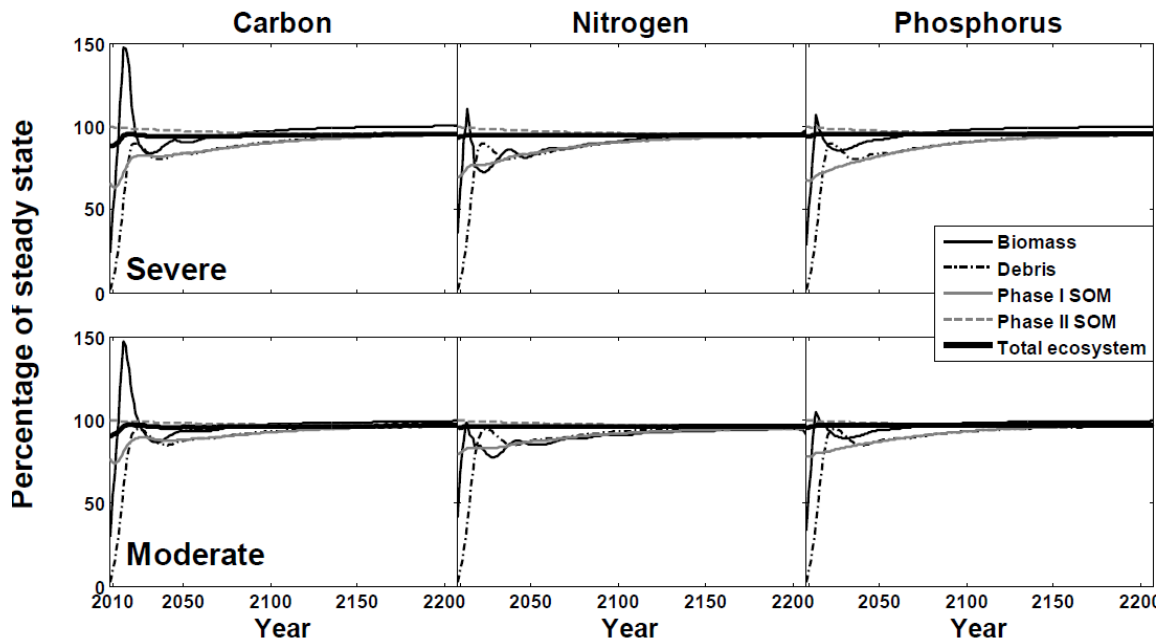
Figure 2: Simulated C, N, and P stocks of biomass, soil organic matter and the entire ecosystem in the severely (top three panels) and moderately (bottom three panels) burned tundra for 200 years following the disturbance under constant climate and external nutrient inputs. Steady-state values are referred to the initial control levels (in this case, values in the year 2008). The values in the end year of simulation are presented in Table S1.
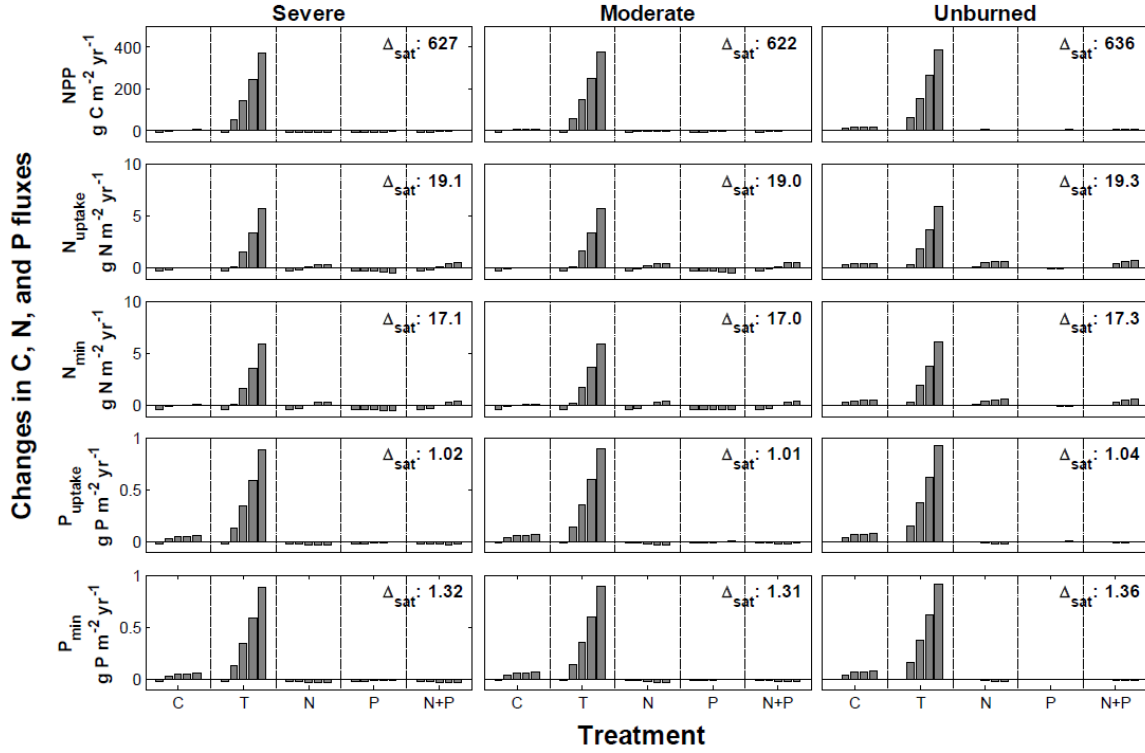
Figure 3: The 200-year changes (Year$_{200}$ – Year$_{1, \text{ unburned}}$) of NPP, N$_{\text{uptake}}$ (nitrogen uptake by plant), N$_{\text{min}}$ (net nitrogen mineralization), P$_{\text{uptake}}$ (phosphorus uptake by plant) and P$_{\text{min}}$ (net phosphorus mineralization) in the severely, moderately burned sites and the unburned site under different conditions. "C" represents five CO_2 treatments (ambient, double, triple, four times, and five times); "T" represents five air temperature treatments (ambient, 3°C, 6°C, 9°C, and 12°C increase); "N" represents five nitrogen deposition rates (ambient, double, five times, 10 times, and 20 times); "P" represents five phosphorus weathering rates (ambient, double, five times, 10 times and 20 times); "N+P" represents combinations of N and P treatment (ambient, double, five times, 10 times and 20 times of each component). The control value in prefire is 218 g C/m^2/yr for NPP, 4.63 g N/m^2/yr for N$_{\text{uptake}}$, 4.74 g N/m^2/yr for N$_{\text{min}}$, 0.54 g P/m^2/yr for P$_{\text{uptake}}$, and 0.54 g P/m^2/yr for P$_{\text{min}}$. Δ_{sat} represents the change relative to the control under a nutrient-saturated environment where ammonium, nitrate, DON and phosphate concentrations exceed plant and microbial demands for N and P.
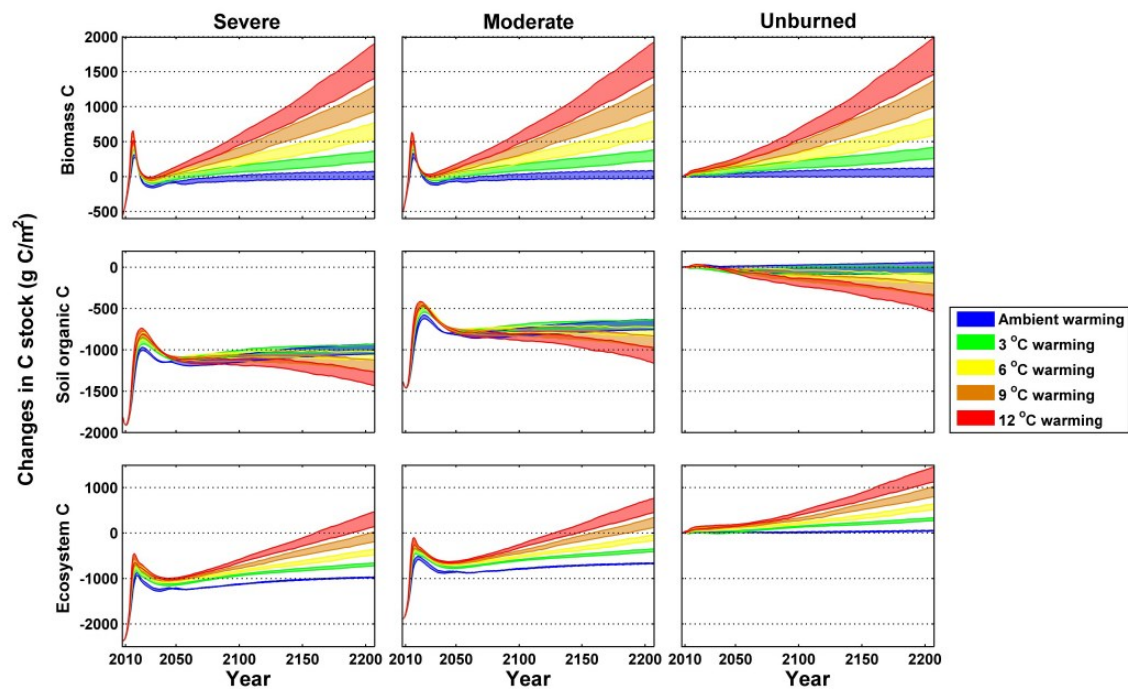
Figure 4: The modeled 200-year changes in C stock of biomass, soil organic matter and the total ecosystem at the severely and moderately burned sites and the unburned site, relative to the pre-fire steady state. The five different colors represent multiple warming scenarios and the shaded area represents the ranges caused by varied atmospheric CO_2 concentrations.
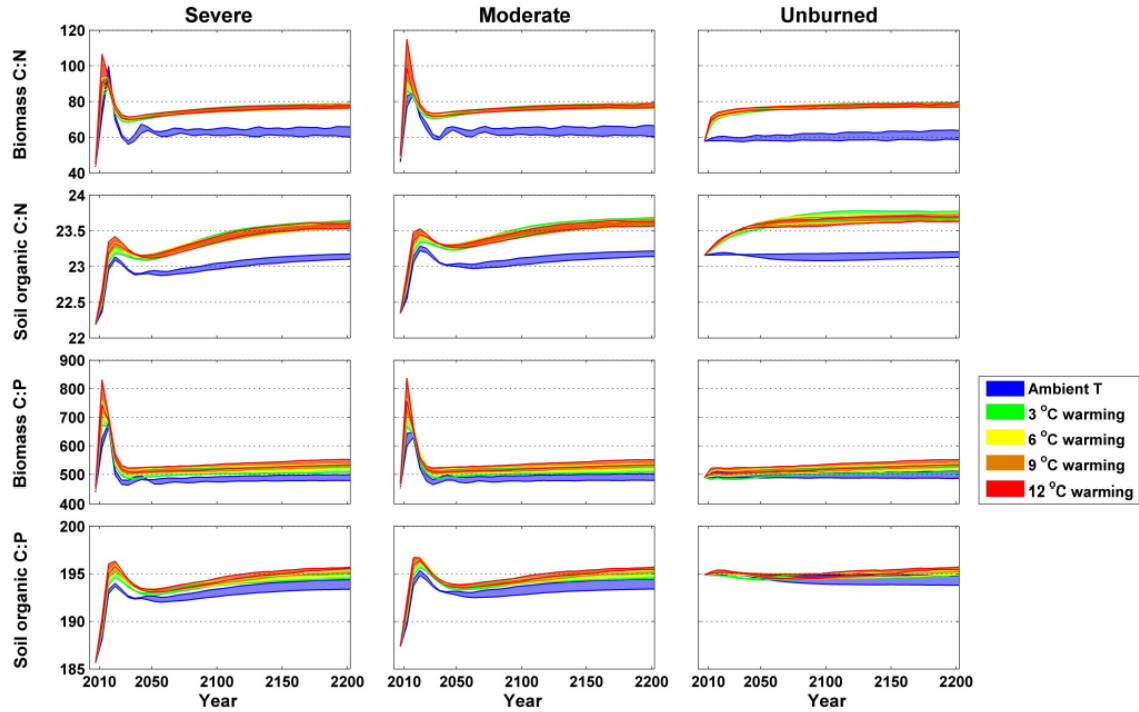
Figure 5: Changes in biomass C:N, soil organic C:N, biomass C:P, and soil organic C:P ratio through the 200-year simulation following fire. The five different colors represent multiple warming scenarios and the shaded area represents the ranges caused by varied atmospheric CO_2 concentrations.