

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-yr post-fire changes in the biogeochemistry of three sites along a burn severity gradient in response to increases in air temperature, CO₂ 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 CO₂ 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.

Key words: climate warming; CO₂ fertilization; fire resilience; nitrogen deposition; nutrient limitation.

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., NH₄⁺, PO₄³⁻) 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 km² of moist acidic tussock tundra on the North Slope of Alaska (Bowman et al.

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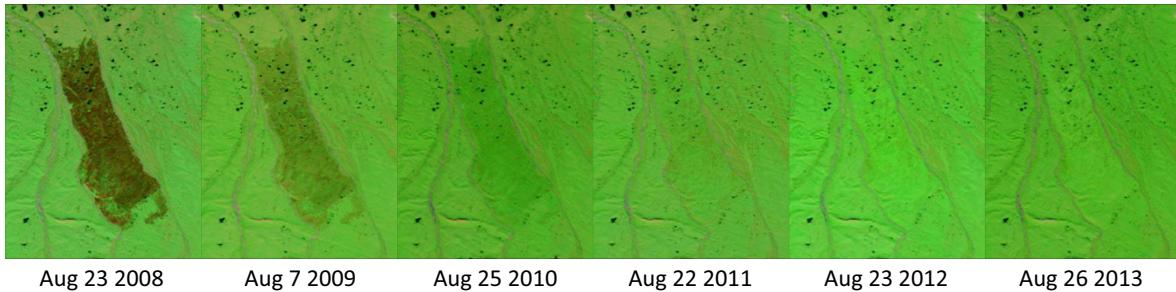


FIG. 1. MODIS summer Band 7-2-1 image for the 2007 Anaktuvuk River fire region from 2008 to 2013. All images are Rapid Response imagery from the Land Atmosphere Near-real time Capability for EOS (LANCE) system operated by the NASA/GSFC/Earth Science Data and Information System (ESDIS) with funding provided by NASA/HQ.

2009, Jones 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 3 yr and was higher than the nearby unburned area thereafter (Fig. 1; Rocha et al. 2012, Hu et al. 2015; *data available online*).⁶ 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 CO₂ 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 CO₂ 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; Galloway et al. 2004, 2008, Dentener et al. 2006, Hobara et al. 2006). 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, Jiang et al. 2015a, Pearce et al. 2015) 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 5 yr 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 5,000 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

⁶ https://lance.modaps.eosdis.nasa.gov/subsets/?subset=Arctic_LTER

regrowth by *Eriophorum* tussocks and herbaceous forbs (e.g., cloudberry; *Rubus chamaemorus* L.), with little moss regrowth.

The severely burned site (68.99°N, 150.28°W) consists of ~1 km² 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°N, 150.21°W) consisted of a mosaic of completely and partially burned patches scattered across the landscape and varying in size from 1 to 100 m². The moderately burned site had ~5% tussock mortality and ~33% remaining moss coverage. The unburned site (68.93°N, 150.27°W) was a large undisturbed area (~10 km²) 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, CO₂ concentration, external apatite input, and deposition of NH₄⁺, NO₃⁻, and PO₄³⁻.

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 (nonuptake 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 (CO₂ and light) vs. 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 (Jiang et al. 2015a, b, Pearce 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 the Arctic Long Term Ecological Research permanent archive (*available online*).⁷

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°N, 149.72°W) and then to

⁷ <http://arc-lter.ecosystems.mbl.edu/melarcimfire>

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 5 yr following fire and were consistent with the data reported by Mack et al. (2011) and Bret-Harte et al. (2013). We use the same routines and parameterization used by Jiang et al. (2015a) to conduct 200-yr 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 yr. As model inputs, the first year climate data were determined as the average of 5-yr (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 nongrowing 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 nongrowing 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. 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°C 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°C 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 the value in 2008 ($0.035 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), with P weathering rate ($1.28 \times 10^{-4} \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ 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 five sets of N treatments and the five sets of P treatments separately, then a total of five 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 (1,000 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

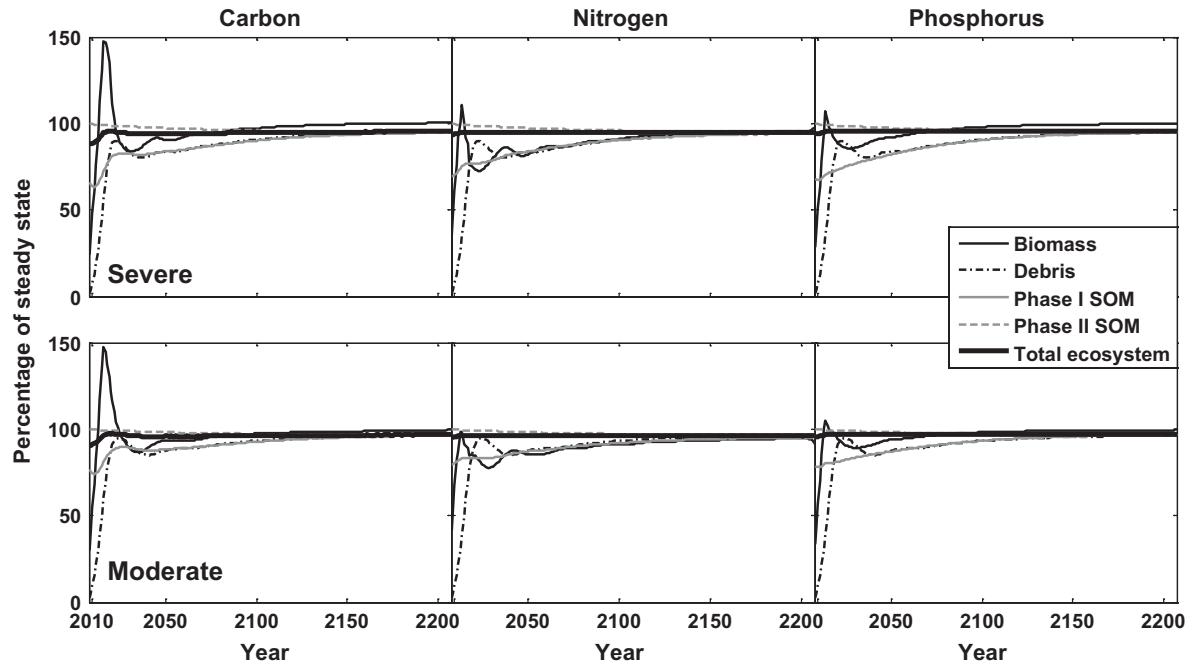


FIG. 2. Simulated C, N, and P stocks of biomass, soil organic matter, and the entire ecosystem in the severely (top three panels) and moderately (bottom three panels) burned tundra for 200 yr following the disturbance under constant climate and external nutrient inputs. Steady-state values are referred 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 1.

unburned tundra within ~ 80 yr (Fig. 2). Vegetation biomass N and P had similar recovery patterns but with a lower overshoot than C. By the end of the 200-yr simulation, vegetation biomass N remained $\sim 2\%$ and 9% lower in the severe and moderate burn, respectively, than the pre-fire level, while vegetation biomass P almost completely recovered (Table 1). Debris stocks rebuilt and gradually leveled off after 100 yr, but remained 5% and 3% lower, respectively, in the severe and moderate burn than the pre-fire level. The phase I SOM C, N, and P stocks had similar increasing trends (Fig. 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 yr after fire and were $\sim 5\%$ lower in the severe burn and $\sim 3\%$ lower in the moderate burn than the pre-fire levels. Overall, burned tundra gradually approached a quasi-steady state within 200 yr following fire (Fig. 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 $10 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 5\%$) even at the highest simulated deposition or weathering rates (Fig. 3). For comparison, when available N and P were held at saturating concentrations, both burned and unburned tundra had more than $620 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 284\%$) higher

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

	Severe burn	Moderate burn
Carbon ($\text{g C}/\text{m}^2$)		
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 ($\text{g N}/\text{m}^2$)		
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 ($\text{g P}/\text{m}^2$)		
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 is soil organic matter.

NPP than the control value ($218 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the first year unburned tundra) after 200 yr. 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

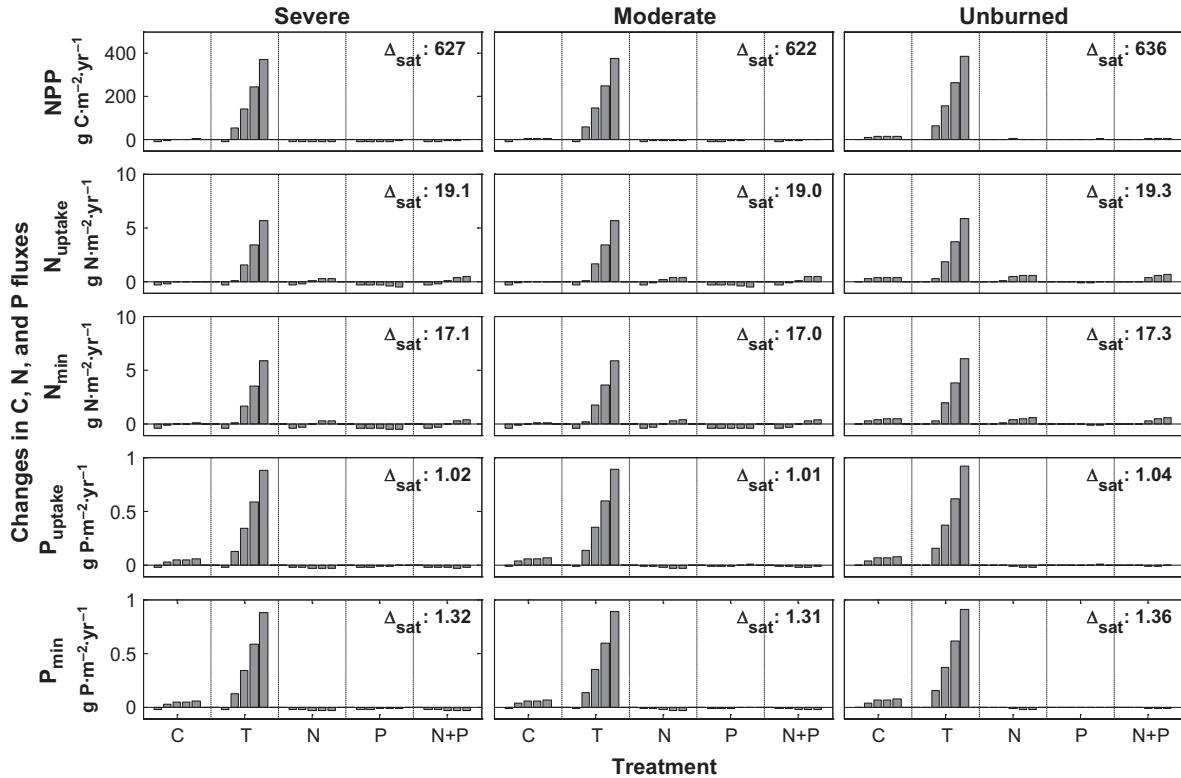


FIG. 3. The 200-yr changes ($\text{Year}_{200} - \text{Year}_1$, unburned) of NPP, N_{uptake} (nitrogen uptake by plant), N_{min} (net nitrogen mineralization), P_{uptake} (phosphorus uptake by plant), and P_{min} (net phosphorus mineralization) in the severely and moderately burned sites and the unburned 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 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for NPP, 4.63 $\text{g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for N_{uptake} , 4.74 $\text{g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for N_{min} , 0.54 $\text{g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for P_{uptake} , and 0.54 $\text{g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for P_{min} . Δ_{sat} represents the change relative to the control under a nutrient-saturated environment where ammonium, nitrate, dissolved organic N (DON), and phosphate concentrations exceed plant and microbial demands for N and P.

saturation plant available N and P, vegetation N uptake rates were $\sim 19 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ higher ($\sim 410\%$) than the control value ($4.63 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and N mineralization rates were $\sim 17 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ higher ($\sim 359\%$) than the control value ($4.74 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) after 200 yr. The responses of P uptake and net mineralization rates to the increase in N deposition and P weathering rates combined were both less than $0.04 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 7\%$). With saturating N and P sources, vegetation P uptake rates were $\sim 1.0 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ higher ($\sim 185\%$) than the control value ($0.54 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and P mineralization rates were $\sim 1.3 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ higher ($\sim 241\%$) than the control value ($0.54 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) after 200 yr.

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 (Fig. 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 $\sim 1.5 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 32\%$) and by $\sim 0.2 \text{ g P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 37\%$) by the end of the 200-yr 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 (Fig. 3). On average, each 3°C warming increased NPP by $\sim 100 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ($\sim 45\%$), 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-yr 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

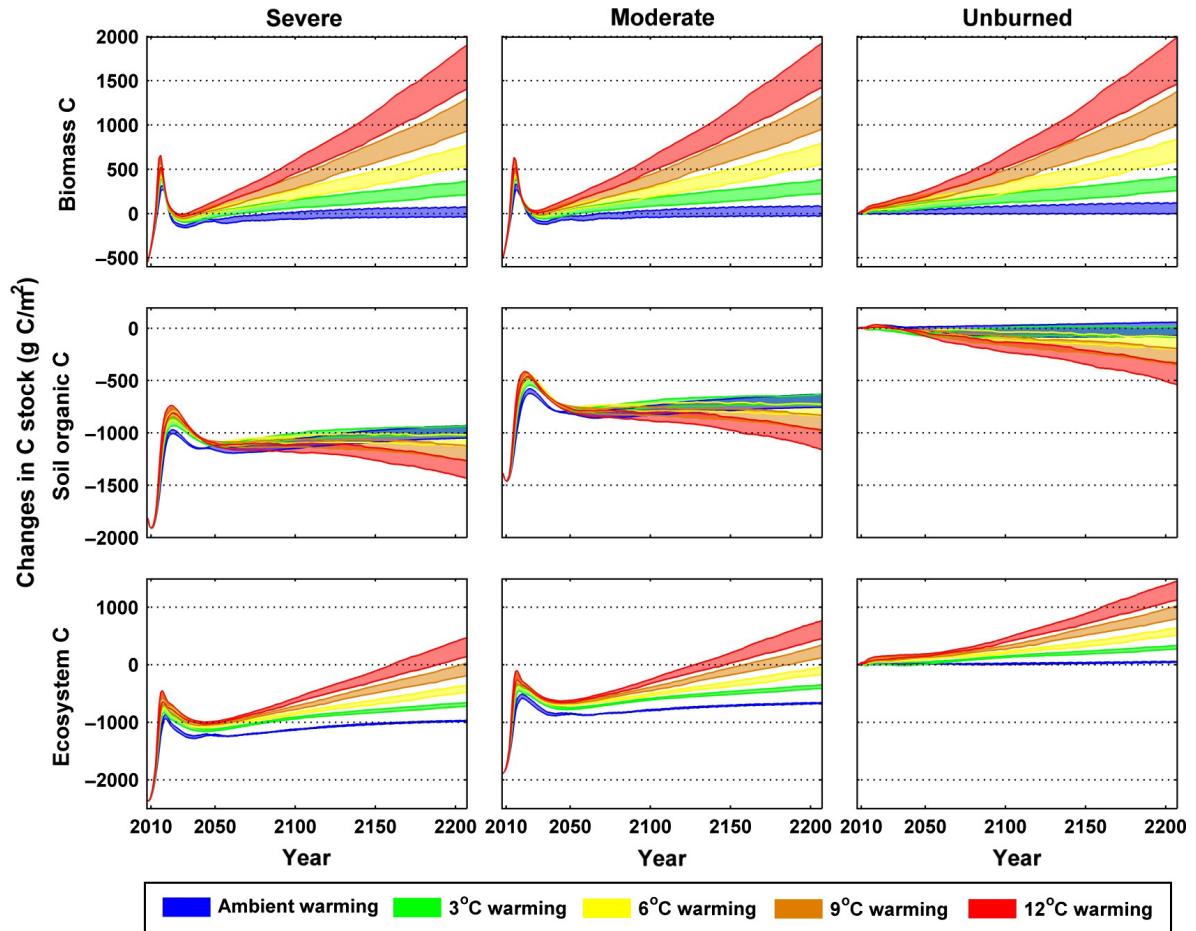


FIG. 4. The modeled 200-yr changes in C stock of biomass, soil organic matter, and the total ecosystem at the severely and moderately burned sites and the unburned site relative to the pre-fire steady state. The five different colors represent multiple warming scenarios, and the shaded area represents the ranges caused by varied atmospheric CO_2 concentrations.

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 (Fig. 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°C warming increased vegetation biomass by 200 g C/m^2 by year 200 and a 12°C warming increased it by 1,400 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°C warming by an additional 500 g C/m^2 (Fig. 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 yr 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 (Fig. 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 (Fig. 4). Only very strong warming can completely recover fire C losses within 200 yr. The MEL simulations indicated that a 12°C warming over 200 yr was required to offset initial losses due to combustion of $\sim 2,300 \text{ g C/m}^2$ in the severe

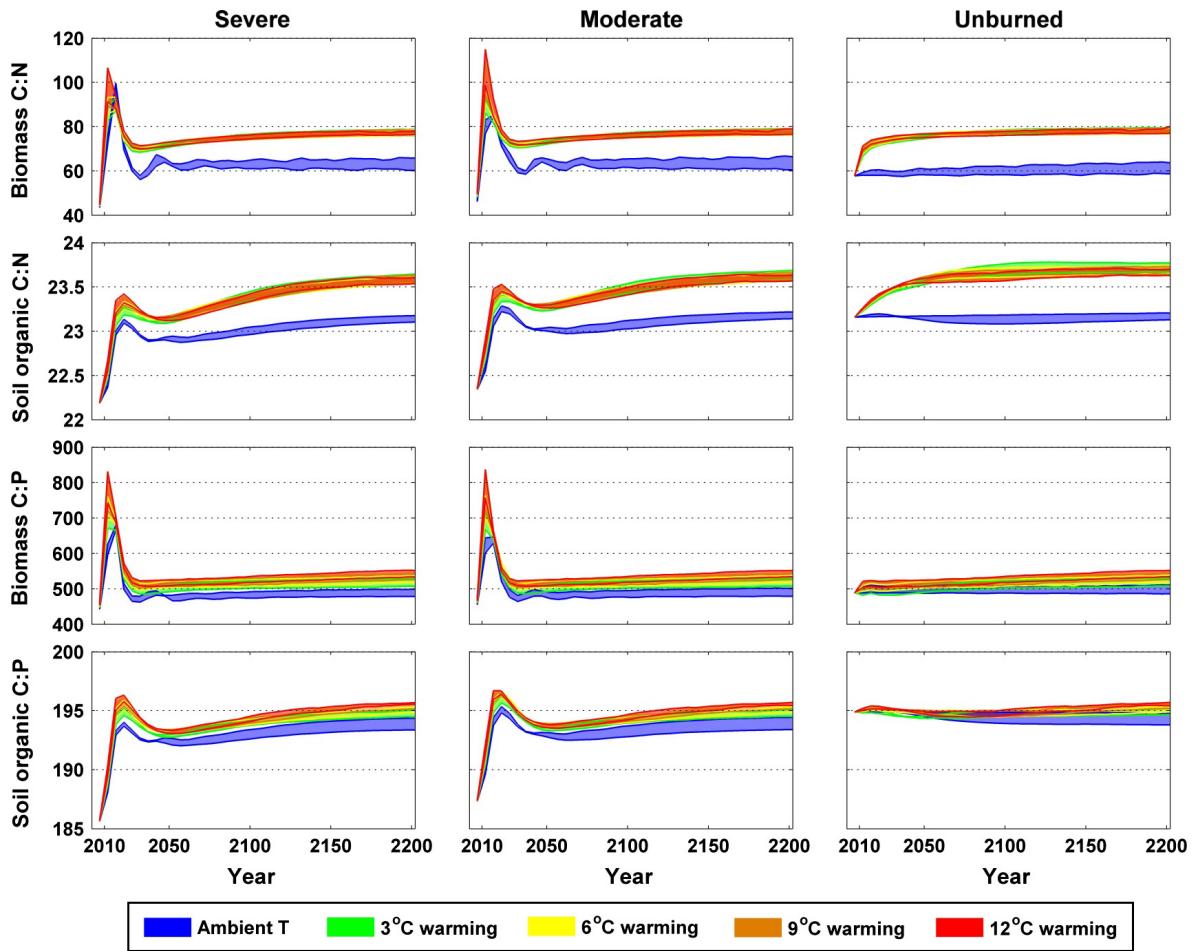


FIG. 5. Changes in biomass C:N, soil organic C:N, biomass C:P, and soil organic C:P ratio through the 200-yr simulation following fire. The five different colors represent multiple warming scenarios, and the shaded area represents the ranges caused by varied atmospheric CO₂ concentrations.

burn; the $\sim 1,900$ g C/m² losses in the moderate burn were offset by the gains from a 9°C or 12°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 yr 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 (Fig. 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 CO₂ 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 yr of recovery from fire were much smaller than those caused by climatic change (Fig. 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°C to +6°C increases the net N mineralization rate by only 33%, but warming from +6°C to +12°C will further increase the

N mineralization by 87% (Fig. 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°C and 9°C but can double as the temperature increases from 9°C to 15°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 and Shaver 2011a 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, CO₂ 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 (Schoor et al. 2008, Jiang et al. 2016). 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 (Fig. 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 CO₂ 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 CO₂ concentration has a smaller effect on plant productivity (Fig. 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 (Fig. 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 unlimited nutrient availability (Fig. 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 (Fig. 4), the stabilized vegetation biomass and SOM C:nutrient ratios (Fig. 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 what are 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 two to three decades after fire (Landhauser 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 (Tape et al. 2006, Myers-Smith et al. 2011, Swanson 2013). However, the expansion of tall shrubs may shade out lichens and other N₂-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 CO₂ 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.

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DATA AVAILABILITY

Data associated with this paper are available in the Long Term Ecological Research Network: <http://dx.doi.org/10.6073/pasta/3c28308d77>