


Effects of long-term nutrient additions on Arctic tundra, stream, and lake ecosystems: beyond NPP

Laura Gough¹  · Neil D. Bettez² · Karie A. Slavik³ · William B. Bowden⁴ · Anne E. Giblin⁵ · George W. Kling⁶ · James A. Laundre⁵ · Gaius R. Shaver⁵

Received: 9 November 2015 / Accepted: 21 August 2016 / Published online: 31 August 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Primary producers form the base of food webs but also affect other ecosystem characteristics, such as habitat structure, light availability, and microclimate. Here, we examine changes caused by 5–30+ years of nutrient addition and resulting increases in net primary productivity (NPP) in tundra, streams, and lakes in northern Alaska. The Arctic provides an important opportunity to examine how ecosystems characterized by low diversity and low productivity respond to release from nutrient limitation. We review how responses of algae and plants affect light availability, perennial biotic structures available for consumers, oxygen levels, and temperature. Sometimes, responses were similar across all three ecosystems; e.g., increased NPP significantly reduced light to the substrate following

fertilization. Perennial biotic structures increased in tundra and streams but not in lakes, and provided important new habitat niches for consumers as well as other producers. Oxygen and temperature responses also differed. Life history traits (e.g., longevity) of the primary producers along with the fate of detritus drove the responses and recovery. As global change persists and nutrients become more available in the Arctic and elsewhere, incorporating these factors as response variables will enable better prediction of ecosystem changes and feedbacks in this biome and others.

Keywords Fertilization · Habitat · Light · Oxygen · Temperature

Communicated by Deron E. Burkepile.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3716-0) contains supplementary material, which is available to authorized users.

✉ Laura Gough
lgough@towson.edu

¹ Department of Biological Sciences, Towson University, Towson, MD 21252, USA

² Cary Institute for Ecosystem Studies, PO Box AB, Millbrook, NY 12545, USA

³ University of Michigan Biological Station, 930 N. University, Ann Arbor, MI 48109, USA

⁴ Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05405, USA

⁵ Marine Biological Laboratory, Ecosystems Center, Woods Hole, MA 02543, USA

⁶ Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

Introduction

A relatively common experiment conducted in both terrestrial and aquatic ecosystems involves manipulating nutrients to better understand the nature of nutrient limitation (e.g., Elser et al. 2007) or to determine how a food web is regulated from the bottom-up (e.g., Gruner et al. 2008). These also aid predictions of effects of increased nutrients entering ecosystems (e.g., Falkowski et al. 2000), particularly nitrogen (N) deposition in terrestrial systems and runoff of N and phosphorus (P) into aquatic systems. This research thus has direct implications for understanding changes that may be occurring now or in the near future, including how climate changes may interact with altered N cycling (e.g., Porter et al. 2013). Several meta-analyses have summarized results of such manipulations across terrestrial and aquatic ecosystems (e.g., Elser et al. 2007) to determine how productivity and autotrophs themselves may be limited or colimited by N and P (Harpole et al. 2011; Bracken et al. 2015), how diversity and evenness of the

producers are affected (Hillebrand et al. 2007), and how changes in bottom-up resource availability interact with top-down herbivore pressure (Gruner et al. 2008; Borer et al. 2014).

Most such studies focus on the changes in the quantity (and sometimes quality) of net primary productivity (NPP) and biomass (e.g., De Schrijver et al. 2011; Phoenix et al. 2012). However, producers also affect physicochemical variables, e.g., light, temperature, and oxygen (Fig. 1). Changes in primary production can affect energy flow to consumers and detritivores while also altering habitat structure, light, dissolved oxygen, and temperature. Changes in these physicochemical variables can then feedback to affect biota (Fig. 1). A well-known example is eutrophication in freshwater ecosystems: after algae bloom in response to excess nutrients, they eventually die, sink to the bottom and are decomposed, thus lowering oxygen levels in the water and negatively affecting producers and consumers. This is a case in which altered production results in physicochemical feedbacks that can cause a state change (Scheffer and Carpenter 2003).

Determining the net effect of these physicochemical changes can be challenging because of the many direct and indirect effects involved (Fig. 1). For example, fertilized marine rocky intertidal systems can promote a newly dominant form of algae that alters wave and light energy to the benthos and provides a different attachment substrate for other organisms (Kraufvelin et al. 2010). Such changes in coastal systems can have major impacts on the benthic invertebrate and attached microalgae by altering shelter, attachment substrates, and the chemical environment, particularly dissolved oxygen (Cebrian et al. 2013). Parsing

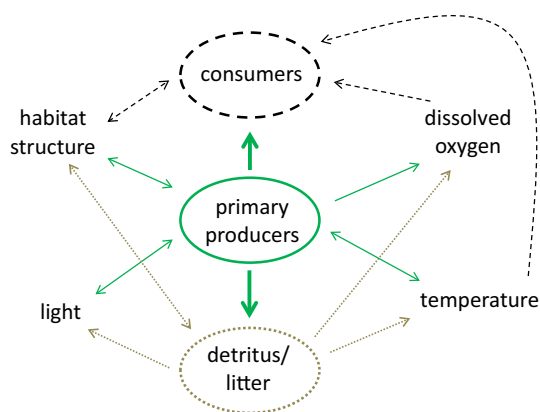


Fig. 1 Conceptual diagram indicating potential relationships and feedbacks in response to nutrient addition. *Solid lines* indicate effects of primary producers, *dotted lines* indicate effects of litter or detritus, and *dashed lines* indicate how physicochemical variables may influence consumers. *Double-headed arrows* indicate possible effects in both directions, because primary producers may alter physicochemical variables that feedback to affect themselves

out the magnitude and direction of these many potential responses requires careful consideration of the important physicochemical factors in that system that can be influenced by the primary producers.

In terrestrial plant communities, a well-studied physicochemical response to fertilization is a reduction of light at the ground surface caused by increased shading from greater plant biomass and litter (Fig. 1). Species richness often decreases when this occurs because of greater light competition for understory plants (Hautier et al. 2009). Similar decreases in light penetration to the benthos in fertilized lakes result from higher pelagic algae biomass (Scheffer and Carpenter 2003).

If the morphology of the primary producers changes in response to fertilization, either because of growth by species already present or a change in community composition, the biotic structure of the ecosystem may be altered and provide different physical habitat niches for other producers and consumers (Fig. 1). For example, increased NPP and litter deposition can affect habitat structure for plant canopy dwelling as well as ground dwelling consumers in a terrestrial ecosystem (note double-headed arrows in Fig. 1 to habitat structure). Similarly, as mentioned above, in some coastal systems that have been fertilized, significant biotic structure changes occurred with substantial effects on associated fauna (Kraufvelin et al. 2010; Antón et al. 2011).

Additional physicochemical effects of greater producer biomass can be changes in dissolved oxygen in aquatic systems (or oxygen availability in saturated soils) and temperature in any ecosystem (Fig. 1). Eutrophication can result in very low dissolved oxygen, as described above. Trees and shrubs may shade the soil surface and stream or lake margins, reducing temperatures. In contrast, in the center of a lake, increased abundance of pelagic algae (particles) may absorb more light and raise water temperatures (e.g., Kling 1988). Our objective in this study was to evaluate the effects of long-term fertilization on these physicochemical effects in Arctic terrestrial and freshwater ecosystems to examine effects of added nutrients that go beyond altering NPP.

Focus on the Arctic

The Arctic is undergoing rapid ecological changes resulting from climate warming (Post et al. 2009; Post and Høye 2013). Because of the low solar energy inputs and nutrient limitation, diversity and productivity in terrestrial and aquatic ecosystems are low (Crawford 2013; Hobbie and Kling 2014). However, warming may affect individual organisms directly by alleviating temperature stress and indirectly by improving related growing conditions. For example, deeper thaw resulting from warming allows

increased rates of decomposition and greater nutrient availability (Hobbie et al. 1999; Hinzman et al. 2005). Thus, the Arctic biome provides an important opportunity to investigate how release from nutrient limitation affects physicochemical variables, primary producers, and consumers.

While recognizing the value of broad-scale meta-analyses across diverse aquatic and terrestrial ecosystems, here, we present results that focus on responses to long-term resource manipulations in tundra, stream, and lake habitats as part of the Arctic Long-Term Ecological Research (LTER) project (Hobbie and Kling 2014). Data reviewed here come from more than three decades of experimental treatments in both terrestrial and aquatic systems performed at the same time in one location, making our synthesis unique among similar ecological studies. Much of the prior analyses of these experiments focused on the responses of NPP and biomass and emphasized changes in carbon (C) and N cycling within each individual ecosystem. Here, we illuminate the context of those effects with two objectives: (1) to review changes in the physicochemical environment caused by nutrient enrichment and associated changes in primary producers within tundra, stream, and lake ecosystems, and (2) to compare among these Arctic ecosystems to determine general drivers of response to the press effects of multi-year nutrient enrichment. For each ecosystem, we describe responses at representative study sites of four physicochemical variables that can affect biota and biogeochemistry: light, perennial biotic structures for consumers, oxygen, and temperature. Perennial structures produced by plants change the physical environment in multiple ways, and thus are included here as a physicochemical variable. Determining the *net* effect of adding nutrients and associated changes in NPP on the physicochemical environment is difficult because of the possibility of multiple, counteracting effects (Fig. 1). By focusing within one biome and removing some of the environmental noise that enters into large-scale meta-analyses, we explore these interactions to illustrate how they should be considered to determine long-term responses to changes in nutrient availability and to better understand potential feedbacks.

Tundra ecosystems

“Tundra” here indicates terrestrial and wetland plant communities, including riparian and littoral areas bordering streams and lakes in the Arctic. Arctic tundra plant communities have low NPP (50–350 g m⁻² year⁻¹) relative to temperate systems, with the greatest NPP in riparian shrub habitats (Shaver et al. 2014). Almost all of the plant species are perennial and reproduce predominantly by clonal growth. Depending on topographic location and soil moisture, the vegetation may be a mixture of dwarf evergreen

and deciduous shrubs, graminoids, few forbs, mosses, and lichens.

Nutrient addition studies have shown that tundra ecosystems may differ in their relative responses to N or P alone, but are often colimited by both (e.g., Shaver and Chapin 1995; Johnson et al. 2000; Gough et al. 2002) like other ecosystems (Harpole et al. 2011). In general, adding nutrients causes initial short-term (several year) increases in growth of all species present, followed by competitive exclusion over the longer term and lower species richness after 10 or more years (Shaver et al. 2014). Although NPP increases significantly, community biomass may not change relative to control plots because of compensatory responses among growth forms (e.g., Chapin et al. 1995). Generally, mosses, lichens, and evergreen shrubs fare poorly in fertilized conditions in the long term; however, concurrent increases in graminoids and deciduous shrubs offset the loss of biomass from these species.

Moist acidic tussock tundra (MAT)

MAT at the Arctic LTER has been subjected to annual addition of both N and P in multiple experiments beginning in 1981 and is the most well-studied and common upland tundra plant community in northern Alaska. Each year 10 g N m⁻² and 5 g P m⁻² have been added to these plots, approximately 5–8 times the amount of N taken up by the MAT vegetation annually (Chapin et al. 1995). In MAT under ambient conditions, the plant community is a mixture of tussock-forming sedges, dwarf deciduous shrubs, dwarf evergreen shrubs, perennial forbs, *Sphagnum* mosses, and lichens. Added nutrients increase NPP (Table 1) and, after 5 years of fertilization, the community shifts toward dominance by *Betula nana* (dwarf birch, a deciduous shrub) and a shade-tolerant understory species, *Rubus chamaemorus* (cloudberry, a perennial forb) (photos in Online Resource 1; Online Resource 2; Hobbie et al. 2005). Other species, including mosses and lichens, are excluded from these plots over time resulting in decreased species richness (Shaver et al. 2001).

Because of the increase in shrub stature, light levels are significantly depleted at the soil surface when MAT is fertilized (Online Resource 1, 2, 3). In an adjacent experiment in MAT, shade houses reduced biomass of all plant growth forms after 9 years of treatment (Chapin et al. 1995), and several of these species fared poorly in similar shading experiments in Scandinavian tundra (Capioli et al. 2012). The ground surface may receive less light not only because of increased living plant biomass but also because of greater litter deposition (Mack et al. 2004).

The shift toward *Betula* with fertilization also significantly changes the perennial biotic structure available for consumers for food and shelter, as the amount of woody

Table 1 Responses of primary producers to long-term fertilization (mean \pm 1 SE if available)

Ecosystem	Productivity units	community/site	Control		Fertilized		Source
Tundra	$\text{g m}^{-2} \text{ year}^{-1}$	MAT	Mixed sedges, shrubs, mosses	145 ± 29	Deciduous shrub, forb	462 ± 88	Gough et al. (2012a)
	$\text{g m}^{-2} \text{ year}^{-1}$	Dry heath	Evergreen shrubs, lichens	39 ± 9	Grass, deciduous shrub	88 ± 17	Gough et al. (2012a)
	$\text{g m}^{-2} \text{ year}^{-1}$	Wet sedge	Rhizomatous sedges	99 ± 16	Rhizomatous sedges	146 ± 30	Shaver (2004)
	$\text{g m}^{-2} \text{ year}^{-1}$	Shrub	Deciduous shrubs	342 ± 75	Deciduous Shrubs	491 ± 18	DeMarco et al. (2014)
Stream	moss % cover	Kuparuk	Phytoplankton, algae	5	Filamentous moss	35	Arscott et al. (1998)
	g C h^{-1}	Kuparuk	Phytoplankton, algae	2.3	Filamentous moss	6.3	Arscott et al. (1998)
Lake*	$\text{mg m}^{-2} \text{ day}^{-1}$	N1	Phytoplankton	110 ± 11	Phytoplankton	304 ± 48	Arctic LTER database**
	$\text{mg m}^{-2} \text{ day}^{-1}$	N2	Phytoplankton	77 ± 6.5	Phytoplankton	262 ± 23	Arctic LTER database**

* Benthic productivity was not consistently measured in these lakes

** Lake values are from the Arctic LTER database but converted to pelagic $\text{mg m}^{-2} \text{ day}^{-1}$ for the growing season by Mary Anne Evans calculated from annual data collected in: control N1 (1989, 1995, 1996, 1998, 1999, 2000), fertilized N1 (1990–1994), control and fertilized N2 (1985–1990)

stem biomass and canopy complexity aboveground dramatically increase (Online Resource 3; Hobbie et al. 2005; Campioli et al. 2012). Abundance of tundra consumers, including arthropods, migratory songbirds, and small mammals, is correlated with shrub abundance in complex ways (e.g., Gough et al. 2012a; Rich et al. 2013). For example, particular species of voles and migratory songbirds preferentially occupy shrub habitat for nesting and overwintering, while others prefer open tundra (Batzli and Lesieutre 1995; Boelman et al. 2014). In addition to the increase in wood biomass, woody and herbaceous litter deposition tend to increase in fertilized MAT, and moss and lichen cover significantly decrease (Gough et al. 2012a), altering the environment for surface-dwelling organisms.

Another potential effect of chronic fertilization on tundra communities could be lowering of soil oxygen availability driven by increased soil moisture. However, after 11 years of fertilization, soil moisture was characteristically high in late July (>400 % water content in the top 5 cm of the organic horizon, L. Gough unpubl.) and was not significantly different between control and fertilized plots, although there was a trend toward lower moisture in the fertilized plots.

Finally, changes in the soil physical environment, particularly temperature, occur because of the increased shading and litter deposition described above. In the winter, Arctic shrubs trap more snow than herbaceous vegetation and thus alter snow depth, albedo, and soil temperature (Myers-Smith et al. 2011). As a result, soils in fertilized plots in MAT are slightly warmer in winter (Sep–May average years 10–14, $+0.7 \pm 0.4$ °C; Shaver 2002) than in control plots. In contrast in the summer, fertilized soils are cooler (Online Resource 3; also see Shaver et al. 2014) and

have shallower maximum depth of thaw (6 ± 1 cm less in fertilized plots, average years 16–22; Shaver 2006). This shallower active layer may restrict soil microbial and root activity relative to control plots.

Other tundra communities

Long-term fertilization experiments have also been conducted in dry heath (DH), wet sedge (WS), and shrub tundra as part of the Arctic LTER and provide an important comparison with the better studied MAT, although some relevant variables have not yet been collected in these communities. Responses differed in terms of shifts in the relative abundance of primary producers. In DH, normally dominated by dwarf evergreen shrubs and lichens, added nutrients for 7–10 years caused a shift towards a grass-dominated community, with an increase in NPP (Table 1), but a decrease in community biomass because of the loss of lichens and evergreen shrubs (Gough et al. 2002, 2012a). In contrast, WS remained dominated by clonal sedges, with leaf mass and litter greater in fertilized plots after 5 years (Johnson et al. 2000), though these differences lessened after 12 years (Boelman et al. 2003). This greater biomass increased shading of the soil surface in both dry and wet tundra (Online Resource 3). In shrub tundra, adding nutrients also resulted in greater NPP (Table 1) and greater shrub height and complexity (DeMarco et al. 2014).

Changes in perennial biotic structures available for consumers in DH and WS are in the opposite direction as MAT, with a shift towards greater graminoid biomass (Johnson et al. 2000; Boelman et al. 2003; Gough et al. 2007). In shrub tundra, however, changes in perennial biotic structures were similar to MAT in that the species that responded

positively were all deciduous shrubs (DeMarco et al. 2014). Litter mass also increased in all three communities, potentially altering the physical environment for surface and soil dwelling consumers. In DH, the dramatic loss of lichens with fertilizer (Gough et al. 2008) likely affects surface and soil-dwelling fauna, while the significant increase in moss biomass in WS also changes the surface environment.

Soil moisture was unaffected by nutrient addition in shrub (DeMarco et al. 2014) and DH tundra (L. Gough unpubl.). Wet sedge tundra soils remain saturated during most years, though after 9 years of fertilization, the top 10 cm of soil was slightly drier in fertilized plots (control vs. fertilized: 662 ± 27 vs. 582 ± 70 %; G.R. Shaver unpubl.).

Finally, summer soil temperatures were cooler in fertilized plots in DH and WS, just as at MAT (Online Resource 3), while there was no difference in shrub tundra (DeMarco et al. 2014). We cannot determine changes in thaw depth in DH and shrub tundra, because rocks prevent this measurement; the soil thaws deeply given the lack of insulation at the surface and the high mineral content. The cooler soils in fertilized WS resulted in substantially shallower depth of thaw relative to controls (-9 ± 2 cm, average years 16–21, Arctic LTER database), similar to results at MAT.

Tundra summary

In summary, nutrient addition in tundra increased NPP, thus providing greater food resources for consumers and driving sometimes dramatic changes in the biotic structure of these habitats. Light at the soil surface decreased, negatively affecting prostrate vascular plants as well as cryptogams. The perennial, overwintering plant structures changed, with an increase in woody material in MAT and Shrub tundra, and an increase in graminoid biomass in DH and WS. However, soil moisture (and therefore potential anoxia) was not affected by fertilization. Finally, soil temperature and thaw depth were affected in three communities, changing the soil environment and likely affecting root and soil microbial activity. None of these experiments have ended, and thus, recovery has not been measured, unlike in the aquatic ecosystems described below.

Stream ecosystems

Streams in Arctic Alaska differ from those at other latitudes in several major ways. In particular, most headwater streams freeze during the winter which greatly restricts productivity (Bowden et al. 2014). Stream organisms, like all Arctic flora and fauna, experience 24-h light during the summer which affects metabolism and behavior. Most streams are underlain by permafrost which affects their

hydrology as well. These streams are generally P limited, and soluble reactive P concentrations are typically near detection limits ($\sim 0.03 \mu\text{M}$), though total dissolved P concentrations are measurable (Peterson et al. 1985; Slavik et al. 2004; Bowden et al. 2014).

The Kuparuk River

The Kuparuk River, a fourth-order tundra stream located at the Arctic LTER site, has been the subject of a long-term P fertilization experiment since 1983 with a target concentration for soluble reactive P of $0.3 \mu\text{M}$. Gross primary productivity of the reference riffles averages $\sim 80 \text{ mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ (Bowden et al. 2014). After approximately 8 years of fertilization, stream productivity increased by a factor of three, primarily because two species of bryophyte new to this reach (*Hygrohypnum alpestre* and *Hygrohypnum ochraceum*) invaded and increased cover of the substrate in riffles from 5 % to more than 35 % (Table 1, photos in Online Resource 1, Online Resource 3). The filaments of these moss species can exceed 15 cm in length and persist for multiple years. Mosses tend to stabilize stream bed substrates and can lead to a higher capacity for nutrient retention and primary production in streams (Stream Bryophyte Group 1999).

Not surprisingly, light availability decreased under the moss (methods in Online Resource 2; Online Resource 3). Although a precise mechanism cannot be assigned, the overall decrease in epilithic chlorophyll in the fertilized reach likely resulted from a combination of this lower light availability, increased abrasion by moss fronds, and competition for nutrients (Slavik et al. 2004).

The increase in moss cover also changed the biotic structure of the community, affecting food and shelter availability for algae and insects in particular (Online Resource 3). The moss filaments increased the surface area available for periphyton to colonize and trapped larger amounts of sestonic fine particulate organic matter (FPOM) compared with rocks (Stream Bryophyte Group 1999; Slavik et al. 2004). These changes benefit shredding and grazing invertebrates, some chironomid taxa and the large mayfly, *Ephemerella*, in particular (Lee and Hershey 2000). Conversely, densities of the diatom tube-building chironomid, *Orthocladius*, and the mayfly, *Baetis*, declined once moss took over the fertilized reach (Online Resource 3), because of less available rock substrate for colonization for *Orthocladius* and a decrease in periphyton food source for *Baetis*. There were no significant differences in fish growth rates between the fertilized reach and the reference reach (Slavik et al. 2004).

Given the short hydrological residence time of water and the turbulent nature of the Kuparuk River, mosses might not be expected to have much influence on either dissolved

oxygen (DO) or temperature. However, recent monitoring data show that the greater moss biomass has resulted in higher rates of gross primary production (GPP) and respiration, and consequently, DO fluctuates more in the moss-dominated fertilized reach with slightly greater daily maximum (after 30 years of treatment, 11.06 ± 0.05 vs. 10.78 ± 0.06 mg L⁻¹) and slightly lower daily minimum values (9.60 ± 0.07 vs. 9.76 ± 0.06 mg L⁻¹; Arctic LTER Database) compared with the reference reach. Because of these counteracting trends, mean daily DO was not different between the two reaches (10.40 ± 0.06 in fertilized vs. 10.31 ± 0.06 mg L⁻¹ in reference; Arctic LTER database). In addition, water temperatures are slightly higher in the fertilized reach compared with the reference reach (Online Resource 3), although these are likely not of biological significance. These differences in DO and temperature are exaggerated during periods of low flow.

Hershey Creek and Oksrukuyik Creek

Two shorter term whole-stream fertilization experiments were conducted at the Arctic LTER site, but a similar response by aquatic bryophytes did not occur. N and P were added to Hershey Creek, a second-order beaded tundra stream, for 1 year, resulting in an increase in algal cover, chlorophyll *a*, macroinvertebrate biomass, and grayling growth (Benstead et al. 2005). For 6 years, P (1991 and 1992) and N plus P (1993–1996) were added to Oksrukuyik Creek, a third-order, lake-fed tundra stream. These enrichments increased production at all trophic levels but did not change bryophyte biomass (Harvey et al. 1998). This lack of response could be related to the different duration of the experiments or to the absence of viable, upstream sources of the bryophyte species in these two creeks. The long (7–9 year) delay before colonizing bryophytes began to dominate the cover and biomass of the experimentally fertilized reach of the Kuparuk River suggests that it took considerable time for propagules from these species to disperse from upstream (or external) source areas and establish in the experimentally fertilized reach.

Recovery from fertilization

Moss colonization strongly affected the trajectory of recovery from nutrient enrichment as well. Recovery from fertilization was measured in the Kuparuk River (following 2 and 13 years of treatment) and Oksrukuyik Creek, where the locations of the nutrient additions were moved downstream or discontinued, respectively. Epilithic algal biomass returned to reference levels in both streams within a year after fertilization ceased. In contrast, the persistent moss cover in the Kuparuk River continued to affect the physical habitat for more than 8 years after fertilization ceased,

resulting in a lag in the recovery response of the macroinvertebrate community (Benstead et al. 2007; Bowden et al. 2014).

Stream summary

In summary, long-term, seasonal fertilization of the Kuparuk River with relatively low levels of P promoted the introduction and growth of two aquatic bryophyte species not previously observed in this reach; this response was not observed in the shorter term stream fertilization studies. In the Kuparuk, these two moss species dramatically altered primary production, the distribution of primary producer biomass, and habitat structure. This change in habitat severely limited light availability to the stream bottom, affected the abundance of periphyton and some benthic macroinvertebrate species, altered stream metabolism (daily maximum and minimum DO), and increased stream temperature in the experimental reach.

Lake ecosystems

Lakes in the Alaskan Arctic are covered by ice up to 1.8 m thick for all but three to four months each summer. Lakes in the Toolik area have very low nutrient concentrations and annual rates of pelagic primary production ($20\text{--}200$ mg C m⁻² d⁻¹), similar to temperate oligotrophic and ultra-oligotrophic lakes (Luecke et al. 2014). These low rates are caused by the short growing season, low rates of external nutrient (N and P) loading into the lakes from streams, and low internal nutrient loading rates from sediments (Whalen and Cornwell 1985). In addition, light penetration is low because of high dissolved organic carbon (DOC) concentrations (Luecke et al. 2014). In the Toolik area lakes, the amount of benthic production, especially in shallow lakes, can also be significant (Whalen et al. 2008; Gettel et al. 2013; Daniels et al. 2015), ranging from $25\text{--}250$ mg C m⁻² day⁻¹ (Luecke et al. 2014).

To better understand the impact of increased N and P loading on nutrient cycling and food webs in Arctic lakes, the Arctic LTER has carried out a series of lake fertilization experiments since the 1980s. Lake N2 was divided in half by a nylon curtain and fertilized on one side with N and P from 1985 to 1990 (details in Online Resource 2; O'Brien et al. 2005). In a second experiment, a larger and deeper lake, Lake N1, was fertilized with N and P from 1990 to 1994 (Bettez et al. 2002). These lakes responded strongly to the addition of N and P by substantially increasing pelagic primary production and chlorophyll *a* (Table 1; Bettez et al. 2002; O'Brien et al. 2005; Lienesch et al. 2005). Fertilization also significantly changed both the pelagic (microplankton, macroplankton, and fish) and

benthic (macroinvertebrates, snails, and fish) food webs in both lakes when phytoplankton biomass and some zooplankton species increased; snails also increased after a two-year lag (Rublee and Bettez 1995, 2001; O'Brien et al. 2005). The effect of fertilization on a pelagic fish (lake trout) was mixed (discussed below).

The increased pelagic algal biomass significantly decreased light penetration through the water column (measured as Secchi depth) (photo in Online Resource 1, Online Resource 3). In Lake N2, Secchi depth was significantly shallower on the fertilized side than on the control side (Online Resource 3). Similarly, in Lake N1, the Secchi depth was less deep throughout the treatment phase of the experiment. This decrease in light availability under fertilized conditions was also evident in light extinction curves in Lake N2 (Online Resource 3).

Unicellular algae continued to dominate the pelagic zone during fertilization, and thus, perennial biotic structures did not change in the water column in such a way as to strongly affect habitat for other species. Benthic producers were not explicitly monitored in these two lakes, although observations suggest that perennial algal mats may have been thicker in the fertilized portion of lake N2 (Kling 1994). Unlike in tundra and streams, these algal mats did not dramatically alter the three-dimensional habitat structure and thus potential shelter habitat for other taxa. Increased pelagic algal production was cumulative because of nutrient retention in the sediments and because dormant algal cells in the sediments may allow the algal population to begin the following growing season with greater numbers. These changes certainly affected the amount of food available to consumers, but did not affect shelter or habitat directly.

The most dramatic effect in the lakes occurred when DO in the hypolimnion, the layer of water in a thermally stratified lake that lies below the thermocline, decreased. In Lake N2, DO in the hypolimnion steadily decreased and averaged less than 1 mg L^{-1} during July and August (Online Resource 3) by the sixth year of the experiment. In Lake N1, by the 4th year of fertilization, DO levels were even lower ($\sim 0.2 \text{ mg L}^{-1}$) during July and August. These low oxygen concentrations have a large influence on higher trophic levels, especially fish. In Lake N1, growth rate of lake trout doubled during fertilization (likely due to the increases in snails and macrozooplankton; Lienesch et al. 2005), but overall numbers of trout did not increase, probably because of the effects of low DO on the survival of lake trout eggs (Luecke et al. 2014). This chemical change in the water affected lake organisms directly as well as indirectly as sediment chemistry continued to be affected over time (Giblin 2014).

In contrast with the dramatic changes in light and oxygen, water column temperature was not affected

by fertilization and associated greater primary production (Online Resource 3). The change in light penetration resulting from increased algal biomass was not enough to cause a change in temperature; relatively weak solar inputs and cool night temperatures likely limited a temperature response. Mixing depth was also not affected in either lake (Giblin and Kling 1985, 1991).

Recovery from fertilization

In some ways, the lakes rapidly recovered from fertilization. For example, Secchi depth returned to pre-fertilization levels in both lakes relatively quickly (Online Resource 3). Because there were no changes in biotic perennial structure, as soon as the algae once again became limited by nutrient availability, they returned to pre-fertilization abundance levels. However, DO in the bottom waters remained lower than pre-fertilization levels even 10 years after fertilization ended, and feedbacks from changes in sediment chemistry also continued (Giblin 2014).

Lake summary

In summary, nutrient addition in these Arctic lakes dramatically increased pelagic algal production resulting in significantly decreased light transmission and DO. Unlike in tundra and streams, no changes in perennial biotic structure occurred. Although most of the changes in community structure and food web composition were short term and occurred only during fertilization, others such as decreased hypolimnetic DO were still evident 10 years later.

Comparison across tundra, streams, and lakes

Overall, long-term nutrient addition in tundra, lakes, and streams caused substantial changes in food quantity, food quality, and subsequent detritus production, but also significantly altered the physicochemical environment. Although there was variability in the responses we observed, certain trends emerged (Table 2; Fig. 2).

In all three ecosystems as primary producers increased in size, number, or both, they shaded the substrate substantially more than under ambient nutrient conditions (Table 2; Fig. 2). This reduction in light negatively affected prostrate terrestrial plants and likely benthic producers as well, drove long-term community change, and affected ecosystem functions via changes to the soil and substrate. In addition, in tundra, litter can shade and physically smother plants on the soil substrate, particularly mosses and lichens.

Producers with perennial structures differed in response to nutrients across these three systems (Table 2; Fig. 2). In stream and tundra ecosystems, perennial plants created

Table 2 Comparison of physicochemical responses across ecosystems in response to long-term fertilization

Ecosystem	Community/site	Detritus changes	Light interception*	Perennial structures/habitat	Dissolved oxygen	Temperature	Sources
Tundra	MAT	Increased shrub, forb leaf litter	32 → 9 %	Shrub height/complexity increased, mosses decreased		Cooler summer, warmer winter	Shaver (2002); Gough et al. (2012a)
	Dry heath	Increased grass and wood litter	40 → 24 %	Tussock grasses increased, lichens decreased		Cooler summer, NS winter	Gough et al. (2012a); Arctic LTER database
	Wet sedge	—	90 → 46 %	Moss cover increased		Cooler summer and winter	Shaver (2004); Arctic LTER database
	Shrub	ND	ND	Shrub height/complexity increased		NS summer, cooler winter	DeMarco et al. (2014)
Stream	Kuparuk	More FPOM trapped in moss	100 → 5 %	Moss cover increased	Bigger daily fluctuations	Slight increase	Arcott et al. (1998); Bowden et al. (2014); Arctic LTER database
Lake	N1	Increased deposition to sediments	5 → 3 m	—	8.5 → <2 mg L ⁻¹	—	Giblin and Kling (1985, 1991)
	N2	Increased deposition to sediments	5 → 2 m	—	6.5 → 1–3 mg L ⁻¹	—	Giblin and Kling (1985, 1991)

see text and Online Resources for details

* For tundra and streams, light levels represent percent of ambient light (PAR) intercepted by primary producers at substrate surface first in control/reference conditions and second under fertilized conditions. In lakes, light interception represents the change in Secchi depth with fertilization

ND no data available, — indicates no difference between control and fertilized treatments, NS indicates no significant difference

persistent changes in the vegetation structure with known (streams) and presumed (tundra) effects on biota that depend on these primary producers for food and habitat. In lakes, the cumulatively greater abundance of unicellular pelagic algae in fertilized conditions created a system that essentially restarted every spring, with more “seeds” and greater nutrients each year, whereas in tundra and streams, the perennial structures were already in place from the previous year, and new growth could continue on existing (as well as newly established) individual plants.

Effects on oxygen availability also differed among the three systems (Fig. 2). Tundra soil moisture was not significantly affected by fertilization and therefore was likely not driving changes in soil oxygen. The streams studied here generally have enough flow to keep DO levels high throughout the summer, although oxygen levels were affected by moss (Bowden et al. 2014). In contrast in lakes, DO in bottom water was dramatically depleted by the greater algal productivity and associated respiration by decomposers (Table 2).

Finally, as a result of fertilization, summer temperature decreased in most tundra soils, slightly increased in streams, and was unaffected in lakes (Table 2; Fig. 2). Greater litter deposition and shading under fertilized conditions caused cooler soils and shallower depth of thaw in three of the tundra communities. In the Kuparuk River, increased nutrients and moss resulted in slightly higher water temperatures, but biological effects on the stream inhabitants are likely slight. Finally, despite the dramatic change in water clarity, fertilization did not affect lake temperatures.

Factors driving similarities and differences across ecosystem

Ecologists often compare ecological processes across aquatic and terrestrial ecosystems to improve understanding of both environments while better developing general theory (e.g., Menge et al. 2009). For example, the study of

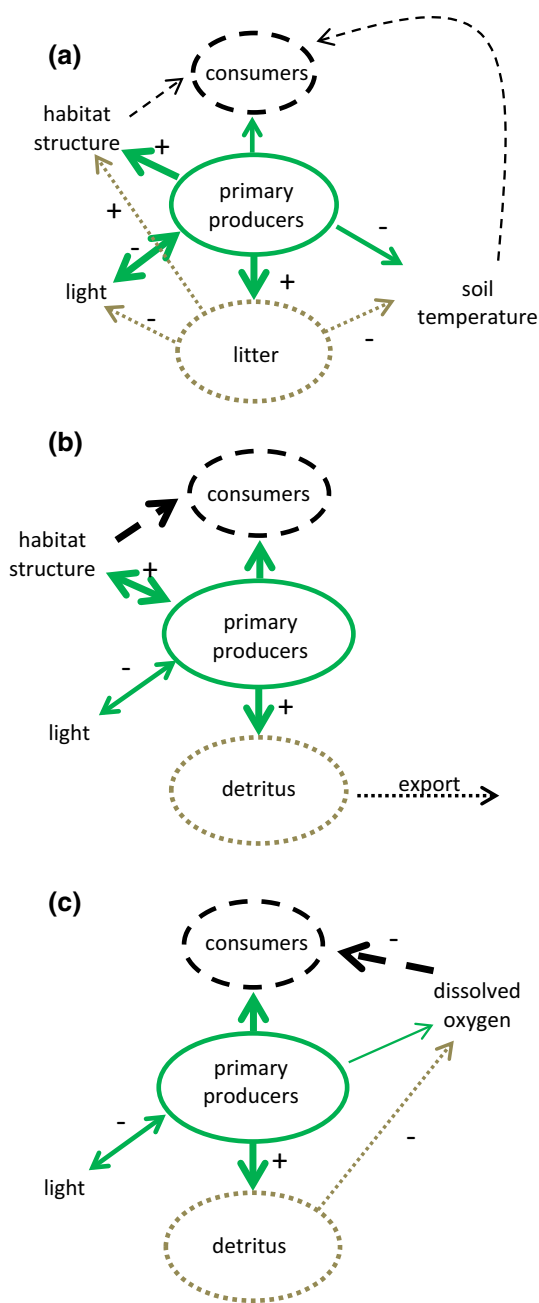


Fig. 2 Effects of changes in primary producers in response to long-term nutrient addition on the physicochemical characteristics of **a** Moist acidic tussock tundra, **b** Kuparuk River, and **c** Lake N2. Plus and minus symbols represent direction of response. If arrows from Fig. 1 are not included, those effects were not manifest in that ecosystem

trophic relationships and food web strength across aquatic and terrestrial systems has received steady attention (e.g., Strong 1992; Shurin et al. 2006; Cebrian et al. 2009), with some generalities emerging. These comparisons are challenging, partly because simply defining a “plant” consistently across ecosystems is difficult (Newman and Rotjan

2013). However, such assessments provide value by highlighting important areas for future research as well as by synthesizing the current state of knowledge.

Our findings summarized above highlight commonalities and differences in response to nutrient enrichment among tundra, lake, and stream ecosystems of the Arctic. They reveal several important ecological factors that affect the ways in which communities respond to greater nutrient availability and suggest how these systems may respond to greater nutrient inputs caused by global change.

Across all three ecosystems, primary producer community response and associated changes in physicochemical variables are controlled to a major extent by the life history and longevity of the resident primary producer species (Smith et al. 2015, also see next paragraph), even after decades of experimental treatment. All the tundra plants described here are perennial, reproduce vegetatively, and may store tissues over winter belowground or aboveground. Thus, gradual, cumulative changes in nutrient availability that favor woody shrubs, for example, changed producer structure available for other trophic levels for food and shelter. This is similar to the fertilized reach of the Kuparuk River where *Hygrohypnum* spp. created a perennial primary producer population and changed the associated food web, because the moss altered physical processes, food availability, and habitat. However, in lakes where pelagic primary producers were not perennial, the algae responsible for increased productivity did not create comparable structures for consumers.

At the community level, species composition, the regional species pool, and dispersal limitations were each crucial elements that drove short- and long-term responses to changes in resource availability in all three ecosystems. Results of fertilization experiments in terrestrial systems including tundra highlight how the ability of a resident species to respond quickly may determine both short- and long-term patterns in NPP and species diversity (e.g., Clark and Tilman 2010; Gough et al. 2012b; Isbell et al. 2013). In several long-term tundra fertilization experiments near Toolik Lake a “new” species has become resident: fireweed (*Epilobium angustifolium*, a boreal species with widely dispersed, wind-blown seeds) has invaded fertilized plots in DH (Moulton and Gough 2011), WS and non-acidic tundra (L. Gough pers. obs.). The long-term responses have otherwise been dominated by resident species. This is true in lakes as well, where to our knowledge “new” phytoplankton species have not invaded the fertilized lakes. And in the Kuparuk River, the ability of one resident but rare moss species, *Hygrohypnum*, to disperse throughout a stream reach has dominated the response of the entire system to increased nutrients. With greater nutrient availability, the exclusion of particular taxa is also to be expected, particularly because Arctic species in general have evolved

to tolerate very low nutrient conditions. In the long-term, additional community reshuffling might occur as greater nutrient availability allows invasion by boreal species (Crawford 2013) causing additional feedbacks to ecosystem function.

Finally, the fate of the increased primary production also affects biophysical feedbacks to the ecosystem (Moore et al. 2004). Some of the producer biomass is consumed by higher trophic levels, leading to changes in food web interactions, as described earlier. But much of the algal and plant biomass will not be consumed by herbivores and will instead become litter and detritus. In terrestrial tundra, this increase in litter changes the physical environment of the soil, affecting temperature and thaw depth and likely microbial activity. In streams, some of this detritus may be exported. But a greater impact may be a change in the quality of detrital matter from the relatively good quality of algal biofilms to the relatively poor quality of bryophyte litter, which is less useful as a substrate for microbial remineralization or as food to higher trophic levels (Stream Bryophyte Group 1999). In lakes, detrital organic matter accumulates in the sediments, where it may ultimately control long-term productivity (although our experiments have not been long enough to demonstrate this). Where the detritus ends up because of physical constraints (degree of “openness” of the system) will affect not only the detritivore community but also nutrient cycling. Furthermore, a recent meta-analysis showed that changes in detritus can also feed back to affect the grazing food web, demonstrating another potential pathway for interactions (Hagen et al. 2012).

Conclusion

Release from nutrient limitation for 5–30+ years had diverse effects on biotic and physicochemical attributes of Arctic aquatic and terrestrial ecosystems (Fig. 2). Life history characteristics and dispersal abilities of the primary producers and consumers, as well as the fate of litter and detritus, drove these changes. In particular, shifts in the life history characteristics of the newly dominant species relative to traits of the usually abundant species caused most of the observed changes in fertilized tundra and streams, whereas the fate of dead primary producers caused substantial changes in lakes, because the detrital biomass was not exported. The degree of openness of these three ecosystems thus plays an important role in their response to added nutrients.

These landscape connections among aquatic and terrestrial ecosystems are likely being intensified by changes associated with climate warming, including greater nutrient availability in the tundra that can be exported into streams

and lakes. Connecting processes across the landscape to understand how aquatic and terrestrial ecosystems are affected simultaneously (Bartels et al. 2012) is crucial to understanding how the region will respond. Examining and going beyond NPP to incorporate measures of the physicochemical changes caused by greater nutrient availability that may feedback to the biota and perpetuate over time should better enable us to predict and potentially mitigate such changes in the Arctic as well as ecosystems in more temperate climates.

Acknowledgments We thank Josh Beneš and Fiona Jevon for help with data collection and summaries. Constructive comments by Phaedra Budy, Just Cebrian, Elsa Cleland, Byron Crump, Jennie McLaren, and Ed Rastetter improved earlier versions of the manuscript. The Arctic LTER is funded by the National Science Foundation in multiple grants to the Marine Biological Laboratory including DEB-1026843.

Author contribution statement LG conceived of the study and wrote the manuscript with NB and KS. All co-authors contributed essential ideas, data, and specific analyses that were critical to the development of this manuscript and edited the manuscript as it evolved.

References

- Antón A, Cebrian J, Heck KL, Duarte CM, Sheehan KL, Miller ME, Foster CD (2011) Decoupled effects (positive to negative) of nutrient enrichment on ecosystem services. *Ecol Appl* 21:991–1009
- Arctic LTER Database. <http://arc-lter.ecosystems.mbl.edu/data-catalog>
- Arcsott DB, Bowden WB, Finlay JC (1998) Comparison of epilithic algal and bryophyte metabolism in an arctic tundra stream, Alaska. *J N Am Benth Soc* 17:210–227
- Bartels P, Cucherousset J, Steger K, Eklöv P, Tranvik LJ, Hillebrand H (2012) Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93:1173–1182
- Batzli GO, Lesieutre C (1995) Community organization of arvicoline rodents in north Alaska. *Oikos* 72:88–98
- Benstead JP, Deegan LA, Peterson BJ, Hurny AD, Bowden WB, Suberkropp K, Buzby KM, Green AC, Vacca J (2005) Responses of a beaded Arctic stream to short-term N and P fertilization. *Freshw Biol* 50:277–290
- Benstead JP, Green AC, Deegan LA, Peterson BJ, Slavik K, Bowden WB, Hershey AE (2007) Recovery of three arctic stream reaches from experimental nutrient enrichment. *Freshw Biol* 52:1077–1089
- Bettez ND, Rublee PA, O'Brien J, Miller MC (2002) Changes in abundance, composition and controls within the plankton of a fertilised arctic lake. *Freshw Biol* 47:303–311
- Boelman NT, Stieglitz M, Rueth HM, Sommerkorn M, Griffin KL, Shaver GR, Gamon JA (2003) Response of NDVI, biomass, and ecosystem gas exchange to long-term warming and fertilization in wet sedge tundra. *Oecologia* 135:414–421
- Boelman NT, Gough L, Wingfield J, Goetz S, Asmus A, Chmura HE, Krause JS, Perez JH, Sweet SK, Guay KC (2014) Greater shrub dominance alters breeding habitat and food resources for migratory songbirds in Alaskan arctic tundra. *Global Change Biol* 21:1508–1520

- Borer ET, Seabloom EW, Gruner DS, Harpole WS, Hillebrand H, Lind EM, Adler PB, Alberti J, Anderson TM, Bakker JD, Biederman L, Blumenthal D, Brown CS, Brudvig LA, Buckley YM, Cadotte M, Chu C, Cleland EE, Crawley MJ, Daleo P, Damschen EI, Davies KF, DeCrappeo NM, Du G, Firn J, Hautier Y, Heckman RW, Hector A, Hille Ris Lambers J, Iribarne O, Klein JA, Knops JMH, La Pierre KJ, Leakey ADB, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Mortensen B, O'Halloran LR, Orrock JL, Pascual J, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Williams RJ, Wragg PD, Wright JP, Yan LH (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508:517–520
- Bowden WB, Peterson BJ, Deegan LA, Hury AD, Benstead JP, Golden H, Kendrick M, Parker SM, Schuett E, Vallino J, Hobbie JE (2014) Ecology of streams of the Toolik Region. In: Hobbie JE, Kling GW (eds) *A warming Arctic: ecological consequences for tundra, streams, and lakes*. Oxford University Press, New York, pp 173–237
- Bracken MES, Hillebrand H, Borer ET, Seabloom EW, Cebrian J, Cleland EE, Elser JJ, Gruner DS, Harpole WS, Ngai JT, Smith JE (2015) Signatures of nutrient limitation and co-limitation: responses of autotroph internal nutrient concentrations to nitrogen and phosphorus additions. *Oikos* 124:113–121
- Campioli M, Leblans N, Michelsen A (2012) 22 years of warming, fertilization, and shading of subarctic heath shrubs promote secondary growth and plasticity but not primary growth. *PLoS One* 7(4):e34842
- Cebrian J, Shurin JB, Borer ET, Cardinale BJ, Ngai JT, Smith MD, Fagan WF (2009) Producer nutritional quality controls ecosystem trophic structure. *PLoS One* 4(3):e4929
- Cebrian J, Stutes JP, Christiaen B (2013) Effects of grazing and fertilization on epiphyte growth dynamics under moderately eutrophic conditions: implications for grazing rate estimates. *Mar Ecol Prog Ser* 474:121–133
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observational changes in climate. *Ecology* 76:694–711
- Clark CM, Tilman D (2010) Recovery of plant diversity following nitrogen cessation: effects of recruitment, litter, and elevated N cycling. *Ecology* 91:3620–3630
- Crawford RMM (2013) *Tundra-taiga biology*. Oxford University Press, New York
- Daniels WC, Kling GW, Giblin AE (2015) Benthic community metabolism in deep and shallow arctic lakes during 13 years of whole-lake fertilization. *Limn Oceanogr* 60:1604–1618
- De Schrijver A, De Frenne P, Ampoorter E, Nevel LV, Demey A, Wuyts K, Verheyen K (2011) Cumulative N input drives species loss in terrestrial ecosystems. *Global Ecol Biogeogr* 20:803–816
- DeMarco J, Mack MC, Bret-Harte MS, Burton M, Shaver GR (2014) Long-term experimental warming and nutrient additions increase productivity in tall deciduous shrub tundra. *Ecosphere* 5:1–22
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine, and terrestrial ecosystems. *Ecol Lett* 10:1135–1142
- Falkowski P, Scholes RJ, Boyle E, Canfield D, Elser J, Gruber N, Hibbard K, Höglberg P, Linder S, Mackenzie FT, Moore B III, Pedersen T, Rosenthal Y, Seitzinger S, Smetacek V, Steffen W (2000) The global carbon cycle: a test of our knowledge of earth as a system. *Science* 290:291–296
- Gettel GM, Giblin AE, Howarth RW (2013) Controls of benthic nitrogen fixation and primary production from nutrient enrichment of oligotrophic, Arctic lakes. *Ecosystems* 16:1550–1564
- Giblin AE (2014) Vignette 8.2 Changes in sediment chemistry induced by fertilization. In: Hobbie JE, Kling GW (eds) *A warming Arctic: ecological consequences for tundra, streams, and lakes*. Oxford University Press, New York, pp 252–254
- Giblin AE, Kling GW (1985) Physical and chemical data for various lakes near Toolik Research Station, Arctic LTER. Summer 1983 to 1989. <http://dx.doi.org/10.6073/pasta/52db341ca154d907e2a82a7ae84c9be2>
- Giblin AE, Kling GW (1991) Physical and chemical data for various lakes near Toolik Research Station, Arctic LTER. Summer 1990 to 1999. <http://dx.doi.org/10.6073/pasta/4d37166727c18052bc444ca5c7bb398c>
- Gough L, Wookey P, Shaver GR (2002) Dry heath arctic tundra responses to long-term nutrient and light manipulation. *Arc Antar Alp Res* 34:211–218
- Gough L, Ramsey EA, Johnson DR (2007) Plant-herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos* 116:407–418
- Gough L, Shrestha K, Johnson DR, Moon B (2008) Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra. *Arc Antar Alp Res* 40:65–73
- Gough L, Moore JC, Shaver GR, Simpson RT, Johnson DR (2012a) Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology* 93:1683–1694
- Gough L, Gross KL, Cleland EE, Clark CM, Collins SL, Fargione JE, Pennings SC, Suding KN (2012b) Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition. *Oecologia* 169:1053–1061
- Gruner DS, Smith JE, Seabloom EW, Sandin SA, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken ME, Borer ET, Bolker BM (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol Lett* 11:740–755
- Hagen EM, McCluney KE, Wyant KA, Soykan CU, Keller AC, Luttermoser KC, Holmes EJ, Moore JC, Sabo JL (2012) A meta-analysis of the effects of detritus on primary producers and consumers in marine, freshwater, and terrestrial ecosystems. *Oikos* 121:1507–1515
- Harpole WS, Ngai JT, Cleland EE, Seabloom EW, Borer ET, Bracken ME, Elser JJ, Gruner DS, Hillebrand H, Shurin JB, Smith JE (2011) Nutrient co-limitation of primary producer communities. *Ecol Lett* 14:852–862
- Harvey CJ, Peterson BJ, Bowden WB, Hershey AE, Miller MC, Deegan LA, Finlay JC (1998) Biological responses to fertilization of Oksrukuyik Creek, a tundra stream. *J N Am Benthol Soc* 17:190–209
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638
- Hillebrand H, Gruner DS, Borer ET, Bracken ME, Cleland EE, Elser JJ, Harpole WS, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Consumer vs. resource control of producer diversity depends on ecosystem type and producer community structure. *Proc Nat Acad Sci* 104:10904–10909
- Hinzman LD, Bettez ND, Bolton WR, Chapin FS, Dyurgerov MB, Fastie CL, Griffith B, Hollister RD, Hope A, Huntington HP, Jensen AM, Jia GJ, Jorgenson T, Kane DL, Klein DR, Kofinas G, Lynch AH, Lloyd AH, McGuire AD, Nelson FE, Nolan M, Oechel WC, Osterkamp TE, Racine CH, Romanovsky VE, Stone RS, Stow DA, Sturm M, Tweedie CE, Vourlitis GL, Walker MD, Walker DA, Webber PJ, Welker J, Winker KS, Yoshikawa K (2005) Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Clim Change* 72:251–298

- Hobbie JE, Kling GW (eds) (2014) A warming Arctic: ecological consequences for tundra, streams, and lakes. Oxford University Press, New York
- Hobbie JE, Peterson BJ, Bettez ND, Deegan L, O'Brien WJ, Kling GW, Kipphut GW, Bowden WB (1999) Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Res* 18:207–214
- Hobbie SE, Gough L, Shaver GR (2005) Species composition differences on different-aged glacial landscapes drive contrasting responses of tundra to nutrient addition. *J Ecol* 93:770–782
- Isbell F, Reich PB, Tilman D, Hobbie SE, Polasky S, Binder S (2013) Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc Natl Acad Sci* 110:11911–11916
- Johnson LC, Shaver GR, Cades D, Stanley A, Nadelhoffer K, Giblin A (2000) Plant carbon-nutrient interactions control CO₂ exchange in Alaskan wet sedge tundra ecosystems. *Ecology* 81:453–469
- Kling GW (1994) Ecosystem-scale experiments in freshwaters: the use of stable isotopes. In: Baker LA (ed) *Environmental chemistry of lakes and reservoirs*, Advances in Chemistry Series 237. American Chemical Society, Washington DC, pp 91–120
- Kling GW (1988) Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West-Africa. *Limnol Oceanogr* 33:27–40
- Kraufvelin P, Lindholm A, Pedersen MF, Kirkerud LA, Bonsdorff E (2010) Biomass, diversity and productivity of rocky shore macroalgae at two nutrient enrichment and wave action levels. *Mar Biol* 157:29–47
- Lee JO, Hershey AE (2000) Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. *J N Am Benthol Soc* 19:697–708
- Lienesch PW, McDonald ME, Hershey AE, O'Brien J, Bettez N (2005) Effects of a whole-lake fertilization on lake trout in a small oligotrophic arctic lake. *Hydrobiologia* 548:51–61
- Luecke C, Giblin AE, Bettez ND, Burkart GA, Crump BC, Evans MA, Gettel G, MacIntyre S, O'Brien WJ, Rublee PA, Kling GW (2014) The response of lakes near the Arctic LTER to environmental change. In: Hobbie JE, Kling GW (eds) *A warming Arctic: ecological consequences for tundra, streams, and lakes*. Oxford University Press, New York, pp 238–286
- Mack MC, Schurr EAG, Bret-Harte MS, Shaver GR, Chapin FS III (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–443
- Menge BA, Chan F, Dudas S, Eerkes-Medrano D, Grorud-Colvert K, Heiman K, Hessing-Lewis M, Iles A, Milston-Clements R, Noble M, Page-Albino K, Rilov G, Rose J, Tyburczy JA, Vinuela L, Zarnetske P (2009) Do terrestrial ecologists ignore aquatic literature? *Front Ecol Environ* 7:182–183
- Moore JC, Berlow EL, Coleman DC, De Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics, and biodiversity. *Ecol Lett* 7:584–600
- Moulton CA, Gough L (2011) Effects of soil nutrient availability on the role of sexual reproduction in an Alaskan tundra plant community. *Arc Ant Alp Res* 43:612–620
- Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Levesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Menard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6(4):045509. doi:10.1088/1748-9326/6/4/045509
- Newman RM, Rotjan RD (2013) Re-examining the fundamentals of grazing: freshwater, marine and terrestrial similarities and contrasts. *Oikos* 122:317–320
- O'Brien WJ, Barfield M, Bettez N, Hershey AE, Hobbie JE, Kipphut G, Kling G, Miller MC (2005) Long-term response and recovery to nutrient addition of a partitioned arctic lake. *Freshw Biol* 50:731–741
- Peterson BJ, Hobbie JE, Hershey AE, Lock MA, Ford TE, Vestal JR, McKinley VL, Hullar MA, Miller MC, Ventullo RM, Volk GS (1985) Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. *Science* 229:1383–1386
- Phoenix GK, Emmett BA, Britton AJ, Caporn SJM, Dise NB, Helliwell R, Jones L, Leake JR, Leith ID, Sheppard LJ, Sowerby A, Pilkington MG, Rowe EC, Ashmore MR, Power SA (2012) Impacts of atmospheric N deposition responses: of multiple plant and soil parameters across contrasting ecosystems in long-term field experiments. *Global Change Biol* 18:1197–1215
- Porter EM, Bowman WD, Clark CM, Compton JE, Pardo LH, Soong JL (2013) Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity. *Biogeochemistry* 114:93–120
- Post E, Høye TT (2013) Advancing the long view of ecological change in tundra systems. *Phil Trans R Soc B* 368:20120477
- Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT, Ims RA, Jeppesen E, Klein DR, Madsen J, McGuire AD, Rysgaard S, Schindler DE, Stirling I, Tamstorf MP, Tyler NJ, van der Wal R, Welker J, Wookey PA, Schmidt NM, Aastrup P (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358
- Rich ME, Gough L, Boelman NT (2013) Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography* 36:994–1003
- Rublee PA, Bettez ND (1995) Change of microplankton community structure in response to fertilization of an arctic lake. *Hydrobiologia* 312:183–190
- Rublee PA, Bettez ND (2001) Lake characteristics influence recovery of microplankton in arctic LTER lakes following experimental fertilization. *Hydrobiologia* 446:229–232
- Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* 18:648–656
- Shaver GR (2002) Hourly weather data from the Arctic LTER Moist Acidic Tussock Experimental plots from 2000 to 2010. Toolik Field Station, North Slope, Alaska. doi:10.6073/pasta/dd1d7302ec6268bba52d1c76540932ec
- Shaver GR (2004) Biomass, nitrogen and carbon of plants in the Arctic LTER experimental wet sedge tundra experimental sites, 2001. Toolik Lake Alaska. doi:10.6073/pasta/07b042676a052d5e6b52f50bbcc65849
- Shaver GR (2006) Late season thaw depth measured in the ARC LTER moist acidic tussock experimental plots at Toolik Field Station, AK, 1993 to current year. <http://dx.doi.org/10.6073/pasta/e7c2be020f700c6452554f56e23bcd4>
- Shaver GR, Chapin FS III (1995) Long-term responses to factorial NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* 18:259–275
- Shaver GR, Bret-Harte MS, Jones MH, Johnstone JF, Gough L, Chapin FS III (2001) Species composition interacts with fertilization to control long-term change in tundra productivity. *Ecology* 82:3163–3181
- Shaver GR, Laundre JA, Bret-Harte MS, Chapin FS III, Giblin A, Gough L, Hobbie S, Kling G, Mack MC, Moore J, Nadelhoffer K, Rastetter E, Schimel J (2014) Terrestrial ecosystems at Toolik Lake, Alaska. In: Hobbie JE, Kling GW (eds) *A warming Arctic:*

- ecological consequences for tundra, streams, and lakes. Oxford University Press, New York, pp 90–142
- Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc R Soc B* 273:1–9
- Slavik K, Peterson BJ, Deegan LA, Bowden WB, Hershey AE, Hobbie JE (2004) Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* 85:939–954
- Smith MD, LaPierre K, Collins SL, Knapp AK, Gross KL, Barrett JE, Frey SD, Gough L, Miller RJ, Morris JT, Rustad LE, Yarie J (2015) Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. *Oecologia* 177:935–947
- Stream Bryophyte Group (1999) Roles of bryophytes in stream ecosystems. *J N Am Benthol Soc* 18:151–184
- Strong DR (1992) Are trophic cascades all wet? *Ecology* 73:747–754
- Whalen SC, Cornwell JC (1985) Nitrogen, phosphorus, and organic-carbon cycling in an arctic lake. *Can J Fish Aquat Sci* 42:797–808
- Whalen S, Chalfant B, Fischer E (2008) Epipelagic and pelagic primary production in Alaskan Arctic lakes of varying depth. *Hydrobiologia* 614:243–257