Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska

Gaius R. Shaver & Sven Jonasson

Long-term field experiments at Abisko, Sweden, and Toolik Lake, Alaska, reveal both similarities and differences in response of contrasting Arctic ecosystems to changes in temperature, light, and nutrient availability. Five different ecosystems were manipulated for 5–15 years by increasing air temperature with greenhouses, by decreasing light with shading, and by increasing available N and P with fertilizers. The ecosystems at Abisko included evergreen-dominated heath and fellfield sites; at Toolik Lake they included wet sedge tundra, moist tussock tundra, and dry heath tundra. In all ecosystems, fertilizer treatment increased plant growth, production, and/or biomass. Plant responses to warming were smaller and occasionally nonsignificant. Responses to shading were generally nonsignificant after 3–6 years, although after 9 years the tussock tundra showed significant decreases in biomass. In general, the ecosystems at Abisko were less responsive to nutrients and more responsive to temperature than the ecosystems at Toolik Lake. Overall, though, the sites were quite similar in their responses to the perturbations, increasing our confidence in predictions of response to climate change over large areas based on small-area studies.

Gaius R. Shaver, The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA; Sven Jonasson, Dept. of Plant Ecology, University of Copenhagen, Ø. Farimagsgade 2D, DK-1353, Copenhagen K, Denmark.

Introduction

Arctic ecosystems have the potential for significant feedbacks on global climate change, through changes in their net C balance which affect atmospheric CO_2 and methane content, and through changes in species composition and plant cover which affect surface energy balance and hydrology. Some of these feedbacks may already be occurring, as shown for example by recent evidence of C losses from Alaskan tundra ecosystems during the warm years of the 1980s and early 1990s, with smaller losses or net C accumulation in the cooler, wetter mid-1990s (Vourlitis & Oechel 1999). Simulation models of the Arctic region also predict changes in C fluxes in response to climate, although the predictions are often smaller than expected by extrapolation from short-term process studies (e.g. McKane et al. 1997a).

A major difficulty in predicting feedbacks on climate change from the Arctic as a whole is that current models simulate the Arctic as consisting of only one or a few similar ecosystem types, yet we know that variables like net primary production differ by more than two orders of magnitude within this region (Bliss et al. 1981). The major classes of Arctic vegetation, including tundra, polar desert and semidesert, differ dramatically in their plant functional type composition, and the accumulation of organic matter in Arctic soils varies similarly (Jonasson & Shaver in press; Shaver & Jonasson in press). A key issue for improving predictions of feedbacks on global change, therefore, is improving our understanding of how different Arctic ecosystem types might respond to broad, regional changes in climate.

Our ability to generalize about responses of Arctic ecosystems to climate change has been improved recently by the completion of several multiyear, whole-ecosystem experiments. While not identical in design, these experiments involved comparable manipulations of key variables like light, temperature and water and nutrient inputs. Their general aim was to evaluate the responsiveness of contrasting ecosystems to change in these variables. The same variables are expected to change as part of global climate change, through warming of the atmosphere, changes in cloudiness, and effects of temperature or precipitation on rates of nutrient cycling (Chapin et al. 1995). The experiments were not intended as simulations of specific scenarios for climate change, however. Their primary value is through the insights they provide into relative importance of major climate-related controls over these ecosystems, and interactions among these controls over time.

This paper summarizes results from experiments in tundra ecosystems at Abisko, Sweden, and Toolik Lake, Alaska (Chapin et al. 1995; Shaver et al. 1998; Jonasson, Michelsen et al. 1999), where experimental designs were similar and the measured responses were often directly comparable. Other multiyear experiments with similar design include those in Svalbard and in subalpine vegetation near Abisko (Wookey et al. 1993; Parsons, Welker et al. 1994; Potter et al. 1995; Jonasson, Lee et al. 1996; Press et al. 1998; Robinson et al. 1998), and the International Tundra Experiment (ITEX; Henry & Molau 1997; Arft et al. in press).

Sites and experiments

Toolik Lake and Abisko are at similar latitudes (68°38′N and 68°20′N, respectively) but are widely separated in longitude (149°34′W versus 18°30′E). Elevation at the Toolik site ranges from 730–780 m, and at Abisko from 400–1150 m. Vegetation at both sites includes diverse tundra types (Table 1). At Toolik, the ecosystems subjected to manipulation were (1) a wet sedge tundra consisting mainly of rhizomatous sedges, (2) a moist tussock tundra including sedges and deciduous and evergreen shrubs, and (3) a dry lichen-evergreen heath. At Abisko the ecosystems included a heath and a fellfield, both dominated by the evergreen *Cassiope tetragona*.

Temperature, light and nutrient availability were manipulated similarly. Air temperature was increased with clear polyethylene greenhouses. At Toolik these were approximately 3 × 5 m, 0.5 m high at the sides and 1 m high in the centre, while at Abisko they were 1.2 × 1.2 m with the polyethylene reaching either to the ground or to 5–10 cm above-ground (raising temperatures to two different levels at Abisko). Light was manipulated by shading, with greenhouse shade cloth at Toolik (3 × 5 m frames) and with hessian at Abisko (1.2 × 1.2 m frames). Nutrients were added as granular fertilizer (Toolik) or dissolved in water (Abisko). At Toolik the rates of addition were $10\,g\,m^{-2}y^{-1}$ N and $5\,g\,m^{-2}y^{-1}$ P (except in the first year when $10\,g\,m^{-2}$ P were added). At Abisko

Table 1. Vegetation characteristics at the study sites. Original data in Shaver & Chapin (1992), Chapin et al. (1995), Shaver et al. (1998), and Jonasson, Michelsen et al. (1999).

Site	Tundra type	Plant functional types	Dominant species	Above-ground vascular NPP ($g\,m^{-2}\,y^{-1}$)	Above-ground vascular biomass ($g\,m^{-2}$)
Toolik Lake	Moist tussock	Tussock-forming sedges, evergreen and deciduous dwarf shrubs, mosses	*Eriophorum vaginatum*, *Ledum palustre*, *Vaccinium vitis-idaea*, *Betula nana*	140	800
	Wet sedge	Rhizomatous sedges, mosses	*Eriophorum spp*, *Carex spp.*	60	60
	Lichen-heath	Evergreen and deciduous dwarf shrubs, lichens	*Loisleuria procumbens*, *Ledum palustre*, *Betula nana*	40	100
Abisko	Heath	Evergreen dwarf shrubs, mosses	*Cassiope tetragona*, *Vaccinium spp.*, *Empetrum hermaphroditum*	n.d.	600
	Fellfield	Evergreen and deciduous dwarf shrubs, mosses	*Cassiope tetragona*, *Salix polaris*, *Salix herbacea*	n.d.	200

the rates were 4.9 g m^{-2} N and 1.3 g m^{-2} P in the first year and 10 g $m^{-2}y^{-1}$ N and 2.6 g $m^{-2}y^{-1}$ P in succeeding years. Fertilizer addition at Abisko also included 9.0 g $m^{-2}y^{-1}$ K and 0.8 g $m^{-2}y^{-1}$ Mg. The greenhouse and shade treatments were maintained annually from soon after snowmelt to late August or early September; fertilizers were added each year after snowmelt except in the year of the principal harvest (1993) at Abisko.

Effects of these treatments have been described elsewhere (Havström et al. 1993; Jonasson, Havström et al. 1993; Chapin et al. 1995; Michelsen et al. 1996; Graglia et al. 1997; Shaver et al. 1998). In general the treatments produce the intended effects. Greenhouses warmed the air by 2.5–5.0°C and the soil (at 4 cm) by 0.4–2.0°C, with greater warming in closed greenhouses than in those with a gap at the soil surface. At Toolik, which is underlain by permafrost, annual soil thaw was increased in the greenhouses from 38 to 43 cm. Shading reduced photosynthetically active photon flux by 50%, and the fertilizer increased N and P inputs to at least 10 times the initial annual uptake requirements of the vegetation. The major confounding effect was the reduction in photon flux in the greenhouses by about 10% at Abisko and up to 30% at Toolik (the difference was due to the thickness of the polyethylene). McKane et al. (1997b) simulated the effects of the greenhouse warming without this reduction in light and concluded that the net C losses in the greenhouse at Toolik were increased due to reduced C fixation at lower light. Additional effects of the greenhouses, such as those due to reduced UV-B irradiance (Björn et al. 1998), were not studied.

The experiments began in different years and were sampled after different periods. Treatment of tussock tundra at Toolik began in 1981, with harvests in 1982, 1983, 1984, 1989 and 1995 (after 2, 3, 4, 9 and 15 years). Treatments in other ecosystems at Toolik began in 1989, with harvests in wet sedge tundra in 1994 (6 years) and lichen-heath in 1996 (8 years). At Abisko, treatments began in 1989 with a harvest in 1993 (5 years) and a second harvest in 1998 from which results are not yet available.

Responses: plant species and vegetation

Overall responses to the treatments were similar in all five ecosystems (Table 2). Fertilization with N and P consistently caused the largest changes, increasing primary production and total or above-ground biomass. Temperature responses were next in magnitude, with smaller increases in production or biomass of vascular plants with higher temperatures. The temperature response was similar in magnitude to the fertilizer response only for total vascular and evergreen biomass in the Abisko fellfield, where evergreens responded strongly to warming while other plant forms responded more strongly to fertilizer (Jonasson, Michelsen et al. 1999). (The evergreen *Vaccinium vitis-idaea* responded most strongly at Abisko [Graglia et al. 1997] and was also the only species to increase in response to warming in moist tundra at Toolik Lake [Chapin et al. 1995.]) Moss biomass either decreased or was unaffected by the warming at all sites. Shading had the least effect on production and biomass, causing a reduction only after 9 years at 50% light in the tussock tundra (vascular plus nonvascular plants) and after 8 years in the lichen-heath at Toolik Lake (vascular plants only).

The production and biomass changes in these experiments are consistent with the hypothesis that nutrient availability is the principal limiting factor in all five ecosystems, and that temperature and light are only secondarily limiting over the 3–15 years of sampling. This conclusion is also consistent with the changes in overall vegetation N and P mass and concentration that were observed (Table 2). In the fertilizer treatments, increases in production and biomass were accompanied by increases in both N and P mass and N and P concentration. In the greenhouse treatments where production and biomass increased, there were only small increases in N and P mass, and N and P concentration often decreased. In the shade treatments where production and biomass decreased, N and P mass either did not change or decreased less than production or biomass, so concentration increased. In wet sedge tundra at Toolik and at both Abisko sites, biomass and N and P mass actually increased (nonsignificantly) with shading.

The greatest difference between the Toolik and Abisko sites was in their temperature response and especially in the temperature × fertilizer interaction (Table 2). Increases in production and biomass in the greenhouses were greater at Abisko, and at Abisko the individual temperature and fertilizer responses were additive when these treatments were combined in both the heath and the fellfield (Jonasson, Michelsen et al. 1999).

Table 2. Summary of vegetation and soil responses to the experimental treatments at Abisko, Sweden, and Toolik Lake, Alaska. Upward-pointing arrows indicate increases, downward-pointing arrows indicate decreases in the indicated variables. Vegetation variables: NPP = Above-ground vascular net primary production; Biomass = live vascular biomass including above-ground parts, roots and below-ground stems at Abisko, and above-ground parts and below-ground stems only at Toolik Lake; N mass and P mass = total N and P mass in live vascular biomass; %N and %P = N and P concentration (% dry mass) in live vascular biomass. Soils variables: Inorganic N = sum of extractable NO3 and NH4; Inorganic P = extractable PO4; N min = Net N mineralization (buried bag method); Microbial C, N, and P = C, N, or P mass in microbial biomass. Original data in Chapin et al. (1995), Shaver et al. (1998; unpubl. data), and Jonasson, Michelsen et al. (1999).

			Vegetation						Soils					
Treatment	Site	Tundra type	NPP	Biomass	N mass	P mass	%N	%P	Inorganic N	Inorganic P	N min	Microbial C	Microbial N	Microbial P
Fertilizer	Toolik Lake	Tussock	↑↑↑	↑	↑↑↑	↑↑↑	↑↑	↑↑↑	↑↑↑	↑↑↑				
		Wet sedge	↑↑↑	↑↑	↑↑↑	↑↑↑	↑↑	↑↑↑	↑↑↑	↑↑↑				
		Lichen-heath	↑↑↑	↓										
	Abisko	Heath		↑↑	↑↑↑	↑↑↑	↑	↑↑	↔	↑↑		↑	↔	↑↑
		Fellfield		↑↑	↑↑↑	↑↑↑	↑	↑↑	↑	↑↑		↑	↑	↑↑
Greenhouse	Toolik Lake	Tussock	↑	↑	↔	↔	↔	↔	↔	↔				
		Wet sedge	↑	↑	↑	↑	↓	↔	↔	↔	↑			
	Abisko	Heath		↑	↑	↑	↓	↓	↔	↑↑		↔	↔	↔
		Fellfield		↑↑	↑	↑	↔	↔	↑	↔		↔	↔	↔
Shade	Toolik Lake	Tussock	↓	↓	↔	↔	↑	↑	↔	↔				
		Wet sedge	↔	↔	↔	↔	↑	↔	↔	↔				
		Lichen-heath	↓	↔										
	Abisko	Heath		↔	↔	↔	↔	↔	↑↑	↑↑		↑	↑	↑
		Fellfield		↔	↔	↔	↑	↑	↑↑	↑↑		↔	↔	↑↑
Greenhouse + NP Fert	Toolik Lake	Tussock	↑↑↑	↔	↑↑	↑↑	↑↑	↑↑	↑↑	↑↑				
		Wet sedge	↑↑	↑↑	↑↑	↑↑	↑↑	↑↑						
	Abisko	Heath		↑↑↑	↑↑↑	↑↑↑	↔	↑	↑↑	↑↑		↑	↔	↑↑
		Fellfield		↑↑↑	↑↑↑	↑↑↑	↔	↑	↑↑	↑↑		↑	↑	↑↑
Shade + NP Fert	Abisko	Heath		↔	↑↑	↑↑	↑	↑↑	↑↑↑	↑↑↑		↑	↔	↑↑
		Fellfield		↔	↑↑	↑↑	↑↑	↑↑↑	↑↑	↑↑		↔	↑	↑↑

At Toolik Lake in both moist and wet sedge tundras (Chapin et al. 1995; Shaver et al. 1998), there was a significant *negative* temperature × fertilizer interaction, such that production and biomass were lower in the fertilized and warmed plots than in either individual treatment. Furthermore, at Abisko the increases in biomass with warming and with warming plus fertilizer were accompanied by nearly proportional increases in N and P uptake, so the changes in N and P concentration were smaller than at the Toolik sites. There are several possible explanations for this difference between sites, but the most likely include:

(1) Soil temperatures are lower at Toolik, which is underlain by permafrost. The effect of warming on nutrient mineralization in the soil (discussed below) may be smaller at Toolik than at Abisko, leading to a smaller increase in nutrient uptake in the warmed plots, and a smaller increase in biomass.
(2) The fertilizer treatment at Toolik, with or without warming, fully overcame the initial nutrient limitation so that factors other than nutrients or temperature were limiting to production and biomass in the fertilized plots at Toolik. At Abisko, however, the fertilizer treatment did not fully eliminate the nutrient limitation, so that additional increases in biomass were possible with warming plus fertilizer.
(3) The higher plant N and P concentrations in the warmed plus fertilized plots at Toolik may have led to increased respiratory C losses (linked to higher maintenance costs of high-nutrient tissues), which would counter nutrient-stimulated growth increases. Air temperatures were also higher at Toolik than at Abisko, which would lead to even higher respiration rates.

In sum, the differences in the temperature responses of vegetation at Abisko versus Toolik may be tied to differences in temperature effects on soil nutrient mineralization and plant nutrient use, not to the direct effect of temperature on plant C accumulation.

At the two Abisko sites, there also was a negative interaction between the shade and the fertilizer treatments, such that biomass did not increase above controls when these treatments were combined despite large increases in N and P mass and concentration (Table 2). This response indicates that, at least at the low light levels in the shade treatments, the vegetation was unable to take advantage of greater nutrient availability with fertilization.

The greatest differences between Abisko and Toolik were changes in species composition that had no clear impact on vegetation biomass or nutrient mass. In particular, the fertilizer treatment had a major impact on species composition at Toolik but relatively little impact at Abisko. In the tussock tundra at Toolik, by the ninth year of treatment the vegetation was dominated (65% of vascular biomass) by the deciduous shrub *Betula nana*, a species that accounted for only 25% of biomass in control plots (Chapin et al. 1995). By the 15th year the tussock vegetation was over 90% *B. nana*. Although *B. nana* also grows at the Abisko heath site, it did not respond strongly to fertilizer treatment there (Graglia et al. 1997). Similarly, the lichen-heath at Toolik responded to fertilizer addition by essentially complete replacement of the dominant evergreens with the grass *Hierochloe alpina*. At Abisko the species composition of both sites did change slightly with fertilizer treatment (e.g. forb plus graminoid biomass increased) but the dominant species (*Cassiope tetragona*) remained dominant. Fertilizer experiments at other sites near Abisko, however, have shown greater increases in grasses or sedges (Jonasson 1992; Parsons, Press et al. 1995).

In the longer term the changes in species composition in the Toolik sites may cause a divergence between Toolik and Abisko in their responsiveness to the experimental treatments. At Toolik the wet sedge, lichen-heath and tussock tundras have been followed for 6, 8 and 15 years, respectively. Preliminary results from 10 years of treatments at the Abisko heath site show a similar pattern of response to that seen after 5 years, but with a stronger increase in the deciduous dwarf shrub *Vaccinium uliginosum* in warmed plots (A. Michelsen, unpubl. data). Because all of the dominant species in these communities are long-lived, with large amounts of slowly-replaced stem, leaf and below-ground biomass, there may be a considerable lag before changes in growth are fully reflected in changes in biomass (Chapin et al. 1995; Jonasson 1997).

Changes in species composition in response to warming or fertilizer addition in the low Arctic also differ from the high Arctic. At Toolik Lake where there is little bare ground, species richness was consistently reduced due to loss of herb species that are minor contributors to biomass and production (Chapin et al. 1995; Shaver unpubl. data). In Svalbard where bare ground is available for colonization, species richness increases with fertilizer addition (Robinson et al. 1998). On the other hand, cover of *Dryas octopetala* in fertilized and watered plots in Svalbard was reduced after a wet and mild growing season, probably because of delayed winter hardening associated with the treatment (Robinson et al. 1998), suggesting that extreme climatic events can cause pronounced stepwise changes in the communities.

Responses: soil nutrients and microbes

The fertilizer treatments increased inorganic N and P pools at Toolik and the Abisko fellfield, even as plant uptake and microbial immobilization also increased (Table 2). The magnitude of these changes was smaller, though, at Abisko, and in the heath at Abisko there was no change in inorganic N (Jonasson, Michelsen et al. 1999; Schmidt et al. 1999). The lack of a fertilizer effect on inorganic N at the Abisko heath, combined with the increases in vegetation biomass, N mass and P mass, suggests that vegetation was still a strong nutrient sink even after 5 years of treatment, and was still capable of reducing available soil N to the level of unfertilized soil. The large accumulations of inorganic N in the other sites, particularly at Toolik, suggest that they were becoming nutrient-saturated.

The shade and greenhouse treatments had different effects on inorganic N and P pools at Toolik versus Abisko (Table 2). At Toolik there was no response to either treatment, while at Abisko both inorganic pools increased with shading, as did inorganic P and, to a lesser degree, inorganic N, with warming. The responses to shade reflect continued vegetation nutrient uptake at Toolik despite reduced productivity there, and perhaps reduced uptake at Abisko. The responses to warming are more complex and probably represent different combinations of increased vegetation uptake and increased N and P mineralization with warming. The fact that vegetation biomass, N mass and P mass consistently increased with warming at Abisko even as inorganic N increased in the fellfield and inorganic P increased in the heath suggests that the warming increased mineralization more than it increased uptake there, while at Toolik vegetation uptake paralleled the increased mineralization.

Microbial immobilization clearly did not drive changes in inorganic N and P pools, as microbial C, N, and P pools increased only when the inorganic pools also increased (Table 2; data available only from Abisko). On the other hand, increases in N mineralization in the greenhouses in the Toolik wet sedge tundra did not cause any corresponding increase in inorganic N pools. The most likely explanation for this pattern is that plants are much more effective competitors for inorganic N and P than expected, such that the changes in both soil-available and microbial pools are inversely related to the plant uptake demand (Jonasson, Michelsen et al. 1999). Differences between Toolik and Abisko in treatment effects on inorganic N and P pools could also be due, in part, to differences in element losses from the treated plots by leaching and/or denitrification. These losses were not measured, although the Abisko sites were not underlain by permafrost, so deeper drainage was possible.

Synthesis

Clearly, a diverse group of five contrasting low Arctic ecosystems on two continents respond similarly when subjected to similar manipulations. This result increases our confidence in predictions of similar responses to climate change over at least the low Arctic, that part of the Arctic where most of the organic matter, C and nutrients are held. Comparable results are still needed from the high Arctic, although recent work suggests that these areas should respond in similar ways (Robinson et al. 1998). In this regard it is less important that the experiments represent explicit simulations of global change than it is important that the experiments cover a broad spectrum of key variables (nutrients, temperature and light), and that the similarities in response among sites were consistent across the full spectrum of treatments.

At the 5–15 year time scale of these experiments, soil nutrient availability and vegetation nutrient demand are clearly of dominant importance. Although temperature and light do affect both vegetation and soils, their effects are relatively small at this time scale and clearly interactive with N and P availability. From the perspective of the vegetation, it appears that changes in N and P availability can cause large and relatively rapid changes in production and/or biomass even if ambient temperature regimes and light levels are unchanged. The vegetation response to warming is constrained by the plants' ability to accumulate additional N and P, such that over several years the effects of temperature on soil processes may be more important than direct effects on plant growth. At low light, continued uptake of N and P in amounts similar to control conditions allows productivity to continue at near control rates, so that even at 50% reduction in light it takes several years for a significant reduction in biomass to occur. The importance of nutrient limitation is also reflected in the soils, where the changes in inorganic and microbial nutrient pools are consistent with highly effective plant uptake in relation to temperature- and light-related changes in uptake requirement.

Additional research is needed to explain the relatively small differences in response that were observed between Toolik Lake and Abisko, but these differences are consistent with the interpretation that nutrient limitation is dominant at both sites. At the levels of fertilizer that were used, this limitation may have been completely overcome at Toolik, while at Abisko the continued increases in biomass with warming plus fertilizer suggest that higher levels of fertilizer might continue to elicit responses. The greater warming responses at Abisko could also be due as much to the effect of temperature on soil nutrient availability and uptake as to direct effects of temperature on photosynthesis and growth, which is consistent with the changes in plant and soil N and P pools that were observed and with the observation that soils at Toolik are wetter and colder at depth, due to permafrost.

A final overall conclusion is that long-term (multiyear) changes in the C cycle of Arctic ecosystems are tightly linked to changes in the cycles of N and P, and thus it is essential to understand long-term controls over each of these cycles and the linkages between them in order to predict long-term change in organic matter cycling. Clearly, there must be a correlation between short-term and long-term controls on element cycles, but we need long-term experiments to understand the mechanisms that determine these correlations, and to understand how long-term change is constrained by interactions among element cycles.

References

Arft, A. M. et al. (29 authors) in press: Response patterns of tundra plant species to experimental warming: a metaanalysis of the International Tundra Experiment. *Ecology.*

Björn, L. O., Callaghan, T. V., Gehrke, C., Johanson, U., Sonesson, M. & Gwynn-Jones, D. 1998: The problem of ozone depletion in northern Europe. *Ambio 27*, 275–279.

Bliss, L. C., Heal, O. W. & Moore, J. J. (eds.) 1981: *Tundra ecosystems: a comparative analysis*. Cambridge: Cambridge University Press.

Chapin, F. S., Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J. & Laundre, J. A. 1995: Responses of Arctic tundra to experimental and observed changes in climate. *Ecology 76*, 694–711.

Graglia, E., Jonasson, S., Michelsen, A. & Schmidt, I. K. 1997: Effects of shading, nutrient application, and warming on leaf growth and shoot densities of dwarf shrubs in two Arctic/alpine plant communities. *Ecoscience 4*, 191–198.

Havström, M., Callaghan, T. V. & Jonasson, S. 1993: Differential growth responses of *Cassiope tetragona*, an Arctic dwarf-shrub, to environmental perturbations among three contrasting high- and subArctic sites. *Oikos 66*, 389–402.

Henry, G. H. R. & Molau, U. 1997: Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biol. 3 (suppl. 1)*, 1–10.

Jonasson, S. 1992: Growth responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos 63*, 420–429.

Jonasson, S. 1997: Buffering of Arctic plant responses in a changing climate. In W. C. Oechel et al. (eds.): *Global Change and Arctic Terrestrial Ecosystems*. Pp. 365–380. New York: Springer.

Jonasson, S. & Michelsen, A. 1996: Nutrient cycling in subArctic and Arctic ecosystems, with special reference to the Abisko and Torneträsk region. In P. S. Karlsson & T. V. Callaghan (eds.): *Plant ecology in the subArctic Swedish Lapland. Ecol. Bull. 45*, 45–53.

Jonasson, S. & Shaver, G. R. in press: Within-stand nutrient cycling in Arctic and boreal herbaceous and forested wetlands. *Ecology.*

Jonasson, S., Havström, M., Jensen, M. & Callaghan, T. V. 1993: In situ mineralization of nitrogen and phosphorus of Arctic soils after perturbations simulating climatic change. *Oecologia 95*, 179–186.

Jonasson, S., Lee, J. A., Callaghan, T. V., Havström, M. & Parsons, A. N. 1996: Direct and indirect effects of increasing temperatures on subArctic ecosystems. In P. S. Karlsson & T. V. Callaghan (eds.): *Plant ecology in the subArctic Swedish Lapland. Ecol. Bull. 45*, 180–191.

Jonasson, S., Michelsen, A., Schmidt, I. K. & Nielsen, E. V. 1999: Responses in microbes and plants to changes temperature, nutrient, and light regimes in the Arctic. *Ecology 80*, 1828–1843.

McKane, R. B., Rastetter, E. B., Shaver, G. R., Nadelhoffer, K. J., Giblin, A. E. & Laundre, J. A. 1997a: Reconstruction and analysis of historic changes in carbon storage in Arctic tundra. *Ecology 78*, 1188–1198.

McKane, R. B., Rastetter, E. B., Shaver, G. R., Nadelhoffer, K. J., Giblin, A. E. & Laundre, J. A. 1997b: Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology 78*, 1170–1187.

Michelsen, A., Jonasson, S., Sleep, D., Havström, M. & Callaghan, T. V. 1996: Shoot biomass, ^{13}C, nitrogen, and chlorophyll responses of two Arctic dwarf shrubs to in situ shading, nutrient application, and warming simulating climatic change. *Oecologia 105*, 1–12.

Parsons, A. N., Press, M. C., Wookey, P. A., Welker, J. M., Robinson, C. H., Callaghan, T. V. & Lee, J. A. 1995: Growth responses of *Calamagrostis lapponica* to simulated environmental change in the sub-Arctic. *Oikos 72*, 61–66.

Parsons, A. N., Welker, J. M., Wookey, P. A., Press, M. C., Callaghan, T. V. & Lee, J. A. 1994: Growth responses of four sub-Arctic dwarf shrubs to simulated environmental change. *J. Ecol. 82*, 307–318.

Potter, J. A., Press, M. C., Callaghan, T. V. & Lee, J. A. 1995: Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-Arctic. *New Phytol. 131*, 533–541.

Press, M. C., Potter, J. A., Burke, M. J. W., Callaghan, T. V. & Lee, J. A. 1998: Responses of a subArctic dwarf heath community to simulated environmental change. *J. Ecol. 86*, 315–327.

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

Schmidt, I. K., Jonasson, S. & Michelsen, A. 1999: Mineralization and microbial immobilization of N and P in Arctic soils in relation to season, temperature, and nutrient amendment. *Appl. Soil Ecol. 11*, 147–160.

Shaver, G. R. & Chapin, F. S. 1991: Production/biomass relationships and element cycling in contrasting Arctic vegetation types. *Ecol. Monogr. 61*, 1–31.

Shaver, G. R. & Jonasson, S. in press: Productivity of Arctic ecosystems. In H. Mooney, J. Roy & B. Saugier (eds.): *Terrestrial Global Productivity*. New York: Academic Press.

Shaver, G. R., Johnson, L. C., Cades, D. H., Murray, G., Laundre, J. A., Rastetter, E. B., Nadelhoffer, K. J. & Giblin, A. E. 1998: Biomass accumulation and CO_2 flux in three Alaskan wet sedge tundras: responses to nutrients, temperature, and light. *Ecol. Monogr. 68*, 75–99.

Vourlitis, G. L. & Oechel, W. C. 1999: Eddy covariance measurements of CO_2 and energy fluxes of an Alaskan tundra ecosystem. *Ecology 80*, 686–701.

Wookey, P. A., Parsons, A. N., Welker, J. M., Potter, J. A., Callaghan, T. V., Lee, J. A. & Press, M. C. 1993: Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. *Oikos 67*, 490–502.