Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities

Citation for published version:
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' Environmental Research Letters, vol 6, no. 4, 045509, pp. -., 10.1088/1748-9326/6/4/045509

Digital Object Identifier (DOI):
10.1088/1748-9326/6/4/045509

Link:
Link to publication record in Edinburgh Research Explorer

Document Version:
Publisher final version (usually the publisher pdf)

Published In:
Environmental Research Letters

IOP PUBLISHING ENVIRONMENTAL RESEARCH LETTERS

Environ. Res. Lett. **6** (2011) 045509 (15pp) doi:10.1088/1748-9326/6/4/045509

Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities

Isla H Myers-Smith[1,2], Bruce C Forbes[3], Martin Wilmking[4], Martin Hallinger[4], Trevor Lantz[5], Daan Blok[6], Ken D Tape[7], Marc Macias-Fauria[8], Ute Sass-Klaassen[6], Esther Lévesque[9], Stéphane Boudreau[10], Pascale Ropars[10], Luise Hermanutz[11], Andrew Trant[11], Laura Siegwart Collier[11], Stef Weijers[12], Jelte Rozema[12], Shelly A Rayback[13], Niels Martin Schmidt[14], Gabriela Schaepman-Strub[15], Sonja Wipf[16], Christian Rixen[16], Cécile B Ménard[17], Susanna Venn[18], Scott Goetz[19], Laia Andreu-Hayles[20,21], Sarah Elmendorf[22], Virve Ravolainen[23], Jeffrey Welker[24], Paul Grogan[25], Howard E Epstein[26] and David S Hik[1]

[1] Department of Biological Sciences, University of Alberta, Edmonton, AB, T6G 2E9, Canada
[2] Département de biologie, Faculté des Sciences, Université de Sherbrooke, Sherbrooke, QC, J1K 2R1, Canada
[3] Arctic Centre, University of Lapland, Rovaniemi, FI-96101, Finland
[4] Institute for Botany and Landscape Ecology, Ernst Moritz Arndt University Greifswald, Greifswald, 17487, Germany
[5] School of Environmental Studies, University of Victoria, Victoria, BC, V8W 3R4, Canada
[6] Centre for Ecosystem Studies, Wageningen University, Wageningen, 6700 AA, The Netherlands
[7] Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[8] Biodiversity Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[9] Département de Chimie-biologie, Université du Québec à Trois-Rivières, Trois-Rivières, QC, G9A 5H7, Canada
[10] Chaire de recherche nordique en écologie des perturbations, Centre d'études nordiques and Département de biologie, Université Laval, Québec, QC, G1V 0A6, Canada
[11] Department of Biology, Memorial University, St John's, NL, A1B 3X9, Canada
[12] Faculty of Earth and Life Sciences, Vrije Universiteit, Amsterdam, 1081 HV, The Netherlands
[13] Department of Geography, University of Vermont, Burlington, VT 05405, USA
[14] Department of Bioscience, Aarhus University, DK-4000 Roskilde, Denmark
[15] Institute of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, CH-8057, Switzerland
[16] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Davos, CH-7260, Switzerland
[17] School of GeoSciences, University of Edinburgh, Edinburgh EH9 3JN, UK
[18] Research Centre for Applied Alpine Ecology, Department of Botany, La Trobe University, Bundoora, VIC, 3086, Australia
[19] Woods Hole Research Center, Falmouth, MA 02540-1644, USA
[20] Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY 10964, USA
[21] Institut Català de Ciències del Clima (IC3), 08005 Barcelona, Catalonia, Spain
[22] Department of Geography, University of British Columbia, Vancouver, BC, V6T 1Z2, Canada
[23] Department of Biology, University of Tromsø, Tromsø, N-9037, Norway
[24] Environment and Natural Resources Institute and Biological Sciences Department, University of Alaska Anchorage, Anchorage, AK 99501, USA
[25] Department of Biology, Queen's University, Kingston, ON, K7L 3N6, Canada
[26] Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904-4123, USA

Received 2 September 2011
Accepted for publication 17 November 2011
Published 20 December 2011
Online at stacks.iop.org/ERL/6/045509

Abstract

Recent research using repeat photography, long-term ecological monitoring and dendrochronology has documented shrub expansion in arctic, high-latitude and alpine tundra ecosystems. Here, we (1) synthesize these findings, (2) present a conceptual framework that identifies mechanisms and constraints on shrub increase, (3) explore causes, feedbacks and implications of the increased shrub cover in tundra ecosystems, and (4) address potential lines of investigation for future research. Satellite observations from around the circumpolar Arctic, showing increased productivity, measured as changes in 'greenness', have coincided with a general rise in high-latitude air temperatures and have been partly attributed to increases in shrub cover. Studies indicate that warming temperatures, changes in snow cover, altered disturbance regimes as a result of permafrost thaw, tundra fires, and anthropogenic activities or changes in herbivory intensity are all contributing to observed changes in shrub abundance. A large-scale increase in shrub cover will change the structure of tundra ecosystems and alter energy fluxes, regional climate, soil–atmosphere exchange of water, carbon and nutrients, and ecological interactions between species. In order to project future rates of shrub expansion and understand the feedbacks to ecosystem and climate processes, future research should investigate the species or trait-specific responses of shrubs to climate change including: (1) the temperature sensitivity of shrub growth, (2) factors controlling the recruitment of new individuals, and (3) the relative influence of the positive and negative feedbacks involved in shrub expansion.

Keywords: shrubs, vegetation, tundra, Arctic, alpine, climate change, feedbacks, ecosystem structure, ecosystem function, disturbance

1. Introduction

High-latitude ecosystems have experienced warmer temperatures in recent decades, and are projected to continue to warm in the future [1]. The implications of this warming for tundra ecosystems are widespread and diverse [2], including permafrost thaw [3], more frequent tundra fires [4] and changing tundra vegetation [5]. Climate change is projected to alter ecosystem boundaries between the various tundra vegetation communities by increasing the relative abundances and cover of shrub species (such as birch, willow and alder: *Betula*, *Salix* and *Alnus* spp. respectively).

Shrubs are woody plants with diverse growth forms including tall multi-stemmed shrubs (0.4–4.0 m), erect dwarf shrubs (0.1–0.4 m) and prostrate dwarf shrubs (<0.1 m) that grow laterally along the ground surface. In this paper we refer to erect dwarf shrubs and prostrate dwarf shrubs simply as dwarf shrubs. Shrub species are often the tallest plants occupying tundra ecosystems upslope or northward of the treeline ecotone, and can form dense thickets with closed canopies in suitable habitats. Shrub species differ in their potential to gain dominance in tundra ecosystems, and some shrub species have a competitive advantage over other tundra plants. In warming and fertilization experiments, woody deciduous shrubs have been reported to increase in canopy cover and height to dominate treatment plots [6–9]. Certain shrub species such as the dwarf birch *Betula nana* can take advantage of more favorable growing conditions, such as an increase in air temperature and nitrogen availability, by rapidly elongating 'short shoots'. These increases in cover and height potentially restrict the growth of other plant species by limiting light availability [6, 7, 10, 11]. The formation of a closed shrub canopy can drastically alter the structure and function of tundra ecosystems.

Changes to tundra vegetation structure, such as an increase in tall shrub species, may either mitigate or exacerbate warming in tundra ecosystems [10]. Shrubs modify a wide range of ecosystem processes including snow depth and associated hydrologic dynamics, nutrient exchange and associated net carbon balance, as well as albedo and associated energy fluxes. At present there is considerable uncertainty about the magnitude and direction of these feedbacks, and it is likely that different processes will drive feedbacks in opposite directions. However, dramatic changes to shrub abundance in tundra ecosystems could result in significant alterations to the global carbon cycle [9], surface reflectance [12] and tundra disturbance regimes [4]. In this review, we document current observations of changes in tundra shrubs, explore ecosystem processes modified by the shrub increases, and outline research priorities to advance a more synthetic understanding of the implications of increased tundra shrub cover.

2. Observations of shrub increase

Increases in shrub biomass, cover and abundance (colloquially termed *shrubification*) have been observed in many Arctic, high-latitude and alpine tundra ecosystems over the past century (table 1, figure 2) [13], including in northern Alaska (primarily alder) [14, 15], the western Canadian Arctic (primarily alder and willow) [16–19, 26], the Canadian High Arctic (dwarf willow and evergreen shrub species) [20, 21], northern Quebec (primarily birch) [22] and Arctic Russia (primarily willow) [23]. Studies in high-latitude mountain and other alpine ecosystems indicate the upslope advancement of willow and alder species in Alaska [24], the Yukon Territory [25], juniper in subarctic Sweden [27] and a variety of shrub species in the Alps [28–30]. In addition to these published studies, northern peoples are observing increases in shrub cover in their traditional lands [31, 32].

Table 1. Recent observations of shrub change in high-latitude or alpine tundra ecosystems.

Region	Site	Shrub change observed	Time period	References
Alaska	(1) Brooks Range, North Slope of Alaska 68.15–69.18 N 159.55–152.30 W	Expanding and stable patches of *Alnus viridis* subsp. *fruticosa*, *Salix* spp. and *Betula* spp.	~50 yr	[14, 15, 132], Hallinger, Tape, Wilmking *et al* unpubl. data
	(2) 'Ice Cut', North Slope of Alaska 69.02 N 148.84 W	Increases in abundance of *Alnus* spp. Significant positive relationship between the *Alnus* ring-width chronology and June–July temperatures	~50 yr	Andreu-Hayles *et al* unpubl. data
	(3) Kenai Peninsula, southcentral Alaska 60.56 N 151.24 W	Expansion of alder shrub patches, new shrub cover at the shrubline ecotone	~50 yr	[24]
Western Canadian Arctic	(4) Herschel Island, Yukon 69.57 N 138.91 W	Increases in canopy height and cover of *Salix pulchra*, increases in patch size of *Salix richardsonii*	10–50 yr	[19]
	(5) Mackenzie Delta Region, NWT 68–69.5 N 32.5–35 W	Increased growth and reproduction of *Alnus viridis* subsp. *fruticosa* in tundra fire scars, and retrogressive thaw slumps	4–~30 yr	[16, 17]
		Increased abundance of tall shrubs in upland tundra in the NWT	~50 yr	Lantz unpubl. data
	(6) Parry Peninsula, NWT 69.43 N 124.88 W	Increase in cover of tall willows on a collapsing pingo	~50 yr	[18]
	(7) Kluane region 61.22 N 138.28 W	Increase in tundra shrubline (*Salix* spp.) in high-latitude mountain valleys	~30 yr	[25]
Central Canadian Arctic	(8) Daring Lake, NWT 64.87 N 111.57 W	Significant increase in ground cover but not height of *Betula glandulosa* plants within a variety of low Arctic tundra habitats	2006–11	Grogan unpubl. data
Eastern Canadian Arctic	(9) Kangiqsualujjuaq, Northern Québec 58.71 N 66.00 W	Increasing *Betula glandulosa* cover both by infilling and new colonization	1964–2003	[22]
	(10) Boniface River, Northern Québec 57.45 N 76.20 W	Increase in *Betula glandulosa* cover on well-drained non-forested sites	~50 yr	[144]
	(11) Northern Labrador, Nain, Nunatsiavut 56.53 N 61.70 W	Increase in *Betula glandulosa* growth rates based on growth rings, diverging patterns of radial growth and temperature, and movement upslope based on age structure	~50 yr	Trant *et al* unpubl. data
		Local increase in height and infilling of various shrub species based on local elder knowledge	~3–10 yr	Siegwart Collier *et al* unpubl. data
	(12) Nakvak Brook, Torngat Mt. NP, Nunatsiavut 58.63 N 63.35 W	Upslope movement and increased density of shrub cover	~50 yr	[137]
Canadian High Arctic	(13) Alexandra Fiord, Ellesmere Island 78.88 N 75.92 W	Increase in dwarf evergreen shrubs, and the dwarf willow *Salix arctica*	1981–2008	[20, 21]
Greenland	(14) Tasiilaq, Southeast Greenland 65.62 N 37.67 W	Stable cover of *Salix glauca*	40 yr	[138]

Table 1. (Continued.)

Region	Site	Shrub change observed	Time period	References
	(15) Zackenberg, Northeast Greenland 74.50 N 21.00 W	Little increase in *Salix arctica*, probably due to high density of muskoxen	1997–2008	Schmidt *et al* unpubl. data
European Arctic	(16) Isdammen and Ny-Ålesund, Svalbard 78.92 N 11.93 E	Increase in shoot length growth of *Cassiope tetragona*	∼20 yr	[68, 69], Weijers *et al*, unpubl. data, Buizer *et al* unpubl. data
	(17) Endalen, Svalbard 78.18 N 15.73 E	Increased shoot length and berry ripening *Empetrum nigrum* ssp *hermaphroditum* with experimental warming		
	(18) Abisko, Sweden 68.35 N 18.82 E			
	(19) Abisko, Sweden 68.21 N 18.49 E	Increases in shrub size and upslope movement of *Juniperus nana*. Growth of *Salix glauca, Betula nana*	∼50 yr	[27, 139], Hallinger *et al* unpubl. data
	(20) Cievrratjåkka, Sweden 68.01 N 18.81 E	Increasing cover of *Empetrum hermaphroditum* in Arctic mountain tundra in northern Sweden	20 yr	[123]
	(21) Varanger Peninsula, Norway 70.30 N 30.10 E	Increase in biomass of *Salix* spp. when released from herbivory by ungulates and/or small rodents	2006–8	[96]
Arctic Russia	(22) Yamal-Nenets Okrug, Russia 67.40 N 68.00 E and 68.54 N 69.57 E	Increases in annual growth of *Salix lanata* at all sites and *Alnus fruticosa* at the southernmost site on Yamal	∼50 yr	[23], Macias Fauria *et al* unpubl. data
	(23) Kytalyk reserve, Northeast Siberia 70.82 N 147.47 E	Positive correlations with annual growth rings and early summer temperatures for *Salix pulchra* and *Betula nana*. No data available on changes in shrub cover	∼60 yr of growth ring data	[34]
Non-polar alpine	(24) European Alps, Multiple sites	Increases in a variety of shrub species with land abandonment and climate change	∼50 yr	[28–30]
		Shrub species detected at higher elevations	100 yr	Wipf, Rixen and Stoecki unpubl. data
	(25) Australian Alps, Bogong High Plains, Australia 147.33 S 36.91 E	Increases in cover of a variety of species leading to vegetation community change	1936–80	[140]
	(26) Snowy Mountains, Australia 148.33 S 36.33 E	Lateral expansion of existing cover of a variety of shrub species	1959–2001	[141]

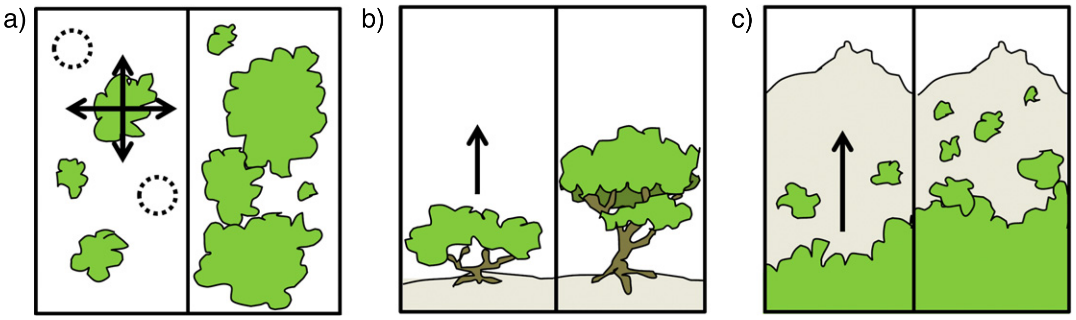

Figure 1. The three general categories of shrub increase including (a) infilling of existing patches, (b) increase in growth and (c) an advancing shrubline.

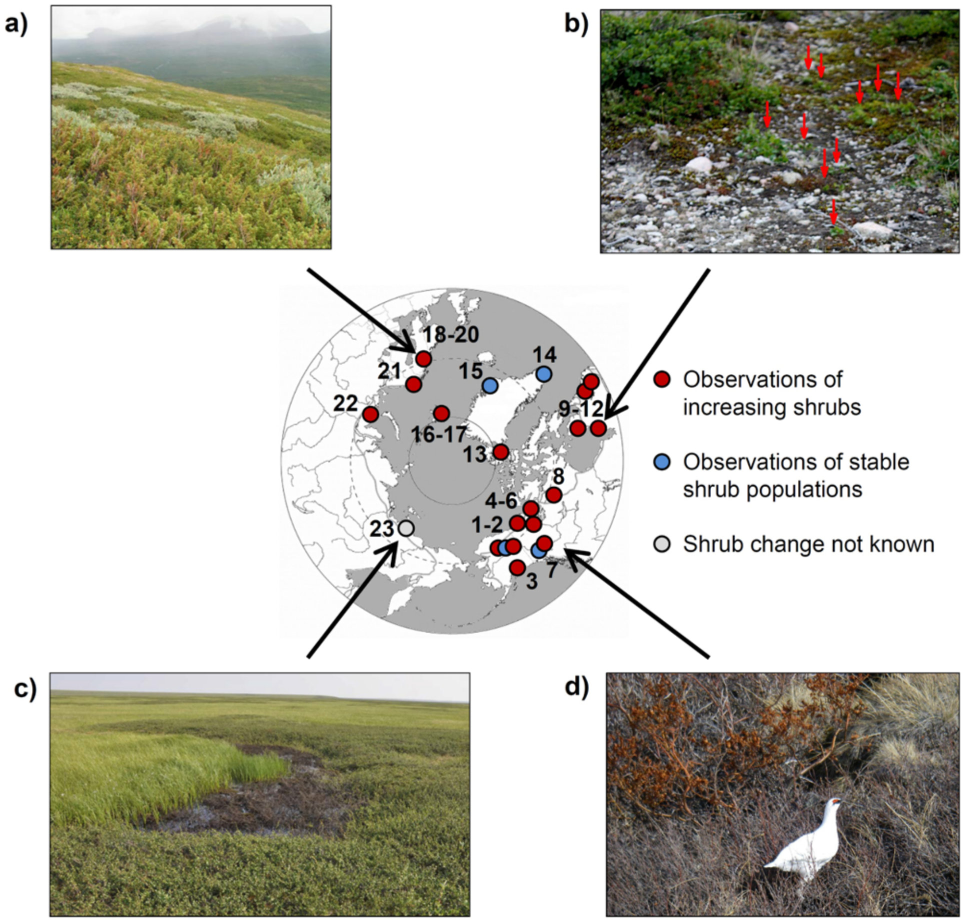

Figure 2. Map of sites at high latitudes where shrub change has been observed (table 1) and some examples of shrub change. (a) Shrubline advance of *Juniperus nana* shrubs, with proliferating patches of *Salix glauca* and *Betula nana* in the background on a south slope in the mountains of North Sweden about 900 m above sea level (©Hallinger, Abisko, Sweden, July 2008). (b) Trampling of ground cover on caribou trails allows for establishment of *Betula glandulosa* seedlings (indicated with red arrows) in Northern Québec (©Ropars, Boniface River, Québec, July 2010). (c) Dieback of *Betula nana* growing on previously ice-rich palsas with shallow active layers located between wet graminoid patches. As palsas degrade, *Betula nana* shrubs are gradually exposed to higher soil moisture and finally drowned in water, while *Eriophorum* and *Carex* species invade the areas. (©Schaepman-Strub, Kytalyk, Indigirka lowlands, NE Siberia, July 2010.) (d) Rock ptarmigan (*Lagopus muta*) standing in a patch of *Betula gladulosa* and next to a patch of *Salix pulchra*. Ptarmigan feed on buds in spring and are one of the major herbivores on willow species in the western North American Arctic [55]. (©Myers-Smith, Pika Valley, Yukon Territory, May 2007.)

Increases in shrub species can be classified into three categories involving either a change in clonal growth or seed recruitment (figure 1). These three categories are: (a) infilling, an increase in shrub cover through lateral growth of currently existing shrubs as well as recruitment between existing patches; (b) increase in growth potential, such as a change of growth form including an increase in the canopy height of shrub cover; and (c) an advanced shrubline, or colonization

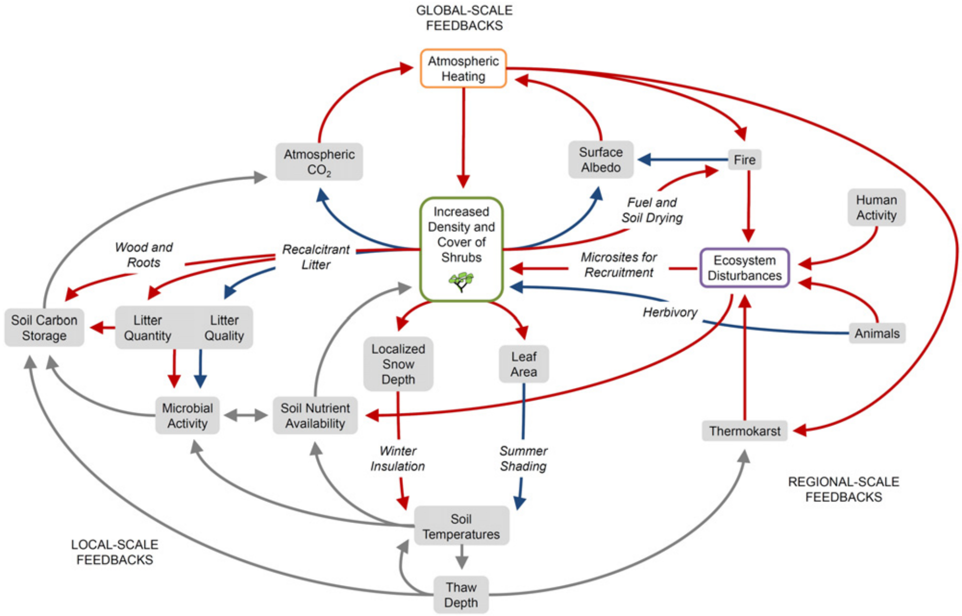

Figure 3. Potential feedbacks from increased density and cover of shrubs to ecosystems processes and properties. Red arrows indicate positive relationships, and blue arrows indicate negative relationships between the two connecting factors; gray arrows indicate as yet undetermined influences.

of areas beyond the previous range limit. Observations of all three types of shrub expansion have been reported in the literature (table 1). The low Arctic transition zone between tall and dwarf shrub tundra is predicted to respond most rapidly to warming [26, 33]; however, advances of shrub species northward into the high Arctic or upslope in mountainous regions are also projected [5].

The ground-based observations of shrub increase are supported by trends observed with satellite imagery [23, 34–36]. Multi-decadal records of the normalized difference vegetation index (NDVI), an indicator of vegetation greenness, show a greening of the Arctic tundra at sites in Alaska, western Canada and Siberia [35–42]. However, the spatial resolution of continuous long-term satellite records (i.e. AVHRR, MODIS or Landsat) covering timespans relevant to climate warming is coarse (250 m–8 km) compared to the spatial heterogeneity of shrub patches in tundra ecosystems (1–200 m) [26]. Changes in NDVI observed using these larger pixel sizes integrate various factors at the landscape scale, including water bodies and changes in NPP and biomass of all functional groups [43]. Therefore, low resolution satellite images can provide indirect evidence of shrub growth, but only when they are validated with high resolution imagery and *in situ* ‘ground-truthed’ observations as have been conducted at sites in Alaska [15, 44], western Canada [26] and Siberia [23, 34].

Contemporary shrub expansion parallels past episodes of Arctic vegetation change. Paleoecological records suggest that shrub species are well adapted to colonize and/or extend their presence in tundra ecosystems during periods with favorable growing conditions. Pollen records indicate that alder, birch and willow species were more widespread in circumpolar mid and high Arctic ecosystems during periods after the last glacial maximum that were warmer and wetter than the present [13, 45–49]. The onset of relatively cool conditions may have restricted the reproduction of shrubs, pushing back the distributions of these species to more southerly limits or to locally favorable environments. For example, the dwarf birch *Betula glandulosa* persists clonally in late snow melt areas at its northern limit on Baffin Island, but it is unable to reproduce sexually due to loss of pollen viability [50]. By contrast, as conditions warm, reproduction can be greatly enhanced. For example, the number of locations with *Empetrum nigrum* ssp *hermaphroditum* (an erect dwarf evergreen shrub) is increasing markedly on Svalbard [51] and range extension of this species is expected with continued climate warming. Together, evidence of higher shrub abundance and expanded northern distributions during warmer periods in the past, combined with current observations of increases in shrub growth and colonization (table 1), suggest that if growing conditions continue to improve, shrubs will become widespread across the Arctic biome [12].

3. Factors influencing shrub increase

Although growth of tundra plants is limited by temperature in Arctic and alpine environments [52, 53], many other factors influence shrub growth (figure 3). Incoming solar radiation, precipitation, soil moisture, nutrient availability, CO_2 concentrations, disturbances, snow pack and melt timing, active layer depth, soil temperatures, and growing season length interact, making it difficult to pinpoint which specific factors control the growth and recruitment of shrub species at a given location. Biotic interactions with herbivores [54, 55], pollinators [56], pathogens [57] or soil mycorrhizae [58], and competing tundra plants [59, 60] add even greater complexity. In the following sections we explore three key drivers of shrub change in tundra ecosystems: temperature, soil disturbances and herbivory.

3.1. Temperature

Temperature limits both the reproduction and growth of shrub species in tundra ecosystems. Growing season temperatures are increasing in northern North America and northwestern Russia [12, 61, 62], and, concurrent with this, the conditions for recruitment and growth of shrub species are also likely changing. Observations of low pollen or seed viability in populations of alder (*Alnus viridis* subsp. *fruticosa*), dwarf birch (*Betula glandulosa*) and willows (*Salix* spp.) near their range limits suggest that temperature limitation of reproduction may determine the northern extent of many shrubs in the low Arctic [16, 50, 63]. Studies of age distributions of shrub species in tundra ecosystems indicate that recruitment has increased in recent years at sites in the western North American and European Arctic [16, 25, 27, 64]. However, there are currently few studies that link warming and new recruitment to shrub increase in tundra ecosystems.

Several recent studies have documented significant positive correlations between ring widths or shoot lengths and early and mid growing season temperatures for some of the most common tall [23, 25, 27, 34, 65] and dwarf [66–70] shrub species found in tundra ecosystems. In some studies, winter temperatures and snow have been found to correlate with growth in the following summer [27, 71–73]. Snow melt timing determines the length of the growing season and the snowpack provides protection from frost damage during the winter and spring [74–76]. These analyses suggest that warmer conditions are likely to promote shrub growth either directly by altering physiological processes or indirectly by enhancing soil microbial activities that supply nutrients for shrub uptake, as long as other factors are not limiting [77]. Also, increased summer temperatures are often accompanied by greater summer moisture deficits, which could offset the expected growth increase created by higher summer temperature alone, as has been observed in boreal trees [78].

3.2. Soil disturbance

Tundra disturbances caused by fire, permafrost degradation, stream channels, animal burrowing or trampling, or human activities create and maintain microsites where tall shrubs can establish and remain dominant for decades to centuries. Recent evidence indicates that many of these disturbances, such as fire [4, 79] and permafrost degradation [3, 80–84], are increasing in high-latitude ecosystems. Increased abundance and growth of tall shrubs on thaw slumps [17], drained lake basins [85], pingos [18], tundra fires [16], vehicle tracks [86] and drilling mud sumps [87] suggest that increases in natural and anthropogenic disturbance could be contributing to increased shrub abundance and distribution.

In the low Arctic, disturbances that expose mineral soils and deepen active layers show rapid changes in functional group abundance, and after several decades are typically dominated by tall shrubs [16, 17, 87, 88]. In the short-term, landscape and soil disturbances are likely to stimulate more rapid recruitment than warming alone [16, 17]. The rate of shrub expansion on recently burned tundra sites is twice as fast as on comparable undisturbed surfaces (Lantz *et al* unpubl. data). Caribou and other animal species can create disturbances by trampling ground cover [89], creating trails that erode soils resulting in either damaged biomass and reduced shrub cover or the provision of sites for the recruitment of shrub seedlings [90]. Soil disturbances could also be a precondition for shrubs to take advantage of improved climate conditions and increase in abundance across the landscape. In contrast, in some ecosystems, landscape disturbances can also reduce shrub abundance. Decreases in shrub cover were observed in northwestern Arctic Russia where willows failed to regenerate in vehicle tracks two decades after the initial disturbance, due to the development of a graminoid-dominated sward [91]. Landscape-scale fires have set back potential shrub increase in Australian alpine areas for 5–20 yr, except in burn scars where species are able to re-sprout [92]. In addition, permafrost degradation of ice-rich palsas in northeast Siberia has resulted in dieback of large *Betula nana* patches and a conversion to graminoid cover (figure 2). Thus, future disturbances and recovery after disturbance in tundra ecosystems could lead to both increases and decreases in shrub abundance.

3.3. Herbivory

Herbivores can reduce the survival of shrubs and limit or reduce shrub patch expansion, as shown by enclosure and exclosure experiments [54, 93]. Animals such as sheep, reindeer, muskoxen, lemmings, ptarmigan, moose and hares have been shown to decrease tundra tree and shrub abundance and canopy structure in Scandinavia, Greenland and Alaska [54, 55, 93–96]. However, current knowledge of the influence of different herbivores on seedling recruitment is limited, and little is known about the influence of insect herbivory and seed predation.

The influence of herbivory on shrub abundance in tundra ecosystems will depend on the size and density of the herbivore populations, intensity of grazing, palatability of the shrub species, and plant and herbivore phenologies [95]. Wild herbivores can migrate over large areas and exhibit cyclic population dynamics; therefore the influence of herbivory on shrub populations will likely change over time and space [5]. Shrub abundance has been reduced by mammalian herbivores in low Arctic Greenland [93] and Norway [96], while no evidence of reduction in shrub expansion by mammalian herbivores was found on the Arctic coast of the Yukon [19].

In tundra ecosystems, the dominant herbivores can be either wild or domesticated. In Fennoscandia and Siberia, land use is dominated by extensive grazing by reindeer and sheep, and this has strongly influenced the abundance of woody species in tundra environments [23, 54, 96, 97]. In northern Scandinavia, herbivory by sheep or reindeer is thought to be the primary factor determining the elevational position of the treeline ecotone [94, 95, 98], and declined use of pastures has

Table 2. Observed impacts of shrub canopies on tundra ecosystem function.

Ecosystem function	Influence of canopy observed	References
Energy exchanges	Higher sensible heat fluxes during melt, and reduced sublimation in winter, from tall shrub canopies	[102, 109]
Reflectance	Lower albedo over shrub tundra	[12, 102–106, 110], Ménard *et al* unpubl. data
Snow melt	Faster snow melt in areas with shrub canopies extending above the snowpack	[12, 102–104]
Soil temperature dynamics	Snow trapping and soil warming in winter, shading and soil cooling in summer under shrub canopies relative to tundra plots	[25, 102, 107, 110, 120], Lévesque unpubl. data
Nitrogen cycling	Greater N availability or faster N-cycling in tall shrub versus low shrub tundra plots	[114, 119, 142]
	No difference in NO_3 and NH_4 availability during summer between shrub and tundra plots	[25]
	No influence of shrub canopies and snow on winter N-mineralization rates, greater summer N-mineralization from soils under a high shrub canopy and with snow addition differences in SOM quality can drive larger differences in net N-mineralization than changes in soil microclimate	[120]
Carbon storage	Greater carbon storage in shrub versus tundra plots	[9, 25, 143]
Carbon flux	No difference in CO_2 soil respiration between shrub and tundra plots	[25]
Decomposition	More recalcitrant litter from shrub species than other tundra plants	[113]
	Greater decomposition rates in tall shrub versus low shrub tundra plots	[143]
	Little difference in decomposition rates between shrub and tundra plots	[25]
Biodiversity	Lower biomass and diversity of species under shrub canopies	[122], Myers-Smith and Hik unpubl. data

resulted in increases in shrubs in the Alps [28]. Herbivores can also influence seed production and seedbed size [89, 99], transport seeds [100] and fertilize soils, which can in turn alter recruitment, dispersal, growth and potential rates of shrub increase.

4. Feedbacks and impacts of shrub increase

Interactions among shrubs, microclimate, litter inputs, carbon storage, nutrient cycling, organic matter decomposition, surface reflectance, erosion, ground temperatures, thaw depth and disturbance have been hypothesized to result in positive and negative feedbacks to further shrub expansion (figure 3, table 2) [12]. In the following sections, we explore feedback mechanisms involving shrubs and albedo, snow cover, soil temperatures, thaw depth, nutrient availability and biodiversity.

4.1. Surface energy exchange and soil temperatures

Tundra shrubs can significantly influence the exchange of energy among the atmosphere, vegetation and soils [101–103]. With an increasing canopy height and density, a higher fraction of the incoming shortwave radiation is absorbed by the canopy and less is reflected to the atmosphere and, therefore, albedo decreases [12, 104–106]. Lower spring and summer albedo has been observed over shrub versus shrub-free tundra in Arctic Alaska [12, 105], alpine areas of the Yukon Territory [102], upland tundra north of Inuvik, NWT (Lantz *et al* unpubl. data) and across the tundra biome [105]. Shrub expansion can therefore significantly alter the interaction of the atmosphere with vegetation, soil and permafrost through changes in energy fluxes.

Shrub canopies and snow cover interact to influence soil and permafrost temperatures. Tundra shrubs can significantly modify the accumulation, timing and physical characteristics of snow, thereby influencing the exchanges of energy and moisture between terrestrial ecosystems and the atmosphere [101–103]. In winter, snow cover protects plant buds and tissue from the effects of extreme cold [74, 75]. Shrubs trap snow, leading to localized increases in snowpack, and also reducing the thermal conductivity of the snowpack by preventing the formation of highly conductive wind-compacted snow layers [110]. As a consequence, winter soil temperatures can be up to 30 °C warmer than air temperatures under shrub canopies [108], whereas soil temperatures may be almost equal to air temperatures in adjacent shrub-free sites [25]. The effect of tall shrubs on snow trapping and albedo can also be moderated by shrubs bending and being buried in the snowpack under the weight of snow [102–104]. In spring, snow melt is first accelerated as a result of the lowered albedo around shrub branches that protrude above the snowpack, but subsequent shading by shrub canopies may promote longer duration snow patches [103, 107, 109]. In summer, shading under shrub canopies decreases soil temperatures [103] and active layer depths [107]. Removal of the *Betula nana* shrub canopy in experimental plots in Siberia resulted in greater active layer depths due the loss of soil shading, despite the increase in surface albedo accompanying shrub removal [107]. Near surface soil temperatures under shrub canopies were found to be ∼2 °C cooler in summer and ∼5 °C warmer in winter in an experimental canopy manipulation conducted in alpine tundra of the Kluane Region [25]. The results of these studies suggest that both the summer soil cooling effect of shading and the winter soil warming effect of snow trapping must be considered to determine the year-round effect of changes in shrub cover on soil temperatures and permafrost conditions.

4.2. Nutrient cycling

Interactions between the abiotic and biotic influences of shrub canopies can alter tundra nutrient cycling. Fertilization experiments show that vascular plant productivity is nutrient limited in tundra ecosystems, as demonstrated by an increase in shrub biomass after nitrogen and phosphorus fertilization [6, 9, 111, 112]. Increases in canopy cover and height of shrub species can increase litter inputs to soils [113], nitrogen mineralization rates [114] and the amount of carbon stored in above and below ground biomass [9]. Although deciduous shrub species produce more litter than other tundra species, this litter is relatively recalcitrant; thus, increases in shrubs could reduce overall decomposition rates in tundra soils [113]. In winter, snow trapped by shrub canopies insulates soils and has been hypothesized to increase decomposition and nutrient release [108]. Experimental manipulations demonstrate that greater snow depth and warmer winter soils under shrub canopies can increase litter decomposition [115] and nitrogen cycling [114, 116–119]. Recent work at Toolik Lake, Alaska showed a positive effect of winter snow addition on summer, but not winter, nitrogen mineralization rates [120]; however, there have not been experimental tests of the influence of summer canopy shading on nutrient cycling and decomposition rates. Carbon dioxide and methane fluxes are likely also altered by shrub canopies. Differences in growing season carbon dioxide effluxes were not explained by the presence of a half-meter-tall willow canopy in alpine tundra in the Kluane region, Yukon Territory [25]. However, increased evapotranspiration from greater shrub biomass could dry soils, and has been suggested to reduce methane emissions and increase carbon dioxide fluxes in areas with expanding shrub cover [121]. This same mechanism of soil drying from increased evapotranspiration when combined with the greater fuel load in shrub tundra could result in increased frequency and intensity of tundra fires with increases in shrubs [48].

4.3. Biodiversity and ecosystem services

Increases in shrub abundance could have negative effects on tundra species richness, through the loss of shade-intolerant species under shrub canopies [122]. At tundra sites in northwestern Fennoscandia and the Yamal Peninsula in Russia, the species richness of vegetation declined with increasing shrub height and cover [122]. The richness of herbaceous species decreased significantly over 20 yr with increasing dwarf shrub cover on an Arctic mountainside in northern Sweden [123]. Fewer species and lower biomass of tundra plants, excluding tall shrub canopies, were found in shrub versus adjacent shrub-free plots in alpine tundra of the Kluane Region in the Yukon Territory [25]. The loss of particular species or functional groups may have implications for tundra food webs and ecosystem services. Lichens have been shown to decline with increases in shrub cover [8, 124, 125]. As important forage species, lichen decline could negatively impact caribou and reindeer populations, and thus influence hunting or herding activities. Increased shrub cover could also reduce moss biomass, which is an important soil insulator. Thus, the loss of the moss layer may alter soil temperatures, active layer depths, and rates of soil decomposition [126]. Willows are an important forage species for caribou, moose, ptarmigan and other wildlife species [55, 127, 128], and either increases or decreases in willow cover may influence the populations of these species. In addition to the potential impacts on biodiversity, ecosystem function and wildlife, altered vegetation structure in tundra ecosystems might influence human access to traditional travel routes, berry harvesting, reindeer herding or hunting of wildlife species.

5. Future research needs

Our analysis of the literature indicates that the following questions must be addressed in order to determine future patterns and impacts of shrub encroachment on tundra ecosystems.

5.1. How will shrub species vary in response to climate and environmental change in tundra ecosystems?

Our review highlights the growing number of observations of shrub increase around the circumpolar Arctic and in high-latitude and alpine tundra ecosystems (figure 2 and table 1); however, the differences in species specific responses to warming have yet to be adequately quantified within and between sites. The International Tundra Experiment (ITEX) tested the response of tundra plots to warming across the Arctic [129, 130]; however, warming experiments with larger plots encompassing larger statured shrub species have only been conducted at a few locations [9, 111, 131]. Understanding the key differences among shrub species responses to climate warming could improve predictions of vegetation change across the Arctic. Birch has been the focus of many experimental field studies [6, 50, 58, 107], but the potential responses of willow, alder and other shrub species to changes in environmental conditions are less well characterized. Furthermore, a whole host of species-level interactions may determine future shrub distributions, with, for example, caribou preferentially browsing willow over birch or alder, birch roots forming an association with an ectomycorrhizal fungal partner, or alder forming a symbiosis with nitrogen-fixing bacteria. Species-level studies are urgently required to evaluate and interpret current patterns of shrub change, as well as to predict future change.

5.2. To what extent is the potential expansion of shrubs across Arctic landscapes constrained by landscape position?

Many of the observations of increasing shrubs are from discrete locations, and variation in rate of shrub change is seldom quantified across the landscape (figure 2 and table 1). Studies that have conducted landscape-level analyses of shrub change find both increasing and more stable patches sometimes located in close proximity [15, 132]. Tall shrubs generally occur in patches across the tundra landscape where conditions favor enhanced nutrient cycling and productivity, such as areas of preferential water flow, or areas where snow accumulates and protects the shoots from winter damage [15]. Topography therefore is likely to be an important constraint on the potential for increased shrub growth and expansion as the climate warms. Thus, landscape-scale studies are required to parameterize realistic models of shrub proliferation and close examination of the current patterns of shrub expansion for key species in relation to local hydrology and wind protection are needed. New applications of remote sensing to measure shrub distributions and changes in shrub cover and associated ecosystem processes in greater detail over large areas will facilitate these avenues of research.

5.3. What controls the recruitment of new individuals that will lead to range expansion of shrub species?

Much of the current research on shrub expansion focuses on the factors that control shrub growth (figure 2 and table 1), and only a few studies have addressed changes in recruitment of shrub species [16, 17, 99]. Since shifts in abundance and range expansions will be mediated primarily by the establishment of new individuals, future research should focus on the factors controlling pollination, germination, recruitment and survival. The interactions between warming, disturbance and increased recruitment of shrub species should also be further explored so that we can better project future shrub increase. Seed viability experiments, demographic studies of shrub populations and experimental studies of seedling establishment would all contribute to our understanding of shrub recruitment in tundra ecosystems.

5.4. Can shrubs growing at the latitudinal or elevational range edge form more dominant and tall canopies if growing conditions improve?

A growing number of studies have identified increases in shrub cover at low Arctic sites, but few have investigated change at the range edge of shrub species (figure 2 and table 1). Many tundra shrub species have very large geographic ranges, and at higher latitudes these species have a more diminutive growth form with lower canopy heights and reduced ground cover [26]. Little is known about whether individuals growing at the range edge have the ability to form larger more dominant canopies if growing conditions improve. The current size and growth form of northern or high-elevation populations of tall shrub species may represent genetically-based local adaptation to extremely harsh growing conditions. The ITEX experiments [129, 130] examined phenological variation in rates of plant growth between warmed and control plots. Common garden experiments or reciprocal transplants [133, 134] have tested how individuals from different sites at different latitudes grow under the same conditions. However, further work exploring phenotypic plasticity, local adaptation and latitudinal clines in size and fecundity should be conducted to improve our understanding of future shrub change at the range edge of tundra shrub species.

5.5. What is the balance between summer and winter feedbacks to shrub encroachment?

Feedbacks of shrub expansion to abiotic processes remain poorly understood (figure 3). Several studies have proposed hypotheses and experimentally tested ecosystem impacts of increasing shrub cover (table 2); however, studies that integrate processes across the entire year have yet to be conducted. Winter biological processes were initially hypothesized to create positive feedbacks to future shrub encroachment [108, 109]; however, recent studies have also highlighted the importance of the summer season [25, 107]. Further observational and experimental work is required to answer questions, such as what the overall effect is of shrubs on soil nutrient availability, integrating the influence of soil temperatures in the summer, winter and shoulder seasons.

5.6. How do feedbacks to shrub encroachment vary across different densities and canopy heights of shrub cover?

The influence of shrub canopies on ground shading, snow depth, soil temperatures and biological processes varies with the cover, height, density and structure of the shrub canopy [135, 136], but additional research is required to characterize the nature of these linear or non-linear relationships. For example, we do not yet know whether shrub expansion is accelerated by positive feedbacks involving snow cover and thickness, surface albedo and atmospheric heating. Nor do we know whether the strength of these potential feedbacks varies with shrub density, cover and canopy height. Future investigations using canopy removals, artificial canopies and other experimental techniques across variation in shrub cover, density and canopy heights will improve our understanding of the relative balance of positive and negative feedbacks to shrub encroachment.

6. Conclusions

Our review highlights the growing number of observations of increases in shrub species in tundra ecosystems at sites around the circumpolar Arctic, high-latitude and alpine areas. These changes are likely to cause significant modifications to the structure and functioning of tundra ecosystems. Recent research highlights that: (1) growth in shrub species is often strongly correlated with growing season temperatures; (2) disturbances such as fire and permafrost thaw can enhance shrub expansion; (3) herbivory can control shrub canopy architecture and limit expansion rates; (4) shrub canopies can alter surface albedo and increase atmospheric heating; and (5) shrub canopies can trap snow and insulate soils in the winter, yet shade soils and maintain shallower active layer depths during the summer. There is growing recognition that increasing rates of shrub encroachment in tundra ecosystems will be determined by large-scale factors such as atmospheric heating, regional factors such as altered disturbance regimes or herbivore populations and site specific factors such as soil moisture conditions or snow insulation. The prediction of future shrub patterns in the tundra biome requires continued monitoring of changes in shrub abundance and research to identify key drivers of this change. Much of the current evidence for increasing shrub cover comes from low Arctic sites in the western North American Arctic, Subarctic Scandinavia and the eastern European Arctic (figure 2). Further research on the patterns of shrub increase and the impacts on ecosystem function at sites across the Arctic biome will improve circumpolar projections of shrub abundance in tundra ecosystems and their role in land–surface feedbacks to climate change.

Acknowledgments

We would like to thank S Villarreal and one anonymous reviewer for providing valuable comments on the manuscript. Funding was provided by an NSERC discovery grant to D S Hik. This review is a collaborative effort of the Shrub Hub Research Network (http://shrubhub.biology.ualberta.ca/) and a legacy of the fourth International Polar Year.

References

[1] Hinzman L D *et al* 2005 Evidence andimplications of recent climate change in northern Alaska and other arctic regions *Clim. Change* **72** 251–98

[2] Serreze M C, Walsh J E, Chapin F S, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel W C, Morison J, Zhang T and Barry R G 2000 Observational evidence of recent change in the northern high-latitude environment *Clim. Change* **46** 159–207

[3] Lawrence D M, Slater A G, Tomas R A, Holland M M and Deser C 2008 Accelerated arctic land warming and permafrost degradation during rapid sea ice loss *Geophys. Res. Lett.* **35** L11506

[4] Mack M C, Bret-Harte M S, Hollingsworth T N, Jandt R R, Schuur E A G, Shaver G R and Verbyla D L 2011 Carbon loss from an unprecedented arctic tundra wildfire *Nature* **475** 489–92

[5] Post E *et al* 2009 Ecological dynamics across the Arctic associated with recent climate change *Science* **325** 1355–8

[6] Bret-Harte M S, Shaver G R, Zoerner J P, Johnstone J F, Wagner J L, Chavez A S, Gunkelman R F IV, Lippert S C and Laundre J A 2001 Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment *Ecology* **82** 18–32

[7] Chapin F S, Shaver G R, Giblin A E, Nadelhoffer K J and Laundre J A 1995 Responses of arctic tundra to experimental and observed changes in climate *Ecology* **76** 694–711

[8] Dawes M A, Hagedorn F, Zumbrunn T, Handa I T, Hättenschwiler S, Wipf S and Rixen C 2011 Growth and community responses of alpine dwarf shrubs to *in situ* CO_2 enrichment and soil warming *New Phytol.* **191** 806–18

[9] Mack M C, Schuur E A G, Bret-Harte M S, Shaver G R and Chapin F S 2004 Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization *Nature* **431** 440–3

[10] Wookey P A *et al* 2009 Ecosystem feedbacks and cascade processes: understanding their role in the responses of arctic and alpine ecosystems to environmental change *Glob. Change Biol.* **15** 1153–72

[11] Bret-Harte M S, Shaver G R and Chapin F S 2002 Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change *J. Ecol.* **90** 251–67

[12] Chapin F S *et al* 2005 Role of land–surface changes in arctic summer warming *Science* **310** 657–60

[13] Naito A T and Cairns D M 2011 Patterns and processes of global shrub expansion *Prog. Phys. Geogr.* **35** 423–42

[14] Sturm M, Racine C H and Tape K D 2001 Increasing shrub abundance in the Arctic *Nature* **411** 546–7

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

[16] Lantz T C, Gergel S E and Henry G H R 2010 Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada *J. Biogeogr.* **37** 1597–610

[17] Lantz T C, Kokelj S V, Gergel S E and Henry G H R 2009 Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps *Glob. Change Biol.* **15** 1664–75

[18] Mackay J R and Burn C R 2011 A century (1910–2008) of change in a collapsing pingo, Parry Peninsula, Western Arctic Coast, Canada *Permafr. Periglac.* **22** 266–72

[19] Myers-Smith I H, Hik D S, Kennedy C, Cooley D, Johnstone J F, Kenney A J and Krebs C J 2011 Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada *Ambio* **40** 610–23

[20] Hudson J M G and Henry G H R 2009 Increased plant biomass in a high arctic heath community from 1981 to 2008 *Ecology* **90** 2657–63

[21] Hill G B and Henry G H R 2011 Responses of High Arctic wet sedge tundra to climate warming since 1980 *Glob. Change Biol.* **17** 276–87

[22] Tremblay B 2010 Augmentation récente du couvert ligneux érigé dans les environs de Kangiqsualujjuaq (Nunavik, Québec) *MSc thesis* Université du Québec à Trois-Rivières, Trois-Rivières, Québec, Canada

[23] Forbes B C, Fauria M M and Zetterberg P 2010 Russian arctic warming and 'greening' are closely tracked by tundra shrub willows *Glob. Change Biol.* **16** 1542–54

[24] Dial R J, Berg E E, Timm K, McMahon A and Geck J 2007 Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: evidence from orthophotos and field plots *J. Geophys. Res.* **112** G04015

[25] Myers-Smith I H 2011 Shrub encroachment in arctic and alpine tundra: mechanisms of expansion and ecosystem impacts *PhD thesis* University of Alberta

[26] Lantz T C, Gergel S E and Kokelj S V 2010 Spatial heterogeneity in the shrub tundra ecotone in the Mackenzie Delta Region, Northwest Territories: implications for arctic environmental change *Ecosystems* **13** 194–204

[27] Hallinger M, Manthey M and Wilmking M 2010 Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia *New Phytol.* **186** 890–9

[28] Anthelme F, Villaret J-C and Brun J-J 2007 Shrub encroachment in the Alps gives rise to the convergence of sub-alpine communities on a regional scale *J. Veg. Sci.* **18** 355–62

[29] Cannone N, Sgorbati S and Guglielmin M 2007 Unexpected impacts of climate change on alpine vegetation *Front. Ecol. Environ.* **5** 360–4

[30] Dullinger S, Dirnböck T and Grabherr G 2003 Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria *Arct. Antarct. Alp. Res.* **35** 434–41

[31] Thorpe N, Eyegetok S, Hakongak N and Elders K 2002 Nowadays it is not the same: Inuit Quajimajatuqangit, climate caribou in the Kitikmeot region of Nunavut, Canada *The Earth Is Faster Now: Indigenous Observations of Arctic Environmental Change* ed I Krupnik and D Jolly (Fairbanks, AK: Arctic Research Consortium of the United States and the Smithsonian Institution) pp 198–239

[32] Forbes B C, Stammler F, Kumpula T, Meschtyb N, Pajunen A and Kaarlejarvia E 2009 High resilience in the Yamal-Nenets social–ecological system, West Siberian Arctic, Russia *Proc. Natl Acad. Sci. USA* **106** 22041–8

[33] Epstein H E, Beringer J, Gould W A, Lloyd A H, Thompson C D C, Chapin F S, Michaelson G J, Ping C L, Rupp T S and Walker D A 2004 The nature of spatial transitions in the Arctic *J. Biogeogr.* **31** 1917–33

[34] Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans M M P D, Sauren P and Berendse F 2011 What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* **8** 1169–79

[35] Bunn A G and Goetz S J 2006 Trends in satellite-observed circumpolar photosynthetic activity from 1982 to 2003: the influence of seasonality, cover type, and vegetation density *Earth Interact.* **10** 1–19

[36] Goetz S J, Bunn A G, Fiske G J and Houghton R A 2005 Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance *Proc. Natl Acad. Sci. USA* **102** 13521–5

[37] Bhatt U S *et al* 2010 Circumpolar arctic tundra vegetation change is linked to sea ice decline *Earth Interact.* **14** 1–20

[38] Jia G J, Epstein H E and Walker D A 2009 Vegetation greening in the Canadian Arctic related to decadal warming *J. Environ. Monit.* **11** 2231

[39] Jia G J, Epstein H E and Walker D A 2003 Greening of arctic Alaska 1981–2001 *Geophys. Res. Lett.* **30** 2067

[40] Raynolds M K, Walker D A and Maier H A 2006 NDVI patterns and phytomass distribution in the circumpolar Arctic *Remote Sens. Environ.* **102** 271–81

[41] Raynolds M K, Comiso J C, Walker D A and Verbyla D 2008 Relationship between satellite-derived land surface temperatures, arctic vegetation types, and NDVI *Remote Sens. Environ.* **112** 1884–94

[42] Stow D 2004 Remote sensing of vegetation and land-cover change in arctic tundra ecosystems *Remote Sens. Environ.* **89** 281–308

[43] Huemmrich K F *et al* 2010 Remote sensing of tundra gross ecosystem productivity and light use efficiency under varying temperature and moisture conditions *Remote Sens. Environ.* **114** 481–7

[44] Beck P S A, Horning N, Goetz S J, Loranty M M and Tape K D 2011 Shrub cover on the North Slope of Alaska: a circa 2000 baseline map *Arct. Antarct. Alp. Res.* **43** 355–63

[45] Brubaker L B, Garfinkee H L and Edwards M E 1983 A late Wisconsin and Holocene vegetation history from the central brooks range: implications for Alaskan palaeoecology *Q. Res.* **20** 194–214

[46] Anderson P M and Brubaker L B 1994 Vegetation history of northcentral Alaska: a mapped summary of late-quaternary pollen data *Q. Sci. Rev.* **13** 71–92

[47] Bigelow N H *et al* 2003 Climate change and arctic ecosystems: 1. Vegetation changes north of 55 N between the last glacial maximum, mid-Holocene, and present *J. Geophys. Res.* **108** 8170

[48] Higuera P E, Brubaker L B, Anderson P M, Brown T A, Kennedy A T, Hu F S and Chave J 2008 Frequent fires in ancient shrub tundra: implications of paleorecords for arctic environmental change *PLoS ONE* **3** e0001744

[49] Kullman L 1995 Holocene tree-limit and climate history from the Scandes Mountains, Sweden *Ecology* **76** 2490–502

[50] Hermanutz L A, Innes D J and Weis I M 1989 Clonal structure of arctic dwarf birch (*Betula glandulosa*) at its northern limit *Am. J. Bot.* **76** 755–61

[51] Alsos I G, Eidesen P B, Ehrich D, Skrede I, Westergaard K, Jacobsen G H, Landvik J Y, Taberlet P and Brochmann C 2007 Frequent long-distance plant colonization in the changing Arctic *Science* **316** 1606–9

[52] Doak D F and Morris W F 2010 Demographic compensation and tipping points in climate-induced range shifts *Nature* **467** 959–62

[53] Klanderud K 2005 Climate change effects on species interactions in an alpine plant community *J. Ecol.* **93** 127–37

[54] Olofsson J, Oksanen L, Callaghan T, Hulme P E, Oksanen T and Suominen O 2009 Herbivores inhibit climate-driven shrub expansion on the tundra *Glob. Change Biol.* **15** 2681–93

[55] Tape K D, Lord R, Marshall H-P and Ruess R W 2010 Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska *Ecoscience* **17** 186–93

[56] Muñoz A A, Celedon-Neghme C, Cavieres L A and Arroyo M T K 2004 Bottom-up effects of nutrient availability on flower production, pollinator visitation, and seed output in a high-Andean shrub *Oecologia* **143** 126–35

[57] Olofsson J, Ericson L, Torp M, Stark S and Baxter R 2011 Carbon balance of arctic tundra under increased snow cover mediated by a plant pathogen *Nature Clim. Change* **1** 220–3

[58] Deslippe J R, Hartmann M, Mohn W W and Simard S W 2011 Long-term experimental manipulation of climate alters the ectomycorrhizal community of *Betula nana* in Arctic tundra *Glob. Change Biol.* **17** 1625–36

[59] Chapin F S, McGraw J B and Shaver G R 1989 Competition causes regular spacing of alder in Alaskan shrub tundra *Oecologia* **79** 412–6

[60] Wipf S, Rixen C and Mulder C P H 2006 Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community *Glob. Change Biol.* **12** 1496–506

[61] ACIA 2005 *Arctic Climate Impact Assessment—Scientific Report* (Cambridge: Cambridge University Press)

[62] Hansen J, Ruedy R, Sato M and Lo K 2010 Global surface temperature change *Rev. Geophys.* **48** 29

[63] Weis I M and Hermanutz L A 1993 Pollination dynamics of arctic dwarf birch (*Betula glandulosa*; Betulaceae) and its role in the loss of seed production *Am. J. Bot.* **80** 1021–7

[64] Danby R K and Hik D S 2007 Variability, contingency and rapid change in recent subarctic alpine tree line dynamics *J. Ecol.* **95** 352–63

[65] McDougall K L, Brookhouse M T and Broome L S 2011 Dendroclimatological investigation of mainland Australia's only alpine conifer, *Podocarpus lawrencei*

Hook.f *Dendrochronologia* at press (doi:10.1016/j.dendro.2011.01.011)

[66] Rayback S and Henry G 2006 Reconstruction of summer temperature for a Canadian high arctic site from retrospective analysis of the dwarf shrub, *Cassiope tetragona Arct. Antarct. Alp. Res.* **38** 228–38

[67] Bär A, Bräuning A and Löffler J 2006 Dendroecology of dwarf shrubs in the high mountains of Norway—a methodological approach *Dendrochronologia* **24** 17–27

[68] Rozema J, Weijers S, Broekman R, Blokker P, Buizer B, Werleman C, El Yaqine H, Hoogedoorn H, Fuertes M M and Cooper E 2009 Annual growth of *Cassiope tetragona* as a proxy for arctic climate: developing correlative and experimental transfer functions to reconstruct past summer temperature on a millennial time scale *Glob. Change Biol.* **15** 1703–15

[69] Weijers S, Broekman R and Rozema J 2010 Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub *Cassiope tetragona Q. Sci. Rev.* **29** 3831–42

[70] Rayback S A, Lini A and Henry G H 2011 Spatial variability of the dominant climate signal in *Cassiope tetragona* from sites in arctic Canada *Arctic* **64** 98–114

[71] Schmidt N, Baittinger C and Forchhammer M 2006 Reconstructing century-long snow regimes using estimates of high arctic *Salix arctica* radial growth *Arct. Antarct. Alp. Res.* **38** 257–62

[72] Schmidt N M, Baittinger C, Kollmann J and Forchhammer M C 2010 Consistent dendrochronological response of the dioecious *Salix arctica* to variation in local snow precipitation across gender and vegetation types *Arct. Antarct. Alp. Res.* **42** 471–5

[73] Rixen C, Schwoerer C and Wipf S 2010 Winter climate change at different temporal scales in *Vaccinium myrtillus*, an arctic and alpine dwarf shrub *Polar Res.* **29** 85–94

[74] Bokhorst S, Bjerke J W, Bowles F W, Melillo J, Callaghan T V and Phoenix G K 2008 Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland *Glob. Change Biol.* **14** 2603–12

[75] Bokhorst S F, Bjerke J W, Tømmervik H, Callaghan T V and Phoenix G K 2009 Winter warming events damage sub-arctic vegetation: consistent evidence from an experimental manipulation and a natural event *J. Ecol.* **97** 1408–15

[76] Wipf S and Rixen C 2010 A review of snow manipulation experiments in arctic and alpine tundra ecosystems *Polar Res.* **29** 95–109

[77] Chapin F S 1983 Direct and indirect effects of temperature on arctic plants *Polar Biol.* **2** 47–52

[78] Barber V A, Juday G P and Finney B P 2000 Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress *Nature* **405** 668–73

[79] Kasischke E S and Turetsky M R 2006 Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska *Geophys. Res. Lett.* **33** L09703

[80] Åkerman H J and Johansson M 2008 Thawing permafrost and thicker active layers in sub-arctic Sweden *Permafr. Periglac.* **19** 279–92

[81] Jorgenson M T, Shur Y L and Pullman E R 2006 Abrupt increase in permafrost degradation in arctic Alaska *Geophys. Res. Lett.* **33** 4

[82] Lacelle D, Bjornson J and Lauriol B 2010 Climatic and geomorphic factors affecting contemporary (1950–2004) activity of retrogressive thaw slumps on the Aklavik Plateau, Richardson Mountains, NWT, Canada *Permafr. Periglac.* **21** 1–15

[83] Lantz T C and Kokelj S V 2008 Increasing rates of retrogressive thaw slump activity in the Mackenzie Delta region, N.W.T., Canada *Geophys. Res. Lett.* **35** L06502

[84] Schuur E A G, Vogel J G, Crummer K G, Lee H, Sickman J O and Osterkamp T E 2009 The effect of permafrost thaw on old carbon release and net carbon exchange from tundra *Nature* **459** 556–9

[85] Marsh P, Russell M, Pohl S, Haywood H and Onclin C 2009 Changes in thaw lake drainage in the Western Canadian Arctic from 1950 to 2000 *Hydrol. Process.* **23** 145–58

[86] Kemper J T and Macdonald S E 2009 Directional change in upland tundra plant communities 20–30 years after seismic exploration in the Canadian low-arctic *J. Veg. Sci.* **20** 557–67

[87] Johnstone J F and Kokelj S V 2009 Environmental conditions and vegetation recovery at abandoned drilling mud sumps in the Mackenzie Delta region, Northwest Territories, Canada *Arctic* **61** 199–211

[88] Olofsson J, Stark S and Oksanen L 2004 Reindeer influence on ecosystem processes in the tundra *Oikos* **105** 386–96

[89] Dufour Tremblay G and Boudreau S 2011 Black spruce regeneration at the treeline ecotone: synergistic impacts of climate change and caribou activity *Can. J. For. Res.* **41** 460–8

[90] Forbes B C, Ebersole J J and Strandberg B 2001 Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems *Conserv. Biol.* **15** 954–69

[91] Kumpula T, Pajunen A, Kaarlejärvi E, Forbes B C and Stammler F 2011 Land use and land cover change in arctic Russia: ecological and social implications of industrial development *Glob. Environ. Change* **21** 550–62

[92] Williams R J, Wahren C, Tolsma A D, Sanecki G M, Papst W A, Myers B A, McDougall K L, Heinze D A and Green K 2008 Large fires in Australian alpine landscapes: their part in the historical fire regime and their impacts on alpine biodiversity *Int. J. Wildland Fire* **17** 793–808

[93] Post E and Pedersen C 2008 Opposing plant community responses to warming with and without herbivores *Proc. Natl Acad. Sci. USA* **105** 12353–8

[94] Hofgaard A, Løkken J O, Dalen L and Hytteborn H 2010 Comparing warming and grazing effects on birch growth in an alpine environment—a 10-year experiment *Plant Ecol. Divers.* **3** 19–27

[95] Speed J D M, Austrheim G, Hester A J and Mysterud A 2010 Experimental evidence for herbivore limitation of the treeline *Ecology* **91** 3414–20

[96] Ravolainen V T, Bråthen K A, Ims R A, Yoccoz N G, Henden J-A and Killengreen S T 2011 Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores *Basic Appl. Ecol.* **12** 643–53

[97] Kitti H, Forbes B C and Oksanen J 2009 Long- and short-term effects of reindeer grazing on tundra wetland vegetation *Polar Biol.* **32** 253–61

[98] Speed J D M, Austrheim G, Hester A J and Mysterud A 2011 Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline *Forest Ecol. Manag.* **261** 1344–52

[99] Munier A, Hermanutz L, Jacobs J D and Lewis K 2010 The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming *Plant Ecol.* **210** 19–30

[100] Klein D R, Bruun H H, Lundgren R and Philipp M 2008 Climate change influences on species interrelationships and distributions in high-arctic Greenland *High-Arctic Ecosystem Dynamics in a Changing Climate* vol 40 (New York: Academic) pp 81–100

[101] Liston G E, McFadden J P, Sturm M and Pielke R A 2002 Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs *Glob. Change Biol.* **8** 17–32

[102] Pomeroy J W, Bewley D S, Essery R L H, Hedstrom N R, Link T, Granger R J, Sicart J E, Ellis C R and Janowicz J R 2006 Shrub tundra snowmelt *Hydrol. Process.* **20** 923–41

[103] Marsh P, Bartlett P, MacKay M, Pohl S and Lantz T 2010 Snowmelt energetics at a shrub tundra site in the western Canadian Arctic *Hydrol. Process.* **24** 3603–20

[104] Sturm M 2005 Changing snow and shrub conditions affect albedo with global implications *J. Geophys. Res.* **110** G01004

[105] Loranty M M, Goetz S J and Beck P S A 2011 Tundra vegetation effects on pan-arctic albedo *Environ. Res. Lett.* **6** 024014

[106] Blok D, Schaepman-Strub G, Bartholomeus H, Heijmans M M P D, Maximov T C and Berendse F 2011 The response of arctic vegetation to the summer climate: relation between shrub cover, NDVI, surface albedo and temperature *Environ. Res. Lett.* **6** 035502

[107] Blok D, Heijmans M M P D, Schaepman-Strub G, Kononov A V, Maximov T C and Berendse F 2010 Shrub expansion may reduce summer permafrost thaw in Siberian tundra *Glob. Change Biol.* **16** 1296–305

[108] Sturm M, McFadden J P, Liston G E, Chapin F S, Racine C H and Holmgren J 2001 Snow–shrub interactions in arctic tundra: a hypothesis with climatic implications *J. Climate* **14** 336–44

[109] Sturm M, Schimel J P, Michaelson G, Romanovsky V E, Welker J M, Oberbauer S F, Liston G E and Fahnestock J 2005 Winter biological processes could help convert arctic tundra to shrubland *Bioscience* **55** 17–26

[110] Bewley D, Essery R, Pomeroy J and Ménard C 2010 Measurements and modelling of snowmelt and turbulent heat fluxes over shrub tundra *Hydrol. Earth Syst. Sci.* **14** 1331–40

[111] Shaver G R and Chapin F S 1980 Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth *Ecology* **61** 662–75

[112] Dormann C F and Woodin S J 2002 Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments *Funct. Ecol.* **16** 4–17

[113] Cornelissen J H C *et al* 2007 Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes *Ecol. Lett.* **10** 619–27

[114] Buckeridge K M, Zufelt E, Chu H and Grogan P 2010 Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks *Plant Soil* **330** 407–21

[115] Baptist F, Yoccoz N G and Choler P 2009 Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient *Plant Soil* **328** 397–410

[116] Buckeridge K M and Grogan P 2010 Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra *Biogeochemistry* **101** 105–21

[117] Buckeridge K M and Grogan P 2008 Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra *Appl. Soil Ecol.* **39** 210–22

[118] Nobrega S and Grogan P 2007 Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra *Ecosystems* **10** 419–31

[119] Schimel J P, Bilbrough C and Welker J M 2004 Increased snow depth affects microbial activity and nitrogen mineralization in two arctic tundra communities *Soil Biol. Biochem.* **36** 217–27

[120] DeMarco J, Mack M C and Bret-Harte M S 2011 The effects of snow, soil microenvironment, and soil organic matter quality on N availability in three Alaskan arctic plant communities *Ecosystems* **14** 804–17

[121] Merbold L, Kutsch W L, Corradi C, Kolle O, Rebmann C, Stoy P C, Zimov S A and Schulze E D 2009 Artificial drainage and associated carbon fluxes (CO_2/CH_4) in a tundra ecosystem *Glob. Change Biol.* **15** 2599–614

[122] Pajunen A M, Oksanen J and Virtanen R 2011 Impact of shrub canopies on understorey vegetation in western Eurasian tundra *J. Veg. Sci.* **22** 837–46

[123] Wilson S D and Nilsson C 2009 Arctic alpine vegetation change over 20 years *Glob. Change Biol.* **15** 1676–84

[124] Joly K, Jandt R R and Klein D R 2009 Decrease of lichens in arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska *Polar Res.* **28** 433–42

[125] Cornelissen J H C *et al* 2001 Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *J. Ecol.* **89** 984–94

[126] Blok D, Heijmans M M P D, Schaepman-Strub G, Ruijven J, Parmentier F J W, Maximov T C and Berendse F 2011 The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site *Ecosystems* **14** 1055–65

[127] den Herder M, Virtanen R and Roininen H 2008 Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone *Basic Appl. Ecol.* **9** 324–31

[128] Viereck L A and Little E L 2007 *Alaska Trees and Shrubs* (Fairbanks, AK: University of Alaska Press)

[129] Arft A M *et al* 1999 Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment *Ecol. Monograph* **69** 491–511

[130] Walker M D *et al* 2006 Plant community responses to experimental warming across the tundra biome *Proc. Natl Acad. Sci. USA* **103** 1342–6

[131] van Wijk M T *et al* 2004 Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change *Glob. Change Biol.* **10** 105–23

[132] Tape K D 2010 *The Changing Arctic Landscape* (Fairbanks, AK: University of Alaska Press)

[133] Maron J L, Vilà M, Bommarco R, Elmendorf S and Beardsley P 2004 Rapid evolution of an invasive plant *Ecol. Monograph* **74** 261–80

[134] Jump A S, Mátyás C and Peñuelas J 2009 The altitude-for-latitude disparity in the range retractions of woody species *Trends Ecol. Evolut.* **24** 694–701

[135] Grogan P and Jonasson S 2006 Ecosystem CO_2 production during winter in a Swedish subarctic region: the relative importance of climate and vegetation type *Glob. Change Biol.* **12** 1479–95

[136] Lantz T C 2008 Relative influence of temperature and disturbance on vegetation dynamics in the low Arctic: an investigation at multiple scales *PhD thesis* University of British Columbia, Vancouver, BC, Canada

[137] Upshall M 2011 Simulating vegetation change in the Torngat Mountains, Labrador using a cellular automata-Markov chain model *MSc thesis* Memorial University of Newfoundland, St. John's, NF, Canada

[138] Daniëls F J A, de Molenaar J G, Chytrý M and Tichý L 2011 Vegetation change in southeast Greenland? Tasiilaq revisited after 40 years *Appl. Veg Sci.* **14** 230–41

[139] Hallinger M and Wilmking M 2011 No change without a cause—why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia *New Phytol.* **189** 902–8

[140] McDougall K L 2003 Aerial photographic interpretation of vegetation changes on the Bogong High Plains Victoria between 1936 and 1980 *Aust. J. Bot.* **51** 251–6

[141] Scherrer P and Pickering C 2005 Recovery of alpine vegetation from grazing and drought: data from long-term photoquadrats in Kosciuszko National Park, Australia *Arct. Antarct. Alp. Res.* **37** 574–84

[142] Chu H and Grogan P 2010 Soil microbial biomass, nutrient availability and nitrogen mineralization potential among vegetation-types in a low arctic tundra landscape *Plant Soil* **329** 411–20

[143] Vankoughnett M 2009 Shrub expansion in the low arctic: the influence of snow and vegetation feedbacks on nitrogen cycling *MSc thesis* Queen's University Kingston, ON, Canada

[144] Ropars P and Boudreau S 2011 Shrub expansion at the forest tundra ecotone: spatial heterogeneity linked to local topography *Environ. Res. Lett.* at press