

Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska

Kyle Joly,^{1,2} Randi R. Jandt³ & David R. Klein⁴

1 National Park Service, Gates of the Arctic National Park and Preserve, 4175 Geist Road Fairbanks, AK 99709, USA

2 Department of Biology and Wildlife, 211 Irving 1, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

3 Bureau of Land Management, Alaska Fire Service, 1541 Gaffney Road, Fort Wainwright, AK 99703, USA

4 Institute of Arctic Biology, University of Alaska Fairbanks, P.O. Box 757000, Fairbanks, AK 99775, USA

Keywords

Climate warming; disturbance; fire; grazing; lichens; *Rangifer tarandus*.

Correspondence

Kyle Joly, National Park Service, 4175 Geist Road, Fairbanks, AK 99709, USA. E-mail: kyle_joly@nps.gov

doi:10.1111/j.1751-8369.2009.00113.x

Abstract

We review and present a synthesis of the existing research dealing with changing Arctic tundra ecosystems, in relation to caribou and reindeer winter ranges. Whereas pan-Arctic studies have documented the effects on tundra vegetation from simulated climate change, we draw upon recent long-term regional studies in Alaska that have documented the actual, on-the-ground effects. Our review reveals signs of marked change in Arctic tundra ecosystems. Factors known to be affecting these changes include wildfire, disturbance by caribou and reindeer, differential growth responses of vascular plants and lichens, and associated competition under climate warming scenarios. These factors are interrelated, and, we posit, unidirectional: that is, they are all implicated in the significant reduction of terricolous lichen ground cover and biomass during recent decades. Lichens constitute the primary winter forage for large, migratory caribou and reindeer herds, which in turn are a critical subsistence resource for rural residents in Alaska. Thus, declines in these lichens are a major concern for rural people who harvest caribou and reindeer for subsistence, as well as for sport hunters, reindeer herders, wildlife enthusiasts and land managers. We believe a more widely distributed and better integrated research programme is warranted to quantify the magnitude and extent of the decline in lichen communities across the Arctic.

Climate warming is predicted to cause unprecedented change in the future (Parry et al. 2007). Rapid and dramatic changes in both terrestrial and aquatic ecosystems were already evident throughout much of the Arctic several years ago (Symon et al. 2005). The Arctic is now experiencing the warmest temperatures it has seen over the past 400 years, and the rate of temperature rise is predicted to increase (Hinzman et al. 2005; Symon et al. 2005). These climatic changes will have, and indeed are already having, a dramatic effect on the flora and fauna of the Arctic.

A comprehensive review of the effects of climate change on the winter range of reindeer (*Rangifer tarandus tarandus*) in Norway was conducted by Heggberget et al. (2002). Their review focused on how climate warming could affect the quality, distribution and availability of winter forage, with lichens being of specific interest

(Heggberget et al. 2002). Terricolous (ground-dwelling) lichens are the preferred winter forage, where available, for *Rangifer* populations, with specific species of interest that include *Cladina mitis*, *Cladina rangiferina*, *Cladina stellaris*, *Cladonia amaurocraea*, *Cladonia gracilis*, *Cladonia uncialis*, *Cetraria cucullata*, *Cetraria ericetorum*, *Cetraria islandica* and *Cetraria nivalis* (Ahti 1959; Scotter 1967; Pegau 1968; Holleman & Luick 1977; Thomas & Hervieux 1986; Thomas & Kiliaan 1998; Brodo et al. 2001). Heggberget et al. (2002) also reviewed the impacts of climate warming on alternative, vascular forage, and the impacts of grazing on lichens, whereas the role of wildfire, uncommon in Norwegian reindeer ranges, was only briefly covered.

The intent with our review is to build upon past reviews, highlighting the major driving factors altering Arctic flora, while focusing on the winter ranges of



caribou (*Rangifer tarandus granti*) and reindeer (*Rangifer*, collectively) in Alaska. By expanding the scope of the review to include the findings of recent long-term field and experimental studies on changes in the tundra ecosystems in Alaska, we believe that the possibility of pan-Arctic changes should be considered.

There is strong agreement in climate change models with regards to temperature changes, and the rate of climate warming in Alaska is predicted to accelerate (Chapin et al. 2005; Symon et al. 2005; Parry et al. 2007). Wildfires, a primary ecosystem driver in the boreal forest regions of Alaska, have increased in frequency and extent in recent years (Kasischke & Turetsky 2006; Shulski & Wendler 2007). Though more common in boreal forest ecosystems, fires do occur within the tundra winter ranges of *Rangifer* (Jandt et al. 2008), and are expected to continue to increase in frequency (Higuera et al. 2008).

Although there is little agreement on how the moisture regime will be affected by climate change, it plays an important role in the ecology of the Arctic (Rouse et al. 1997), especially for lichens. The reliance of lichens on atmospheric moisture and nutrients, and their slow growth, make them vulnerable to the disturbance and environmental changes driven by climate warming and drying. Summer warming and drying, with increased evaporative loss, would lead to decreased growth rates in lichens if there was not an increase in precipitation, be it rain, fog or dew. Continued climate warming is expected to have a direct impact on lichens in Arctic and sub-Arctic plant communities, and to indirectly impact them through industrial development activities (Klein & Vlasova 1991), leading to concern that declining lichen communities could lead to reduced *Rangifer* populations. *Rangifer* populations are heavily utilized by rural residents in Alaska, and are therefore important in their subsistence-dominated economies. Caribou are sought after by sport hunters, and are appreciated by wildlife enthusiasts: groups that are important to the broader economy of Alaska.

Because of the importance of lichens in tundra ecosystem dynamics in Alaska, investigators have used long-term monitoring studies to understand their response to disturbance factors that affect their presence and distribution within the northern landscape. We highlight four recent long-term studies in this review. On St. Matthew Island (Fig. 1), in the northern Bering Sea, permanent plots were originally established in 1957, in conjunction with a study of feral reindeer (Klein 1968). On the eastern Seward Peninsula, permanent plots were established in 1981 to monitor caribou grazing pressure and changes in vegetative cover within the core winter range of the Western Arctic Herd (WAH; Fig. 1; Joly, Jandt et al.

2007). Jandt et al. (2008) monitored post-fire succession from 1981 to 2006 using adjacent, paired burned and unburned transects within the same region. Holt et al. (2008) investigated plots on the western Seward Peninsula: a region used by both caribou and reindeer.

Twenty-nine reindeer were introduced to St. Matthew Island in 1944, as an emergency source of human food for personnel at a navigational station that was abandoned only two years later (Klein 1968). Much of the vegetated portion of the island was initially blanketed with dense lichen mats. The herd faced no predation pressure, and in the absence of humans the reindeer population rapidly increased, reaching 6000 animals in 1963. By that time, the herd had decimated the lichen community, and, in conjunction with severe weather, a population crash occurred during the late winter of 1964 (Klein 1968). The population expired shortly after the crash, as no viable males survived that winter, and the island has remained free of reindeer and other large herbivores ever since. Lichen re-growth on the island was tracked during subsequent studies (Klein 1987; Klein & Shulski 2009)

The WAH, Alaska's largest caribou herd, reached a population of nearly 500 000 in 2003 (Dau 2005a). It occupies a total range of about 363 000 km² in north-western Alaska. The centre of the herd's wintering area lies just east of the Seward Peninsula, and is dominated by tussock tundra, but also contains extensive areas of boreal forest and alpine ecosystems. The herd is highly migratory, and faces predation from wolves (*Canis lupus*), bears (primarily *Ursus arctos*), other carnivores and golden eagles (*Aquila chrysaetos*). The WAH remains an important resource in the subsistence-dominated lifestyle of the people of the region, which emphasizes the need for an increased understanding of caribou-habitat relationships for the effective management and conservation of the herd. In recent years there has been an increased focus on changes in plant community structure within the winter range of the herd, primarily associated with the influences of wildfire and climate change, and their effects on habitat quality for *Rangifer* and other herbivores (Racine et al. 1985; Racine et al. 1987; Sturm et al. 2001; Joly et al. 2007; Jandt et al. 2008). The role of terricolous lichens, which constitute the majority (60–80%) of the diet of WAH caribou in winter (Saperstein 1996), in the ecosystem dynamics of tundra and boreal forest habitats, remains poorly understood.

Reindeer were first introduced to the Seward Peninsula in 1892 through the efforts of Sheldon Jackson, then Commissioner for Education in Alaska, for the purpose of providing a stable supply of food for the native inhabitants (Stern et al. 1980). Reindeer herding on the Seward Peninsula was at its apex in the 1930s, when more than 100 000 animals were present, but numbers since have

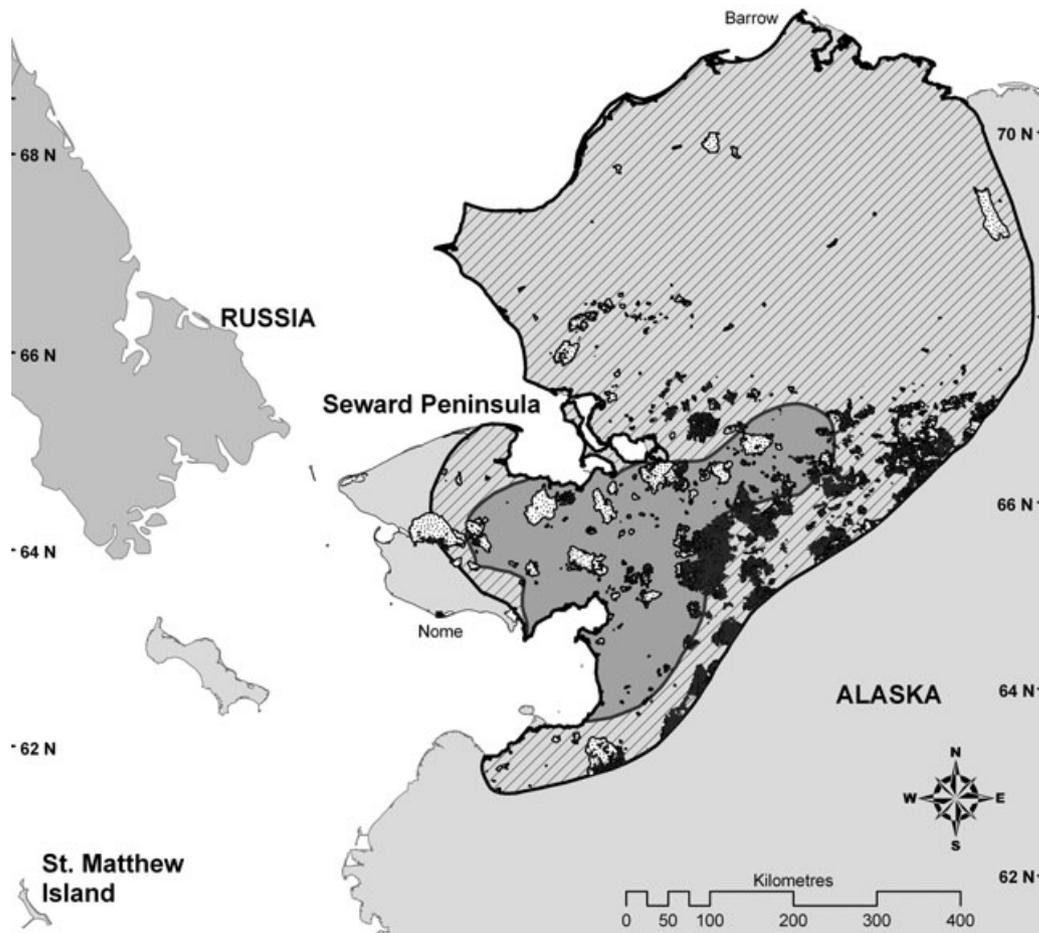


Fig. 1 Total annual range of the Western Arctic Caribou Herd, shown outlined by the thick, solid black line, within which the dark-grey shaded area is the core winter range, in north-western Alaska (courtesy of the Alaska Department of Fish and Game). Areas shaded black within the range of the herd depict recent burns (<55 years old) in boreal forest habitats while stippled areas depict burns within tundra habitats, for the period 1950–2007 (courtesy of the Alaska Fire Service).

greatly declined (Stern et al. 1980). With the expansion of the WAH in recent decades making herding of reindeer no longer feasible over all but the westernmost portion of the peninsula, the industry has been reduced to less than 10 000 reindeer (Dau 2000). Studies of the effects of wildfire and grazing by both *Rangifer* species on the Seward Peninsula have been carried out by Holt et al. (2008).

Wildfire

The role of wildfire in boreal forest succession is relatively well studied. In Alaska, the burn area correlates strongly with increased summer temperature (Duffy et al. 2005). The frequency and extent of wildfires in North American boreal ecosystems have increased in recent decades (Kasischke & Turetsky 2006). Caribou forage lichens are especially vulnerable to being consumed by fire during

dry summers (Auclair 1983; Dunford et al. 2006), because of their growth form and rapid loss of moisture content in response to decreases in relative humidity that proceed a fire front. Caribou are known to avoid recently burned areas in the boreal forest: that is, areas burned within the last 50 years (Thomas et al. 1996; Thomas et al. 1998; Joly et al. 2003; Dalerum et al. 2007).

Less is known about the role of fire in Arctic tundra ecosystems. Fires are relatively uncommon, and are of limited extent, in tundra ecosystems (Wein 1976; Payette et al. 1989), although they are somewhat more common in the Noatak River valley and the Seward Peninsula (Racine et al. 1985; Racine et al. 1987)—both are areas within the range of the WAH. Similarly, the incidence of fires is increasing within the range of the WAH (Fig. 2; this study). However, a corresponding trend in the acreage burned has not yet been identified, which may be because of improved firefighting capabilities. In 2007, a

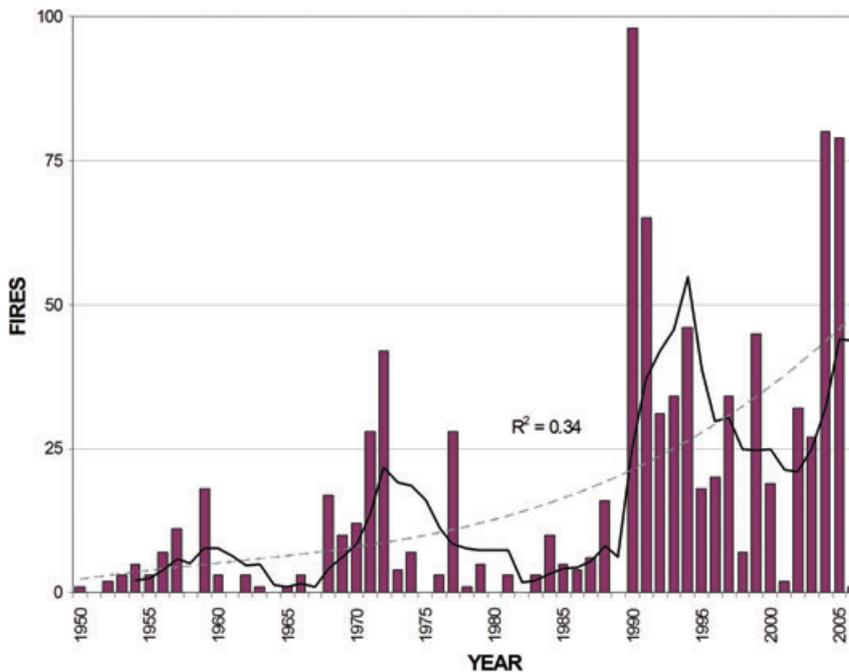


Fig. 2 The incidence of reported fires from 1950 to 2007 occurring within the range of the Western Arctic Caribou Herd, north-western Alaska (compiled from Alaska Fire Service data). The solid black line represents the 5-year moving average, and the dashed grey line is a best-fit trend polynomial.

single fire burned over 100 000 ha of tundra, making it the largest fire on record north of the Arctic Circle in Alaska (the north-easternmost fire in Fig. 1; this study). In addition to the unusual size of this tundra fire, the fact that it burned so late into the season (e.g., late September, when small lakes had already frozen) was remarkable. This fire elicited concern from local rural residents that Arctic tundra fires may become an issue in the future.

Caribou forage lichens are also vulnerable to being consumed by wildfire in tundra habitats, and are a major component of these ecosystems. The response of caribou to burned tundra habitat has received much less attention than in boreal ecosystems. In fact, only one regional study of these effects has been undertaken so far. This recent analysis using satellite telemetry data determined that caribou avoided burned tundra habitat in mid-winter for up to 55 years (Joly, Bente et al. 2007). In complementary studies, it was shown that the lichen cover in burned tundra areas was less than 5% at 30 or 35 years post-fire (Holt et al. 2008; Jandt et al. 2008, respectively). This level of lichen cover is not likely to be great enough for caribou to seek it out as foraging habitat (Arseneault et al. 1997; Joly, Jandt et al. 2007). Wildfires reduce the abundance of lichens, especially the late-succession fruticose lichens that are the primary caribou forage lichens, for decades in tundra ecosystems (Morneau & Payette 1989; Arseneault et al. 1997; Racine et al. 2004; Holt et al. 2006; Holt et al. 2008; Jandt et al. 2008). Furthermore, post-fire lichen recovery is taking longer than has been predicted (Jandt et al. 2008). The Natural Resource

Conservation Service forecasted lichen cover of >20% at 10 years post-fire, and of >30% at 20 years post-fire, on the Seward Peninsula (Swanson et al. 1985), whereas lichen cover has remained at under 5% for 20–35 years post-fire on the plots examined by Jandt et al. (2008).

Caribou and reindeer

Rangifer directly affect lichen abundance through grazing and trampling (Ahti 1959; Klein 1968, 1982, 1987; Pegau 1969; Moser et al. 1979; Helle & Aspi 1983; van der Wal et al. 2001; van der Wal 2006). These effects can occur at local and regional levels (Moser et al. 1979; Morneau & Payette 1989; Arseneault et al. 1997). On St. Matthew Island, Klein (1968, 1987) reported on the population increase and crash of the introduced reindeer, and their impact on the island flora. Heavy grazing pressure exerted by reindeer on St. Matthew Island as the population increased to its peak, without the option for dispersal or movement from the island, resulted in the near total removal of lichens, with few live fragments from which forage lichen species could regenerate (Klein & Shulski 2009). Although lichen cover and biomass recovered somewhat from 1985 to 2005, it was still below historic levels (Klein & Shulski 2009). Lichen biomass on St. Matthew Island was just 12% of that on neighbouring Hall Island, which had not been populated by reindeer (Klein & Shulski 2009).

The WAH reached a record high population level (490 000 caribou) by 2003, causing the general public and

land managers to become concerned about the possibility of deteriorating winter ranges through heavy grazing pressure (Dau 2005a). In fact, lichen cover had declined by more than 50% (Joly, Jandt et al. 2007) on permanent unburned transects in the winter range between 1981 and 2005, coincident with the population rise. Joly, Jandt et al. (2007) determined that the decline in lichen cover was significantly related to the amount of caribou utilization: 31% of the variation in the decline of lichens was explained by caribou utilization. On the Seward Peninsula, areas that were heavily grazed by reindeer had lower lichen cover and shorter thallus heights than areas that were lightly grazed (Holt et al. 2008). The recovery of lichen communities from heavy grazing by caribou and reindeer can take a few to many decades, depending on the intensity and duration of grazing, past history of grazing, the suite of lichen species present, characteristics of snow cover at the time of use by the caribou or reindeer, and the duration of the growth season and its favourability for lichen growth (Pegau 1969; Thing 1984; Messier et al. 1988; Henry & Gunn 1990).

Competition with vascular plants

Graminoids (grasses and sedges) are known to increase under heavy grazing pressure from reindeer and caribou in lichen-dominated plant communities (Klein 1968; Thing 1984; Post & Klein 1999), and are also predicted to increase under global warming scenarios (Chapin et al. 1995; Walker et al. 2006). These taxa rapidly increased in the WAH winter range over a 25-year period, more than doubling their percentage cover (Joly, Jandt et al. 2007). Holt et al. (2008) revealed a strong negative correlation between lichen and graminoid cover. Shrub height and cover extent is also expected to increase with climate warming (Chapin et al. 1995; van Wijk et al. 2003; Walker et al. 2006), and studies using aerial photography indicate that shrub expansion is already occurring in Arctic and sub-Arctic Alaska (Sturm et al. 2001; Tape et al. 2006). Dwarf shrub cover has increased by more than 35% in north-western Alaska over the past 25 years (Joly, Jandt et al. 2007). Tall shrubs (e.g., *Alnus* spp.) have noticeably increased within the WAH winter range, based on time-paired photos (Bureau of Land Management, unpubl. data). Vascular plant species compete with lichens for sunlight and available ground surface substrate. This competition can lead to declining lichen cover in Arctic tundra ecosystems. These vascular taxa not only directly compete with lichens, but they also alter the snow-melt patterns, which could lead to even greater shrub cover (Sturm et al. 2005). Although the shrubs may interfere with the winter grazing of lichens by *Rangifer*, the smothering (by shed leaves of deciduous shrubs)

and shading effects of the shrubs may be more detrimental to the lichens. The expansion of vascular plants has also come at the expense of some mosses, which have declined by 67% in the WAH winter range (Joly, Jandt et al. 2007). This may prove to be important regionally, as Holt et al. (2008) determined that there was a positive correlation between lichen and moss cover.

Climate change

The observed reduction in lichen cover in north-western Alaska over the past 25 years cannot be attributed solely to wildfire and the effects of *Rangifer* grazing. The slow rate of the re-establishment of lichens on St. Matthew Island, and their subsequent growth, has been further retarded by pronounced climate warming in recent decades, with associated atmospheric drying (Klein & Shulski 2009). In areas that contain high densities of *Rangifer* or other animal populations in summer, atmospheric drying could result in increased damage to lichen communities by trampling (Cooper et al. 2001).

Lichen cover has declined on some unburned Seward Peninsula transects that have only experienced light caribou grazing (Joly, Jandt et al. 2007). Jandt et al. (2008) also revealed that lichen cover dropped from 20 to 6% on unburned transects with low caribou use. Furthermore, the recovery of lichen communities after wildfire has regressed on transects on the Seward Peninsula over the past decade (Jandt et al. 2008). Analyses of the implications of climate change on tundra ecosystems as well as experimental warming studies predict that lichens and mosses will be negatively affected as a result of warming and drying (Chapin et al. 1995; Robinson et al. 1998; Cornelissen et al. 2001; van Wijk et al. 2003; Epstein et al. 2004; Hollister et al. 2005; Walker et al. 2006; Wiedermann et al. 2007), and we posit that recent observations from north-western Alaska augment this body of evidence. Furthermore, decreases in lichen and moss cover have also been detected on the North Slope of northern central Alaska between 1984 and 2002 (Jorgensen & Buchholtz 2003). Alternatively, lichens in alpine habitats may benefit from increased temperatures if there is little competition with vascular species (Molau & Alatalo 1998) and sufficient atmospheric moisture (Cooper et al. 2001). The effects of climate change on Arctic ecosystems will not, however, be easy to predict, especially changes in the moisture regime (Rouse et al. 1997; Wookey 2007).

Snow is a critical factor in determining the accessibility of winter forage for *Rangifer* (Hegggerget et al. 2002). *Rangifer* prefer to forage in areas where the snow is less hard and shallow (Collins & Smith 1991). Exceptionally deep snow, in conjunction with depleted lichens, was a

factor in the crash of the reindeer herd on St. Matthew Island. In the Arctic, warming will be especially pronounced during winter (Hinzman et al. 2005; Symon et al. 2005). Warmer winters could be accompanied by increased rain-on-snow events that form ice crusts, or engulf vegetation, at ground level on *Rangifer* winter ranges. Within the winter range of the WAH, two of these events have been documented, along with the associated caribou die-offs (Dau 2005b).

Interactions

Wildfire, disturbance by *Rangifer*, competition with vascular plants and climate change all independently act to reduce lichen cover in Arctic tundra ecosystems. These factors, however, are also interactive. Wildfires consume lichens, but also facilitate rapid increases in shrub and graminoid cover through nutrient release and soil warming (Racine et al. 2004; Jandt et al. 2008). Darker surfaces left by wildfire charring may reduce surface albedo, leading to more melting, which would give competitive advantage to vascular taxa over lichens. Deep burns also expose suitable mineral soil seedbeds for the establishment of new shrubs: particularly willows, which have efficient wind-aided seed dispersal. The establishment of new willows (*Salix pulchra*) following fire on the Seward Peninsula has been documented (Racine et al. 2004). Greater shrub cover could also reduce the surface albedo, over that of the pre-burn tundra vegetation (Chapin et al. 2005).

Herbivory can also induce fairly rapid changes in tundra plant community structure, both directly and indirectly (Thing 1984; Arseneault et al. 1997; van der Wal 2006; Klein & Shulski 2009). Areas heavily grazed by reindeer had 26% higher vascular plant cover than areas that were lightly grazed (Holt et al. 2008). The reduction of lichens by grazing *Rangifer* may also affect the surface albedo and plant community structure, which could lead into a feedback loop with further declines in lichens.

Climate warming induces change more slowly, and is the most difficult factor to document with field studies. However, longer growing seasons, increased photosynthetic activity and accelerated leaf tissue maturation have all been detected in tundra ecosystems (Goetz et al. 2005). Climate warming could lead to more dwarf birch (*Betula nana*) across tundra ecosystems in northern Alaska (van Wijk et al. 2003), which was the primary fuel when this region had significantly more frequent fires (Higuera et al. 2008). Thus, climate warming may induce changes in shrub species dominance and cover, which, in conjunction with warmer temperatures, could increase fire frequency (Higuera et al. 2008). Climate warming and summer drought are correlated with more frequent

and extensive wildfires in Alaska, northern Canada and Siberia (Wein 1976; Duffy et al. 2005; McCoy & Burn 2005; Soja et al. 2007), which could accelerate lichen declines and the potential disappearance of old-growth lichen tussock tundra communities in north-west Alaska (Rupp et al. 2000), thereby further degrading the caribou winter range (see Rupp et al. 2006). The decline in lichen biomass within plant communities that previously had a major lichen component appears to result from the warmer summers of recent decades, which favour vascular plant growth. Moreover, the associated dryer conditions at the ground surface inhibit lichen re-growth following either wildfire or moderate to heavy winter grazing by *Rangifer* species. In other words, climate change may extend the lichen regeneration time lines following disturbance by either wildfire or *Rangifer* grazing (Gough et al. 2008; Jandt et al. 2008; Klein & Shulski 2009).

The negative effects of climate warming on the *Rangifer* winter range may be partially offset by the improved spring forage quality resulting from earlier snowmelt (Cebrian et al. 2008). However, as spring forage quality and availability are temperature dependent, whereas caribou migration and calving are cued by changes in day length, a trophic mismatch may arise (Post & Forchhammer 2008). In West Greenland, this trophic mismatch has resulted in decreased calf production and increased calf mortality (Post & Forchhammer 2008).

Conclusions

Our review of the theoretical, experimental and actual outcomes of climate warming reveals a decrease in the extent and biomass of fruticose lichens over recent decades in north-western Alaska. Our current understanding of the primary factors influencing Arctic tundra ecosystems, inclusive of wildfire, grazing by *Rangifer* species, competition with vascular plants and climate change, leads us to conclude that these factors are unidirectional, interrelated and most likely have led to a marked decline in lichens among plant communities at high latitudes across Alaska. Changes in Arctic and sub-Arctic lichen communities in Alaska may be representative of changes elsewhere in the Arctic (Shaver & Jonasson 1999), with the possible exception of the Fennoscandian Arctic (Callaghan et al. 1999). Our review, in concert with others (e.g., Heggberget et al. 2002), leads us to question if these changes may well be pan-Arctic in nature, and may foreshadow major changes in plant community structure throughout the world's circumpolar regions.

Lichens are considered to be critical winter forage for the large, migratory herds of caribou in North America,

for the wild reindeer in Eurasia, as well as for the semi-domesticated reindeer throughout the Arctic, particularly for herds that face predation (White et al. 1981; Klein 1982; Syroechkovskii 1995; Heggberget et al. 2002). Thus, the decline of lichens in Arctic and sub-Arctic plant communities should concern land managers, subsistence and sport hunters, reindeer herders and wildlife enthusiasts.

Some researchers have postulated that the transition from a lichen-rich winter diet to one dominated by graminoids may not adversely affect *Rangifer* populations (Bergerud 1974; Heggberget et al. 2002; van der Wal 2006). This postulation, however, is based on ad libitum feeding trials with individual animals in captivity (Jacobsen & Skjennneberg 1975), and extrapolation from High-Arctic, low-density populations of Peary caribou (*Rangifer tarandus pearyi*; Thomas & Edmonds 1983) and the Svalbard caribou (*Rangifer tarandus platyrhynchus*). The latter, in the absence of predators, with little winter snow accumulation and with little need for efficient mobility, acquired morphological, physiological and behavioural adaptations that, unlike other caribou, equip them for winter survival through low energy expenditure, a greater capacity for fat storage, and an increased efficiency in the digestion of graminoids and mosses (Tyler 1987). On predator-free, High-Arctic islands, low-density populations of *Rangifer* can survive without abundant fruticose lichens (van der Wal et al. 2001; Heggberget et al. 2002). Lichens, as a component of the winter diet of the continental WAH, have declined during the past decade, with corresponding increases in graminoids (Joly, Cole et al. 2007). Therefore, the WAH may serve as a test case for assessing the importance of lichens for large, migratory caribou herds that face predation. Declining recruitment in the herd (Dau 2005a) concurrent with the decline in lichens on the landscape and in the diet, and the avoidance of recently (within 55 years) burned areas on the winter range (Joly, Bente et al. 2007), despite the quick and vigorous regrowth of graminoids (Jandt et al. 2008), appear to be initial evidence supporting the importance of climate warming and a lichen-rich winter diet for this herd. Furthermore, the initial population estimate for the WAH in 2007 revealed a 20% decline from the population high of 490 000 in 2003 (Dau, pers. comm.). It has been hypothesized that *Rangifer* herds may become smaller, more sedentary and utilize mountainous habitat more, as a result of climate warming and declining lichen communities (Heggberget et al. 2002). The work of Holleman et al. (1979) also supports the theory that more mobile *Rangifer* utilize greater proportions of lichen in their diets. Thus, the potential loss of dense and extensive lichen communities in the Arctic could lead to declines in herd sizes, and changes in distribution, behaviour and

diet of *Rangifer*, rather than leading towards their extirpation.

The role of wildfire in caribou winter ecology has long been debated (Leopold & Darling 1953; Scotter 1970; Klein 1982). However, of the four factors affecting lichen abundance, wildfire appears to be the one that land managers have the most control over, and thus garners the most attention. We promote the idea of improving the synthesis of existing research, supporting new research projects to address knowledge gaps and using this information to develop fire management plans for the winter ranges of large, migratory *Rangifer* herds. In addition, an integrated, international effort is needed to investigate the role of lichens in Arctic and sub-Arctic ecosystems, and the responses of lichens to changes in the environment: changes that have accelerated in recent decades (Symon et al. 2005). Such an effort should encompass: climate change detection and modelling; the assessment of the long-term impacts of boreal forest and tundra wildfires, and the related soil dynamics; determining the competitive feedbacks between lichens, shrubs and graminoids in plant community structure; and impacts on caribou ecology. Furthermore, dramatic changes in sea-ice dynamics, which strongly influence Arctic weather patterns, may lead to even more pronounced changes on terrestrial Arctic ecosystems. Land managers throughout the Arctic could use such data to guide strategies for fire and resource management that fit with the changing climate.

Acknowledgements

We thank all the Bureau of Land Management employees that have worked on the various projects mentioned in this paper, especially R. Meyers and J. Cole. J. Allen, T. Chapin, K. Kielland, R. Meyers, G. Theisen, R. van der Wal and anonymous reviewers provided comments and discussions that were helpful for developing this manuscript.

References

- Ahti T. 1959. *Studies on the caribou lichen stands of Newfoundland*. *Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo* 30. Helsinki: Societas Zoologica Botanica Fennica Vanamo.
- Arseneault D., Villeneuve N., Boismenu C., Leblanc Y. & Deshayes J. 1997. Estimating lichen biomass and caribou grazing on the wintering grounds of northern Quebec: an application of fire history and Landsat data. *Journal of Applied Ecology* 34, 65–78.
- Auclair A.N.D. 1983. Role of fire in lichen-dominated tundra and forest-tundra. In R.W. Wein & D.A. MacLean (eds.):

- Role of fire in northern circumpolar ecosystems*. Pp. 235–256. New York: John Wiley and Sons.
- Bergerud A.T. 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38, 757–770.
- Brodo I.M., Sharnoff S.D. & Sharnoff S. 2001. *Lichens of North America*. New Haven: Yale University Press.
- Callaghan T.V., Press M.C., Lee J.A., Robinson D.L. & Anderson C.W. 1999. Spatial and temporal variability in the response of Arctic terrestrial ecosystems to environmental change. *Polar Research* 18, 191–197.
- Cebrian M.R., Kielland K. & Finstad G. 2008. Forage quality and reindeer productivity: multiplier effects amplified by climate change. *Arctic, Antarctic and Alpine Research* 40, 48–54.
- Chapin F.S. III, 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.
- Chapin F.S. III, Sturm M., Serreze M.C., McFadden J.P., Key J.R., Lloyd A.H., McGuire A.D., Rupp T.S., Lynch A.H., Schimel J.P., Beringer J., Chapman W.L., Epstein H.E., Euskirchen E.S., Hinzman L.D., Jia G., Ping C.-L., Tape K.D., Thompson C.D.C., Walker D.A. & Welker J.M. 2005. Role of land-surface changes in Arctic summer warming. *Science* 310, 657–660.
- Collins W.B. & Smith T.S. 1991. Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*). *Arctic* 44, 217–222.
- Cooper E.J., Smith F.M. & Wookey P.A. 2001. Increased rainfall ameliorates the negative effect of trampling on the growth of High Arctic forage lichens. *Symbiosis* 31, 153–171.
- Cornelissen J.H.C., Callaghan T.V., Alatalo J.M., Michelsen A., Graglia E., Hartley A.E., Hik D.S., Hobbie S.E., Press M.C., Robinson C.H., Henry G.H.R., Shaver G.R., Phoenix G.K., Jones D.G., Jonasson S., Chapin F.S., Molau U., Neill C., Lee J.A., Melillo J.M., Sveinbjornsson B. & Aerts R. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89, 984–994.
- Dau J. 2000. Managing reindeer and wildlife on Alaska's Seward Peninsula. *Polar Research* 19, 57–62.
- Dau J. 2005a. Western Arctic Herd. In C. Brown (ed.): *Caribou management report of survey and inventory activities, 1 July 2002–30 June 2004*. Pp. 177–218. Juneau: Alaska Department of Fish and Game.
- Dau J. 2005b. Two caribou mortality events in northwest Alaska: possible causes and management implications. *Rangifer Special Issue* 16, 37–50.
- Dalerum F., Boutin S. & Dunford J.S. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. *Canadian Journal of Zoology* 85, 26–32.
- Duffy P.A., Walsh J.E., Graham J.M., Mann D.H. & Rupp T.S. 2005. Impacts of large-scale atmospheric–ocean variability on Alaskan fire season severity. *Ecological Applications* 15, 1317–1330.
- Dunford J., McLoughlin P., Dalerum F. & Boutin S. 2006. Lichen abundance in the peatlands of northern Alberta: implications for boreal caribou. *Ecoscience* 13, 469–474.
- Epstein H.E., Calef M.P., Walker M.D., Chapin F.S. III & Starfield A.M. 2004. Detecting changes in Arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology* 10, 1325–1334.
- Goetz S.J., Bunn A.G., Fiske G.J. & Houghton R.A. 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Science* 102, 13521–13525.
- Gough L., Shrestha K., Johnson D.R. & Moon B. 2008. Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra. *Arctic, Antarctic and Alpine Research* 40, 65–73.
- Heggberget T.M., Gaare E. & Ball J.P. 2002. Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage. *Rangifer* 22, 13–32.
- Helle T. & Aspi J. 1983. Effects of winter grazing by reindeer on vegetation. *Oikos* 40, 337–343.
- Henry G.H.R. & Gunn A. 1990. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. *Arctic* 44, 38–42.
- Higuera P.E., Brubaker L.B., Anderson P.M., Brown T.A., Kennedy A.T. & Hu F.S. 2008. Frequent fires in ancient shrub tundra: implications of paleorecords for Arctic environmental change. *PLoS ONE* 3(3), e0001744. doi: 10.1371/journal.pone.0001744.
- Hinzman L.D., Bettez N.D., Bolton W.R., Chapin F.S. III, Dyurgerov M.B., Fastie C.L., Griffith B., Hollister R.D., Hope A., Huntington H.P., Jensen A.M., Jia G.J., Jorgenson T., Kane D.L., Klein D.R., Kofinas G., Lynch A.H., Lloyd A.H., McGuire A.D., Nelson F.E., Oechel W.C., Osterkamp T.E., Racine C.H., Romanovsky V.E., Stone R.S., Stow D.A., Sturm M., Tweedie C.E., Vourlitis G.L., Walker M.D., Walker D.A., Webber P.J., Welker J.M., Winker K.S. & Yoshikawa K. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. *Climate Change* 72, 251–298.
- Holleman D.F. & Luick J.R. 1977. Lichen species preference by reindeer. *Canadian Journal of Zoology* 55, 1368–1369.
- Holleman D.F., Luick J.R. & White R.G. 1979. Lichen intake estimates for reindeer and caribou during winter. *Journal of Wildlife Management* 43, 192–201.
- Hollister R.D., Webber P.J. & Tweedie C.E. 2005. The response of Alaskan Arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology* 11, 525–536.
- Holt E.A., McCune B. & Neitlich P. 2006. Defining a successional metric for lichen communities in the Arctic tundra. *Arctic, Antarctic, and Alpine Research* 38, 373–377.
- Holt E.A., McCune B. & Neitlich P. 2008. Grazing and fire impacts on macrolichen communities of the Seward Peninsula, Alaska, U.S.A. *The Bryologist* 111, 68–83.
- Jacobsen E. & Skjenneberg S. 1975. Some results from feeding experiments with reindeer. In L.R. Luick et al.

- (eds.): *Proceedings of the First International Reindeer and Caribou Symposium. Biological Papers of the University of Alaska Special Report 1*. Pp. 95–107. Fairbanks, AK: University of Alaska.
- Jandt R.R., Joly K., Meyers C.R. & Racine C. 2008. Slow recovery of lichen on burned caribou winter range in Alaska tundra: potential influences of climate warming and other disturbances. *Arctic, Antarctic and Alpine Research* 40, 89–95.
- Joly K., Bente P. & Dau J. 2007. Response of overwintering caribou to burned habitat in northwest Alaska. *Arctic* 60, 401–410.
- Joly K., Cole M.J. & Jandt R.R. 2007. Diets of overwintering caribou, *Rangifer tarandus*, track decadal changes in Arctic tundra vegetation. *Canadian Field-Naturalist* 121, 379–383.
- Joly K., Dale B.W., Collins W.B. & Adams L.G. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. *Canadian Journal of Zoology* 81, 1192–1201.
- Joly K., Jandt R.R., Meyers C.R. & Cole M.J. 2007. Changes in vegetative cover on Western Arctic Herd winter range from 1981–2005: potential effects of grazing and climate change. *Rangifer Special Issue* 17, 199–207.
- Jorgensen J.C. & Buchholtz C.A. 2003. Eighteen years of vegetation monitoring in the Arctic National Wildlife Refuge, Alaska. Accessed on the internet at www.arcus.org/SEARCH/meetings/2003/webcast.php on 19 February 2009.
- Kasischke E.S. & 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. *Geophysical Research Letters* 33, L09703, doi: 10.1029/2006GL025677.
- Klein D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management* 32, 350–367.
- Klein D.R. 1982. Fire, lichens, and caribou. *Journal of Range Management* 35, 390–395.
- Klein D.R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management* 40, 336–338.
- Klein D.R. & Shulski M. 2009. Lichen recovery following heavy grazing by reindeer delayed by climate warming. *Ambio* 38, 11–16.
- Klein D.R. & Vlasova T.J. 1991. Lichens, a unique forage resource threatened by air pollution. *Rangifer* 12, 21–27.
- Leopold A.S. & Darling F.F. 1953. *Wildlife in Alaska: an ecological reconnaissance*. New York: Ronald Press.
- McCoy V.M. & Burn C.R. 2005. Potential alteration by climate change of the forest-fire regime in the boreal forest of central Yukon Territory. *Arctic* 58, 276–285.
- Messier F., Huot J., Le Henaff D. & Luttich S. 1988. Demography of the George River Caribou Herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41, 279–287.
- Molau U. & Alatalo J.M. 1998. Responses of subarctic–alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio* 27, 322–329.
- Morneau C. & Payette S. 1989. Postfire lichen–spruce woodland recovery at the limit of boreal forest in northern Quebec. *Canadian Journal Botany* 67, 2770–2782.
- Moser T.J., Nash T.H. III & Thomson J.W. 1979. Lichens of Anaktuvuk Pass, Alaska, with emphasis on the impact of caribou grazing. *The Bryologist* 82, 393–408.
- Parry M.L., Canziani O.F., Palutikof J.P., van der Linden P.J. & Hanson C.E. (eds.). 2007. *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Payette S., Morneau C., Sirois L. & Despons M. 1989. Recent fire history of the northern Quebec biomes. *Ecology* 70, 656–673.
- Pegau R.E. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. *Arctic* 21, 255–259.
- Pegau R.E. 1969. Effect of reindeer trampling and grazing on lichens. *Journal of Range Management* 23, 95–97.
- Post E. & Forchhammer M.C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B* 363, 2369–2375.
- Post E. & Klein D.R. 1999. Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management* 63, 335–345.
- Racine C.H., Patterson W.A. III & Dennis J.G. 1985. Tundra fire regimes in the Noatak River watershed, Alaska: 1956–1983. *Arctic* 38, 194–200.
- Racine C.H., Jandt R., Meyers C. & Dennis J. 2004. Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research* 36, 1–10.
- Racine C.H., Johnson L.A. & Viereck L.A. 1987. Patterns of vegetation recovery after tundra fires in northwestern Alaska, U.S.A. *Arctic and Alpine Research* 19, 461–469.
- 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 polar semi-desert. *Ecology* 79, 856–866.
- Rouse W.R., Douglas M.S.V., Hecky R.E., Hershey A.E., Kling G.W., Lesack L., Marsh P., McDonald M., Nicholson B.J., Roulet N.T. & Smol J.P. 1997. Effects of climate change on the freshwaters of Arctic and subarctic North America. *Hydrological Processes* 11, 873–902.
- Rupp T.S., Chapin F.S. III & Starfield A.M. 2000. Response of the subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Change Biology* 6, 541–555.
- Rupp T.S., Olson M., Adams L.G., Dale B.W., Joly K., Henkelman J., Collins W.B. & Starfield A.M. 2006. Simulating the influences of various fire regimes on caribou winter habitat. *Ecological Applications* 16, 1730–1743.

- Saperstein L.B. 1996. Winter forage selection by barren-ground caribou: effects of fire and snow. *Rangifer Special Issue 9*, 237–238.
- Scotter G.W. 1967. The winter diet of barren-ground caribou in northern Canada. *Canadian Field-Naturalist 81*, 33–39.
- Scotter G.W. 1970. Wildfires in relation to the habitat of barren-ground caribou in the taiga of northern Canada. *Annual Proceedings Tall Timbers Conference 10*, 85–106.
- Shaver G.R. & Jonasson S. 1999. Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Research 18*, 245–252.
- Shulski M. & Wendler G. 2007. *The climate of Alaska*. Fairbanks: University of Alaska Press.
- Soja A.J., Tchebakova N.M., French N.H.F., Flannigan M.D., Shugart H.H., Stocks B.J., Sukhinin A.I., Parfenova E.I., Chapin F.S. III & Stackhouse P.W. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change 56*, 274–296.
- Stern R.O., Arobio E.L., Naylor L.L. & Thomas W.C. 1980. *Eskimo, reindeer and land*. Bulletin 59. Fairbanks: University of Alaska Fairbanks.
- Sturm M., Racine C. & Tape K. 2001. Increasing shrub abundance in the Arctic. *Nature 411*, 546–547.
- Sturm M., Schimel J., Michaelson G., Welker J.M., Oberbauer S.F., Liston G.E., Fahnestock J. & Romanovsky V.E. 2005. Winter biological processes could help convert Arctic tundra to shrubland. *Bioscience 55*, 17–26.
- Swanson J.D., Schuman M. & Scorup P.C. 1985. *Range survey of the Seward Peninsula reindeer ranges, Alaska*. Anchorage AK: USDA Soil Conservation Service.
- Symon C., Arris L. & Heal B. (eds.) 2005. *Arctic climate impact assessment*. Cambridge: Cambridge University Press.
- Syroechkovskii E.E. 1995. *Wild reindeer*. Washington, D.C.: Smithsonian Institution Libraries.
- Tape K., Sturm M. & Racine C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Global Change Biology 12*, 686–702.
- Thing H. 1984. *Feeding ecology of the West Greenland caribou (Rangifer tarandus groenlandicus) in the Sisimuit-Kangerlussuaq Region*. Danish Review of Game Biology 12. Copenhagen: Vildtbiologisk Station.
- Thomas D.C., Barry S.J. & Alaie G. 1996. Fire–caribou–winter range relationships in northern Canada. *Rangifer 16*, 57–67.
- Thomas D.C. & Edmonds J. 1983. Rumen contents and habitat selection of Peary caribou in winter, Canadian Arctic Archipelago. *Arctic and Alpine Research 15*, 97–105.
- Thomas D.C. & Hervieux D.P. 1986. The late winter diets of barren-ground caribou in north-central Canada. *Rangifer Special Issue 1*, 305–310.
- Thomas D.C. & Kiliaan H.P.L. 1998. *Fire–caribou relationships: (IV) recovery of habitat after fire on winter range of the Beverly Herd*. Technical Report Series 312. Edmonton: AB: Prairie and Northern Region, Canadian Wildlife Service.
- Thomas D.C., Kiliaan H.P.L. & Trottier T.W.P. 1998. *Fire–caribou relationships: (III) movement patterns of the Beverly Herd in relation to burns and snow*. Canadian Wildlife Service, Prairie & Northern Region Technical Report Series 311. Edmonton: AB: Prairie and Northern Region, Canadian Wildlife Service.
- Tyler N.J.C. 1987. Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. *Symposia of the Zoological Society of London 57*, 203–229.
- van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos 114*, 177–186.
- van der Wal R., Brooker R., Cooper E. & Langvatn R. 2001. Differential effects of reindeer on High Arctic lichens. *Journal of Vegetation Science 12*, 705–710.
- van Wijk M.T., Clemmensen K.E., Shaver G.R., Williams M., Callaghan T.V., Chapin F.S. III, Cornelissen J.H.C., Gough L., Hobbie S.E., Jonasson S., Lee J.A., Michelsen A., Richardson S.J. & Rueth H. 2003. 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. *Global Change Biology 10*, 105–123.
- Walker M.D., Wahren C.H., Hollister R.D., Henry G.H.R., Ahlquist L.E., Alatalo J.M., Bret-Harte M.S., Calef M.P., Callaghan T.V., Carroll A.B., Epstein H.E., Jonsdottir I.S., Klein J.A., Magnusson B., Molau U., Oberbauer S.F., Rewa S.P., Robinson C.H., Shaver G.R., Suding K.N., Thompson C.C., Tolvanen A., Totland Ø., Turner P.L., Tweedie C.E., Webber P.J. & Wookey P.A. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Science 103*, 1342–1346.
- Wiedermann M.M., Nordin A., Gunnarsson U., Nilsson M.B. & Ericson L. 2007. Global change shifts vegetation and plant–parasite interactions in a boreal mire. *Ecology 88*, 454–464.
- Wein R.W. 1976. Frequency and characteristics of Arctic tundra fires. *Arctic 29*, 213–22.
- White R.G., Bunnell F.L., Gaare E., Skogland T. & Hubert B. 1981. Ungulates on Arctic ranges. In L.C. Bliss et al. (eds.): *Tundra ecosystems: a comparative analysis*. Pp. 397–483. Cambridge: Cambridge University Press.
- Wookey P.A. 2007. Climate change and biodiversity in the Arctic—Nordic perspectives. *Polar Research 26*, 96–103.