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Slow Recovery of Lichen on Burned Caribou Winter Range in Alaska Tundra: Potential Influences of Climate Warming and Other Disturbance Factors

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Abstract

Lichen regeneration timelines are needed to establish sound fire management guidelines for caribou (*Rangifer tarandus*) winter range. Paired burned and unburned permanent vegetative cover transects were established after 1981, 1977, and 1972 tundra fires in northwestern Alaska to document regrowth of tundra vegetation including caribou forage lichens in the wintering range of Alaska's largest caribou herd. Following fire, lichen had recovered very little compared to unburned transects (1% cover vs. 15% cover) after 14 years. After 24 or 25 years, lichen cover in the burns remained low (3–4%), whether or not caribou were present during the recovery period. In addition, lichen cover on unburned transects at one study site had decreased from 14% to 6%. Shrub cover was higher on the burned plots than the unburned plots. Cover of cottongrass (*Eriophorum vaginatum*) initially increased following the fire and tussocks quickly became more vigorous than on paired unburned transects, remaining so for more than 14 years. Persistent changes in vegetation following fire likely reflect the cumulative impacts of seasonal caribou use and favorable growing conditions (warmer soils, longer growing season) for rooted vascular species during the recovery period. The actual recovery of forage lichens after fire on our study sites is slower than predictions based on ideal growth potential.

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Introduction

North American caribou (*Rangifer tarandus*) herds are largely dependent on lichens for winter forage. Prevalence of ground lichens in the winter diet was 68% based on rumen content samples in Canada (Thomas and Hervieux, 1986). Lichen comprised 63–83% of winter fecal pellets from caribou of the Western Arctic Herd (WAH; Jandt et al., 2003). Findings from a study in eastern Alaska showed that caribou strongly selected against burned areas <35 years old throughout the winter and that lichen availability was a large factor influencing habitat selection (Joly et al., 2003). The WAH, Alaska's largest caribou herd, increased in population steadily after a drastic decline between 1970 and 1976, when it dropped from 240,000 to 70,000 animals (Davis and Valkenburg, 1978). Population of the WAH grew rapidly during the 1980s and early 1990s, but leveled off during the last 10 years at just under 500,000 animals (Dau, 2005). Although individual members of the WAH can be found across a broad swath of northwest Alaska, the Buckland River valley (Fig. 1) has been and continues to be the core winter range (Davis and Valkenburg, 1978; Dau, 2005). The only ongoing assessment of the range conditions for this herd, which is a vital subsistence resource to 36 villages in western Alaska, are permanent transects established by the Bureau of Land Management, including pairs on burned ranges (Jandt et al., 2003; Joly et al., 2007).

The abundance of lichen available to caribou has important management implications. Lichen biomass varies greatly across the Alaskan arctic but is relatively high in the treeless tussock tundra of the Buckland River valley and Seward Peninsula. Mean biomass of live lichen in lichen tussock tundra for the Buckland River valley was estimated by Adams and Connery (1983) at $161 \pm 22 \text{ g m}^{-2}$ and vascular production at $64 \pm 5 \text{ g m}^{-2} \text{ yr}^{-1}$.

Macrolichen abundance is dependent on a variety of conditions but is often associated with low-nutrient, high sunlight, and relatively dry conditions in tundra. The influence of wildfire, climate warming, grazing, and trampling has the potential to change lichen abundance relative to vascular species on a landscape scale (Cornelissen et al., 2001; van der Wal, 2006). The primary goals of this study were to document successional changes in lichen tussock tundra vegetation and to present the management implications.

Presently, tundra fires in Alaska are infrequent except for a limited area in the northwest including the Seward Peninsula and Noatak River area (Racine et al., 1985), but are expected to increase in size and frequency with a warming climate (Rupp et al., 2000; McCoy and Burn, 2005). Fire changes the composition and structure of tundra vegetation on both a short and long time scale, although biomass and net primary production recovers quickly (Wein and Bliss, 1973). This may have important implications for carbon, surface energy balance, winter snow depth, and forage for herbivores. In the Low Arctic where most tundra fires occur, vegetation is primarily sedge tussock tundra, sometimes lichen- or dwarf shrub-dominated. Fires do not typically consume tussock bases and usually burn only the surface of the thick organic horizon. Terricolous lichens dry rapidly in response to low atmospheric humidity and provide a ready surface fuel for tundra wildfires. Due both to their structure and position in the tundra canopy they are consumed or killed by fire's radiant heat even in relatively light burns. Short-term recovery of tundra vascular vegetation has been well-documented (Wein and Bliss, 1973; Vavrek et al., 1999). Vascular plants quickly recover to pre-fire levels, regaining pre-fire primary production and biomass, including shrubs, within 10 years (Wein and Bliss, 1973; Racine et

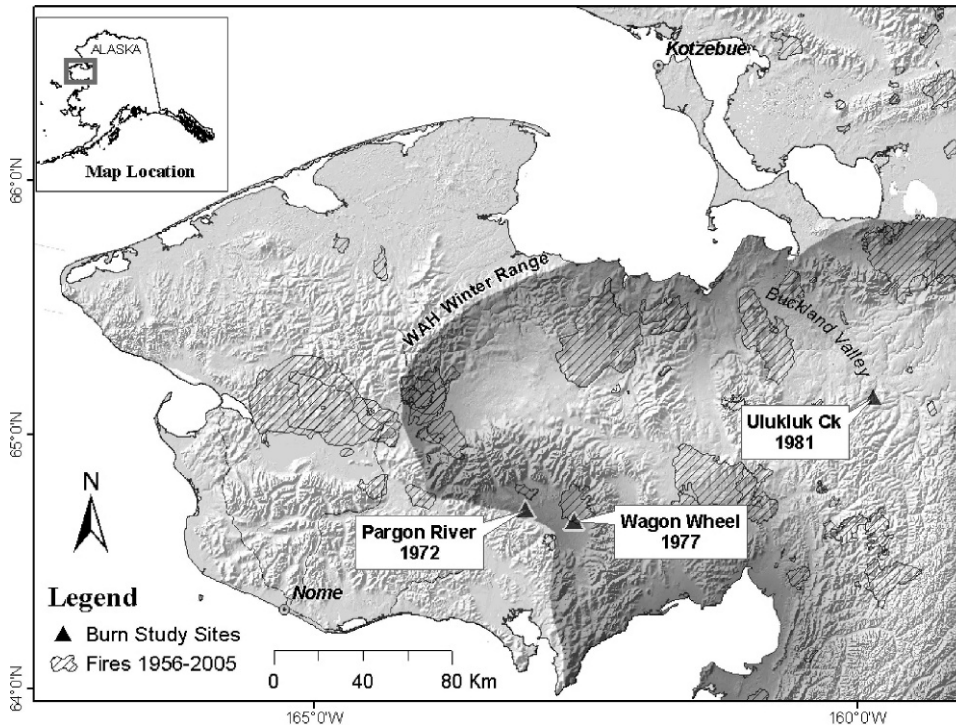


FIGURE 1. Map location of three tundra fire recovery study sites in northwestern Alaska in relation to the Western Arctic caribou herd winter range. The 1981 burn was sampled in 1981–1984, 1995, and 2005, while 1972 and 1977 burns were sampled in 1997 and 2006. Polygons with crosshatching identify scars of fires >400 ha in size from 1956 to 2005.

al., 1987; Fetcher et al., 1984). Much of early recovery is due to vigorous regrowth of graminoid sedges. Lichen species important as winter caribou forage take much longer to recover after disturbance (Thomas, 1996; Jandt and Meyers, 2000), and the influence of compounding factors, such as continued grazing or trampling and climate warming on recovery timelines, remains unknown.

Study Area

The three recovering burns we studied were in lowland tundra valleys in northwestern Alaska (Fig. 1). The 1981 burn study site (Ulukluk Creek) lies in the Buckland River Valley, central to the WAH core winter range. The 1972 (Pargon River) and 1977 (Wagon Wheel) burn sites are in a broad basin on the eastern Seward Peninsula, topographically isolated from the main winter range by the Darby Mountains. Caribou grazing has been documented in the basin only sporadically during the recovery period. Vegetation is characterized by treeless tussock tundra on flats or rolling hills up to 900 m dominated by graminoid sedges (primarily *Eriophorum vaginatum*), deciduous shrubs (*Betula nana*, *Salix* sp., and *Vaccinium uliginosum*), and evergreen shrubs (*Empetrum nigrum*, *Ledum palustre*, and *V. vitis-idaea*). Fruticose lichens (*Cladina* spp., *Cetraria* spp.) were important components of the tundra tussock community, with the “reindeer lichens” preferred by caribou, including *Cladina rangiferina*, *C. stellaris* (formerly *C. alpestris*), and *C. mitis* (Pegau, 1968), well represented in undisturbed plots. The vegetation type at all study sites prior to disturbance was lichen tussock tundra, as described by Swanson et al. (1985). Plant nomenclature follows Hultén (1968) for vascular plants and Thomson (1984) for lichens.

Kotzebue, the most representative regional long-term weather station, has a mean annual temperature of -5.7°C (Alaska Climate Research Center, 2006). Temperatures can drop to -45°C during the winter months. Mean annual precipitation is 41 cm

with about half (16 cm) falling during June, July, and August. Since 1949, mean annual temperatures at Kotzebue and Nome have increased 1.8°C (Alaska Climate Research Center, 2006), with new highs set in 2004 when large, deep-burning fires occurred on the Seward Peninsula. Mean summer temperature at Kotzebue and Nome increased 1.5°C from 1949 to 2005, while springtime (March–May) average Nome temperature increased a remarkable 2.4°C .

Methods

Paired permanent transects were established at each of the three sites beginning with the Ulukluk Creek study site in July 1981 to monitor recovery of vegetation. Transects at Ulukluk Creek were established 3 days after lightning ignited a fire that burned about 2 ha before it was extinguished by humidity. Plots were established in 1997 at the burns dating from 1972 and 1977. The original burn perimeter could still be readily observed when the plots were established. Percent cover of low-growing tundra plants correlates strongly with biomass (Jonasson, 1988), so we used cover estimates to indicate forage availability.

At Ulukluk Creek, ocular estimates of cover were made on paired 50-m transect lines located inside and outside the burn perimeter along each side of the burn, with twenty-five 0.1-m^2 quadrats spaced every 2 m along the transect lines. Burn severity on each quadrat was evaluated based on plant and substrate consumption after Viereck et al. (1979). Within quadrats, the cover of each plant species was recorded as 0–5%, 6–25%, 26–50%, 51–75%, 76–95%, or >95%. Quadrat cover values were summed as the mean of the cover class (i.e. 2.5, 15, 37.5, etc.) for determining the transect means. Sampling was conducted using the same methods in July 1981, August 1981, 1982, 1983, 1984, and 1995. After completing the ocular cover estimates in 1995, we repeated sampling on each transect using a point-sampling frame, with 50 string intersections over a 0.5-m area (frame size: $1\text{ m} \times$

TABLE 1

Changes in vegetative canopy cover over time in a tussock tundra community burned in July 1981 (B) compared to paired unburned (U) transects*, Ulukluk Creek, northwestern Alaska.

Cover (%)	1981		1982		1983		1984		1995	
Treatment:	<u>B</u>	<u>U</u>	<u>B</u>	<u>U</u>	<u>B</u>	<u>U</u>	<u>B</u>	<u>U</u>	<u>B</u>	<u>U</u>
Lichen	0.5	28.4	1.2	39.9	0.8	38.2	0	35.0	3.2	27.2
Moss	7.8	12.8	7.0	7.7	4.9	10.2	1.1	9.9	2.6	6.0
Grass/Sedge	0.3	12.6	16.4	15.6	27.4	20.0	34.1	18.0	53.9	40.2
Forb	0	5.4	2.8	5.3	3.0	4.2	4.0	5.2	3.5	3.6
Shrub	0	28.0	10.0	33.2	13.4	39.4	19.0	48.4	30.4	35.7

* Results based on ocular estimates of two paired transects.

0.5 m). Ocular estimates overestimate smaller plants and rare species due to the assumption that cover values are uniformly distributed about the midpoints of the cover classes; that is, a trace of lichen would be counted as 2.5% (Floyd and Anderson, 1987). Point estimates of cover are less biased and more repeatable for long-term studies with inevitable turnover of observers. In addition, sampling time at the remote study sites, accessible only by helicopter, was reduced by 50%, and lower cost will facilitate continuance of long-term monitoring (Jandt and Meyers, 2000). Twelve quadrats were spaced every 4 m along each transect, and the first plant species encountered directly under an intersection was recorded. Cover values were calculated as the percentage of total hits. In 2005 only point-intercept sampling was conducted.

To see whether repeated caribou disturbance was responsible for the observed recovery times at Ulukluk Creek, paired 50-m transects were established in 1997 at 2 older burn sites in lichen tussock tundra on the southern Seward Peninsula that had not been used by caribou or reindeer for at least 50 years (Fig. 1). These transects were sampled and analyzed using the same point-intercept frame method as Ulukluk Creek.

Statistical inference between burned and unburned areas for the early recovery at Ulukluk Creek (years 0–4) was limited due to the small number of transects. In subsequent years, point-intercept quadrats were spaced at sufficient distance to consider them independent so that significance of mean differences could be evaluated. Data from succeeding years on the same transect were compared using *t*-test for dependent (paired) samples, while burned/unburned treatments were compared using *t*-test for independent samples.

Results

The overall burn severity at Ulukluk Creek was light, with charred vegetation but little consumption of the peaty organic duff layer. The burn was relatively uniform in that only 2% of the total quadrat area was unburned. Quadrats had no mineral soil exposure and only slight damage to tussock bases, so tussock mortality was minimal. Burn severity at 1970s burn sites was not measured but would likely be higher than observed at Ulukluk Creek based on review of old photographs and known environmental conditions prevailing during those burns. During the first 3 years cottongrass (*Eriophorum vaginatum*) recovered quickly, demonstrating vigorous basal sprouting from tussock bases and heavy flowering. Graminoid cover (<1% in 1981) rose to equal unburned cover in 1 year and by the third summer was almost double that in unburned transects (Table 1, Fig. 2). After 14 years, graminoid cover remained 11% greater on burned than on unburned transects ($t = 2.20$, $P = 0.033$; Table 2). Graminoid and shrub cover in the *unburned* transects also appeared to increase between years 4 and 14 (Table 1), but statistical significance of the ocular estimates could not be evaluated. Sedges (85% *Eriophorum*, 15% *Carex*) covered about 50% of both burned and unburned transects after 24 years (Table 2).

During the first 3 years of monitoring at Ulukluk Creek only trace amounts of lichen were recorded on burned transects, and relative cover of lichen actually appeared to decline as cottongrass and shrubs increased (Table 1, Fig. 2). On the burned transects, lichen cover recorded by the point-intercept method was 1.2% after 14 years at Ulukluk Creek, compared to 15.4% on unburned

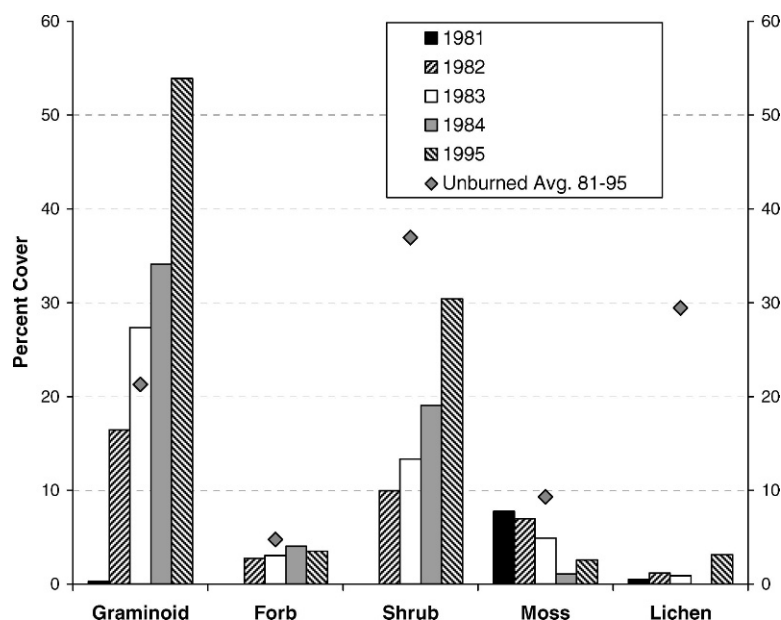


FIGURE 2. Changes in percent cover of vegetation classes on burned transects at Ulukluk Creek from 0 to 14 years after burning; percent cover based on ocular estimates. Diamonds show average value of unburned paired transects.

TABLE 2

Comparison of burned and unburned transects 14 and 24 years after 1981 fire in a lichen tussock tundra, Ulukluk Creek, northwestern Alaska. Results are derived from 24 point-intercept quadrats (each with 50 hits) per treatment. An * indicates significance ($P < 0.05$).

ULUKLUK CREEK COVER TYPE	1995 % COVER			2005 % COVER		
	Burned	Unburned	Mean Difference: B – Unb	Burned	Unburned	Mean Difference: B – Unb
<i>Carex bigelowii</i>	8.8	9.3	-0.6	6.0	9.7	-3.7
<i>Eriophorum vaginatum</i>	45.9	34.5	11.4	43.0	42.1	0.9
Total Graminoid:	54.7	43.8	10.8	49.1	51.8	-2.8
<i>Rubus chamaemorus</i>	2.0	2.3	-0.3	2.3	3.0	-0.7
Total Forb:	2.0	2.3	-0.3	2.3	3.0	-0.7
<i>Ledum palustre</i>	15.2	11.2	4.0	15.0	9.6	5.4
<i>Vaccinium uliginosum</i>	7.2	5.8	1.4	10.0	8.1	1.9
<i>Betula nana</i>	3.2	2.2	1.0	1.6	1.6	0.0
<i>Vaccinium vitis-idaea</i>	2.2	4.2	-2.0	6.2	4.9	1.3
<i>Empetrum nigrum</i>	0.9	2.9	-2.0	3.1	2.3	0.8
Total Shrub:	31.1	28.4	2.7	36.4	28.2	8.2*
<i>Cladonia rangiferina</i>	0.1	5.0	-4.9*	0.2	1.3	-1.1
<i>Cladina mitislarbuscula</i> ¹	0.1	2.5	-2.4	1.3	1.3	-0.1
<i>Cetraria cucullata</i>	0.2	6.1	-5.8	1.4	2.8	-1.3
<i>C. islandica</i>	0.1	1.1	-1.0*	0.1	0.2	-0.1
<i>Cladonia</i> spp.	0.8	0.8	0	0.6	0.2	-0.4
Total Lichen:	1.2	15.4	-14.2*	3.7	6.0	-2.3
Total Moss:	2.4	3.0	-0.6	1.3	1.6	-0.3

¹ Species of lichens which cannot be distinguished without chemical tests.

transects ($N = 24$, $t = 6.26$, $P < 0.0001$; Table 2). Lichens in the burn consisted primarily of *Cladonia* squamules which were difficult to identify to species. Between years 14 and 24, post-fire lichen cover increased to 3.7% in the burn ($t = -2.76$, $P = 0.011$, $n = 24$) but had declined to 6.0% in the unburned quadrats ($t = 4.27$, $P = 0.0003$; Table 2). In fact, by 2005 the difference in lichen cover on burned versus unburned quadrats was no longer statistically significant ($t = 1.58$, $P = 0.12$; Fig. 3).

The 1972 and 1977 burns on ranges undisturbed by caribou also demonstrated very low lichen cover. At the 1977 burn site (Wagon Wheel Burn), lichen cover was $4.3 \pm 1.1\%$ compared to $48.8 \pm 4.2\%$ ($n = 12$) on the unburned quadrats after 20 years (Table 3). In the 25-year-old 1972 burn site (Pargon River Burn), lichen cover was $2.7 \pm 1.0\%$ compared to $39.5 \pm 3.8\%$ ($n = 12$) for the unburned (Table 3). Remeasurement of these transects in 2006 showed a slight decrease in relative lichen cover. After 29 and 34 years, respectively, both burn sites had about 1% lichen cover

(Table 3). Lichen cover also declined on the associated unburned transects from 1997 to 2006, mainly due to caribou utilization that occurred during this interval (Table 3).

Dwarf birch (*Betula nana*) and ericaceous shrubs, primarily Labrador tea (*Ledum palustre*), blueberry (*Vaccinium uliginosum*), and lingonberry (*V. vitis-idaea*) recovered by resprouting and increased steadily over time on burned plots. After 3 years, shrub cover in burned transects was 40% of unburned shrub cover and by 14 years had essentially recovered to match unburned values (Table 1, Fig. 2). Crowberry (*Empetrum nigrum*) however, did not recover as rapidly as other dwarf and heath shrubs. After 14 years only 0.9% crowberry cover was recorded on burned transects compared to 2.9% outside the burn (Table 2). By 24 years after fire, shrub cover on the Ulukluk Creek burn (36.4%) exceeded that on the unburned transects (28.2%, $t = 2.21$, $P = 0.03$; Table 2). The 1972 and 1977 burn plots also demonstrated higher shrub cover on burned quadrats than on unburned transects in all years,

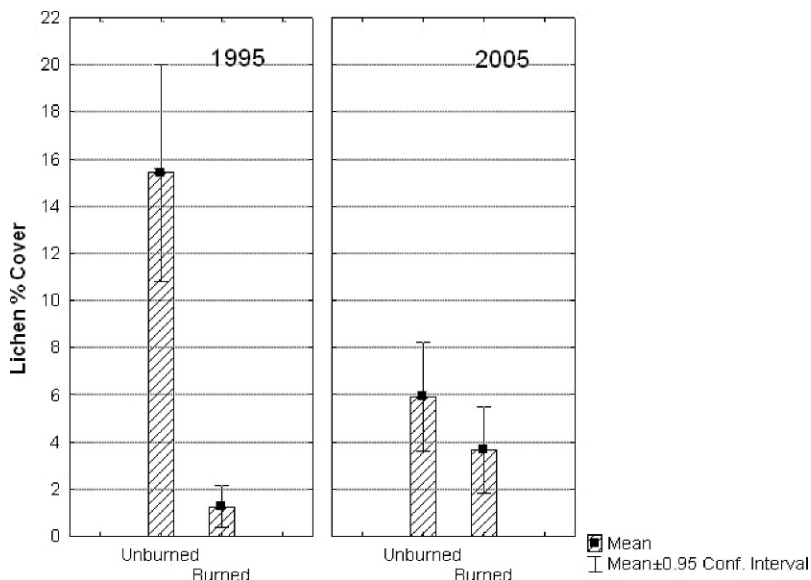


FIGURE 3. Change in lichen cover based on point-intercept sampling between year 14 (1995) and year 24 (2005) following fire at Ulukluk Creek, Alaska. Error bars represent 95% confidence interval of the mean.

TABLE 3

Comparison of vegetation cover on paired burned vs. unburned transects at two sites 20–34 years after fire (percent canopy cover based on point-intercept quadrats, $N = 12$). An * indicates significance ($P < 0.05$). Sampling was conducted in August 1997 and August 2006. Transects were undisturbed by caribou grazing prior to 1995.

WAGON WHEEL 1977 Burn		1997 %COVER			2006 %COVER		
COVER TYPE	Burned 20 yrs	Unburned	Mean Difference: B – Unb	Burned 29 yrs	Unburned	Mean Difference: B – Unb	
Lichen	4.3	48.8	-44.5*	0.8	15.0	-14.2*	
Moss	0.8	2.0	-1.2	0.8	2.2	-1.4	
Grass/Sedge	34.2	18.8	15.4*	54.6	47.0	7.6	
Forb	4.8	2.3	2.5	8.7	2.3	6.4*	
Shrub	34.8	15.3	-31.8*	33.6	24.0	9.6*	
PARGON RIVER 1972 Burn		1997 %COVER			2006 %COVER		
COVER TYPE	Burned 25 yrs	Unburned	Mean Difference: B – Unb	Burned 34 yrs	Unburned	Mean Difference: B – Unb	
Lichen	2.7	39.5	-36.8*	1.3	22.5	-21.2*	
Moss	1.3	3.3	-2.0	0.5	3.7	-3.2*	
Grass/Sedge	37.8	17.7	20.1*	51.5	30.3	21.2*	
Forb	4.0	1.8	2.2	7.5	3.5	3.7*	
Shrub	38.8	32.3	-6.5	36.7	35.2	0.2	

although the difference was significant only on the 1977 burn (Table 3). Shrub cover 20 years after fire averaged $34.8 \pm 2.8\%$ while the unburned quadrats averaged $15.3 \pm 1.6\%$ (Table 3). The 1977 burn site still had more shrub cover after 29 years (33.6% vs. 24.0% on paired unburned quadrats).

Forbs were poorly represented in this tundra ecotype. Cloudberry (*Rubus chamaemorus*) was the primary forb present, with trace amounts of *Andromeda polifolia* and cranberry (*Oxycoccus microcarpus*). Forb cover recovered quickly at Ulukluk Creek and was not significantly different in burned (2.5%) and unburned (2.1%) quadrats after 14 years ($t = -0.31$, $P = 0.760$; Fig. 2, Table 2). Although forb cover was consistently higher on burned than unburned plots at the older burn sites, the differences were significant only after 29 and 34 years (Table 3). Moss cover was light and showed the opposite trend, with more moss on unburned plots, but no statistically significant differences (Table 3).

Discussion and Conclusions

On tundra rangelands, permafrost hinders root penetration into the mineral soil layer and confines root growth to the organic mat. The resulting nutrient-poor environments are more favorable to lichens and mosses than to vascular plants. Recent burns have higher soil moisture and temperature in the organic horizon which increases both nutrient availability and rate of decomposition (Weintraub and Schimmel, 2005). Thawing of permafrost on burned tundra can persist for many years (Racine et al., 2004) providing warmer soil and more rapid nutrient cycling which promote vascular plant growth. Our data show increased vascular plant cover on burned tussock tundra compared to unburned transects, suggesting such nutrient enrichment.

Lichens rely on a developed organic mat for support, protection, and moisture retention, but may be out-competed by faster-growing vascular plants where the mineral soil is available for nutrients (such as when thawing occurs in a burn due to lower surface albedo and removal of insulating organic mat; Cornelissen et al., 2001). Our data reflect the expected short-term shift from lichen to graminoid cover on burned transects, but also show that increased graminoid cover persisted many years on the burns and also increased on unburned transects during the study period

(Table 3). The warmer climate and longer growing seasons which prevailed in northwestern Alaska during the course of the studies would have promoted vascular plant growth. Studies using aerial photographs and satellite imagery have documented increases in shrub cover over the last 25–50 years in northwestern Alaska (Sturm et al., 2001; Silapaswan et al., 2002), but graminoid changes would be more difficult to identify by remote sensing. Long-term monitoring studies such as ours indicate a dynamic plant community response, possibly in response to climate warming, is occurring at a stand scale. Lichen cover decreased through time on the unburned Ulukluk Creek transects from 1995 to 2005 ($t = 4.3$, $P < 0.001$; Table 2). Temporal declines in lichen cover on unburned transects at 1977 and 1972 burn sites were also significant from 1997 to 2006 (1977 burn, $t = 6.8$, $P < 0.0001$; 1972 burn, $t = 4.5$, $P = 0.0009$; Table 3). Ulukluk Creek is continually subjected to caribou disturbance due to its location near the core of the traditional wintering area of the WAH. The older burn sites on the Seward Peninsula were grazed by caribou sporadically between 1995 and 2005. Joly et al. (2007) reported decreased lichen and increased vascular cover on unburned range monitoring transects over a broad section of northwestern Alaska during the same years. We saw no signs of use or caribou disturbance on the recovering burns but disturbance by caribou clearly impacted the unburned transects on our study. Grazing was at least partly responsible for the decline in lichen although increased vascular and shrub cover due to warmer and longer growing seasons would also reduce the relative cover of lichen. Removal of the reflective and insulating lichen mats by grazing may also induce warming of the soil active layer, further stimulating vascular plant growth. Plant community changes associated with concentrated grazing (such as a large reindeer population confined to an island) include marked increases in graminoids and slight increases in prostrate shrubs as well as decreased lichen abundance (Klein, 1987; Van der Wal, 2006). Studies of overgrazed ranges also documented dramatic increases in moss cover which we did not observe on either burned or unburned transects. Grazing disturbance leaves more lichen remnants and fragments for regeneration, whereas the fires we studied consumed or killed virtually all the lichens within the burn areas.

Our data indicate a long timeline for reestablishment of caribou forage lichens on burned ranges. Extrapolating the present

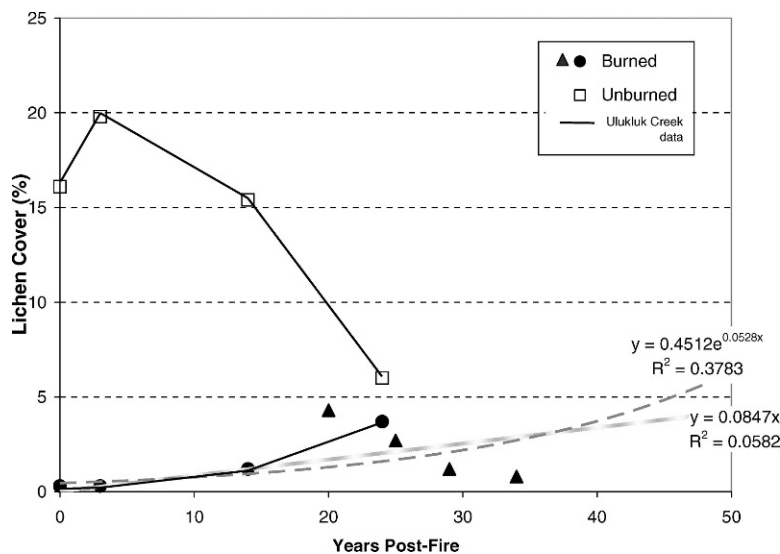


FIGURE 4. Lichen cover over time on burned and unburned transects. Best-fit recovery timeline for lichen in the burn is shown based on either exponential or linear rate of increase. Black triangles indicate data from 1972 and 1977 burn study sites. (Note: Lichen cover from 1981 and 1984 Ulukluk Creek ocular estimates were adjusted for this graph based on ratio derived by dual sampling with point-intercept estimates in 1995.)

rate of increase linearly to year 50 would predict lichen cover about 4%, substantially less than the original unburned cover of 16%, and probably not enough to be utilized by caribou (Fig. 4). If the growth curve were more exponential than linear, a more rapid increase should be expected after 35 years. Our results do not support recovery timelines that were proposed by the Natural Resource Conservation Service (Swanson et al., 1985) for the Seward Peninsula, which predict lichen cover restored to >20% at 10 years, and 30% at 20 years following fire. We are not aware of any field data from Alaska that support these post-fire recovery rates, even though Pegau (1968) documented growth rates of 3–5 mm annually for individual lichen podetia. On the WAH's eastern ranges, in the upper Kobuk Valley, Swanson (1996) found that *Cladina mitis* and *Cladonia* spp. reached peak abundance in 50- to 100-year-old stands, while *Cladina stellaris* and *C. rangiferina* increased almost fivefold on dry terraces and uplands older than 100 years compared to stands aged 10–50 years. At Ulukluk Creek, scant lichen cover present after 24 years was primarily *C. mitis* and *Cladonia* spp., while unburned transects had about equal amounts of *C. mitis* and *C. rangiferina*.

Twenty-four years after a more severe tussock tundra burn on the central Seward Peninsula, Racine et al. (2004) found little or no recovery of fruticose lichens or sphagnum moss, but did show dwarf shrub recovery to pre-fire levels as well as new willow shrub colonization. No new colonization by willows was noted on our burn study sites. We expected lichen re-establishment might be more rapid at Ulukluk Creek due to the small fire size and light burn severity but found little difference between the sites with respect to lichen recovery. Thirty-four years after fire, lichen cover at the oldest burn study site (1972) was still a fraction of that outside the burn scar (Table 3). These results differ markedly from retrospective studies on burned caribou ranges in northern Quebec where Arseneault et al. (1997) reported 17% lichen cover on post-fire stands aged 0–30 years and 52% cover on stands aged 31–50 years.

Lichen tussock tundra, as the study sites were initially described, typically has high cover values for lichens (25–50%), with moderate graminoid cover (12–25%) (Swanson et al., 1985). In contrast, low shrub-sedge tussock tundra is characterized by high cover values for graminoids (25–50%), with moderately low amounts of lichen (6–12%). By the end of the study, both burned and unburned transects at Ulukluk Creek and burned sites on the

Seward Peninsula are more accurately characterized as low shrub-sedge tussock tundra. Shifts to shrub community types are predicted as the climate warms and their expansion will result in more blowing snow trapped during the winter resulting in further warming of soils, and higher rates of decomposition (Sturm et al., 2005).

Climate warming has been implicated as a factor that may reduce lichen abundance in the tundra ecosystem (Chapin et al., 1995) and may be contributing to slow recovery of lichens on burned tundra sites as well as the declining lichen cover on the unburned transects we observed. In fact, experimental warming of research plots in arctic tundra communities by just 1–3 °C produced substantial vegetation changes in a single year (Walker et al., 2006). Shrubs and graminoids increased in height and density, resulting in decreased cover of shade-intolerant lichens and bryophytes (Walker et al., 2006). We observed similar changes on control quadrats over the course of this study. Although climate is likely to be a factor in these changes, care should be taken in interpreting this as a response to climate change, since we have no experimental control for the climate effect and the interannual variability in vegetation cover is not known. If climate warming is primarily responsible for the vegetation community shifts on the control transects, it raises the important question of whether retrospective studies still have validity for predicting rates of lichen recovery under current climatic conditions.

Fire, climate change, and animal disturbance all act unidirectionally in forcing vegetation communities to shift from cryptogram to vascular dominance. Declining winter range condition is expected to be detrimental to the fitness of the WAH, although other factors such as predation, insect harassment in summer, summer range, and snow conditions will also affect the herd's response. Land and wildlife managers need to understand lichen regeneration timelines specific to their region in order to establish sound fire management guidelines for caribou winter range. This study illustrates the importance of inventorying the present caribou winter range and its status relative to past fire occurrence. Based on knowledge of how much old-growth lichen range is available for caribou, fire management goals should be tailored to reflect the present size and needs of the herd and its users. The area utilized by caribou for winter range should be managed for long fire return intervals, and suppressing fires in critical winter range is justified when the threat of large fires is great and supply of alternative winter range is limited.

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References Cited

- Adams, L. G., and Connery, B. A., 1983: *Buckland River reindeer/caribou conflict study final report*. Fairbanks, Alaska: Bureau of Land Management Open File Report 8.
- Alaska Climate Research Center, 2006: (<http://climate.gi.alaska.edu>).
- Arseneault, D., Villeneuve, N., Boismenu, C., Leblanc, Y., and Dehay, J., 1997: Estimating lichen biomass and caribou grazing on the wintering grounds of northern Québec: an application of fire history and Landsat data. *Journal of Applied Ecology*, 34: 65–78.
- Chapin, F. S., III, 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.
- Cornelissen, J. H. C., Callaghan, T. V., Alataso, 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, D. K., Gwynn Jones, D., Jonasson, S., Chapin III, F. S., Molau, U., Neill, C., Lee, J. A., Melillo, J. M., Sveinbjornsson, B., and 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., 2005: Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A caribou management report. In Brown, C. (ed.), *Caribou management report of survey and inventory activities July 1 2002–June 30 2004*. Juneau, Alaska: Alaska Department of Fish and Game, 177–218.
- Davis, J. L., and Valkenburg, P., 1978: Western Arctic Caribou Herd studies. Alaska Department of Fish and Game Report W-17-8R and W-17-9R, 99 pp.
- Fetcher, N., Beatty, T. F., Mullinax, B., and Winkler, D. S., 1984: Changes in arctic tussock tundra thirteen years after fire. *Ecology*, 65: 1332–1333.
- Floyd, D. A., and Anderson, J. E., 1987: A comparison of three methods for estimating plant cover. *Journal of Ecology*, 75: 221–228.
- Hultén, E., 1968: *Flora of Alaska and neighboring territories*. Stanford, California: Stanford University Press, 1008 pp.
- Jandt, R. R., and Meyers, C. R., 2000: *Recovery of lichen in tussock tundra following fire in northwestern Alaska*. Fairbanks, Alaska: Bureau of Land Management Open File Report 82, 25 pp.
- Jandt, R. R., Meyers, C. R., and Cole, M. J., 2003: *Western Arctic Caribou Herd winter habitat monitoring and utilization, 1995–1996*. Fairbanks, Alaska: Bureau of Land Management Open File Report 88, 26 pp.
- Joly, K., Dale, B. W., Collins, W. B., and 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., and 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*: (in press).
- Jonasson, S., 1988: Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, 52: 101–106.
- Klein, D. R., 1987: Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management*, 40(4): 336–338.
- McCoy, V. M., and Burn, C. R., 2005: Potential alteration by climate change of the forest-fire regime in the boreal forest of central Yukon Territory. *Arctic*, 58(3): 276–285.
- Pegau, R. E., 1968: Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. *Arctic*, 21: 255–259.
- Racine, C. H., Patterson III, W. A., and Dennis, J. G., 1985: Tundra fire regimes in the Noatak River Watershed, Alaska: 1956–1983. *Arctic*, 38: 194–200.
- Racine, C. H., Johnson, L. A., and Viereck, L. A., 1987: Patterns of vegetation recovery after tundra fires in northwestern Alaska, U.S.A. *Arctic and Alpine Research*, 19(4): 461–469.
- Racine, C. H., Jandt, R. R., Meyers, C. R., and 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): 1–10.
- Rupp, T. S., Chapin III, F. S., and Starfield, A. M., 2000: Response of subarctic vegetation to transient climatic change on the Seward Peninsula in north-west Alaska. *Global Change Biology*, 6: 541–555.
- Silapaswan, C. S., Verbyla, D. L., and McGuire, A. D., 2002: Land cover change on the Seward Peninsula: the use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Canadian Journal of Remote Sensing*, 27: 542–554.
- Sturm, M., Racine, C., and 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., and Romanovsky, V. E., 2005: Winter biological processes could help convert arctic tundra to shrubland. *Bioscience*, 55: 17–26.
- Swanson, D. K., 1996: *Fruticose lichen distribution in the Kobuk Preserve Unit, Gates of the Arctic National Park*. Anchorage, Alaska: National Park Service Technical Report AFA RNR/NRTR-96/28, 22 pp.
- Swanson, J. D., Schuman, M., and Scorup, P. C., 1985: *Range survey of the Seward Peninsula reindeer ranges, Alaska*. Anchorage, Alaska: USDA Soil Conservation Service, 77 pp.
- Thomas, D. C., and 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., Barry, S. J., and Alaie, F., 1996: Fire–caribou–winter range relationships in northern Canada. *Rangifer*, 16(2): 57–67.
- Thomson, J. W., 1984: *American arctic lichens I. The macrolichens*. New York: Columbia University Press, 504 pp.
- van der Wal, R., 2006: Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, 114(1): 177–186.
- Vavrek, M. C., Fetcher, N., McGraw, J. B., Shaver, G. R., Chapin III, F. S., and Bovard, B., 1999: Recovery of productivity and species diversity in tussock tundra following disturbance. *Arctic, Antarctic, and Alpine Research*, 31: 254–258.
- Viereck, L. A., Foote, M. J., Dyrness, C. T., Van Cleve, K., Kane, D., and Siefert, R., 1979: Preliminary results of experimental fires in the black spruce type of interior Alaska. Portland, Oregon: USDA Forest Service Resource Note PNW-332, 27 pp.
- 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., Jónsdóttir, I. S., Klein, J. A., Magnússon, 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., and Wookey, P. A., 2006: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, 103(5): 1342–1346.
- Wein, R. W., and Bliss, L. C., 1973: Changes in arctic *Eriophorum* tussock communities following fire. *Ecology*, 54(4): 845–852.
- Weintraub, M. N., and Schimmel, J. P., 2005: Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *Bioscience*, 55: 408–415.

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