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Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska[1]

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Abstract: Large, late-winter ptarmigan migrations heavily impact the shoot, plant, and patch architecture of shrubs that remain above the snow surface. Ptarmigan browsing on arctic shrubs was assessed in the vicinity of Toolik Lake, on the north side of the Brooks Range in Alaska. Data were collected in early May 2007, at maximum snow depth, after the bulk of the ptarmigan migration had passed through the area. In an area of tall shrubs, half of the buds on *Salix alaxensis* were browsed by ptarmigan. Three percent of the buds that were buried beneath the snow were browsed, 90% of the buds that were less than 30 cm above the maximum snow level were browsed, and 45% of the buds above that height were browsed. Ptarmigan browsing was found to be a major height limiter for tall shrubs, thereby controlling shrub architecture by brooming stems at the snow surface and inducing stump shoots. These results were qualitatively extrapolated by photographing shrub morphology over a region approximately 300 km wide across a series of north-flowing arctic rivers with headwaters in the Brooks Range. Ptarmigan "hedging" of shrub patches, and shrub growth under a warmer climate, are opposing forces mediated by snow distribution.
Keywords: browsing, greening, ptarmigan, shrubs, snow, tundra.

Résumé : Les grandes migrations de lagopèdes à la fin de l'hiver ont un impact important sur l'architecture des pousses, des plants et des parcelles d'arbustes dépassant la surface de la neige. L'effet du broutement des lagopèdes sur les arbustes arctiques a été examiné aux alentours du lac Toolik, du côté nord de la chaîne Brooks en Alaska. Les données ont été récoltées au début mai 2007, au moment où la neige avait atteint son épaisseur maximale, après que la majeure partie de la migration des lagopèdes soit passée dans le secteur. Dans une zone d'arbustes de grande taille, la moitié des bourgeons de *Salix alaxensis* avaient été broutés par les lagopèdes. Trois pour cent des bourgeons enterrés sous la neige avaient été broutés, 90 % de ceux qui dépassaient de moins de 30 cm le niveau maximal de la neige avaient été broutés et 45 % des bourgeons dépassant cette hauteur avaient été broutés. Nous avons trouvé que le broutement par les lagopèdes était un facteur principal limitant la hauteur des arbustes de grande taille, modifiant ainsi leur architecture en causant la formation de tiges en forme de balai et la pousse de rejets à la surface de la neige. Ces données ont été extrapolées de façon qualitative en photographiant la morphologie des arbustes dans une région d'approximativement 300 km couvrant une série de rivières arctiques coulant vers le nord et prenant leur source dans la chaîne Brooks. La taille des parcelles d'arbustes par les lagopèdes et la croissance des arbustes résultant d'un climat plus chaud, sont deux forces qui travaillent en opposition et qui sont médiées par la distribution de la neige.
Mots-clés : arbustes, broutement, lagopède, neige, reverdissement, toundra.

Nomenclature: Hulten, 1968; Wilson & Reeder, 2005.

Introduction

Evidence from repeat photography, remote sensing, and vegetation plot studies suggests that shrubs are increasing in northern Alaska (Figure 1) (Chapin *et al.*, 1995; Myneni *et al.*, 1997; Tape, Sturm & Racine, 2006). Temporal trends in satellite vegetation indices, namely the Normalized Difference Vegetation Index (NDVI), show a generic "greening" in tundra regions (Zhou *et al.*, 2001; Jia, Epstein & Walker, 2003; Goetz *et al.*, 2005; Verbyla, 2008). While it is not clear exactly what this greening actually represents in terms of shifts in plant communities (Fung, 1997), it is believed that an increase in deciduous shrubs is responsible for much of the greening (Jia, Epstein & Walker, 2004). It has been projected that the increase in shrubs will alter the surface energy balance and carbon balance at high latitudes, with potential for strong positive feedbacks to climate warming (McFadden, Chapin & Hollinger, 1998; Mack *et al.*, 2004; Chapin *et al.*, 2005; Sturm *et al.*, 2005).

One factor that has been largely overlooked in discussions of shrub expansion is the potential interaction between herbivores and changing arctic vegetation. This interaction involves not just how the changing vegetation affects forage availability and quality for herbivores, but how the herbivores affect net primary production, plant architecture, and community composition. Such herbivore effects can be substantial in high-latitude terrestrial ecosystems, and often lead to a reduction in aboveground biomass and slow recovery (Crête & Doucet, 1998; den Herder, Virtanen

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& Roininen, 2004; Hansen *et al.*, 2007). For example, in southern Greenland, 20% of the increased growth from experimental warming was consumed by caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). The biomass reduction was even more extensive for dwarf birch (46%), the main shrub species at the site (Post & Pedersen, 2008). In Norway, fertilization of a tundra heath led to a four-fold increase in rodent density and an increase in winter grazing but no change in aboveground plant biomass (Aunapuu *et al.*, 2008). In western Alaska, recent declines in lichens and forbs and increases in shrubs and grasses were attributed to increases in caribou (*Rangifer tarandus*) grazing and possibly climate change (Joly *et al.*, 2007). In interior Alaska, moose (*Alces alces*) can consume 100% of current annual growth of preferred shrub species, which has significant effects on a suite of vegetation characteristics, including canopy structure, age distribution, species composition, and survival (Kielland & Bryant, 1998; Bowyer & Neville, 2003; Butler & Kielland, 2008). Snowshoe hares (*Lepus americanus*) also browse shrubs in interior Alaska, especially *Salix alaxensis* (Bryant *et al.*, 1985). Hare browsing was found to increase plant biomass and decrease plant height (Bryant, 1987). Both moose and hare browsing accelerated succession from willow shrubs to alder shrubs (Bryant, 1987; Butler & Kielland, 2008).

FIGURE 1. Photos taken from the same location near the top of a > 10 000 year-old moraine on the west side of the Jago River, (69° 27.83' N, 143° 44.73' W): (top) from 1957 (George Kunkel), showing no vegetation higher than 0.5 m, and (bottom) from 2007 (Ken Tape), showing dense stand of *Salix alaxensis* > 3 m tall. The perspective in the latest photo is close but not exactly the same as in the old photo, because the permafrost has collapsed, making the exact old photo location inaccessible, hanging above the collapse.

Ptarmigan browsing could similarly be a major factor influencing the species composition and canopy structure of shrubs throughout the Arctic. Despite the considerable literature on willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*Lagopus mutus*) diet and behaviour (Weeden, 1969; Moss, 1973; Helle, 1981; Pulliainen & Iivanainen, 1981), few studies have examined the impact of ptarmigan on vegetation or how browsing by ptarmigan might interact with snowfall to influence shrub architecture. Studies from northern Alaska show that ptarmigan, including a fraction of rock ptarmigan among the majority willow ptarmigan (Irving, 1953; Pitelka, 1974), migrate from summer breeding grounds north of the Brooks Range to winter habitat in the boreal forest of the southern Brooks Range. These movement patterns are characterized by 1 broad southward migration in November and 2 broad northward migrations in January/February and April/May (Irving *et al.*, 1967). When ptarmigan return to arctic feeding grounds in spring, snow depth restricts access to forage, which forces them to feed almost exclusively on taller shrub species, particularly *S. alaxensis* (West & Meng, 1966). This reduces the number of catkins on tall, but not short willows, because the short shrubs are buried by the snow (Hakkarainen *et al.*, 1980; Williams *et al.*, 1980). Browsing of this severity slows the growth of willow shrubs and could affect shrub architecture to such an extent as to retard the greening trend or alter the snow regime, but these direct effects and feedbacks have never been explored explicitly.

The purpose of this study was to examine the interactive effects of snow depth and ptarmigan browsing on shrub growth and architecture in arctic Alaska. The project had 2 questions: (1) How does accumulating snow affect ptarmigan browsing on shrub buds, and (2) is there a long-term impact of ptarmigan browsing on shrub architecture? To answer these questions, we excavated snow surrounding *S. alaxensis* shrubs near the end of the winter. We then compared browsing of buds on shoots above the snow to buds on shoots buried beneath the snow. A conceptual model that outlines the complex interactions between tall shrubs, snow, and ptarmigan browsing within the framework of changing arctic vegetation is presented.

Methods

SITE DESCRIPTION

This study was conducted between April and June 2007 in an area within 1.5 km of the Toolik Lake Field Station (68° 37.69' N, 149° 35.61' W) in arctic Alaska. The area is broadly classified as tussock-sedge, dwarf-shrub, moss tundra (CAVM, 2003), while the specific areas where shrubs were sampled are classified as riparian shrublands (Walker *et al.*, 1994). This includes the shrubs *Betula nana*, *Salix pulchra*, *S. lanata*, and *S. alaxensis* growing in water tracks and peaty-stream floodplains (Walker, Walker & Auerbach, 1994). The first 3 species are typically < 1.2 m tall, while the last regularly grows up to 4 m in height. Ptarmigan prefer willow species, but they also feed on *B. nana* catkins and foliar buds (Bryant & Kuropat, 1980). The terrain is an amalgamation of glacially derived sediments, some of which have been reworked by streams or cryoturbation. The area is underlain by permafrost.

The region is dominated by long, cold winters and short, cool summers, with a mean annual temperature of –13 °C. The snow period extends from September to May, but snow depth varies inter-annually and across short distances due to wind and topography. Shrubs also play an important role in affecting snow depth, by trapping blowing snow and increasing snow depth (Sturm *et al.*, 2000). This study was conducted during a year with a steady accumulation of snow, starting in October and ultimately becoming a typical snowpack by the time of the spring ptarmigan migration (Berezovskaya *et al.*, 2008). All vegetation sampled was in pristine areas devoid of anthropogenic disturbance.

Flocks of hundreds of ptarmigan were commonly seen feeding in tall shrub communities, particularly during the late winter. Although caribou migrate through the region, heading south in the fall and north in the spring, they feed almost exclusively on lichens during the snow-covered months, with shrubs composing a minimal portion of their diet (Boertje, 1984). Moreover, during the spring migration, caribou typically utilize windswept higher ground where snow is shallow or nonexistent, while avoiding shrubby areas with deep snow (Schaefer, Stevens & Messier, 1996; K. Tape, pers. observ.). Moose are rare in the immediate region and were not seen during the study. Voles (*Microtus oeconomus*, *M. miurus*) and ground squirrels (*Spermophilus parryii*) can be abundant, but their browsing on tall shrub buds is negligible (Batzli & Henttonen, 1990). Hares (*L. americanus* and *Lepus othus*) are beyond their range limit in this region (Rausch, 1951) and were not seen during the study. Therefore, during winter and spring, ptarmigan are the primary herbivore feeding on shrubs in this area.

SAMPLING

PTARMIGAN BROWSING ON SHRUBS, AND PROTECTION BY SNOW

In September 2006, 2 representative shrub patches (2–4 m in diameter) of *Betula nana* and 2 similarly sized patches of *Salix pulchra* were selected northeast of Toolik Lake. Four ramets (main stems emanating from the base of the plant) of each species were randomly selected within each patch; 2 were staked upright to prevent snow burial, while the other 2 were tagged but left untreated. By May 2007, all new shoots on the staked ramets were sticking above the snow, while control ramets remained buried beneath the snow. At least 10 new (most recent annual growth) shoots were chosen from the control and experimental ramets, and all buds were counted on each shoot. Bud scars were classified as browsed (if the bark was ripped near the bud location) or missing (if the bud was not present and no bark was ripped near the bud scar).

In early May 2007, we quantified bud browsing by ptarmigan on all new shoots of *Salix alaxensis* within 3 large patches (75 m^2) with ramets sticking out of the snow. This was the predominant species that had exposed stems and buds during late spring. Three height classes (strata) were delineated and sampled: buried, low, and high. The "buried" stratum included shoots below the snow (~1 m depth), the "low" stratum included shoots between 0 and 50 cm above the snow surface, and the "high" stratum included shoots greater than 50 cm above the snow surface. When the measurements were taken, snow had melted approximately 20 cm from the maximum accumulation. We estimated that when standing on the snow pack, ptarmigan could reach and browse up to approximately 30 cm above the snow surface. Therefore the low stratum was established to include buds readily accessible to ptarmigan while foraging from the ground, in contrast to above this height, where ptarmigan would be browsing while roosting. Shoots of new growth were haphazardly selected and assessed (total $n = 1143$) in each stratum. On each shoot, all bud locations were counted and classified according to the protocol described above for staked shrubs. Each new shoot was also classified as no stripping (N), low stripping (L), medium stripping (M), or high stripping (H), according to the fraction of bark (green felt) stripped from the stem (N = 0%, L = 0–10%, M = 10–50%, H = 50–100%). We also recorded whether or not the shoot was broken.

PTARMIGAN BROWSING ON DOMINANT SHRUB SPECIES

To include more shrub species and a larger area, in late May 2007, 39 tall individuals (13 from each species) of *Salix lanata*, *S. pulchra*, and *Betula nana* shrubs were assessed for ptarmigan browsing intensity. Four *Salix alaxensis* shrubs were similarly assessed (total $n = 43$ shrubs). The snow was completely melted, and 10 new shoots were randomly selected for each shrub. Bud locations on each of 10 shoots were classified as browsed, missing, or live bud, and whether or not the shoot was broken was recorded. For *B. nana*, bud locations were only classified as missing or present because the characteristic ptarmigan browse was difficult to identify on this species. The characteristic ripped bark beneath the bud location is more difficult to discern because new growth on dwarf birch is not fuzzy or easily ripped.

PTARMIGAN INFLUENCE ON REGIONAL SHRUB ARCHITECTURE

In late winter, spring, and summer of 2007 and 2008, we photographed a variety of shrub and branch morphologies that contained a visible record of ptarmigan browsing to evaluate whether results from Toolik Lake could be extrapolated across arctic Alaska. From these photos, an index of ptarmigan browsing influence on shrub architecture was developed. The index, i, is the number of broomed shoots or resprouted stump shoots divided by the total number of shoots ($0 < i \leq 1$).

During April/May 2007, photographs were taken of ptarmigan-browsed shrubs from Toolik and Galbraith Lake westward to the Itkillik River (15 km), May Creek (25 km), and the Nanushuk River (55 km) while traveling via dog sled. In the summer of 2007, photographs of ptarmigan-browsed shrubs were taken along a section of the Jago River, which is approximately 150 km east of Toolik Lake.

A 180-km transect from Anaktuvuk Pass (north-central Brooks Range) to Toolik Lake was skied during the April/May ptarmigan migration of 2008. Along the transect widespread browsing-controlled shrub architecture was photographed. In most cases, it was possible to identify ptarmigan browsing by the signature bark and bud stripping, tracks, and actual observation of the browsing. Moose break shoots rather than plucking individual buds, and moose are at the fringe of their range in these generally low-stature drainage habitats. Some of the area surveyed was also close to the village of Anaktuvuk Pass, where subsistence hunting is important and moose density is very low. Ultimately, only 2 moose were sighted (both at the head of May Creek) in the combined 2 months of spring and summer travel in the northern Brooks Range and southern North Slope foothills, so we assume the browsing to be primarily that of ptarmigan. In some cases drainages were choked with thick aufeis during the winter and spring, thus restricting available forage by burying portions of the shrub in layered overflow ice, instead of snow.

Statistics

Data were not normally distributed, so differences in browsing rates on *Salix alaxensis* among strata were tested using the Kolmogorov–Smirnov two-sample test (KS-test) for independence (*e.g.*, Massey, 1951). The maximum difference between the 3 strata was evaluated using the Kolmogorov distribution. KS-tests were also used for comparing browsing rates among shrub species. Unless otherwise mentioned, means and standard errors of untransformed data are presented throughout the text and in the figures.

Results

Ptarmigan browsing on shrubs, and protection by snow

Snow protects shoots that are buried but facilitates access to shoots immediately above the snow level. Buds on *Betula nana* and *Salix pulchra* ramets that were buried by snow early in the winter were not browsed, whereas buds on their counterparts that were staked upright were heavily browsed (Table I). Ptarmigan browsing on current annual *Salix alaxensis* shoots (n = 1143) examined at maximum snow depth, including bud removal, breaking of new shoots, and bark removal, was highest in the low stratum (90 ± 2%), lowest in the buried stratum (3 ± 2%), and moderate in the high stratum (45 ± 2%) (stratum effect: P < 0.0001) (Figure 2 and Table II).

Ptarmigan browsing on dominant shrub species

The taller shrub species, *Salix alaxensis*, was subject to heavier browsing than the shorter shrub species. Data from our survey northeast of Toolik Lake show that 42 ± 4% of the new buds on *S. alaxensis* were browsed by ptarmigan, while browsing on buds of *S. lanata*, *S. pulchra*, and *B. nana* averaged 27 ± 5%, 25 ± 5%, and 20 ± 5%, respectively (species effect: P < 0.02) (Table III).

TABLE I. Mean percent of bud locations browsed per new shoot ± SE.

Species	Buried by snow (n = 40 shoots)	Exposed (n = 40 shoots)
Salix pulchra (n = 2 ramets)	0.0 ± 0	54.6 ± 6
Betula nana (n = 2 ramets) *	0.0 ± 0	43.5 ± 6

*Value includes "browsed" and "missing" bud locations.

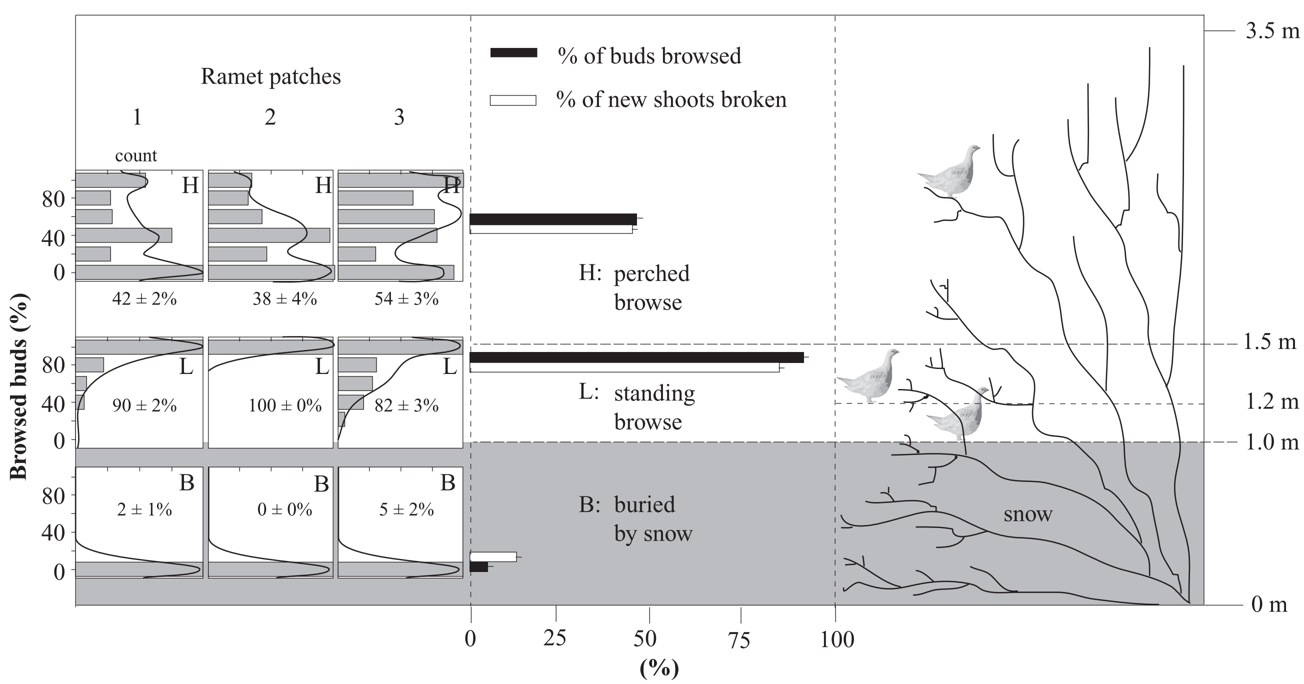

FIGURE 2. Patterns of ptarmigan browsing on 3 *Salix alaxensis* ramet patches measured during spring migration at Toolik Lake. The curves are nonparametric probability distribution functions, including means and standard error for each patch. Because of the similarity between the browsing distributions of the 3 *S. alaxensis* patches (left column), independence of new shoots is assumed for computing means and standard errors of each height stratum (centre column). Ptarmigan browsing on *S. alaxensis* is heaviest in the low stratum, where the snow surface permits easy access to the buds.

PTARMIGAN INFLUENCE ON REGIONAL SHRUB ARCHITECTURE

Repeated browsing by ptarmigan can have substantial effects on the architecture of shrubs. When browsing intensity is high, all buds on new shoots are removed, except the small buds near the base of the shoot, which are often protected by the branch intersection. In the following year, new shoots originate from surviving buds near the branch intersection, or from the base of the shrub (hereafter stump shoots). Repeated heavy browsing eventually creates a "broom"-like branch architecture (Figure 3) and hedged or partially hedged stump shoots (Figure 4).

Photographs of shrubs taken during surveys across arctic Alaska showed that branches on tall shrubs (n = 49) were often broomed shoots or stump shoots resulting from intense browsing. Along the Anaktuvuk River, $i = 0.79 \pm 0.04$, and along the Jago River, $i = 0.82 \pm 0.03$, which means that approximately 80% of the shoots on these shrubs were hedged by ptarmigan. Photographs from Toolik Lake and the surrounding area taken during spring 2007 were unusable, due to deeper snow in 2007 concealing stump shoots.

TABLE II. Percentage of *Salix alaxensis* shoots in each stratum categorized by the percent of bark stripped (No stripping = 0%, Low stripping = 0.1–10%, Medium stripping = 10–50%, High stripping = 50–100%). Each row adds up to 100%.

	No stripping	Low stripping	Medium stripping	High stripping
Buried stratum	96%	3.7	0	0.2
Low stratum	1	30	37	32
High stratum	28	68	3.6	0.2

TABLE III. Mean percent of bud locations browsed per new shoot on dominant shrub species.

Shrub species	% bud locations browsed ± SE
Salix alaxensis	42 ± 4
Salix lanata	27 ± 5
Salix pulchra	25 ± 5
Betula nana	20 ± 5 *

*Value includes "browsed" and "missing" buds.

Discussion

Snow deposition, ptarmigan browsing, and shrub architecture interact in ways that strongly couple trophic dynamics with the physical environment (Figure 5). Accumulating snow (1) protects smaller shrubs or those that readily lie down during winter, (2) leaves the taller shrubs exposed

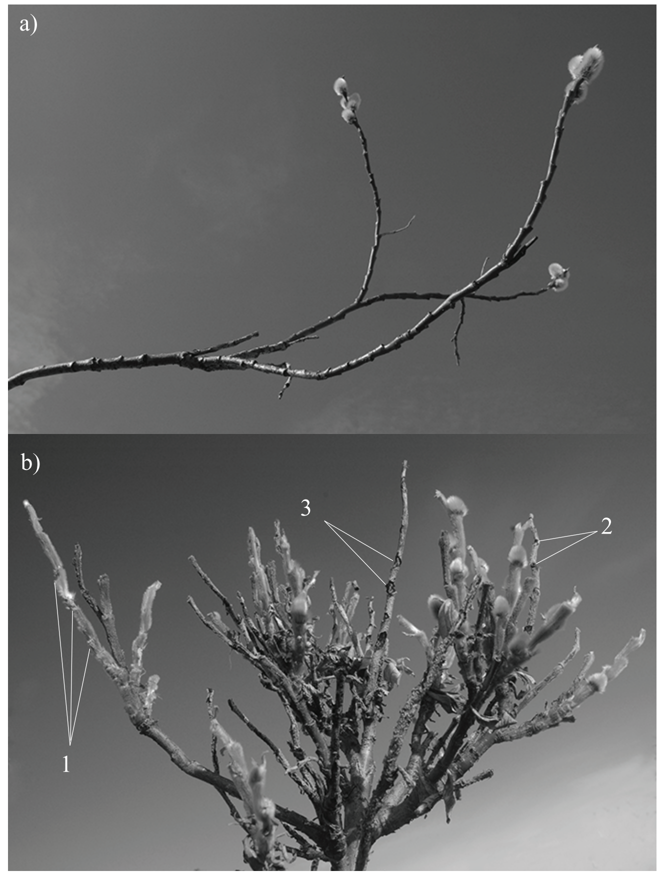

FIGURE 3. Influence of ptarmigan browsing on shoot architecture of *Salix alaxensis*: a) unbrowsed growth form at 3 m tall and b) repeatedly browsed ("broomed") growth form at 1.5 m tall, showing evidence of (1) this year's browsing, (2) last year's browsing, and (3) browsing from at least 3 y ago.

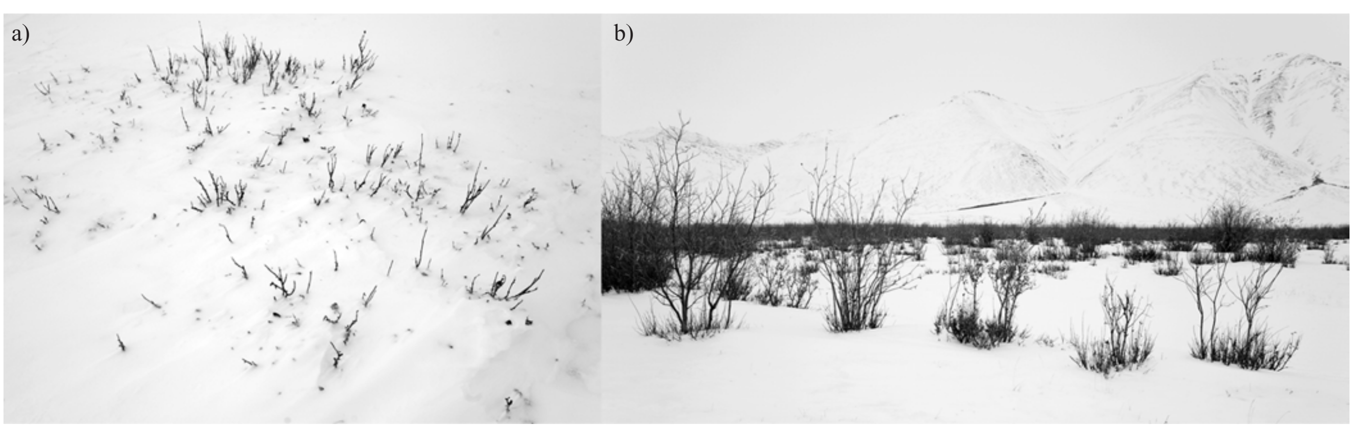

FIGURE 4. Photo (a) shows hedged shrub architecture at maximum snow depth, 15 km east of Anaktuvuk Pass (i ~ 1). In the same valley, photo (b) shows hedged architecture at mean snow depth but also some ramets growing above the standing browsing level of ptarmigan (i ~ 0.8). The hedged shoots are mostly stump shoots that were initiated by severe browsing events.

above the snow, and (3) enables ptarmigan to access buds higher on the shrub. (4) Ptarmigan populations depend on tall shrubs for forage during the spring. (5) Ptarmigan browsing alters shrub architecture and reduces shrub heights through hedging, which (6) decreases future snow accumulation (Figure 5).

Snow timing and distribution mediate the impact of ptarmigan browsing on shrubs. If snow arrives late or is insufficient to bury most of the shrubs, then ptarmigan browsing is spread over a larger number of smaller shrubs of varying heights. This lessens the impact of browsing on tall shrubs. In contrast, during winters with average to deep snow, most shrubs are buried at the time of spring ptarmigan migrations so only the remaining exposed tall shrubs are browsed heavily. Years with average to deep snow may lead to high fidelity of large ptarmigan flocks to exposed shrub patches due to food limitations at the landscape scale. In our study, the taller shrub species, *Salix alaxensis*, was subject to heavier browsing (42 ± 4%) than the shorter shrub species (27 ± 5%, 25 ± 5%, and 20 ± 5%), because the shorter shrubs were buried by snow during the spring ptarmigan migration, while the tall shrubs had ramets exposed throughout the winter.

Legacies of ptarmigan browsing intensity and snow depth can be inferred from the architecture of shrubs. When deep snow restricts ptarmigan browsing to tall shrubs, and when ptarmigan abundances are high relative to shrub density, ptarmigan maintain shrubs in a hedged or partially hedged growth form (Figure 4). The height of the hedge is approximately the browsing height of a ptarmigan above the average snow depth.

Because ptarmigan browsing appears to affect arctic shrubs in a manner similar to how snowshoe hare browsing affects boreal shrubs (Bryant, 1987), it might be expected that much of the associated plant–herbivore dynamics documented for boreal browsing systems apply to ptarmigan browsing on arctic shrubs. Effects of intensive browsing on growth of *Salix alaxensis* and *S. interior* can be seen along the Tanana River in central Alaska, where high moose and snowshoe hare populations maintain "browsing lawns" (similar to hedges here) of shrubs close to the snow surface (K. Tape, pers. observ.).

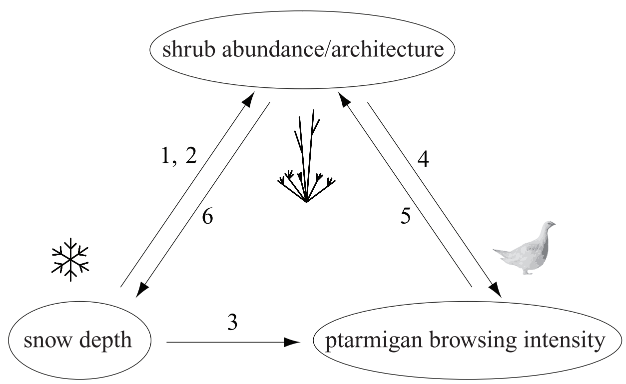

FIGURE 5. Complex interactions between snow, shrubs, and ptarmigan. Numbers correspond to processes described in the Discussion.

Severe snowshoe hare browsing causes *S. alaxensis* to revert to stump shoots, which are initially of lower nutritional quality, although they regain nutritional content after several years, when they grow high enough to be available to hares during the winter (Bryant *et al.*, 1985). The stump shoots and hedges resulting from severe hare browsing in central Alaska are also prevalent in arctic *S. alaxensis* shrubs (Figure 4b). Stump shoots and broomed shoots constituted approximately 80% of the ramets on surveyed shrubs along the Anaktuvuk and Jago Rivers, and most of that 80% were stump shoots rather than broomed shoots (Figure 4b). In the central and eastern Brooks Range and arctic foothills of Alaska, however, hares and moose are rare (Best & Henry, 1994; K. Tape, pers. observ.), and the stump shoots and hedges in the study area are instead likely a response to severe ptarmigan browsing. Stump shoots constitute additional shoots, which widen the effective base of the shrub, while the brooming truncates and broadens the branch structure. Combined, these architectural modifications resulting from browsing create a hedged shrub.

Average to deep snow years and associated heavy ptarmigan browsing can trigger another positive feedback that promotes architecture amenable to ptarmigan browsing. Repeated browsing during average to deep snow years produces a thickening of the junction of the broom in the following year (Bowyer & Neville, 2003); new shoots grow from that junction, rather than growing well above maximum snow depth and above the reach of ptarmigan standing on the snow. This allows ptarmigan to maintain new growth within reach and control shrub canopy structure to their advantage, in a manner reminiscent of the positive feedback between grazers and graminoids (McNaughton, 1984; Person *et al.*, 2003; Frank, 2007).

Because taller shrubs trap more snow and create deeper snow than shorter shrubs (Sturm *et al.*, 2000), intense ptarmigan browsing has the potential to reduce snow-trapping by shrubs at the landscape scale. Shallower snow in heavily browsed shrub patches permits higher winter energy exchange between the ground and the atmosphere. The lower winter ground temperature as a result of shallower snow is a negative feedback to warming and greening (Sturm *et al.*, 2005). Similarly, ptarmigan browsing reducing shrub height may increase winter albedo, another negative feedback to warming and greening (Chapin *et al.*, 2005), but the complexity of snow–shrub interactions confounds these predictions.

The increase in shrub abundance across arctic Alaska (Jia, Epstein & Walker, 2003; Tape, Sturm & Racine, 2006) may have fostered an increase in ptarmigan over-winter survival, maternal nutrition, and overall population size. More tall shrubs create more forage above the snow surface available to ptarmigan during the winter. The fact that only 6% of buds on *S. alaxensis* remained unbrowsed in the heavily browsed low stratum suggests that late-winter forage availability may be a factor limiting ptarmigan populations. Territorial behaviour of ptarmigan (Moss, 1973) and other birds (Greenberg, Ortiz & Caballero, 1994) and the association of that behaviour with food resources also suggest that winter forage is a limiting resource. For example, the mid-continent population of the lesser snow goose has grown 5–7% annually in response to nitrogen fertilizers enhancing the growth of agricultural forage on wintering grounds and along flyways (Abraham, Jefferies & Alisauskas, 2005). The estimated annual 50 000 ptarmigan migrating biannually through Anaktuvuk Pass in 1960–1964 (Irving *et al.*, 1967) constitutes only a fraction of the total number of ptarmigan passing through a dozen similar meridional migration routes through the Brooks Range, and the current increase in shrubs is a potential mechanism for population growth since that period.

Some of the dramatic greening observed in repeat photography over the last half-century in arctic Alaska is the result of green alders (*Alnus viridis* spp. *fruticosa*) colonizing floodplains (Tape, Sturm & Racine, 2006). In boreal floodplain succession, moose and snowshoe hares facilitate a similar vegetation shift by browsing heavily on willows while avoiding and indirectly cultivating the dominance of the thin-leaf alder (*Alnus tenuifolia*), an important N_2-fixing species (Bryant, 1987; Uliassi & Ruess, 2002; Butler & Kielland, 2008). Browsing also has both direct (feces) and indirect (litter quality, rhizosphere processes) effects on nutrient cycling processes (Hamilton & Frank, 2001; Butler & Kielland, 2008). It is possible that by browsing willows and avoiding alders (Moss, 1973), ptarmigan are similarly facilitating the spread of green alder and influencing ecosystem N balance, both within and outside of arctic floodplains.

Conclusion

Ptarmigan browsing, snow cover, and shrub architecture are tightly interconnected in a complex way. Ptarmigan populations may be responding to recent shrub expansion, and, as a major limiter of shrub height in arctic Alaska, they may also be affecting arctic floodplain succession. The interactions presented here involve both positive and negative feedbacks to greening, and although the cumulative impact on the system is unknown, the outcome of these interactions is encoded in the height and architecture of shrubs across arctic Alaska.

Acknowledgements

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