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Acceleration of vegetation turnover and element cycling by mammalian herbivory in riparian ecosystems

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Summary

1. We examined the effects of browsing by moose and snowshoe hares on vegetation structure, species composition, plant demography and element cycling in 25 riparian (willow) vegetation stands along the Tanana River, interior Alaska, across a 250-km gradient that represented a fivefold range in moose densities (0.2–1.0 km^{-2}).

2. Browsing frequency was much greater in areas with high moose densities. The combined browsing pressure (% of annual browse production consumed by herbivores) of moose (*Alces alces*) and snowshoe hares (*Lepus americanus*) on forage species was over fivefold greater in the high moose density areas (33%) than the low moose density areas (6%), reflecting the fivefold difference in moose densities.

3. Above-ground biomass of preferred willow species was lower in high moose density areas, and the age structure of the vegetation was significantly skewed towards younger age classes. This shift in age structure was accompanied by higher proportion of dead to live ramets, indicating higher mortality under increased browsing pressure. Increasing browsing pressure favoured later-successional species (*Alnus tenuifolia* and *Populus balsamifera*) on the landscape, as shown by both a reduction in the number and size of willow stands in high-density areas.

4. High rates of fecal input resulted in a doubling of above-ground N input in high moose density areas. The rates of carbon and nitrogen input from willow communities to the soil as mediated by moose herbivory were approximately fivefold and eightfold greater in high moose density areas than in low moose density areas, respectively.

5. *Synthesis*. The effects of herbivory were manifested at several ecological hierarchies, including the individual, the community, and the landscape. Across these spatial scales herbivory appears to accelerate the ecosystem turnover of carbon and nitrogen by a combination of both plant- and animal-based processes.

Key-words: Alaska, boreal forest, herbivory, moose, riparian communities, succession

Introduction

In the taiga forests of interior Alaska, riparian corridors represent hot spots of biodiversity and productivity compared with adjacent uplands (Van Cleve *et al.* 1993; Magoun & Dean 2000).

Riparian shrub communities that dominate the open and closed shrub stages of primary succession on river floodplains in interior Alaska (Van Cleve *et al.* 1993) are an important resource for many vertebrate herbivores (Bryant & Kuropat 1980). This is especially true for moose (*Alces alces*) that concentrate in these areas during winter and browse heavily on a variety of willow species (*Salix* spp.) (Wolff & Zasada 1979; Collins & Helm 1997). Vegetation nomenclature follows Hultén (1968).

Since 1989 nine herbivore exclosures (50 m × 20 m) have been maintained along the Tanana River as part of the Bonanza Creek Long-term Ecological Research (LTER) Programme to study the effects of mammalian herbivory on succession. This study has documented several effects of mammalian herbivores on willow communities and provided plot-level information of how herbivores may influence stand characteristics and soil processes (Kielland *et al.* 1997; Rossow *et al.* 1997; Kielland & Bryant 1998; Ruess *et al.* 1998). Other studies have also addressed herbivore effects on successional change (Wolff & Zasada 1979; Bryant & Chapin. 1986; Walker *et al.* 1986; Bryant 1987; Pastor & Naiman 1992; Binkley *et al.* 1997; Helm & Collins 1997). Willow responds to herbivory by growing fewer stems that are longer and less palatable (Bryant *et al.* 1985; Molvar *et al.* 1993). The reduction in twig density increases light penetration through the plant canopy, increasing the productivity of emergent later-successional

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species. As these species reach into the canopy and increasingly shade the willows, the latter decrease their production of secondary compounds, again making them more susceptible to herbivory (Bryant *et al.* 1983). This sequence of events, triggered by herbivores, accelerates the replacement of willow by alder, and eventual domination by late-successional species.

The central idea driving this study was that browsing by herbivores influences plant longevity and successional turnover, thereby exerting control over large-scale landscape vegetation patterns along the Tanana River. In particular, we hypothesized that: (i) increased herbivore density would result in a reduction of forage biomass due to high rates of forage consumption; (ii) in areas with high moose-densities, the riparian zone would be dominated by less-preferred shrubs such as thin-leaf alder (*Alnus tenuifolia*); and (iii) high-density areas would have a greater degree of soil development due to more rapid turnover of vegetation, higher rates of fecal input and larger soil carbon pools due to increased litter input from alder. Here we examine if the observations of herbivore–vegetation interactions from plot-level studies can be generalized to larger spatial scales in ways that are relevant for resource management.

To address these hypotheses we examined vegetation characteristics and foraging behaviour of moose across an extensive (250 km) section of the Tanana River in interior Alaska. This extensive riparian zone represents a natural gradient of moose densities from a high of approximately 1.0 moose km^{-2} near Fairbanks (Dale 1998) to 0.2 moose km^{-2} near Manley Hot Springs (Boudreau 1998). We measured plant architecture, removal of stems, bite mass, and annual forage production. We also measured canopy height, nutrient inputs, plant age distribution and species composition of willow communities, as well as the composition and abundance of shrub communities at the landscape level.

Methods

STUDY AREA

The study was conducted in 2001–02 along the Tanana River in Interior Alaska between Fairbanks (64°50.50′ N, 147°43.30′ W) and Manley Hot Springs (65°0.0′ N, 150°36.0′ W). The Tanana River forms at the junction of the Chisana and Nabesna Rivers, and flows approximately 850 km before entering the Yukon River at the village of Tanana (65°10.4′ N, 152°5.5′ W). Early successional floodplain soils are primarily sandy with a layer of silt loam on the surface. Willow typically colonizes new soils deposited along the river after 2 years and can persist for the next 20+ years (Van Cleve *et al.* 1993). Daily air temperatures in this region ranged from 28 °C to to – 41 °C during the study (2000–02) with an average daily temperature of – 2 °C. Annual precipitation in 2001 was 220 mm (National Oceanic & Atmospheric Administration 2003). Average snow depth recorded at the field sites in the spring of 2001 was approximately 40 cm (Butler 2003).

Two extensive sampling areas were selected based on winter moose density surveys conducted by the Alaska Department of Fish and Game (ADF & G). Moose densities in the Fairbanks to Nenana area (approximately 88 river-km) were approximately 1 moose km^{-2} (Dale 1998), whereas the area around Manley Hot Springs had relatively low densities, with estimates of 0.2 moose km^{-2} (Boudreau 1998). Area-wide moose densities have been estimated by the ADF & G several times during the last 10 years, and the densities of moose have remained relatively stable during this time period (Boudreau 1998; Dale 1998). Snowshoe hare populations peaked in 1999 (Rexstad & Kielland 2006). We assumed that the majority of herbivory by snowshoe hares occurred during the period when the hare population was reaching its peak. Hare densities were assumed to be similar across the gradient (Rexstad & Kielland 2006).

We examined 25 willow stands along the Tanana River between Fairbanks and Manley Hot Springs Slough. Twelve of the willow stands were selected from the low moose density areas (hereafter denoted low-density areas) near Manley Hot Springs. These stands were compared with 13 stands from the relatively high moose density areas (hereafter denoted high-density areas) between Fairbanks and Nenana. Willow stands sampled in this study were no more than 50 m from banks of the Tanana River. The stands ranged in size from 0.04 ha to 3.72 ha, and site selection favoured mature felt leaf willow (*Salix alaxensis*) stands. These stands were composed of several *Salix* species (*S. alaxensis*, *S. brachycarpa*, *S. interior*, *S. lasiandra* and *S. nova angliae*), as well as alder (*Alnus tenuifolia*) and balsam poplar (*Populus balsamifera*).

Information on moose population densities and wolf abundances were obtained from the Alaska Department of Fish & Game management reports (Osborne 1996; Boudreau 1998; Dale 1998; Seaton 2006; Young 2006a; Young 2006b).

HERBIVORE USE

Moose and hare browsing were measured on plants of each species closest to three random locations at each willow stand during the spring of 2001. Browsing frequency was measured by counting the number of browsed stems and dividing by the total number of live stems per plant (ramet). A maximum of 10 randomly selected current annual growth (CAG) twigs between 0.5 and 3 m above the ground on each plant were included in the survey. Plant and twig selection continued until a total of 30 twigs per species had been recorded at each stand. Sampled twigs were classified as browsed by moose, browsed by hare, or unbrowsed. Browsed twigs were classified by herbivore based on the characteristics of the browsed point. Browse points that appeared jagged were classified as moose browsing, while points that were removed in a smooth, angular cut were classified as hare browsing. While estimating browsing intensity, measurements were also taken on the CAG base diameter and the diameter at the point of browsing (DPB) (Kielland & Osborne 1998).

Forage species were also classified by their architecture to qualitatively assess historic browsing levels. Plants were assigned to one of three categories: unbrowsed, browsed or broomed. In each category current and historic browsing was assessed by proportions of live and dead twigs less than 3 m above the ground for evidence of browsing, as well as the growth form of the plant. Unbrowsed plants were defined as plants that display no evidence of moose or hare browsing. Browsed plants showed evidence of browsing on less than half of their twigs. Broomed plants had more than half of their twigs removed by browsing or exhibited stunted growth due to removal of the apical meristem (Seaton 2002).

The apical growth stem from one randomly selected plant of each species was harvested at each stand. The branch was divided into segments by cutting through the branch at each diameter that was measured as a whole number in millimetres (i.e. 1 mm diameter,

Table 1. Regression relationships between twig diameter and twig mass for six species of shrubs browsed by moose along the Tanana River, interior Alaska. The general equation takes the form: *Twig mass* = $a + b \times diameter + c \times diameter^2$.

	Regression coefficients			Coefficient of determination
Species	a	b	c	r^2
Salix alaxensis	2.82	–2.07	0.38	0.92
Salix brachycarpa	0.19	–0.33	0.16	0.70
Salix lasiandra	1.80	–1.51	0.33	0.97
Salix nova-angliae	0.43	–0.66	0.26	0.87
Alnus tenuifolia	0.46	–0.64	0.24	0.91
Populus balsamifera	1.27	–1.07	0.27	0.92

2 mm diameter, etc.). The twigs were then oven dried for 48 h at 50 °C. Diameter-specific mass of CAG stems of each species was determined (Hjeljord *et al.* 1982), and fitted to the following regression model to estimate off-take by herbivores and to estimate forage productivity:

$$TwigBiomass = a + b * Diameter + c * Diameter^2$$

where a, b and c are estimated coefficients (Table 1).

CANOPY HEIGHT

Canopy height was measured in September 2001 (fall) and March 2002 (spring) to assess the effects of browsing on canopy height. At each stand, 50 locations were randomly selected during each sampling event. The height of the tallest plant regardless of species was measured to the nearest centimetre using a telescoping height pole.

SOIL CHEMISTRY

Five soil cores were collected at randomly selected locations from each of the 25 stands to determine the effect of herbivores on total soil carbon (C) and nitrogen (N) concentrations. After homogenizing the top 5 cm of each soil core (including both organic and inorganic layers), 20 g of soil were placed in a drying oven for 2 days at 60 °C. The dry soil was then ground and passed through a 2-mm sieve to remove coarse roots. After processing the samples 1 g of soil was analysed in a LECO 2000 CNS Analyser (LECO Instruments, St Joseph, MI, USA) to determine total C and N concentrations in the samples. Organic layer depth was measured on each soil core prior to homogenization and used as a covariate in analysis.

FAECAL SAMPLES

Moose and hare faecal samples ($n = 5$) were collected from each of the 25 willow stands during winter of 2001. The pellets were oven dried for 48 h at 60 °C, ground in a 20-mesh Wiley mill, and analysed for total N and C using a LECO 2000 CNS Analyser. Pellet production over-winter was estimated in early spring by counting faecal pellets groups in five 2 m × 2 m plots randomly located in each of the 25 willow stands. Total carbon and nitrogen input (m^{-2}) via moose pellets was estimated as the product of pellet biomass ($g\ m^{-2}$) and their C and N concentrations ($mg\ g^{-1}$).

PLANT DENSITY

Stem density was measured at five randomly selected 2 m × 2 m plots at each stand in the spring of 2001. Due to the high likelihood that an individual plant will produce multiple ramets originating below the soil surface, we defined an individual as a ramet that was at least 5 cm away from the nearest ramet of a plant of the same species. Dead ramets were considered unidentifiable and lumped into a single category in order to examine differences in overall plant survival in each of the areas with different browsing intensity.

STAND AGE

The ages of willow stands were compared to determine how long the willow successional stage had persisted and how herbivory affects the age distribution of browse species. Twenty randomly selected plants of each species were harvested at each of the willow stands. After harvesting the plant, growth rings were counted under a dissecting microscope to determine plant age. The age of the oldest plant detected at each stand was assumed to represent the amount of time since the terrace was colonized and was used as a conservative estimate of stand age.

COMMUNITY ABUNDANCE AND DISTRIBUTION

During the summer of 2002, a 21-km line transect was randomly established upriver of Nenana (high moose density area) and downriver of Nenana (low-density area) (two transects total) to estimate average size and distribution of shrub communities. All shrub communities observed were classified by the predominant genera as willow or alder communities. The location of each community was recorded using a Magellan 2000 Global Positioning System unit (Magellan Navigation, Inc., Santa Clara, CA, USA). The size (ha) of the stands was estimated using a Bushnell Yardage Pro 600 Range Finder (Bushnell Outdoor Products, Overland, KS, USA).

DATA ANALYSIS

Data were analysed using SAS statistical software (SAS Institute Inc. 2001; Cary, NC, USA). All tests were evaluated at $\alpha = 0.05$. Herbivore use was assessed based on three different estimates of removal (browsing frequency, plant architecture, and forage production and offtake) as well as changes in CAG base diameters and DPB. Browsing frequency percentages were arcsine transformed before analysis. ANOVAS were used to test for differences in the removal by moose and hares. Differences in plant architecture, CAG base diameters and browse selection between the high and low moose density areas were tested using nested ANOVAS, where measurements were nested in individual stands within the treatment areas. The analysis was repeated for all plant species.

Forage production and offtake were calculated based on the twig diameter-biomass relationship in combination with species density, twig density per plant, CAG base diameters, and DPB measurements. A quadratic regression between twig diameter and biomass was calculated for each plant species and used to convert CAG base diameters and DPB measurements to forage production and offtake. Nonlinear regression (Oldemeyer 1982) was preferred over the natural log transformed linear regression (Telfer 1969; Brown 1976) because it provided a normal scale standard error that could be used to calculate a standard error for forage production and offtake using the delta method (Oehlert 1992). Estimates of aforementioned parameters were compared using a t-test.

Remaining plant parameters (canopy heights, species composition, stand age, and soil characteristics) were analysed using ANOVAS with appropriate transformations and covariate analyses as noted.

A single (21 km) transect along the river corridor in each of the upriver (high density) and downriver (low density) areas was used to estimate the number of willow and alder communities present. This precluded the calculation of means and standard errors and therefore statistical testing. However, an ANOVA was used to test for differences in the size of willow and alder communities between high- and low-density areas.

Results

Overall, the frequency of browsed twigs in high moose density areas was greater (69%) than in low moose density areas (15%) ($F_{1,16} = 35.85$, $P < 0.001$). At the species level, only the proportion of *S. alaxensis* (65%) and *S. novae-angliae* (43%) twigs browsed by moose (Fig. 1a) were significantly different between areas ($F_{1,19} = 24.26$, $P < 0.001$ and $F_{1,12} = 13.34$, $P = 0.003$, respectively). This difference was attributed to moose ($F_{1,19} = 21.81$, $P < 0.001$), because snowshoe hare browsing was very low and did not differ significantly across the gradient ($F_{1,19} = 2.58$, $P = 0.124$; Fig. 1b). Moreover, we did not observe any browsing by moose or snowshoe hares on *S. novae-angliae* and *P. balsamifera* in low-density areas.

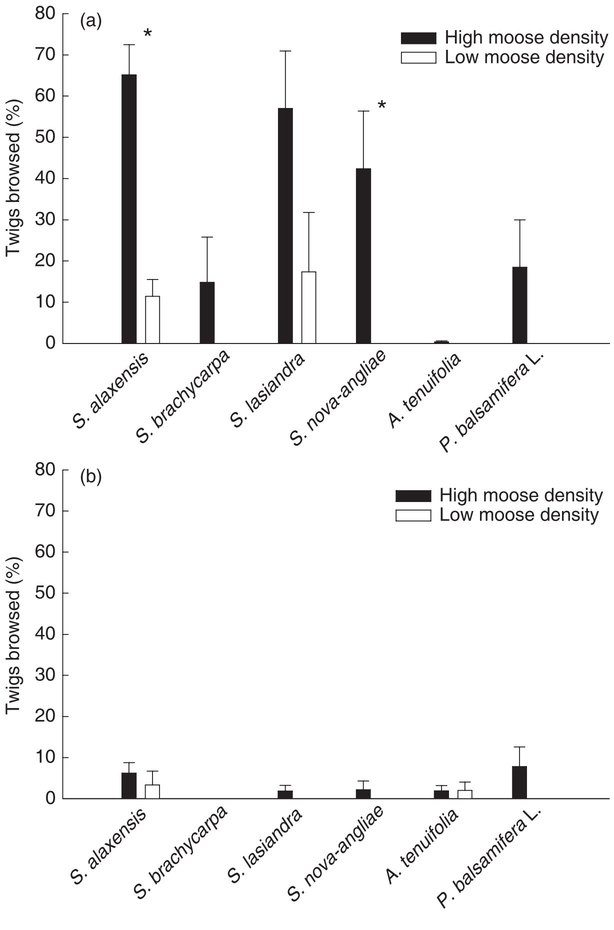

Fig. 1. Frequency (%) of browsing on deciduous shrubs by (a) moose and (b) snowshoe hares along the Tanana River between Fairbanks and Manley, interior Alaska. Bars indicate means, and SEs are shown above the bars. Significant differences are denoted by asterisk.

Of the forage plants in willow communities in the high-density areas, 3% were unbrowsed, 11% were browsed, and 86% were broomed. In the low-density areas, 0% was unbrowsed, 32% were browsed, and 68% were broomed. The difference in the proportion of forage plants assigned to the browsed architectural category was significant ($F_{1,19} = 4.49$, $P = 0.044$). *S. alaxensis* was the only individual species with significant differences in the browsed (7% in the high-density area and 35% in the low-density area) and broomed (93% in the high-density area and 65% in the low-density area) architectural categories, suggesting high historical use of this species by herbivores in the high-density areas and reflecting its importance as a major forage species of moose (Wolff & Zasada 1979; Kielland & Osborne 1998; Seaton 2002). Moose browsing differed between areas both at the individual plant species and at the community level. The primary forage species for moose in riparian areas along the Tanana River was *S. alaxensis* followed by *S. lasiandra* and *S. nova-angliae*, while hares browsed primarily on *S. alaxensis* and *P. balsamifera* L.

Species-specific base diameters of current annual growth (CAG) did not differ between high- and low-density areas, with the exception of *S. lasiandra* ($F_{1,12} = 8.06$, $P = 0.015$). Similarly, differences in diameter-at-point of browsing (DPB) were not significant for any forage species at high or low densities of moose. Combining information on plant densities, twig densities, twig base diameters, and twig biomass for forage species, we estimated that 657 kg ha^{-1} (SE = 92) of CAG biomass was produced in the high-density areas and 750 kg ha^{-1} (SE = 127.4) in the low-density areas. Moose removed 220 kg ha^{-1} (SE = 26.7) in the high-density areas and 42 kg ha^{-1} (SE = 7.8) in the low-density areas during the winter (Table 2). The consumption : production ratio calculated from these data clearly shows the much higher relative browsing pressure in the high-density areas (33.5%) compared with the low-density areas (5.6%) on the lower Tanana River (Table 2), reflecting the fivefold range in moose densities across this section of the Tanana River. The shrub canopies were higher in the low-density area ($F_{1,23} = 7.25$, $P = 0.013$) and remained stable at 282 cm between seasons ($F_{1,11} = 0.04$, $P = 0.845$). By contrast, canopy heights in high-density areas were lower and the average canopy height decreased over the winter (from 233 cm in the fall to 211 cm in the spring; $F_{1,19} = 9.43$, $P = 0.013$), as has been documented in similar studies (Beschta & Ripple 2006).

Contrary to our initial hypothesis, total C and N concentrations in soil were highest in the low-density areas (Fig. 2) and were positively correlated with organic layer depth ($r = 0.778$, $n = 60$, $P < 0.001$ and $r = 0.807$, $n = 60$, $P < 0.001$, respectively) and stand age ($r = 0.801$, $n = 60$, $P < 0.001$ and $r = 0.834$, $n = 60$, $P < 0.001$, respectively). Soil concentrations of C and N in high-density areas were also correlated with organic layer depth ($r = 0.685$, $n = 65$, $P < 0.001$ and $r = 0.663$, $n = 65$, $P < 0.001$ for carbon and nitrogen, respectively), but were poorly correlated with stand age ($r = 0.21$, $n = 65$,

Table 2. Twig off-take and production (kg ha^{-1}) by herbivores in willow communities along the Tanana River in the high and low moose density areas. Mean (SE)

	S. alaxensis	*S. brachycarpa*	*S. lasiandra*	*S. nova-angliae*	*P. balsamifera*	Total
Offtake						
Moose						
High moose density	158.6 (17.6)	0.7 (1.2)	7.5 (2.1)	2.1 (0.9)	1.3 (0.6)	170.5 (22.4)
Low moose density	30.4 (4.9)	0.0 (0.0)	1.0 (0.6)	0.0 (0.0)	0.0 (0.0)	34.0 (5.5)
Hare						
High moose density	47.1 (3.6)	0.0 (0.0)	0.1 (0.3)	0.9 (0.4)	1.7 (0.6)	48.9 (4.3)
Low moose density	11.0 (2.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	11.0 (2.3)
Production						
High moose density	588.9 (62.0)	7.4 (4.7)	17.4 (5.5)	14.1 (5.5)	29.8 (14.4)	657.5 (92.1)
Low moose density	713.9 (116.3)	1.0 (1.1)	12.6 (5.5)	1.1 (0.7)	3.7 (3.7)	750.3 (127.4)
Consumption : production ratio						
High moose density	0.35	0.10	0.44	0.15	0.10	0.33
Low moose density	0.06	0.00	0.08	0.00	0.0	0.06

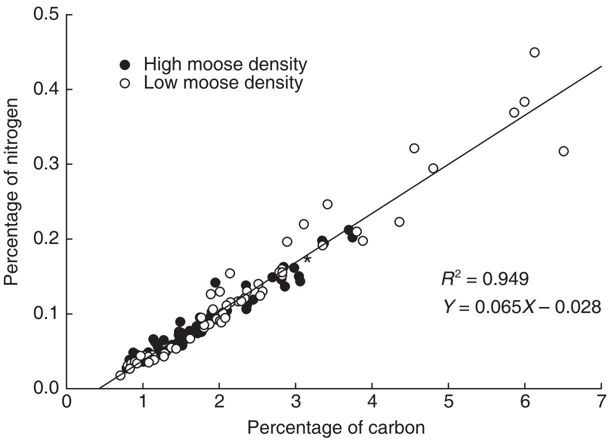

Fig. 2. Relationship between soil carbon and nitrogen concentrations expressed as percentage of the dry weight of soil in 25 willow communities along the Tanana River (n = 125).

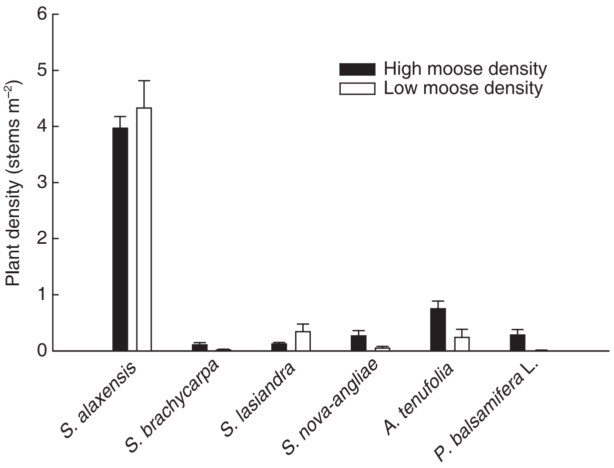

Fig. 3. Plant density of the dominant willow species, as well as alder and balsam poplar across willow communities on the Tanana River (n = 25).

$P = 0.093$ and $r = 0.253$, $n = 65$, $P = 0.042$ for carbon and nitrogen, respectively). Soil nitrogen concentrations correlated with soil carbon concentrations ($R^2 = 0.95$, Fig. 2), but the C/N ratio did not differ between areas.

Densities of current-year moose pellet groups were eightfold greater along the upper parts of the Tanana River (high moose density) than the lower river (mean = 0.24 vs. 0.03 pellet groups m^{-2}, respectively, $F_{1,23} = 12.17$, $P = 0.002$). By contrast, densities of hare pellet groups did not differ between areas (mean = 0.2 pellet groups m^{-2}, $F_{1,23} = 0.01$, $P = 0.905$). Winter faecal pellets exhibited no significant variation in N concentration across the gradient (mean = 1.49% N, SE = 0.036; $F_{1,19} = 0.05$, $P = 0.818$). This rate of faecal input (largely from moose) represented, however, an estimated annual addition of 29.6 g C m^{-2} and 0.6 g N m^{-2} to soils in high-density areas and 4.8 g C m^{-2} and 0.1 g N m^{-2} to soils in low-density areas. The higher rate of C and N addition represents nearly a doubling of the annual C and N input via leaf litter fall typical of similar-aged shrub stands (Kielland & Bryant 1998).

Willow communities along the entire section of the river were dominated by *S. alaxensis*, with all other species making up less than 30% of the community (Fig. 3). No significant differences were found between high and low moose density areas regarding frequency of willow or later-successional species. However, we found much higher density of standing dead ramets in high moose density areas ($F_{1,23} = 40.19$, $P <$ 0.001) as well as a much higher proportion (approximately fourfold) of dead to live plants (Table 3), suggesting higher plant mortality. The mean age of plants in the willow communities was significantly younger in areas of high browsing pressure ($F_{1,25} = 8.77$, $P = 0.007$, Table 4). However, whereas age distribution of each species changed towards younger age classes, these demographic shifts were only significant for preferred browse species, including *S. alaxensis*, *S. lasiandra*, and *S. nova-angliae* ($F_{1,23} = 9.44$, $P = 0.005$; $F_{1,20} = 4.62$, $P = 0.044$; and $F_{1,20} = 4.75$, $P = 0.042$, respectively; Fig. 4). The earliest colonization of alder in low-density areas is estimated to have occurred when the willow stands were approximately 14 years

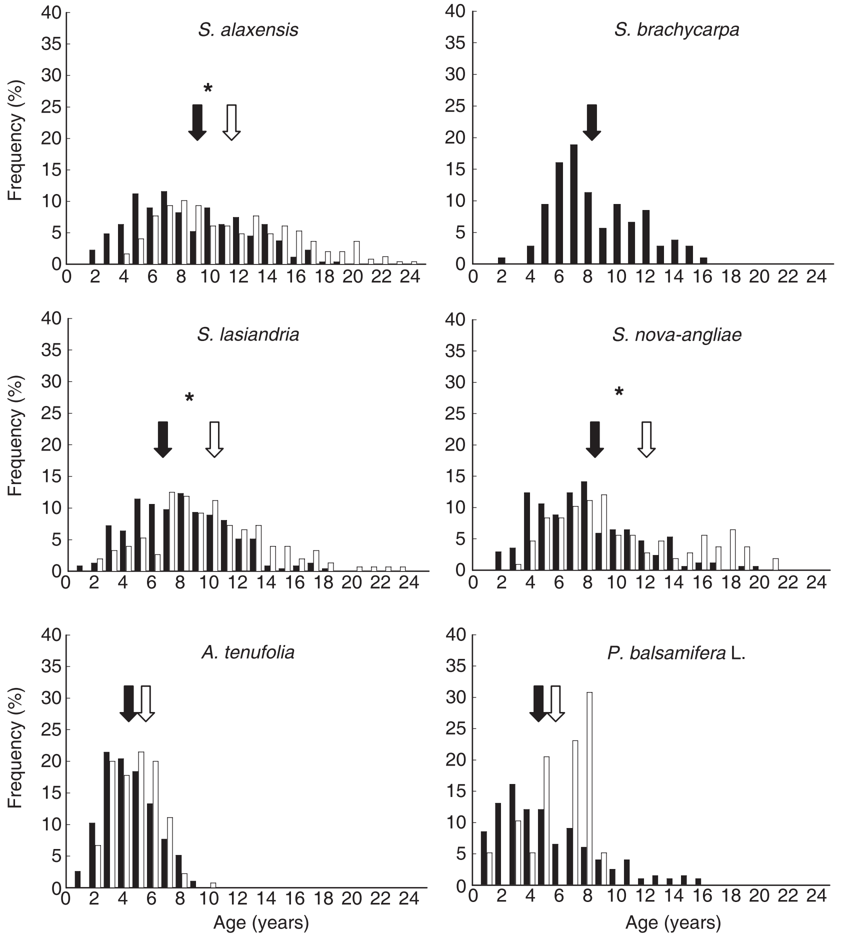

Fig. 4. Age (years) distribution of four willow species, alder and poplar in willow communities found along the Tanana River in the high (solid) and low (open) moose density areas. Arrows indicate the average age. Significant differences are denoted by asterisk.

Table 3. Density (stems m^{-2}) comparison of plant species found in willow communities along the Tanana River in areas of high and low moose density

	High moose density		Low moose density		
	Mean	SE	Mean	SE	*P*-value
S. alaxensis	4.0	0.2	4.3	0.3	0.345
S. brachycarpa	0.1	< 0.1	0.0	< 0.1	0.073
S. lasiandra	0.1	0.1	0.3	0.1	0.021
S. nova-angliae	0.3	0.1	0.1	0.1	0.055
A. tenuifolia	0.8	0.1	0.2	0.1	0.004
P. balsamifera L.	0.3	0.1	0.0	0.1	0.005
Standing dead ramets	2.7	0.1	0.6	0.1	< 0.001

(SE = 1.02), whereas colonization of alder stands in high-density areas was estimated to be 10 years (SE = 0.83) on average ($F_{1,18} = 8.99$, $P = 0.008$). Colonization time of *P. balsamifera* did not differ between areas, but this species occurred in only four out of 12 willow communities in the low-density areas as opposed to 12 out of 13 communities in the high-density areas, suggesting a spatial difference in colonization along this stretch of the river.

No difference between areas was detected in the average stand age. However, several of the willow communities in low-density areas were older than any willow community in the high-density areas. Natural variation in the minimum age of selected stands precluded statistical testing of community age. As all of the mature willow communities found in both study areas were aged, we conclude that the lack of older stands in the high-density area is evidence of differences in the successional transition of willow to alder communities between these two areas.

At the landscape scale, willow communities comprised a larger percentage of the shrub communities in the low-density areas than in the high-density areas (Table 5, Fig. 5a). The size of willow communities along the Tanana River tended to be larger in low-moose areas (11.4 ha), in contrast to the high-moose areas (3.4 ha) ($F_{1,36} = 1.36$, $P = 0.252$). This comparison was statistically significant when age (of known-age communities) was used as a covariate ($F_{1,22} = 13.88$, $P = 0.001$). Though we found the same number of alder communities in areas of low and high moose densities, these communities were smaller in size in the low-density areas ($F_{1,34} = 4.18$, $P = 0.049$). Because of the much lower contribution of willow to the landscape in the high-density areas, the relative proportion of willow and alder was driven by this component of the vegetation (Fig. 5b). The ratio of willow to alder (47.0 ha/58.5 ha) was

Table 4. Comparison of mean and maximum ages (years) of species found in willow communities along the Tanana River in the high and low moose density areas

	High moose density		Low moose density		
	Mean age (SE)	Maximum	Mean age (SE)	Maximum	*P*-value
A. tenuifolia	4.4 (0.1)	9	4.7 (0.1)	10	0.106
P. balsamifera L.	5.3 (0.3)	16	6.1 (0.4)	9	0.162
S. alaxensis	8.6 (0.2)	19	11.8 (0.3)	37	< 0.001
S. brachycarpa	8.5 (0.3)	16	NA	NA	NA
S. lasiandra	7.9 (0.2)	18	9.8 (0.3)	23	< 0.001
S. nova-angliae	7.9 (0.3)	20	10.4 (0.5)	21	< 0.001

Table 5. Comparison of the proportion of shrub communities dominated by willow and alder along 21-km transects along the Tanana River in each study area

	High moose density	Low moose density
River distance (km)	20.9	20.9
Straight line distance (km)	16.4	18.0
Observed stands	32	42
Number of willow communities	14 (43.8%)	24 (57.1%)
Number of alder communities	18 (56.2%)	18 (42.9%)
Total willow area (ha)	47.0 (45%)	274.2 (66%)
Total alder area (ha)	58.5 (55%)	142.9 (34%)
Willow (ha) : alder (ha) ratio	0.8	1.9

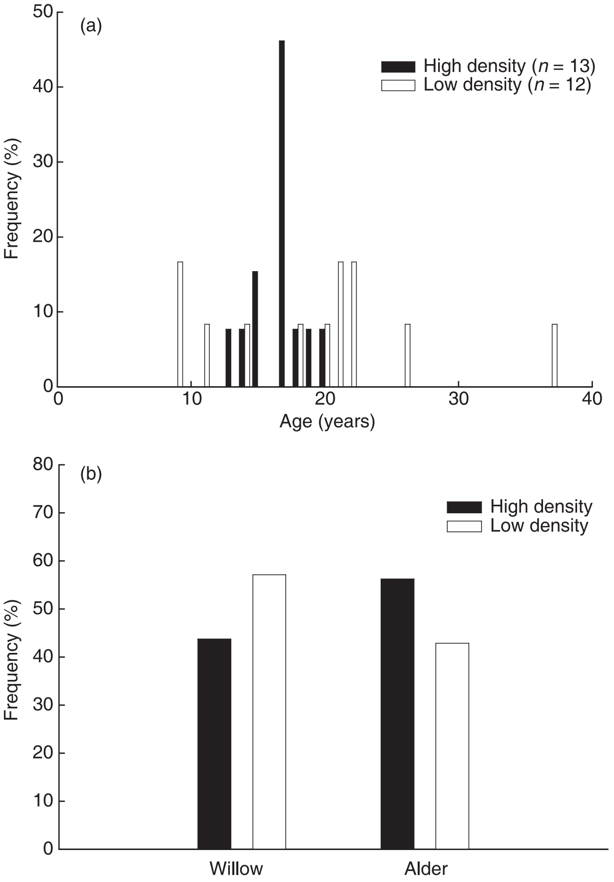

Fig. 5. Vegetation composition along the Tanana River pertaining to: (a) age distribution of the 25 willow communities used as field sites in the high and low moose density areas, and (b) proportion of shrub communities classified as willow or alder on a 21-km transect along the Tanana River in each study area.

0.8 in the high-density area, whereas this ratio (274.2 ha/142.9 ha) was approximately 1.9 in the low moose density areas. These data are consistent with the apparent suppression of willow abundance under high browsing pressure, as has been observed under plot-level experimental conditions using large herbivore exclosures (Kielland *et al.* 2006).

Discussion

We found that changes of interactions between herbivores and vegetation at the plot level (Bryant *et al.* 1985; Kielland *et al.* 1997; Kielland & Bryant 1998) could be extended to the level of the Tanana River landscape, where herbivores modified the structural properties of willow communities and altered the numbers and sizes of these communities at the landscape level. These changes linked browsing by moose (and hares) to a shortening of the life span of individual willow plants and willow communities as a whole. High consumption : production ratios of willows associated with higher moose densities accelerated both carbon and nitrogen vegetation turnover, and faecal deposition represented both a considerable redistribution of nitrogen and a significant increase in above-ground N input to riparian willow stands. Thus, in these productive systems (relative to other taiga ecosystems) element cycling appeared to be promoted by herbivory (*sensu* Bardgett & Wardle 2003).

We recognize that the strong gradient in moose densities along the Tanana River begs the question of a possible trophic cascade (Paine 1980; Ripple *et al.* 2001; Peterson *et al.* 2003) involving interactions of predators (wolves), herbivores (moose) and vegetation. Interior Alaska has healthy populations of both moose and wolves (Magoun & Dean 2000; Kielland *et al.* 2006). The range in moose densities across our study area spanned the general range of moose densities in North America, where these populations are hunted by wolves, bears and humans (Peterson *et al.* 2003).

The threefold lower ratio of moose to wolves (moose : wolf ratio ≈ 22) along the lower Tanana River around Manley Hot Springs (Game Management Unit 20C) compared with the Tanana Flats near Fairbanks (moose : wolf ratio ≈ 68) (Seaton 2006; Young 2006a; Young 2006b), suggests that differences in the strength of trophic-level interactions could partly explain our observations. For example, there is ample demographic evidence showing that moose are food-limited in the high-density areas in the Tanana Flats (i.e. delayed age of first reproduction, very low twinning rates, low yearling and adult body weights; Boertje *et al.* 2007). By contrast, there are no documented cases in the interior of Alaska of a low-density moose population (such as in GMU 20C near Manley Hot Springs) that was limited by food rather than by predation (Gasaway *et al.* 1992; Boertje *et al.* 2007). Thus, variation in landscape patterns of riparian vegetation across interior Alaska may be functionally linked to differences in herbivore densities and predator-prey dynamics, as has been suggested for temperate wolf-ungulate systems (e.g. Bradner *et al.* 1990; Beschta 2003; Larsen & Ripple 2003; Peterson *et al.* 2003; Beschta & Ripple 2006).

The effects of herbivory documented in this study were attributed to moose (and to a lesser extent to snowshoe hares). Beavers (*Castor canadensis*) have also been identified as a mammalian herbivore that can modify the habitat and affect succession (Moen *et al.* 1990; Naiman *et al.* 1994; Nolet *et al.* 1994; Helm & Collins 1997). However, beaver activity was documented in only two of the 25 stands, and thus was not an important factor affecting the vegetation in this study. Similarly, we observed little defoliation by insects during the 2 years of our study, though we recognize they may have been important historically.

Moose faecal C input was approximately equal to the annual carbon input from leaf litter fall (Kielland *et al.* 1997). The rate of nitrogen input from moose faeces in high-density areas was approximately twice as high as previous estimates and demonstrates the potential for herbivory to affect rates of nitrogen cycling (Bryant & Chapin 1986; Pastor *et al.* 1988; Pastor *et al.* 1993; Kielland & Bryant 1998; Kielland *et al.* 2006).

Despite the proportional effect of moose densities on browsing pressure and ramet mortality, we found no differences in the densities of the different species in willow communities. This lack of differences may be due to vegetative reproduction of the willow plants replacing dead ramets or due to site selection. As mature willow stands were selected, all of the stands had high willow densities and low densities of later successional species. The absence of *S. brachycarpa* and the infrequent occurrence of *S. nova-angliae* in the low moose density areas may be a consequence of taller canopy height, which may select against shorter, small-leaved species. We do not think that seed dispersal would limit the distribution of these species along the Tanana River, because the light seeds of *S. brachycarpa* and *S. nova-angliae* can be dispersed for long distances by wind.

Further, we did not detect a great difference in plant architecture, particularly in the proportion of broomed plants, across the gradient of moose densities. We suspect this was because the degree of brooming is largely a function of how many twigs are clipped per plant (i.e. removal of meristems), not how much mass of a given twig that is removed. The number of twigs clipped by moose, as opposed to the consumption : production ratio, appears rather insensitive to variation in moose density, at least above moderate densities (e.g. 0.1 moose km^{-2}). For example, a fivefold increase in moose densities along the Koyukuk River in the western part of interior Alaska during the 1980s resulted in only 5% increase in proportion of twigs browsed by moose (Osborne 1996).

Shifts in the age distribution of the three primary forage species at the landscape scale and the increase in the density of standing dead ramets implies a decreased life span in plants that can be attributed to herbivory. Associated increases in density of later successional species suggest an accelerated rate of successional turnover from the willow to alder due to moose and hare browsing (Kielland & Bryant 1998). This conclusion was further supported by observations on the river transects that showed not only a change in landscape composition, but also a change in the size of shrub communities. These changes resulted in a landscape with fewer, smaller willow communities and larger alder communities associated with increased herbivory.

Our results are consistent with previous research showing that herbivory is manifested at several levels of ecological organization, including at the individual, species, population and community levels. Here we have shown how these herbivore-driven processes at local spatial scales translate to the landscape level. The coupling of these regional vegetation patterns to available information on moose demography and relative wolf–moose abundance across the study region suggests that these ecological patterns may be augmented by predator–prey interactions.

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