Effects of Moose Foraging on Soil Nutrient Dynamics in the Gustavus Forelands, Alaska

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Abstract. We are studying how selective foraging by moose is affecting soil nutrient dynamics in the Gustavus forelands, where current over-winter moose densities (ca. 3.9 animals/km^2) are among the highest recorded in Alaska. We examined variation in inorganic N and microbial N pools between paired exclosure-control plots located in willow thicket habitats, both within and adjacent to the Gustavus airport, and used buried bags to measure *in situ* net nitrogen (N) mineralization rates. The fence surrounding the airport has functioned as a moose exclosure since 1998, and thus samples collected inside the airport boundary were treated as unbrowsed controls. Results of this study provide preliminary insight into the extent to which the moose population on the Gustavus forelands may be altering soil nutrient dynamics. In addition to this baseline sampling, we also have established three 12×12 m moose exclosures in other areas of the forelands that span a gradient of soil moisture and willow cover. These additional exclosures will allow a more rigorous evaluation of the impact of moose herbivory on local plant community structure and soil nutrient dynamics.

Introduction

Ungulate herbivores can modify ecosystem structure and function through the timing and extent of their activities and may have pronounced effects on soil nutrient dynamics. In Alaska, moose are an important component of many ecosystems and have the potential, at high densities, to significantly alter soil processes (cf. Pastor and others, 1993) and community composition (Butler, 2003). Although both grazers and browsers are expected to reduce above-ground plant biomass and litter inputs, their effects on soil C and N availability and turnover appear to be mediated by differences in the timing and selectivity of their foraging (Danell and others, 1994). Grazers generally enhance net N turnover (Frank and Groffman, 1998; Stark and others, 2000) and N retention (Frank and others, 2000), although browsers such as moose tend to reduce soil N pools and net N mineralization (Pastor and others, 1988; Pastor and others, 1993), perhaps through enhanced carbon turnover and sequestration.

The exclusion of moose has been shown to increase soil nutrient availability, microbial activity, and C and N mineralization rates in a boreal forest system, where moose densities were estimated to be 2.8 animals/km^2 (Pastor and others, 1993). In the Gustavus forelands and parts of Glacier Bay National Park (GBNP), the moose population has increased from low, colonization levels in the 1960s, to an over-winter density (ca. 3.9 animals/km^2) that is among the highest recorded in the states. The nearly two-fold increase in winter moose densities over the last 5 years has resulted in high levels of foraging and changes in plant community structure in preferred foraging habitats (i.e. *Salix* thickets; White and others, this issue). However, the effects of moose foraging on soil nutrient dynamics are unknown.

The objective of this study was to examine how the current level and timing of moose activity observed in the Gustavus forelands may be affecting soil nutrient dynamics and site productivity, and to relate these findings to projected population trends for the Gustavus moose population. We sampled soils inside and outside of the Gustavus airport boundary to examine short-term effects of moose browsing on inorganic N pools, microbial N, and net N turnover. The area surrounding the Gustavus airport is heavily utilized by over-wintering moose, and the fence surrounding the airport has functioned as a moose exclosure since its construction in 1998. Thus, productivity measurements and soil samples collected inside the airport boundary were treated as unbrowsed controls.

Methods

Soils of the Gustavus forelands consist of weathered and reworked glacial till derived from metamorphosed sandstone, limestone and igneous intrusions. Open stands of willow (*Salix barclayi*, *S. commutata, S. sitchensis*) provide winter forage areas for moose. Plots were located in a bluejoint-forb meadow vegetation type, dominated by bluejoint reedgrass (*Calamagrostis canadensis*) and fireweed (*Chamerion angustifolium*). No nitrogen-fixing species were present. We measured soil parameters at three sites near the Gustavus airport, two of which utilized the fence surrounding the airport as a moose exclosure (Sites A, B), and one of which was in a browsed area about 1 km south of the airport (Site C; fig. 1). Sites A and B were characterized by loamy, well-drained soils dominated by willow, while Site C was characterized by

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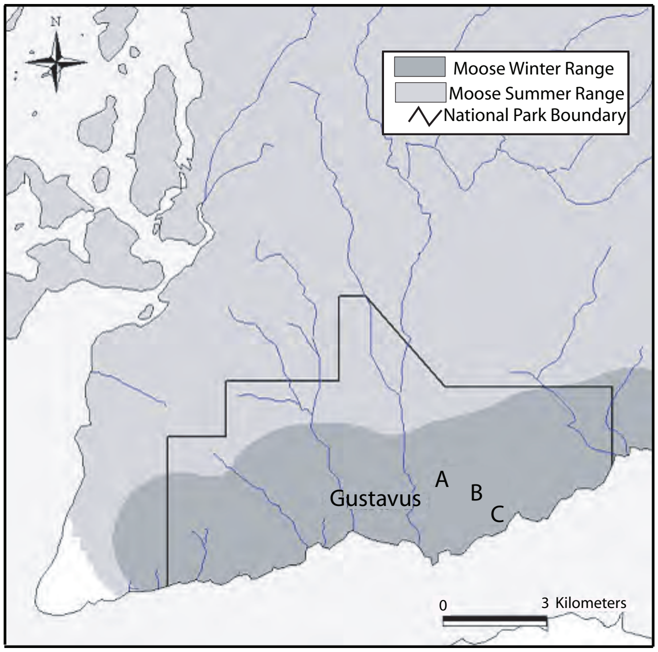

Figure 1. Summer and winter moose range and soil sampling sites, Gustavus forelands and Glacier Bay National Park.

organic soils underlain by a sandy mineral horizon and was dominated by a mixed overstory of willow and sweet gale (*Myrica gale*).

At each site, we collected five pairs of soil cores (3.8 cm diameter, 10 cm deep) from browsed and unbrowsed plots (Sites A, B), or from a browsed plot only (Site C) in April 2004. One core was returned to the laboratory and processed within 12 hr of collection for determination of microbial biomass and inorganic N pools. The second core, used for determination of *in situ* net N mineralization, was enclosed in a semipermable polyethylene bag and incubated in the field until October 2004. Microbial N was determined on the initial set of cores using a chloroform fumigation-extraction method over a 2-day fumigation period, and extracts were analyzed for total N using a persulfate digestion technique. We did not apply a correction for extraction efficiency to our estimates of microbial N, and thus these values are interpreted as chloroform-labile N rather than total microbial biomass. Net N mineralization will be calculated over the growing season as the difference in inorganic N concentrations (NH_4^++NO_3^-) between paired soil cores collected in April and October (*analyses in progress*). Soil C:N will be determined on a subsample of all soils collected in October (*analyses in progress*). Browsing effects on soils at Sites A and B were determined by ANOVA (Systat Version 10, SPSS, Inc.).

As part of a long-term study of the effects of moose browsing on willow productivity, we permanently marked 80 individuals of *Salix barclayi* (Sites A, B). Individual plants were selected using a stratified random sampling approach based on size class (i.e., rooted stem diameter) within paired control and browsed plots (360 m^2). We estimated willow productivity on each plot by measuring basal diameter of all current annual growth twigs for each plant in October 2003. We re-examined each twig for evidence of moose browsing and associated twig bite diameters in April 2004. Twig biomass and bite biomass were calculated using twig diameter (mm) by biomass (g) regression equations (White). Within and between site differences in productivity were determined by ANCOVA, using plant size as a covariate.

Results

Browsed plots showed consistently lower soil inorganic N pools than unbrowsed plots following 5 years of moose exclosure (Sites A, B). Moose browsing reduced extractable NO_3^- (df=1, F=5.02-5.46, P<0.05), and to a lesser degree NH_4^+ concentrations, across sites (fig. 2*A*, *B*). In contrast, browsing effects on microbial N were site specific, with browsing reducing the microbial pool at Site A, but enhancing it at Site B (fig. 2*A*, *B*). Across browsed plots (Sites A, B, C), significant site effects were observed for all soil N parameters (*data not shown*), although Sites A and B did not differ for any one parameter (fig. 2*A*–*C*).

At the time of the initial sampling (April 2004), inorganic N pools at all sites comprised a substantial fraction of microbial N, ranging from 45 to greater than 100 percent of chloroform-labile N, regardless of browsing effects (fig. 2*A*–*C*). Soil NO_3^- concentrations equaled or exceeded soil NH_4^+, indicating the presence of a potentially large, plant-available N pool prior to the start of the growing season (leaf initiation).

Current annual growth of willow, estimated as change in twig biomass per plant (October 2003–April 2004), did not differ between browsed and unbrowsed plots (table 1). Nevertheless, over-winter moose browsing resulted in a 25–43 percent reduction in current annual growth, relative to unbrowsed plots. Site differences in productivity also were evident, as current annual growth was greater at Site B than Site A (df=1, F=15.41, P<0.001), and differences in mean current annual growth ranged from 0 g (Site B) to 4.5 g (Site A) between browsed and unbrowsed plots (table 1).

Discussion and Conclusions

Winter browsing by moose in the Gustavus forelands has decreased soil inorganic N pools over the last 5 years, relative to adjacent unbrowsed areas, but has had little effect on willow productivity in spite of 25–43 percent twig consumption rates. Herbivore effects have been shown to alternately enhance (Frank and Groffman, 1998) and limit (Pastor and others, 1993) rates of soil N cycling through associated changes in plant productivity, litter C:N ratios and litter inputs, as well as through trampling and the deposition of urine and feces.

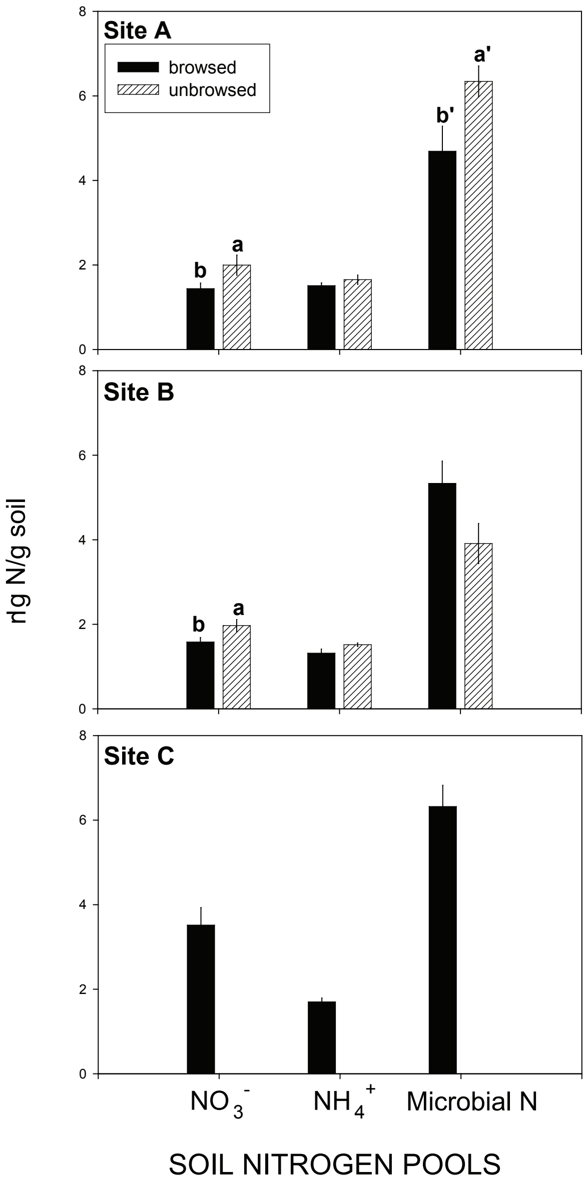

Figure 2. Effects of browsing on soil NO3⁻, NH4⁺ and microbial N pools in browsed and unbrowsed plots (Sites A, B), and at a browsed site only (Site C), April 2004. Data are expressed as means ±1 SE. Lower case letters indicate browsing effects significant at *P*<0.05.

Table 1. Summary of current annual growth (CAG) willow productivity estimated in October 2003 and the proportion of willow biomass consumed by moose at the end of the following winter (April 2004). Sites A and B represent paired control-browsed sites located inside and adjacent to the Gustavus airport fence. Data are expressed as means ±1 SE.

Site	CAG twig biomass per plant (g)		CAG twig biomass Consumed per plant (percent)	
	Control	Browsed	Control	Browsed
A	14.6	10.1 (2.6)	—	26.4 (4.3)
B	22.4 (6.0)	22.4 (4.8)	—	42.5 (2.7)

In some cases, winter browsing has induced morphological changes in shrubs without concurrent changes in biomass (Peinetti and others, 2001). However, even where litter inputs increased with moose browsing, concomitant increases in litter C:N have resulted in a net reduction in soil N pools (Pastor and others, 1988).

Over-winter densities of moose in Gustavus (3.9 animals/km^2) were about 40 percent greater than those reported from a boreal forest system in Minnesota (2.8 animals/km^2), where moose browsing decreased soil N pools and microbial respiration (Pastor and others, 1988), as well as primary productivity and C and N mineralization (Pastor and Naiman, 1993). Significant reductions in inorganic N (NO_3^-) with browsing, were consistent with the results above, although changes at our sites in Gustavus occurred over a much shorter time frame (5 vs. 20+ years). Indeed, the irruptive growth of the Gustavus moose population over this period, the concentration of moose activity during the winter months, and the limited extent of activity in the area prior to the last 5–10 years together suggest that the effects of moose herbivory on soil nutrient stocks can be manifested in a relatively short period of time.

Over-winter moose browsing reduced current annual growth in willows by 25–43 percent. On average, 85 percent of the current year's twigs were browsed and 37 percent of the total current annual growth twig biomass was consumed at these sites (White and others, 2007). While woody browse comprised the majority (76–90 percent) of winter food items consumed by over-wintering moose between 2001–2004, there is evidence that an increasing proportion of their diet is being supplemented by lower quality forage (White and others, 2007). Such changes in foraging patterns (and thus reduced quality of moose inputs), paired with decreases in soil N availability and N turnover, could result in negative feedbacks at the ecosystem scale.

Variation in willow productivity, and thus potential litter inputs, may account for some of the observed variation in microbial pools between our sites, as browsing reduced both current annual growth (twig biomass) and microbial N at Site A, but did not affect either parameter at Site B, where overall productivity was nearly twice as great. Site factors have had a greater effect than grazers on soil C and N cycling in Yellowstone National Park (Verchot and others, 2002), and potentially control much of the variation we observed across browsed sites.

In October 2004, we constructed an additional two 12×12 m exclosures in the area, which span a gradient of soil moisture and willow cover and will be used to expand our monitoring efforts across a broader range of soil and community types. Results of the *in situ* net N mineralization and C:N analyses from Sites A–C, as well as future work at newly established exclosure sites (fig. 3) are expected to provide greater insight into the relative importance of site versus herbivore effects in this system.

Figure 3. Newly constructed moose exclosure, Site B, October 2004. (Photograph taken by Eran Hood, University of Alaska Southeast.)

Management Implications

Our findings regarding moose browsing effects on soil nutrient pools, while preliminary, have implications for larger ecosystem processes (e.g., nutrient turnover, nutrient loss, plant-soil feedbacks) within the study area and in adjacent GBNP. First, changes in moose diet toward lower quality forage (and thus reduced quality of moose inputs), paired with decreases in soil N availability and N turnover, could result in negative feedbacks at the ecosystem scale. Additionally, because the winter range of the Gustavus population is largely contained within non-Park lands open to subsistence and sport hunting, the summer range, largely contained within GBNP, likely will be impacted by management activities that occur outside the Park. Thus, policies implemented by Alaska Department of Fish and Game designed to reduce moose population densities below carrying capacity in the Gustavus forelands are expected to have implications that transcend park boundaries and raise important issues regarding the natural regulation of wildlife populations.

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Uplifted tidal flat supports an emergent meadow. (Photograph taken by Bill Eichenlaub, National Park Service.)