Moose herbivory and carbon turnover of early successional stands in interior Alaska

Knut Kielland, John P. Bryant and Roger W. Ruess


In the taiga of interior Alaska, early successional stands are dominated by deciduous species. These species represent the main forage base for many mammalian herbivores. In a long-term study employing large, permanent exclosures, we measured the impact of winter browsing by moose and snowshoe hares on carbon flux in riparian willow/alden communities. We found that browsing-induced changes in leaf litter chemistry increased the rate of litter decomposition both in the laboratory and under field conditions, and increased the pool of mineralizable carbon in litter. The aboveground input of higher-quality litter-carbon following browsing may explain the increased respiration potentials of soils sampled outside the exclosures. Moreover, winter browsing tends to reduce the production of fine roots and appears to decrease fine root longevity. Thus, the net effect of moose browsing on aboveground and belowground processes in these early successional stands is to accelerate carbon turnover. These results demonstrate that the effects of mammalian herbivory on element cycling in taiga is a two-stage process, involving interspecific as well as interspecific responses at different time scales. Winter browsing by moose offer one example of how mammalian herbivory modify ecosystem-level processes that govern major functions in these ecosystems.

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The early stages of primary succession of taiga forests in interior Alaska are dominated by deciduous species, in particular willow (Salix spp.) and alder (Alnus tenuifolia). By late successional the deciduous species have largely been replaced by evergreens such as white spruce (Picea glauca L.). Life history processes play major roles in explaining this successional pattern (Walker et al. 1986), but the rate of species replacement is significantly affected by selective browsing by mammals (Kielland and Bryant unpubl.). By feeding selectively on deciduous species such as willow, moose (Alces alces) and snowshoe hare (Lepus americanus) favor the eventual dominance of evergreens in the vegetation (Bryant and Chapin 1986, Pastor et al. 1988, McInnes et al. 1992, Pastor and Naiman 1992).

Increasing dominance by evergreens is associated with reduced rates of soil organic matter turnover and nutrient cycling (Flanagan and Van Cleve 1983, Van Cleve et al. 1991). One important component of organic matter decomposition relates to litter chemistry. Litter of evergreens such as spruce has lower nitrogen and phosphorus concentrations, but higher concentrations of recalcitrant toxic compounds such as lignin, tannin, and resin compared to deciduous species such as willows (Bryant and Kuropat 1980). These chemical characteristics cause evergreen litter to decompose much slower than deciduous litter (Fox and Van Cleve 1983, Berg and Wessén 1984, Berg and Staaf 1987). Thus, high concentrations of indigestible substances and chemical defenses that deter herbivory (Bryant and
Kuropat 1980) are inversely related to intrinsic rates of litter decomposition. Viewed in the context of this long-term effect, mammalian herbivory is seen, correctly, as decreasing the rates of organic matter turnover and element cycling (Pastor et al. 1993).

However, previous research has shown that browsing on paper birch (Betula papyrifera) results in more rapid litter processing by stream insects (Irons et al. 1991). Moreover, unrelated experiments with snowshoe hares have found increased nitrogen leach concentration and higher digestibility of previously browsed fellleaf willow (Bryant unpubl.), which mirror the observations of moose browsing (Kielland and Bryant unpubl.). These findings suggest that browsing may increase litter decomposition and element cycling in the short term, within the successional stage that browsing occurs. The purpose of the present study was to test this hypothesis, and try to resolve the apparent opposing views of how mammalian herbivores affect ecosystem functions in taiga forests.

**Methods**

The study area was a 17-km segment of the Tanana River floodplain within the Bonanza Creek LTER site which is located 20 km SW of Fairbanks, Alaska (64°51’N, 147°43’W, elevation 305 m). Within this segment of the Tanana River floodplain we constructed nine enclosures in 1988. The enclosures are large (50 × 20 m) permanent structures, constructed of 10-cm diameter, 5-m long treated posts planted 2 m into the ground. On this framework high-tensile-strength steel wire and 2.5-cm mesh fence wire were strung. These fences have prevented browsing by moose and hares even in winters of very deep snow. At each enclosure the site was divided into treatment (enclosure) and control, with the control plots separated from the enclosure by a 10-m buffer strip that limited the edge effect of fencing and access trails. Within enclosure and control plots, permanent subplots were placed in a stratified random design. In these subplot measurements of phytosociological parameters, litter fall, and browsing intensity have been made yearly (Table 1). Other measurements, such as litter decomposition and soil chemistry were carried out along transects at each site. Decomposition of native litter was measured in the laboratory and in the field.

**Litter decomposition**

In the laboratory gas flux measurements were carried out on litter contained in sealed 980-ml glass jars fitted with rubber septa. Each jar contained 5 g fresh weight litter. Moisture was adjusted to 75% water-holding capacity with distilled water after determining the water-holding capacity of each litter type. Samples were pre-incubated for two d in the dark at the incubation temperature (15°C) before gas measurements started. Carbon dioxide concentration in the head space was determined five times over the course of the experiment, and analyzed using gas chromatography (by thermal conductivity) on a Shimadzu GC-14A fitted with a 0.5-ml sample loop and a 200-cm Poropak Q column. In a short-term (2-week) experiment we measured the respiration potential of three species, separately and in their natural mixture (determined from litter traps). The individual species examined were thin-leaf alder (Alnus tenuifolia), balsam poplar (Populus balsamifera), and fellleaf willow (Salix alaxensis). Long-term (7-month) respiration potential was measured on fellleaf willow, the dominant species in the willow stage of succession. Gas flux measurements were done on a monthly basis. Between measurements the jars were covered with a 0.02-mm polyethylene sheet to prevent moisture loss, but allow free gas exchange (Gordon et al. 1987). Each experiment comprised six composite litter samples from eight enclosures (n = 48). The data were fit to single exponential models of the form

\[ X_t = X_0(1 - e^{-kt}) \]

where \( X_t \) is the cumulative carbon mineralization up to time \( t \) (d), \( X_0 \) is the pool (mg g\(^{-1}\)) of potentially mineralizable carbon in the litter, and \( k \) is the instantaneous release rate (d\(^{-1}\)) of that pool. Data were fit to the model by non-linear regression, using the DUD algorithm (Rabson and Jennrich 1978).

In the field experiment, leaf litter of fellleaf willow was collected (from five litter traps per treatment from five enclosures, \( n = 50 \)) in late September. The litter (4 g fresh weight) was enclosed in 15 × 15 cm, 2-mm mesh, polyester bags, and placed in the litter layer in late September 1994, and retrieved 12 months later.

A similar experiment evaluating the importance of site factors on carbon cycling, examined the rate of cellulose decomposition (a neutral substrate). This experiment was conducted at the same time as the litter decomposition experiment using the same methodology and sample sizes, but additionally including bags placed in the alder stage.

**Table 1. Vegetation and soil properties on the willow and alder stage of succession on the Tanana River floodplain. Mean (S.E.).**

<table>
<thead>
<tr>
<th>Source</th>
<th>Willow stage</th>
<th>Alder stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m(^{-2}))</td>
<td>200–400</td>
<td>2500–3000</td>
</tr>
<tr>
<td>Litter fall (g m(^{-2}) yr(^{-1}))</td>
<td>33.0 (4.0)</td>
<td>290 (24.1)</td>
</tr>
<tr>
<td>Litter N (%)</td>
<td>1.3 (0.0)</td>
<td>1.7 (0.1)</td>
</tr>
<tr>
<td>Total soil N (%)</td>
<td>0.1 (0.0)</td>
<td>2.5 (0.1)</td>
</tr>
<tr>
<td>Total soil C (%)</td>
<td>1.2 (0.9)</td>
<td>37.4 (1.3)</td>
</tr>
</tbody>
</table>

2. This study.
Soil respiration

Soil respiration potentials were measured in the laboratory at 15°C. Samples of 50-g dry weight soil were placed in 980-ml glass jars and moisture content adjusted to 60% WHC. Samples were kept in dark environmental chambers and pre-incubated for two d before CO₂ measurements were initiated. We report the average of six replicate measurements that were made over a three-week period.

Root dynamics

Fine root production and mortality were measured using a minirhizotron system. Five clear butyrate plastic minirhizotron tubes (2 m in length, 5 cm ID), each etched with 120 1.4 × 1.4-cm frames along the length of the tube, were installed at a 45° angle to the soil surface, inside and outside 3 of 9 enclosures in September 1991. Monthly images of roots were taken throughout the growing season beginning in 1992 using a color microvideo camera (Barth Technology, Santa Barbara, CA, USA) and saved to SVHS video tape. Images were then digitized using the ROOTS program (Michigan State University). The program allows for the tracking of individual roots over time by saving length and diameter tracings of each root from each (monthly) sampling period. We then used a dBASE program to independently calculate production and mortality based on extension growth and/or death of new and preexisting roots (Hendrick and Pregitzer 1992). For statistical purposes, root length data for live and dead roots from five tubes inside and outside each enclosure were summed, resulting in n = 3 for comparisons of browsed vs unbrowsed plots. Here we report data summarizing total annual production and mortality for fine roots growing during the 1993 growing season.

Data were analyzed using the SYSTAT statistical package (Wilkinson 1987). Differences among means were tested using 1-way ANOVA, simple t-tests, and the Kruskal-Wallis test for non-parametric data.

Results

*Short-term* respiration rates of the natural litter mixture of leaf litter from browsed plants were significantly greater (P = 0.005) than unbrowsed plants in the enclosure (Fig. 1). Among individual species browsing increased the short-term respiration potential between 16 and 30%, but the increase was only significant with respect to poplar (P = 0.015). Respiration rates of litter, irrespective of treatment, was highest in feltleaf willow and lowest in alder.

Further, the *long-term* rate of decomposition of feltleaf willow, the dominant, most preferred forage species, was significantly greater in browsed than unbrowsed plants (Fig. 2). The difference in decomposition between treatments was not evident until after 30 d of incubation, which is consistent with the finding of the short-term respiration experiment. After 30 d of incubation, the respiration rate of browsed litter was significantly greater than unbrowsed litter, and remained as such for the duration of the experiment.

Whereas the turnover time (1/λ) of browsed litter was only slightly shorter than that of unbrowsed litter (97 vs 105 days), the estimated pool of mineralizable carbon was nearly 30% greater in litter from browsed plants (Table 2). Thus, the average daily flux (the product of the pool size and the rate constant [C₀ × k]) of carbon from litter of browsed plants was over 50% greater than from unbrowsed plants.

Decomposition of feltleaf willow leaf litter in the field showed similar treatment effect as in the Laboratory (Fig. 3). Total mass loss over one year was approximately 30% greater in litter from browsed than from
unbrowsed plants, again indicating substantially faster litter turnover as a consequence of browsing.

We found large differences in soil respiration potentials both in the willow and alder stage of succession (Fig. 4). Respiration potentials (per gram dry weight soil) of soils from outside the enclosures were approximately twice as high as inside the enclosures.

Browsing decreased fine root production by 41% during 1993 ($P = 0.004$) (Fig. 5). Fine root mortality was also less in browsed plots, but the difference was not statistically significant ($-25\%, P = 0.33$). The ratio of production to mortality averaged $2.37 \pm 0.31$ for unbrowsed sites and $1.68 \pm 0.16$ for browsed sites. This indicates that production and mortality were not at equilibrium, and suggest that browsing decreased fine root longevity. Hence, the direction of the treatment response was consistent with more rapid turnover of soil carbon, as indicated by the respiration potentials of litter. Thus, browsing appears to accelerate the turnover of both recent (leaf and root litter) and older (soil) organic matter pools.

**Discussion**

Species-specific differences in short-term respiration of litter is a function of the biochemical makeup of the different litter types. The high respiration potentials of feltleaf willow is a function of both high nitrogen concentrations and low lignin content. By contrast, the low respiration potentials of alder litter is likely a function of very high lignin content (20–30%), up to 5-fold higher than feltleaf willow (Van Cleve et al. pers. comm.).

The faster rate of decomposition of leaf litter from browsed plants is partially explained by higher concentrations of total nonstructural carbohydrates (Chapin 1980), the greater overall pool of mineralizable carbon, higher litter nitrogen concentrations, and lower C/N ratio of the decomposing litter (Table 2).

In addition to browsing-induced changes in litter chemistry, there has been changes in the physical environment as well as a consequence of moose foraging (Kieland and Bryant unpubl.) that appears to improve the conditions for decomposition. Evidence for this hypothesis is found in the faster rate of cellulose decomposition (a neutral substrate) outside the enclosures (Fig. 6). Thus, decomposition of leaf litter in the field is

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**Table 2. Chemical characteristics of feltleaf willow litter from unbrowsed and browsed plants. Mean (S.E.). Different letters indicate significant differences ($P < 0.05$).**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unbrowsed</th>
<th>Browsed</th>
</tr>
</thead>
<tbody>
<tr>
<td>C&lt;sub&gt;0&lt;/sub&gt; (mg g&lt;sup&gt;-1&lt;/sup&gt; litter)</td>
<td>281 (8.5)a</td>
<td>395 (14.5)b</td>
</tr>
<tr>
<td>% total C</td>
<td>60.9 (1.9)a</td>
<td>86.8 (3.2)b</td>
</tr>
<tr>
<td>% C</td>
<td>46.1 (0.1)a</td>
<td>45.5 (0.2)a</td>
</tr>
<tr>
<td>% N</td>
<td>1.0 (0.1)a</td>
<td>1.3 (0.0)b</td>
</tr>
<tr>
<td>C/N</td>
<td>43.5 (0.1)a</td>
<td>34.2 (0.1)b</td>
</tr>
</tbody>
</table>

<sup>1</sup> Potentially mineralizable carbon.
enhanced by browsing through an apparent combination of biochemical and physical factors. The somewhat faster mass loss rate of cellulose compared to leaf litter is similar to that found in other studies (Fox and Van Cleve 1983).

Moose urine and fecal input to the soil represent about 30% of the total nitrogen input in the willow stage of succession (Kielland and Bryant unpub.). However, nitrogen amendments to soil tend not to enhance soil respiration. Indeed, in general the opposite appears to be true (Söderström et al. 1983).

The higher soil respiration potentials outside the exclosures is not due to greater soil organic matter content, since browsing has significantly reduced both the total soil carbon pool (Kielland and Bryant unpub.), in part due to lower root biomass (Rosow et al. 1997) and fine root production (Fig. 5). The much higher (2.7-fold) respiration potential per gram soil organic matter of soil from outside the exclosures strongly suggests higher soil organic matter quality. One source of this higher-quality carbon is probably litter carbon as indicated by the estimates of mineralizable litter carbon.

Another important source of readily decomposable carbon is dead fine roots. Although both fine root production and mortality were lower in browsed sites, fine root longevity also appears to be lower, suggesting that the turnover of fine roots is accelerated by above-ground herbivory. It is also possible that the actual decomposition of dead fine roots may be faster in browsed plots. Such an effect could be due to higher carbon quality of fine roots, as found for leaves, as a consequence of being younger or due to some other chemical characteristic unrelated to age.

In summary, the effects of moose browsing on carbon cycling in taiga ecosystems is a two-stage process. In the short-term (<50 yr), herbivory speeds up soil organic matter turnover, and facilitates vegetation change (from the willow to the alder stage) that is accompanied by order-of-magnitude increases in productivity and soil nitrogen stocks. In the long-term (50–100+ yr), herbivory contributes to the ultimate dominance of conifers, which is associated with increased forest floor thickness, slower carbon turnover, and conservation of the soil nutrient capital. Thus, mammalian herbivores such as moose, play a significant role in modifying ecosystem-level processes that govern major functions in these taiga ecosystems.

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References

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