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MOOSE BROWSING AND SOIL FERTILITY IN THE BOREAL FORESTS OF ISLE ROYALE NATIONAL PARK[1]

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Abstract. Selective foraging by moose on hardwoods and avoidance of conifers alters community composition and structure, which in turn can affect nutrient cycles and productivity. The effect of moose browsing on the nutrient cycles of boreal forests was studied using three 40-yr-old exclosures on Isle Royale, Michigan. Two alternative mechanisms by which moose affect ecosystems were tested: (1) moose depress both the quantity and quality of litter return to the soil, and hence N mineralization and net primary productivity, by browsing on hardwoods and avoiding conifers; (2) moose stimulate N mineralization, and hence net primary productivity, by opening the canopy and by dropping fecal pellets. Soil nutrient availability and microbial activity, including exchangeable cations, total carbon and nitrogen, nitrogen mineralization rates, and microbial respiration rates, were uniformly higher in exclosures than outside. These differences were more significant where browsing intensity was high and less often significant where browsing intensity was low. N mineralization in browsed plots declined with increasing moose consumption rates. Net primary production in exclosures and browsed plots was strongly correlated with N mineralization. N mineralization in turn was positively correlated with litter N return and negatively correlated with litter cellulose content. These differences in litter quantity and quality were caused by an increased abundance of unbrowsed spruce outside the exclosures. Moose pellets alone mineralized less N but more C than soil alone, but pellets combined with soil stimulated N and C mineralization more than the sum of the two separately. However, this did not appear to be sufficient to offset the depression in nitrogen and carbon mineralization in soil resulting from the increased abundance of unbrowsed spruce. We conclude that, in the long term, high rates of moose browsing depress N mineralization and net primary production through the indirect effects on recruitment into the tree stratum, and subsequent depression of litter N return and litter quality. These results suggest that the effects of herbivores on ecosystems may be amplified by positive feedbacks between plant litter and soil nutrient availability.

Key words: Alces; *boreal forests; exclosures; food webs; herbivory; Isle Royale, Michigan; moose; nitrogen cycling; nitrogen mineralization.*

INTRODUCTION

The effects of herbivores on boreal forests are potentially large and long lasting (Krefting 1974, Snyder and Janke 1976, Wolff and Zasada 1979, Bryant and Chapin 1986, Bryant 1987, Naiman et al. 1988, Pastor et al. 1988, McInnes et al. 1992). How herbivores affect nutrient cycles in these forests is particularly important because nutrient availability is generally low (Flanagan and Van Cleve 1983, Pastor et al. 1987*a*, Bonan and Shugart 1989), and changes in nutrient availability are major factors driving succession (Van Cleve and Viereck 1981). Furthermore, populations of boreal herbivores fluctuate drastically between years and decades (Haukioja et al. 1983 and references therein), and these fluctuations may in turn be related to changes in nutrient cycles and inherent lag times imposed by herbivory (Schultz 1964, Bryant and Chapin 1986).

There are several important links between foraging behavior of boreal mammals, the responses of boreal plants to browsing, and the way these plants cycle nutrients. Coley et al. (1985) hypothesize that the slow growth and low nutrient uptake by plants adapted to soils of low N availability, particularly conifers, requires continuous production of secondary defensive compounds to protect their tissues; in contrast, plants adapted to high nutrient availability, particularly early successional hardwoods, do not invest highly in secondary compounds but rather have high nutrient up-

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take, which allows them to grow fast, escape mammalian browsing, and compensate for removal of browsed material. In addition, both ruminant feeding rates and litter decomposition are depressed by secondary metabolites such as phenolics and terpenes as well as by structural cellulose and lignin (Bryant and Kuropat 1980, Horner et al. 1988). This happens because both decomposition and ruminant digestion are microbial processes. Furthermore, the palatabilities of different boreal plant species are indirectly correlated with their abilities to tolerate nutrient stress but directly correlated with their growth rates, litter production, and litter decomposition (Bryant and Chapin 1986).

Bryant and Chapin (1986), Pastor et al. (1987*b*, 1988), and Pastor and Naiman (1992) propose that these community- and ecosystem-level processes result from feedbacks between chemical and morphological traits of boreal tree species, browsing preferences of moose, and the effects of litter chemistry on decomposition and nutrient availability. In particular, selective browsing by moose could reduce nutrient availability by shifting plant community composition towards evergreens with slow growth rates, high leaf-retention rates and hence low litterfall, and slowly decomposing litter with high concentrations of lignin and secondary metabolites (Bryant and Chapin 1986, Pastor et al. 1988, Pastor and Naiman 1992).

Moose (*Alces alces*) are the largest member of the deer family and the largest herbivore in boreal forests (Peterson 1955). An adult moose consumes 3000–5000 kg of dry matter per year, mainly the growing shoots of aspen (*Populus tremuloides*), willow (*Salix* spp.), birch (*Betula papyrifera, B. pendula, B. pubescens*), and hazel (*Corylus cornuta, C. americana*). Moose do not eat spruce (*Picea glauca, P. mariana*), but occasionally eat balsam fir (*Abies balsamea*). Over time, this selective foraging increases the dominance of spruce (Krefting 1974, Snyder and Janke 1976, Risenhoover and Maass 1987, McInnes et al. 1992). Spruce in turn depresses N mineralization because of low N return in poor-quality litter.

Alternatively, excretion of fecal pellets and urine may increase nutrient availability, at least locally, but this has been tested only in grazing systems and has not been studied with moose pellets (McKendrick et al. 1980, Schimel et al. 1986, Ruess and McNaughton 1987, Ruess et al. 1989, Day and Detling 1990). An opening of the canopy observed in areas of intense moose browsing (Risenhoover and Maass 1987, McInnes et al. 1992) might also stimulate nutrient availability through soil warming.

These alternative hypotheses yield several predictions testable with exclosure experiments:

1) If moose depress nutrient availability indirectly through changes in community composition related to tissue chemistry (Bryant and Chapin 1986, Pastor et al. 1988), then nutrient return in litter and nutrient availability should be higher inside exclosures than outside, and nutrient availability should correlate directly with nutrient quantity and quality in litter and inversely with consumption rates;

2) If moose increase nutrient availability through opening of the canopy or through manuring, then nutrient availability should be greater outside exclosures than inside;

   a) if microclimatic changes caused by opening the canopy are the major mechanism increasing nutrient availability, then differences between exclosures and controls should be observed only in the field and not in the laboratory under controlled temperatures and moistures;

   b) if manuring is the major mechanism increasing nutrient availability, then nutrient availabilities should be enhanced not only in the field but under controlled conditions where addition of pellets to soil should stimulate N mineralization above that expected by decay of pellets and soil alone.

Accordingly, the objective of this study was to determine the ways by which moose affect nutrient cycling and productivity. We measured soil nutrient availability and litter quantity and quality inside and outside moose exclosures on Isle Royale, Michigan, and experimentally tested the fertilizing effect of moose pellets on soil nitrogen and carbon dynamics.

STUDY SITES

Isle Royale is located in the western arm of Lake Superior (48° N, 89° W) and is ≈544 km^2 (Fig. 1). The forests of Isle Royale are predominantly boreal and composed of aspen, birch, spruce, and fir except for northern hardwoods on glacial till in the southwestern sector (Linn 1957). The history of moose and wolf populations has been reviewed by Mech (1966) and Peterson (1977). Moose colonized the island around the turn of the century and by the 1930s they numbered some 3000 individuals. Because of severe overbrowsing, their population declined drastically and by the late 1930s numbered some 500 individuals. Several large forest fires between 1936 and 1938 regenerated sufficient browse of aspen and paper birch to allow recovery of the moose population. Wolves (*Canis lupus*) arrived on Isle Royale in the late 1940s, and early research appeared to show that predation, rather than food supply, limits the size of the moose population (Mech 1966). Recent research indicates that wolves and vegetation play somewhat different roles in controlling the moose population. Predation may determine the rate of population increase but browse supply in turn affects susceptibility to predation, limits moose biomass, and introduces a time lag in the recovery of the moose population from predation (Peterson 1977, Peterson et al. 1984). The current moose population is ≈1500 individuals, or 2.8 animals/km^2 (Peterson 1987).

To study the effects of the moose population on forest dynamics, L. Krefting and coworkers built four ex-

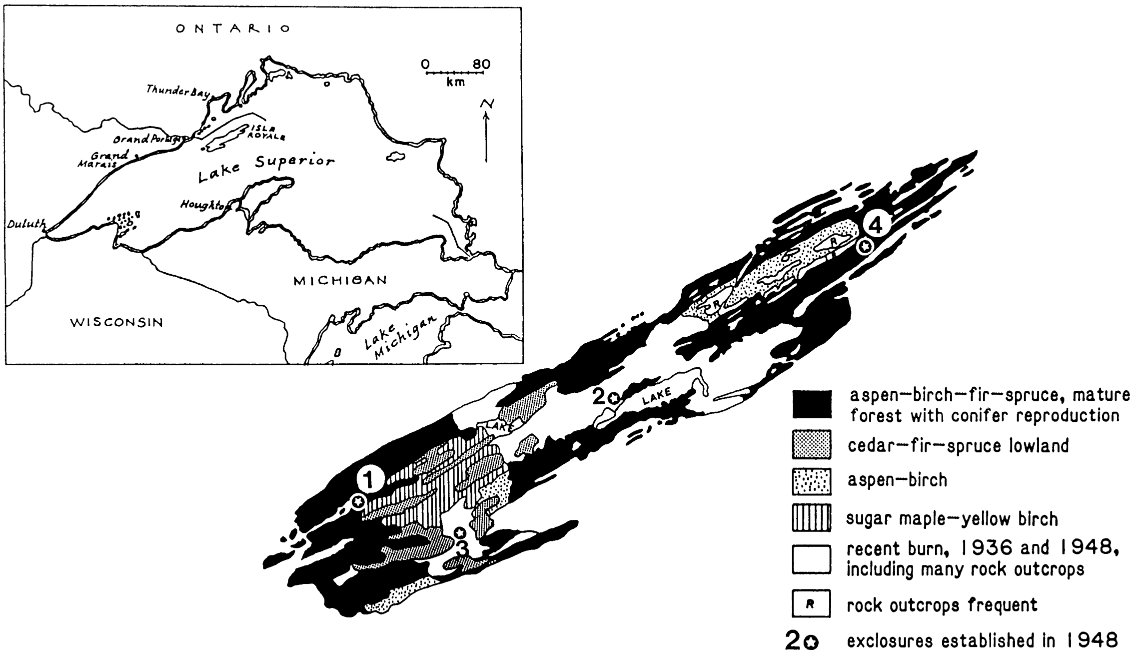

FIG. 1. Vegetation map of Isle Royale, Michigan, from Krefting (1974) and Peterson (1975), showing locations of exclosures: (1) Windigo; (2) Siskiwit Lake (not used in this study, but see McInnes et al. 1992); (3) Siskiwit Camp; (4) Daisy Farm.

closures between 1948 and 1950 in various communities on Isle Royale (Krefting 1974). The exclosures are 15 × 15 m square and made of 3 m high wire fencing between cedar posts. They exclude only moose, not snowshoe hare (*Lepus americanum*), the other herbivore of importance at these sites. Control plots were established adjacent to each exclosure at the time of construction; the vegetation in these control plots was initially similar to that of the exclosure (Krefting 1974). Further discussion of initial vegetation composition and present composition and productivity can be found in Risenhoover and Maass (1987) and McInnes et al. (1992).

Three of the exclosures are in upland forests: (1) Windigo—aspen–birch–spruce on sandy outwash in the southwest; (2) Siskiwit Camp—birch–spruce originating after fire in 1936 on raised gravel beach ridge in the south-central portion of the island; and (3) Daisy Farm—birch–spruce–fir on compacted ground moraine over granite in the northeast sector. A fourth exclosure near Siskiwit Lake is in a stand originating after a fire in 1938 and is in a wetland; its soil properties were not investigated as part of this study. Current moose densities are 4.6 animals/km^2 (Windigo), 3.4 animals/km^2 (Daisy Farm), and 1.5 animals/km^2 (Siskiwit Camp), although moose densities at Siskiwit Camp were higher 20–30 yr ago. Further descriptions of the vegetation are in Krefting (1974), Risenhoover and Maass (1987) and McInnes et al. (1992). The salient findings of these studies are that intensive moose browsing has reduced the abundance of hardwoods and balsam fir, net primary production, and litterfall, but that the community has partially compensated by an increase in herb and, in some cases, shrub production.

A separate experiment on the decomposition of moose pellets was performed with material from Raspberry Island, a small island ≈200 m from the main island of Isle Royale. Quaking aspen and paper birch form the overstory and balsam fir the understory of the forests of Raspberry Island, with the main browse species being aspen and birch sprouts in gaps, dogwood (*Cornus racemosa*), and yew (*Taxus canadensis*) (Snyder and Janke 1976, McInnes 1989). Raspberry Island has no resident moose population, being visited for a few weeks in spring by one or two cows seeking protection from wolves to give birth to calves. Thus, unlike the soil on the main island, the soil of Raspberry Island has been little affected by either fecal material or long-term, intensive browsing (Pastor et al. 1988). It is therefore a logical site to investigate the initial stages of how fecal material interacts with humus.

METHODS

Sampling and analysis

Soil.—Sampling was confined to the A1 or O2 horizons, where most of the soil organic matter and nitrogen is mineralized and is therefore the most likely horizon to be affected. Ten samples of these horizons in each exclosure and control plot were collected in June 1987 with a brass core 5 cm in diameter. The air-dried samples were weighed and moisture corrections were made by drying subsamples at 100°C overnight. Bulk densities were determined by dividing the moisture-corrected mass by volume. Exchangeable cations, namely Na, K, Ca, and Mg, were extracted with pH 7 ammonium acetate and analyzed with a Perkin-Elmer atomic absorption spectrophotometer. The results were expressed in moles per unit soil mass and summed to estimate cation exchange capacity.

Field N mineralization was measured with buried polyethylene bags (Eno 1960, Gordon and Van Cleve 1983). For each incubation period, ammonium and nitrate were extracted with 1 mol/L KCl from 10 samples in each exclosure and control. Paired samples were buried in 50 μm thick polyethylene bags, incubated monthly from June through September and over the winter from October through May, recollected, and extracted as above. Field mineralization was calculated as the final sum of mineral nitrogen as ammonium and nitrate minus the amounts initially present. All samples were recovered, enabling statistical analyses without missing data.

Potential C and N mineralization was measured on 10 samples, each collected from exclosures and controls in June, August, and October. Soil samples mixed 1:1 with sand were incubated in the laboratory at 30°C with tensions drawn down to field moisture content after leaching, using the method of Stanford and Smith (1972) and the closed incubation chambers of Nadelhoffer (1990). Mineralized ammonium and nitrate were leached from the chambers after 0, 2, 4, 8, 16, 24, and 30 wk with 0.01 mol/L $CaCl_2$ followed by addition of nutrient solution minus nitrogen; the leachate was analyzed using a Lachat autoanalyzer. The initial, time 0 leaching was discarded as it contains standing amounts of ammonium and nitrate that had been mineralized in the field. Microbial respiration was measured during intervening weeks until week 26 by flushing the chamber with CO_2-free air scrubbed through a potassium hydroxide solution, closing the chamber, and sampling the chamber headspace with a syringe through a septum after 6 h. The gas sample was analyzed on a Tracor gas chromatograph with a thermal conductivity detector. The rate of CO_2 evolution was estimated by multiplying its concentration by the headspace volume and divided by the amount of time each chamber was closed. Integration of these measurements over the entire 26-wk period yielded cumulative carbon mineralization. Both nitrogen and carbon mineralization were expressed on a per-gram soil or pellet as a percentage of total nitrogen or carbon in the incubated samples.

Total C and N were measured on a dried subsample of each lab-incubated sample using a LECO CHN 800 analyzer.

Moose pellets.—Pellets were collected in June and in August 1987 from a large, fresh pile deposited in spring 1987 on Raspberry Island (snowmelt, soil thaw, and ice-out are usually in May, so at first collection in June these pellets were at most only a few weeks old). Three samples of five pellets (≈10 g) apiece were sampled in June and in August. Although it is not possible to generalize about all moose from this one sample, it does constitute a rejection of the null hypothesis (moose manuring never increases soil N availability) if nutrient availability in soil is enhanced in the presence of the pellets. Accordingly, three samples of O2 horizon soil ≈5 m away from the fecal pellets were also collected simultaneously. Total C and N contents were measured as above. Pellets and soil were incubated in the laboratory both separately and combined by the methods described above. Pellets were combined with soil by placing intact pellets atop soil in the chamber; the pellets were not ground and the two materials were not mixed. In each replicate, ≈5 g of soil and/or 2 g of pellets were used.

Litter.—Six 0.25-m^2 litter traps with 2-mm wire mesh bottoms were randomly installed in each exclosure and control. These were sampled once or twice a month from July 1987 to July 1988, except in winter. The samples were dried at 60°C and sorted by species. Overwinter mass loss by leaching was estimated with litterbags of samples in Duluth, Minnesota; values ranged from 10 through 30% depending on species (McInnes et al. 1992). The first collection in spring of 1988 was then corrected for overwinter leaching by the appropriate amount, since without this correction litter mass during late fall and early winter would have been underestimated.

Litter samples were composited by site, treatment, and species. Dried samples were ground to uniform powder to pass through an ≈250-μm mesh screen. Subsamples were ashed at 450°C for 4 h. Total C and N was measured using a LECO CHN 800 analyzer. Each sample was analyzed for carbon fractions by sequential extraction (McClaugherty et al. 1985): first for nonpolar compounds (waxes, fats, and oils) by repeated filtration through Gooch crucibles with dichloromethane following sonication; next for polar compounds (sugars, starches, and tannins) by hot-water extraction with the extract analyzed for tannins by Folin-Denis reaction; finally, in concentrated sulfuric acid digest followed by autoclaving in 1 mol/L of sulfuric acid to remove cellulose and hemicellulose. The residue after these extractions was assumed to be lignin + ash. The mass of all fractions was then expressed on an ash-free basis.

Hypothesis testing

We report means and standard deviations of analyses. We report standard deviations rather than standard errors because on many of the graphs standard errors are smaller than the size of the symbols, visually implying no variance. The reader can calculate standard errors by dividing the standard deviation by the square root of the number of samples indicated.

The results were analyzed with treatments (moose–no moose) nested within stand type to statistically separate the main effect of treatment from stand type. This design cannot detect which stand properties are re-

TABLE 1. Concentration of exchangeable cations in soil at three sites on Isle Royale, Michigan. E = Exclosure; C = Control. Data are means ± 1 SD; $n = 10$.

	Na (cmol/kg)	K (cmol/kg)	Mg (cmol/kg)	Ca (cmol/kg)	CEC† (cmol/kg)
Windigo					
E	0.032 ± 0.012*	1.003 ± 0.824*	1.284 ± 0.269*	6.361 ± 1.825	8.680 ± 2.164**
C	0.021 ± 0.005	0.270 ± 0.265	0.817 ± 0.233	4.402 ± 1.896	5.511 ± 2.304
Siskiwit Camp					
E	0.022 ± 0.008	0.505 ± 0.152	2.039 ± 0.321	10.177 ± 2.628	12.744 ± 2.784
C	0.020 ± 0.004	0.480 ± 0.169	1.966 ± 0.490	10.886 ± 3.661	13.352 ± 4.249
Daisy Farm					
E	0.078 ± 0.013**	0.194 ± 0.038	4.243 ± 0.676*	14.686 ± 2.284	19.201 ± 2.986
C	0.040 ± 0.014	0.186 ± 0.035	3.867 ± 0.439	13.726 ± 1.791	17.819 ± 2.196

* $P < .05$, ** $P < .01$ (Asterisks show where excluding moose caused significant increases in concentrations.)

† CEC = cation exchange capacity, expressed as the sum of the four cations shown.

sponsible for significant differences between stands, but it does remove the effect of site differences from treatment effects. Elsewhere we have shown that the tree, shrub, and herb biomass in the browsed control plots is statistically similar to that of the surrounding area; moreover, exclosure tree biomass is significantly greater and herb biomass is significantly less than that of the surrounding area (McInnes 1989). We therefore conclude that the controls are representative of the surrounding forest and the vegetation in the exclosures departs significantly from that of the surrounding forest. Nevertheless, caution should be used when extrapolating these results to dissimilar sites.

We tested main effects of stand and treatment (moose–no moose) nested within stand on exchangeable cations and litterfall using single-degree-of-freedom nested ANOVA in SYSTAT (Wilkinson 1989). Normally, time is also included as a main effect in many ecological studies that sample several times during a year. However, in our case, differences in N and C mineralization in any one month are not independent of the previous month because the time course of mineralization is partly a consequence of the continuous changes in organic matter quality during the season. Therefore, we tested the main effect of stand and treatment on C and N dynamics using ANOVA with repeated measures nested as above. This method has the advantage of testing for consistency of effect of treatment across the growing season, even though the effect may not be significant at particular times. The method has the disadvantage of not detecting when differences between treatments are significant. However, testing the consistency, rather than the seasonality, of an effect is our main objective.

Single exponential models of carbon and nitrogen mineralization of the form

$$X_t = X_0(1 - e^{-kt}) \qquad (1)$$

were fit to data from each incubation, where X_t is the cumulative mineralization of carbon or nitrogen up to time t, X_0 is the pool of potentially mineralizable carbon or nitrogen in the sample, and k is the instantaneous release rate of that pool. Data were fit to the model by non-linear regression as recommended by Talpaz et al. (1981) using the quasi-Newton method of approximation in SYSTAT (Wilkinson 1989). Convergence was tested using starting points above and below the final value; the final values were accepted after convergence from several starting points was demonstrated.

Carbon and nitrogen quality were assessed by comparing potentially mineralizable carbon and nitrogen

TABLE 2. Concentrations of total nitrogen and carbon in soils at three sites on Isle Royale, Michigan. Data are means ± 1 SD; $n = 10$. Excluding moose caused significant changes in total C and N only at Windigo during the October sampling ($P < .05$).

	Windigo		Siskiwit Camp		Daisy Farm	
	Exclosure	Control	Exclosure	Control	Exclosure	Control
Nitrogen (% of dry mass)						
Jun	0.93 ± 0.29	0.71 ± 0.14	1.01 ± 0.22	0.91 ± 0.33	2.20 ± 0.47	2.12 ± 0.59
Aug	0.37 ± 0.086	0.40 ± 0.10	0.47 ± 0.19	0.41 ± 0.17	0.46 ± 0.14	0.43 ± 0.14
Oct	0.44 ± 0.18	0.25 ± 0.09*	0.46 ± 0.17	0.31 ± 0.14	0.42 ± 0.26	0.38 ± 0.17
Carbon (% of dry mass)						
Jun	9.0 ± 4.1	5.2 ± 1.3	8.5 ± 2.7	8.2 ± 5.5	34.9 ± 11.9	30.4 ± 11.7
Aug	7.0 ± 1.2	5.9 ± 1.5	8.5 ± 4.4	7.3 ± 4.0	9.5 ± 2.9	9.2 ± 2.8
Oct	12.0 ± 6.1	7.0 ± 3.1*	9.2 ± 2.4	7.6 ± 4.0	10.9 ± 5.7	10.1 ± 4.5

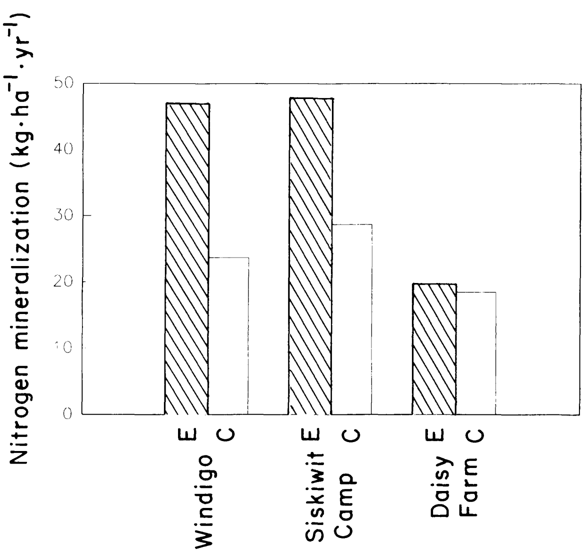

FIG. 2. Annual N mineralization in exclosures (hatched) and controls (white). Values are means of 10 buried-bag incubations summed over each month during the growing season and throughout the winter. Sites are arranged in order of highest (Windigo) to lowest browsing intensity.

pools both per unit of soil mass and per unit of total carbon or nitrogen mass, and the decay constants from the regressions.

These models were also used to test the manuring effect of fecal pellets on nutrient availability in soil. If fecal pellets do not stimulate soil nutrient dynamics, then the combined mineralization of carbon or nitrogen from both should be equal to that predicted by the sum of their exponential decay models (Eq. 1). Predictions of the additive model were compared to data from the combined pellet–soil incubations to determine if pellets stimulate C and N mineralization from soil.

RESULTS

Exchangeable cations

Excluding moose significantly increased concentrations of exchangeable soil Na, K, and Mg, and cation exchange capacity at Windigo, the most heavily browsed site ($P < .03$, .00, .02, and .02, respectively), and only slightly increased the concentration of Ca at Windigo ($P < .08$). At Daisy Farm only the concentrations of Na and Mg were increased. Moose browsing did not affect the concentrations of other nutrients at any other site (Table 1). The concentrations of each exchangeable cation as well as cation exchange capacity also differed significantly among stands ($P < .001$ for each).

Total carbon and nitrogen

Excluding moose increased the concentrations of total nitrogen by ≈14% and carbon by ≈20% above control levels across all stands, but the differences were significant only in October at Windigo ($P < .02$ for each). Carbon and nitrogen varied significantly between stands only in June ($P < .001$, Table 2). Essentially, whatever differences there are between stands or treatments in carbon and nitrogen pools are temporary.

Carbon and nitrogen mineralization

Field.—Excluding moose significantly increased field nitrogen mineralization at Windigo and Siskiwit Camp ($P < .001$), the most heavily browsed sites, but not at Daisy Farm, the least heavily browsed site (Fig. 2). Annual nitrogen mineralization was twice as high in the Windigo exclosure compared with its paired control, nearly twice as high at Siskiwit Camp, but not significantly greater at Daisy Farm (Fig. 2). Stand history and type also affected N mineralization nearly as much as excluding moose ($P < .001$).

These differences are not attributable to different total pool sizes of nitrogen because these were not consistently different nor did they vary by two-fold across treatments and stands. Soil moisture content inside the enclosure was not significantly different from that outside. Furthermore, the differences are not attributable to either warming or manuring, since these factors would increase mineralization outside the exclosures rather than depress it relative to controls. Therefore, the differences are attributable solely to changes in substrate quality upon excluding moose (hypothesis 1), which we further tested by data on potential mineralization under optimal laboratory conditions.

Laboratory potentials.—The cumulative amount of nitrogen and carbon mineralized per unit of soil mass after 30 or 26 wk, respectively, under optimal conditions was slightly but consistently greater in exclosure soils than in control soils, across all stands and across all months (Figs. 3 and 4). As in the field, differences between exclosure and control were greatest and significant at Windigo ($P < .05$ for June and August carbon mineralization and June and October nitrogen mineralization and $P < .10$ for the other months). Differences were less but not significant at Siskiwit Bay, and least and not significant at Daisy Farm. Variations in potential N and C mineralization per unit of soil mass are attributable solely to the presence or absence of moose browsing and its intensity; they were never significantly different between stands.

The pools of potentially mineralizable nitrogen and carbon (N_0 and C_0) and their release rates (k_N and k_C) were slightly but consistently greater in exclosure soils than in controls (Table 3). Since non-linear fitting of a model (Eq. 1) to the data is an approximation rather than exact solution, it is not possible to estimate statistical differences between treatments or stand types for these parameters with an associated probability level. However, the consistency of the pattern is in accord with the statistical tests of cumulative amounts of N and C mineralized in the laboratory and differences in N mineralization in the field. Excluding moose con-

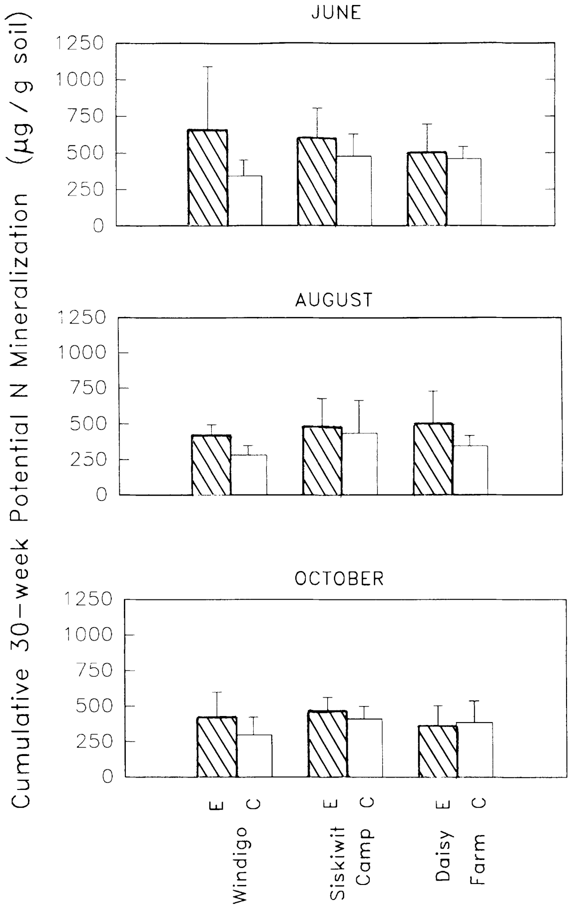

FIG. 3. Cumulative N mineralization under optimal conditions in the laboratory for exclosures (hatched) and controls (white). Values are means and standard deviations of 10 samples.

sistently increased pools of potentially mineralizable N and C, and differences between exclosures and controls were greater than differences between stands for respective treatments. As in field mineralization, excluding moose had the greatest effect at Windigo, a moderate effect at Siskiwit Camp, and the least effect at Daisy Farm.

Convergence to the single exponential decay model implies that there is one pool each of potential mineralizable N and C during the 30-wk incubation. We tested convergence to a double exponential decay model, which implies two pools each with different turnover rates (Deans et al. 1986). However, we found no improvement over the single exponential decay model (in fact, the double exponential decay model collapsed to a single exponential model during the fitting procedure). Occasionally, such as N mineralization from the Daisy Farm samples in June and October, the single exponential decay model could not be fit to the data.

Moose pellets.—The chemical properties of moose pellets differed significantly from those of humus (Table 4). Pellet carbon content was greater than that of humus in both June and August. Pellet C-to-N ratio was greater than that of humus during June, while nitrogen content was greater during August. Pellet nitrogen content was less than those reported for cattle (Schimel et al. 1986) and snow geese (Reuss et al. 1989).

However, differences in mineralization dynamics were even greater and more consistent. The soil mineralized an order of magnitude more nitrogen than did pellets, while pellets mineralized four times as much carbon as did soil (Figs. 5 and 6). The sizes of the potentially mineralizable carbon and nitrogen pools dominated these dynamics. Potentially mineralizable nitrogen in soil was an order of magnitude greater than that in pellets in June, and four times greater in August (Table 4). In contrast, potentially mineralizable carbon in pellets was twice that in soil during both months. The instantaneous release rate of carbon from pellets was greater than that from soil, particularly in June. The instantaneous release rate of nitrogen from pellets was greater than that from soil in June but less than that from soil in August.

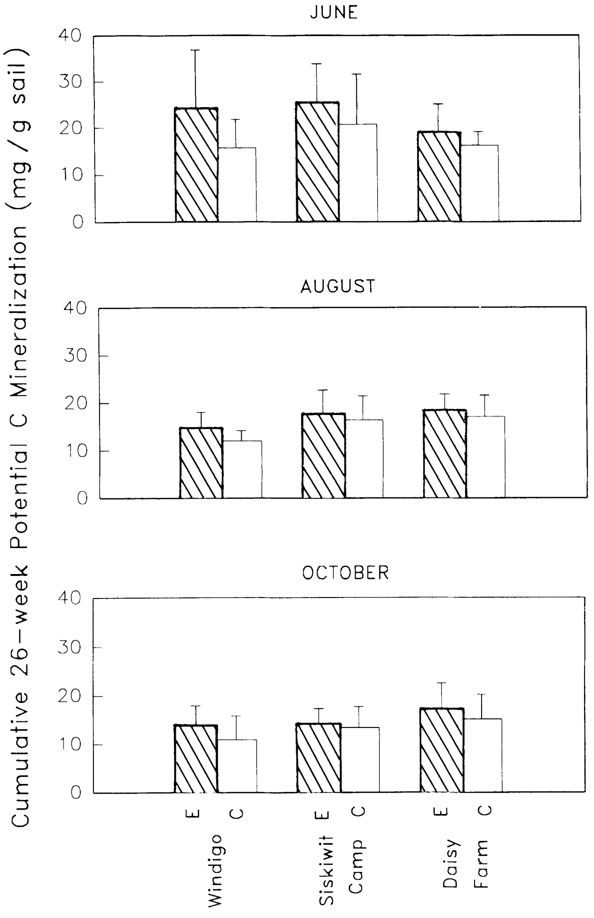

FIG. 4. Cumulative C mineralization (respiration) in the same 10 samples as in Figure 3. Values are means and 1 SD.

TABLE 3. Potential nitrogen and carbon mineralization at three sites on Isle Royale, Michigan. Data are means ± 1 SE from the quasi-Newton solution to the non-linear convergence of laboratory incubation data to Eq. 1. k_N and k_C = instantaneous weekly release rate. nc = no convergence in solution to equation.

	Windigo		Siskiwit Camp		Daisy Farm	
Exclosure	Exclosure	Control	Exclosure	Control	Exclosure	Control
			June			
N_0 (potentially mineralizable nitrogen)						
mg/g soil	982 ± 203	772 ± 330	1640 ± 1040	1340 ± 650	nc	nc
% N	10.6 ± 2.2	10.7 ± 4.3	17.6 ± 11.5	18.2 ± 9.1	nc	nc
k_N	0.038 ± 0.012	0.021 ± 0.011	0.016 ± 0.012	0.015 ± 0.009	nc	nc
C_0 (potentially mineralizable carbon)						
mg/g soil	27.5 ± 2.4	18.2 ± 2.7	29.4 ± 3.9	27.6 ± 5.5	22.2 ± 1.8	20.5 ± 1.8
% C	31.2 ± 3.1	34.3 ± 4.9	35.6 ± 4.8	40.6 ± 9.7	30.4 ± 2.7	30.0 ± 2.7
k_C	0.080 ± 0.013	0.081 ± 0.023	0.080 ± 0.020	0.056 ± 0.019	0.075 ± 0.011	0.061 ± 0.009
N_0/C_0						
mg N/mg C	35.7	42.4	55.8	48.5	...	...
			August			
N_0 (potentially mineralizable nitrogen)						
mg/g soil	404 ± 21	284 ± 16	517 ± 23	457 ± 26	589 ± 53	465 ± 29
% N	11.4 ± 0.60	7.3 ± 0.43	10.9 ± 0.46	11.3 ± 0.67	12.6 ± 1.1	11.3 ± 0.73
k_N	0.121 ± 0.018	0.106 ± 0.016	0.078 ± 0.007	0.080 ± 0.010	0.058 ± 0.009	0.046 ± 0.005
C_0 (potentially mineralizable carbon)						
mg/g soil	15.4 ± .80	12.5 ± .78	19.2 ± 1.3	18.8 ± 1.3	20.1 ± 1.4	18.8 ± 1.4
% C	30.3 ± 1.6	16.0 ± 1.0	32.5 ± 2.5	24.8 ± 1.6	30.3 ± 2.1	27.7 ± 1.9
k_C	0.105 ± 0.013	0.106 ± 0.016	0.088 ± 0.013	0.076 ± 0.010	0.088 ± 0.013	0.090 ± 0.014
N_0/C_0						
mg N/mg C	26.2	22.1	26.3	24.3	29.3	24.1
			October			
N_0 (potentially mineralizable nitrogen)						
mg/g soil	425 ± 41.5	349 ± 61.5	477 ± 56.8	500 ± 61.2	nc	nc
% N	10.3 ± 1.0	13.3 ± 1.6	11.6 ± 1.1	16.9 ± 1.4	nc	nc
k_N	0.094 ± 0.022	0.061 ± 0.020	0.075 ± 0.019	0.055 ± 0.012	nc	nc
C_0 (potentially mineralizable carbon)						
mg/g soil	14.9 ± 1.7	12.0 ± 1.2	14.6 ± 1.8	15.5 ± 2.6	21.1 ± 4.5	16.5 ± 1.7
% C	14.3 ± 1.6	17.6 ± 1.8	16.2 ± 2.1	22.4 ± 3.9	21.3 ± 4.8	17.8 ± 2.0
k_C	0.089 ± 0.023	0.083 ± 0.018	0.094 ± 0.026	0.070 ± 0.023	0.058 ± 0.022	0.085 ± 0.019
N_0/C_0						
mg N/mg C	28.5	29.1	32.7	32.3	...	...

TABLE 4. Properties of soil and moose pellets used in the experiment. Values are means ± 1 SD; $n = 3$.

	June		August	
Property	Soil	Pellets	Soil	Pellets
% C	36.2 ± 3.81	52.0 ± 0.0*	33.5 ± 4.7	52.5 ± 0.0*
% N	2.2 ± 0.2	2.5 ± 0.0	1.50 ± 0.2	2.3 ± 0.0*
C/N	16.8 ± 0.7	20.7 ± 0.0*	22.3 ± 1.6	23.1 ± 0.2
N_0 (potentially mineralizable nitrogen)				
mg/g soil or pellet	9.3 ± 7.4	1.2 ± 0.3*	4.0 ± 0.2	1.8 ± 0.5*
% total N	4.3 ± 2.3	0.48 ± 0.10*	2.7 ± 0.09	0.80 ± 0.3*
k_N	0.025 ± 0.025	0.080 ± 0.45*	0.191 ± 0.29	0.069 ± 0.45*
C_0 (potentially mineralizable carbon)				
mg/g soil or pellet	105 ± 8.1	234 ± 18.7*	80 ± 5.7	205 ± 12.1*
% total C	29.2 ± 1.0	45.0 ± 2.77*	21.8 ± 1.6	39.1 ± 2.6
k_C	0.069 ± 0.008	0.098 ± 0.15*	0.115 ± 0.020	0.141 ± 0.020

* $P < .05$ (Soil and pellets significantly different for these properties.)

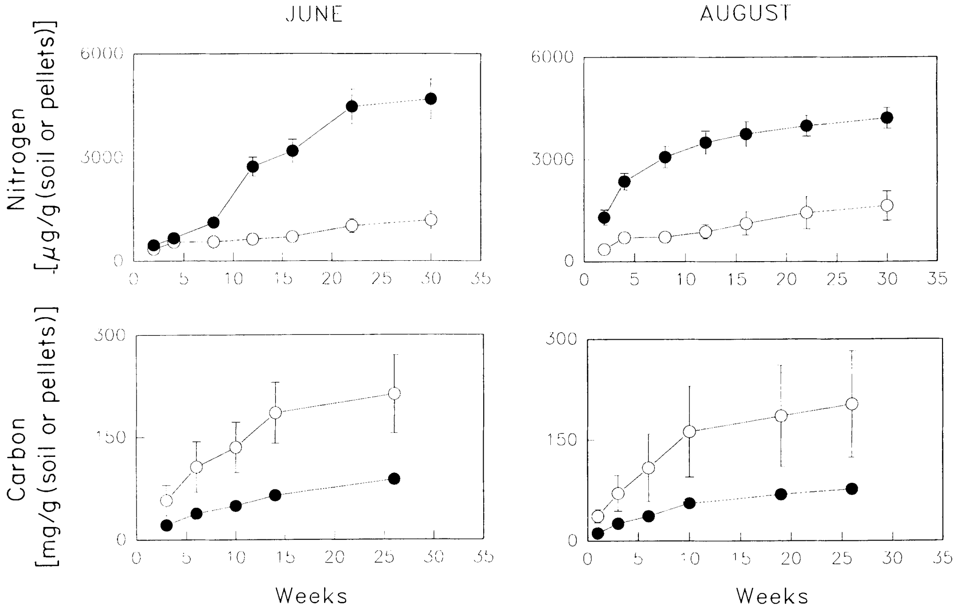

FIG. 5. Cumulative nitrogen and carbon mineralization for moose pellets (○) and soil (●) from Raspberry Island, an island near Isle Royale, Michigan, with no resident moose population. Values are means ± 1 SD of three samples incubated under optimal conditions in the laboratory. Where standard deviations are not shown, they are smaller than symbol size.

The additive model described nitrogen mineralization from the combined soil and pellets in June, implying that pellets and soil mineralized N independently (Fig. 6). Carbon mineralization from combined soil and pellets was slightly underpredicted by the additive model in June. However, in August, there was significantly more nitrogen and carbon mineralized from the combined soil and pellets than predicted by the additive model (Fig. 6), indicating that soil and pellets have a co-fertilizing effect on each other late in the season.

Litterfall and chemistry

Excluding moose significantly increased total litterfall and nutrient return (Table 5). The increased nutrient return in litter was due mainly to greater production inside than outside the exclosures (McInnes et al. 1992), rather than to consistent differences in litter

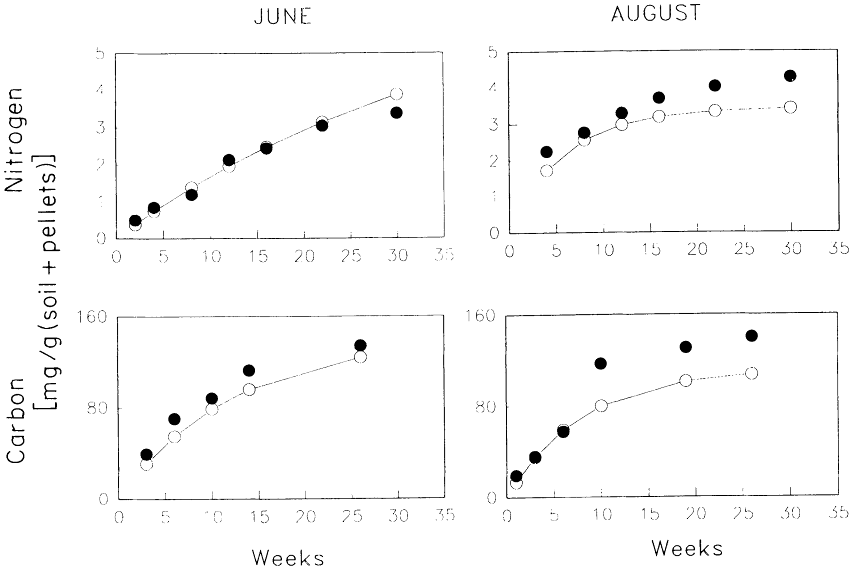

FIG. 6. Comparisons of cumulative nitrogren and carbon mineralization from pellets incubated with soil (●) compared with an additive model of pellet and soil mineralization assuming no co-fertilizing effect (○).

TABLE 5. Total litterfall at Isle Royale, Michigan. E = Exclosure, C = Control; NPE = non-polar extractives (waxes, resins); WS = water-soluble extractives (sugars, starches, non-structural proteins); AS = acid-soluble extractives (cellulose, hemicellulose). All values are in kilograms per hectare.

Site	Treatment	Component	Mass	N	NPE	WS	AS	Lignin	Tannin	Lignin : N
Windigo	E	Leaves	6743.4	59.4	819.7	1905.9	2414.6	1603.3	896.1	27.0
		Total	8545.4	76.4	952.1	2063.8	3157.0	2372.5	954.5	31.1
	C	Leaves	1930.0	15.6	180.6	497.7	787.5	464.2	157.4	29.8
		Total	2232.0	18.0	203.4	539.1	924.3	565.2	165.8	31.4
Siskiwit Camp	E	Leaves	2820.7	32.7	311.0	641.7	1100.9	767.1	183.0	23.5
		Total	3070.7	34.8	330.9	659.3	1196.3	884.2	186.8	25.4
	C	Leaves	2271.3	26.8	336.7	447.1	882.9	604.6	125.0	22.6
		Total	2610.0	29.6	361.7	474.1	1030.3	743.8	130.9	25.1
Daisy Farm	E	Leaves	2669.4	24.4	79.1	702.2	1065.6	882.6	182.9	36.2
		Total	3000.1	26.7	88.1	736.0	1234.3	941.8	189.5	35.3
	C	Leaves	2332.0	24.4	198.7	591.9	943.7	597.8	144.6	24.5
		Total	2896.7	29.3	224.1	651.6	1179.0	842.0	152.1	28.7

chemistry (Table 6). Inconsistent trends in litter chemistry were partly due to stand differences in vegetation. However, at Windigo, excluding moose increased both the quantity and quality of litter, as indicated by higher N concentrations and lower lignin-to-N ratios and cellulose contents. This was because conifer litter comprised a smaller proportion of litterfall inside the exclosure compared with outside. At Siskiwit Camp, excluding moose only increased the quantity of litter, not its quality. At Daisy Farm, excluding moose had no effect on either quantity or quality of litterfall.

DISCUSSION

Annual N mineralization declined significantly with increased moose consumption in the control plots (Fig. 7; see McInnes et al. [1992] for data on moose browsing). N mineralization was positively correlated with net primary production ($r = 0.95$, $P < .01$) and leaf litter N ($r = 0.76$, $P < .05$). N mineralization was not correlated with total litter N return including N in wood, possibly because N is released from decomposing wood only over long periods (Harmon et al. 1986), and changes in leaf litter N would affect N mineralization more rapidly. Nitrogen mineralization declined with increased cellulose concentrations in leaf litter ($r^2 = 0.62$, $P < .05$) and total litter ($r^2 = 0.81$, $P < .01$). Thus, declining amounts of leaf litter N and declining litter quality depressed soil N mineralization in proportion to the intensity of moose browsing. These results are in accord with the predictions of hypothesis 1, namely, that selective foraging by moose depresses N mineralization and productivity through changes in plant community composition and associated changes in litter quantity and quality.

Fecal pellet deposition may compensate somewhat for this depression of N availability. During late summer, combining fecal pellets with soil stimulates N mineralization above levels found for either fecal pellets or soil alone, and urine deposition presumably has the same effect (Schimel et al. 1986). However, this enhancement was small compared with browsing-induced depression of nitrogen in litterfall and nitrogen mineralization in the control plots. Because N mineralization was lower in control (browsed) plots both in the field and in laboratory conditions, manuring appears not to compensate over the long term for the

TABLE 6. Concentrations of nitrogen and carbon compounds in litterfall at Isle Royale, Michigan (percentage of dry mass). E = Exclosure, C = Control; NPE = non-polar extractives (waxes, resins); WS = water-soluble extractives (sugars, starches, non-structural proteins); AS = acid-soluble extractives (cellulose, hemicellulose).

Site	Treatment	Component	% N	% NPE	% WS	% AS	% Lignin	% Tannin
Windigo	E	Leaves	0.88	12.16	28.26	35.81	23.78	13.29
		Total	0.89	11.14	24.15	36.94	27.76	11.17
	C	Leaves	0.81	9.36	25.79	40.80	24.05	8.15
		Total	0.81	9.11	24.15	41.41	25.32	7.43
Siskiwit Camp	E	Leaves	1.16	11.03	22.75	39.03	27.20	6.49
		Total	1.13	10.78	21.47	38.96	28.79	6.08
	C	Leaves	1.18	14.82	19.68	38.87	26.62	5.50
		Total	1.13	13.86	18.17	39.48	28.50	5.02
Daisy Farm	E	Leaves	0.91	2.96	26.31	39.92	30.82	6.85
		Total	0.89	2.94	24.53	41.14	31.39	6.32
	C	Leaves	1.04	8.52	25.38	40.47	25.63	6.20
		Total	1.01	7.74	22.49	40.70	29.07	5.25

decline in litter quantity and quality even though locally and within the first season after deposition it may stimulate N mineralization. Therefore, the depression of productivity, litter N, and litter quality through selective foraging on hardwoods appear to override the potentially stimulatory and probably local effect of manuring on soil N mineralization.

To demonstrate how moose populations could be sustained even though increases in consumption depress N mineralization, consider a simple model composed of the following equations derived from the data presented here or by McInnes et al. (1992) for the same sites ($n = 6$ for all, i.e., two treatments × three sites, except for Eq. 8 where $n = 3$):

Tree production

$$= 5904.1 - 108.96\ (\text{moose consumption}), \tag{2}$$

$$r = -0.964, \quad P < .05;$$

Leaf litter N

$$= -0.326 + .005\ (\text{tree production}), \tag{3}$$

$$r = 0.839, \quad P < .05;$$

Leaf litter cellulose

$$= 44.9 - 0.001\ (\text{tree production}), \tag{4}$$

$$r = -0.893, \quad P < .01;$$

Nitrogen mineralization

$$= 1.7 + 1.01\ (\text{leaf litter N}), \tag{5}$$

$$r = 0.755, \quad P < .05;$$

Nitrogen mineralization

$$= 253.1 - 5.68\ (\text{leaf litter cellulose}), \tag{6}$$

$$r = -0.786, \quad P < .05;$$

Net primary production

$$= 5662.4 + 108.9\ (\text{nitrogen mineralization}), \tag{7}$$

$$r = 0.946, \quad P < .01; \quad \text{and}$$

Moose consumption

$$= 87.6 - 0.010\ (\text{net primary production}), \tag{8}$$

$$r = -0.996, \quad P < .01;$$

where all units except cellulose concentrations (which are percentage of dry mass) are in kilograms per hectare. These equations form a feedback loop from moose consumption through vegetation and litterfall and their effect on soil N availability, followed by the limitation of N availability on net primary production and its inverse relationship to moose consumption. They are solved graphically in Fig. 8. Assume as a starting point zero moose consumption (Fig. 8a). Assume an increase in the moose population such that moose consumption increases to 10 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. For our purposes, it doesn't matter if this increased consumption arises because of an expanding moose population or immigration into the area of browse production: both have the same net result. As moose consumption increases, tree production declines (Fig. 8a) because moose prevent the ingrowth of browsed seedlings and saplings to the tree stratum (McInnes et al. 1992) thereby enhancing the ingrowth of unbrowsed spruce (Krefting 1974, McInnes et al. 1992). This decline in tree production corresponding to a shift to spruce dominance decreases the chemical quality of leaf material (i.e., cellulose content increases; Fig. 8b). Tissue chemical quality is doubly important because it determines both foraging behavior (Bryant and Kuropat 1980) and decomposition rates (Flanagan and Van Cleve 1983). The decline in litter quality subsequently causes a decline in N mineralization (Fig. 8c); this in turn depresses total net primary productivity (Fig. 8d). Consumption in turn increases (Fig. 8e) because, while there is an overall decline in productivity, the productivity of the shrub layer and hence browse supply increases because of the opening of the canopy (Risenhoover and Maass 1987, McInnes et al. 1992). Tree production in turn decreases as the increased consumption prevents the entry of still more seedlings and saplings into the tree layer except for spruce. This positive and degenerative feedback can continue until all of net primary production is concentrated in unbrowsed spruce and moose consumption exceeds browse production. At this point, the moose population collapses because of food limitations.

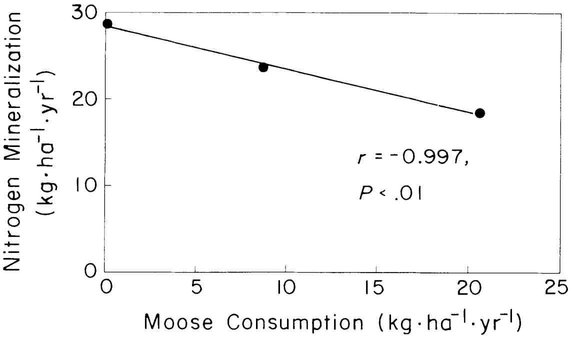

FIG. 7. An inverse relation between annual N mineralization and moose consumption (data from McInnes et al. [1992]).

Spruce has several properties that depress rates of nitrogen cycling. First, the growth rates and nitrogen uptake rates of spruce are inherently slower than those of associated hardwoods (Coley et al. 1985, Bryant and Chapin 1986). The browsing-induced shift towards spruce therefore weakens the plant sink for nitrogen, thereby increasing the potential for leaching below the rooting zone if mineralization is greater than uptake. Second, needle retention time is >3 yr and often as much as 7 yr (Fowells 1965). Thus, whatever nitrogen is taken up is retained in the plants for a longer time than in deciduous plants, resulting in lower litterfall

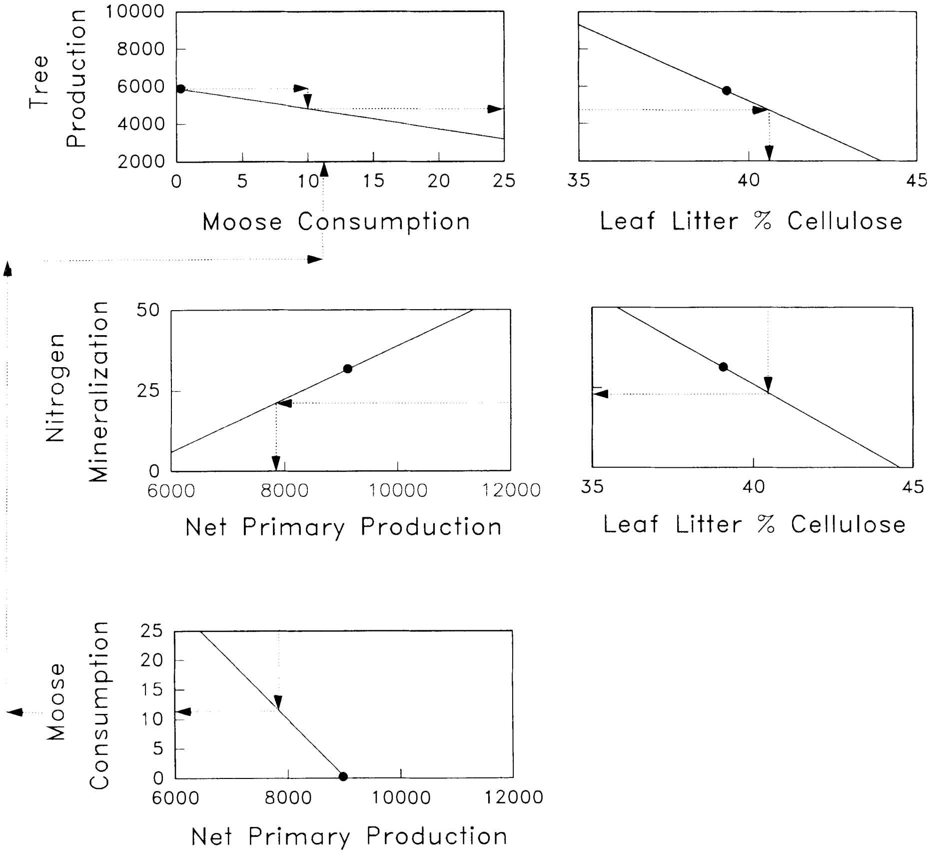

FIG. 8. Graphical solution of the model of interactions between moose and vegetation on Isle Royale (Michigan) that is presented in the text (Eqs. 3 through 9 except for Eq. 6, which is not shown for simplicity). Starting with the upper left part, follow the arrows sequentially to determine the net changes in ecosystem properties from starting values (●) assuming an increase in moose consumption from 0 to 10 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$.

rates and a slower replenishment of the soil nitrogen pools. Third, spruce litter is of lower quality than hardwood litter, and whatever nitrogen is returned in litter is released at slower rates than from deciduous leaf litter (Flanagan and Van Cleve 1983, Melillo et al. 1984, Moore 1984). Both the quantity of nitrogen in litterfall and its carbon quality were equally valid descriptors of the depression of N availability. Where both were depressed at Windigo, differences in nitrogen mineralization were greatest. Where only the quantity of litter N was depressed by moose browsing at Siskiwit Camp, differences in N mineralization were less, but still significant. At Daisy Farm, moose browsing depressed neither litter nitrogen nor litter quality, and differences between exclosure and control nitrogen mineralization rates were negligible.

If nitrogen mineralization is sufficiently depressed through these feedbacks, the subsequent recovery of the ecosystem may be severely limited. Selective browsing thus introduces hysteretic behavior into the system to the extent that it alters processes that have slower time dynamics, such as tree recruitment and soil organic matter turnover.

This net depression of N availability through the indirect effects of moose browsing on vegetation and litterfall corroborates a more detailed simulation model that considers the population dynamics of browsed and unbrowsed species (Pastor and Naiman 1992). This degenerative positive feedback can be altered by factors inhibiting spruce dominance, such as fire, disease, or insect herbivory. These may reset the system to earlier successional stages dominated by aspen and other hardwoods. Alternatively, browsing by moose themselves on balsam fir could slow this feedback, but not if balsam fir densities are high (Brandner et al. 1990).

In summary, by changing the plant communities and the arrays of litters decomposed from them, moose browsing indirectly controls the nitrogen cycle and the long-term productivity of Isle Royale's boreal forests. Failure to consider the indirect effects of herbivores on decomposers through changes in litterfall may cause incomplete models of food webs to be seriously in error.

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Literature Cited

Bonan, G. B., and H. H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecology and Systematics **20**:1–28.

Brandner, T. A., R. O. Peterson, and K. L. Risenhoover. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology **71**:155–164.

Bryant, J. P. 1987. Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology **68**:1319–1327.

Bryant, J. P., and F. S. Chapin, III. 1986. Browsing–woody plant interactions during boreal forest plant succession. Pages 213–225 *in* K. Van Cleve, F. S. Chapin, III, P. W. Flanagan, L. A. Viereck, and C. T. Dyrness, editors. Forest ecosystems in the Alaskan taiga. Springer-Verlag, New York, New York, USA.

Bryant, J. P., and P. J. Kurpoat. 1980. Selection of winter forage by subarctic browsing vertebrtes: the role of plant chemistry. Annual Review of Ecology and Systematics **11**: 261–285.

Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant antiherbivore defense. Science **230**:895–899.

Day, T. A., and J. K. Detling. 1990. Grassland patch dynamics and herbifore grazing preference following urine deposition. Ecology **71**:180–188.

Deans, J. R., J. A. E. Molina, and C. E. Clapp. 1986. Models for predicting potentially mineralizable nitrogen and decomposition rate constants. Soil Science Society of America Journal **50**:323–326.

Eno, C. F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Science Society of America Proceedings **24**:277–299.

Flanagan, P. W., and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. Canadian Journal of Forest Research **13**: 795–817.

Fowells, H. A. 1965. Silvics of forest trees in the United States. Agricultural Handbook Number 271, United States Department of Agriculture, Forest Service, Washington, D.C., USA.

Gordon, A. M., and K. Van Cleve. 1983. Seasonal patterns of nitrogen mineralization following harvesting in the white spruce forests of interior Alaska. Pages 119–130 *in* R. W. Wein, R. R. Riewe, and I. R. Methven, editors. Resources and dynamics of the boreal zone. Association of Canadian Universities for Northern Studies, Ottawa, Canada.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133–302.

Haukioja, E., K. Kapiainen, P. Niemela, and J. Tuomi. 1983. Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? Oikos **40**:419–432.

Horner, J. D., J. R. Gosz, and R. G. Cates. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. American Naturalist **132**: 869–883.

Krefting, K. W. 1974. The ecology of the Isle Royale moose. Technical Bulletin 297, Forestry Series 15. University of Minnesota Agricultural Experiment Station, Saint Paul, Minnesota, USA.

Linn, R. M. 1957. The spruce–fir, maple–birch transition in Isle Royale National Park, Lake Superior. Dissertation. Duke University, Durham, North Carolina, USA.

McClaugherty, C. A., J. Pastor, J. D. Aber, and D. M. Melillo. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology **66**:266–275.

McInnes, P. F. 1989. Moose browsing and boreal forest vegetation dynamics, Isle Royale, Michigan, USA. Thesis, University of Minnesota, Saint Paul, Minnesota, USA.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litterfall of the boreal forests of Isle Royale, Michigan, U.S.A. Ecology **73**:2059–2075.

McKendrick, J. D., G. O. Batzli, K. R. Everett, and J. C. Swanson. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. Arctic and Alpine Research **12**:565–578.

Mech, L. D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the United States, Fauna Series **7**:1–210.

Melillo, J. M., R. J. Naiman, J. D. Aber, and A. E. Linkens. 1984. Dynamics of plant litter decay in northern streams. Bulletin of Marine Science **35**:341–356.

Moore, T. R. 1984. Litter decomposition in a subarctic spruce–lichen woodland, eastern Canada. Ecology **65**:299–308.

Nadelhoffer, K. J. 1990. Microlysimeter for measuring nitrogen mineralization and microbial respiration in aerobic soil incubations. Soil Science Society of America Journal **54**:411–415.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience **38**:753–763.

Pastor, J., R. H. Gardner, V. H. Dale, and W. M. Post. 1987*a*. Successional changes in nitrogen availability as a potential factor contributing to spruce declines in boreal North America. Canadian Journal of Forest Research **17**:1394–1400.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist **139**:690–705.

Pastor, J., R. J. Naiman, and B. Dewey. 1987*b*. A hypothesis of the effects of moose and beaver foraging on soil carbon and nitrogen cycles, Isle Royale. Alces **23**:107–124.

Pastor, J., R. J. Naiman, B. Dewey, and P. F. McIness. 1988. Moose, microbes and the boreal forest. BioScience **38**:770–777.

Peterson, R. L. 1955. North American moose. University of Toronto Press, Toronto, Ontario, Canada.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. Scientific Monograph Series, Number eleven. National Park Service, Washington, D.C., USA.

Peterson, R. O. 1987. Ecological studies on wolves in Isle Royale. Annual Report 1986–1987. Michigan Technological University.

Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. Science **224**: 1350–1352.

Ruess, R. W., D. S. Hik, and R. L. Jefferies. 1989. The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia (Berlin) **79**:23–29.

Ruess, R. W., and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos **49**:101–110.

Risenhoover, K. L., and S. A. Maass. 1987. The influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research **17**:357–364.

Schimel, D. S., W. J. Parton, F. J. Adamsen, R. G. Woodmansee, R. L. Senft, and M. A. Stillwell. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. Biogeochemistry **2**:39–52.

Schultz, A. M. 1964. The nutrient-recovery hypothesis for arctice microtine cycles. Pages 57–68 *in* D. J. Crips, editor. Grazing in terrestrial and marine environments. Blackwell, Oxford, England.

Snyder, J. D., and R. A. Janke. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. American Midland Naturalist **95**:79–92.

Stanford, G., and S. J. Smith. 1972. Nitrogen mineralization potentials of soils. Soil Science Society of America Proceedings **36**:465–472.

Talpaz, H., P. Fine, and B. Bar-Yosef. 1981. On the estimation of N-mineralization parameters from incubation experiments. Soil Science Society of America Journal **45**: 993–996.

Van Cleev, K., and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. Pages 185–211 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest succession. Springer-Verlag, New York, New York, USA.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, USA.

Wolff, J. O., and J. Zasada. 1979. Moose habitat and forest succession on the Tanana River floodplain and Yukon–Tanana upland. Proceedings of the North American Moose Conference **15**:213–244.