A HYPOTHESIS OF THE EFFECTS OF MOOSE AND BEAVER FORAGING ON SOIL NITROGEN AND CARBON DYNAMICS, ISLE ROYALE

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Abstract. Selective foraging by moose (Alces alces) and beaver (Castor canadensis) alter the species composition of forests. We hypothesize that this affects the types of litter returned to the soil, soil carbon and nitrogen pools and soil nitrogen availability. Preliminary analyses of soils collected from areas with various combinations of moose and beaver foraging on Isle Royale, Michigan, support this hypothesis. Soil carbon and nitrogen pools and nitrogen availability are significantly greater where beaver cutting of large diameter (> 10 cm) aspen (Populus tremuloides), mountain ash (Sorbus americana) and other hardwoods maintains their dominance because they sprout prolifically from roots and stumps. These species have easily decomposible litter which increases soil nitrogen availability. In contrast, moose browsing of young hardwoods suppresses their growth, allowing unbrowsed spruce (Picea glauca, P. mariana) to gain dominance. Spruce litter is low in nitrogen and difficult to decompose. Soil nitrogen pools and nitrogen availability are significantly lower in areas of heavy moose browsing. Because nitrogen is the limiting nutrient in boreal forests, moose and beaver may have long-term effects on ecosystem properties.

ALCES 23 (1987)

Recent theories of nutrient cycling in the boreal forest have emphasized the differences between tree species in the decomposibility of their litter and in their nutrient requirements (Gordon 1983, Flanagan and Van Cleve 1983, Van Cleve and Viereck 1981, Van Cleve et al. 1983, Chapin et al. 1986, Pastor et al. 1987). Emphasis has been placed on the cycle of nitrogen because it is the most limiting nutrient to tree growth (Weetman 1968, Van Cleve and Zasada 1976, Van Cleve and Oliver 1982). Early successional species, such as aspen (Populus tremuloides), balsam poplar (P. balsamifera) and paper birch (Betula papyrifera) have easily decomposible, nitrogen-rich litter which enhances soil nitrogen availability (Flanagan and Van Cleve 1983). They are generally succeeded by spruce (Picea glauca, P. mariana) and balsam fir (Abies balsamea), whose slowly decomposing litter depresses soil nitrogen availability (Flanagan and Van Cleve 1983, Pastor et al. 1987). These conifers are able to survive their depression of soil nitrogen availability because of low requirements (Chapin et al. 1986), but eventually severe nitrogen stress and even dieback may occur (Pastor et al. 1987).

Although the successional sequence of 5-10 decades of hardwood dominance followed by a conifer climax forest is true in a broad sense, there are multiple successional pathways in the boreal regions (Larsen 1980), depending largely on the frequency and intensity of disturbances. Fire is the most intensively studied disturbance to succession and the carbon and nitrogen cycles of the boreal forest (Wien and MacLean 1983). Intensive browsing by mammals may be another, perhaps equally important, disturbance affecting boreal ecosystems, although it is not often recognized as such. A lack of understanding of how moose, beaver, and other herbivores influence plant communities strongly limits our ability to predict sucession in northern ecosystems (Wien and El-Bouyami 1983).

We have developed a general hypothesis that mammalian herbivores affect nutrient cycling in boreal forests through their selective foraging which alters forest species composition and therefore the array of litter types returned to the soil. We are testing this hypothesis by examining soils of boreal forests whose composition has been greatly altered by moose (Alces alces) and beaver (Castor canadensis).

Beaver selectively cut large diameter (generally > 10 cm) hardwoods, particularly aspen, mountain ash (Sorbus americana), willow (Salix spp.), paper birch, and other species (Aldous 1938, Northcott 1971, Jenkins 1980, Belovsky 1984). Normally, without heavy browsing or fire, these species would eventually succeed to spruce or fir because they are shade intolerant. However, the opening of the canopy by beaver causes these species to sprout prolifically from roots and stumps, forming dense sucker and stump-sprouted stands around beaver ponds. These stands are often heavily browsed by moose (Wolfe 1974).

In contrast, moose selectively browse small diameter hardwoods and avoid spruce because the hardwoods have lower lignin and resin and higher nitrogen contents, allowing these species to be more easily digested by the moose's gut flora (Peek et al. 1976, Belovsky 1981, Bryant and Kuropat 1980, Miquelle and Jordan 1980). These same chemical properties also determine litter decay and nutrient release rates (Mcentemeyer 1978, Melillo et al. 1982, Flanagan and Van Cleve 1983, Moore 1984) for the simple reason that both ruminant digestion and litter decomposition are microbially mediated. Intensive moose

browsing can convert stands from aspen and other hardwoods to spruce (Houston 1968, Krefting 1974, Snyder and Janke 1976).

If beaver foraging retards succession of shade intolerant hardwoods to spruce and fir and moose browsing accelerates that succession, then we would expect the following effects on soil properties: 1. Soils where shade intolerant hardwoods are maintained by beaver cutting should have high carbon and nitrogen contents and high nitrogen availability. 2. Soils where heavy moose browsing on small diameter hardwoods gives a competitive advantage to spruce should have low C and N contents and low soil nitrogen availability.

STUDY SITES

Isle Royale, Michigan, is a 544 km^2 island in Lake Superior about 20 km from the Minnesota-Ontario shore. The forests are predominantly boreal, with aspen, paper birch, spruce, and balsam fir predominating, particularly in the northeastern portion. Details of the climate, geology, and vegetation are given in Hansen et al. (1973), Krefting (1974), Snyder and Janke (1976), Peterson (1977), and Huber (1983). Moose have had a major effect on the vegetation since their invasion around the turn of the century (Murie 1934, Hansen et al. 1973, Krefting 1974, Snyder and Janke 1976). In general, the abundance of american yew (Taxus canadensis), aspen and birch have declined because of heavy moose browsing. White spruce, which is unbrowsed, is increasing steadily.

On Sept. 22-25, 1986 we collected soil samples from six stands on northeastern Isle Royale and on Passage Island, a smaller island approximately 5 km northeast of Isle Royale. These stands were chosen to represent various combinations of moose and beaver foraging (Table 1).

Passage Island has not had an active moose population within historic times. The forest there is fully described by Krefting (1974), Hansen et al. (1973) and Snyder and Janke (1976). It is spruce-fir with mountain ash in gaps or in large groves with spruce-fir understory, and abundant american yew in the understory. Mountain ash seems to be the preferred food of an active beaver colony on the island, there being little or no willow, aspen or paper birch. Little seems to be known about the ecology of mountain ash or american yew in boreal forests, although they are common subordinates in forests along the north shore of Lake Superior (Peattie 1963, Rosendahl 1975, Larsen 1980). Soils were sampled in an active beaver-created opening dominated by unbrowsed mountain ash, stump sprouts of beaver-browsed mountain ash, and american yew. We also sampled soils in an adjacent spruce-fir mature forest with lesser amounts of ash and yew, mainly in single-tree gaps.

A third site sampled was adjacent to recently abandoned beaver pond off the Lane Cove Trail on the northeastern end of Isle Royale. Beaver are actively cutting aspen > 15 cm diameter around this pond, thereby opening the canopy which results in prolific production of aspen root sprouts and a shrub cover of hazel (Corylus spp.). Moose are heavily browsing these sprouts as well as hazel stems while avoiding spruce, resulting in increased dominance by spruce. Moose also browse lower branches of balsam fir, but the fir seems to be growing beyond the browse height of moose in this area of the island. The invasion of spruce around this and other ponds we examined seems to be due to intensive browsing of aspen and hazel by moose rather

than to beaver cutting of mature aspen and releasing of understory spruce.

Three additional sites were located around the Daisy Farm moose exclosure in the Rock Harbor area of Isle Royale. This exclosure was built in 1949 after nearly 40 years of intensive moose browsing had seriously curtailed hardwood growth and reproduction (Krefting 1974). The vegetation inside and outside this moose exclosure has been described in detail by Krefting (1974) and Hansen et al. (1973). Outside the exclosure, heavy moose browsing has virtually eliminated aspen and pin cherry (Prunus pensylvanica). The current vegetation is composed of patches of thimbleberry (Rubus parviflorus) and groves of spruce. The spruce groves usually have one or two mature trees in their center and progressively younger trees towards their edges. Inside the exclosure, the forest is mixed aspen-paper birch overstory with spruce-fir understory. Soils were sampled in an adjacent thimbleberry patch, several adjacent spruce groves, and inside the exclosure.

METHODS

Ten samples of the A1 or H horizons were randomly taken at each site with a tulip bulb planter. Each sample was approximately 5 cm dia by 5-8 cm deep. These samples were transported to our laboratories in Duluth within 4 days and immediately sieved of all roots in the lab. Approximately 15 g of each sample was incubated at 30 degrees C for 16 weeks to determine potentially mineralizable (plant available) nitrogen by the method of Stanford and Smith (1972). Each sample was also analyzed for total C and N with a LECO CHN analyzer.

Data were statistically analyzed by one way analysis of variance testing the main effect of foraging type, by a least significance difference test between pairs when the main effect of foraging was significant, and by regression analysis to examine correlation among these properties.

RESULTS

Soil carbon and nitrogen contents were highest in the beaver created gap on Passage Island, followed by the mature forest on Passage Island, the beaver pond, outside the Daisy Farm exclosure, and inside the exclosure (Table 1). Analyses of variance show significant main effect of browsing on these soil properties. Further comparisons using a least significance difference test at $P < 0.05$ indicates that beaver foraging significantly elevates soil carbon and nitrogen pools over that found in the spruce-fir stand without moose or beaver, but that moose browsing (either with or without the influence of beaver) significantly depresses these pools.

The amount of soil nitrogen mineralized after 16 weeks of laboratory incubation both per g soil and as a proportion of the total N pool also differed significantly between the sites (Table 1). Differences in the proportion of total N mineralized are attributable to differences in the quality of organic-N. Different rates of mineralization per g soil are attributable to differences in both quality and quantity of organic nitrogen. Cumulative N mineralization was greatest in the active beaver cutting on Passage Island, and was significantly lower ($P < 0.05$) in areas of heavy moose browsing, both adjacent to the beaver pond as well as outside the Daisy Farm Exclosure. Even after four decades of protection from moose inside

TABLE 1. Sampling areas, type of foraging, and soil properties. Data are means and standard deviations of 10 replicates. Entries within a column followed by the same letter are not significantly different ($P < .05$) according to a least significance difference test.

		Soil Properties			
Location	Type of foraging	% C	% N	Cumulative N mineralization (% of total N)	Cumulative N mineralization (mg/g soil)
Passage Island					
Spruce-fir	No moose or beaver	31(8.6)	1.6(.37)	6.8(2.2)a	1.14(.56)
Mountain ash-yew	Beaver, no moose	38(7.3)	2.3(.32)	7.1(1.1)a	1.61(.32)
Isle Royale					
Lane Cove Trail	Beaver and moose	24(6.9)	1.2(.24)	7.0(1.5)a	0.86(.29)
Daisy Farm Exclosure					
Outside: Spruce	Moose, no beaver	14(8.0)a	.73(.36)	4.7(1.5)	0.36(.23)a
Outside: Thimbleberry	Moose, no beaver	9.7(2.1)a	.53(.09)a	3.1(.77)b	0.17(.05)a
Inside: Aspen-birch-spruce-fir	Recovery from moose	7.9(2.0)a	.49(.10)a	3.6(1.0)b	0.17(.07)a

the exclosure, soil N availability had not increased compared to that outside.

Soil C and N were highly correlated ($r = 0.973$, $P < 0.001$). The proportion of total N mineralized after 16 weeks was more highly correlated with %C ($r = 0.923$, $P < 0.01$) than it was with %N ($r = 0.865$, $P < 0.05$). This indicates that nitrogen availability may be determined not only by the quantity of nitrogen but also by the quality and quantity of carbon.

DISCUSSION

These findings support our hypothesis that selective foraging by mammals alters the array of litter types returned to the soil and eventually soil nitrogen availability. Changes observed are consistent with feeding preferences of moose and beaver (Aldous 1939, Jenkins 1980, Belovsky 1981, Miquelle and Jordan 1980), changes in plant communities caused by selective foraging (Hansen et al. 1973, Krefting 1974), and known differences between these tree species in their affect on soil properties (Flanagan and Van Cleve 1983, Moore 1984). Soil carbon and nitrogen contents and N mineralization rates are highest where beaver cutting appears to maintain the presence of hardwood species with easily decomposible litter, and lowest where heavy moose browsing on these same species causes spruce dominance to increase.

It is possible that factors other than foraging effects, such as topographic position of the sites or soil parent material, may explain these differences. However, we tend to discount this for several reasons, but recognize that this deserves more research. First, all soils were stony, loamy sands or stony loams of strongly podsolized

nature. Although minor differences may exist, they are generally of the same type. Second, only the A1 or H horizons were sampled. These soil horizons would be more strongly affected by vegetation dynamics, in turn strongly affected by browsing, than by subsoil differences related to parent material or topographic position.

The similarity of nitrogen mineralization inside the exclosure compared with that outside is consistent with findings of slow recovery of vegetation from moose browsing on some sites in boreal regions (Bergerud and Manuel 1968). Results here suggest that soil properties also recover slowly, particularly those properties which are most influenced by vegetation. However, excluding moose may have a greater effect on soil properties of other sites: in 1985, we examined another 38 year old exclosure on a sandy soil in southwestern Isle Royale and found a 5 cm thick forest floor inside the exclosure while outside the forest floor was thin to absent and composed mainly of spruce needles. What factors enhance or prevent recovery from moose browsing remain poorly known, but may include soil type (particularly water holding capacity), and community composition.

Soil properties in the thimbleberry patch were similar to those in the adjacent spruce groves. Thimbleberry is not eaten in large quantity by moose on Isle Royale (Murie 1934, Aldous and Krefting 1946, F. Jordan, personal communication) or elsewhere (Peterson 1955). It would be interesting to determine if thimbleberry is unpalatable to moose because of high lignin or phenolic or low nitrogen contents. If so, then this would explain why soils beneath thimbleberry are similar to those beneath spruce.

Effects of plant-herbivore interactions on soil nutrient availability have been observed elsewhere, but are poorly understood. In arctic salt marshes, areas grazed by geese have less litter accumulation than ungrazed areas (Cargill and Jefferies 1984). When large mammals were excluded from African savannas, soil nutrient and organic matter contents increased over 24 years (Hatton and Smart 1984). Litter accumulation is greater in elk exclosures in the Cascades compared with outside (Tiedemann and Berndt 1972). These studies and results presented here indicate that herbivores may affect ecosystem processes far beyond their food requirements through their effects on the plant community.

Both moose and beaver depend on early successional species whose presence on a large scale in turn depends on fire or other large disturbances. By cutting mature hardwoods and causing proliferation of root sprouts, beaver in some cases retard succession after fire, thereby maintaining ecosystems with high rates of nitrogen cycling. By browsing on small diameter aspen and other hardwood stems, moose do not accelerate succession through a hardwood phase to conifers so much as they prevent the normal course of succession through the hardwood phase. Thus, the recovery of the forest floor nutrient pools and soil nitrogen availability associated with this early successional phase (Stoeckeler 1961, Covington 1981, Federer 1984, Pastor and Post 1986) is prevented by heavy moose browsing. This results in smaller nitrogen and carbon pools and lower nitrogen availability. Moose browsing may therefore cause a different pathway of ecosystem succession rather than an acceleration of succession.

These changes in soil carbon and nitrogen pools and nitrogen availability induced by selective feeding of moose and beaver may have

long range implications for tree growth and browse supply. These results suggest that beaver foraging enhances productivity and browse supply, but moose foraging depresses them. However, other factors influence both the spatial and temporal scales of these processes, and deserve more research. For example, beaver influence the forest within 100 m or less of most streams (Aldous 1938, Jenkins 1980, Johnston and Naiman 1987), while moose home ranges are 300-500 ha in size. On the other hand, when beaver populations are high, large proportions of the landscape may be affected by their foraging and dam building (Naiman et al. 1986, Johnston and Naiman 1987) and moose may preferentially feed around beaver ponds (Wolfe 1974). Therefore, beaver and moose foraging may increase the heterogeneity of the forest by locally altering successional pathways and soil properties.

Studies in Alaska show that soil nitrogen availability decreases during succession as aspen and birch are replaced by spruce (Van Cleve et al. 1983, Flanagan and Van Cleve 1983). Bryant and Chapin (1986) have independently proposed ideas similar to those presented here, emphasizing the relation between plant palatability to herbivores and the ease by which plant tissues decompose. We suggest that the importance of moose and beaver as agents of disturbance in boreal forests have been overlooked by both ecosystem ecologists and wildlife biologists, and deserve further attention.

CONCLUSIONS

1. Soil C and N pools and nitrogen availability are greatest where beaver forage in the absence of moose, maintaining communities of hardwood species with easily decomposible litter.

2. Soil C and N pools and nitrogen availability are lowest where moose browse heavily on species with easily decomposible litter while avoiding spruce which has slowly decomposing litter.

ACKNOWLEDGEMENTS

This research was supported by grant NSF/BSR-8614960 from the Ecosystems Studies Program of the National Science Foundation. Logistic support for the fieldwork provided by the National Park Service is greatly appreciated.

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