SELECTIVE FORAGING AND ECOSYSTEM PROCESSES
IN BOREAL FORESTS

JOHN PASTOR* AND ROBERT J. NAIMAN†

*Natural Resources Research Institute, University of Minnesota, Duluth, Minnesota 55811;
†Center for Streamside Studies, University of Washington, Seattle, Washington 98195

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Abstract.—We suggest that selective foraging alters feedbacks between plants and decomposers and between plants and herbivores. Plant tissue chemistry is an important link between herbivores and decomposers. Plants that produce easily decomposable litter are also heavily browsed, because the same chemical properties that determine litter decay also determine digestibility. This trait links theories of food webs and nutrient cycles by positing a role of herbivores as functional switches determining both plant community composition and the array of litters returned to the soil. This role appears to be particularly strong in boreal forests, where nutrient availability is low and limits productivity and determines successional pathways, where effects of herbivores are strong and long lasting, and where the same plant traits that determine herbivore preference and response to browsing also determine interactions with soil nutrient availability. Such feedbacks cause the effects of herbivores on ecosystems to persist even after the herbivores are no longer present.

Herbivores influence ecosystems by their interactions with food and habitat over several trophic, organizational, and spatial levels and produce complex feedbacks with unexpected results (Starfield and Bleloch 1986; Naiman 1988; DeAngelis et al. 1989). Despite many attempts, there is as yet no general theory that explains how or under what conditions animals alter ecosystems as they search for food and other necessities of life.

Some models of the role of herbivores in ecosystem dynamics assume, sometimes implicitly, that vegetation is a homogeneous food source (Chew 1974; DeAngelis et al. 1989). This implies that herbivores can alter nutrient cycles only by redirecting nutrient flow through their bodies and into the soil as fecal material, urine, or carcasses (Kitchell et al. 1979; Woodmansee et al. 1981; Jefferies 1988). Simple calculations, however, show that in most ecosystems this is usually less than 10% of net primary production, although in graminoid-dominated ecosystems it can be as high as 80%–90% (Ball et al. 1979; Bazeley and Jefferies 1985; Schimel et al. 1986; Ruess and McNaughton 1987; Ruess et al. 1989).

However, current theory falls short in two ways: (1) it does not consider how unbrowsed species respond to the environmental changes wrought by herbivory on the browsed species, and (2) it does not consider lag times in the responses of soils and other ecosystem components to changes in vegetation. Herbivores control ecosystem processes not only by what and how much they eat but also by what they do not eat. If both browsed and unbrowsed species alter nutrient flows through soils, then the ultimate response of the ecosystem depends to a large extent on the direction, degree, and lags in the responses of soil nutrient pools.

The effects of herbivores on community composition and the effects of different plant species on soil nutrient availability are particularly acute in boreal forests, where nutrient availability is generally low (Flanagan and Van Cleve 1983; Pastor et al. 1987; Bonan and Shugart 1989), where changes in nutrient availability are major factors driving succession (Van Cleve and Viereck 1981), and where herbivores can greatly alter plant community composition through selective foraging (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). Furthermore, populations of boreal herbivores fluctuate drastically (Haukioja et al. 1983, and references therein), and these fluctuations may in turn be related to changes in nutrient cycles imposed by herbivory (Schultz 1964; Bryant and Chapin 1986).

In this article, we explore how plant chemistry and its correlation with growth and nutrient uptake link feeding behavior with ecosystem processes in boreal forests. The chemical quality of the plant material partly determines which plants are eaten (Bryant and Kuropat 1980) as well as their fate once they enter the soil (Horner et al. 1988). Production of defensive compounds also appears to be inversely correlated with growth rates, nutrient uptake rates, and retention time of leaves (Coley et al. 1985). Here, we explore how selective herbivory can change ecosystem processes in boreal communities of plants with different chemistries and browsing responses.

We propose that selective foraging by herbivores shifts community structure toward unbrowsed stems or species, changing the quantity and chemical quality of litter returned to the soil, soil nutrient availability, and nutrient cycles. We examine this potentially important process in boreal forests using foraging by moose (Alces alces) and beaver (Castor canadensis) as examples.

NITROGEN CYCLING AND HERBIVORY IN BOREAL FORESTS

Nitrogen and Carbon Cycles

Boreal forests are composed of a few tree species that differ sharply in nutrient cycling properties and landscape distribution (Larsen 1980; Van Cleve et al. 1983). Recent theories of nutrient cycling in boreal forests emphasize the different nutrient requirements and decay rates of litter from various tree species (Van Cleve and Viereck 1981; Flanagan and Van Cleve 1983; Gordon 1983; Van Cleve et al. 1983; Chapin et al. 1986; Pastor et al. 1987). These theories emphasize 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 (*Populus balsamifera*), and paper birch (*Betula papyrifera*), have easily decomposable, nitrogen-rich litter that enhances soil nitrogen availability (Planagan and Van Cleve 1983), but they also require large amounts of nitrogen for production because they grow rapidly and are deciduous (Van Cleve and Oliver 1982; Pastor and Bockheim 1984). They are generally succeeded by spruce (*Picea glauca, Picea mariana*) and balsam fir (*Abies balsamea*), whose slowly decomposing litters depress soil nitrogen availability (Planagan and Van Cleve 1983; Pastor et al. 1987). These conifers are able to survive their depression of soil nitrogen availability because of low requirements, low inherent growth rates, and retention of nitrogen for several years in photosynthetically active needles (Chapin et al. 1986), but eventually severe nitrogen stress and even dieback may occur (Pastor et al. 1987).

To varying degrees, most northern species produce carbon-based compounds that have multiple consequences, one of which may be deterrence of herbivores (Bryant and Kuropat 1980; Palo et al. 1983; Talvanainen et al. 1983). Fast-growing, early successional species seem to produce some of these compounds, such as phenolics, only during juvenility; once beyond the reach of most herbivores, these plants decrease their production of secondary compounds (Bryant et al. 1983; Chapin et al. 1985). In contrast, slower-growing species, such as spruce, maintain production of phenolic polymers that form lignin and other secondary compounds throughout their lives (Bryant et al. 1983).

These secondary compounds are carbon-based rather than nitrogen-based because nitrogen is a scarce resource to boreal plants (Coley et al. 1985). Both low nitrogen content and high lignin content reduce digestibility (Feeney 1970; Rhoades and Cates 1976; Fox and McCauley 1977; McNeil and Southwood 1978; Bryant and Kuropat 1980; Mattson 1980; Palo et al. 1985). However, low nitrogen and high lignin contents also make the litter difficult to decompose (Fogel and Cromack 1977; Meentemeyer 1978; Melillo et al. 1982; Planagan and Van Cleve 1983) for the simple reason that both ruminant digestion and decomposition are microbially mediated. Other secondary compounds may have similar effects (Horn et al. 1988).

Therefore, the carbon and nitrogen cycles of boreal forests are tightly linked by positive and negative feedback loops between decomposers, plants, and herbivores, because nitrogen availability controls net carbon fixation but the types of carbon compounds produced control both nitrogen availability and browsing intensity. The sharp differences between boreal tree species in palatability, litter quality, and growth responses to nitrogen add the extra dimensions of plant population and community dynamics to the role of herbivores in ecosystem functioning.

*Selective Foraging Strategies of Moose and Beaver*

Moose and beaver are two important and interacting herbivores of boreal forests. Although they browse on the same plant species, their foraging strategies and consequently their effect on ecosystems differ substantially.
SELECTIVE FORAGING AND BOREAL ECOSYSTEMS

Beaver cut large-diameter trees of early successional species, particularly aspen and willow (*Salix* sp.), near their ponds (Aldous 1938; Northcott 1971; Gill 1972; Jenkins 1980; Belovsky 1984; McGinley and Whitham 1985; Johnston and Naiman 1990b). The canopy openings that are created in beaver-worked areas are often large gaps with sufficient light penetration to permit regeneration of shade-intolerant species. Therefore, beaver often convert mid-successional stands to early successional stands (Aldous 1938; Gill 1972), although sometimes they release understory for and spruce and thus hasten succession (Naiman et al. 1988; Johnston and Naiman 1990b).

In contrast, moose browse young aspens and other hardwoods and avoid spruce (R. L. Peterson 1955; Peek et al. 1976; Belovsky 1981). This selective foraging seems to be related to the high nitrogen and low lignin content of aspen leaves and twigs (Bryant and Kuropat 1980). Moose browse aspen year-round, stripping leaves in summer and eating current twigs in winter (R. L. Peterson 1955). Consequently, aspen is often killed by continuous, heavy browsing (Krefting 1974), and intensive moose browsing can hasten succession to spruce (Houston 1968; Krefting 1974; Snyder and Janke 1976; McInnes et al. 1992).

There are several consequences of these foraging strategies. First, by maintaining populations of early successional species in large gaps, beaver should indirectly maintain the high rates of nitrogen cycling and productivity characteristic of aspen ecosystems beyond the point when it would normally succeed to conifers. Second, if moose browsing hastens succession to spruce, productivity and nitrogen cycling should decrease earlier in succession. Therefore, browsing by beaver and moose on different individuals of the aspen population should cause ecosystem properties to diverge, depending on the nature of herbivory and the time course of succession.

*Simulation Experiments of Moose and Beaver Foraging*

We examined the logic of these hypotheses with the LINKAGES forest ecosystem model (Pastor and Post 1986). LINKAGES is a member of the JABOWA/FOREST class of models (Botkin et al. 1972; Shugart 1984), derived most directly from the FORNITE (Aber et al. 1982) and FORENA (Solomon 1986) versions. LINKAGES simulates the birth, growth, and death of individual stems in a 1/12-ha plot and the decay and nutrient dynamics of annual cohorts of litter from these trees. Like other models of the JABOWA/FOREST class, the structure is that of a population model except that it also simulates those properties of individuals important to ecosystem functions, such as their morphologies, effects on resource availabilities, and nutrient contents.

Competition for light is simulated by species-specific leaf production, and hence shading of all shorter trees, and by photosynthetic response curves. Species also affect the nitrogen cycle by having different responses to soil nitrogen availability and by differences in the lignin:N ratio, and hence decomposability, of their leaf litter. The model has been well validated against independent data on species composition, biomass, productivity, and nitrogen cycling in northern forests (Pastor and Post 1986, 1988; Pastor et al. 1987). Of particular interest to this article is the potential for a stable limit cycle between early successional hardwoods and late successional conifers in boreal forests because they have opposite responses
to and effects on light and nitrogen availabilities (Pastor et al. 1987). Earlier versions of the FORET models have been used to examine the effect of forest structure on animal populations and habitat suitability (Shugart 1984; Smith 1986; Urban and Smith 1989). However, we believe this is the first use of these models to demonstrate the converse effects of animals on ecosystems.

In these simulations, the boreal forest for the western Lake Superior region was simulated from climatic data from the U.S. Department of Commerce (1968). The forest was simplified to two of the most common boreal tree species, quaking aspen and white spruce. Aspen represents a shade-intolerant, early successional hardwood that is food for either beaver or moose and that has high litter quality that enhances nitrogen availability. Spruce represents a shade-tolerant, late successional conifer that is not eaten by either herbivore and that has calcitrate litter that can depress nitrogen availability. While many boreal forests are composed of these two tree species (Larsen 1980; Van Cleve and Viercock 1981; Van Cleve et al. 1983), some contain various amounts of birch, balsam poplar, black spruce, and balsam fir. However, each of these others is either a shade-tolerant, late successional conifer not heavily browsed or a shade-intolerant, early successional hardwood that is heavily browsed and has high litter quality. Therefore, simplifying the forest to these two species should not distort results and enables us to determine more fully the interaction of browsing and litter quality.

We simulated herbivory by moose and beaver at two intensities. However, because these animals forage in different ways, the method of simulation differed. Moose browsing does not immediately kill the stem. Rather, browsing alters the subsequent growth of the stem and it survives or dies because of competition with other stems (Houston 1968; Kretting 1974). Therefore, the effect of moose browsing on aspen was simulated not by directly changing mortality but by altering growth rates and allowing simulated competitive interactions for nitrogen and light to determine mortality. We assumed that light browsing up to 30% removal of annual aboveground production increases the growth of individual stems and higher levels depress it, borrowing an aspen response curve from the deer-browsing model of Mello and Hauffer (1983). Browsing was simulated by removing 30% or 50% of the current twig biomass and 30% or 50% of current twig biomass. The diameter and height growth of each aspen and spruce stem was then limited by nitrogen or light, whichever was more restrictive, with the growth of browsed aspen stems additionally modified by the response curve at the 30% and 50% browsing intensities.

This is essentially the herbivore optimization hypothesis of McNaughton (1979, 1983) and Dyer and Bokhari (1976). We wish at this time to avoid arguing the validity of an increase in growth at low browsing intensities (Belsky 1987). Such an increase in growth could be a direct, compensatory response of the browsed plants themselves or could be caused by increased rates of nutrient cycling. If the latter were the only cause, this would introduce some degree of circularity into our results. However, there is some evidence that browsing of early successional species by moose, deer, and hare generates such a response within the first year,
Fig. 1.—Simulated effects of moose and beaver browsing on net primary production. See the text for details of simulations. Straight line, no moose or beavers browsing; dashes, 30% probability that a 10-cm diameter at breast height (dbh) aspen will be felled by beaver; dark dots, 50% probability that a 10-cm dbh aspen will be felled by beaver; light dots, 30% probability that an aspen 3 m tall or shorter will be browsed by moose; dots and dashes, 50% probability that an aspen 3 m tall or shorter will be browsed by moose.

well before any changes in soil nutrient availability are possible (Aldous 1952; Wolff 1978; Fox and Bryant 1984; Danell et al. 1985; Bryant and Chapin 1986). In any case, we wish simply to demonstrate the possible logical consequences of this particular response of individual plants for ecosystem properties.

Herbivory by beaver was simulated by increasing the probability of mortality of individual aspen stems to 30% or to 50% once the diameter exceeded 10 cm; smaller trees are not preferred by beaver (Jenkins 1980; Johnston and Naiman 1990a). This simulates the felling of large stems by beaver; once felled, the stem is dead and there is no compensatory regrowth of that particular stem, although sprouting from the parent root stock is allowed to the extent that light availability increases because of the death of the parent tree.

The results are shown in figures 1–3. The no-browsing, control simulation followed the classical pattern of succession in the boreal forest of early occupancy by aspen, with subsequent elevation of N availability, succeeding to spruce, with subsequent depression of N availability (Flanagan and Van Cleve 1983; Gordon 1983; Pastor et al. 1987).

Moose browsing on 30% of the current twigs of aspen within browse height elevated both net primary production (fig. 1) and nitrogen availability (fig. 2) above the no-browsing, control scenario. This is because the growth of small aspen was accelerated at this browsing intensity (fig. 3, top left and top right). In this case, moose browsing enhanced soil N availability because the more easily decomposable aspen litter dominated litter fall. Aspen grew beyond the reach of moose after approximately 10 yr, and the regeneration of additional aspen browse within reach of moose was curtailed because of self-shading. Actual moose
browsing then ceased. However, aspen biomass and net primary production continued to diverge from the control because the enhanced dominance of aspen increased nitrogen availability, which in turn increased the growth of aspen more than that of spruce.

At the other extreme, when moose browsed 50% of the current twigs of aspen within browse height, net primary production and nitrogen availability were lower than in the other simulations. The depression of aspen growth at this browsing intensity allowed spruce to dominate the forest (fig. 3, bottom left and bottom right). The decreased return of aspen litter and the increased proportion of spruce litter depressed nitrogen availability, which in turn constrained the growth of both species to low levels. Note again that this ecosystem-level effect persisted long after the aspen browse supply was curtailed because of self-shading. Again, a shift in species dominance caused by selective foraging had consequences for ecosystem properties beyond the time that the herbivore could occupy the forest. These results are partially validated against independent data from Isle Royale, Michigan. These forests with similar or greater browsing intensities during the past 80 yr have net primary production of approximately 4 Mg/ha/yr, a biomass
of 50–80 Mg/ha (McInnes et al. 1992), and N availabilities of 25–30 kg/ha/yr (Pastor et al., in press), similar to that predicted by the model.

Browsing by beaver caused responses intermediate between these two extremes. There were no differences in forest response under either browsing intensity because an annual intensity of 30% was sufficient to kill most aspen trees within a few years after they attained 10 cm in diameter. This kept aspen biomass lower during early succession than in the no-browsing control but also allowed aspen to maintain dominance later in succession because it created canopy openings. Consequently, soil nitrogen availability eventually surpassed that of the control. However, eventually the unbrowsed spruce began to succeed aspen, and aspen dominance and ecosystem net primary production also declined.

The responses of spruce are particularly interesting because they were caused solely by changes in the altered growth rates of aspen and consequent changes in resource availability. They arise because of the indirect effects of browsing on competition between these two species for nitrogen and light. Spruce growth was greatest when moose browsing stimulated aspen growth (fig. 3, bottom left) because the enhanced nitrogen availability from the aspen litter benefited both tree species. However, the relative dominance of spruce was least under this scenario (fig. 3, bottom right). Spruce biomass was depressed under more intense moose browsing (fig. 3, bottom left) because of the depression of nitrogen availability, although it made up a greater proportion of total forest biomass (fig. 3, bottom right). Beaver browsing depressed both total spruce biomass and its proportion of total ecosystem biomass by maintaining the ecosystem in an early stage of succession.

Thus, changes in growth rates and competitive interactions caused by selective browsing on different-sized individuals of the same plant species caused different responses of ecosystem properties. Changes to these properties, particularly the availability of soil nitrogen, in turn enhanced the changes initially caused by these herbivores. Consequently, ecosystem properties continued to diverge. Thus, by altering the relative abundance of species, the effect of herbivory on ecosystem properties persists even after the ecosystem no longer can support the herbivore.

In these simulations, herbivores are important functional switches that alter the nature of positive feedbacks between plant species and soil nitrogen availability. This contrasts with hypotheses of herbivores as alternative pathways of nutrient flow (Kitchell et al. 1979; Woodmansee et al. 1981; DeAngelis et al. 1989; Jefferies 1989). In the latter view, the effect of herbivores on ecosystem properties would necessarily diminish soon after they were gone, but in the current simulations their effect is more long-term because the changes in plant community composition persist for many decades.

TOWARD A MORE GENERAL MODEL OF BOREAL FOOD WEBS

The link between plant chemistry, foraging behavior, and litter decomposition provides a basis for a general model of boreal food webs. We suggest that a general model of boreal food webs requires four trophic levels (decomposers, primary producers, herbivores, and predators) linked by a set of positive and
negative feedbacks with resource supplies. Primary producers in turn should be divided into palatable and unpalatable plants, partly on the basis of plant chemistry. This property links decomposers with herbivores by affecting both decay rates and digestibility. Decomposition in turn determines nutrient availability and feeds back on primary producers by limiting growth and thus influencing plant competition. Herbivores in turn alter species dominance and food supply, thereby determining the pathways of ecosystem development. Once a pathway is initiated by a particular foraging behavior, feedbacks between the plant species and resource availability amplify the trend. Ecosystem processes in different locations may diverge, depending on initial conditions, the nature of the feedback, and the resultant pathway. This affects future food supplies to all herbivores.

The theory presented here contrasts with that of Oksanen (1983, 1988) and Oksanen et al. (1981), which has been applied to northern ecosystems. The theory of Oksanen and his coworkers derives from the classic article of Hairston et al. (1960), which argued that predators limit herbivores, which in turn cannot therefore limit plant production. Competition for resources therefore determines the structure of plant communities. However, Hairston et al. recognized only water and light as limiting resources to producers. While they recognized that the decomposers' trophic level is limited by the supply of plant litter, they failed to recognize that the decomposition of that litter determines the supply of limiting nutrients to plants. Thus, the feedbacks between plants and decomposers via nitrogen availability presented here were not recognized by Hairston et al. Oksanen (1988) extended the theory of Hairston et al. by relating the structure of trophic levels to gradients of plant productivity. Oksanen argued that the top trophic level always regulates the next lower, and, as one moves down a food chain, regulation of trophic levels alternates between top-down regulation and competition between species within a level. Oksanen and his coworkers further argued that, because northern environments are harsh, plant populations are limited by climatically determined resource availability and cannot support a large enough herbivore population to affect them. As the potential productivity of a site increases, plant productivity becomes more able to support larger herbivore populations and is in turn regulated by them rather than resources. Very productive environments can support a third trophic level, namely predators, which in turn regulate the herbivores. However, like Hairston et al., Oksanen and his coworkers assumed that primary productivity is regulated by physical factors of the environment over which the plants have little influence. They also assumed that the biomass of the top trophic level is proportional to that of its prey and that prey are always available.

The application of the theories of Hairston et al. (1960) and Oksanen and his coworkers to northern environments contrasts with the theory presented here because they assumed that there is no feedback between plants and decomposers and, therefore, no biotic regulation of limiting resources, such as mineral nitrogen. However, in the tundra, recent experiments indicate that plant production is indeed limited by N and P availability (Haag 1974; McKendrick et al. 1978; Shaver and Chapin 1980; Chapin and Shaver 1985) and that the decomposition of humus in tundra is partially controlled by the chemistry of the plant litter from
which it is derived (Rosswall and Granhall 1980; Nadelhoffer et al., in press). Therefore, there is a significant potential for such feedback between plants and decomposers in tundra communities.

Oksanen (1988) also cites supportive experiments in which moose populations in exclosures were maintained at densities as high as five per square kilometer without damage to boreal forest vegetation (Bergstrom 1987). However, these experiments have been maintained only for five years, and we (Pastor et al. 1988; McInnes et al. 1992) and others (Krefting 1974; Snyder and Janke 1976), as well as the simulations presented here, demonstrate that moose do indeed affect plant communities with consequent changes in soil fertility over longer time periods. Oksanen et al. (1981) cite the early work of Mech (1966) on Isle Royale as an example of how moose populations in boreal forests regulate plant productivity until predators are introduced, whereupon the predators begin to control the moose populations. However, more recent research suggests that the situation is more complex and that both vegetation and wolves may play important but different roles in regulating moose populations, depending on the stage in the moose population cycle. Vegetation may set a ceiling on moose and wolf biomass (Botkin and Levantin 1977), especially if overbrowsing leads to malnutrition and predisposes moose to wolf predation (R. O. Peterson 1977). We suggest further that, if overbrowsing alters the composition of the vegetation sufficiently to depress soil nitrogen availability, then recovery of the vegetation on collapse of the moose population may be extremely limited.

Others have suggested that plant chemical defenses rather than predators regulate herbivores (Murdoch 1966; White 1978). The evidence for this remains somewhat controversial (Krebs and Myers 1974; Bryant 1987), and this may be one of several complementary rather than mutually exclusive hypotheses (Haukioja et al. 1983). We suggest that chemical defenses may have several consequences for ecosystems by partially regulating the quality of food to both herbivores and decomposers and thereby regulating food production through their effects on soil nutrient availability. Evidence for the multiple roles of particular secondary compounds has been recently presented by Horner et al. (1988).

Others also propose that herbivory creates positive feedbacks to nutrient cycles (Kitchell et al. 1979; Woodmansee et al. 1981; Jefferies 1988), mainly by return of fecal material. This feedback was not incorporated in the model simulations here. Although both feedbacks through feces and changes in plant composition may operate simultaneously, they operate on different time scales because they involve components with different turnover rates. Decomposition of fecal material is relatively rapid (Schimel et al. 1986; Ruess and McNaughton 1987; Ruess et al. 1989), but decomposition of plant litter and changes in species composition are slower. Therefore, the detection of their effects depends to a great degree on the time scales of the relevant experiments. A short-term experiment might detect an initial and local enhancement of nutrient availability through dung and urine deposition, but a long-term experiment might detect a decrease in nutrient availability associated with changes in plant community composition.

The model presented here could explain the extreme fluctuations in herbivore populations characteristic of boreal regions (Haukioja et al. 1983, and references
therein), some of the heterogeneity in boreal communities that is not explained by topography, climate, or disturbances (Larsen 1980; Van Cleve et al. 1983), and the interactions between resource heterogeneity and population fluctuations (Rosenzweig and Abramsky 1980). It is not inconceivable that such a model may apply to other terrestrial ecosystems as well.

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