

MOOSE-VEGETATION-SOIL INTERACTIONS: A DYNAMIC SYSTEM

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ABSTRACT: We review the processes by which moose (*Alces alces*) interact with vegetation at the module (leaf and shoot) and genet (individual plant) levels of organization, and show the consequences of these interactions for plant population, community, ecosystem, and landscape dynamics. Moose forage selectively on photosynthetic and meristematic tissues of a few preferred species. These species respond with compensatory growth and often tissues of higher forage quality, leading to a positive feedback at the module and genet level. However, height growth of browsed genets is often reduced or even curtailed by browsing, leading to higher levels of mortality and eventual replacement of browsed species by unbrowsed ones. These unbrowsed species (predominantly conifers) grow more slowly and have litter of low nutrient content that decomposes slowly. Consequently, even though moose browsing stimulates growth and browse availability at module and genet levels, ecosystem productivity and nitrogen cycling decline. Such feedbacks eventually lead to spatial patterns in the landscape. Genotypic and phenotypic differences within forage species modify these responses somewhat, and plant responses to moose browsing all differ somewhat along productivity gradients. Other herbivores, notably invertebrates, are also affected by these changes in vegetation. We conclude by suggesting some unanswered questions and new directions for future research.

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Through their foraging behavior, moose (*Alces alces*), the largest extant herbivore in boreal regions, exert many changes to plants, plant communities, and ecosystems. The purpose of this paper is to review the interactions between moose, vegetation, and soil at a number of hierarchical levels and to suggest gaps in our knowledge, and some experimental and modeling approaches to fill them.

These complex interactions between moose and plants occur at several nested hierarchical levels (Danell et al. in press). The lowest is the module level of meristematic tissues of leaves and shoots, the level of the primary foraging decisions of moose. The genet, or individual plant level, responds to the removal of

meristematic tissue through reallocations of carbon and nutrients to compensate for consumptive removals. In addition, the plant's responses to browsing affect the intensity and probability of future browsing. The genet must contend not only with removal of portions of its tissues, but also competition with its neighbors that may or may not have been browsed by moose. These interactions between the browsed genet and its neighbors affect both population dynamics (through changes in distributions of genotypes, sex ratios, reproductive potential, mortality, and age structure) and community composition (through shifts in dominance between browsed and unbrowsed species). To the extent that browsed and unbrowsed species differ in

functional attributes important to ecosystem processes, such as litter quality or N fixation rates, the changes in community structure caused by differential browsing translate into changes in ecosystem productivity and nutrient cycling rates. These higher order changes, especially in the cycling of limiting nutrients such as nitrogen, in turn feed back on all individuals in the plant community through changes in soil fertility. This cascade of interactions has both beneficial and detrimental consequences to the energy and nutrient balances of moose. Therefore, the effects of moose on vegetation are best viewed as a continuum of interactions (Hjältén et al. 1993) that constitute a dynamic system of multiple feedbacks of different temporal and spatial scales.

INTERACTIONS BETWEEN MOOSE AND PLANT MERISTEMS: THE MODULAR LEVEL

Moose Behavioral Decisions at the Modular Level

Browsing of leaves and shoots, both meristematic tissues, are the decisions made by moose that most immediately affect plants. Whether to browse shoots or leaves or both depends on plant species and growth form (deciduous vs. coniferous), season, and whether the plant has been previously browsed.

Deciduous trees, especially *Salix*, *Populus*, *Betula*, and *Sorbus* spp., are generally the preferred food of moose, especially in summer. Browsing of these species during summer consists almost entirely of leaf stripping. In winter, the bare current shoots of these species are also browsed, along with the current shoots (twigs and needles) of two conifers, *Pinus sylvestris* in Fennoscandia and Russia and *Abies balsamea*, particularly in the Maritime Provinces and New England, in North America.

Moose maximize energy intake per unit

time at the modular level by browsing larger shoots (Belovsky 1978, Spalinger and Hobbs 1992). As bite size increases, so does energy intake rate, but digestibility decreases because larger shoots contain higher proportions of lignified woody material (Vivas and Saether 1987). Moose therefore optimize shoot diameter to maximize energy intake rate within the constraints of decreasing digestibility; the optimal shoot diameter selected across a wide range of species appears to be 3 – 5 mm, depending on plant species (Shipley et al. 1999). Pastor et al. (1999a) showed that moose maximize energy intake rates per unit time by taking single bites most often and browsing approximately 3.5 g per bite. This bite size is similar to measurements independently made by Gross et al. (1993), Risenhoover (1987), and others reviewed by Renecker and Schwartz (1998).

Average dry matter intake rates by moose range between 30 – 45 g per minute (Belovsky and Jordan 1978; Belovsky 1981; Renecker and Hudson 1985, 1986; Shipley and Spalinger 1992; Spalinger and Hobbs 1992; Gross et al. 1993; Renecker and Schwartz 1998; Pastor et al. 1999a), or approximately 10 bites per minute of foraging. Given that foraging bouts last approximately 30 – 60 minutes and moose have 4 – 5 foraging bouts to meet daily requirements of 5 – 10 kg per day (Belovsky and Jordan 1978, Renecker and Hudson 1986, Renecker and Schwartz 1998), moose take approximately 1,500 – 3,000 bites or more per day.

Such a large number of bites each day can have a substantial impact on plants, especially since the bites are concentrated on photosynthetic or apical meristems. However, moose distribute these bites over a large portion of the landscape and rarely consume all available bites within a patch, usually taking only approximately 20% of bites available or 1 – 2 bites per individual plant (Shipley et al. 1998), except when a

food species is rare, whereupon it is heavily and repeatedly browsed (Brandner et al. 1990). Nonetheless, by making a large number of biting decisions per day and concentrating their impact on the browsing tips of a few plant species, moose have a great ability to affect growth of plants, competitive abilities between browsed and adjacent unbrowsed plants, plant succession, and ecosystem properties. Therefore, decisions made by moose at the modular level are also reflected at higher levels of vegetation organization.

Responses of Modules to Browsing

Deciduous trees whose leaves have been stripped have some capacity to regrow leaves the same season, but the ability to regrow leaves depends on shoot morphology, growth strategy, intensity and frequency of stripping, and site fertility. Experimental leaf stripping from *Betula pendula* resulted in lower standing leaf biomass by the end of the growing season, but refoliation produced a second crop of leaves such that total leaf production during the growing season (removed leaves plus regrown leaves) did not differ between stripped and control trees (Bergström and Danell 1995). However, 1 year after defoliation, total leaf biomass was lower than controls because defoliation decreased the number of shoots.

Responses of birches to current shoot removal during the non-growing season differ substantially from the above responses to defoliation and also depend on the type of shoot browsed. Birches and many other deciduous species (especially in the Betulaceae, Salicaceae, and Rosaceae) produce two types of shoots, termed “long” and “short” for obvious reasons. Long shoots are exclusively vegetative growth and are characterized by extreme apical dominance (hormonal suppression of bud emergence lower on the stem by the apical bud). Short

shoots are smaller side shoots with reproductive structures such as catkins, fruits, etc., that often emerge at their base. Long shoot dry mass, leaf dry mass, leaf number, leaf area, and chlorophyll and N content of leaves on long shoots are higher on moderately browsed *B. pendula* and *B. pubescens* than on slightly browsed trees (Danell et al. 1985, Bergström and Danell 1987). Some short shoots on moderately browsed birches can sometimes develop into long shoots, thus compensating for leaf biomass declines when short shoots are browsed (Danell et al. 1985). Although the number of long shoots sometimes declines following moderate browsing, the frequency of branched shoots increases (Bergström and Danell 1987). Senn and Haukioja (1994) show that these responses are primarily the result of removal of the apical buds and reduction in hormonal suppression of buds lower on the stem.

Shoot browsing also increases leaf nitrogen and chlorophyll contents in birches (Bergström 1984, Danell and Huss-Danell 1985, Danell et al. 1985, Danell et al. in press) and feltleaf willow (*Salix alaxensis*; Kielland et al. 1997). In contrast, defoliation decreases food quality of *B. pubescens* ssp. *tortuosa* leaves because of induced defenses (Haukioja et al. 1985, Hanhimäki 1989, Ruohomäki et al. 1992). Therefore, shoot browsing results in higher quality foliage the following year in birch and willow but defoliation results in lower quality leaves in subsequent crops during the same year. Because shoot and leaf browsing occur at different times of the year, the effect of removal of either tissue on subsequent leaf quality may also be a seasonal effect. Therefore, new experiments are needed in which shoots are removed in summer as well as winter to determine the interactive effects of shoot removal *per se* and season of removal on leaf chemistry.

Like deciduous species, *Pinus sylvestris*

also compensates for winter (shoot plus needles) browsing, but the compensation can be delayed for one or more years (Edenius et al. 1995) because growth in these pines is determinate rather than indeterminate as in the birches (Millard et al. 2001). Edenius et al. (1995) also found that densely grown pines compensate more for lost biomass than open grown pines.

Balsam fir (*Abies balsamea*) generally shows very little compensatory growth following browsing, and browsed stems eventually become progressively weaker and then die (Brandner et al. 1990, Thompson and Curran 1993).

Feedbacks between Modular Responses and Moose Foraging

The different responses of modules of deciduous and coniferous species to moose browsing affect the frequency and intensity of subsequent browsing on individual genets. Birches whose shoots were previously browsed by moose have a higher probability of being browsed again than unbrowsed or slightly browsed birches because of the higher leaf and stem chemical quality, large long shoots, and greater proportion of shoots within reach of moose (Bergström 1984, Danell and Huss-Danell 1985, Danell et al. 1985, Danell et al. in press). Thus, the compensatory growth response of birches to browsing at the modular level establishes a positive feedback loop at the genet level, resulting in even greater consumption in subsequent years.

These positive feedbacks between shoot browsing during winter, the higher quality of regrown leaves, and subsequent browsing are the opposite of that noted for leaves that had been stripped by moose during summer (Miquelle 1983) or wounded by insects during summer (Haukioja et al. 1985, Hanhimäki 1989, Ruohomäki et al. 1992). In summer, leaf stripping induces defenses that reduce probabilities of being consumed again. Thus,

leaf stripping in summer results in a negative feedback between moose and the browsed plant while winter browsing on shoots gives positive feedbacks. As noted above, new experiments are needed to sort out the direct effects of browsing vs. stripping *per se* from the indirect effects of season of browsing on changes in food quality.

In pines, the delay in compensatory response may temporarily release browsed pines from subsequent browsing, allowing some recovery (Edenius et al. 1995). As we shall see below, these different compensatory responses between deciduous species and conifers greatly affect competition with neighboring plants.

Balsam fir is also repeatedly browsed by moose, leading to a highly pruned growth form (Brandner et al. 1990). However, because compensatory regrowth is very small, many balsam fir escape from repeat browsing, especially on sites of high fir and low moose density (Brandner et al. 1990).

INTERACTIONS BETWEEN MOOSE AND WHOLE PLANTS: THE GENET LEVEL

Here, we consider how the decisions made by moose at the individual plant level depend in part on responses of the plant modules to browsing. We also consider the effect of genotype and phenotype on browsing intensity and recovery of plants, and the effect of browsing on whole plant growth and height growth.

Moose Foraging Decisions at the Genet Level

Besides decisions made at the modular level reviewed above, decisions made at the genet (individual tree) level are also important. Danell et al. (1991a) showed that moose foraging decisions are made at this level (consumption and preferences of individuals of a given species within stands are

the same regardless of stand composition) more than at the stand level (consumption and preference of individuals did not depend on stand composition, and so stand composition was not the primary decision on where to forage). Because of the compensatory and generally higher quality regrowth reviewed above, browsed plants, especially deciduous plants, have a higher probability of being rebrowsed, resulting in even greater consumption in subsequent years (Bergström 1984, Danell and Huss-Danell 1985, Danell et al. 1985, Danell et al. in press).

Genotypic and Phenotypic Differences in Susceptibility of Genets to Browsing

In a provenance study, Danell et al. (1991b) found that, when transplanting pines from different sites and exposing them in cafeteria tests to free-ranging moose, *P. sylvestris* individuals from fertile habitats were browsed more intensively than pines from infertile habitats because of their larger shoot size and higher quality food. Jia et al. (1995) showed that moose adjust bite diameters among phenotypes of *P. sylvestris* shoots according to shoot characteristics such as growth rate and nutrient contents: in general bite diameters are larger from phenotypes of higher productivity than lower productivity. Such differences in browsing preference and bite size may be at least partly genetically based because slowly growing northern genotypes of *P. sylvestris* are less preferred by moose than more rapidly growing southerly genotypes, even when grown in a common garden (Niemelä et al. 1989).

Balsam fir from the open habitats of thinned stands are more intensively browsed than those from unthinned stands because of higher crude fat, protein, and nutrient concentrations (Thompson et al. 1989). The fact that these chemical differences were responses to thinning rather than phenotypic

sorting along a fertility gradient shows that some of the phenotypic susceptibility of genets to browsing is environmentally rather than genetically based. On the other hand, balsam fir from the Maritime Provinces are much less defended than balsam fir from continental North America, and these broad geographic differences are believed to be genetically based (Hunt 1993). This may account for the greater proportion of balsam fir in the diet of moose in the Maritime Provinces (Bergerud and Manuel 1968) than in continental North America (Krefting 1974, Risenhoover and Maass, 1987, McInnes et al. 1992).

Within several birch species, genets also differ in susceptibility to browsing depending on biogeographic origin. In a common garden experiment, Bryant et al. (1989) found that Icelandic *B. pubescens* was more preferred by snowshoe hares (*Lepus americanus*) and Finnish mountain hares (*L. timidus*) than Finnish *B. pubescens* or *B. pendula*, which in turn were more preferred than Siberian *B. middendorffi*. This rank order is inversely related to the concentrations of resins and triterpene acids in internodes of these provenances. Moreover, Iceland did not have a resident mammalian population until settlement by Vikings in the 9th century, and Finnish hare populations are less dense than Siberian. This relationship between susceptibility to browsing and long-term coexistence with hare populations strongly suggests that biogeographic differences between genets in browse preference have resulted from co-evolution between the plants and browsing animals. Although no studies have demonstrated this specifically, the discrimination of moose between genotypes within a species may also lead to changes in the distribution of genotypes in the population, thus making moose a selection pressure on its forage species (Danell et al. in press).

Growth Responses of Genets to Browsing

Although compensatory growth of new shoots and side shoots often results in little or no decrease in total dry matter production in birches (Danell et al. 1985, Bergström and Danell 1987, Hjältén et al. 1993), height growth of birch can be greatly affected by browsing, depending on the type of tissue consumed. Defoliation of *B. pubescens* decreases height growth by almost 50% (Hjältén et al. 1993, Bergström and Danell 1995), presumably because of decreased shoot growth due to reductions in photosynthate. For established trees, shoot browsing decreases height growth of *B. pubescens* and *B. pendula* when large proportions of current shoots are removed (Bergström and Danell 1987, Hjältén et al. 1993). Height growth of *P. sylvestris* was also similarly decreased when 100% of current shoots were clipped (Edenius et al. 1995).

The height growth of seedlings and small suckers and ramets of deciduous species such as *Betula*, *Populus*, and *Salix* is almost always curtailed by browsing because such individuals consist almost entirely of a single shoot with one apical meristem. Browsing of this apical meristem releases the shoot from apical dominance (Senn and Haukioja 1994) and often kills the main stem (Krefting 1974, Heinen and Sharik 1990, McInnes et al. 1992). Although the total dry matter production of an individual genet is usually not curtailed outright by browsing, height growth of browsed seedlings and suckers is then curtailed in favor of increased production of new side shoots or new ramets.

EFFECT OF MOOSE BROWSING ON PLANT POPULATION DYNAMICS

The effects of moose at the module and genet levels are translated to the population level by their consequences for reproduc-

tion and establishment, mortality, and seed dispersal.

Reproductive Potential of Genets in Response to Browsing

Browsing generally decreases reproduction. The number of female catkins (and hence seed production) is reduced in *B. pendula* and *B. pubescens* with higher browsing intensity, although mean viable seed mass increased slightly, suggesting partial compensation in potential seed germination success to the reduction of seed number (Bergström and Danell 1987). In part, this may be due to reduced short shoot production of browsed plants, as noted above. Beaked hazelnut (*Corylus cornuta*), an important winter forage species for moose in North America, also usually does not set seed when browsed (Trottier 1981). Browsing also decreases cone production in *P. sylvestris*, especially with severe browsing on productive sites (Edenius et al. 1995).

Moose damage seedlings by trampling and uprooting, resulting in severe repression of establishment in some areas (Bergerud and Manuel 1968).

Mortality of Genets in Response to Browsing

In many studies, mortality of individuals was directly proportional to browsing intensity and the more preferred deciduous plant species had higher rates of mortality (Krefting 1974, Heinen and Sharik 1990, McInnes et al. 1992, Edenius et al. 1995, Danell et al. in press). Mortality rates are particularly high in the smaller size classes.

Mortality in response to browsing is higher on infertile soils, presumably because limiting nutrients and water are scarce enough to severely inhibit compensatory growth after browsing (Edenius et al. 1995).

Severe bark-stripping by moose almost always causes the stem to die because the

cambial tissue is removed when the stem is girdled (Miquelle and Van Ballenberghe 1989). In contrast, shoot or leaf browsing rarely appears to directly cause mortality, at least in deciduous species. Instead, mortalities of leaf stripped or shoot-browsed plants are directly proportional to the suppression of their height growth (Risenhoover and Maass 1987, Danell et al. in press).

This suggests that browsed individuals die because of increased light limitations as they become overtopped by adjacent unbrowsed individuals. The reduced height growth of seedlings of shade intolerant species puts them at a disadvantage when they are overtopped by unbrowsed neighbors, especially of less preferred conifer species. The recruitment of browsed deciduous seedlings and suckers into larger tree size classes is greatly reduced because of suppression of their growth by light limitations imposed by unbrowsed neighbors.

Support for this comes from experiments performed by Hjältjén et al. (1993), who found that compensatory height growth of *B. pubescens* decreases with increasing stand density, presumably because of increased severity of light competition to re-growing shoots from neighbors. McLaren (1996) also found that shoot-browsed balsam fir is more likely to die when canopy cover was greater than 60% compared to browsed individuals grown under a more open canopy.

Changes in Sex Ratios in Response to Browsing

Some of the most preferred species (*Populus* and *Salix*) are dioecious, that is, the male and female reproductive organs occur on different individuals. There is some limited evidence that some herbivores appear to prefer male individuals (Ågren et al. 1999), although whether this is enough to alter sex ratios and if so, if the alteration is large enough to be important evolutionarily,

is not known. This is an area deserving further investigation.

Changes in Forest Age Structure

Because moose populations cycle, they can change age structure of plant species as their foraging pressure waxes and wanes. For example, moose populations on Isle Royale cycle with a period of 38 ± 13 years (Peterson et al. 1984). Age structure of balsam fir also cycles coincident with this period (McLaren and Peterson 1994). McLaren and Peterson (1994) suggest that the moose-wolf predator-prey cycle results in periodic suppression (when moose populations are high) and release (when moose populations are low) of balsam fir, resulting in age gaps in the balsam fir population. Snyder and Janke (1976) also show dependence of age class distributions on moose population densities, not only of forage species, but of non-preferred species such as *Picea*, indicating that cycles in populations of preferred species affect competitors through imposition and release of competition for light and perhaps soil resources.

EFFECTS OF MOOSE BROWSING ON THE PLANT COMMUNITY AND ECOSYSTEM PROCESSES

Early successional boreal forests are often dominated by deciduous species such as *Populus*, *Betula*, and *Salix*, that not only are the preferred species of moose but also respond positively to moose browsing with regrowth of leaves that are higher in nitrogen, protein, and other nutrients. These leaves decompose more quickly than leaves from unbrowsed individuals of the same species (Irons et al. 1991, Kielland et al. 1997), leading to a temporary increase in ecosystem carbon turnover and nutrient cycling rates (Molvar et al. 1993, Kielland et al. 1997).

In the long run, however, numerous

studies comparing plant community composition inside and outside exclosures have shown that the abundances of preferred species, especially the deciduous species, decline as they are replaced by non-preferred species, especially *Picea* (Krefting 1974, Risenhoover and Maass 1987, McInnes et al. 1992, Thompson et al. 1992). In North America, there is a consistent shift from an aspen-birch-spruce-fir community to a more open and unbrowsed spruce (*Picea glauca*, *P. mariana*) community with an understory of heavily browsed preferred species with increased moose population density. In many areas, unbrowsed spruce is often the only species able to grow above browse height (Janke et al. 1978, Bryant and Chapin 1986, McInnes et al. 1992, Thompson and Curran 1993). The primary reason for this species replacement is the suppression of height growth of plants that are repeatedly browsed by moose, leading to their shade-induced mortality as noted above.

These long-term successional shifts in plant community composition towards non-preferred species greatly depress rates of ecosystem properties such as net primary productivity (McInnes et al. 1992) and nitrogen cycling (Pastor et al. 1993). The decline in productivity occurs for two reasons. First, non-preferred species grow more slowly than preferred species (Danell et al. 1985, Bryant and Chapin 1986, McInnes et al. 1992, Pastor and Naiman 1992). Secondly, non-preferred species have litter that is difficult to decompose because of low nitrogen and high lignin contents, the same reasons why moose, with microbially mediated ruminant digestion avoid them (Bryant and Chapin 1986, Pastor and Naiman 1992). The same chemical properties of tissues that cause moose to forage selectively also result in a depression of soil nitrogen availability of up to half that for forests without moose (Pastor et al.

1988, 1993; Pastor and Cohen 1997). This depression of soil nitrogen availability because of vegetation changes is not offset by local increases in nitrogen from fecal and urine deposition (Pastor et al. 1993, 1996; Pastor and Cohen 1997). Thus, decisions made by moose at the modular and genet level are reflected at the ecosystem level because the same plant chemical properties affect both digestive rate and nutrient cycling. Such effects on ecosystem properties are widely distributed across the landscape in characteristic patterns: patches of high density browse are heavily browsed, allowing unbrowsed conifers to invade and create coincident patches with lower available nitrogen (Pastor et al. 1998). Moose must therefore contend not only with changes at modular and individual plant levels, but also with the effect of these plant responses on the distribution of food across the landscape and the cycling of limiting nutrients to support that food.

Thus, at the module and genet levels, shoot browsing by moose, especially on deciduous species, has a positive effect on growth and tissue quality, which leads to repeated browsing. The repeated browsing keeps these shoots and individuals within browse height, thus temporarily increasing browse supply for moose. But in the long run, reproductive potential is decreased, height growth is suppressed, and these species yield to unbrowsed species that depress availability of soil nitrogen, leading to a decrease in the food supply, nitrogen cycling, and net primary production of the entire ecosystem.

Therefore, the effects of moose on vegetation appear to be a continuum of responses at several levels, sometimes positive (especially at the finest levels of vegetation organization) and other times negative (especially at plant community and ecosystem levels over the long run).

SECONDARY EFFECTS OF MOOSE BROWSING ON OTHER ANIMAL SPECIES

Moose browsing on vegetation has secondary effects on other animals, especially insects, at all levels of plant organization. Danell and Huss-Danell (1985) found greater abundance of a wide variety of insect types on shoots of moderately browsed *B. pendula* and *B. pubescens* than on shoots of unbrowsed individuals because of the higher nitrogen and chlorophyll contents of regrown leaves on browsed shoots. Surprisingly, mountain hare (*Lepus timidus*) did not appear to discriminate between browsed and unbrowsed birch shoots (Danell and Huss-Danell 1985).

Recently, Suominen et al. (1999a,b) showed that moose browsing increases light penetration to the forest floor, that in turn increases temperature and decreases soil moisture, thus favoring some invertebrate species, such as carabid beetles and disfavoring others, such as gastropods.

Increased leaf litter nitrogen and changes in tannin chemistry of browsed Alaskan paper birch (*Betula papyrifera* var. *humulis*, formerly *B. resinifera*) result in faster decay when these leaves are deposited in streams by trees growing in riparian zones (Irons et al. 1991). The effects of moose on litter chemistry of terrestrial species are thus translated into adjacent aquatic ecosystems as litter is transported across ecological boundaries.

Such secondary effects of moose on other trophic levels are only beginning to be recognized and deserve much more attention. For example, it would be particularly interesting to determine if bird communities differ between areas heavily impacted by moose compared with areas of low moose population.

SOME UNANSWERED QUESTIONS AND SUGGESTIONS FOR FUTURE RESEARCH

The Genetic Basis of Foraging Decisions by Moose and Plant Responses: Co-evolution of Moose and Plant Species?

A number of the studies reviewed above (e.g., Danell et al. 1985, 1991b; Bryant et al. 1989; Niemelä et al. 1989) have suggested that there are genotypic differences between individuals within the same species with respect to moose browsing preferences and plant responses. In general, faster growing genotypes are more preferred, have higher quality plant tissues, and show more compensatory growth than slower growing phenotypes. To determine the relative contributions of genetic and environmental controls on these plant properties, common garden experiments are needed across a wide range of site fertilities. It is entirely possible that some plant responses are controlled more by genotypic differences and others are controlled more by environmental differences. The relative expression of genetic and environmental factors may also differ along fertility gradients. The same genetic mechanisms that may determine quality of forage for moose also determine quality and decomposability of litter. We therefore have the fascinating possibility that moose selection among genotypes has consequences at the ecosystem level (Cohen et al. 2000).

Plant community dynamics may also exert a selection pressure on moose populations. Geist (1974) proposed that there are two phenotypes of moose: large bodied individuals with a high consumption rate that are at a selective advantage after large disturbances such as fire that generate much high quality food, such as regenerating *Populus*, and small-bodied individuals that persist when disturbances are small. Geist suggested that these phenotypes have

a genetic basis, but thus far this has not been demonstrated. It is also not clear whether these phenotypic differences in moose are a response to differences in quantity of food vs. quality of food in these two disturbance regimes. Nevertheless, there are some differences between resident and migratory moose populations in foraging behavior that suggest a genetic basis: Histøl and Hjeljord (1993) showed that migratory moose in Norway used habitats of lower quality, had a higher proportion of poorer quality *P. sylvestris* and *B. pubescens* in their diet, and rebrowsed previously browsed individuals more so than did resident moose. Histøl and Hjeljord (1993) suggest that this implies some genetic differences in foraging behavior between partly sympatric subpopulations with overlapping ranges. Although it is possible that genetic differences underlie these different behaviors in sympatric populations, other mechanisms are also possible (and not mutually exclusive), including learned behavior, stochastic differences in previous experience between populations, exclusion of migratory individuals from better habitats by resident individuals, etc. Nonetheless, the genetic basis of moose foraging clearly deserves more experimental attention.

There are also intriguing patterns in the fossil record that suggest co-evolution between moose and the plant species that constitute the current boreal forest biome. Moose arose fairly recently in the fossil record during the northern glacial advances of the late Pleiocene and early Pleistocene (Bubenik 1998), represented by the genera *Cervalces* and *Libralces*. The genus *Alces* arose from *Libralces* represented by at least 4 species, of which only *A. alces* survives. *A. alces* is believed to have originated in far eastern Siberia from ancestral stocks of *Alces gallicus* that previously had migrated east from Europe (Bubenik 1998, Hundertmark et al. 2002).

A. alces migrated east into the rest of North America and west into Scandinavia and the rest of Europe shortly after the last advance of the Wisconsin/Würm ice sheet, although the exact time is not certain (Bubenik 1998, Hundertmark et al. 2002). During these migrations, *A. alces* radiated into 8 subspecies, of which 7 survive (Groves and Grubb 1987).

At the same time that *A. alces* was undergoing these migrations and adaptive radiations, boreal species of the genera *Populus*, *Betula*, *Picea*, and *Abies* that constitute its present habitat also migrated northward following the retreat of the ice sheet, at least in North America (Larsen 1980). Hundertmark et al. (2002) propose that a cool climate during the last glacial period contracted and fragmented moose habitat, which led to sparse and isolated populations from which the current subspecies evolved during the expansion and reorganization of habitat in the subsequent current interglacial period. Therefore, it is interesting to speculate that the current complex relationships between moose and vegetation reviewed above arose when the circumpolar boreal forest became assembled, suggesting possible co-evolution between moose and the plant species they require for food and shelter (Bryant et al. 1989).

Moose-Vegetation Interactions along Productivity Gradients

Studies reviewed above (e.g., Danell et al. 1991a,b; McInnes et al. 1992; Edenius et al. 1993) show that moose browsing affects plant performance and responses differently along site productivity gradients. However, moose population densities also vary along productivity gradients (e.g., Peterson et al. 1984, McLaren and Peterson 1994) and so the performance and responses of plants along productivity gradients is confounded with moose population density

and hence foraging pressure. To sort out these confounding factors, controlled experiments comparing simulated browsing at different intensities to natural browsing are required along productivity gradients.

We and our colleagues and students have been engaged in one such experiment for the past 4 years. Exclosures, 70 x 70 m in size, have been established on 8 sites representing a productivity gradient in northern Sweden. The sites were all clearcut 8-10 years ago and planted to *P. sylvestris*. On the least productive sites, the pines coexist mainly with dwarf shrubs and lichens while on the most productive sites the pines coexist with deciduous species such as *B. pendula*, *P. tremula*, *Rubus chamaemorus*, grasses, and herbs. We have subdivided each exclosure into 4 subplots. Within each subplot (25 x 25 m) we are simulating moose browsing by clipping at an intensity corresponding to 0, 1, 3, and 5 moose per 100 ha, distributed amongst species according to dietary preferences of moose on these sites. We also add urine and fecal material at rates corresponding to these population densities. Our colleagues and we are measuring changes in plant growth, litter fall, soil temperature and moisture, soil nitrogen availability, and soil invertebrate diversity and population density. Preliminary results after 3 years of the experiment indicate reductions in litter fall with increasing browsing pressure and proportionally greater reductions of litter fall on productive than unproductive sites (Inga-Lill Persson et al., unpublished data).

Moose-Landscape Interactions: How Do Moose Forage in Landscapes Previously Affected by Other Moose?

Older studies of moose-habitat relations (Phillips et al. 1973, Peek et al. 1976) have assumed that habitats change independently of moose and moose adjust their movements accordingly. The research re-

viewed here suggests otherwise, namely that through their foraging decisions moose greatly affect the abundance and distribution of both browsed and unbrowsed plant species and ecosystem properties, and that such interactions produce patterns in the landscape (e.g., Pastor et al. 1998). This raises the interesting question of how moose and their progeny deal with landscape patterns that previous generations of moose have made.

To answer this question, Moen et al. (1997a, 1998) developed a simulation model of the energetics of a foraging moose in a spatially explicit landscape, parameterized by many of the empirical relations and data in the above papers and in the moose physiology literature (Hudson and White 1985). Foraging decisions are made on the basis of several rules: how much to eat at a given spot; when to stop eating; and where to move to next. The model has been well validated against independent data (Moen et al. 1997a, 1998). Moen et al. (1997a, 1998) show that the foraging strategy of moose creates different patterns in the landscape, which in turn affect the energy balance of a moose. In particular, foraging according to the marginal value theorem generates a landscape that cannot support moose populations in the long run: areas of high browse density are browsed heavily to reduce them to the average browse density of a landscape and areas of browse density lower than the marginal value criteria are bypassed and then grow out of reach. The net result is a landscape of low forage availability because of suppression of growth in areas of heavy browsing coupled with areas where forage has grown out of reach when not browsed. A strategy which seems to sustain moose populations at positive energy balances appears to be to browse 20-30% of that available at a feeding station then move to the best nearest patch until the rumen is full, then begin randomly at some

other point in the landscape for the next foraging bout (Moen et al. 1998), similar to that found for free-ranging moose by Shipley et al. (1998). Pastor et al. (1999b) showed that this strategy produces a simulated landscape whose pattern matches that of real landscapes on Isle Royale (Pastor et al. 1998). Therefore, there may be a strong feedback between the generation of landscape pattern and the energetics of foraging moose and how they expend energy to search for food. If so, the effect of moose on landscape patterns could be a strong selection pressure for genotypes of certain foraging behaviors.

Testing of the predictions of moose movement patterns requires the sampling intensity, continuity, and accuracy of GPS collars (Moen et al. 1996, 1997b). Our colleagues and we are now engaged in analyzing such data gathered over the past 7 years or so, and data are also being gathered by others. Further advances in GPS collar technology and model development should help clarify the answers to this question, but may also raise others. For example, do some moose “cheat” on other moose – that is, can some moose employ the marginal value strategy if other moose employ other strategies that maintain a landscape that enables a positive energy balance? How do moose simultaneously adjust their movement patterns in response to both their effects on the landscape and also to avoid predators?

In conclusion, the interactions of moose with vegetation are a continuum of nested responses and feedbacks, some positive and some negative, and are more extensive than previously thought. Studies of these interactions have caused us to revise older, more static ideas of moose-habitat relationships. Instead the current picture is a more dynamic one of nested responses at different levels of ecological organization.

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