Effects of moose *Alces alces* population density and site productivity on the canopy geometries of birch *Betula pubescens* and *B. pendula* and Scots pine *Pinus sylvestris*

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De Jager, N.R. & Pastor, J. 2008: Effects of moose *Alces alces* population density and site productivity on the canopy geometries of birch *Betula pubescens* and *B. pendula* and Scots pine *Pinus sylvestris*. - Wildl. Biol. 14: 251-262.

The instantaneous rate of food intake for mammalian herbivores is controlled by the geometry of plant communities which regulates the encounter rate with bites, bite mass and the processing rate of bites. The geometry of plant canopies is fractal because bite density only occupies a fraction of the entire dimension of the tree canopy and scales allometrically with the search resolution of herbivores. We tested the hypothesis that both the population density of moose *Alces alces* and site productivity alter the fractal geometry of plant canopies as well as bite mass, and therefore the mechanisms regulating herbivore functional response. Sapling birch *Betula pubescens* and *B. pendula* and Scots pine *Pinus sylvestris* in northern coastal Sweden were sampled in five exclosures that spanned the range of site productivities for the region. Within each exclosure and over four years, the effects of four population densities of moose (0, 10, 30, and 50 moose/1,000 ha) were experimentally simulated within treatment plots. The fractal dimension of bite density of Scots pine decreased non-linearly with increasing moose population density regardless of site productivity. In contrast, the fractal dimension of bite density for birch increased strongly from low to intermediate moose densities regardless of site productivity, but decreased with further increases in moose population density. For birch, the decreases in fractal dimension were greater on sites of low productivity. Bite mass decreased linearly with increases in experimental moose density for both species, but the decrease was moderated by increases in site productivity. The different geometric responses of birch and Scots pine saplings to moose population density resulted in an increase in predicted plant biomass for birch, a decrease in plant biomass for Scots pine, and decreases in predicted herbivore intake rate for both species with increased moose population density. Thus, there are strong feedbacks between population density, site productivity and the geometry of plant canopies regulating herbivore functional response.

Key words: allometry, birch, bite mass, foraging, fractal geometry, Scots pine, soil fertility

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Received 4 December 2006, accepted 28 June 2006

Associate Editor: Atle Mysterud

The functional response of herbivores may underlie their population dynamics (Illius 2006) and control the cycling of nutrients and energy through ecosystems dominated by herbivores (Hilder & Mottershead 1963, Schimel et al. 1986, Detling 1988, Ruess & McNaughton 1988, Hobbs et al. 1991). Functional response is the change in an animal's feeding rate with changes in food abundance (Solomon 1949, Holling 1959) and controls the amount of time animals invest in feeding and thus their potential impacts on vegetation. It was long held that the feeding rates of herbivores increased with food biomass (Allden & Whittaker 1970, Wickstrom et al. 1984, Hudson & Watkins 1986, Renecker & Hudson 1986, Hudson & Frank 1987). But mechanistic models of functional response have shown that the geometric properties of plant communities, rather than total plant biomass, control intake through the rate at which herbivores encounter bites and the processing rates of plant tissue which in turn depends on bite mass (Spalinger & Hobbs 1992, Hobbs et al. 2003). Plant biomass only controls herbivore functional response when it is correlated with these aspects of plant geometry. This is often the case in grazing systems, but not in browsing systems (Spalinger & Hobbs 1992).

Moose *Alces alces* are large browsing herbivores that require 5-10 kg dry mass of forage per day (Schwartz et. al 1984, Renecker & Hudson 1985), and to achieve that they can take 3,000 bites daily (Pastor & Danell 2003). By changing plant growth and morphology and the composition of litter returned to the soil, these bites eventually stimulate large changes in both forage production and the soil fertility that sustains long-term forage production (Pastor & Danell 2003). Previous studies suggest that the geometric structure of tree crowns may respond to such a large number of bites in a variety of ways (Danell et al. 1985, Hjältén et al. 1993). Browsing of apical shoots of deciduous trees and shrubs may stimulate the indeterminant growth of lateral shoots within the same year as herbivory because of the removal of apical dominance, which tends to restrict lateral growth in plants (Aarssen & Irwin 1991). In contrast to deciduous trees, growth of conifers is usually determinate rather than indeterminate (Millard et. al 2001) and any compensation by conifers for tissue lost to herbivory can be delayed for one or more years. Although the different growth responses between conifers and deciduous trees to herbivory suggest that moose can alter the geometries of these species in different ways, no study has systematically examined how they differ among different species, with different population densities, and on sites of different productivities.

Fractal geometry provides a simple mathematical framework for quantifying and understanding geometric changes in plant crowns and relating them to the mechanisms regulating feeding rates and ecosystem dynamics. Woody plants with branching architecture are self-similar fractal objects (Mandelbrot 1983, Frontier 1987, Vleck & Cheung 1986, Crawford & Young 1990, Zeide 1990). In fractal structures, the measured quantities vary as a power of the resolution at which the measurements are made (Mandelbrot 1983, Stanley 1986, Lauwerier 1991). Because foraging is hierarchical (Senft et al. 1987) multiple resolutions (i.e. scales) pertain to foraging animals. At a very fine scale the volume of the animal's mouth may set the measurement resolution (Gordon & Illius 1988). At fine scales, bites of plant tissue scale as a $1/3$ power of mouth volume (T. Hobbs, pers. comm.). But we focus on larger scales in this study, such as when animals survey the density of bites on plants. At the level of the individual plant the search width of the animal determines the resolution at which measurements are made. In the case of animals foraging on individual trees, the density of bites piercing the outermost hemispheric surface of the tree crown (and therefore accessible to the animal) is the measured quantity of interest. Each bite represents the intersection of the center of a twig with the outermost hemispheric surface of the crown. The pertinent measurement resolution is the search width (W, cm) of the animal. Essentially, the herbivore 'measures' or samples the density of bites as it swings its head from side to side. If the bites are regularly distributed over the surface, then the density is

constant for all search widths. If the bites are randomly distributed over the surface, then density varies as a normally distributed random variable about a stationary mean. If, however, the bites are distributed over the surface in a fractal (self-similar) pattern because of an underling fractal branching structure, then the total number of bites on the surface varies with some power, d, of some linear dimension of the surface, namely, the animal's search width W (Fig. 1). The fractal density of bites per area (D_f, in bites/cm^2) is then equal to the total number of points divided by the linear dimension squared as follows:

$$D_f = \frac{kW^d}{W^2} = kW^{d-2} \qquad (1)$$

where k is bite density (bites/cm^3) when W = 1, and the exponent (d-2) is a function of the fractal dimension of bites (see Appendix A in Spalinger & Hobbs 1992).

In fractal geometry, as in Euclidean geometry, the dimension describes the tendency of the measured objects to fill the space within which they occur (Milne et al. 1992). However, unlike Euclidean objects, fractal objects occupy only a fraction of the entire dimension and consequently exhibit 'fractional' or fractal dimensions (Mandelbrot 1983, Zeide 1990, Lauwerier 1991). In the case of the fractal density of the points where the twigs pierce the outermost surface of tree crowns, if the bites are regularly or randomly distributed over the surface, then as the density increases the bites eventually cover the entire surface. But for a fractal distribution, the bites will never completely cover the surface as the density increases.

Recently, West et al. (1997, 1999) have proposed a general allometric theory for scaling of metabolic rate to body mass in organisms, such as trees, in which resources are delivered to growing tips through branching structures or fractal networks. West et al. (1997, 1999) examine the fractal geometry of these networks as an optimum solution to a static problem such as continuity of flow and the delivery of water and nutrients to growing tips. But these and other studies have not considered the possibility that the fractal geometry of woody plants can change over time in response to changes in growing conditions such as with herbivory and site productivity. We are aware of only two studies that treat the fractal geometry of plant canopies as a dynamic property of a plant-herbivore system rather than an optimal solution in a static system with fixed constraints, and those are Escos et al. (1997) and Alados et al. (1999). Escos et al. (1997) found increases in the fractal dimension of the Mediterranean shrub *Anthyllis cytisoides* with moderate herbivory by sheep and goats, but decreases in fractal dimension at higher levels of grazing. Using the same species, Alados et al. (1999) found higher fractal dimensions for grazed than for ungrazed shrubs and higher fractal dimensions for shrubs on northern exposures than on southern exposures. We hypothesize that moose population density and site productivity alter the fractal geometry of woody plants through the removal of stems and by altering subsequent plant growth.

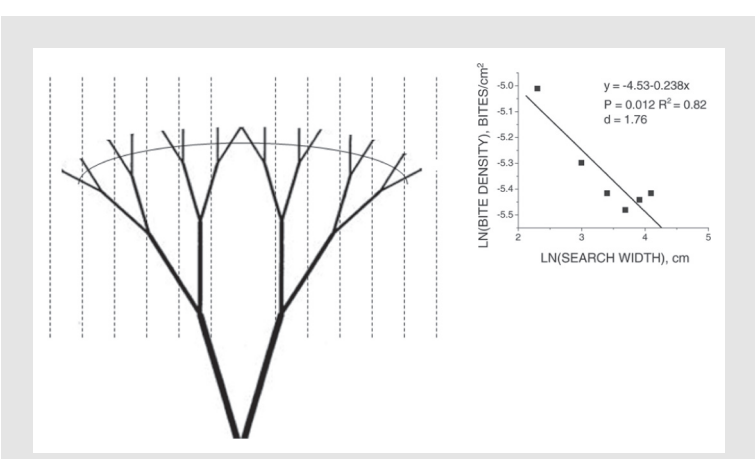

Figure 1. An idealized fractal branching structure (tree) with dashed lines indicating animal search width (W, cm) and a solid curved line exposing the twigs on the outermost hemispheric surface of the tree crown, which the animal surveys as bites of plant tissue. By plotting the ln cumulative bite density against ln search width, the fractal dimension of bite density can be calculated from Equation 1. For this idealized tree d = 2.0-0.24 = 1.76 and k = exp(-4.53) = 0.01078.

Material and methods

Study sites

We made use of a large ongoing experiment in northern coastal Sweden to examine the interactive effects of moose population density and site productivity on plant and ecosystem responses to browsing (Persson et al. 2005a,b). Five, 70 × 70 m exclosures were constructed

50-90 km north and northwest of Umeå, Sweden (63°50'N, 20°18'E) in young forest stands of Scots pine *Pinus sylvestris* planted following clear-cutting approximately 11 years previously and interspersed with naturally reproducing birches *Betula pubescens* and *B. pendula*. The sites were selected along a forest productivity gradient spanning the range of productivities for the region (Hägglund & Lundmark 1987, Fridman et al. 2001). Site productivity was estimated by the maximum height growth of Scots pine at 100 years, otherwise known as 'site index' (Lindgren et al. 1994, Elfving & Kiviste 1997). Other measures of productivity included litter production in the control plot (0 moose/1,000 ha). The amount of litter collected from the control plot at each site is from Persson et al. (2005b) and given in Table 1 along with the site index.

Within each exclosure, browsing at four moose population densities (0, 10, 30, and 50 moose/1,000 ha) were each simulated in 25×25 m plots beginning in early spring 1999. A full description of the methods used to simulate moose foraging are given in Persson et al. (2005a) and briefly summarized here. Simulated browsing occurred at random but in proportion to the dietary composition of moose (Belovsky & Jordan 1978, Cederlund et al. 1980, Shipley et al. 1998). Throughout the summer, leaves were stripped from hardwoods, while twigs of conifers and hardwoods were clipped during winter in proportion to the appropriate moose population density. Dung and urine were also applied to the sites at random and in proportion to the appropriate population density. At a couple of sites it was not possible to obtain enough biomass to support 50 moose/1,000 ha. If this was the case, as much biomass was removed as possible and 1/5 and 3/5 of that amount were taken from the '10 and 30 moose/1,000 ha' plots, respectively. In this manner, the same proportional moose densities were maintained at each site. The actual experimental moose densities in the '50 moose/1,000 ha' plots are given in Table 1.

Measurement of the fractal dimension of bite density and other architectural features

We measured architectural changes in two of the most important food plants for moose in Sweden, Scots pine during winter and birch year round, in response to increasing moose population density and site productivity. During early June, 2003, after four years of simulated browsing within the four treatment plots at each of the five sites, the fractal dimension of bite density, bite mass, tree crown width and tree height were measured on the nearest birch and pine trees >50 cm in height at 5 m intervals along transects 5 m apart until a total of nine trees for both birch and pine were measured in each treatment plot.

To aid these measurements, we used a definition of a feeding station as the volume of food on trees accessible to a browsing animal without moving both forefeet (Senft et al. 1987). We then constructed a sampling frame (Fig. 2) to serve as a template for the area of a feeding station. The sampling frame was 80 cm in lateral width because most trees in the experimental plots were less than 80 cm wide, and because moose are able to swing their head to cover at least 80 cm (N.R. De Jager & J. Pastor, pers. obs.). The frame was 30 cm deep, the distance measured from the tip of the nose to the bell of a bull moose specimen in the collections of the Department of Biology, University of Minnesota Duluth, and therefore the distance into the crown that a moose can forage. The frame was 60 cm in vertical width, twice the distance measured from the tip of the nose to the bell of an average adult bull moose, a reasonable minimum estimation of the range of vertical head movement. The volume of the frame therefore represents a portion of a hemispheric shell in which a moose can forage when at a feeding

Table 1. Exclosures were constructed at five sites that varied in terms of annual litter production (g/m^2/year; $\pm$SE) and site index (m) for pine. Within these exclosures the activities of four moose population densities were simulated (0, 10, 30, and 50 moose/1,000 ha). At some sites it was not possible to remove enough biomass to support 50 moose/1,000 ha and the actual supportable moose population is given.

Site	Litter	Site index	Age	Geographic position	Moose density
Lögdåberget	15.34 (4.14)	13	16	64°00'N, 18°45'E	32
Skatan	22.75 (3.82)	15	9	64°13'N, 19°09'E	38
Ralberget	32.22 (7.17)	27	9	64°13'N, 20°42'E	51
Mörtsjöstavaren	60.16 (7.96)	26	7	64°22'N, 20°07'E	50
Åtmyrberget	87.28 (8.53)	25	9	64°12'N, 19°17'E	47

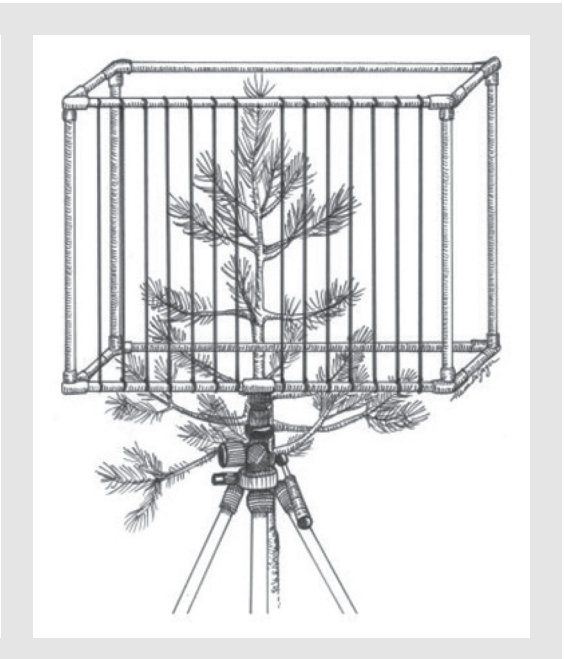

Figure 2. We constructed a 3-dimensional sampling frame in order to quantify the fractal dimension of bite density across the surface of tree crowns.

station. In the field, the frame was placed on an adjustable tripod adjacent to each sampled tree. The frame was adjusted against a sample tree to encompass the top shoot and centered with the outermost branch just protruding through its front face (see Fig. 2). The maximum height of the frame and tripod was 350 cm, which is at most, how high an adult moose can forage (N.R. De Jager & J. Pastor, pers. obs.).

Once the frame was positioned on the tree, the number of twigs (bites) was counted at different lateral search widths beginning with the center 10 cm and moving outward toward the edges of the frame at 10 cm intervals. The width between the teeth rows of an adult moose as measured in our laboratory is approximately 10 cm. The parameters d and k in Equation 1 were estimated by regressing the logarithm of bite density (D_f) against the logarithm of search width (W). The fractal dimension of bite density (d) was estimated by adding two to the slope of the regression line (d-2), and k was estimated by taking the anti-logarithm of the y-intercept.

Total tree crown width (W_T, cm) was measured as the width of the entire tree crown that resided within the 80 cm sampling frame shown in Figure 1. Otherwise, if the tree was larger than the sampling frame, total tree crown width was set at 80 cm to correspond to the effective crown width reachable by moose at a feeding station. Tree height was estimated with a standard height pole and rounded to the nearest cm.

Bite mass (S, g/bite) was measured by selecting the first 10 twigs within the sampling frame and measuring twig length from the tip to the mean bite diameters observed to be browsed in the areas, which are 2.5 mm for birch and 4.0 mm for pine (R. Bergström & K. Danell, unpubl. data). If the diameter of a twig was less than 2.5 or 4.0 mm for the respective trees, the length of the twig was measured from the tip to the point where it branched into a second twig large enough to be considered a distinct bite (approximately >10 cm in length or about the amount one can fit in the hand when mimicking the act of a moose biting a twig) and both the diameter and length were recorded. If a total of 10 twigs were not found within the sampling frame, twigs from outside the sampling frame but on the same tree were sampled to obtain data on 10 twigs on each tree sampled. Regression equations developed by Persson et al. (2005a) were then used to determine the dry weight of birch and Scots pine twigs from their basal diameters and lengths. These estimates yield the average bite size a moose would be expected to take from these trees during winter.

Statistical analyses

Statistical analyses were carried out in the statistical computing environment 'R' (R Development Core Team 2006). We began by examining the relationship between the logarithm of fractal bite density (D_f) and the logarithm of animal search width (W, cm) for the 351 trees sampled. Trees with P-values of >0.1 were considered to have a high level of variability in the slope of the regression, making the estimate of the fractal dimension of bite density inaccurate. We chose to use $P=0.1$ as the criterion because many heavily browsed trees were reduced to very narrow crown widths, which resulted in few degrees of freedom for the regression. In further analyses of fractal dimension, we only used trees that had reliable estimates for d to avoid bias due to inaccurate fractal dimensions in further results. We included all plants sampled in analyses of bite mass, tree height and crown width. There is currently no accepted protocol for accepting or rejecting whether something has a significant fractal dimension (Halley et al. 2004).

We used analysis of covariance (Ancova) to determine how the fractal dimension of bite density

(d), bite density at the unit crown width (k), bite mass, tree height and the width of tree crowns responded to increasing experimental moose density, and whether site productivity interacted with moose density to alter the slope of regression equations, similar to Persson et al. (2005b). We used Kolmogorov-Smirnov to test for normality. We used the most accurate estimate of moose population density at the treatment plots because '50 moose/1,000 ha' was not always attained at each plot (see above). This provided 20 estimates of experimental moose density. We then pooled sites into high or low productivity to obtain replication within two broad productivity categories. The low productivity sites were Lögdåberget and Skatan where both measurements of site index and litterfall were lowest. Therefore, site productivity was used as the categorical factor and experimental moose density as the covariate in Ancova.

We tested for higher order effects of moose density by including a second order term for experimental moose density. We also tested for interactions between site productivity and second order moose density with Ancova models. Note that moose population density controls the coefficient of the linear term and the second order term for moose population density controls the coefficient of the non-linear term in the model, while site productivity regulates the y-intercept. Interactions between site productivity and moose density alter the coefficients of both linear and non-linear terms. Beginning with the most complex model (all terms), we used the 'step' function in 'R' (R Development Core Team 2006) to choose the more parsimonious model that explained the most variation in each plant architecture measurement. The 'step' command causes all the terms in the model to be tested to see whether they are needed in the minimum adequate model. 'Step' uses the Akaike Information Criterion, AIC, as model selection criterion. In the general case, the AIC is

$$AIC = 2k\text{-}2\ln(L),$$

where k is the number of parameters, and L is the likelihood function. AIC weighs the trade-off between degrees of freedom and model fit. AIC adds two times the number of parameters to the model deviance. Deviance is twice the log likelihood of the current model (Burnham & Anderson 2002). We selected models with the lowest AIC, but only if all coefficients in the model were significant (t-test: $P < 0.05$).

Estimates of plant biomass and changes in functional response

We predicted available forage biomass for a particular moose population density and site productivity by first calculating the average density of bites per feeding station ($\overline{D}$, bites/cm^2) by inserting the Ancova regression equations for d, k, and W_T into Equation 1.

$$D_{m,i,j} = k_{m,i,j} W_{m,i,j}^{\,d_{m,i,j}-2} \qquad (2).$$

Here m represents moose population density and i represents site productivity, which are both used to estimate the parameter of interest (d, k, W, and eventually D) for plant species i. Then we multiplied this estimate by the bite mass ($\overline{S}_{i,j,m}$, g/bite) at those feeding stations and the average projected surface area of the feeding station ($\overline{W}_{i,j,m} \times 60$ cm in height, cm^2):

$$F_{i,j,m} = D_{i,j,m} \times S_{i,j,m} \times W_{i,j,m} \times 60 \qquad (3).$$

This is the predicted amount of available forage biomass a moose views as it faces a sapling of species i located in a landscape with moose population density m and site productivity j. We then multiplied the available forage biomass by two to attain the predicted biomass available per plant (g/plant).

We also calculated predicted changes in the intake rate (g/minute) of moose feeding on saplings of species i located in a landscape with moose population density m and site productivity j by the following equation:

$$I_{i,j,m} = \frac{R_{max} S_{i,j,m}}{R_{max}\overline{h} + S_{i,j,m}} \qquad (4),$$

where R_{max} is the maximum food processing rate in the mouth in absence of cropping additional bites (g/minute) and $\overline{h}$; is cropping rate (minutes/bite). We used 48.5 g/minute for R_{max} (Shipley & Spalinger 1992) and 0.037 minute/bite for $\overline{h}$; (Shipley et al. 1994) and the equations developed in this paper for changes in bite mass in response to experimental moose density and site productivity were substituted for S (g/bite).

Results

Fractal architecture

Out of 171 birch saplings, 145 (84.79%) had significant regressions between search width and fractal bite density (Equation 1) on the outermost hemispheric surface of the tree crown and out of 180 pines

sampled, 135 (75%) had significant regressions. The limiting factor for trees conforming to Equation 1 appeared to be the width of tree crowns because narrower tree crowns, often as a result of heavy browsing, imparted fewer data points for the regressions between search width and fractal bite density.

For birch, the fractal dimension of bite density responded quadratically to increasing experimental moose density ($R^2 = 0.52$, $P = 0.009$; Fig. 3), first increasing with moose density to moderate levels and decreasing thereafter. The model with the lowest AIC consisted of both linear and non-linear effects of experimental moose density and an interaction between experimental moose density squared and site productivity. The interaction between experimental moose density squared and site productivity produced a sharper decline in fractal dimension with increasing moose density at sites of low productivity (see Fig. 3).

In contrast to birch, the fractal dimension of bite density for pine decreased monotonically with increasing experimental moose density ($R^2 = 0.56$, $P < 0.001$; see Fig. 3). The model with the lowest AIC value consisted of a non-linear decrease in fractal dimension with increasing experimental moose density and no effect of site productivity or interactions between site and experimental moose density.

A null model consisting of a y-intercept but no significant slope terms or interactions between site productivity and experimental moose density had the lowest AIC value for bite density at the unit crown width (k) for both birch and pine. Therefore, this term, k, in Equation 1 was not affected by either moose population density or by site productivity, and can be modeled as a constant 0.0279 ($\pm$0.001314 SE) for birch and 0.0218 ($\pm$0.001335 SE) for pine.

Other architectural features of plants, i.e. bite mass, crown width and tree height

A linear model consisting of site differences in y-intercept and experimental moose density by site interactions altering the slope of the line had the lowest AIC ($R^2 = 0.7251$, $P < 0.001$) for bite mass of birch. This indicates that bite mass declines more rapidly with increased moose density at sites of low productivity than at sites of high productivity (Fig. 4). Bite mass of pine also decreased with increasing moose density. The model with the lowest AIC was a linear decrease in bite mass with increases in experimental moose density and site differences in y-intercept ($R^2 = 0.65$, $P < 0.001$; see Fig. 4).

A non-linear model consisting of site differences in y-intercept, a non-linear decrease in crown width with increasing moose density, and site by moose density interaction had the lowest AIC ($R^2 = 0.77$, $P < 0.001$) for birch. The model shows a sharper decline in the crown width of birch trees at sites of lower productivity than sites of higher productivity (see Fig. 4). Crown width of pine also decreased non-linearly with increasing moose density, and there was a significant interaction between moose density and site productivity producing a sharper decrease in crown width at sites of low productivity ($R^2 = 0.69$, $P < 0.001$; see Fig. 4).

Tree height decreased with increasing moose density for both species. A non-linear decrease in tree height with no effect of site productivity or interactions had the lowest AIC value for birch ($R^2 = 0.41$, $P = 0.003$; see Fig. 4). A linear model consisting of different y-intercepts due to site productivity and linear decreases in tree height with increasing moose density had the lowest AIC value for pine ($R^2 = 0.52$, $P = 0.002$; see Fig. 4).

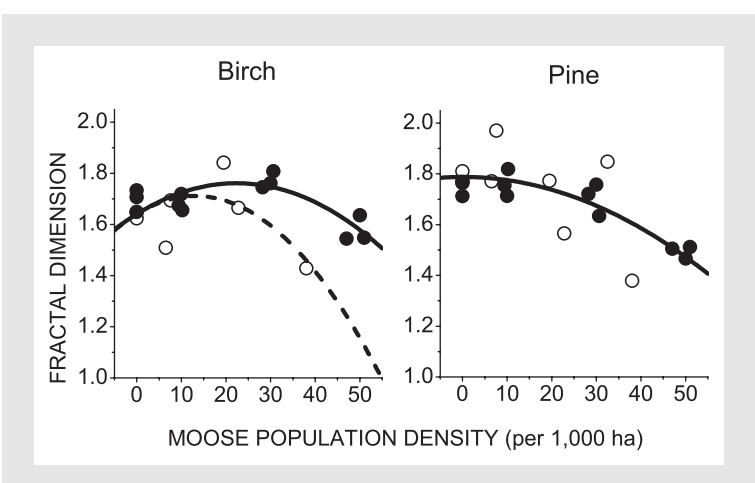

Figure 3. Fractal dimension varied quadratically for birch and decreased non-linearly for Scots pine with increasing experimental moose density. Open circles correspond with the low productivity sites and dark circles with the high productivity sites. For birch, the dashed line is the Ancova model for the low productivity sites and the solid line applies to the high productivity sites. For Scots pine, the dark line applies to all sites.

Changes in plant biomass and functional response

Unless they are exactly compensatory, both the changes in the fractal dimension of bites and bite mass at different moose population densities and site productivities alters plant biomass, but they may affect plant biomass in different ways. The quadratic response of the fractal dimension of birch overrides the linearly decreasing bite mass with increasing moose density, resulting in increased plant biomass to a maximum at six moose/1,000 ha at low productivity sites and 16 moose/1,000 ha at high productivity sites and decreased plant biomass thereafter (Fig. 5).

In contrast to the quadratic response of birch, predictions of plant biomass for Scots pine decline monotonically with increases in moose density because of decreases in both bite mass and the fractal dimension of bite density (see Fig. 5). This prediction applies to both low and high productivity sites with only minor differences between productivities.

Because the changes in the fractal dimension of bite density and bite mass were not exactly compensatory, changes in intake rate should also occur in response to increasing moose population density. Despite increases in plant biomass for birch, the feeding rate of moose on these plants decreases with any increase in moose density because of the impact of browsing on bite mass (see Fig. 5). For pine, because declines occurred in both bite mass and fractal dimension, both plant biomass and intake rate decrease correspondingly with increasing moose density (see Fig. 5).

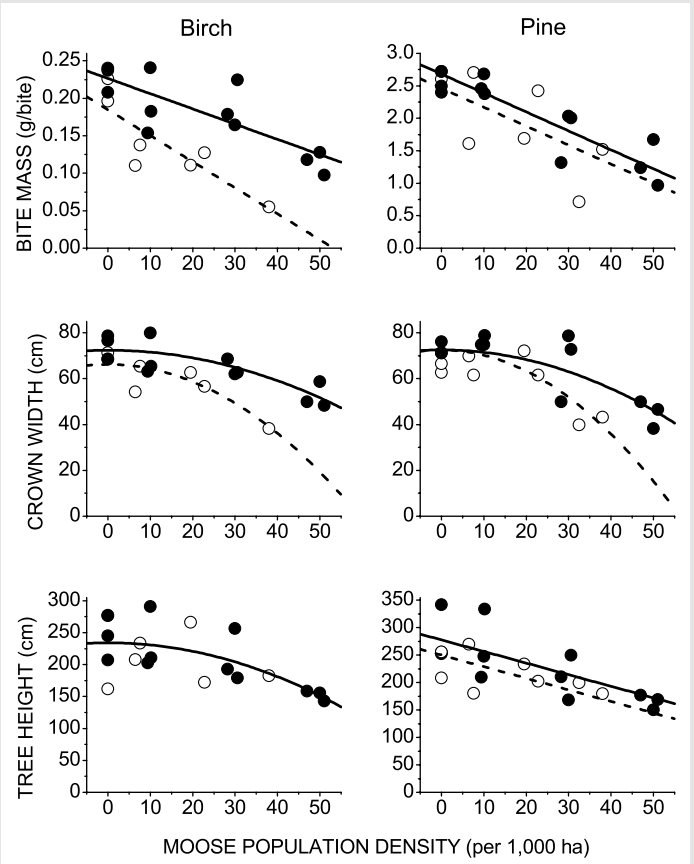

Figure 4. Bite mass (g/bite), crown width and tree height all decreased with increasing experimental moose density for both birch and Scots pine. Open circles correspond with the low productivity sites and dark circles with the high productivity sites. Dashed lines correspond with Ancova models for the low productivity sites and solid lines with high productivity sites or all sites if site was not significant.

Discussion

Increasing experimental moose population density altered the fractal geometry of tree canopies for both birch and Scots pine and site productivity modified many of these responses. In our study, moose browsing was simulated using the best available knowledge of foraging pattern and intake rate of moose (Persson et al. 2005a), and our results only hold under the assumption that we were able to adequately simulate moose foraging at different densities. For Scots pine, the fractal dimension of bite density decreased non-linearly with increasing moose population density regardless of site productivity. In contrast, the fractal dimension of bite density for birch increased strongly from low to intermediate moose densities regardless of site productivity before decreasing with further increases in moose population density. The rate of decrease in the fractal dimension of birch was greater at sites of low productivity. We acknowledge that the stronger decrease in fractal dimension of birch at high moose densities and low site productivities is

highly dependent on a single data point (see Fig. 3). There were no data available for the fractal dimension of birch trees at high moose densities at the other low productivity site (Lögdåberget) because all deciduous trees in the '50 moose/1,000 ha' plot had died from such a high intensity of simulated moose browsing. Thus, it is possible that the decrease in fractal dimension that occurs in response to high levels of moose browsing and low levels of site productivity are actually stronger than shown in Figure 3 and over time may lead to plant mortality. Furthermore, sharper declines in both bite mass and crown width of birch trees also occurred at sites of low productivity, suggesting that rates of changes for many plant properties, including fractal dimension, differ with site productivity.

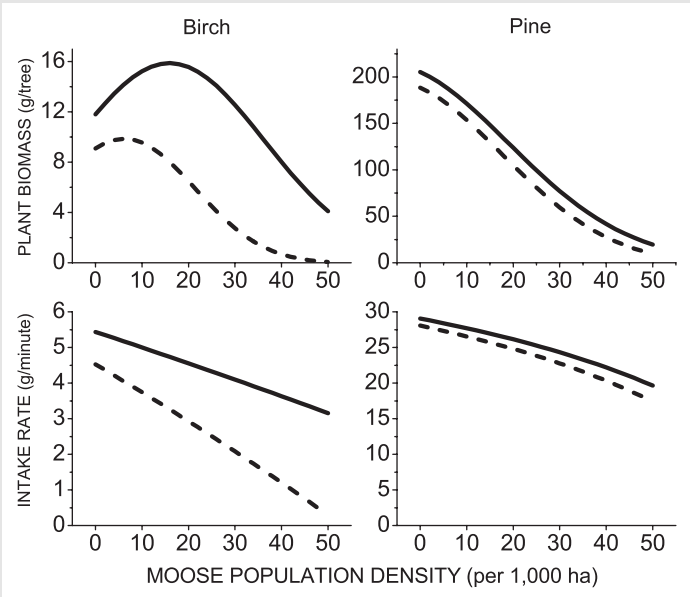

Figure 5. Predictions of plant biomass and moose intake rate are shown for the low (dashed line) and high (solid line) productivity sites. Note the increase in plant biomass with increasing moose density for birch, but a decrease in the feeding rate of moose.

These and other changes in plant architecture (bite mass, crown width and tree height) are consistent with previous studies where moose browsing decreases growth and forage production of Scots pine (Dannell et al. 1991, Edenius et al. 1995, Persson 2005a) and deciduous trees became more branched in response to moderate herbivory (Bergström & Danell 1987, Hobbs 1996, Strauss & Agrawal 1999). The fractal dimension of the Mediterranean shrub *Anthyllis cytisoides* has also increased with moderate levels of herbivory (Escos et al. 1997, Alados et al. 1999). The primary physiological mechanism behind the increased branching frequency, and thus fractal dimension, of the deciduous species is the removal of apical buds, which reduces the hormonal suppression of buds and side shoots lower on the stem (Senn & Haukioja 1994) and promotes highly branched plant architectures. If such changes in branching architecture result in increased plant biomass, it may constitute overcompensation (Paige & Whitham 1987). Overcompensation to browsing for some woody plants has been found by Persson (2005a), McInness et al. (1992), Du Toit et al. (1990), Bergström & Danell (1987), Danell (1983) and here.

The results of our study suggest that, as moose density increases to intermediate levels (10-30 moose/1,000 ha), the fractal dimension of browsed trees increases for birch, even at sites of low productivity, but the size of bites decreases. Even though individual trees are still nutrient limited, the removal of apical dominance can increase forage availability by increasing the branching frequency, and therefore fractal dimension. Such changes in plant fractal geometry may account for the apparent overcompensation found in the studies mentioned above. Moreover, different responses of bite mass and the fractal density of bites have important and different consequences for herbivore foraging.

Changes in plant geometry affect the instantaneous feeding rates of herbivores, but small changes can have large cumulative effects on intake over an entire day. For example, according to Equation 3, the decrease in both fractal dimension and bite size of Scots pine causes plant biomass to decrease with increased moose population density. To gain 5,000 g of dry mass during a single day, a moose in a highly productive habitat with a population density of one moose/1,000 ha must visit >200 fewer plants when browsing Scots pine than a moose in the same habitat with a population density of 50 moose/1,000 ha, a substantial reduction in time spent foraging and in search energy. In contrast, for moose that are browsing birch, gaining 5,000 g per day

requires visiting 110 fewer plants when moose density is 16 instead of one moose/1,000 ha and nearly 900 fewer plants when the population density is 16 instead of 50 moose/1,000 ha, again substantial savings in foraging time and search energy. In addition, predictions of herbivore intake rate decreased monotonically with increasing moose population density in response to decreases in bite mass. These changes in canopy geometry induced by past browsing therefore result in considerably different amounts of time and travel that must be allocated to meet daily forage requirements. In terms of optimal foraging theory (Charnov 1976), the changes in plant fractal geometry and bite mass cause a steeper increase in the gain function, thereby reducing the optimal amount of time that must be spent in a patch.

These results can also improve our current theoretical understanding of interactions between herbivores and plant geometry. West et al. (1997, 1999) have proposed a general allometric theory for scaling of metabolic rate to body mass in organisms, such as trees, in which resources are delivered to growing tips through branching structures or fractal networks. They derive their theory by making the reasonable assumption that each 'tube' in a network branches into n_k smaller tubes at a level k from the basal tube at $k = 0$. For a tree to be fractal, n_k must be constant. Each branch at a level k also has a characteristic length l_k. Therefore, the total number of branches, N_c, emerging through a hemispherical surface at the uppermost level c of radius $r \propto \sum_{k=0}^{c} l_k$ is $N_c = n_0\ n_1\ n_2 \ldots n_c$. This is the density of growing points that the moose sees and which we have measured.

West et al. (1997, 1999) show that in order to minimize the energy dissipated in the branching system to deliver resources throughout the volume of the branching structure, various properties, such as metabolic rate and growth, should scale to mass in characteristic fractal dimensions. Such fractal dimensions have a genetic basis and are heritable plant traits (Bailey et al. 2004). Given the constraints outlined by West et al. (1997, 1999), a plant's fractal dimension ought to evolve as an optimal solution to a static problem.

However, we have found that the fractal dimension of crowns changes with moose population density and site productivity. Thus, fractal geometry of plants is a dynamic property of a plant-herbivore system rather than simply an optimal solution derived from fixed constraints. In terms of the model of West et al. (1997, 1999), what moose (or any other browsing animal) do is to change the characteristic length of an internode, l_k, at some level k and perhaps also change the number of smaller tubes, n_k, branching from the previous level k-1. Thus moose browsing alters the density of growing points emerging from the hemispherical surface by changing n_k and l_k. Site productivity modifies these alterations. Our results therefore suggest an extension of the West et al. (1997, 1999) model to a dynamic model in which n_k and l_k respond to population density and site productivity. Such additions could account for the diversity of fractal dimensions within a given species that we tend to see in ecosystems with large browsing herbivores and converts the problem explored by West et al. from one of static optimization of geometry to minimize energy dissipation to a dynamic optimization problem including herbivory and site productivity.

Acknowledgements - this research was made possible by a grant from the National Science Foundation's Long-term Research in Environmental Biology Program. The continued support of this organization is greatly appreciated. We thank Kjell Danell, Inga-Lill Persson and Åke Nordström for their hospitality while we were living in Umeå and anyone who has helped to maintain the exclosures in Sweden. Alesa De Jager's assistance in fieldwork and data collection as well as drawing Figure 2 is greatly appreciated. David Schimpf, Bruce Peckham, Tom Hobbs and three anonymous reviewers made helpful comments on previous versions of this paper and we thank them for their efforts. This is contribution number 487 from the Center for Water and the Environment at NRRI, University of Minnesota Duluth. All methods carried out in this study comply with current laws of the United States of America and Sweden.

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