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Original article

Effects of simulated moose *Alces alces* browsing on the morphology of rowan *Sorbus aucuparia*

Nathan R. De Jager & John Pastor

In much of northern Sweden moose *Alces alces* browse rowan *Sorbus aucuparia* heavily and commonly revisit previously browsed plants. Repeated browsing of rowan by moose has created some concern for its long-term survival in heavily browsed areas. We therefore measured how four years of simulated moose browsing at four population densities (0, 10, 30 and 50 moose/1,000 ha) changed plant height, crown width, available bite mass, the number of bites per plant and per plant forage biomass of rowan saplings. Increased biomass removal led to a significant decline in plant height ($P < 0.001$), but a significant increase in the number of bites per plant ($P = 0.012$). Increases in the number of bites per plant more than compensated for weak decreases in bite mass, leading to a weak increase in per plant forage biomass ($P = 0.072$). With the decline in plant height and increase in the number of stems per plant, a greater number of bites remain within the height reach of moose relative to unbrowsed controls. Moose therefore stand to benefit from revisiting previously browsed plants, which may result in feeding loops between moose and previously browsed rowan saplings.

Key words: Alces alces, bite mass, forage biomass, herbivory, moose, plant morphology, rowan, Sorbus aucuparia

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Different woody plant species demonstrate a variety of growth responses to increasing browsing intensity by large herbivores (McInnes et al. 1992, Edenius et al. 1993, Danell et al. 1994, 1997, Persson et al. 2005, De Jager & Pastor 2008, De Jager et al. 2009). Some species may compensate for lost tissue due to browsing, whereas others may not. Plants that do compensate for lost tissue often do so at the cost of height growth, which keeps them within easy reach of herbivores and leads to even more browsing in the future (Pastor & Danell 2003). Over time, highly palatable plants that are repeatedly browsed are often overtopped and subsequently replaced with less palatable plants, thereby changing patterns of plant community composition (Krefting 1974, Risenhoover & Maass 1987, McInnes et al. 1992, Thompson et al. 1992, De Jager & Pastor 2009), soil fertility (McInnes et al. 1992, Pastor et al. 1993, 1998, De Jager & Pastor 2009) and in some cases decreasing biodiversity (van Wieren & Bakker 2008).

Among the characteristics on which moose *Alces alces* select plants are available bite size, bite density and forage biomass (Belovsky 1978, Renecker & Hudson 1986, Vivås & Sæther 1987, Shipley & Spalinger 1995, Shipley et al. 1998, 1999, Shipley 2007). Tree height and crown width can influence rates of browsing by moose and also control plant survival, forest succession and biodiversity. However, if moose browsing influences tree height, then

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it can determine whether plants remain within reach and therefore are available for browsing in the future. Thus, the changes in the mass and density of bites that regrow in response to browsing and changes in tree height and crown width ought to subsequently affect the future forage supply to moose and their preference for previously browsed plants.

Although there has been much work on the effects of moose on these properties for many tree species within the boreal biome (see the above references), we are not aware of any study that has systematically examined the response of these morphological features of rowan *Sorbus aucuparia* to a year-round gradient of known moose browsing. Ungulate browsing is suggested to be the most important biotic factor in limiting the growth of rowan in northern Europe (Raspé et al. 2000). Moose find rowan highly palatable, presumably due to its high nutrient content (Heroldova et al. 2003) and because rowan offers moose relatively large and nutritious bites within easy reach (Shipley et al. 1999). Although rowan can be the most abundant species in the seedling cohort in productive forests of northern Sweden, it is often almost entirely absent from the tree layer in highly browsed areas (Linder et al. 1997, Motta 2003). This has created some concern for the long-term survival of rowan in heavily browsed areas (Moen 2004, Mysterud 2006).

In our study, we measured the responses of available bite mass, number of bites per plant, forage biomass, plant height and the width of plant crowns of rowan following four years of four different simulated intensities of moose browsing (0, 10, 30 and 50 moose/1,000 ha) and at two sites of high productivity in northern Sweden. Our previous studies of the responses of birch *Betula pubescens* and *B. pendula* and Scots pine *Pinus sylvestris* in this same experimental setting suggest that the deciduous species have a greater ability to replace lost tissue than conifers (Persson et al. 2005, De Jager & Pastor 2008). Despite declines in plant height and crown width, forage production of birch saplings were either unaffected at the '10 moose' level of tissue removal or responded unimodally with initial increases in forage production at the '10 and 30 moose' levels, followed by declines in forage production at the '50 moose' levels. We therefore hypothesize that increasing moose population density will cause monotonic declines in sapling height and crown width of rowan, but that forage biomass will compensate for lost tissue due to simulated moose browsing. Such a growth response would suggest that rowan has a high capacity to replace lost tissue due to moose browsing and that previously browsed saplings may become even more palatable to moose relative to unbrowsed controls. On the other hand, if increased population density results in monotonic declines in forage biomass, we will conclude that rowan has a low tolerance for browsing and that previously browsed plants are less palatable to moose than unbrowsed control trees.

Material and methods

We simulated the interactive effects of moose population density and site productivity on plant and ecosystem responses in eight exclosures measuring 70×70 m, and were situated 50-90 km north and northwest of Umeå, Sweden (63°50'N, 20°18'E; Persson et al. 2005). The exclosures were constructed in young forest stands of Scots pine planted following clear-cutting approximately 11 years previously and interspersed with naturally reproducing deciduous trees, mainly birch, but also rowan, aspen *Populus tremula* and willows *Salix* spp. Sites were selected along a forest productivity gradient spanning the range of productivities for the region (Hägglund & Lundmark 1987, Fridman et al. 2001). In our study, we examined data from two of the most productive sites, Mörtsjöstavaren and Åtmyrberget, because these were the only sites where rowan was common. These sites had comparable estimates of site productivity and litterfall (Persson et al. 2005), and are typical of the types of plant communities and fertile soil types where rowan is commonly found (Linder et al. 1997).

Within each exclosure, browsing at four moose population densities (0, 10, 30 and 50 moose/1,000 ha) was simulated in 25×25-m plots beginning in early spring 1999. A full description of the methods used to simulate moose foraging is given in Persson et al. (2005) and is briefly summarized here. We calculated the consumption per month in the treatment plots for the different moose densities based on an estimated daily food intake of moose of 5 kg dry mass in winter and 10 kg in summer (Persson et al. 2000). The species composition of food plants in each monthly harvest was based on the seasonal composition of a moose's diet (Cederlund et al. 1980, Bergström & Hjeljord 1987, Shipley

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et al. 1998). During winter (November-April) living twigs > 50 cm above ground were clipped at the mean diameter observed to be browsed by moose in the area, which was 4 mm for rowan and corresponding diameters for other species encountered such as birch, pine, aspen and willow. The mass of all removed plant material was measured each time to 0.1 g precision and then deposited outside the study area. Dung (natural) and urine (artificially made by dissolving urea in water) corresponding to the amounts expected from the simulated moose densities were also added to the treatment plots (Persson et al. 2000).

During early June 2003, after four years of simulated browsing, we measured the number of bites that would be available to moose per tree, the available bite mass, forage biomass per tree, tree height and crown width on the nearest rowan trees > 50 cm in height at 5 m intervals along transects 5 m apart until a total of nine trees were measured in each treatment plot. Tree height was estimated from the ground to the tallest shoot on the plant and crown width was the distance measured across the widest portion of the tree canopy. Available bite mass (g/bite) was measured by selecting all of the twigs on the tree and measuring twig length from the tip to the mean bite diameter observed to be browsed in the areas, which is 4 mm for rowan (Persson et al. 2005). If the diameter of a twig was <4 mm, 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 (> 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.

We then developed regression equations to determine the dry weight of rowan bites from basal diameters and lengths (ln bite mass = -3.379 + 0.537 (ln length) + 1.714 (ln diameter); $R^2 = 0.97$). Estimates made using twig basal diameter and length yielded the average bite mass available to moose during winter. The total potential number of bites per tree was the total number of these shoots on a tree, and forage biomass was estimated by adding together the dry mass of each shoot on the tree.

We pooled the data from both sites because they had comparable estimates of litterfall and site productivity (Persson et al. 2005) and because there were only two of them. We then tested the effects of the increasing moose browsing treatments on plant height, crown width, bite mass, number of bites per plant and forage biomass using ANOVA and post-hoc Tukey's t-tests. For ANOVAs that were not significant ($P > 0.05$), we also tested for differences between the trees in the control plots (without moose) and trees from all treatments combined (with moose).

Results

After four years of simulated browsing at both sites, the height of rowan trees decreased as biomass removal increased ($P < 0.001$; Fig. 1). Decreases in rowan height were greatest in the '50 moose' plot where mean plant height declined by ~ 75 cm relative to unbrowsed control trees. We did not detect a significant change in tree crown width with increasing population density ($P = 0.213$), but there was a difference of ~ 10 cm in width between the trees found in the control plots and those found in all treatment plots combined and this difference was significant ($t = 2.04$, $P = 0.037$). The number of bites per plant increased with increasing population density ($P = 0.012$) and was greatest in the '50 moose' plot where there was an increase of about two bites per plant relative to the control trees. Available bite mass declined with increasing population density ($P = 0.045$) but the only pairwise difference was between the '10' and '50 moose' plots (see Fig. 1). Finally, we observed a weak and statistically insignificant ($P = 0.072$) increase in per plant forage biomass with increasing moose browsing. However, we observed a significant increase in forage biomass of approximately 1.5 g, or the size of one bite, when comparing trees from all treatments with the unbrowsed control trees ($t = 2.69$, $P = 0.01$).

Discussion

Simulated moose browsing increased forage biomass of rowan by approximately 1.5 g/plant over unbrowsed control trees. This plant response to browsing resulted from an increase of about one or two bites per tree, a response that compensated for a slight decrease in bite mass. Therefore, the small change in forage biomass resulted from two almost compensating processes. This weak effect did not happen because of 'no response' on the part of the plant; indeed, the increased number of bites which compensated for the decreased bite mass at least prevented forage biomass from declining.

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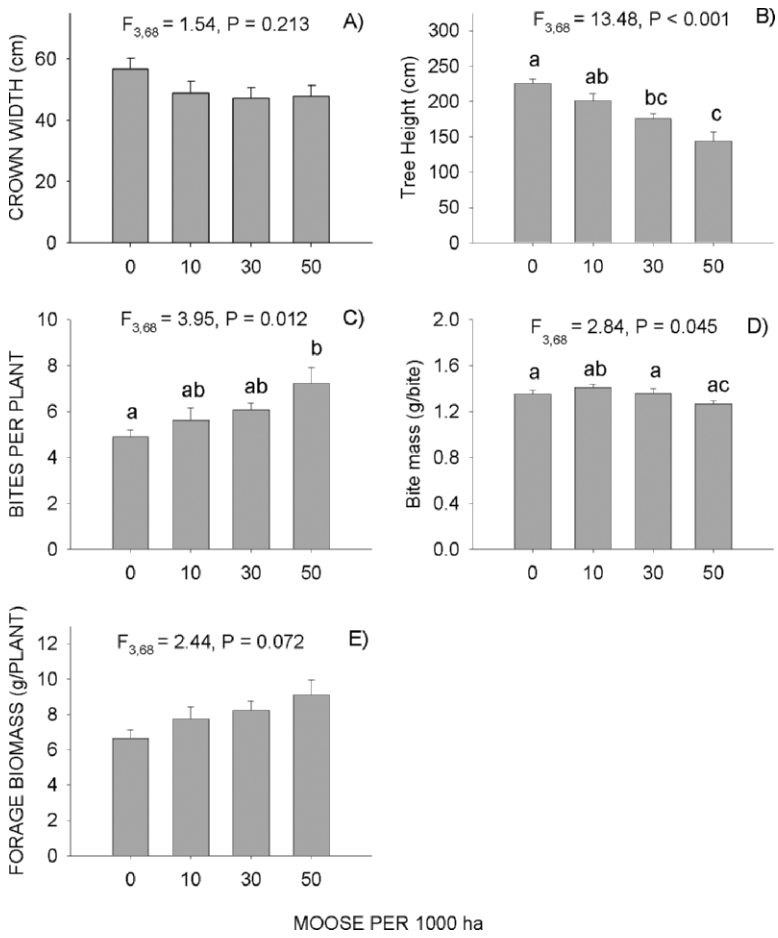


Figure 1. Mean and standard error of crown width (A), tree height (B), bites per plant (C), bite mass (D) and forage biomass (E) of rowan trees measured in 2003 in relation to browsing treatments (0, 10, 30 and 50 moose/1,000 ha) administered during 1999-2002. N = 18 within each treatment, and differing letters above bars indicate significant differences at $\alpha = 0.05$.

In contrast, plant height of rowan declined strongly and significantly to these same simulated browsing rates. Furthermore, similar tissue removal rates strongly decreased forage biomass of other plant species such as birch and Scots pine (Persson et al. 2005, De Jager & Pastor 2008). Thus, biomass production by rowan appears to at least compensate for lost tissue and may even increase production at moose population densities (equivalent to 50 moose/1,000 ha) which would otherwise decrease the productivity of Scots pine and birch, which are its main competitors.

In contrast to the increased number of twigs produced, simulated browsing decreased the height and width of plants, causing browsed plants to remain within the height reach of moose for a longer time period and the biomass produced to be concentrated within a smaller volume. Reductions in plant height resulted from replacement of the terminal shoot with several lateral shoots that only differed slightly in size. As a result, plant height declined monotonically with increased moose density because the terminal shoots were removed with increasingly high probability with increasing moose density. However, because the lateral shoots that continually re-grew were only slightly smaller than those of unbrowsed trees, crown width remained relatively constant across all levels of the moose density treatment. This all-or-nothing response in crown width therefore results from the replacement of terminal shoots (reduction in plant height) with compensatory growth of multiple side shoots that maintain a relatively large size.

Declines in plant height appear to be a common effect of moose browsing (Pastor & Danell 2003, Persson et al. 2005, De Jager & Pastor 2008). The decreased plant height coupled with the increased number of side shoots and only slightly decreased bite mass suggests that even plants receiving extremely high levels of browsing may compensate for lost tissue and hence provide more food to moose relative to unbrowsed control plants. Bio-

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mass production of the two species of birch, aspen and willow all increase under some conditions following browsing at low to moderate levels (Danell et al. 1985, Stolter 2008, De Jager & Pastor 2008, De Jager et al. 2009), and in many cases moose revisit these plants in preference to unbrowsed plants of the same species (Bergström 1984, Danell et al. 1985, Stolter 2008). Similar feedbacks most likely exist between moose and rowan but are probably sustained at even greater levels of moose browsing intensity given the monotonic growth responses presented here.

More than 90% of the winter food base of moose in northern Sweden is composed of three commonly occurring species (commercially planted Scots pine and the two naturally regenerating birch species; Persson et al. 2005). Rowan appears to have a much greater capacity to respond to browsing than either birch or pine. This may explain why rowan is often heavily and repeatedly browsed by moose even though it is far less common in the environment than these other species. In fact, moose browse as much as 80% of the rowan in some areas (Solbraa 2002). Rowan is thus highly palatable but low in abundance. The decline in plant height reported here and the ability of rowan to replace lost tissue at extremely high moose densities likely make previously browsed plants especially susceptible to browsing, when they occur alongside more abundant but less palatable plants. Under such conditions, generalist herbivores, such as moose, can reduce the abundance of the highly preferred but uncommon plant species (Solberg et al. 2003). Because the uncommon but highly preferred plant species constitutes a quantitatively small part of the total food intake of the herbivore, they may have little return impact on herbivore population density. Consequently, rare but palatable species may be continually browsed and not released from herbivory because the more abundant forage species support the herbivore population and thereby maintain high foraging rates (Coomes et al. 2003, Mysterud 2006). Thus, feeding loops between moose and rowan could eventually lead to local extinction of the seed source and long-term impacts on plant abundance and diversity despite maintenance of forage biomass.

Taking the results presented here and those presented in Persson et al. (2005) and De Jager & Pastor (2008) into account, a moose population density of 10 moose/1,000 ha will have very little influence on the growth of birch, Scots pine or rowan, while divergent responses of these species occur at population densities of $>$ 10 moose/1,000 ha. In many areas of Sweden moose densities are only 5-10/1,000 ha (Ball et al. 2000), but in some young forest stands during winter, population densities can be even higher than the densities we simulated. Thus, managers interested in the long-term effects of different sustained moose densities on plant community composition, soil fertility and biodiversity ought to be aware of the different species-specific growth responses to short-term browsing and the subsequent palatability of previously browsed plants, especially where moose populations exceed 10 moose/1,000 ha.

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