

1 EFFECTS OF SIMULATED MOOSE BROWSING ON THE MORPHOLOGY OF ROWAN
2 (*Sorbus aucuparia*)

3
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18

19 **Abstract**

20 In much of northern Sweden moose browse rowan (*Sorbus aucuparia*) heavily and commonly
21 revisit previously browsed plants. Repeated browsing of rowan by moose has created some
22 concern for its long-term survival in heavily browsed areas. We therefore measured how four
23 years of simulated moose browsing at four population densities (0, 10, 30, and 50 moose per
24 1000 ha) changed plant height, crown width, available bite mass, the number of bites per plant,
25 and per plant forage biomass of rowan saplings. Increased biomass removal led to a significant
26 decline in plant height ($p < 0.001$) but a significant increase in the number of bites per plant ($p =$
27 0.012). Increases in the number of bites per plant more than compensated for weak decreases in
28 bite mass, leading to a weak increase in per plant forage biomass ($p = 0.072$). With the decline in
29 plant height and increase in the number of stems per plant, a greater number of bites remain
30 within the height reach of moose relative to unbrowsed controls. Moose therefore stand to
31 benefit from revisiting previously browsed plants, which may result in feeding loops between
32 moose and previously browsed rowan saplings.

33

34 **Introduction**

35 Different woody plant species demonstrate a variety of growth responses to increasing
36 browsing intensity by large herbivores (McInnes et al. 1992, Edenius et al. 1993; Danell et al.
37 1994, 1997; Persson et al. 2005, De Jager and Pastor 2008, De Jager et al. 2009). Some species
38 may compensate for lost tissue due to browsing, while others may not. Plants that do compensate
39 for lost tissue, often do so at a cost to height growth, which keeps them within easy reach of
40 herbivores and leads to even more browsing in the future (Pastor & Danell 2003). Over time,
41 highly palatable plants that are repeatedly browsed are often overtopped and subsequently
42 replaced with less palatable plants, thereby changing patterns of plant community composition
43 (Krefting 1974; Risenhoover & Maass 1987; McInnes et al. 1992; Thompson et al. 1992; De
44 Jager & Pastor 2009), soil fertility (McInnes et al. 1992; Pastor et al. 1993; Pastor et al. 1998; De
45 Jager & Pastor 2009), and in some cases decreasing biodiversity (van Wieren & Bakker 2008).

46 Moose select plants based on the available bite size, bite density, and forage biomass,
47 among other characteristics (Belovsky 1978, Renecker & Hudson 1986, Vivas & Sæther 1987,
48 Shipley & Spalinger 1995, Shipley et al. 1998, 1999; Shipley 2007). Tree height and crown
49 width determine the ability of plants to escape moose browsing and thus control plant survival,
50 forest succession and biodiversity. But if moose browsing controls tree height, then it can
51 determine whether plants remain within reach and therefore available for browsing in the future.
52 Thus, the changes in the mass and density of bites that regrow in response to browsing and
53 changes in tree height and crown width ought to subsequently affect the future forage supply to
54 moose and their preference for previously browsed plants.

55 Although there has been much work on the effects of moose on these properties for many
56 tree species within the boreal biome (see above references), we are not aware of any study that

57 has systematically examined the response of these morphological features of rowan (*Sorbus*
58 *aucuparia*) to a year-round gradient of known moose browsing. Ungulate browsing is suggested
59 to be the most important biotic factor limiting the growth of rowan in northern Europe (Raspé
60 2000). Moose find rowan highly palatable, presumably due to its high nutrient content
61 (Heroldova et al. 2003) and because rowan offers moose relatively large and nutritious bites
62 within easy reach (Shipley et al. 1999). Although rowan can be the most abundant species in the
63 seedling cohort in productive forests of northern Sweden, it is often almost entirely absent from
64 the tree layer in highly browsed areas (Linder et al. 1997, Motta 2003). This has created some
65 concern for the long-term survival of rowan in heavily browsed areas (Moen 2004, Mysterud
66 2006).

67 In this study we measured the responses of available bite mass, number of bites per plant,
68 forage biomass, plant height, and the width of plant crowns of rowan following four years of four
69 different simulated intensities of moose browsing (0, 10, 30 and 50 moose per 1000 ha) and at
70 two sites of high productivity in northern Sweden. Our previous studies of the responses of birch
71 (*Betula pubescens* and *B. pendula*) and Scots pine (*Pinus sylvestris*) in this same experimental
72 setting suggest that the deciduous species have a greater ability to replace lost tissue (Persson et
73 al. 2005; De Jager and Pastor 2008). Despite declines in plant height and crown width, forage
74 production of birch saplings were either unaffected at the "10 moose" level of tissue removal or
75 responded unimodally, with initial increases in forage production at the "10 and 30 moose"
76 levels followed by declines in forage production at the "50 moose" levels. We therefore
77 hypothesize that increasing moose population density will cause monotonic declines in sapling
78 height and crown width of rowan, but that forage biomass will compensate for lost tissue due to
79 simulated moose browsing. Such a growth response would suggest that rowan has a high

80 capacity to replace lost tissue due to moose browsing and that previously browsed saplings may
81 become even more palatable to moose relative to unbrowsed controls. On the other hand, if
82 increased population density results in monotonic declines in forage biomass, we will conclude
83 that rowan has a low tolerance for browsing and that previously browsed plants are less palatable
84 to moose than unbrowsed control trees.

85

86 **Material and Methods**

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

99 Within each exclosure, browsing at four moose population densities (0, 10, 30, and 50
100 moose per 1000 ha) was simulated in 25 x 25 m plots beginning in early spring 1999. A full
101 description of the methods used to simulate moose foraging are given in Persson et al. (2005)
102 and briefly summarized here. The consumption per month in the treatment plots was calculated

103 for the different moose densities based on an estimated daily food intake of moose of 5 kg dry
104 mass in winter and 10 kg in summer (Persson et al. 2000). The species composition of food
105 plants in each monthly harvest was based on the seasonal composition of a moose's diet
106 (Cederlund et al. 1980, Bergström & Hjeljord 1987, Shipley et al. 1998). During winter
107 (November through April) living twigs > 50 cm above ground were clipped at the mean diameter
108 observed to be browsed by moose in the area, which was 4.0 mm for rowan and corresponding
109 diameters for other species encountered such as birch, pine, aspen, and willow. The mass of all
110 removed plant material was measured each time to 0.1 g precision and then deposited outside the
111 study area. Dung (natural) and urine (artificially made by solving urea in water) corresponding to
112 that expected from the simulated moose densities were also added to the treatment plots (Persson
113 et al. 2000).

114 During early June 2003, after four years of simulated browsing, we measured the number
115 of bites that would be available to moose per tree, the available bite mass, forage biomass per
116 tree, tree height, and crown width on the nearest rowan trees greater than 50 cm in height at 5 m
117 intervals along transects 5 m apart until a total of 9 trees were measured in each treatment plot.
118 Tree height was estimated from the ground to the tallest shoot on the plant and crown width was
119 the distance measured across the widest portion of the tree canopy. Available bite mass (g/bite)
120 was measured by selecting all of the twigs on the tree and measuring twig length from the tip to
121 the mean bite diameter observed to be browsed in the areas, which is 4 mm for rowan (Persson et
122 al. 2005). If the diameter of a twig was less than 4.0 mm, the length of the twig was measured
123 from the tip to the point where it branched into a second twig large enough to be considered a
124 distinct bite (approximately >10 cm in length or about the amount one can fit in the hand when
125 mimicking the act of a moose biting a twig) and both the diameter and length were recorded.

126 We then developed regression equations to determine the dry weight of rowan bites from
127 basal diameters and lengths ($\ln \text{ bite mass} = -3.379 + 0.537(\ln \text{ length}) + 1.714(\ln \text{ diameter})$,
128 $R^2=0.97$). Estimates made using twig basal diameter and length yield the average bite mass
129 available to moose during winter. The total potential number of bites per tree was the total
130 number of these shoots on a tree and forage biomass was estimated by adding together the dry
131 mass of each shoot on the tree.

132 We pooled the data from both sites because they had comparable estimates of litterfall
133 and site productivity (Persson et al. 2005) and because there were only two of them. We then
134 tested the effects of the increasing moose browsing treatments on plant height, crown width, bite
135 mass, number of bites per plant, and forage biomass using ANOVA and post-hoc *t*-tests (Tukey).
136 For ANOVA's that were not significant ($P > 0.05$), we also tested for differences between the trees
137 in the control plots (0 moose) and trees from all treatments combined (>0 moose).

138

139 **Results**

140 After four years of simulated browsing at both sites, the height of rowan trees decreased as
141 biomass removal increased ($p < 0.001$) (Fig. 1). Decreases in rowan height were greatest in the
142 "50 moose" plot where mean plant height declined by ~75 cm relative to unbrowsed control
143 trees. We did not detect a significant change in tree crown width with increasing population
144 density ($p = 0.213$), but there was a difference of ~10 cm in width between the trees found in the
145 control plots and those found in all treatment plots combined and this difference was significant
146 ($t=2.04$, $p=0.037$). The number of bites per plant increased with increasing population density (p
147 $= 0.012$) and was greatest in the "50 moose" plot where there was an increase of about 2 bites per
148 plant relative to the control trees. Available bite mass declined with increasing population

149 density ($p = 0.045$) but the only pairwise difference was between the "10" and "50 moose" plots
150 (Fig. 1). Finally, we observed a weak and statistically insignificant ($p = 0.072$) increase in per
151 plant forage biomass with increasing moose browsing. However, we observed a significant
152 increase in forage biomass of approximately 1.5 grams, or the size of one bite, when comparing
153 trees from all treatments with the unbrowsed control trees ($t = 2.69$, $p = 0.01$).

154

155 **Discussion**

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

163 In contrast, plant height of rowan declined strongly and significantly to these same
164 simulated browsing rates. Furthermore, similar tissue removal rates strongly decreased forage
165 biomass of other plant species such as birch (*Betula pendula* and *B. pubescens*) and Scots pine
166 (*Pinus sylvestris*) (Persson et al. 2005, De Jager & Pastor 2008). Thus biomass production by
167 rowan appears to at least compensate for lost tissue and may even increase production at moose
168 population densities (equivalent to 50 moose/1000 ha) which would otherwise decrease
169 productivity of Scots pine and birch, its main competitors.

170 In contrast to the increased number of twigs produced, simulated browsing decreased the
171 height and width of plants, causing browsed plants to remain within the height reach of moose

172 for a longer time period and the biomass produced to be concentrated within a smaller volume.
173 Reductions in plant height resulted from replacement of the terminal shoot with several lateral
174 shoots that only differed slightly in size. As a result, plant height declined monotonically with
175 increased moose density because the terminal shoots were removed with increasingly high
176 probability with increasing moose density. However, because the lateral shoots that continually
177 re-grew were only slightly smaller than those of unbrowsed trees, crown width remained
178 relatively constant across all levels of the moose density treatment. This all-or-nothing response
179 in crown width therefore results from the replacement of terminal shoots (reduction in plant
180 height) with compensatory growth of multiple side shoots that maintain a relatively large size.

181 Declines in plant height appear to be a common effect of moose browsing (Pastor &
182 Danell 2003; Persson et al. 2005; De Jager & Pastor 2008). The decreased plant height coupled
183 with the increased number of side shoots and only slightly decreased bite mass suggests that
184 even plants receiving extremely high levels of browsing may compensate for lost tissue and
185 hence provide more food to moose relative to unbrowsed control plants. Biomass production of
186 birch (*B. pendula* and *B. pubescens*), aspen (*Populus tremuloides*), and willow (*Salix spp.*) all
187 increase under some conditions following browsing at low to moderate levels (Danell et al. 1985;
188 Stotter 2008; De Jager & Pastor 2008; De Jager et al. 2009) and in many cases moose revisit
189 these plants in preference to unbrowsed plants of the same species (Bergstrom 1984; Danell et al.
190 1985, Stotter 2008). Similar feedbacks most likely exist between moose and rowan but are
191 probably sustained at even greater levels of moose browsing intensity given the monotonic
192 growth responses presented here.

193 Over 90% of the winter food base of moose in northern Sweden is composed of three
194 commonly occurring species (commercially planted Scots pine (*Pinus sylvestris*) and two

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

212 Taking the results presented here and those presented in Persson et al. (2005) and De
213 Jager and Pastor (2008) into account, a moose population density of 10 moose per 1000 ha will
214 have very little influence on the growth of birch, Scots pine or rowan, while divergent responses
215 of these species occur at population densities that exceed 10 moose per 1000 ha. In many areas
216 of Sweden moose densities are only five to 10 per 1000 ha (Ball et al. 2000), but in some young
217 forest stands during winter, population densities can be even higher than those simulated here.

218 Thus, managers interested in the long-term effects of different sustained moose densities on plant
219 community composition, soil fertility, and biodiversity ought to be aware of the different
220 species-specific growth responses to short-term browsing and the subsequent palatability of
221 previously browsed plants, especially where moose populations exceed 10 moose per 1000 ha.

222

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228

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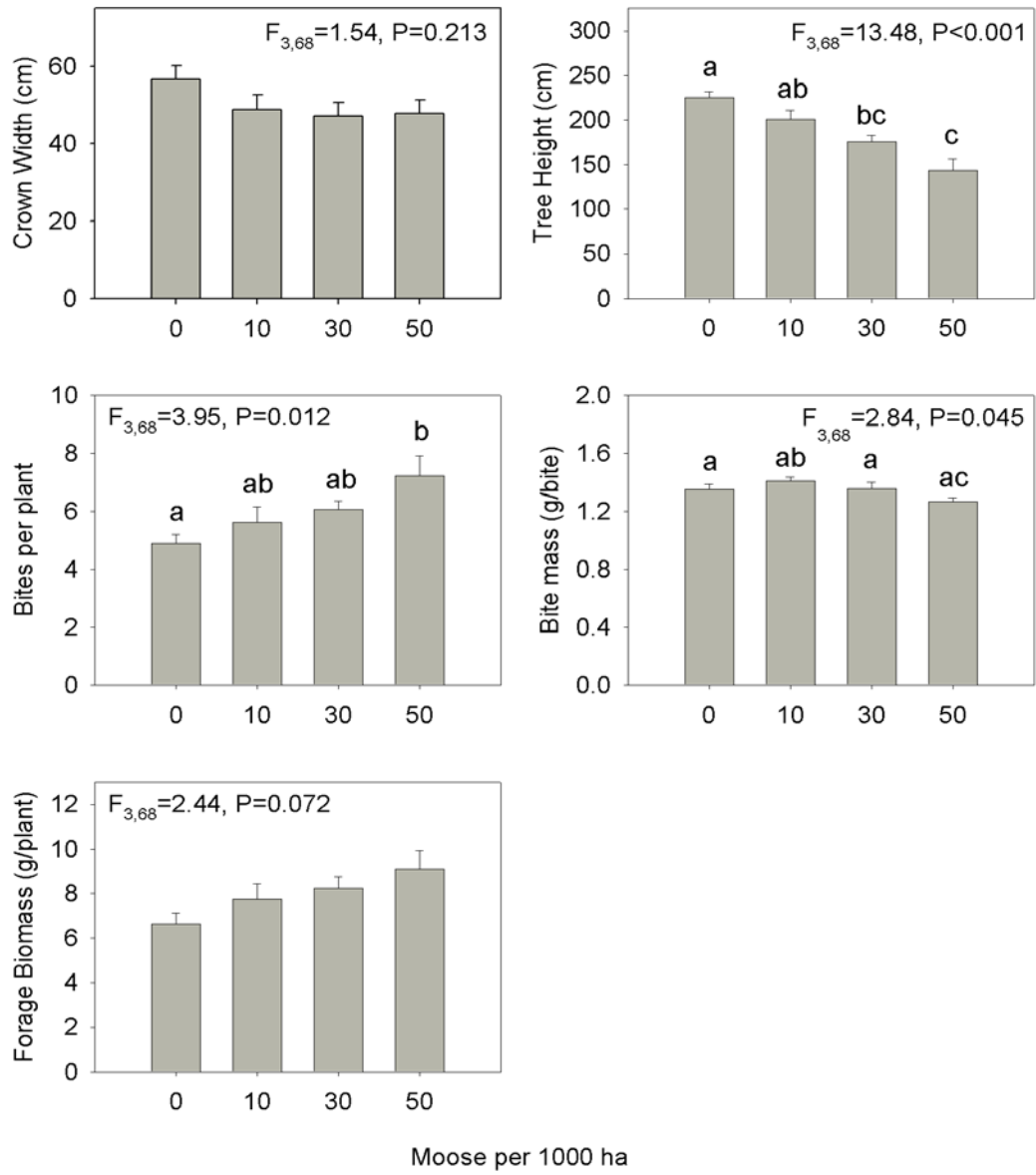
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374

375 **Figure Captions**

376

377 Fig. 1. The mean and standard error of morphological features of rowan trees measured in 2003
378 in relation to browsing treatments (0, 10, 30, 50 moose per 1000 ha) administered from 1999-
379 2002. N=18 within each treatment and different letters indicate significant differences at $\alpha=0.05$.

380



381

382 Fig. 1