SHOOT GROWTH RESPONSES AT SUPPLEMENTARY FEEDING STATIONS FOR MOOSE IN NORWAY

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ABSTRACT: Moose browsing pressure in the vicinity of supplementary winter feeding stations eventually declines over time. It is believed that continual winter browsing over multiple years causes locally reduced shoot growth and forage availability for moose (*Alces alces*). We tested this hypothesis by comparing the size of annual shoots of Scots pine (*Pinus sylvestris*), downy birch (*Betula pubescens*), and Norway spruce (*Picea abies*) along a distance gradient from supplementary feeding stations. Contrary to our hypothesis, we found that shoot size was larger at feeding stations than at distances out to 1500 m. This increase in shoot size was probably not related directly to browsing, but to higher nutrient and light availability associated with moose activity at feeding stations. Increased use of Norway spruce, yet reduced browsing overall at feeding stations, probably reflects the overall decline in abundance of preferred Scots pine and downy birch in a local environment substantially altered by an artificially and abnormally high density of moose.

Understanding plant-herbivore interactions is important for management of moose (*Alces alces*) populations and habitat. Plant morphology and architecture influence forage selection of moose (Shipley 2007), which in turn can affect plant growth patterns (Danell et al. 2003, Pastor and De Jager 2013). In general, plants respond to herbivory through compensatory growth, thereby reducing the impact of herbivory on growth and fitness (McNaughton 1983). However, plant species differ in their responses to herbivory; for example, after browsing, deciduous plants may show stronger compensatory growth than conifers because conifers have predetermined shoot growth, and different storage sites for nutrients and distribution of meristems (Millard et al. 2001).

Herbivores may affect forage plants such that the quantity and accessibility of their food source is altered (Christie et al. 2014). Browsing by moose over time can reduce biomass production in Scots pine (*Pinus sylvestris*), downy birch (*Betula pubescens*), and silver birch (*B. pendula*) depending on the intensity of browsing and the productivity of the environment (Persson et al. 2005). Moderate browsing may increase biomass production in birch, but high intensity browsing over an extended period generally leads to reduced biomass production in both birch and Scots pine (Persson et al. 2007). Shoot size of birch can increase in response to winter-browsing by moose, but the number of shoots and shoot biomass production are reduced (Danell et al. 1985, Danell

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et al. 1997). Shoot size in Scots pine can increase at low browsing intensity and decline at high browsing intensity (Edenius 1993, Edenius et al. 1993). Although short term browsing may have positive effects on shoot biomass, accumulated browsing over multiple years, or at high intensity, reduces shoot biomass.

Shoot size is an important selection criterion of moose (Belovsky 1981). According to the plant vigor hypothesis, herbivores prefer large shoots from vigorous, fast-growing plant modules (Price 1991); therefore, moose may avoid smaller shoots from slow growing trees. Selection of stems can be predicted by the tradeoff between fast harvesting and high quantity (large twigs), and quick digestion and high quality (small twigs) (Shipley 2010), but moose select larger bite diameters when forage availability declines (Shipley and Spalinger 1995). Further, secondary chemical compounds influence shoot selection during winter; for example, moose select tea-leaved willow (*Salix phylicifolia*) stems with lower concentration of phenolics (Stolter et al. 2013).

Supplementary or diversionary winter feeding of moose is a common management practice in Fennoscandia (Gundersen et al. 2004, Sahlsten et al. 2010) that affects the local environment at feeding sites and modifies plant-herbivore interactions (Doenier et al. 1997, Smith 2001, Putman and Staines 2004, Cooper et al. 2006, Rajsky et al. 2008). It also affects spatial distribution, activity, and movement of moose around feeding stations. To some degree, it can be described by central-place foraging theory-high moose density at feeding stations and an inverse relationship between moose density and distance from the feeding station (van Beest et al. 2010a, 2010b, Mathisen et al. 2014). The high browsing impact at feeding stations often leads to local food depletion (van Beest et al. 2010a), and high nutrient input from dung and urine may alter vegetation

composition and structure, with cascading effects on birds and mammals (Mathisen and Skarpe 2011, Mathisen et al. 2012, Pedersen et al. 2014). Browsing on Scots pine and downy birch increases initially (Gundersen et al. 2004) but eventually declines at annual feeding stations (van Beest et al. 2010a), coincident with increased browsing of Norway spruce (*Picea abies*), a less preferred forage species (Shipley et al. 1998, Månsson et al. 2007b). Van Beest et al. (2010a) suggested that accumulated browsing over time reduces shoot production in downy birch and Scots pine in the vicinity of feeding stations, perhaps explaining the eventual reduced browsing pressure at feeding stations. The goal of this study was to investigate the hypothesis that trees at moose feeding stations produce small shoots due to long-term browsing impact, compared with trees further from feeding stations.

STUDY AREA

The study occurred in the Stor-Elvdal municipality in Hedmark County in southeast Norway (~61 °N, 11 °E). The vegetation was primarily boreal forest (Moen et al. 1999) below commercial timberline (700 m). It consisted of managed stands of pure or mixed Scots pine, Norway spruce, downy birch, and silver birch, interspersed with grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), and willows (*Salix* spp.). The field layer vegetation was dominated by dwarf shrubs such as *Vaccinium* spp.. The 30-year average summer (May–September) and winter (October–April) temperatures at the valley bottom were 11.2 and −4.8 °C, respectively. The average 30-year annual precipitation and snow depth (October–April) were 766 mm and 31.3 cm, respectively (NMI 2014).

Moose are the dominant large herbivore in the area with a winter population density between 1.1–3.4 moose per km² (Gundersen

et al. 2004, Storaas et al. 2005, Milner et al. 2012). In winter the population concentrates in the lower valleys, leading to browsing damage in young Scots pine stands and vehicular collisions on the main road and railway. Landowners have winter-fed moose with grass silage since 1990 (initially to divert moose away from the main road and railway) and this supplementary food now provides ~60% of the population's winter forage (Gundersen et al. 2004, van Beest et al. 2010a, Milner et al. 2012), and is pro-vided *ad libitum* at fixed sites throughout the winter (November–March). The amount has increased from a few hundred kg in 1990 to ~200 tons in 1998, and almost 2000 tons in 2010. Feeding stations now number >100 in Stor-Elvdal alone, and the radius around feeding stations with heavy browsing impact and local browse depletion has expanded from 0.2 km in 1998 to 1 km in 2008 (van Beest et al. 2010a).

METHODS

Moose density can be 50 x higher at feeding stations than at the landscape level during winter, causing high browsing impact on vegetation and a high deposition rate of moose dung and urine. With increasing distance from feeding stations, browsing im-pact and dung deposition declines rapidly following a negative exponential function (Mathisen et al. 2014). We measured shoot morphology along a gradient at 3 distance categories from feeding stations using a study design employed in previous surveys (Mathisen et al. 2012, Pedersen et al. 2014): feeding station (FS), 0–30 m; inter-mediate (INT), 150–400 m; far (FAR), 900–1500 m. To minimize variation among plots, we focused on young, mixed conifer-birch forest in the Norwegian forestry cutting classes 2 (trees up to 8 m) and 3 (trees above 8 m but not mature for felling), with a field layer dominated by bilberry (*Vac-cinium myrtillus*) or cowberry (*V. vitis-idaea*)

(Moen et al. 1999). These criteria yielded a balanced design of 11 plots in each of the 3 distance categories (FS, INT, FAR). Since the plots were not designated by random allocation, the study design was not strictly experimental. Rather, it was quasi-experimental that includes highly structured observational studies, with some non-random treatments unlikely to be fraught with confounding factors (Shadish et al. 2002).

At each site, samples of current annual shoots from Scots pine, downy birch, and Norway spruce were clipped after the growing season (3 September – 2 October 2013). These tree species were the most common and present at all 3 distances categories, whilst other species were less abundant and not present at all distances. Trees were selected for clipping by starting with the closest tree to plot center, and moving sequentially outwards until we clipped a minimum of 10 lateral shoots per species. If the closest tree had no twigs at browsing height, we moved to the next closest tree, and proceeded sequentially outwards.

The maximum 3 lateral shoots were clipped from the same tree. Shoots were sampled at 3 height intervals (0.5–1, 1.1–1.5, and 1.51–2.0 m) reflecting the height of trees available and avoiding shoots <50 cm height which are normally covered by snow. The closest shoot to the plot center at each height interval was clipped. Top shoots were sampled if they were <3 m (maximum moose browsing height). For each tree, an index of accumulated browsing was assigned: 0 = no previous browsing; 1 = previous browsing present, but architecture of the tree had not changed; 2 = previous browsing present and architecture of the tree had changed; 3 = previous browsing present and architecture of tree had strongly changed (Skarpe et al. 2000). Stem di-ameter was measured (nearest 0.1 mm) at

the base of the shoot, and length was measured (nearest 0.1 cm) from the base of the shoot to the base of the terminal bud. Stem samples were then collected, oven dried at 100 °C to constant weight, and weighed (nearest 0.01g).

The relationship between distance to feeding station and shoot diameter, length, and dry weight of each species were analyzed separately using linear mixed models in the package nlme in R 3.1.0 (R Development Core Team 2014). Although these are essentially 3 different measurements to describe the size of a shoot and are not independent variables, we chose to analyse them as such to investigate if they responded differently to distance to feeding station. Distance to feeding station (FS/INT/FAR), accumulated browsing index, shoot type (top/lateral), and height interval were included as explanatory variables. In addition, the interaction between distance to feeding station and an accumulated browsing index was included for Scots pine and downy birch to test if the effect of feeding station differed from the effect of previous browsing; Norway spruce was not included because it was only browsed at feeding stations. Specific tree identification and specific tree within site identification were included as random intercepts to account for dependency within shoots sampled from the same tree or site. Shoot length and dry weight were log-transformed to fulfill assumptions of normal distribution and homogeneity of variance. The effect of explanatory variables was assessed by comparison of nested models by dropping one explanatory variable at a time following Zuur et al. (2009). The likelihood ratio between models including/excluding each variable was evaluated, and variables showing a significant relationship ($P < 0.05$) with shoot morphology were included in the model with estimates presented for these variables.

RESULTS

We measured 1253 shoots from 580 trees. Shoot length and dry weight of all 3 species varied with distance to feeding stations (Table 1, Fig. 1). Shoots tended to be larger at feeding stations compared to INT and FAR plots, whilst shoot size was more similar between INT and FAR plots (Fig. 1). Scots pine had the strongest response to feeding stations with shoot length, diameter, and dry weight significantly greater at feeding stations than at INT and FAR plots; dry weight increased 140%, length 102%, and diameter 42% at feeding stations compared with FAR plots. For downy birch and Norway spruce, shoot dry weight and length increased from feeding stations to FAR plots 49% and 56%, and 34% and 67%, respectively. Shoot diameter of downy birch and Norway spruce did not vary significantly with distance to feeding stations (Table 1). Shoot size was generally larger for top shoots than lateral shoots in all 3 species (Fig. 1), and increased with height (Table 2).

Accumulated browsing of downy birch declined slightly with increasing distance from feeding stations, whereas, it was high at all distance categories in Scots pine (Fig. 2). Many Scots pine were unbrowsed at feeding stations but <50 cm high, shorter than the average snow depth in the area and protected from browsing. For Norway spruce, accumulated browsing was high at feeding stations, but browsing levels were minimal at further distances (Fig. 2). We found no effect of the interaction between accumulated browsing and distance to feeding stations on shoot morphology of downy birch and Scots pine (Table 1). Shoot length of Scots pine was the only response variable that differed significantly with accumulated browsing; it declined as the accumulated browsing index increased (Table 1, Fig. 3). The difference in shoot length of Scots pine between feeding stations and FAR plots was greater (102%) than the relationship

Table 1. Significance of distance to supplementary feeding stations (FS.dist) for accumulated browsing (Acc.br) and their interaction, height above ground, and shoot type (top/lateral) on current annual shoot morphology analysed by linear mixed models, Stor-Elvdal, Norway. Likelihood ratio (L), P, and df are presented for each variable.

Species	Response variable	Interaction FS. dist*Acc.br (df = 6)	Distance to FS (df = 2)	Accumulated browsing (df = 3)	Height (df = 2)	Top / lateral (df = 1)
Scots pine	Diameter	$L = 2.89$	$L = 14.54$	$L = 0.74$	$L = 13.68$	$L = 134.4$
		$P = 0.823$	$P < 0.001$	$P = 0.864$	$P = 0.001$	$P < 0.001$
	Length	$L = 6.74$	$L = 15.02$	$L = 7.95$	$L = 5.10$	$L = 110.10$
		$P = 0.348$	$P < 0.001$	$P = 0.047$	$P = 0.078$	$P = 0.078$
	Dry weight	$L = 1.37$	$L = 15.06$	$L = 1.70$	$L = 11.81$	$L = 136.76$
		$P = 0.968$	$P < 0.001$	$P = 0.637$	$P = 0.003$	$P < 0.001$
Downy birch	Diameter	$L = 4.05$	$L = 3.45$	$L = 1.71$	$L = 7.53$	$L = 16.31$
		$P = 0.671$	$P = 0.178$	$P = 0.634$	$P = 0.110$	$P < 0.001$
	Length	$L = 11.46$	$L = 10.88$	$L = 2.28$	$L = 2.42$	$L = 19.56$
		$P = 0.075$	$P = 0.004$	$P = 0.516$	$P = 0.660$	$P < 0.001$
	Dry weight	$L = 8.71$	$L = 7.97$	$L = 2.78$	$L = 11.91$	$L = 24.56$
		$P = 0.190$	$P = 0.019$	$P = 0.427$	$P = 0.018$	$P < 0.001$
Norway spruce	Diameter	–	$L = 1.48$	$L = 1.42$	$L = 48.82$	$L = 230.90$
			$P = 0.477$	$P = 0.702$	$P = <0.001$	$P < 0.001$
	Length	–	$L = 17.53$	$L = 2.04$	$L = 30.11$	$L = 24.28$
			$P < 0.001$	$P = 0.563$	$P = <0.001$	$P < 0.001$
	Dry weight	–	$L = 7.30$	$L = 0.70$	$L = 60.04$	$L = 115.52$
			$P = 0.026$	$P = 0.874$	$P = <0.001$	$P < 0.001$

between accumulated browsing and shoot length. Shoot length with an accumulated browsing index of 3 was 26% shorter than where the index was 0 (Fig. 3).

DISCUSSION

Moose browsing on natural vegetation declined over time at the feeding stations in our study area. Our starting hypothesis was that this decline was related to intensive accumulated browsing at feeding stations which causes production of smaller shoots avoided/less preferred by moose. We found some weak support for this hypothesis in Scots pine, but overall and contrary to our hypothesis, shoot size in all 3 tree species was larger at feeding stations.

The increase in shoot length and dry mass was predominantly at feeding stations as the increase in shoot size did not extend to the farther distance plots. The increase could reflect a compensatory response to previous browsing (McNaughton 1983) as several studies indicate that trees browsed by moose produce larger, but fewer shoots (Danell et al. 1985, Bergström and Danell 1987, Danell and Bergström 1989). A strong gradient between accumulated browsing data and distance to feeding stations was evident only in Norway spruce, although it was only browsed measurably at feeding stations. Browsing on downy birch and Scots pine was high at all distance categories as the accumulated browsing index was 2–3 on >70% of trees. Previous studies at the
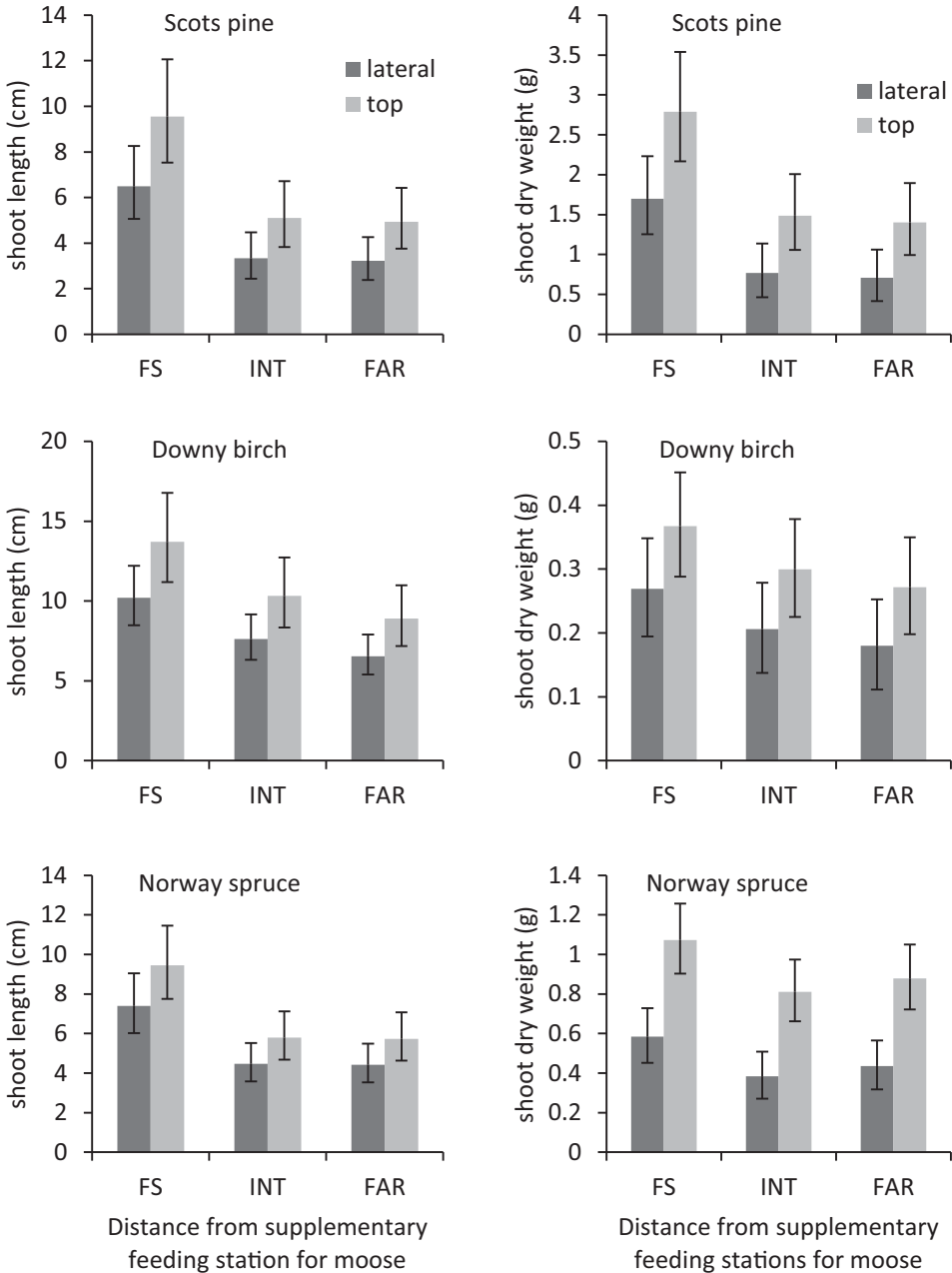
Fig. 1. Effects of distance from supplementary feeding stations for moose on shoot length and dry weight (mean ± 2 SE) of current annual shoots of common tree species in Stor-Elvdal, Norway (FS = feeding station, INT = intermediate distance [150–400 m], and FAR [900–1500 m]).

feeding stations noted that a distance gradient in browsing pressure occurs from preferred species such as downy birch and Scots pine to less preferred species such as Norway spruce (van Beest et al. 2010a, Mathisen et al. 2014). Further, accumulated browsing had no effect on shoot size in Norway spruce and downy birch, but was related negatively

with shoot length in Scots pine. Therefore, it seems unlikely that the increase in shoot size at feeding stations (compared to farther

Table 2. Relationship between shoot dry weight (mean ± 2 SE) and height above ground for lateral current annual shoots at moose feeding stations in Stor-Elvdal, Norway.

Species	Height (m)	Shoot mass (g)	
		Mean 2	SE
Downy birch	0.5–1	0.14	0.02
	1–1.5	0.15	0.03
	1.5–2	0.18	0.05
Norway spruce	0.5–1	0.23	0.04
	1–1.5	0.29	0.05
	1.5–2	0.27	0.05
Scots pine	0.5–1	0.98	0.13
	1–1.5	1.35	0.63
	1.5–2	1.82	1.37

distances) is explained entirely by browsing, at least for Scots pine and downy birch.

An alternative explanation may be that the increase in shoot size at feeding stations is related to fertilization by an abnormally high input of moose dung and urine. For example, fertilization increases shoot length and twig biomass in downy birch (Månsson et al. 2009). In Stor-Elvdal up to 2000 tons of silage is converted to moose feces and urine annually, and most is deposited within 50 m of feeding stations (Mathisen et al. 2014). Although local Scots pines have access to abundant nutrients because their canopies are limited from heavy browsing, these trees presumably invest in regrowth of a few large shoots. Increased shoot growth could also be an indirect result of heavy browsing at feeding stations that promotes more open canopy and sunlight (Persson et al. 2005, Mathisen et al. 2010). Previous studies found
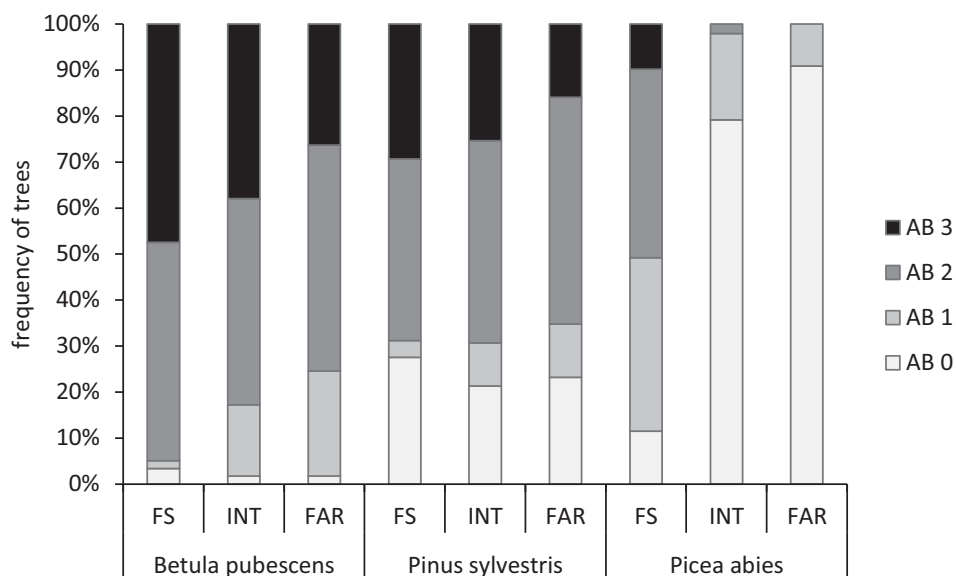

Fig. 2. Frequency of trees with different accumulated browsing index (AB 0 = no previous browsing; AB 1 = previous browsing present, but architecture of the tree had not changed; AB 2 = previous browsing present and architecture of the tree had changed; AB 3 = previous browsing present and architecture of tree had strongly changed) sampled at different distances from supplementary feeding stations for moose in Stor-Elvdal, Norway (FS = feeding station, INT = intermediate distance [150–400 m], and FAR [900–1500 m]).
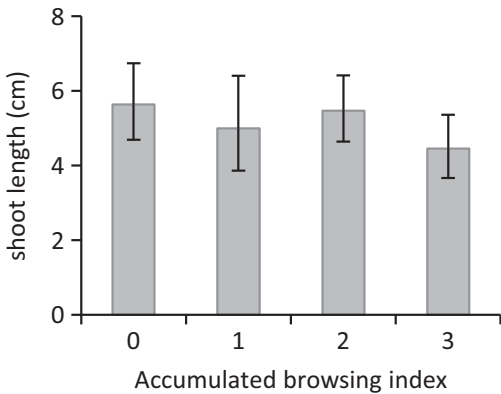
Fig. 3. Effects of accumulated browsing on shoot length (mean ± 2SE) in Scots pine at feeding stations for moose in Stor-Elvdal, Norway. Results are averaged over levels of distance to feeding stations and shoot type. The accumulated browsing index was defined as: 0 = no previous browsing; 1 = previous browsing present, but architecture of the tree had not changed; 2 = previous browsing present and architecture of the tree had changed; 3 = previous browsing present and architecture of tree had strongly changed.

that species composition in the field layer vegetation at feeding stations changed towards more nitrogen and light-demanding species (Mathisen and Skarpe 2011, Mathisen et al. 2012, Pedersen et al. 2014). Interestingly, limitation of light can have an equally suppressive effect on plant height as browsing (McLaren 1996).

Chemical defense and nutrient composition in shoots may also have changed due to the combination of previous browsing and altered environmental conditions at feeding sites. As nutrients are often more limiting than light in boreal forests, trees utilize carbon-based rather than nitrogen-based defenses (Bryant et al. 1983). Trees at feeding sites had high nutrient availability due to fertilization, yet minimal canopy that may reduce the availability of carbon. Consequently, these trees could have a relative

surplus of nutrients and shortage of carbon. How the artificial environment at feeding stations affects plant chemistry and forage choice is uncertain; however, because previous browsing, in general, increases palatability of shoots for moose (Bergqvist et al. 2003), as does increased nutrient availability (Ball et al. 2000, Mansson et al. 2009), it seems an unlikely explanation for the reduction in browsing pressure over time.

In general, moose select diets to optimize digestible energy intake per day, and are more sensitive to changes in plant morphology than plant chemistry (Shipley 2010). Seasonal diets and consumption levels, particularly in winter, are largely influenced by environmental conditions that dictate forage quality and quantity. Stolter et al. (2013) investigated moose browsing in the study area year-round, and found that the relative importance of plant morphology and plant chemistry varied seasonally. Browsing on less preferred tree species such as Norway spruce at feeding stations (van Beest et al. 2010a) may indicate that supplementary feeding changes browsing preferences; however, we did not directly measure consumption or availability of the 3 browse species, and it is highly unlikely that fundamental forage preferences changed. In fact, over time the peak in browsing pressure on Scots pine moved outwards from 12.5 to 500 m from feeding stations (van Beest et al. 2010a), and GPS-collared moose at feeding stations traveled daily up to 500 m distant (Mathisen et al. 2014). Because supplementary food measurably elevates the nutritional status of local moose (Milner et al. 2012) and represents 60% of their winter forage requirements, it is more likely that fed moose demonstrate less selective browsing than unfed animals, and simply consume the mix of browse available at feeding stations where they consume the majority of their food.

Our results suggest that the temporal decline in browsing pressure at feeding stations was not due to higher availability of smaller shoots, as hypothesized previously (van Beest et al. 2010a). An alternative explanation is that the number of shoots per tree and total production of browse biomass decline at feeding stations over time (Danell et al. 1997, Persson et al. 2007). Indeed, the number of shoots per tree on both Scots pine and downy birch at feeding stations decreased over time (F. van Beest, unpublished data), which might reduce preference at the individual tree level (Senft et al. 1987, Månsson et al. 2007a), a hierarchal level of browse selection above our measurements and study design.

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