IMPACT OF MOOSE BROWSING ON FOREST REGENERATION IN NORTHEAST VERMONT

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ABSTRACT: Moose (*Alces alces*) play an important role in the ecological and economic resources of northern New England, a landscape dominated by commercial forests. This study measured the impact of moose browsing on forest regeneration in Wildlife Management Unit E1 in northeastern Vermont where moose density was considered high in the 1990–2000s. We surveyed 37 clearcuts categorized into 4 age classes (3–5, 6–10, 11–15, and 16–20 years old). The stocking rate (stems/plot) of commercial species ranged from 74–76% in the 3–5, 6–10, and 11–15 year age classes, increasing to 86% in the 16–20 year age class. The proportion of plots containing a commercial tree without severe damage was above the accepted threshold stocking level of 40–60% in all age classes. The proportion of plots containing a commercial hardwood stem declined with increasing age class; the opposite occurred with softwood stems indicating a possible shift from hardwood- to softwood-dominated stands from selective browsing pressure. Height of 11–20 year old stems was less than in New Hampshire, indicating that growth was possibly suppressed in Vermont due to higher moose density. Overall, browsing was not considered a major problem based upon stocking rates. Further study is warranted to evaluate whether compensatory growth occurs in response to reduced browsing as forests age and/or moose population density declines.

ALCES VOL. 50: 67–79 (2014)

Key words: *Alces alces*, browsing, clearcut, damage, moose, New England, regeneration, stocking.

Moose (*Alces alces*) populations have experienced a regional increase in northern New England over the last several decades, making them an increasingly valuable wildlife resource. They play an important role ecologically and economically in Vermont, with 78% of the state open to regulated moose hunting and 406 hunting permits issued statewide in 2011 (VTFW 2008, 2011). With forests also covering 78% of Vermont's landscape, the state generates over $1.5 billion annually from forest-based manufacturing and forest-related recreation and tourism (NEFA 2007). The majority of forestland, 4 million acres, is owned privately or by timber investment management organizations; local, state, and federal government owns ~19% (919,440 acres) (NEFA 2007). Forest and wildlife management aimed at sustainable forest production is critical for the long-term stability of both Vermont's economy and moose population.

With adult moose weighing 300–600 kg, substantial browse is required to maintain such large body size (Bubenik 1997), estimated at daily dry matter intake of 2.8 kg/moose/day in January (Pruss and Pekins 1992). Moose have the ability to substantially alter plant communities and are capable of damaging woody plants (Renecker and Schwartz 1997); repeated browsing can suppress height growth and recruitment of saplings into the canopy (Risenhoover and Maass 1987). Moose browsing has the capability to affect the structure and dynamics of forest ecosystems over the long-term (McInnes et al. 1992), which has important implications for the management of forests where moose populations are regulated. Moose show preference for forage in clear-cut and early-successional habitat that is typical of the commercially managed forests of the northeast (Thompson et al. 1995, Scarpitti et al. 2005). For example, productive moose habitat in New Hampshire was linked directly to the early successional forage created by commercial forest harvesting and early-successional browse is a dietary component year-round (Scarpitti et al. 2005, Scarpitti 2006). Clearcuts 5–20 years old provide suitable early winter habitat, as regenerating hardwood and softwood species provide both browse and cover for moose (Thompson and Stewart 1997). While the impact of moose browsing on forest regeneration has received substantial attention elsewhere, little attention has been paid to the potential and actual effects in northern New England (Pruss and Pekins 1992, Scarpitti 2006, Bergeron et al. 2011).

In order to manage moose and forest resources with respect to moose density and damage to regeneration, it is important to have extensive ecological knowledge of the relationships among moose, the ecosystems they inhabit, the plants they use as forage (Edenius et al. 2002), and the associated impacts on forest production such as timber quality impairment. As moose populations have increased in northern New England, land managers have implied that a relationship exists between high population density and reduced forest regeneration in clearcuts. On Isle Royale, McInnes et al. (1992) found that moose browsing affected the structure and dynamics of forest ecosystems on a long-term scale; however, in larger landscapes such impacts are usually more localized and often relate to high seasonal density.

In northern New Hampshire, Bergeron et al. (2011) evaluated the impact of browsing on the regeneration of commercial tree species in 3 regions with different moose population density (0.26–0.83 moose/km^2). While regeneration of commercial trees was not considered a regional problem at any density, specific clearcut sites with low regeneration were found adjacent to traditional moose wintering areas. It was predicted that such sites could change from hardwood to softwood dominance over time (Bergeron et al. 2011).

By the early 2000s, there was anecdotal evidence that the moose population in northeastern Vermont, specifically wildlife management unit (WMU) E, was causing measurable damage to forest regeneration; moose densities in WMU E were thought to be well over 1.5 moose/km^2 (4 moose/mile^2) (C. Alexander, VTFW wildlife biologist, pers. comm.). To achieve the desired population level, hunting permit numbers were dramatically increased by the Vermont Department of Fish and Wildlife (VTFW) from 440 to 833 permits in 2004, when it was believed moose had approached their biological carrying capacity (VTFW 2008). The number of hunting permits rose to 1046 in 2005 and continued to increase until 2009, when 1223 permits were issued statewide in an effort to accelerate population reductions to protect forest habitat. By 2008, the population density was approaching the goal set by the 10-year moose management plan (0.7 moose/km^2 [1.75 moose/mile^2]) and the number of permits was reduced to 765 in 2010 and 405 in 2011. In response, this study was designed to evaluate the impact of moose browsing on the regeneration of commercial tree species in WMU E1 in northeast Vermont by conducting qualitative assessments of damage in clearcuts between 3–20 years of age.

METHODS

Study Area

The study area was located in northeast Vermont and encompassed all of

VTFW WMU E1, covering an area of 682 km[2] bordered by New Hampshire and Quebec (Fig. 1). Elevation ranges from ~250–1,130 m, and it is dominated by maple (*Acer saccharum, A. pensylvanicum, A. rubrum*) and birch (*Betula alleghaniensis, B. papyrifera*) hardwoods, and coniferous stands of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens.*) While heavily forested, timber harvesting is common throughout as the majority of the land is privately owned and commercially harvested (NEFA 2007). The 2011 moose density was estimated at 0.77 moose/km[2] (1.96 moose/mi[2]) based on a rolling 3-year average of moose sightings by early winter (November) deer hunters, and was previously estimated in 2010 as 0.93 moose/km[2] (2.41 moose/mile[2]) based on aerial surveys (Millette et al. 2011).

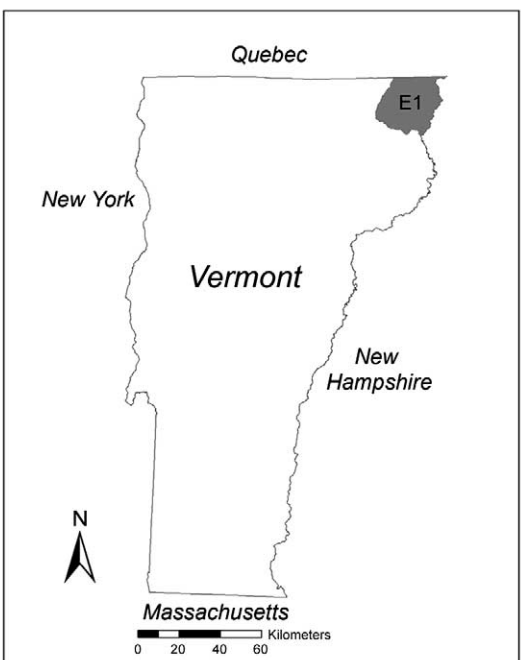

Fig. 1. The location of the study area in Vermont used to assess the impact of moose browsing on forest regeneration, 2012. The area included all of WMU E1 in northeast Vermont.

Field Measurements

Regeneration surveys were performed in June 2012 to measure the impact of moose browsing on forest regeneration in clear-cuts 3–20 years old (Leak 2007, Bergeron et al. 2011). Clear-cuts were separated into 4 age classes (3–5, 6–10, 11–15 and 16–20 years old) in order to assess temporal changes during both the period of typical browsing (0–10 years) and at least 10 years post-browsing (11–20 years). In each age class, 8–11 clear-cuts were located using aerial photography; each was a minimum of 4.1 ha (10 acres) and a maximum of 16.2 ha (40 acres) in size to reflect the typical range in size of clear-cuts in the region (M. Langlais, Vermont Department of Forests, Parks & Recreation County Forester, pers. comm.). In certain cases, clear-cuts >16.2 ha were used to achieve appropriate sample sizes within an age class; a section ≤16.2 ha was surveyed.

Small plot surveys (milacre, ~2.3 m diameter circle) were evenly spaced on equidistant transects throughout each clear-cut (Fig. 2). In each milacre plot, the dominant stem (tallest tree) was recorded as a commercial or non-commercial tree species. If the dominant stem was non-commercial, the plot was searched for the presence of commercial species; commercial species included yellow and white birch, sugar and red maple, American beech (*Fagus grandifolia*), aspen (*Populus* spp.), black cherry (*Prunus serotina*), balsam fir, red and black spruce (*Picea mariana*), and tamarack (*Larix laricina*). Stem damage was assessed on a qualitative basis as fork, broom, or crook (Fig. 3). The height of the damage above or below breast height (approximately 1.4 m) was recorded, as well as the number of forks and crooks, and the severity of crooks based on angle. Light crooks were those ≤30°, moderate crooks were those 30–60°, and severe crooks were those ≥60° from the dominant stem. The relative height of the

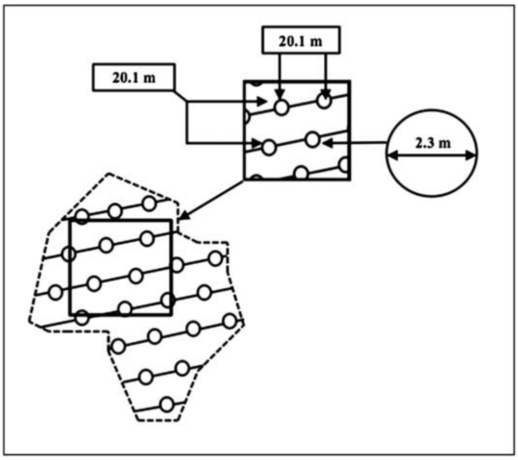

Fig. 2. Example of the sampling design used to measure browse damage in clearcuts in northeast Vermont, summer 2012. Equidistant transects were established upon which 100–400, 2.3 m diameter plots were established to measure the presence of dominant commercial stems, stem quality, and relative height; modeled after Bergeron et al. 2011.

dominant stem was estimated to the nearest foot when <3.05 m (10 ft), or as ≥3.05 m.

Data Analysis

Broomed stems and multiple forks above breast height were considered browse defects indicative of a severely damaged tree; otherwise, damage was considered light or moderate. Trees with lesser damage are expected to recover during future growth (Switzenberg et al. 1955, Carvell 1967, Trimble 1968, Jacobs 1969). Stems with single forks above breast height, or multiple forks either above or below breast height were considered to have moderate damage. Stems with a single fork below breast height or crooks were considered to have light damage. A fully stocked stand (average density for undisturbed stand) at 80 years was assumed if a minimum of 40–60% of plots (threshold) contained a dominant commercial stem without severe damage (Leak et al. 1987). To evaluate relative height between age classes and further assess browse impact, comparisons were made of the proportion of plots containing a dominant commercial stem ≥3.05 m height without severe damage, as vegetation ≥3.05 m was presumed to be above the typical height of moose browsing (Bergström and Danell 1986).

Temporal comparisons were made to assess if younger age classes with high initial browse pressure recover to fully stocked stands after 10–15 years. Analysis of variance (ANOVA) and pairwise Tukey's test were used to look for differences in browse damage between clear-cuts and age classes. Analyses were performed with Systat v. 13. Significance for all tests was assigned a

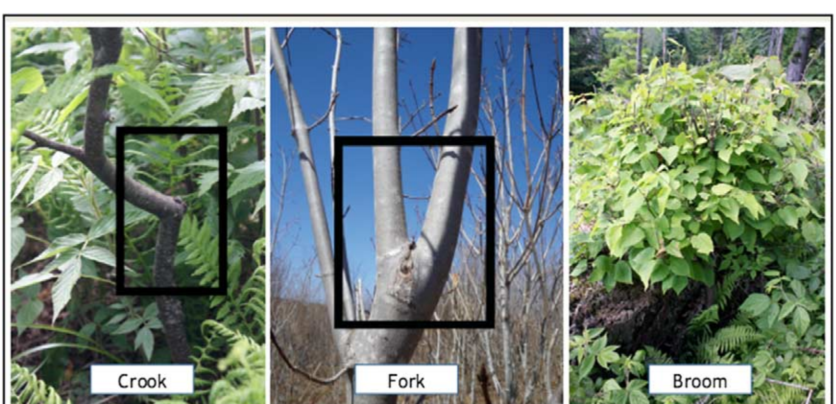

Fig. 3. The 3 qualitative browse categories used to describe browsing damage of dominant stems in milacre sample plots (Bergeron et al. 2011).

priori at α = 0.05. Results are presented throughout as б ± SE.

RESULTS

A total of 37 clearcuts were surveyed: 11, 8, 8, and 10 in the 3–5, 6–10, 11–15, and 16–20 year age classes, respectively. There were 1709, 1291, 1442, and 1585 milacre plots surveyed in the 4 age classes, respectively. Stocking rate of commercial trees (stems/plot) was high in all age classes, and increased with age class (Table 1); it ranged from 74–76% in the 3–5, 6–10, and 11–15 year age classes, increasing to 86% in the 16–20 year age class. The proportion of commercial trees with severe damage was low overall, with <10% damaged severely in all age classes except in the 16–20 age class (11%, Table 1).

The proportion of plots containing a commercial tree without severe damage was above the defined threshold stocking level of 40–60% in all age classes (Table 1, Fig. 4), ranging from 67–68% in the 3–5, 6–10, and 11–15 year age classes, and increasing to 75% in the 16–20 year class. The proportion of dominant commercial trees ≥3.05 m without severe damage increased with age class with 1, 25, and 39% in the 6–10, 11–15 and 16–20 year age classes, respectively. The proportion of plots containing a commercial hardwood stem declined with age class, averaging 62, 51, 43, and 40% in the 4 age classes, respectively. Conversely, the proportion of plots containing a commercial dominant softwood stem increased with age class, averaging 12, 24, 33 and 46% in the 4 age classes, respectively (Fig. 5). The highest stocking rates (>80%) were restricted to softwood-dominated stands. The majority of plots with a dominant non-commercial stem also contained commercial stems (70–81% across age classes).

The stocking rate of dominant commercial trees was lower (*P* = 0.02) in the 3–5 year age class than in the 16–20 year age class, although stocking rate was above the threshold stocking level in all age classes. The proportion of dominant commercial hardwoods was higher (*P* = 0.014) and the proportion of dominant commercial softwoods lower (*P* = 0.015) in the 3–5 year age class than in the 16–20 year age class. The proportion of plots beyond browse height (≥3.05 m) and without severe damage in the 6–10 year age class was lower than the 11–15 year (*P* = 0.022) and the 16–20 year age classes (*P* < 0.001).

At least 3 commercial species accounted for ≥50% of the species composition within each age class (Table 2). The majority of these species were classified with light to no damage, and the proportion of non-commercial species declined as age class increased (Tables 1 and 2). The proportion of dominant commercial stems classified as hardwood declined with age class, averaging 83 ± 7.6, 69 ± 8.5, 58 ± 8.5 and 49 ± 7.2% in the 4 age classes, respectively; the opposite occurred with the proportion of dominant commercial stems classified as softwood that averaged 17 ± 7.6, 31 ± 8.5, 42 ± 8.5, and 51 ± 7.2%.

Red maple and yellow birch accounted for 24 and 20% of total species composition in the 3–5 year age class; no other commercial species accounted for more than 6%. In the 6–10 year class, red maple, balsam fir, and yellow birch accounted for the highest proportion of species composition (14–16% each) and in the 11–15 year age class, these 3 species accounted for 11–17% each, and red spruce 11%. Red maple, balsam fir, and red spruce accounted for the greatest proportion of dominant commercial stems (21–23% each) in the 16–20 year age class; yellow birch fell to 6% (Table 2).

DISCUSSION

Overall, the impact of moose browsing on the regeneration of commercial tree

Table 1. Summary values indicating the stocking of commercial tree species, stocking of commercial trees with and without severe damage, the proportion of commercial trees ≥3.05 m in height without severe damage, and the proportion of dominant commercial hardwood and softwood stems in clearcuts in northeastern Vermont, 2012. Rows with the same letter within columns are not statistically different ($P > 0.05$).

Age Class	Stocking rate of dominant commercial trees (%)[1]	Stocking rate of dominant commercial trees w/o severe damage (%)[2]	Stocking rate of dominant commercial trees w/ severe damage (%)[3]	Proportion of dominant commercial trees w/o severe damage and ≥3.05 m tall (%)	Proportion of dominant commercial hardwoods (%)	Proportion of dominant commercial softwoods (%)
3–5	74[a]	67	6	N/A	83[a]	17[a]
6–10	75[ab]	68	7	1[a]	69[ab]	31[ab]
11–15	76[ab]	67	9	25[b]	58[ab]	42[ab]
16–20	86[b]	75	11	39[b]	49[b]	51[b]

[1]Proportion of plots containing dominant stems considered to be commercial species
[2]Proportion of plots containing dominant commercial stems not considered to be severely damaged
[3]Proportion of plots containing dominant commercial stems considered to be severely damaged

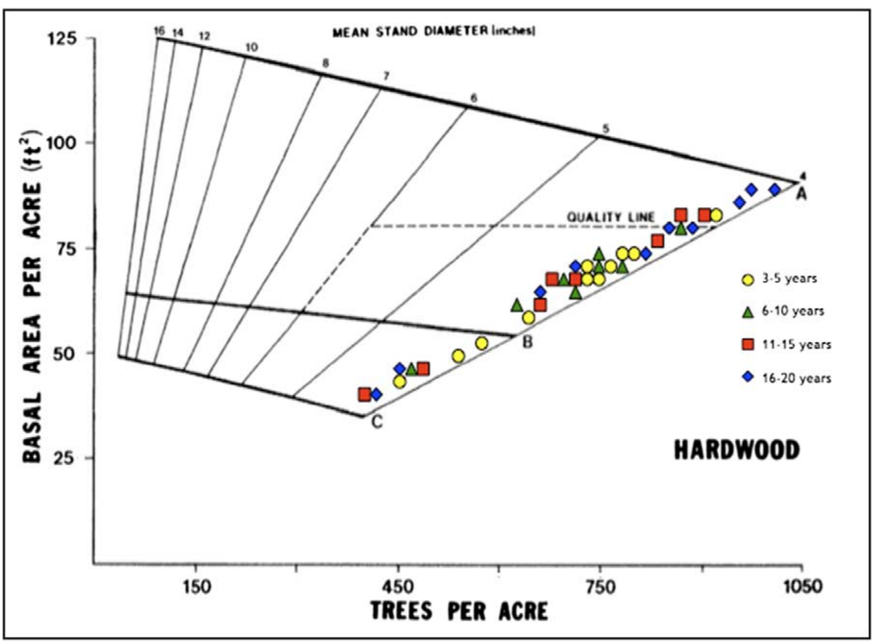

Fig. 4. Stocking guide for main crown canopy of even-aged hardwood and mixed-wood stands relative to basal area, number of trees per acre, and mean stand diameter. The A-line is fully stocked, the B-line is suggested residual stocking (~60%), and the C-line is minimum stocking (~40%) (Leak et al. 1987). The proportion (%) of commercial trees without severe damage are plotted by age class; stocking is projected to a 4" mean stand diameter.

species in northeast Vermont was considered minor. The stocking rate of commercial trees without severe damage was acceptable in all age classes based upon the minimum threshold stocking level of 40–60%, and severe damage from browsing was low in all age classes with regard to acceptable levels, ranging from 6–11% (Table 1). While damage was low in all age classes, site-specific severe browsing can shift species composition (Edenius et al. 2002). For example, moose drastically altered localized species composition on Isle Royale, Michigan where browsed sites had lower overall tree density than unbrowsed sites due to decline in balsam fir and mountain ash (*Sorbus americana*) and concurrent increase in white spruce (*Picea glauca*) densities (Snyder and Janke 1976).

The increasing proportion of dominant softwood stems with age indicates a possible shift to softwood-dominated stands due to selective browsing of hardwood species (Fig. 5). The highest stocking rates (>80%) were restricted to softwood-dominated stands, and stands experiencing the highest levels of damage were stocked predominantly with hardwood species that had much higher damage relative to the softwood species (Table 2); softwood species will likely dominate these stands as they mature. The most commercially valuable hardwood species in the study region are yellow birch and sugar maple, and they were dominant species in the youngest 2 age classes, but accounted for only 6 and 5% of dominant stems in the 16–20 year class.

Conversely, the commercial softwood species, balsam fir and red spruce, were minimal in the youngest age classes, but accounted for a large proportion of the dominant stems (21% each) in the 16–20 year class. Red maple, a less valuable commercial species, was the most common deciduous tree species in all age classes ranging from 13–24% of dominant stems (Table 2). A

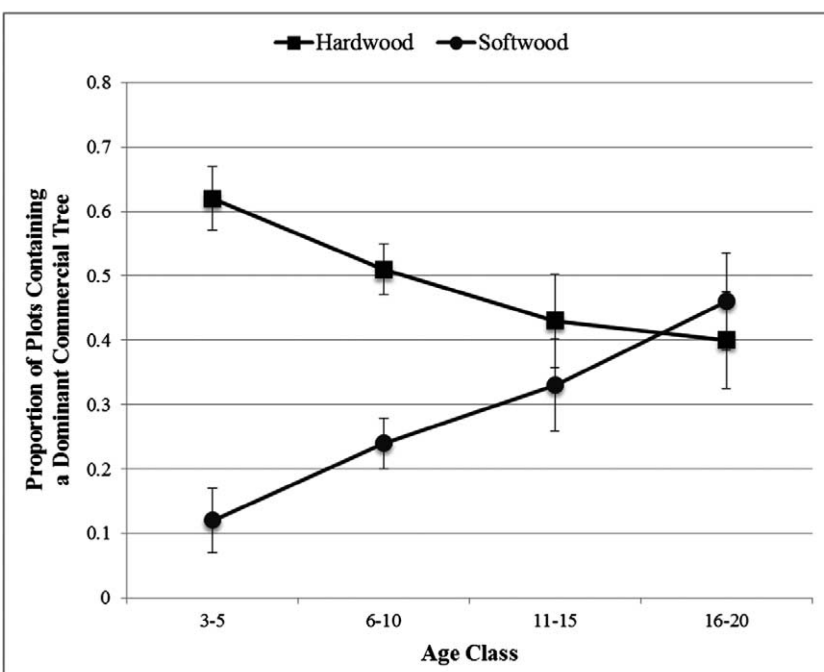

Fig. 5. Proportion (%) of plots containing either dominant commercial hardwood or softwood stems by age class in nothereastern Vermont, 2012.

Table 2. Species composition (%) and browse damage category of dominant stems by age class in clearcuts in northeastern Vermont, 2012.

Age Class	Species	Severe Damage	Moderate Damage	Light Damage	No Damage	Total
3–5	American beech	0	0	2	1	3
	Aspen spp.	0	0	3	0	3
	Balsam fir	1	0	2	3	6
	Black cherry	1	0	0	0	1
	Red maple	0	0	15	8	24
	Red spruce	0	0	1	3	5
	Sugar maple	0	0	4	2	6
	Tamarack	0	0	0	1	2
	White ash	0	0	0	0	1
	White birch	1	0	1	1	3
	Yellow birch	1	0	13	5	20
	Non commercial	NA	NA	NA	NA	26
6–10	American beech	0	0	2	1	3
	Aspen spp.	0	0	1	0	2
	Balsam fir	1	1	4	9	15
	Red maple	1	1	12	3	16
	Red spruce	0	0	0	9	9
	Sugar maple	0	0	8	2	10
	White ash	1	0	0	0	1
	White birch	2	0	2	0	4
	Yellow birch	1	0	11	3	14
	Non commercial	NA	NA	NA	NA	25
11–15	American beech	1	0	1	0	3
	Aspen spp.	0	0	3	2	6
	Balsam fir	2	1	7	7	17
	Black spruce	0	0	0	1	1
	Red maple	3	2	8	0	13
	Red spruce	0	0	1	9	11
	Sugar maple	1	0	3	0	4
	White birch	4	1	4	0	9
	Yellow birch	2	0	8	1	11
	Non commercial	NA	NA	NA	NA	24
16–20	American beech	1	1	3	2	6
	Aspen spp.	0	0	0	1	1
	Balsam fir	2	0	5	14	21
	Black spruce	0	0	0	1	1
	Red maple	7	1	14	1	23

Table 2 continued . . . .

Table 2 continued

Age Class	Species	Severe Damage	Moderate Damage	Light Damage	No Damage	Total
	Red spruce	0	0	1	20	21
	Sugar maple	0	0	4	1	5
	White birch	1	0	1	0	1
	Yellow birch	3	0	3	0	6
	Non commercial	NA	NA	NA	NA	14

similar trend occurred in New Hampshire (Bergeron et al. 2011) where the proportion of dominant commercial hardwood stems also declined with age class. Heavy browsing pressure could potentially accelerate successional development by arresting or retarding the height development of preferred browse species in the region (McInnes et al. 1992, Davidson 1993). While previous site compositions are unknown, it is possible a shift from hardwood to softwood dominated stands may be the natural successional trend for these sites. Although harvest records were unavailable for most sites, it appeared that many were originally mixed wood stands.

The proportion of dominant commercial trees ≥3.05 m (beyond browse height) without severe damage increased with age class, peaking at 39% at 16–20 years (Table 1). These stems are expected to recover from any moderate or light damage during future growth without browsing. In contrast, average values in adjacent northern New Hampshire were 36, 60, and 71% in the 3 older age classes, suggesting that growth was more suppressed in Vermont. Intense browsing in areas of high moose density can arrest or retard growth of preferred browse species (Bergerud and Manuel 1968, Angelstam et al. 2000). A study with exclosures on Isle Royale, Michigan indicated that repeated browsing by moose retarded vertical growth of palatable species such as aspen and paper birch, and prevented stems from growing beyond browsing height resulting in a more open canopy (Risenhoover and Maass 1987). Although heavy browsing of the same species in successive years can result in hedgy growth and lower height potential (Peek et al. 1976, Peek 1997), such stems can compensate if browsing declines or if removed in successive years; for example, after release of a dominant stem in forked stems (Jacobs 1969) and the straightening of crooked stems with secondary growth over time (Switzenberg et al. 1955, Trimble 1968). A clipping study on Isle Royale indicated that the site-dependent survival and growth of balsam fir were related to suppression brought about by severe browsing in previous years (McLaren 1996). Accurate prediction of damage is complicated by this dynamic process that is likely influenced by local site conditions, and seasonal moose density and site fidelity.

In studies assessing browse damage in both southern and northern New England, time since harvest was negatively correlated with foraging intensity (Faison et al. 2010, Bergeron et al. 2011) which may allow compensatory growth by desirable hardwood species beyond the 16–20 year age class. However, an increasing dominance of softwood species coupled with suppressed growth of hardwood species indicates a possible shift in species composition in WMU E1. Several studies have indicated change in forest composition due to heavy moose browsing. In Finland, Heikkila et al. (2003) measured reduced height of preferred browse species resulting in the release of conifers from competition. On Isle Royale, moose prevented aspen, birch, and balsam fir from growing into the canopy, with little impact to spruce, resulting in a forest with fewer trees in the canopy, a well-developed understory of shrubs and herbs, and an increase in spruce biomass (McInnes et al. 1992). Similarly, selective pressure resulted in rapid occupation of spruce (*Picea* spp.) as the dominant species in study stands in Russia (Abaturov and Smirnov 2002). A similar trend is possibly occuring in northeast Vermont where coniferous species account for >50% of total species composition in the 16–20 year age class (Table 2). A reduction in moose density, as implemented in the study area, may also reduce future browsing pressure and provide for the release of preferred hardwood species. A population reduction in Newfoundland in the early 1960s resulted in dramatic decline in the proportion of white birch and balsam fir stems browsed in 6–11 and 12–17 year old stands (Bergerud et al. 1968).

High-density moose populations have the potential to damage preferred forage species (Peek 1997), but the negative impacts of over-browsing can be minimized if moose density is kept at low-moderate levels (Brandner et al. 1990). In Russia, a density of 0.3–0.5 moose/km^2 retarded growth of preferred forage species such as aspen, whereas normal stand development occurred at 0.2–0.3 moose/km^2 (Abaturov and Smirnov 1992). In Sweden, simulated densities of 0.8–1.5 moose/km^2 did not impact winter browse availability; impact was predicted at >2.0 moose/km^2 (Persson et al. 2005).

Both northern Vermont and New Hampshire are classified as a combination of spruce-fir, northern hardwood, and mixed forest types (DeGraaf and Yamasaki 2001), and presumably measurable differences in forest regeneration reflect different moose density. Bergeron et al. (2011) found a direct correlation between browse damage and moose density in northern New Hampshire; the region with highest density had most damage. Densities in northeast Vermont were estimated at 1.2–1.8 moose/km^2 in 1999–2009 and were probably higher than those in the highest density region of New Hampshire estimated at 0.8–1.5 moose/km^2 for the same time period (C. Alexander, pers. comm., K. Rines, NHFG wildlife biologist, pers. comm.).

In both states significant differences were found in the stocking rate of dominant commercial trees, and the proportion of both dominant hardwood and softwood commercial tree species between the youngest and oldest age classes. However, the temporal comparisons among age classes indicate that sites with high initial browse pressure are often released from that pressure and recover to commercially valuable stands. In both Vermont and New Hampshire, stocking rate increased and damage declined over time with relative differences seemingly influenced by local moose density. Compensatory growth in the region was measurable in the 16–20 year age class, but likely begins earlier when stems grow beyond browsing height. However, heavy browsing pressure on preferred tree species may result in lower stand height as measured in Vermont and a possible shift in forest composition to coniferous species. Further assessment is warranted to best evaluate the extent of compensatory tree growth in response to reduction in browsing due to forest aging and/or moose population density.

ACKNOWLEDGEMENTS

We are grateful to the numerous commercial and private landowners for their cooperation and providing access to their property including, but not limited to, Silvio

O. Conte National Fish and Wildlife Refuge, Plum Creek, Heartwood Forestland Fund, and Devost Leasing. We thank D. Bergeron, C. Alexander (VTFW moose biologist), and K. Rines (NHFG moose biologist) for providing useful data. We are also thankful to T. Millette, H. Stabins, W. Leak, and M. Yamasaki for providing knowledge and guidance throughout the project, and to J. Trudeau, N. Fortin, and J. Comeau for assistance in the field.

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