The Effects of Moose (Alces alces L.) on Hemlock (Tsuga canadensis (L.)Carr.) Seedling Establishment in Algonquin Provincial Park, Ontario, Canada

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Abstract

The effects of moose on eastern hemlock (*Tsuga canadensis*) natural seedling establishment in Algonquin Provincial Park, Ontario, were examined. Two thousand seedlings were tagged on 56 sites in 1992 and monitored for six years. Initial data collected included seedling height, browsing history and percent crown closure. At the end of the growing season of the following six years, heights of these seedlings were remeasured; damages on seedlings were assessed according to browsing, physical, logging and unknown factors. After six years, 10.4% of the seedlings had died. Browsing caused 60% of the mortality, followed by unknown factors (18%). Growth rates of healthy, unbrowsed seedlings were significantly affected by initial height, health and percent crown closure. Growth was best at 60% crown closure and least at 80% to 100% crown closure. Healthy, undamaged seedlings grew better than seedlings with browse damage, dieback or both. Mean height losses were 11.1 cm with each browsing incident. Growth rates indicated that seedlings may need to avoid being browsed for up to 30 years to ensure leaders are out of the reach of moose. A negative correlation between moose density and browsing suggested that low moose density in recent years may provide a better opportunity for establishment and canopy recruitment.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.)Carr.) is a shade tolerant conifer common in the Great Lakes - St. Lawrence and Acadian forest regions of Canada. In the United States it is found from Wisconsin east to New England and south in the Appalachians to Tennessee and northern Alabama (Farrar 1995). Common associates include yellow birch (*Betula alleghaniensis* Britt.), beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) (Fowells 1965).

Hemlock seedling and sapling growth can be slow under heavy shade. In the dense shade of a hemlock-beech forest, growth can be 3 - 5 cm/yr, while under a more open canopy, growth can be 6 - 10 cm/yr (Fowells 1965). Vigorous saplings can grow 20 - 30 cm/yr under light to medium shade, and up to 45 cm/yr with full light and adequate moisture (Anderson *et al.* 1990). Optimal seedling growth under nursery conditions was at 45% light intensity (66 cm in 7 years) (Logan 1973). Most papers describe the slow growth of hemlock saplings under suppression and their rapid growth after release (Marshall 1927, Fowells 1965). Saplings can tolerate shade for up to 400 years (Fowells 1965). Seedling mortality is high, especially in the youngest seedlings. The main causes are desiccation and smothering by hardwood leaf litter (Fowells 1965). Mortality rates of older, established seedlings are unknown.

Browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) is known to inhibit eastern hemlock growth and establishment (Stoeckler *et al.*1957, Webb 1957, Anderson and Loucks 1979, Euler and Thurston 1980, Frelich and Lorimer 1985, Alverson *et al.* 1988, Anderson and Katz 1993). A recent study in Algonquin Provincial Park, Ontario, identified an age gap in the hemlock population caused by past deer browsing. High deer populations promoted by the creation of suitable habitat from fires and logging resulted in intense browsing pressure on hemlock and other woody species between the 1890's and the 1950's. During this period relatively few hemlock seedlings survived to reach the sapling stage and recruit into the canopy. This created a gap in the age distribution with a distinct lack of hemlock stems between 40 and 100 years of age (Vasiliauskas 1995).

With the final demise of the deer population in Algonquin during the 1970's, moose became the dominant ungulate (Strickland and Rutter 1987). A concern by park staff on the lack of hemlock regeneration led to a study by Vasiliauskas (1995) who determined that current browsing by moose (*Alces alces* L.) on hemlock seedlings was limiting growth and canopy recruitment. Deer were not considered to be a factor in hemlock browsing as they are uncommon and the study by Vasiliauskas (1995) found deer pellets in less than 1% of the plots. Very few studies have examined the effects of moose browsing on hemlock growth and mortality (Vasiliauskas 1995). Browsing may have a major influence on survival as browsed seedlings stand little chance of recruiting into the canopy (Curtis 1959). A better understanding of moose browsing effects on hemlock seedling growth and mortality would empower forest managers in management decision-making, particularly in predicting stand development.

The main objective of this study was to examine the effects of moose browsing on hemlock seedling establishment. Questions addressed include:

- How much does moose browsing attribute to seedling mortality?
- How does height growth respond to moose browsing pressure?
- How does canopy closure affect seedling growth?

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Materials and Methods

Study area - The study area was in the western part of Algonquin Provincial Park, (Algonquin) Ontario, between 78°15' to 78°51' W and 45°19' to 45°40' N. The park is located on the Algonquin Dome (elevation 400 to 550 m a.s.l.), an area 200 to 300 m higher than the surrounding area with a cooler, more humid climate. Soils on the upland areas are primarily sandy loams that originated from glacial tills and till veneers and are usually less than 1 m deep. The area is covered by northern hardwood forest dominated by sugar maple, yellow birch, eastern hemlock and beech. Lakeshores are dominated by hemlock, balsam fir (*Abies balsamea* (L.)Mill.), white pine (*Pinus strobus* L.), white cedar (*Thuja occidentalis* L.) and yellow birch (Strickland 1987).

Seedlings - Fifty-six naturally established seedling populations were randomly selected in the autumn of 1992. Sites we variable in area, but did not have a radius greater than 15 metres for facilitating seedling relocation. At each site, 10 - 40 seedlings were randomly selected from the large number that were available and tagged with numbered aluminum tags for a total of 2000 seedlings. After tagging, height of each seedling was measured. Seedling heights ranged from 10 cm to 3.1 m. Canopy closure above each seedling was measured using a spherical densiometer. Browsing history of tagged seedlings was attributed to moose or hare (*Lepus americanus*), based on the type of damage. Browsing species can be identified by the type of break on the twig. Hares cut cleanly through the twig, while moose or deer leave a ragged end. Because moose and deer browsing is similar, pellet groups in the vicinity of the plot indicated which ungulates were present. The proportion of a seedling damaged by browsing was determined by measuring the distance between the lowermost and uppermost twigs with browse damage, dividing this by seedling height, and expressing it as a percent. Recent germinants were observed on some of the sites and we took the opportunity to determine mortality rates of these seedlings. Twenty-six patches were selected within these sites and all recent germinants were counted. Patch boundaries were outlined with tree-marking paint for relocation. Because snow depth affects the accessibility of seedlings to herbivores, we measured maximum snow depths in March 1993 at five randomly located points in each site. The snow was considered to be at the maximum depth based on observations during the winter.

We defined early September as the end of the growing season and monitored the seedlings from 1993 to 1998. In each year, we recorded seedling height to leader tip, browse damage since the previous year, and cause of mortality if it could be determined. Mortality causes were classified as browsing, unknown, physical damage, and logging damage. Unknown included undamaged seedlings that may have died from any of several different factors, such as disease, desiccation, insect damage or competition. Physical damage included trampling, snow damage, trees falling on the seedlings or being uprooted by falling trees. Seedlings were classified at each survey into several health classes. These classes include healthy (no browse damage ever), browsed once, browsed more than once, leader dieback (not from browsing damage), and dieback with browsing damage. Recent germinants were recounted in 1993 and 1994.

Data analyses - Mortality was summarized by cause and by year for the complete data set, because of the low levels of mortality. Annual seedling growth rates were determined for each seedling by calculating the difference between 1998 and 1992 heights and dividing by six. Percent damaged by browsing and amount of height lost in each browsing incident was determined for each seedling for the complete data set and annual values were calculated from this. Means were calculated by site for crown closure class and annual seedling growth by health class. Analysis of variance was used to determine seedling growth responses to browsing and canopy closure. Linear regression was used to determine individual healthy seedling growth rates as affected by initial height. Statgraphics Version 7.0 (Manugistics 1992) was used in all analyses.

Results

Mortality - Seedling mortality was relatively low (1.7%/yr), with 207 seedlings (10.4%) dying over six years. Over half of the seedlings (60%, Table 1) died from browsing, either from being cut through the stem below the foliage, consumption of all foliage, or declining after heavy browsing. Unknown factors that affected unbrowsed seedlings were the next main cause of death (18.8%). Logging damage, which occurred on five sites, accounted for another 15%. Physical damage from treefalls or trampling accounted for the rest of the seedling mortality (6.2 %).

Mortality was high in the youngest age classes. Forty-nine percent of the 1992 germinants (n=74) and 18.7 % of the 1990 germinants (n=819) died between 1992 and 1994. The difference in mortality between these two cohorts could be attributed to the age difference. Most of the mortality may have occurred for the 1990 germinants by 1992, hence the lower mortality rate. Mortality was due to desiccation, browsing by hares or voles, trampling by moose, or being on a poor microsite. Monitoring of these patches was discontinued after 1994 due to fading of markings around patches.

Table 1.—Number of hemlock seedling dying each year by cause for 2000 tagged seedlings in Algonquin Provincial Park.

Year	Browsed	Unknown	Physical	Logging
1993	6	6		
1994	13	7		18
1995	18	8	2	
1996	29	5	7	13
1997	34	7	3	
1998	24	6	1	
Total	124	39	13	31

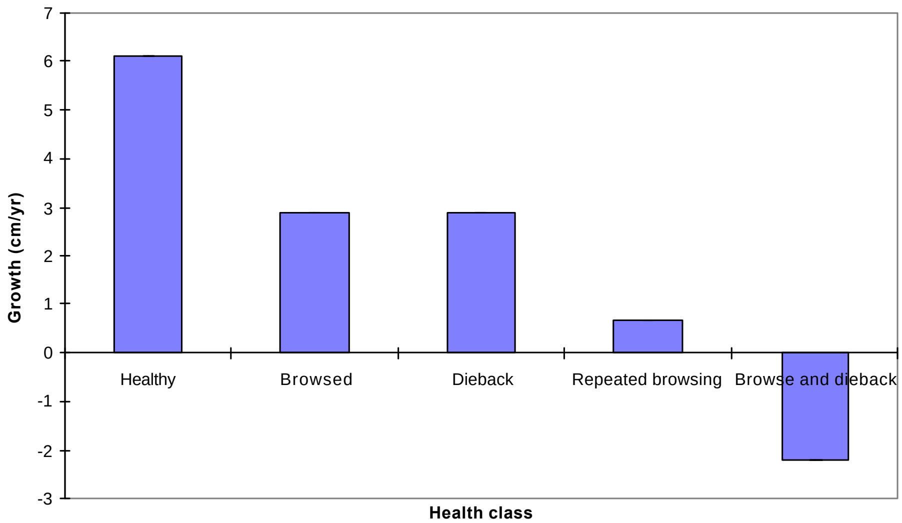

Figure 1.—Mean annual growth rates by health class in 1998 for 2000 tagged seedlings from 56 sites in Algonquin Provincial Park

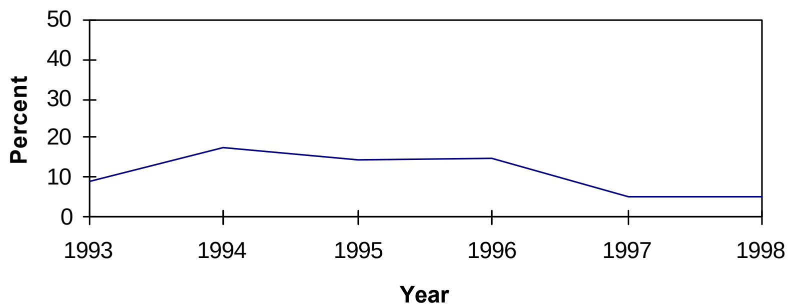

Figure 2.—Percentage of seedlings browsed each year from 2000 tagged seedlings in Algonquin Provincial Park

Browsing - Seedling health class had a significant effect on height growth (Fig. 1, F-ratio = 59.9, $p < 0.001$). Healthy, undamaged seedlings had a mean annual growth rate of 6.6 cm/yr, significantly better than seedling with dieback or browsing damage. Seedlings which had been browsed once, or had leader dieback, had similar growth rates (2.9 cm/yr). Seedlings browsed more than once grew only 0.67 cm/yr. Browsed seedlings that also suffered dieback lost 2.2 cm/yr. Seedlings from these last two classes are most likely to die in the near future.

Browsing rates are probably influenced by moose densities. The higher percentages of seedlings browsed each year during the first half of this study (9.2% to 18%/yr, Fig. 2), coincided with the higher moose densities (0.5 moose km^2, OMNR, unpublished data) at that time. The lower value for 1993 (9.2%) is probably due to moose concentrating their browsing on hemlock tops brought down by a windstorm in November 1992 (pers. obs.). The percentage of seedlings browsed each year has decreased to 5.3 %/yr during the last two years, coincident with a recent drop in moose densities to 0.35 moose /km^2 (January 1998 estimate, OMNR unpublished data). No data is available on snowshoe hare populations during this time, but they are of minor importance compared to moose (Vasiliauskas 1995).

Mean height loss of browsed seedlings after each browsing incident was 11.1 cm ($\pm$ 0.45 cm), or almost two years of height growth. The mean percentage of a seedling that was damaged from a browsing incident was 34.5 % ($\pm$ 1.1%).

The other concern during the first part of the trial was the rapid decrease in unbrowsed seedlings, decreasing from 71% in 1992 to 52.3% by 1995 (Fig. 3), a rate of 6.2%/yr. If this trend had continued, there would have been few unbrowsed seedlings by 2003. This decrease abruptly slowed to 0.5%/yr since 1995, and coincided with the decrease in moose densities. It is not known why it started a year before the moose population decreased.

Snow depths in March 1993 ranged from 30 to 70 cm with less snow found under conifer cover. The percentage of seedlings browsed per site that winter was not significantly affected by maximum snow depths (linear regression, F-ratio=2.98, r^2=0.052, p=0.09). This was not continued in subsequent winters because browsing starts in the fall before there is any snow cover.

Growth Rates - Growth over 6 years of healthy, undamaged seedlings was significantly affected by initial height (linear

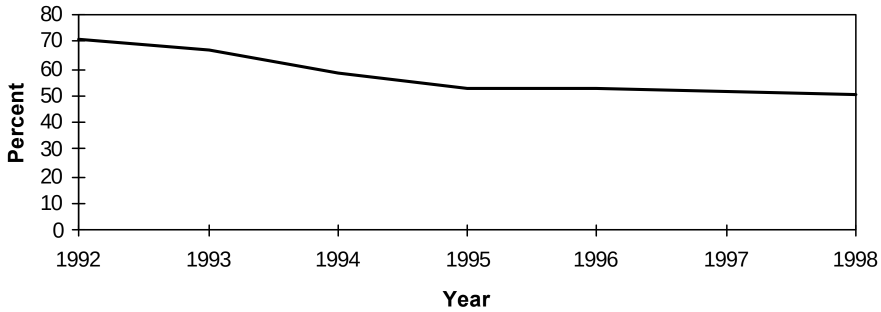

Figure 3.—Percentage of seedlings with no browse damage by year from 2000 tagged seedlings in Algonquin Provincial Park.

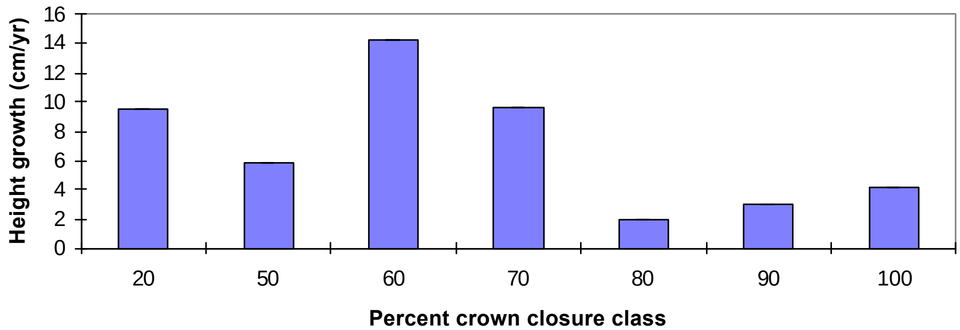

Figure 4.—Annual growth rates by canopy cover class for 828 healthy seedlings from 56 sites in Algonquin Provincial Park.

regression, n=828, F-ratio=654.2, r^2 =0.442, $p < 0.001$). This is described by the model:

Total annual growth increment (m) = 0.12 m + 0.41 (1992 height)

Current annual height increment was also significantly related to seedling height (linear regression, n=828, F-ratio=406.5, r^2=0.33, $p<0.001$), and is described by the model:

Current annual height increment (m) = 0.0065 m + 0.054 (seedling height)

Effect of crown closure on seedling growth - Percent crown closure significantly affected height growth of healthy, undamaged seedlings (Fig. 4, F-ratio = 8.1, $p < 0.001$). The best growth was at 60 % - 70 % crown closure. Competition from other vegetation may be a limiting factor for seedlings growing under higher light conditions (crown closure ≤ 50 %). Under deep shade conditions, limited light availability was the primary factor affecting seedling growth.

Discussion

Mortality - Hemlock seedling mortality rates were highest in the youngest seedlings (< 4 yrs old), as would be expected (Fowells 1965). Although seedlings can germinate on unsuitable microsites, they eventually die from desiccation, lack of nutrients, or smothering by hardwood leaves. Unbrowsed, established seedlings appear to have very low mortality rates (0.43%/yr) and die from physical damage or unknown causes such as desiccation, disease or other factors. At this low rate it would take over 200 years for all of the seedlings to die, reflecting the high shade tolerance of hemlock. Browsing is an additive source of mortality, and could cause mortality of most of the seedling population within a few decades, especially if browsing pressure returns to the same high levels as at the start of the study. Browsing intensity tends to be higher at lower seedling densities (Vasiliauskas 1995). Seedlings that could have grown into saplings at these densities have a low probability of doing so due to browsing. At higher seedling densities, browsing may kill some seedlings that would eventually have died from competition effects, but browsing usually affects all larger seedlings in a stand.

The present seedling population originated after the crash in the deer population in Algonquin Park during the late 1950's, based on the age structure from Vasiliauskas (1995). Most seedlings are less than 30 years old, and there is little evidence of earlier high seedling mortality. A dead seedling count by Vasiliauskas (1995) found only 487 dead seedlings out of 20,281, or 2.4% of all seedlings. Dead seedlings are visible for several years (>5) based on observations from this study. Hemlock does not appear to follow the pattern of sugar maple, which is known to have high turnover rates in dense shade (Curtis 1959, Rogers 1978, OMNR 1983). The low turnover rates of hemlock seedings are due to its high shade tolerance and persisting in the understorey for decades before dying from lack of light.

Browsing - Browsing is the main factor influencing seedling growth and survival. Browsed seedlings have little potential to recover lost height and recruit into the future canopy (Curtis 1959) due to leader and foliage loss, resulting in a decrease of hemlock stem density in the long term. Some seedlings are more likely to recover provided that initial browsing was light. Rebrowsed seedlings have little potential to become saplings, because they become bushy and multi-stemmed, and grow at only 10% of the rate for healthy seedlings. In addition, the probability of being rebrowsed doubles if a seedling has been previously browsed (Vasiliauskas 1995). Snowshoe hares play a minor role in hemlock browsing and have the greatest effect on small seedlings that can be nipped off at the base (Vasiliauskas 1995). Snow does not protect seedlings, as browsing starts in the fall before there is any snow cover. The steady decrease in the number of unbrowsed seedlings at the start of the study suggested that few seedlings would escape browsing. The recent decrease in browsing intensity and in the rate of loss of unbrowsed seedlings suggests that there may be a much better chance of seedlings recruiting into the canopy.

If lower browsing levels are maintained, the age gap in the hemlock population started by past deer browsing could end. Hemlock should maintain itself on the landscape at about current levels. However, if browsing intensity increases, the age gap will be extended. This would decrease the area dominated by hemlock and restrict it to areas with little or no browsing pressure. Forest cover will shift to dominance by other species such as sugar maple, as mature hemlock die and are not replaced.

Growth - Seedling growth is similar to other studies (Fowells 1965, Anderson *et al*. 1990). Seedling growth appears to maximize under partial shade (60% canopy closure). Larger seedlings have faster growth rates since they have more photosynthetic surface area, as determined for white spruce (*Picea glauca* Moench.)(Lieffers *et al*. 1996). It is unknown if the lower growth rates under higher light levels was due to increased hardwood competition, or to seedlings producing more side branches and more lateral growth. Monitoring more saplings under open canopy conditions would help to answer this question.

Implications to management

Hemlock is highly sensitive to browsing pressure. Seedlings can lose at least two years of height growth with each browsing incident and recover slowly. Naturally established seedlings can require up to 30 years before the leaders are at least 3 metres above the ground and out of the reach of moose. Ungulate populations need to remain low, or seedlings have to be protected for this length of time to ensure hemlock recruitment. At the stand level, foresters can consider manipulating canopy openings to maximize seedling growth, reducing browsing pressure or protecting seedlings. At the landscape level, foresters can consider managing hemlock in areas with low browsing pressure rather than trying to maintain it in areas with heavy browsing pressure. In areas where hunting is permitted, ungulate populations may be lowered through increased hunting.

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