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Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuja occidentalis* forests

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Abstract

Regeneration success of canopy dominants is linked to multiple factors, including the ability of their seedlings to survive browsing and to utilize available resources in the understory. In remnant upland northern white cedar *Thuja occidentalis* L. forests, effects of browsing on recruitment of cedar seedlings were evaluated at 7 sites, including known deer yards, located on a portion of the Lake Superior Highlands in northeastern Minnesota. Experimental plantings and vegetation surveys were conducted inside and outside large deer exclosures constructed between 1937 and 1997. Objectives were to determine severity and intensity of browsing by *Odocoileus virginianus* Zimmerman, the ability of seedlings to survive browsing in environments beneath *T. occidentalis* and adjacent paper birch (*Betula papyrifera*) Marshall canopies, and potential long-term sapling recruitment under different browsing scenarios. From 1994 to 1997, 76% of unexclosed planted *T. occidentalis* seedlings had been browsed at least once, compared with 0% of exclosed seedlings. Increased browsing intensity and decreased light availability increased *T. occidentalis* mortality rates. Simulation models and vegetation surveys demonstrated that the best recruitment rates occurred for seedlings planted under *Betula* canopy and subjected to low browsing severity, but no recruitment occurred under high browsing pressure under either canopy type. The current level of browsing in these forests has the potential to alter the future composition of canopy tree species through sustained prevention of *T. occidentalis* recruitment. © 2000 Published by Elsevier Science Ltd. All rights reserved.

Keywords: Upland *Thuja occidentalis* forests; Remnant forests; Browsing and canopy interactions; Human-altered landscapes; Conservation

1. Introduction

The impact of herbivory on species composition in plant communities has been demonstrated by many authors (e.g. Beals et al., 1960; Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Tilghman, 1989; Strole and Anderson, 1992; Van Deelen et al., 1996). In forests, seedlings of some late successional conifers may be especially vulnerable to herbivory (e.g. Little and Somes, 1965; Anderson and Katz, 1993; Alverson and Waller, 1997). If high levels of herbivory are sustained, species sensitive to browsing, especially if they experience other stress factors, may fade from the forest over time, while browse tolerant species persist.

In the northern Great Lakes region (Ontario, Minnesota, Michigan and Wisconsin), conifer-dominated forests were once more common. Since European settlement, natural dynamics, extensive logging, ensuing fires, and residential development have greatly altered the landscape. Human activity has homogenized and simplified the composition and structure of the region's forests (Mladenoff and Pastor, 1993). A wide variety of forest types once intermingled on multiple spatial scales. Today, even-aged, early successional forests, particularly of quaking aspen (*Populus tremuloides*) Michx. and paper birch (*Betula papyrifera*) Marshall, are most common (Frelich, 1995). Embedded within this early-successional forest matrix are occasional remnant stands of the presettlement landscape, including upland northern white cedar (*Thuja occidentalis* L.) forest.

The logging history and current forest management practices have also impacted the region's fauna. Originally, the extreme winters and vast forests with little undergrowth for browse in many cases made the northern Great Lakes region poor habitat for white-tailed deer (*Odocoileus virginianus*) Zimmerman (Bartlett, 1950; Dahlberg

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and Guettinger, 1956). *O. virginianus* may have been completely absent from northeastern Minnesota prior to the early 1900s (Shiras, 1935; Nelson and Mech, 1986).

Harvesting practices, such as the large-scale clear-cutting that took place early this century throughout Minnesota, created early-successional plant communities with abundant browse (Krefting, 1975). As a result, by 1938 *O. virginianus* densities in northeastern Minnesota ranged from 4 to 16 deer/km^2 (Mech and Karns, 1977). Since the 1930s, the *O. virginianus* population in northeastern Minnesota has fluctuated, the average densities over the past few decades ranging from 3 to 10/km^2 (Joselyn and Lake, unpubl. rep., 1987; Dexter, unpubl. rep., 1997). There is evidence, however, that winter densities on the Lake Superior Highlands are substantially higher than the rest of northeastern Minnesota. For example, in the Jonvik Deer Yard, a 2,500 ha wintering yard on the Lake Superior Highlands, winter densities of 45/km^2 were reported in 1973, and 50/km^2 were observed in 1994 in heavily used areas, based on 13 pellet groups/day/individual (Mech and Karns, 1977; Lankester and Peterson, 1996; but see Rogers, 1987). Moreover, *O. virginianus* tend to concentrate in stands of *T. occidentalis* during winter months, exposing them to extreme herbivory damage (Verme, 1965).

Historically, *T. occidentalis* was present on approximately 8% of the presettlement landscape in northeastern Minnesota, growing in both upland and lowland areas as stand dominants and in mixed species stands (US Surveyor General, unpubl rep., 1847–1908; S. Friedman, unpubl. data). Today, *T. occidentalis* constitutes only around 4% of the canopy cover in remaining forested areas of the northeastern Minnesota (S. Friedman, unpubl. data).

Poor recruitment within remaining stands has caused concern that upland *T. occidentalis* forests will not persist as an important forest type in the Great Lakes Landscape (Rusterholz, unpubl rep., 1992; Heitzman et al., 1997). For example, recent surveys of canopy species recruitment in upland *Thuja-Betula* forests detected no seedlings of *T. occidentalis* between 30 cm tall and 1.2 m (Cornett et al., 1997), the range of heights most frequently browsed (Beals et al. 1960; Saunders and Puettmann 1999a). *T. occidentalis* is considered to be a favored browse species (Beals et al., 1960), and browsing by *O. virginianus* is thought to be one of the main causes for the lack of *T. occidentalis* seedling recruitment for the last several decades (Aldous, 1949; Krefting, 1975; Alverson et al., 1988). The lack of saplings suggests that browsed seedlings do not readily survive these conditions. In testing this hypothesis, the feedback loop (sensu Wilson and Agnew, 1992) of the overstory composition on the understory's susceptibility to browsing was explored.

This study examined the interacting effects of two major changes in the landscape of northeastern Minnesota on the recruitment of *T. occidentalis*, the expansion of the range and increased density of *O. virginianus* and early-successional deciduous forest. Deer browsing and canopy type may interact as part of a feedback process with the potential to influence future species composition. The creation of more favorable *O. virginianus* habitat, for example, may have changed the recruitment environment for canopy tree species. To investigate this interaction, four major objectives were addressed. The first was to determine the severity and intensity of current levels of deer browsing on seedlings of *T. occidentalis* in *Thuja-Betula* forests. The second was to compare the degree to which *T. occidentalis* seedlings survive and grow in the different environments beneath *Thuja* and *Betula* canopies, subsequent to being browsed. The third objective was to determine potential long-term recruitment rates of *T. occidentalis* to height classes (> 2.1 m) less vulnerable to deer browsing. Finally, the long-term effect of browsing on other vegetation in *Thuja-Betula* forests was evaluated.

2. Methods

2.1. Study area

Conducted along a portion of the of Lake Superior Highlands in northeastern Minnesota (Fig. 1), the study area comprised roughly 150 km of shoreline containing 7 study sites spanning from southwest (47°08′N, 91°30′W) to northeast (47°58′N, 90°04′W). The climate is continental with a mean annual temperature of 4.7°C, and mean annual precipitation of 739 mm (Midwestern Climate Center, Ill. State Water Survey, Champaign, Ill.). Mean winter temperature within 2.5 km of Lake Superior (−5.5°C) is higher than inland temperatures, which range from −6.7 to −12.2°C from 3 to 50 km inland (Eichenlaub, 1979). Elevation is around 244 m, with surface elevation of Lake Superior at approximately 184 m. Topography is gently-rolling to steep, and soils are shallow Boralfs (< 0.5 m to bedrock in places) (Minnesota Department of Natural Resources, unpubl. reps., 1979, 1980,1997; Anderson and Grigal, 1984).

Dominant canopy species at the study sites included *B. papyrifera*, *P. tremuloides* and *T. occidentalis*. The prevalence of old stumps suggested a history of timber harvesting at or near all study sites. Early spring surveys (1995 and 1996) of percentage available twigs browsed during the preceding winter demonstrated that background levels of browsing on woody vegetation ranged from 4 to 28% per year.

2.2. Experimental design

The 7 sites were selected on the basis of having both *Thuja* and *Betula* canopy types. The study was conducted at different levels of intensity among the sites, in terms

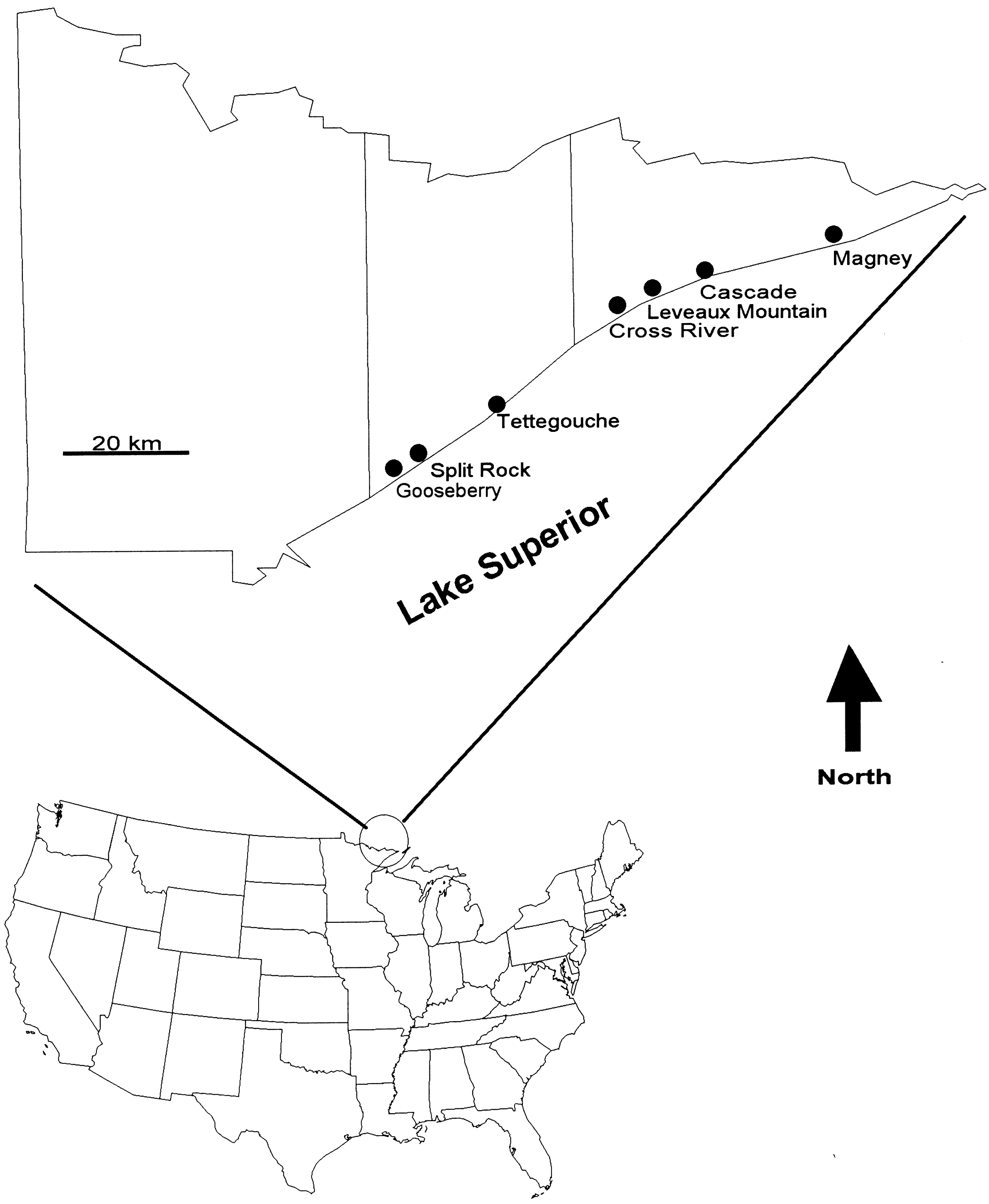

Fig. 1. Study area containing 7 sites on the Lake Superior Highlands, northeastern Minnesota.

of numbers of activities conducted, seedlings planted, and years monitored (Table 1). The rationale for nested levels of intensity included to take advantage of long term exclosures and to document trends at several sites over time, using experimental resources efficiently.

Most research at the three intensively-studied sites (Split Rock, Tettegouche, and Gooseberry Falls) was conducted within 6 macroplots, ranging from 1.5 to 3 ha in size. Each macroplot contained a 2×2 factorial layout with two canopy types (*Thuja* vs. *Betula*) and two browsing treatments (exclosed vs. unexclosed) in adjacent areas (Fig. 2). Exclosures were 4.5 m tall, constructed of wire mesh that excluded deer, but not hare (*Lepus americanus* Erxl.). Logistical constraints prevented the construction of all exclosures in the same year. Sufficient funding was available for exclosure construction at only the three sites with the largest stands of *Thuja occidentalis*. However, additional plantings not associated with exclosures were subjected to the same canopy treatments (Fig. 2).

Table 1
Summary of field activities conducted at 7 sites on the Lake Superior Highlands. Split Rock was the most intensively studied site, followed by Tettegouche and Gooseberry. Relevés were only conducted at exclosures whose construction date is designated with an [a]

Site	Macroplot pair establishment[b]	Exclosure construction	Planting of seedlings	Detailed survey	Relevé
Gooseberry	1996 (8.2, 0.8)	1987[a], 1997	1996		1997
Split Rock	1994 (0.6, 1.2)	1994	1994	1994, 1997	
Tettegouche	1996 (0.4, 0.7)	1996	1995, 1996		
Cross River			1995		
Leveaux		1937[a]			1997
Cascade		1937[a], 1938[a], 1950[a], 1953[a], 1953[a] 1986[a]	1995		1997
Magney			1995		

[a] Pre-existing exclosures.

[b] Approximate size in ha of exclosed portions of macroplots shown in parentheses.

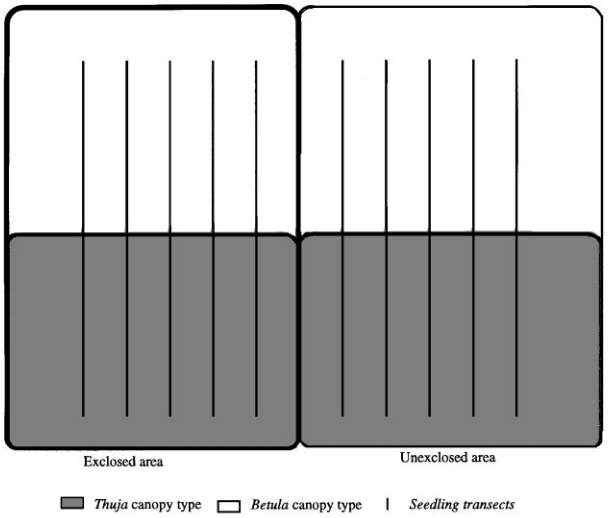

Fig. 2. Layout of macroplots at the Split Rock, Tettegouche, and Gooseberry Falls sites.

2.3. Impact of deer browsing on planted seedlings

In the absence of seedlings of browsable height, seedlings of this height class were planted at 6 of 7 sites. Seedlings were purchased from the Minnesota Department of Natural Resources (MNDNR) Forestry Nursery in Willow River, Minnesota. In compliance with their Seed Source Control Guidelines, the MNDNR matched our study site locations with 3-year-old nursery grown seedlings of local seed origin. Seven hundred and fifty seedlings (mean height $=0.3$ m) were planted at 1 per 9 m^2 in the spring of 1994 at the two Split Rock macroplots (Table 1, Fig. 2). To confirm whether trends observed at Split Rock could be generalized to other sites, an additional 400 seedlings were planted at the Tettegouche and Gooseberry exclosure sites in 1996 (Table 1, Fig. 2). As a means of gathering additional data from sites and portions of sites at which exclosures were not constructed, an additional 400 *T. occidentalis* seedlings were planted in the spring of 1995 at Cross River, Tettegouche, Cascade, and Judge Magney (Table 1). For all planted seedlings, height and evidence of browsing by *O. virginianus* and *L. americanus* were recorded each year until the end of the study.

Data from seedlings planted in 1994 (Split Rock only) were analyzed separately as a larger, longer-term data set, with 1995 and 1996 data used to confirm that trends occurred at >1 site. Non-parametric Wilcoxon tests were used to evaluate whether seedlings were browsed with equal frequency (severity) under the two canopy types. The effects of canopy type and percent height removed during browsing (intensity) on seedling survival were evaluated with logistic regression models. To avoid the confounding effects of mortality due to transplant shock, *T. occidentalis* seedlings that died within the first season after planting were excluded from the analyses.

2.4. Canopy openness

Paired LAI-2000 (Licor Inc., Lincoln, Nebraska) plant canopy analyzers were used to estimate light availability (canopy openness). Measurements were taken under full-leaf conditions in September of 1994 and 1995 at Split Rock. A below-canopy sensor was held just above *T. occidentalis* seedlings, and an above sensor for comparison was placed in an open area (ca. 1 km from the exclosure sites).

Logistic regression models were used to evaluate the effects of canopy type and canopy openness on seedling survival. Canopy openness analyses were based on a subset of the planted *T. occidentalis* seedlings at Split Rock: 112 below the *Betula* canopy, and 128 below the *Thuja* canopy.

2.5. Long-term effects of browsing

2.5.1. Planted seedlings

As a means of exploring possible recruitment rates into height classes less vulnerable to browsing (>2.1 m), the relationships between the effects of browsing and canopy conditions on *T. occidentalis* seedling growth and survival were integrated through the development of a simulation model. The model structure consisted of four height classes and four variables, adjusted for each height class (e.g., Table 2). Browsing and survival were stochastic variables.

Rules determined the fates of individual seedlings. A seedling's height increased by the centimeters assigned to its height class each year, unless browsed (Table 2). If browsed, the seedling risked mortality and was reduced in height by the probability and percent assigned to its height class. Height classes >2.1 m were not modeled.

Data generated by the present study were used as starting values for each of the variables in the first height class, from which additional estimates were made for larger height classes (Table 2). For example, Logan's (1969) relationship between age of *T. occidentalis* seedlings and height under different light conditions was used to determine the annual height increase for larger seedlings (Table 2). The relationship between seedling height and likelihood of browsing was a compromise between conflicting information that there is a decreasing relationship when leaders only are browsed (Saunders and Puettmann, 1999a) and that the relationship is an increasing one (Shabel and Peart, 1994). The only source of mortality introduced in the model is browsing.

Table 2
Baseline values for summary model for *T. occidentalis* seedlings growing under *Thuja* and *Betula* canopies

	Seedling height class (m)			
	<0.5[a]	0.5–1.2	1.21–1.8	>1.8
Thuja canopy				
Browsing probability/year	0.19	(0.25)[b]	(0.3)	(0.3)
Survival probability if browsed	0.55	(0.6)	(0.65)	(0.7)
Annual height increase (cm)	3.25	(9.9)	(14.9)	(14.9)
Percent height removed if browsed	35	(25)	(15)	(10)
Betula canopy				
Browsing probability/year	0.19	(0.25)	(0.3)	(0.3)
Survival probability if browsed	0.88	(0.9)	(0.95)	(1)
Annual height increase (cm)	4.6	(13.9)	(21)	(21)
Percentage height removed if browsed	35	(25)	(15)	(10)

[a] Values in the first height class were based on 4 years of observation of 750 planted seedlings.

[b] Numbers in parentheses indicate estimated values.

Runs of 1000 replicates modeled several different scenarios representing approximately 1 ha at typical spacing over 60 years. A run length of 60 years was used because this was the longest period over which existing exclosures had been in place (below), and as a comprehensible period over which resource management plans might extend. In a baseline set of two runs, growth and survival rates specific to the *Thuja* and *Betula* canopy types in the present study were used (Table 2).

A sensitivity analysis was conducted by means of additional sets of runs to evaluate the influence of each variable on recruitment into the >2.1 m height class. Four sets of runs were conducted to evaluate the importance of different growth rates under *Thuja* and *Betula* canopy types subjected to extremely low (i.e., exclosure conditions) and extremely high (60–65%) likelihoods of browsing. The interaction between browsing likelihood and growth rate was further evaluated by running four sets using combinations of high and low browsing likelihoods with growth rates halved and doubled. Finally, two sets were run with percentage height browsed halved and doubled.

2.5.2. Other vegetation

For the two Split Rock sites combined, vegetation was compared between exclosed and unexclosed areas in 1997. A total of 200 points were surveyed at the beginning and end of the study period. Percent cover data were obtained from circular plots (2 m radius) centered on each point. Wilcoxon non-parametric tests were used to evaluate differences in vegetation.

To determine longer term effects of herbivory on structure and composition of *Thuja*-*Betula* forests, vegetation within exclosures established over a decade ago was compared with adjacent, unexclosed areas for 8 locations at 3 sites (Table 1). Depending on the size of the exclosed area, data were collected inside and outside exclosures in plots ranging from 98 to 400 m^2. Data were collected using relevés, a semi-quantitative means of examining the structure and composition of plant communities. Percent cover for species within the three height classes most vulnerable to browsing during time since construction were recorded: 2 (0.1–0.5 m), 3, (0.5–2.0 m) and 4 (2.0–5.0 m). Vegetation in exclosed and unexclosed areas were compared with Wilcoxon non-parametric tests.

3. Results

3.1. Severity and intensity of deer browsing

Browsing by *O. virginianus* on planted *T. occidentalis* seedlings was severe at most of the study sites, both in terms of percentage seedlings browsed and the effect of browsing on seedling height class distributions (Figs. 3 and 4). Browsing by *L. americanus* on planted seedlings was detected only on two occasions at all sites between 1994 and 1997. In a given year, the percentage of unexclosed *T. occidentalis* seedlings browsed ranged from 13% at Split Rock to 61% at Cascade (Fig. 3).

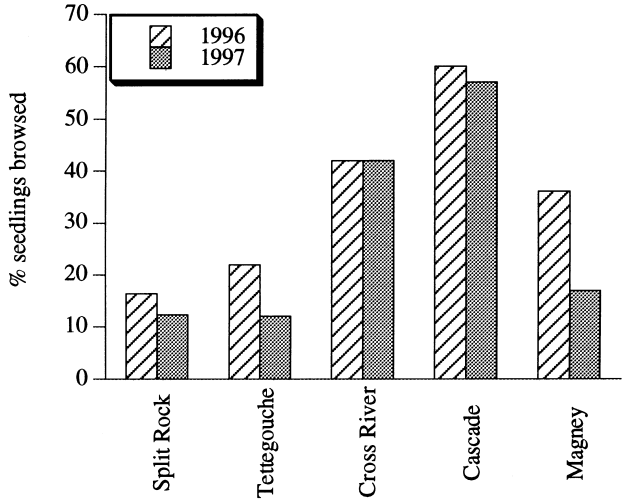

Fig. 3. Percentage (non-cumulative) planted *T. occidentalis* seedlings browsed in 1996 and 1997 at all five sites planted in 1994 and 1995. *T. occidentalis* seedlings were planted one year earlier at Split Rock than at the other sites, but for comparison are only shown here for the overlapping years.

Browsing directly impacted the height class distributions of planted seedlings. From 1994 to 1997 at Split Rock, the height class distribution of exclosed *T. occidentalis* seedlings shifted, with larger numbers of seedlings in the larger size classes ($\chi^2 = 107_{[1]}$; $p < 0.0001$), (Figs. 4A and 4B). In contrast, the distribution of unexclosed *T. occidentalis* seedlings shifted in the opposite direction, with larger numbers of seedlings in smaller size classes ($\chi^2 = 42.5_{[1]}$; $p < 0.0001$), (Figs. 4C and 4D). Similar trends in height class distributions were observed at the 1996 exclosure sites, but data were only collected over a two year period and were therefore not as dramatic (data not shown). Mortality of *T. occidentalis* seedlings was higher with greater browsing intensity (Table 3).

3.2. Canopy influence on seedling mortality

Although canopy type influenced the likelihood of seedling mortality following browsing, *T. occidentalis* seedlings were equally likely to be browsed beneath the *Thuja* and *Betula* canopies both at Split Rock ($\chi^2 = 0.004_{[1]}$; $p = 0.95$) and the other sites ($\chi^2 = 0.84_{[1]}$; $p = 0.4$). However, logistic regression models revealed

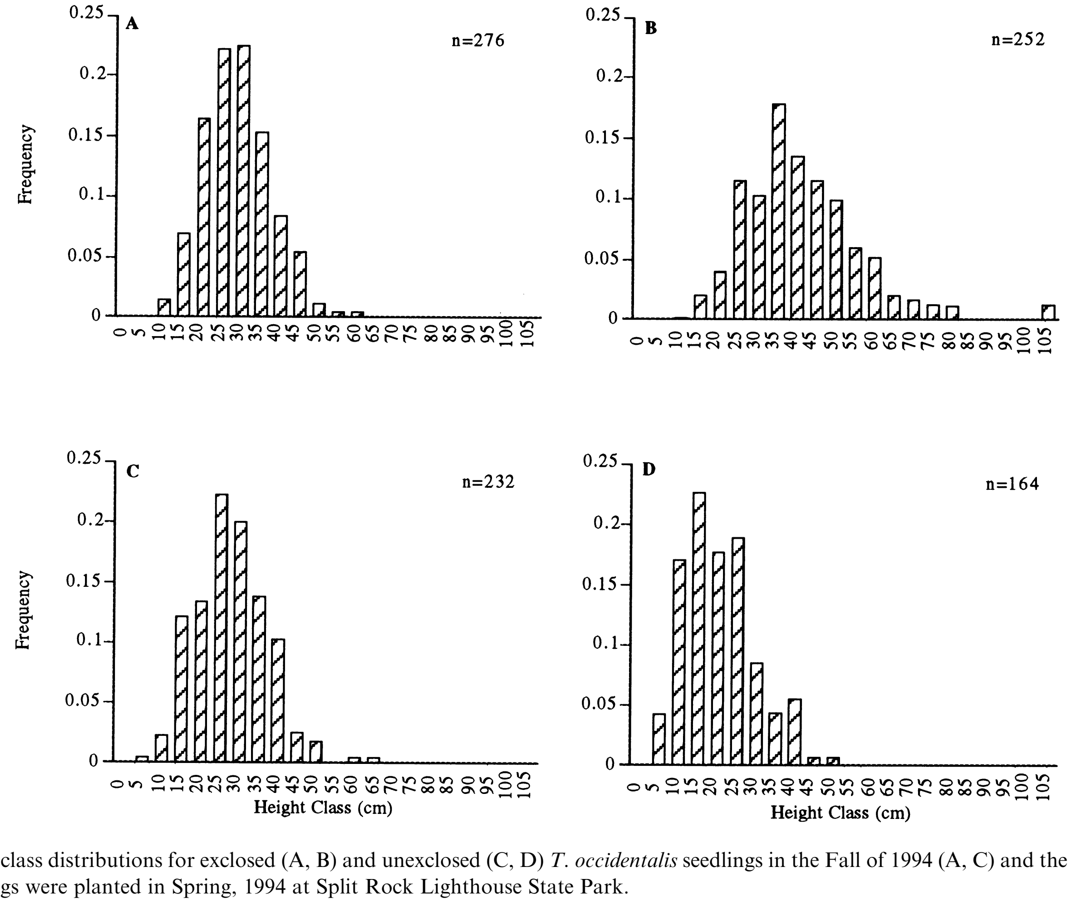

Fig. 4. Height class distributions for exclosed (A, B) and unexclosed (C, D) *T. occidentalis* seedlings in the Fall of 1994 (A, C) and the Spring of 1997 (B, D). Seedlings were planted in Spring, 1994 at Split Rock Lighthouse State Park.

that canopy type and browsing intensity affected seedling mortality (Table 3). Higher mortality rates occurred for browsed seedlings growing beneath the *Thuja* canopy at all sites (Fig. 5). None of the above trends were detected for macroplots where seedlings were planted in 1996. Mortality rates for unbrowsed seedlings did not differ beneath the two canopy types.

Canopy openness was on average twice as high beneath the *Betula* canopy [0.10 ± (0.007)] than the *Thuja* canopy [0.05 (± 0.004)] at the two Split Rock sites. There is evidence that light levels at a given canopy openness are lower beneath evergreen conifers than hardwoods (M. Tobin and P. Reich, unpubl. data), further distinguishing light availability between these two canopy types.

Table 3
Significant results from logistic regressions of the effects of canopy type (Canopy), browsing intensity (Intensity), and interactions on mortality of *T. occidentalis* seedlings at Split Rock Lighthouse State Park and the other North Shore state parks in combination (Tettegouche, Cross River, Cascade, and Magney)[a]

Site(s)	Variable	$\chi^2_{[1]}$	*P*
Split Rock (*n* = 148)	Canopy	8	0.001
	Openness	0.5	0.5
	Intensity	4.0	0.05
	C*O	7.7	0.006
	O*I	1.0	0.3
	C*I	0.6	0.4
	C*O*I	0.1	0.7
North Shore (*n* = 625)	Canopy	37.2	< 0.0001
	Intensity	22.7	< 0.0001
	C*I	12.6	0.002

[a] Canopy openness measurements were only available for a subset of seedlings at Split Rock, not for the North Shore sites. *P* values are the result of effect likelihood ratio tests.

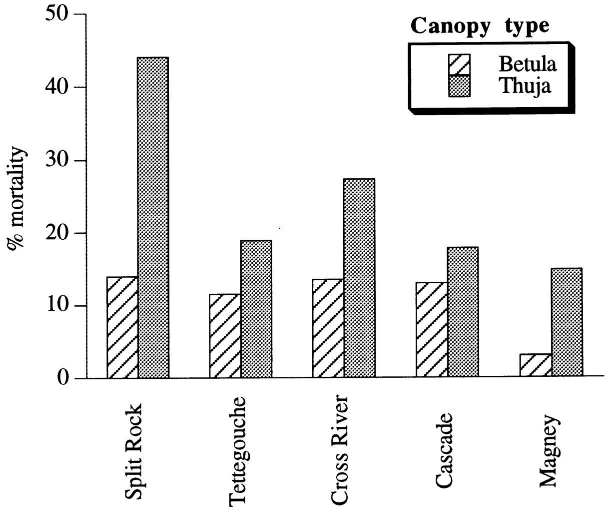

Fig. 5. Mean percentage mortality between 1995 and 1997 for browsed *T. occidentalis* seedlings at all five sites planted in 1994 and 1995.

3.3. Long-term effects of browsing

3.3.1. Planted seedlings

For baseline model runs, the different canopy conditions had a long-term influence on *T. occidentalis* recruitment rates (Table 4). Nearly half of the seedlings under the *Betula* canopy type reached heights of ⩾2.1 m by the end of the 60 year simulation period, while only 6% of seedlings under the *Thuja* canopy type reached 2.1 m (Table 4). For runs in which browsing levels were extremely high (i.e. > 60% mimicking levels that occurred at Cascade), differences in growth and survival rates beneath the two canopy types had little influence on recruitment to height classes ⩾2.1 m (Table 4). Even doubling the highest published growth rates did not compensate for extremely high browsing levels (Table 4). In contrast, good recruitment rates occurred even when lowest growth rates were halved if browsing levels were low. Halving and doubling the browsing intensity resulted in corresponding differences in the proportion of seedlings surviving and reaching 2.1 m (Table 4).

3.3.2. Other vegetation

Exclosures were equally effective at reducing browsing of naturally occurring shrub and tree species. The highest percentage of twigs browsed in an exclosed area was 3.2%, with appearance of browsed twigs implicating *L. americanus* and grouse. *O. virginianus* browsing rates as high as 45% occurred in unexclosed areas over a single winter season.

Percent cover of small shrubs was higher on average in exclosed [30 ± 2% (SE)] than unexclosed [22 ± 2% (SE)] areas at Split Rock in 1997 ($\chi^2_{[1]} = 8$; $p = 0.0005$, Wilcoxon). Differences in percentage cover for exclosed and unexclosed areas were not significant for herbaceous plants nor large shrubs. For portions of sites exclosed between 11 and 60 years, differences in percentage cover between exclosed and unexclosed areas were not significant for herbaceous plants, or small and large shrubs (data not shown). Significant differences were observed, however, for individual species. For example, percentage cover of *Abies balsamea* and *T. occidentalis* in height class 3 was greater within exclosed areas than in unexclosed areas, and cover of *Diervilla lonicera* was greater in unexclosed than exclosed areas (Table 5).

4. Discussion

Evidence was strong that browsing is impacting future *T. occidentalis* recruitment in upland *Thuja-Betula* forests on the Lake Superior Highlands. On decaying wood seedbeds under *Thuja* canopy at Split Rock, Cornett et al. (1997) observed densities as high as 35/m^2 of *T.*

Table 4
Results from simulation model predicting sapling recruitment for a planted population of 1000 *T. occidentalis* seedlings under different scenarios over a 60 year period

Model run	Proportion > 2.1 m at 60 years	Mean years for first seedlings to reach 2.1 m (± SE)	Proportion alive at 60 years	Mean life span in years (± SE)
THUBS[a]	0.06	28.6 (0.8)	0.06	10.2 (0.3)
BETBS[a]	0.48	29.2 (0.4)	0.50	15.3 (0.5)
THULO[b]	0.74	24.2 (0.09)	0.74	12.0 (0.4)
THUHI[b]	0.0	N/A	0.0	3.7 (0.09)
BETLO[b]	0.94	18.3 (0.08)	0.94	9.7 (0.7)
BETHI[b]	0.0	N/A	0.01	13.4 (0.4)
HISL[c]	0.0	N/A	0.01	13.4 (0.4)
HIRA[c]	0.01	22.0 (2.3)	0.01	12.8 (0.4)
LOSL[c]	0.69	47.4 (0.4)	0.83	25.8 (1.1)
LORA[c]	0.97	9.4 (0.03)	0.97	4.7 (0.4)
PBHA[d]	0.59	23.9 (0.02)	0.59	11.7 (0.4)
PBDO[d]	0.24	33.0 (0.8)	0.37	20.8 (0.6)

[a] THUBS, BETBS = Baseline runs under *Thuja* (THU) and *Betula* (BE) canopy types.

[b] THULO, THUHI, BETLO, BETHI = Runs evaluating low (LO) and high (HI) browsing [under *Thuja* (THU) and *Betula* (BE) canopy types].

[c] HISL, HIRA, LOSL, LORA = Runs evaluating slow (SL) and rapid (RA) growth [under low (LO) and high (HI) browsing (ignoring canopy type)].

[d] PBHA, PBDO = Percentage height browsed (PB) halved (HA) and doubled (DO) (ignoring canopy type).

Table 5
Survey results of percentage cover from plots located inside and outside seven exclosures established from 1937 to 1986. Results presented below are for species with strongest differences in mean percentage cover between exclosed and unexclosed areas

	Unexclosed (SE)	Exclosed (SE)	$\chi^2_{[1]}$	*p*
Height class 2 (0.1–0.5 m)				
Abies balsamea	7.4 (2.9)	9.9 (2.6)	0.83	0.36
Amelanchier sp.	1.8 (0.5)	0.7 (0.5)	2.4	0.12
Diervilla lonicera	29.6 (12.3)	13.8 (6.6)	0.3	0.60
Lonicera canadensis	2.9 (2.1)	9.6 (2.8)	3.3	0.07
Picea glauca	1.8 (0.5)	0.7 (0.5)	2.4	0.12
Thuja occidentalis	8.4 (5.4)	6.8 (2.6)	0.18	0.67
Height class 3 (0.5–2 m)				
Abies balsamea	3.3 (2.1)	13.3 (2.2)	4.9	0.03
Amelanchier sp.	1.1 (0.5)	0	3.5	0.06
Diervilla lonicera	17.4 (12.1)	2.2 (2.2)	2.5	0.11
Lonicera canadensis	7.0 (3.0)	7.0 (3.0)	0.0	1.0
Picea glauca	2.9 (2.1)	1.1 (0.5)	0.05	0.83
Thuja occidentalis	0 (0)	19.0 (7.1)	4.4	0.03
Height class 4 (2–5 m)				
Abies balsamea	2.2 (2.2)	14.6 (4.6)	6.0	0.01
Amelanchier sp.	–	–	–	–
Diervilla lonicera	–	–	–	–
Lonicera canadensis	–	–	–	–
Picea glauca	3.3 (2.1)	2.2 (2.2)	1.8	0.17
Thuja occidentalis	2.2 (2.2)	2.6 (1.9)	0.67	0.41

occidentalis seedlings < 15 cm tall, indicating that seed supply is not limiting regeneration provided adequate seedbed conditions are met. Densities on similar seedbeds were up to 10-fold lower under *Betula* canopy in adjacent stands, apparently the result of low seed supply (Cornett et al. 1997). Browsing by *O. virginianus* appears to be a major factor in the lack of naturally-occurring *T. occidentalis* seedlings > 25 cm tall in these forests.

4.1. Severity and intensity of deer browsing

The expansion of *O. virginianus* earlier this century has introduced a new factor to forested ecosystems on the Lake Superior Highlands, operating at all 7 sites as a keystone herbivore (sensu Waller and Alverson, 1997). The differences in level of browsing between sites may be explained by different land use histories, and corresponding differences in habitat. For example, unlike the other sites where seedlings were planted, the Cascade site lies within the Jonvik Deer Yard, which has been actively managed for decades to provide good habitat for *O. virginianus*.

Densities of *O. virginianus* near Lake Superior, particularly in the late winter and early spring, are exceptionally high relative to the rest of northeastern Minnesota because higher mean winter temperatures create a more hospitable climate (Bartlett, 1950). In a study of eastern hemlock (*Tsuga canadensis* L.) Carr., another slow-growing, shade tolerant conifer, Frelich and Lorimer (1985) found that regeneration is much poorer for Michigan sites near Lake Superior than several kilometers inland, and suggest it is because deer concentrate close to the lake in winter. A Wisconsin study concluded that average densities of $\geqslant 8/\mathrm{km}^2$ are likely to be far too high to maintain the diversity of plants native to cold temperate forests (Alverson et al., 1988). Therefore, although winter densities of *O. virginianus* are considered extreme on the Lake Superior Highlands, trends detected in the present study likely to have relevance throughout much of the northern Great Lakes region.

4.2. Canopy influence on seedling mortality

The same forces that opened the landscape of northeastern Minnesota to invasion by deer also created new recruitment environments for late-successional species such as *T. occidentalis*. As a slow-growing species, *T. occidentalis* generally has difficulty recovering from deer browsing (Alverson et al., 1988). Many slow growing conifers do not exhibit compensatory growth after browsing events and are vulnerable to browsing for decades (e.g., Hough, 1965; Rogers, 1978; Saunders and Puettmann, 1999b). In the distinct environments beneath the *Thuja* and *Betula* canopies, however, the degree to which browsing thwarts *T. occidentalis* recruitment appears to differ.

In the present study, the close link between canopy type and seedling mortality for browsed seedlings was consistent with other studies. Heitzman et al. (1997) raised the possibility that *T. occidentalis* recruitment may be generally dependent upon sufficient availability of light. Scott and Murphy (1987) found that in an old-growth dune forest, *T. occidentalis* seedlings taller than 25 cm only occurred near canopy gaps. The additional stress of browsing under low light conditions probably contributed to higher mortality and lower growth rates of *T. occidentalis* seedlings beneath the *Thuja* canopy type on the Lake Superior Highlands. Studies conducted in Michigan and Minnesota have also demonstrated that survival rates for heavily-clipped conifer seedlings are lower under dense canopy cover than in more open settings (McLaren, 1996; Saunders and Puettmann, 1999b).

4.3. Long-term effects of browsing

4.3.1. Planted seedlings

The simulation model suggested that two major changes in the northeastern Minnesota landscape, expansion of *O. virginianus* populations and early successional deciduous forest, may have long-term implications for the process of recruitment in remnant conifer stands. Browsing alone was a powerful force, with high levels overwhelming canopy conditions and preventing recruitment of *T. occidentalis*. By the same token, for low to moderate levels of browsing, canopy conditions and browsing damage form a feedback loop that influences future species composition of the forest canopy. Given what is known about *T. occidentalis* growth and survival rates under the two canopy types, for example, some recruitment of *T. occidentalis* into the canopy may occur in *Betula* stands where <20% of seedlings are browsed annually, but not in *Thuja* stands. However, the model overestimated the percentage of *T. occidentalis* recruitment, as it did not account for other sources of mortality. The model also assumed a planted population of *T. occidentalis* seedlings, but in reality sufficient seed deposition and appropriate seedbed conditions are much less likely to occur beneath the *Betula* than the *Thuja* canopy (Cornett et al., 1997).

4.3.2. Other vegetation

Because of the long-term nature of forest development, stronger evidence of long-term impacts of browsing on future forest composition was detected at sites with exclosures constructed prior to 1986 than for recently exclosed areas. In recently exclosed areas (1994), the difference in percentage cover of small shrubs was largely driven by SR1, where they may have pre-existed construction. For longer-term exclosures, the greatest differences observed were for two species of contrasting browsing preferences, *T. occidentalis* and *A. balsamea*. Both species had a substantially larger percentage cover in height class 3 (0.5–2 m) inside than outside exclosures, i.e. herbivory may reduce their future recruitment into the canopy. This result was consistent with Krefting (1975), who conducted a 25 year study at 21 northern Minnesota exclosure sites, four of which were resurveyed in the present study. Similarly, Van Deelen et al. (1996) found that species sensitive to browsing (e.g. *T. occidentalis*) decrease over time in northern Michigan deer yards. That such differences did not occur for *T. occidentalis* in height class 2 suggested that exclosures are not a panacea for problems with regeneration at all stages of development. For example, exclosures do not ensure appropriate safe sites for germination and early establishment, nor do they provide a suppression-free growth environment for maturing saplings.

Unlike *T. occidentalis*, *A. balsamea* is not preferred unless there is little other available browse (Dahlberg and Guettinger, 1956; Beals et al., 1960). The increase in percentage cover of *A. balsamea* in both height classes 3 and 4 in exclosed areas indicated that high deer densities may also alter vegetation dynamics by reducing occurrences even of less-preferred canopy species. Likewise, the higher cover of *D. lonicera* in unexclosed than exclosed areas suggested that browsing is altering the species composition of these communities.

The similarity of percentage cover of herbaceous plants in exclosed and unexclosed areas was consistent with the notion that higher deer densities occur within a few kilometers of Lake Superior during the winter than the summer. Herbaceous vegetation is unavailable as browse until leaf-out in the spring. Although some slow-growing, long-lived herbaceous plants can be greatly impacted by deer browsing (Van Deelen et al., 1996; Augustine and Frelich, 1998), abundant browse combined with lower deer densities may lead to saturated conditions in the summer (e.g. Augustine et al., 1998).

4.4. Conservation implications

Our results demonstrated that *O. virginianus* has the potential to markedly change the future composition of canopy trees in upland *Thuja-Betula* forests. Although other factors are likely to contribute to the lack of *T. occidentalis* recruitment in upland *Thuja-Betula* forests (Cornett et al., 1997), deer browsing appears to pose a major barrier that can interact with these factors. Under current conditions, *T. occidentalis* is more likely to germinate and establish beneath the *Thuja* canopy than the

Betula canopy (Cornett et al., 1997). However, the *Thuja* forest understory is also generally a low-light environment, lessening chances of surviving a browsing event.

The results of this study have several implications for the long-term conservation of upland *T. occidentalis* forests. In areas with extremely low browsing severity, it may be advantageous to concentrate *T. occidentalis* plantings in microenvironments with higher light availability. Under special circumstances, such microenvironments may occasionally be created by opening the canopy through light thinning. In cases of high browsing severity (e.g. ⩾60% of all seedlings/year), it appears that protecting *T. occidentalis* seedlings is absolutely necessary. Depending on seedling growth rates as influenced by canopy conditions, maintaining seedling protection may be necessary for 30–50 years in order for a single cohort to be recruited to height classes ⩾2.1 m. The decision to protect seedlings from browsing should be made as early as possible, particularly within dense conifer stands.

If browsing continues at current levels, it is likely that losses of *T. occidentalis* overstory trees will not be replaced by recruitment from the understory, resulting in a landscape increasingly dominated by species that are more tolerant of browsing. This potential future change in canopy species composition represents a secondary, unforeseen effect of past and current forest management practices, and has the potential to impact forested landscapes throughout the northern Great Lakes region.

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