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Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA

Thomas P. Rooney^{a,*}, Stephen L. Solheim^b, Donald M. Waller^a

^aDepartment of Botany, University of Wisconsin-Madison, 430 Lincoln Drive, Madison, WI 53706, USA

^bDepartment of Biology, University of Wisconsin-Whitewater, Whitewater, WI 53190, USA

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Abstract

Regeneration of northern white cedar (*Thuja occidentalis*) has been poor in the Upper Great Lakes region for decades. To understand why, we used a spatially extensive approach to examine which factors limit regeneration in lowland swamp forests at a regional scale. We investigated patterns of seedling establishment and sapling recruitment in 1990–1991 and 1996 among 77 lowland stands distributed across northern Wisconsin and the eastern Upper Peninsula of Michigan. These stands differed in ownership, local site conditions, and ambient deer densities, allowing us to evaluate several factors potentially limiting regeneration. Lowland cedar seedlings in this region typically require 10 years to grow to 30 cm and 30 years to attain 3 m. Regression and path analyses demonstrate that initial seedling establishment increases in areas with greater seed input (as inferred from cedar basal area) and (in 1996) higher light levels. Subsequent recruitment to saplings +30 cm tall, however, depends far more on demographic inertia (the number of smaller seedlings) and escape from deer browsing. Surprisingly, estimated deer browse was as significant a factor as demographic inertia, reflecting cedar's palatability, slow growth, and chronic high browsing pressure. Efforts to regenerate this species seem unlikely to succeed without significant and sustained reductions in deer density or extensive efforts to mechanically protect saplings from browsing. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Northern white cedar; Regeneration; Deer browsing

1. Introduction

Shade-tolerant tree species frequently form multi-cohort stands in which seedlings establish and persist in the forest understory until they are released by a disturbance (Oliver and Larson, 1990). This seedling bank, or “regeneration”, is a reproductive strategy used by species adapted to environments in which opportunities for recruitment are infrequent (Grime,

1979). Differential mortality among species in the seedling bank strongly influences future stand composition (Peterson and Pickett, 1995; Clark et al., 1999), so it is useful to identify the biotic and abiotic determinants of seedling density and distribution. Well-executed studies conducted in one or a few stands are useful for identifying which factors are important within a locality, but spatially extensive studies are needed to generate robust generalizations about which factors consistently influence seedling density and distribution (James et al., 1997; Clark et al., 1999; Rooney et al., 2000). Here, we used a spatially extensive approach to examine which factors

* Corresponding author. Tel.: +1-608-265-2191;
fax: +1-608-262-7509.
E-mail address: tprooney@facstaff.wisc.edu (T.P. Rooney).

are most responsible for limiting northern white cedar (*Thuja occidentalis*) regeneration in the lowland swamp forests of the Upper Great Lakes region.

Northern white cedar is a slow-growing, shade-tolerant, long-lived boreal conifer distributed throughout northeastern North America (Johnston, 1977, 1990). In the Upper Great Lakes region, lowland swamp forests (or “cedar swamps”) are relatively scarce, occupying only 810,000 ha in Michigan, Wisconsin, and Minnesota (Johnston, 1977). However, cedar swamps are regionally significant for many reasons. Northern white cedar is a valuable timber species, and cedar swamps provide the majority of winter habitat for white-tailed deer (*Odocoileus virginianus*) and other wildlife (Curtis, 1959; Doepker and Ozoga, 1990). The tree is also used by the Great Lakes Ojibwe tribes for medicinal and ceremonial purposes (Meeker et al., 1993). Cedar stands also provide habitat for many rare species. Among these are the regionally rare calypso orchid (*Calypso bulbosa*), showy lady’s slipper (*Cypripedium reginae*), large roundleaf orchid (*Platanthera orbiculata*), and the globally threatened ram’s head lady’s slipper (*Cypripedium arietinum*) (Epstein et al., 1999).

Regeneration of white cedar has been scant in the Upper Great Lakes region for decades. Published research indicates northern white cedar seed production varies year to year (Johnston, 1977; Heitzman et al., 1997). Seedling establishment is largely constrained to a narrow regeneration niche consisting of rotting wood (Nelson, 1951; Scott and Murphy, 1987; Cornett et al., 1997) and hummocks (St. Hilaire and Leopold, 1995; Chimmer and Hart, 1996; Cornett et al., 1997). Established seedlings are killed by many factors, including desiccation and late frost (Nelson, 1951). Because the number of seedlings that survive to the next season are a function of the number of seedlings initially present, “demographic momentum” increases when the initial density of seedlings is high. Finally, browsing activity by white-tailed deer reduces the survivorship of taller plants (Aldous, 1941; Nelson, 1951; Beals et al., 1960; Johnston, 1977; Pregitzer, 1990; Heitzman et al., 1997; Van Deelen, 1999; Epstein et al., 1999; Cornett et al., 2000). Some or all of these factors limit cedar regeneration throughout the region.

We examined the relative importance of light availability, microtopography, demographic momentum,

and deer browsing for each of three stages of northern white cedar seedling development. Our goal is to generate robust generalizations about regeneration in Wisconsin and Michigan cedar swamps. Our sampling is both spatially extensive, allowing us to incorporate recruitment variability among stands into our analysis (Clark et al., 1999), and temporally extended, including surveys in both 1990–1991 and 1996. Our analysis was two-tiered. First, we performed a series of univariate analyses to determine which factors consistently affected regeneration in three successive seedling height classes. Second, we integrated our findings using path analysis, a multivariate procedure that combines multiple causal relationships to summarize how factors directly or indirectly influence cedar recruitment at different stages of regeneration.

2. Methods

2.1. Study sites

We selected study sites from a master list of northern white cedar stands, using a stratified (by land ownership) random sampling procedure (Rooney et al., 2000 for additional details). These ownerships differ in both land management objectives and deer densities, but all contain cedar swamps. We chose a large number of sites for a geographically extensive survey. This allowed us to average over local differences in regeneration due to disturbance history, hunter activity, deer yard history, and other local nuances, and thus to explore robust regional patterns of white cedar recruitment. All stands were located in northern Wisconsin and the western Upper Peninsula of Michigan (Fig. 1). Sites sampled were distributed among many land owners (county, state, and national forests, national lakeshore, Menominee and Ojibwe tribal lands, and private lands).

To assess regional variation in recruitment success, we surveyed 77 stands in 1990–1991. At each site, we established a single 14 m × 21 m plot consisting of six contiguous 7 × 7 quadrats arranged in a 2 × 3 array. We counted all the white cedar seedlings 4–9 cm tall, and counted and measured the height of all cedar regeneration between 10 and 300 cm tall in two randomly selected quadrats at each stand. In 1996, we revisited 49 of these stands. Our sampling was

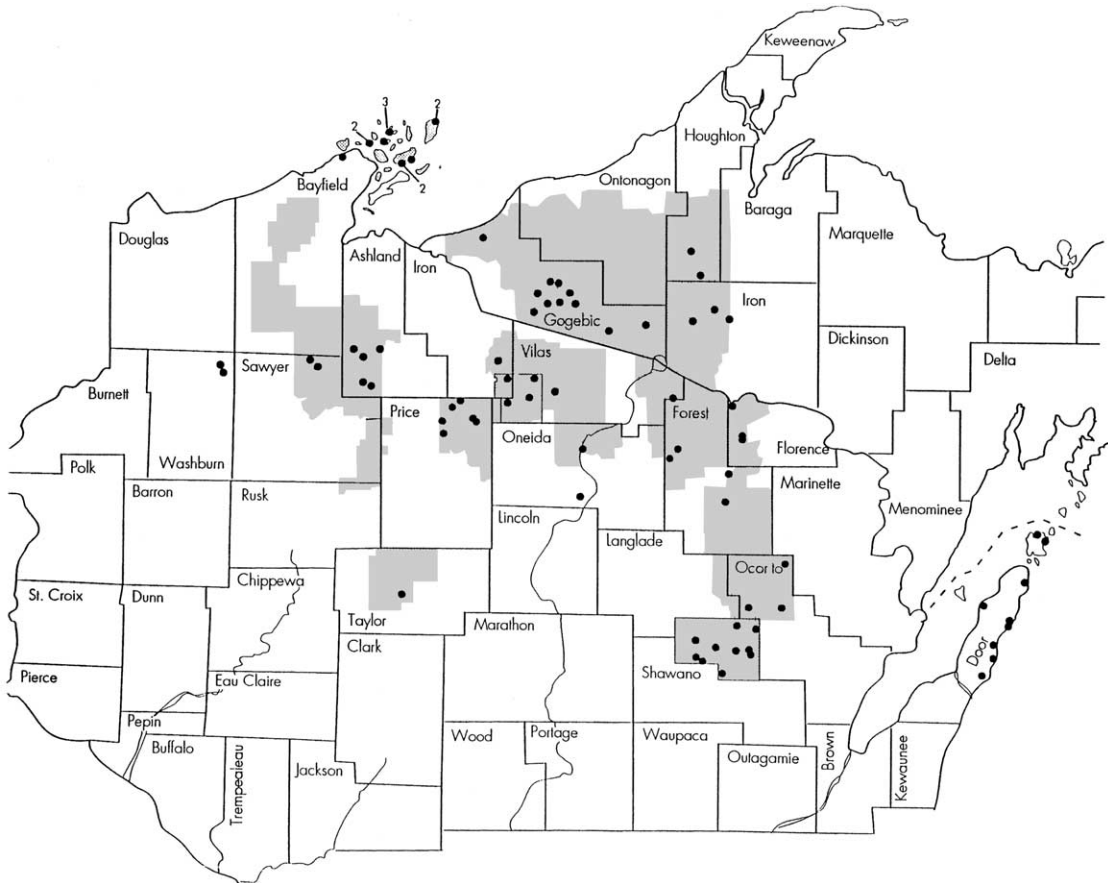


Fig. 1. Location of stands sampled in northern Wisconsin and the western Upper Peninsula of Michigan in 1990–1991 and 1996.

more intensive in 1996, as we counted seedlings and measured heights in all six quadrats. At 28 of the 49 resurveyed sites (57.1%), we successfully relocated and conducted sampling in our original study plots. We could not find our study plots at the remaining 21 sites (42.9%), perhaps because our plot markers were illegally removed. In these cases, we established new plots close as possible to the inferred location of the original plots.

2.2. Size classes of cedar regeneration

We distinguished three demographic categories for cedar regeneration based on seedling height. We classified cedar plants between 4–9 cm tall as “seedlings”, those 10–29 cm tall as “small saplings”, those 30–300 cm tall as “large saplings”. We did not

distinguish between sexual (seed origin) and asexual (branch layering) reproduction. Over 99% of the seedlings we observed were of seed origin, as indicated by the presence of juvenile leaves along the stem (Nelson, 1951). While we did not directly measure seedling ages, we established height–age relationships by measuring the height and ages (via annual growth rings) of 42 white cedar saplings (15–100 cm tall) collected from six study sites. Correlation analysis shows that age and (ln) height are positively related (Fig. 2).

2.3. Data collection and analysis

2.3.1. Regional variation in cedar regeneration

To summarize regional variation white cedar regeneration among sites, we calculated the mean and

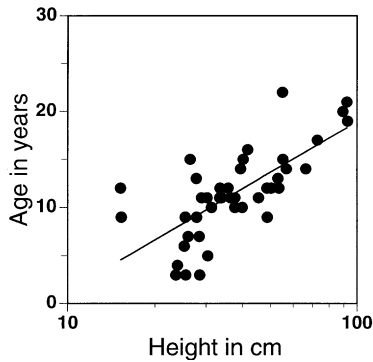


Fig. 2. The relationship between northern white cedar sapling height and age. $\text{Age} = 7.73(\ln \text{height in cm}) - 16.22$ ($n = 42$; $r^2 = 0.50$; $P < 0.001$). This model predicts that small saplings will be between 1.6 and 9.8 years old, and large saplings will be between 9.8 and 27.9 years old.

standard error of seedling, small sapling, and large sapling abundance in 1990–1991 and 1996. We characterized the range of variation in cedar regeneration by reporting the lowest and highest values observed for each demographic category. The mean abundance of northern white cedar regeneration present in 1990–1991 is compared graphically with abundance in 1996 for each demographic size class.

2.3.2. Abiotic factors: light and microtopography

We determined incident light levels during both survey periods by measuring the percentage of open canopy from a point 1.5 m above each quadrat. We recorded vertical canopy images with fish-eye (hemispherical) photographs on high contrast Kodak 2415 Technical Pan Film (1990–1991) and still frames obtained from a “HI-8” video camera (Sony TR700) fitted with a wide-angle accessory lens to encompass a 90° field (1996). We analyzed images in a pixel-based image analysis program (Adobe Photoshop) by lightening all sky pixels to white and darkening canopy foliage, trees, and other obstructions to black. The ratio of white to total (black + white) pixels provides an estimate of percent open canopy above a quadrat. We averaged light measurements over all surveyed quadrats in a plot to estimate light availability. We analyzed the relationship between light and cedar regeneration density in each demographic category using regression analysis, with percent open sky used as the independent variable. Light data collected in

1990–1991 were used in conjunction with the 1990–1991 regeneration data, and 1996 light was used with 1996 regeneration data.

During the 1990–1991 field season only, we examined the distribution of white cedar regeneration among different substrates. We recorded the abundance of northern white cedar regeneration in each of the three height classes (2–5, 6–25, and 26–300 cm) growing on each of the three microtopographic substrates (raised mound, decaying wood, and “else”—a category that included pits, sphagnum moss, standing water, and all other non-wood, non-tip-up mound substrates). The demographic categories deviate slightly from those analyzed in the rest of the study, because at the time we were more interested in distinguishing between initial germination (2–5 cm), establishment (6–25 cm), and subsequent growth (26–300 cm) on these various microtopographical features. For each of the three substrate types, we tested the null hypothesis that the proportion of white cedar seedlings or saplings did not differ among different size classes within a substrate. We assessed significance of results using a *G*-test for goodness of fit (Sokal and Rohlf, 1981).

2.3.3. Biotic factors: demographic momentum and deer browsing

Size-structured populations exhibit ‘demographic momentum’ (Harper, 1977; Caswell, 1989), the term describing the process in which individuals in smaller size classes are recruited into larger size classes. Species employing the seedling bank strategy typically maintain high densities of small seedlings and lower densities of larger saplings in a stand (Rooney et al., 2000). Thus, we expect a priori that the number of saplings present at a site will be a function of the number of established seedlings at that site, and hence conditions for seedling establishment. Following this logic, we incorporated demographic momentum into our study by including the number of white cedar in the preceding size class as a predictor variable when analyzing the number of white cedar regeneration in the size class of interest. We used regression analysis to test for the significance of demographic momentum. We also recorded the basal area of all trees to be >2.5 cm DBH in each study plot. We assumed that as the basal area of white cedar increased, the maximum local seed input also increased. Hence, we used cedar

basal area as the “preceding size class” for seedling abundance, and evaluated the significance of this relationship using regression analysis.

We used two approaches to examine the relationship between deer browsing and white cedar regeneration. First, we estimated local deer browsing pressure using a sugar maple (*Acer saccharum*) browse index (cf. Frelich and Lorimer, 1985). Sugar maple saplings occur in abundance near all study sites. We counted the number of browsed and unbrowsed terminal twigs located 30–200 cm above the ground on 12–20 maple saplings per site. We estimate browsing intensity on a scale from 0 (lowest) to 1 (highest) by taking the ratio of browsed terminal twigs to total number of twigs sampled (Frelich and Lorimer, 1985; Waller et al., 1996; Rooney et al., 2000). We determined the sugar maple browse index in 1990–1991 and 1996 for each of our study sites. We used regression analysis to relate the browse index to the abundance of northern white cedar in each regeneration size class.

Second, we summarized regional variation in white cedar regeneration across ownership categories. We divided ownership a priori into two groups: ownerships with lower deer densities and ownerships with higher deer densities, based in part on data from Rooney et al. (2000). Ownerships classified as having higher deer densities actually represent prevailing conditions throughout most of the region. For 1990–1991, our low deer ownerships ($n = 26$) included tribal lands (Ojibwe and Menominee) and deer-free islands in Lake Superior (outer Apostle Islands). High deer ownerships ($n = 51$) included all other lands (national, state, and county forests, state parks, and national lakeshore lands with deer (mainland and inner Apostle Islands). In 1996, we did not resurvey any deer-free sites on the outer Apostle Islands, but otherwise the classification of low deer ($n = 8$) and high deer ($n = 41$) ownerships remained the same. We tested our assumption that deer browsing, as measured by our browse index, significantly differed between low deer and high deer ownerships, using one-way ANOVAs. Separate tests were done for the 1990–1991 and 1996 data.

We performed a series of one-way ANOVAs to analyze differences in white cedar abundance between low deer and high deer ownerships. Separate tests were done for each of the three cedar size classes in

each of the two survey periods. For all demographic categories, white cedar abundance was $1 + \ln$ -transformed prior to analysis to meet the assumption of normality.

2.3.4. Multivariate model: path analysis

Our multivariate approach (path analysis) combines multiple causal relationships, including both direct and indirect effects, to summarize the effects of a logical succession of dependent variables (Li, 1975; Sokal and Rohlf, 1981). This technique relies on standardized partial regression coefficients (path coefficients). These are derived from a multiple linear regression model that includes all predictor variables (light, deer browsing, demographic momentum) from regression analyses that accounted for significant variation in the abundance of individuals in each white cedar height class. Variables not significant at the 0.05 level were eliminated from each model using a backward elimination procedure. Although, all variables were significant in the univariate tests, collinearities among some variables resulted in low partial correlations with cedar abundance and were consequently removed from the multivariate model.

Path analysis makes three assumptions: (a) the variables can be placed into an unambiguous causal order; (b) effects are linear; (c) effects of different predictor variables are additive. As recruitment into each successive height class necessarily depends on the presence of smaller seedlings or saplings, and as environmental variables clearly affect small white cedar (but not vice versa), the causal order assumption is met. Similarly, the natural log transformations linearized relationships between predictor and dependent variables. Finally, we checked for significant interaction terms between predictor variables using general linear models, but found none. Separate models were calibrated for 1990–1991 and 1996 cedar abundance data.

3. Results

3.1. Regional variation in cedar regeneration

White cedar seedling (4–9 cm) abundance was similar during both survey periods (Fig. 3). The number of seedlings per hectare ranged from 0 to 29,886 in

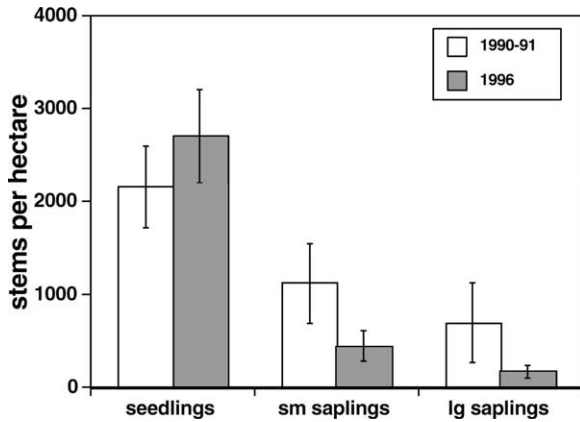


Fig. 3. The number of northern white cedar stems per hectare in the seedling (4–9 cm), small sapling (10–29 cm), and large sapling (30–300 cm) height class tallied in 1990–1991 (open bars) and 1996 (shaded bars). Error bars represent 1 S.E.

1990–1991, and 0 to 18,190 in 1996. Small sapling (10–29 cm) abundance declined from 0 to 14,178 stems per hectare in 1990–1991 to 0–7990 stems per hectare in 1996. Large sapling (30–300 cm) abundance declined from 0 to 11,118 stems per

hectare in 1990–1991 to 0–2992 stems per hectare in 1996. For all northern white cedar size classes, densities are highly variable among sites.

3.2. Abiotic factors: light and microtopography

Canopy openness, our measure of light availability, ranged from 5.3 to 51.4% in 1990–1991 (mean = 23.9%), and from 4.8 to 43.7% in 1996 (mean = 25.8%). Seedling abundance did not increase with light levels in 1990–1991, but it did in 1996 (Table 1). Small sapling and large sapling abundance also appeared unrelated to canopy openness in both 1990–1991 and 1996 (Table 1).

We found important differences when we examined the proportion of northern white cedar stems in a given height class for each microtopographic substrate type. The greatest proportion of seedlings and small saplings occurred on decaying wood (Fig. 4). The proportion of white cedar stems on wood microsites declined with demographic size category (d.f. = 2; $G = 79.7$; $P < 0.0001$). In contrast, the proportion of stems on raised mound (d.f. = 2; $G = 20.8$; $P <$

Table 1

Univariate regression analysis of variables hypothesized to influence the abundance of northern white cedar seedlings (4–9 cm), small saplings (10–29 cm), and large saplings (30–300 cm) in 1990–1991 and 1996

Size class	Variable	<i>n</i>	<i>P</i>	<i>r</i> ²
1990–1991				
(ln) Seedlings	Cedar basal area	77	<0.001	0.194
	Light	58	0.94	0.001
	Deer browsing	46	0.13	0.051
(ln) Small saplings	(ln) Seedlings	77	<0.001	0.433
	Light	58	0.71	0.003
	Deer browsing	46	0.39	0.017
(ln) Large saplings	(ln) Small saplings	77	<0.001	0.393
	Light	58	0.75	0.002
	Deer browsing	46	<0.001	0.378
1996				
(ln) Seedlings	Cedar basal area	45	0.038	0.096
	Light	46	0.005	0.169
	Deer browsing	46	0.84	0.001
(ln) Small saplings	(ln) Seedlings	49	0.029	0.097
	Light	46	0.34	0.021
	Deer browsing	46	0.01	0.143
(ln) Large saplings	(ln) Small saplings	49	<0.001	0.501
	Light	46	0.97	0.001
	Deer browsing	46	<0.001	0.258

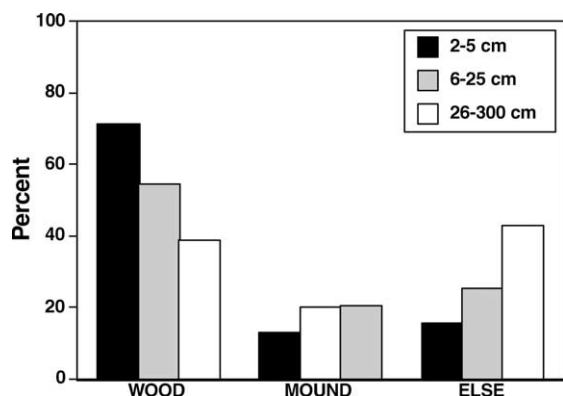


Fig. 4. The observed proportion of seedlings, small saplings, and large saplings growing on decaying wood (WOOD), raised mounds (MOUND), or other (ELSE) substrates during the 1990–1991 field season. Sample sizes were: $n = 3303$ (seedlings 2–5 cm), $n = 1448$ (small saplings 6–25 cm), and $n = 799$ (large saplings 26–300 cm).

0.0001) and “else” substrates (d.f. = 2; $G = 92.8$; $P < 0.0001$) increased with demographic size category, indicating higher survivorship on these microtopographic features than on wood.

3.3. Biotic factors: demographic momentum and deer browsing

In both 1990–1991 and 1996, demographic momentum was important for all white cedar regeneration size classes examined according to univariate regression analyses (Table 1). At each site, (ln) seedling

densities increased with northern white cedar basal area in both 1990–1991 and 1996. Also, (ln) small sapling densities increased with (ln) seedling densities during both sampling periods. Both of these relationships were stronger in 1990–1991 than in 1996, as indicated by the larger r^2 value. The natural log of large sapling densities increased with (ln) small sapling densities during both periods, but this relationship was stronger in 1996 than in 1990–1991.

The mean deer browsing index was lower in 1990–1991 (0.48 ± 0.04 S.E. in 1990–1991) than in 1996 (0.58 ± 0.03 S.E.). In both 1990–1991 and 1996, (ln) seedling densities were not influenced by the deer browsing index, indicating that seedlings were unaffected by deer (Table 1). The natural log of small sapling densities were also unaffected by deer in 1990–1991, but in 1996 there was a negative relationship between (ln) small sapling densities and the deer browsing index. During both sampling periods, there was a pronounced negative relationship between (ln) large saplings and the deer browsing index. These data indicate deer reduce northern white cedar regeneration at a regional scale.

Analysis of regional variation in white cedar regeneration across ownership categories reinforced the importance of deer browsing. We confirmed that deer browsing, as measured by our browsing index, was lower on lands classified a priori as “low deer density” in 1990–1991 (0.23 ± 0.06 S.E. of all terminal sugar maple twigs browsed) than on lands

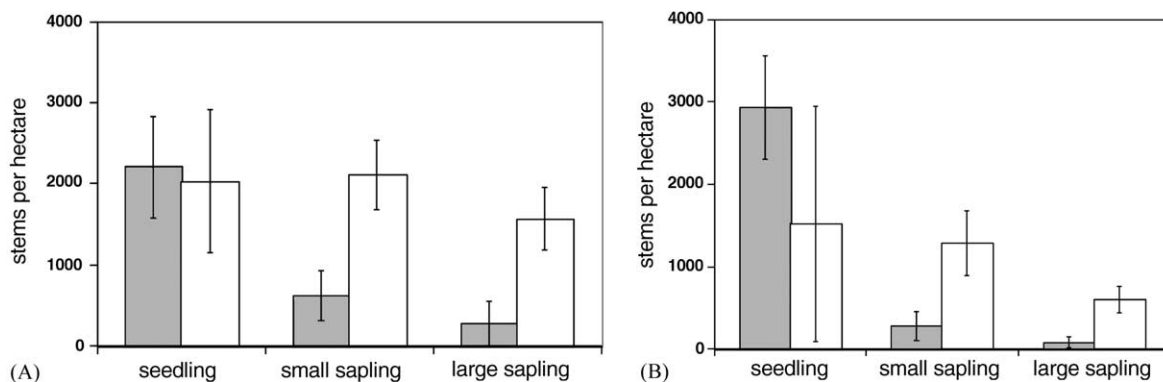


Fig. 5. The number of northern white cedar stems per hectare in the seedling (4–9 cm), small sapling (10–29 cm), and large sapling (30–300 cm) height class tallied in high deer density ownerships (shaded bars) and lower deer density ownerships (open bars) in (a) 1990–1991 and (b) 1996. Sample sizes for low deer were $n = 26$ in 1990–1991 and $n = 8$ in 1996, and for high deer $n = 51$ in 1990–1991 and $n = 41$ in 1996. Error bars represent 1 S.E., and an asterisk indicates a significant difference in stem densities of a given size class between high deer density and low deer density sites as determined by one-way ANOVA.

classified as “high deer density” (0.58 ± 0.04 S.E.; one-way ANOVA; $F_{1,44} = 22.46$; $P < 0.001$). This difference persisted in 1996, but browsing intensity was greater in low (0.30 ± 0.06 S.E.) and high (0.63 ± 0.02 S.E.) deer density ownerships in 1996 ($F_{1,44} = 28.24$; $P < 0.001$) than in 1990–1991.

There were no differences in seedling densities between ownership categories classified as having low deer density and high deer density in 1990–1991 ($F_{1,75} = 0.019$; $P = 0.89$) or 1996 ($F_{1,47} = 0.07$; $P = 0.79$; Fig. 5). However, there were significantly more small saplings at sites in low deer density ownerships than in high deer density ownerships in 1990–1991 ($F_{1,75} = 4.86$; $P = 0.031$; Fig. 5a). In 1996, there also appeared to be more small saplings at sites in low deer

density ownerships, but this fell short of statistical significance ($F_{1,47} = 2.90$; $P = 0.095$; Fig. 5b). Large saplings were significantly more abundant in low deer density ownerships in both 1990–1991 ($F_{1,75} = 12.30$; $P = 0.006$) and 1996 ($F_{1,47} = 7.76$; $P = 0.008$; Fig. 5).

3.4. Multivariate model: path analysis

Our path analysis models for the 1990–1991 and 1996 surveys summarize and synthesize the results from univariate regression analyses. In 1990–1991, white cedar basal area solely explains 19.4% of the total observed variation in seedling abundance (Table 2; Fig. 6). Small sapling abundance, in turn,

Table 2
Path analysis of the 1990–1991 and 1996 data

Dependent variable/height class, predictor variable	Effects		Proportion of variance explained ^b (%)
	Direct ^a	Indirect	
1990–1991			
(ln) Seedlings			19.4
Cedar basal area	0.44		
(ln) Small saplings			43.3
(ln) Seedlings	0.66		
Basal area → (ln) seedlings		0.29	
(ln) Large saplings			52.4
(ln) Small saplings	0.39		
Deer browsing	−0.57		
(ln) Seedlings → (ln) small saplings		0.25	
Basal area → (ln) seedlings → (ln) small saplings		0.05	
1996			
(ln) Seedlings			26.7
Cedar basal area	0.32		
Light	0.40		
(ln) Small saplings			22.5
(ln) Seedlings	0.29		
Deer browsing	−0.39		
Cedar basal area → (ln) seedlings		0.09	
Light → (ln) seedlings		0.12	
(ln) Large saplings			57.4
(ln) Small saplings	0.61		
Deer browsing	−0.28		
Deer browsing → (ln) small saplings		−0.24	
Cedar basal area → seedlings → (ln) small saplings		0.06	
Light → seedlings → (ln) small saplings		0.07	

^a All listed direct effects are significant at the 0.05 level.

^b The squared multiple correlation coefficient (r^2) of the backwards elimination multiple regression procedure provides the proportion of variance explained.

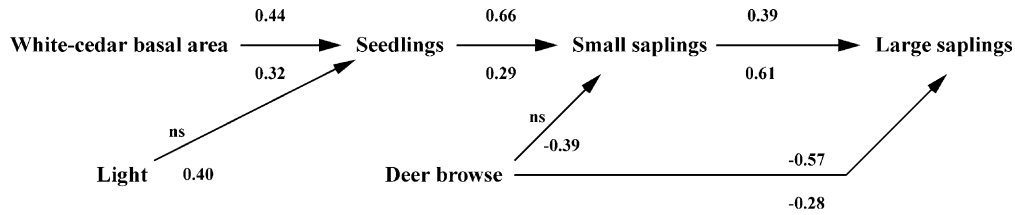


Fig. 6. Path analysis based on inferred causal relationships among variables. Numbers are standardized partial regression coefficients (path coefficients). Numbers above arrows are path coefficients from 1990–1991 data, and numbers below arrows are 1996 path coefficients. Direct paths not statistically significant ($P < 0.05$) are denoted as “ns”.

is directly influenced by the abundance of seedlings present at a site and indirectly by basal area, accounting for 43.3% of the variation observed. Finally, large sapling abundance is diminished by deer browsing and enhanced by the abundance of small saplings, and indirectly by the abundance of seedlings present. By this stage, seed input, as estimated by local cedar basal area, accounts for only 0.25% of the variation in large sapling abundance (0.05^2), while more than 32% (-0.57^2) of the variation appears attributable to deer browsing. In total, demographic momentum, deer browsing, and other indirect effects explain 52.4% of the variation in large sapling abundance.

The path model for the 1996 data resembled that of the 1990–1991 (Table 2; Fig. 6). White cedar basal area and light explain 26.7% of the observed variation in seedling abundance. However, these variables dwindle in importance over time, ultimately accounting for less than 1% of the variation in large sapling abundance. In contrast, deer browsing directly accounts for 15.2% of the variation in small sapling abundance and 13.6% ($0.28^2 \pm 0.24^2$) of the variation in large sapling abundance. In total, seedling abundance in combination with estimated deer browsing accounts for 22.5% of the variation we observed in small sapling abundance. The abundance of small saplings and estimated deer browsing contribute most of the variance accounted for by the abundance of large saplings in this path model.

4. Discussion

4.1. Regional variation in cedar regeneration

Density of northern white cedar regeneration was generally sparse, but varied widely among stands

during both survey periods. Some other tree species that establish a seedling bank can also be characterized as having sparse and spatially variable regeneration. Eastern hemlock (*Tsuga canadensis*) and yellow birch (*Betula alleghaniensis*) tend to fit this pattern (Houle, 1994; Rooney and Waller, 1998; Rooney et al., 2000). Interestingly, white cedar, eastern hemlock, and yellow birch reach their highest densities on spatially restricted microtopographic features (Nelson, 1951; Houle, 1992; Rooney and Waller, 1998; Cornett et al., 2000). Other species, such as sugar maple (*Acer saccharum*) tend to maintain denser and less spatially variable regeneration (Houle, 1994; Marks and Gardescu, 1998). Sugar maple produces larger seeds, and this trait is strongly associated with seedling survivorship in shaded forest understories (Walters and Reich, 2000). Additional research may indicate strong linkages among seedling banks, germination niches, seed size, and spatial variation in seedling abundance.

4.2. Abiotic factors: light and microtopography

Light availability appeared to enhance seedling abundance in 1996 but not in 1990–1991. Also, small and large sapling abundance did not increase in response to more light in 1990–1991 or 1996. Stands surveyed during both periods had fairly open canopies, so seedlings and saplings probably had enough light to survive once established. On South Manitou Island, a deer-free island in Lake Michigan, Scott and Murphy (1987) reported that saplings > 25 cm tall were only found in canopy gaps. The whole-plant light compensation point increases as plants grow larger (Givnish, 1988), so light demands increase as plant size increases. We suspect deer eliminate most small and large saplings before light becomes a limiting factor.

Regeneration densities also appear to be influenced by microtopography. As expected, we found that seedlings and small saplings were disproportionately found on rotting wood and not on raised mounds or other substrates (Nelson, 1951; Scott and Murphy, 1987; Cornett et al., 1997), yet the proportion of white cedar stems on wood declines as plants grow larger. This result paralleled findings on South Manitou Island, where Scott and Murphy (1987) reported that most northern white cedar seedlings occurred on rotting logs. They found that only 1% of newly germinated seedlings survive to a height of 25 cm or taller. Other studies also report higher densities of cedar seedlings on hummocks or wood than in microsites closer to the water table, such as pits (Chimmer and Hart, 1996). Lanasa (1987) recommended prescribed burns to increase cedar seedling densities. We did not have the opportunity to observe cedar regeneration on burned substrates in this study. While prescribed burns may successfully increase white cedar seedling densities (Verme and Johnston, 1986), increasing fire frequencies above their historic norm to regenerate cedar may compromise other species associated with cedar swamps. For example, we do not know how rare plants associated with cedar swamps respond to fire.

4.3. Biotic factors: demographic momentum and deer browsing

We observed ‘demographic momentum’ in most white cedar populations, with the abundance of taller height classes reflecting the abundance of shorter height classes during both sampling periods. This attrition represents mortality as commonly observed in most seedling populations (Nelson, 1951; Harper, 1977). However, northern white cedar populations in the upper Midwest in the 1990s appear to be experiencing extraordinary rates of seedling and sapling mortality, especially outside of tribal lands and deer-free islands (Fig. 5). Much of this attrition appears attributable to local browse pressure. We were surprised to find that estimated deer browsing appears to affect the abundance of large saplings as much as demographic momentum (Table 2; Fig. 6). Because our browse index primarily reflects browse pressure in spring and summer, it likely underestimates winter browse pressure on cedar which

tends to be more concentrated, particularly in winters when deer congregate in deer yards. We are not aware of any other study where such clear and significant regional effects of deer browsing have been documented.

Deer browsing impacts also differed between 1990–1991 and 1996 in that estimated deer browsing appeared to affect only large saplings in 1990–1991 but significantly reduced the abundance of small saplings as well in 1996. As deer exhaust the supply of large saplings, they need to shift to smaller plants. The increase in our browse index values also suggests that deer became more abundant between 1990–1991 and 1996, which accelerated mortality of white cedar regeneration. Data collected by the Wisconsin DNR confirms an increase in deer densities. Between 1989 and 1996, overwintering deer densities fluctuated around a mean density of 10.1 ± 1.0 deer per km^2 , with a low of 6.4 ± 0.2 deer per km^2 occurring in 1992 and a high of 15.3 ± 0.7 deer per km^2 occurring in 1995 (Wisconsin DNR, unpublished data). These deer densities are far in excess of the estimated 2–4 deer per km^2 that occupied the region during presettlement times (Alverson et al., 1988).

4.4. Multivariate model: path analysis

In general, these results parallel the patterns of recruitment we documented for eastern hemlock, *Tsuga canadensis* (Waller et al., 1996; Rooney et al., 2000). Both species have relatively low seedling establishment, but these seedlings are shade tolerant and capable of surviving for long periods. Their persistence and growth, however, appear to be threatened by chronic deer browsing throughout the Upper Great Lakes region. The importance of deer browsing is evident in the high path coefficients relating local browse index values to the abundance of white cedar and hemlock saplings ≥ 30 cm tall (Fig. 6; Rooney et al., 2000). Thus, both demographic momentum and deer browsing affect the abundance of these species, but deer may be exerting a decisive effect, given the general scarcity of seedlings. Although, this inference is based on correlative and thus somewhat circumstantial evidence, it is buttressed by our field observations of browsing damage on these species and field experiments involving

fenced exclosures of hemlock populations (Alverson and Waller, 1997).

5. Conclusion

After returning from Germany in the 1935, Leopold (1936a,b) expressed concern about the incompatibility between what he termed “wood factory” forestry and sound wildlife management. The abundance of shrubs and early successional saplings favored by intensive forestry tends to inflate deer populations (Clark and Gilbert, 1982; Masters et al., 1993). This, in turn, tends to eliminate preferred browse species from the landscape (Waller and Alverson, 1997). Leopold (1936b) advocated removing the less productive half of forested lands from active timber management, maintaining ungulate predators, and managing deer populations below densities that would produce a maximum sustained yield. These prescriptions still need testing, and researchers are eager to study the efficacy of this approach (Alverson et al., 1994; Van Deelen, 1999).

The prognosis for cedar swamps is poor. It is clear to us that without human intervention, cedar swamps are “living dead”—canopy trees will persist for decades or centuries, but have little chance of passing on their genes to the next generation because of deer-induced sapling mortality (Alverson et al., 1994). Without significant and sustained reductions in deer densities, northern white cedar stands in future centuries could become confined to ‘browsing refugia’ (Rooney, 1997; Borgmann et al., 1999), such as limestone cliffs (Habeck, 1958), islands without deer, and tribal lands.

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