

Landscape and Local Factors Affecting Northern White Cedar (*Thuja occidentalis*) Recruitment in the Chequamegon-Nicolet National Forest, Wisconsin (U.S.A.)

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ABSTRACT.—Northern white cedar (*Thuja occidentalis* L.) stands throughout the upper Midwestern United States have failed to recruit individuals to the canopy consistently for several decades. To examine local and landscape factors that influence cedar regeneration we recorded the abundance of cedar seedlings and saplings in 24 lowland cedar stands in the Chequamegon-Nicolet National Forest, Wisconsin, during summer 2001. Cedar seedlings (height <22 cm) were common (median = 1800 ha⁻¹), but the largest size class (height ≥100 cm) was extremely rare (~1 ha⁻¹) and heavily browsed. We used information-theoretic model averaging of linear mixed-effects models to identify local and landscape variables important for predicting the density of seedlings and saplings. The density of newly germinated seedlings was higher along transects farther from roads and with more mature cedar. Large seedling and small sapling densities were higher along transects with open canopies located in landscapes with a higher ratio of deciduous to coniferous forest. Increased edge-to-area ratios of cedar stands and edge density of the surrounding forest were associated with lower densities of large seedlings and small saplings, respectively. Results indicated a strong demographic effect with the density of large size classes being strongly dependent on the density of smaller size classes. Because the landscape factors considered are linked to browsing intensity, a reduction in deer (*Odocoileus virginianus* Zimmermann) density coupled with landscape-sensitive forest management may help to foster cedar regeneration in northern Wisconsin.

INTRODUCTION

Northern white cedar (*Thuja occidentalis* L.) stands throughout much of the Great Lakes region have shown recruitment failure for nearly 60 y (Curtis, 1946; Habeck, 1960; Chimner and Hart, 1996; Swihart and Picone, 1998; Van Deelen, 1999; Rooney *et al.*, 2002). Northern white cedar is a long-lived, shade-tolerant species that is dominant on many alkaline wetlands throughout the upper Midwestern United States (Gates, 1942; Curtis, 1959; Johnston, 1990; Pregitzer, 1990). At one time this species was considered to be tolerant of variable environments and easy to regenerate (Zon and Graves, 1911; Curtis, 1946; Johnston, 1977). The current lack of recruitment has largely been attributed to high densities of white-tailed deer (*Odocoileus virginianus* Zimmermann) because northern white cedar is a preferred browse species (Beals *et al.*, 1960; Ullrey *et al.*, 1968). Broad-scale reduction of deer densities presents numerous political and logistical problems (WI DNR, 2001); however, it is crucial to manage for cedar regeneration because these lowland stands are one of the most diverse plant communities in the region (Pregitzer, 1990) and provide

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important habitat to over 80 wildlife species (Doepker and Ozoga, 1991), as well as many rare species of orchids and lilies (Curtis, 1959; USDA Forest Service, 2004).

The role that herbivory plays in the consistent loss of cedar cohorts has been discussed at length in the literature. Over 40 y ago, after showing that northern white cedar saplings were more common in areas with lower deer browsing activity, Beals *et al.* (1960) noted that high deer densities had, “presented a serious problem in northern Wisconsin and adjacent areas,” for at least two decades. At the same time, Habeck (1960) reported that intense use of lowland cedar swamps by deer could alter the species composition of the canopy. More recent studies have confirmed that cedar saplings, when subjected to ubiquitous browsing pressure, are not recruited into the canopy (*e.g.*, Verme and Johnston, 1986; Heitzman *et al.*, 1999; Van Deelen, 1999; Rooney *et al.*, 2002). Furthermore, other herbivores such as snowshoe hares (*Lepus americanus* Erxleben) and meadow voles (*Microtus pennsylvanicus* Ord) are also known to affect tree regeneration and may be playing a role in this lack of recruitment (Ostfeld *et al.*, 1997; Davis *et al.*, 1998; Cadenasso and Pickett, 2000; Manson *et al.*, 2001)

A recent region-wide study (Rooney *et al.*, 2002) and numerous stand-level studies (*e.g.*, Verme and Johnston, 1986; Davis *et al.*, 1998; Heitzman *et al.*, 1999; Van Deelen, 1999) have shown that there may be small pockets of cedar recruitment in the upper Midwest. On a broad scale, Rooney *et al.* (2002) demonstrated that more cedar saplings were found in areas of low deer densities; however local factors such as light availability, seed source and “demographic momentum” (*i.e.*, the density of small seedlings) were also important. This suggests that landscape-level factors that influence habitat selection by herbivores may interact with local conditions to affect cedar recruitment. For example, proximity to roads may affect seed germination and survival because of changes in the hydrology and water quality of the stand (Ehrenfeld and Schneider, 1991; Jones *et al.*, 2000; Trombulak and Frissell, 2000). Nearby roads could also affect browsing intensity because roads are used as movement corridors and refugia by some herbivores (Bellamy *et al.*, 2000). Sapling establishment may be influenced by the variation in local deer density and browsing intensity induced by distance to and area of logging activity and other land-cover types (Tierson *et al.*, 1985; Filipiak, 1994; Augustine and Jordan, 1998; St-Louis *et al.*, 2000; Takada *et al.*, 2002; Morrison *et al.*, 2003).

To determine if landscape structure and composition influence the fine-scale variation in cedar recruitment, we addressed two questions: (1) Do stands of northern white cedar in the Chequamegon-Nicolet National Forest show evidence of recruitment? (2) What landscape and local factors best explain the variation in seedling and sapling densities? For the purposes of this study, we used the density of cedar in smaller size classes as a proxy for the demographic potential of the stand, because that density indicates the ability of the stand to produce viable offspring that could be recruited into the canopy given the right combination of external conditions. Likewise, we used the density of saplings taller than 2 m to indicate recruitment because those individuals are beyond the reach of deer and no longer greatly affected by browsing. If stands are recruiting individuals into the canopy, we expect the histogram of diam classes to approximately follow the negative exponential or power function models typical of shade tolerant species (Hett and Loucks, 1976). We hypothesized that cedar seedling densities could be related to local factors that influence seedling establishment and growth such as light availability, potential seed source and overstory stand density (Table 1). We also hypothesized that seedling and sapling densities may be influenced by landscape and local factors related to habitat use by herbivores such as landscape composition and the edge density of forest (Table 1).

TABLE 1.—The original suite of independent variables used in regression models to explain variation in cedar presence and abundance

Names	Description	Sample level	Mean	Range	Units	Transform	Hypothesized effect
Canopy	proportion of 10 m sections with a closed canopy	Transect	0.47	0–1	proportion		–
CedarBA	basal area of cedar in 10 × 10-m tree plot	Transect	2725	0–7886	cm ²	ln(x + 1)	+
Decid:Conif	Ratio of deciduous to coniferous forest in a 2-km radius	Stand	6.84	0.57–31.3	ratio		–
Prop regen	proportion of 5–10 y old stands in a 2-km radius	Stand	0.040	0–0.088	proportion		–
Dist. Roads	Distance to county, state and logging roads	Transect	356	30–1060	meters		+
Edgearea	Edge to area ratio of the cedar stand	Stand	127.5	59.9–306.7	m ha ⁻¹		–
Forest ED	Edge density of forest cover in a 2-km radius	Stand	0.54	0.31–0.76	m m ⁻²		–
DensS1	Small seedlings ha ⁻¹	Transect	1669	50–10,900	# ha ⁻¹	ln(x + 1)	+
DensS2	Large seedlings ha ⁻¹	Transect	974.7	0–13,050	# ha ⁻¹	ln(x + 1)	+

METHODS

STUDY AREA

This study was conducted during summer 2001 in the Great Divide District of the Chequamegon-Nicolet National Forest (GDD CNNF) located in north-central Wisconsin (Fig. 1). The study area surrounds the town of Clam Lake and covers 186,340 ha in Ashland, Bayfield, Price and Sawyer counties. The topography ranges from flat to rolling, with glacial moraines and outwash areas dominating the landscape. Although the uplands consist of predominantly well drained soils, many of the lowland areas are poorly drained. Thus bogs, forested wetlands, lakes and streams are common throughout the district. The Chequamegon portion of the CNNF consists of approximately 23% aspen (*Populus tremuloides* Michx.), 32% mixed hardwoods, 13% mixed pine and spruce (*Pinus* spp., *Picea* spp.), 2% balsam fir (*Abies balsamea* [L.] Miller), 2% upland openings, 1.5% northern white cedar and 26.5% other lowland cover types (USDA Forest Service, 1986; USDA Forest Service, 2004).

The climate of this area is cool and moist with annual precipitation ranging from 76 to 86 cm per year and a mean annual air temperature of 5 C (40 F). Snow depths typically peak at around 60 cm in late Jan. and begin to decline in mid Mar. with a final melt in early Apr. (Copper Falls State Park, unpubl. provided by Bruce Bacon—WI DNR). Snow accounts for less than 25% of the total precipitation, although it can accumulate to depths greater than 60 cm (USDA Forest Service, 1986).

The GDD contains portions of three Department of Natural Resources (DNR) deer management units. The 2002 overwinter deer population density estimates for these areas were 7.0, 7.7 and 8.9 deer/km² of deer range (WI DNR, 2004) while the management goals were 4.6, 5.4 and 5.8 deer/km² of deer range respectively (WI DNR, 1998). The estimated carrying capacity of the landscape was estimated at 10.3 deer/km² of deer range (WI DNR, 1998). In addition, a herd of 25 elk (*Cervus elaphus* L.) initially reintroduced in 1995, had grown to approximately 80 individuals in 2001 occupying a 117 km² area of the GDD (L. Stowell, pers. comm.).

SAMPLING DESIGN

All lowland cedar stands in the GDD CNNF were identified using the Forest Service stand map. Of the stands with an area of at least 6 ha and a stand age of at least 60 y ($n = 458$), 24 stands were randomly selected for sampling. These stands ranged in age from 60 to 162 y old (mean = 117 y, $SD = 28$ y) and 6 to 128 ha (mean = 36 ha, $SD = 30$ ha). We randomly distributed four belt transects (100 × 2 m) separated by ≥100 m within 18 stands (total number of transects = 83). Six stands were not large enough to accommodate four transects, so only two transects were established in these smaller stands. Of these, one transect was removed as an outlier because it fell entirely in an extensive alder thicket misclassified as cedar. The beginning location of each transect was recorded with a map grade GPS unit. Each transect was divided into ten contiguous 10-m sections for sampling.

Within each belt transect, we recorded a visual estimate of canopy cover (open [1], partly closed [2] and closed canopy [3]) for every 10-m section. The proportion of sections with a closed canopy was used as an approximation for light availability along the transect. We also recorded the number of cedar stems in each of five height classes in each section (small seedling, <7.5 cm; large seedling, 7.5–22 cm; small sapling-A, 22–44 cm; small sapling-B, 44–100 cm; large sapling, ≥100 cm; any heights exactly between size classes were recorded in the taller group). While trees <44 cm are not normally considered “saplings,” the stout heavily-browsed individuals typical to the small sapling-A size class were more similar to saplings than seedlings and were thus, lumped with small sapling-B individuals into a single

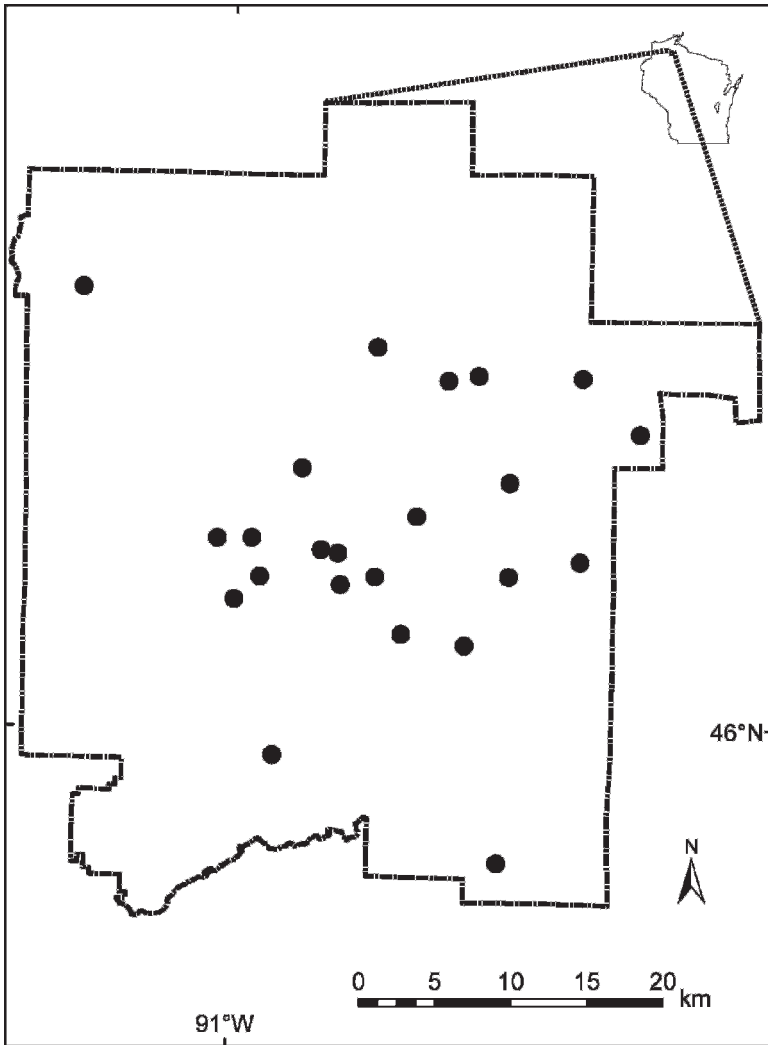


FIG. 1.—Stand locations within the Great Divide District of the Chequamegon-Nicolet National Forest in northern Wisconsin, U.S.A.

“small sapling” class for all statistical analyses (the small sapling sub-classes were used separately only for graphical representations of size distributions). Presence of browse damage was recorded (0 or 1) for each individual.

The numbers of seedlings and saplings on six microsite types (log, stump, tipup mound, ground, unidentified mound, depression) were totaled for each transect. Overstory stand composition was measured in a 10×10 m tree plot centered randomly between meters 35 and 65 along each transect, in which we recorded the species and diam at breast height (dbh) of every tree >5 cm dbh and all cedar >2 m in height. Because large saplings were expected to be rare in our study area (Rooney *et al.*, 2002), we established three supplementary transects (100×2 m) in each stand in which only large saplings were

recorded for qualitative analyses. In the six stands that contained two transects, only one additional transect was established. These supplemental transects were only used to give a more accurate description of the stand-wide density of large saplings.

A Geographical Information System (GIS; ArcGIS 8.1, Environmental Systems Research Institute, Inc.) was used to calculate map metrics for each transect and stand. The final suite of metrics was chosen based on biological relevance and a lack of strong between-variable correlation ($|r| < 0.5$; Table 1). The only transect-level map metric used, distance to road, represents the linear distance from each transect's center point to the nearest road (including all logging roads county roads and state routes). The edge-to-area ratio was calculated for each stand in addition to several landscape metrics calculated within a 2-km buffer from the stand center. The proportion of 5 to 10 y-old clearcuts were used as an indicator of logging activity through time because their high productivity of herbaceous and low-statured woody forage could have affected herbivore movements for at least 5 y. The ratio of the proportions of upland deciduous and coniferous forests was used to represent within-forest heterogeneity of cover types while the edge density of forest represented the overall complexity of forest and open cover types. The 2-km radius was chosen because smaller distances would have included mostly cedar (*i.e.*, omitting attributes of the surrounding landscape) and larger distances would have overlapped many sites and also included extensive areas beyond the extent of the National Forest database. Data layers of land-cover types and the road network were obtained from the Wisconsin Department of Natural Resources (WI DNR, 2002). The location and history of stands were provided by the U.S. Forest Service (USDA Forest Service, 2001).

DATA ANALYSES

Linear mixed-effects regression models were used to examine how variation in stem density within transects was related to local and landscape metrics. The regression parameters were estimated using maximum likelihood techniques as implemented in the nlme library of R (Pinheiro and Bates, 2000; R Development Core Team, 2007). Stem density was normalized using a natural log transformation ($\ln[x + 1]$) prior to model selection. Natural log transformations were also applied to the basal area of cedar in each transect's tree plot to improve the linear relationship with stem density.

The linear mixed-effects models included all covariates as fixed effects with a random stand-level grouping factor. Grouping by stand allowed us to simultaneously compare transect- and stand-level covariates despite residual variability among stands. This hierarchical model structure as expressed in matrix notation by Pinheiro and Bates (2000) is:

$$y_i = X_i\beta + Z_i b_i + \varepsilon_i,$$

$$b_i \sim \mathcal{N}(0, \Psi) \quad \varepsilon_i \sim \mathcal{N}(0, \sigma^2\Lambda_i)$$

Where the vector y_i represents the densities of cedar by transect within stand i . The matrix of covariate values for a given stand is represented by X_i and β is a vector that includes the mean intercept and fixed-effect slopes associated with each covariate. The random-effect term is the vector b_i , which is assumed to be normally distributed with mean 0 and variance-covariance matrix Ψ ; in this formulation, Z_i is a vector of ones. The within-stand errors are represented by ε_i , a normally distributed random variable with mean 0 and variance-covariance matrix $\sigma^2\Lambda_i$.

Model selection was implemented by first determining the appropriate predictor variables to include in the global model. We chose this set of covariates based on hypotheses about

how cedar recruitment was likely to be affected by local growing conditions and how local deer density was likely to be affected by landscape characteristics. Because we had no way of explicitly estimating cedar growth rates or deer density through time, we had to rely upon empirical relationships published in the literature to guide our selection of variables. The global model was the same for all three size classes with one exception: to take into account potential demographic effects, the $\ln(\text{density} + 1)$ of the next smaller size class was also included as a local covariate in the models for large seedlings and small saplings. All covariates, their hierarchical level (transect or stand) and hypothesized effect are listed in Table 1.

Our goal for the regression analysis was to develop an understanding of the relative importance of the covariates in predictive models of cedar seedling and sapling densities. Rather than using formal hypothesis tests to describe the system, we chose a multimodel inference approach based on all-subsets regression (Burnham and Anderson, 2002). To avoid the appearance of data dredging, we re-iterate that the variable set was chosen *a priori*, and further, we use model averaging to account for model-selection uncertainty.

All possible combinations of fixed effects within each global model were computed for each size class. Interaction and polynomial terms were not included in this analysis because we did not have strong biological reasons to include them and moreover, wanted to avoid over-fitting the data. For each model, we first calculated the small sample Akaike's Information Criterion (AIC_c) because the sample size to parameter ratio was less than 40 (Sugiura, 1978; Burnham and Anderson, 2002, p. 66). The second statistic we computed for each model was the predicted residual sum of squares (PRESS) also known as the k-fold cross-validation (CV) statistic formulated as:

$$CV(y) = \sum_{i=1}^k (y_i - y_{pred})^2$$

Where k is the number of stands and y_i is a vector of the observations within the i -th stand. The vector y_{pred} is calculated by removing the i -th stand observations from the dataset, fitting the model on the remaining data and then predicting the removed observations based on that model.

For purposes of interpretation, it is useful to determine how well a given model predicts the data. Turchin (2003, p. 195) suggests the use of a coefficient of prediction in order to express prediction accuracy:

$$R_{pred}^2 = 1 - \frac{\sum_{i=1}^k (y_i - y_{pred})^2}{\sum_{i=1}^k (y_i - \bar{y})^2}$$

The numerator represents the PRESS statistic and the denominator is simply the sample sum of squares. If the R_{pred}^2 is < 0 the model is fitting noise and the mean is a superior predictor. If R_{pred}^2 is close to 0, we know the model in question does not predict much better than the sample mean. However, the closer R_{pred}^2 is to 1, the better the given model predicts unknown data.

One of the disadvantages of using a cross-validation statistic for model selection is that many models may have nearly identical values. Because there is no critical test, maximizing R_{pred}^2 will determine the best predictive model without regard to parsimony. Thus, we ranked the models using AIC_c and used R_{pred}^2 values to provide some intuition about model fit.

To generate model coefficients averaged over all models, we first calculated the ΔAIC_c values and Akaike weights (w) for each model (Burnham and Anderson, 2002, p. 71, 75).

We then calculated the model-averaged estimator, $\tilde{\beta}$, a weighted average of each $\hat{\beta}$ over the entire model set. Finally, we determined the relative importance, w_i , of each covariate by summing the w values for the set of models in which each variable appeared (Burnham and Anderson, 2002, p. 152).

The residuals of the top ten models from each size-class set were checked for approximate normality using a quantile-quantile plot. Residual plots were used to check for heteroscedasticity. We tested for spatial dependence within sites by re-fitting each model using restricted maximum likelihood (REML) both with and without an exponential variogram, and then comparing the model fits using Likelihood Ratio tests. We checked for spatial autocorrelation among sites by examining semi-variogram plots of model residuals.

We used permutation t -tests with Holm corrections to test for pair-wise differences in stem density and browsing intensity by size class. This method was also used to test for differences between the numbers of stems found on each microsite type. All analyses were carried out using R (R 2.5.0, R Development Core Team, 2007).

RESULTS

PRESENCE AND DENSITY OF CEDAR SEEDLINGS AND SAPLINGS

Cedar seedlings were present in more than 90% of transects while small and large saplings occurred in 63% and 1% of the transects respectively (Fig. 2a). Likewise, throughout the study area, small and large seedlings occurred in densities (median = 1250 and 500 stems ha^{-1} , respectively) that were much higher than the density of small and large saplings (median = 100 and 0 stems ha^{-1} , Fig. 2b). Across all transects, cedar seedlings and saplings were more abundant on downed logs than on any other microsite type (Fig. 3).

The proportion of stems browsed increased significantly with each size class, and over 60% of the small saplings showed some browse damage (Fig. 4). Only three large saplings were observed in 145 transects (~ 1 stem ha^{-1}) and all three were heavily browsed. Two of the large saplings were classified as "unhealthy" because $>50\%$ of their branches were dead or dying. Because of the small sample size, large saplings were not included in any statistical analyses.

Northern white cedar was the dominant overstory species in the tree plots and contributed a mean total basal area of $26.9 \text{ m}^2 \text{ ha}^{-1}$ ($\text{SD} = 19.4 \text{ m}^2 \text{ ha}^{-1}$, range = 0.0 to $78.9 \text{ m}^2 \text{ ha}^{-1}$), while other species contributed an average of $12.6 \text{ m}^2 \text{ ha}^{-1}$ ($\text{SD} = 10.3 \text{ m}^2 \text{ ha}^{-1}$, range = 0.2 to $52.5 \text{ m}^2 \text{ ha}^{-1}$). Most of the cedar trees represent larger size classes while other species make up most of the understory (Fig. 5). The mean ratio of cedar to non-cedar basal area per plot was 9.5; however, the variability was high ($\text{SD} = 37.2$) with cedar contributing less than half of the total basal area in 29% of the plots and zero basal area in 8% of the plots. The mean density of mature cedar was 600 stems ha^{-1} ($\text{SD} = 500$ stems ha^{-1} , range = 0 to 1900 stems ha^{-1}) and the mean stand density including all species was 1800 stems ha^{-1} ($\text{SD} = 700$ stems ha^{-1} , range = 200 to 3500 stems ha^{-1}). The plots with no cedar overstory were typically large canopy gaps associated with blowdowns and were dominated by speckled alder (*Alnus rugosa* Du Rois) or black ash (*Fraxinus nigra* Marsh.).

REGRESSION ANALYSES

Model weights were low for all of the regression models in part because of the all-subsets approach. To define a model selection window of 0.95 (*i.e.*, a sum of w_i values ≥ 0.95) for the small seedling, large seedling and small sapling models, we had to include 45 of 127, 96 of 256 and 47 of 256 models, respectively. This indicates a large degree of model-selection uncertainty, so we focus on the model-averaged coefficients for each model and specifically

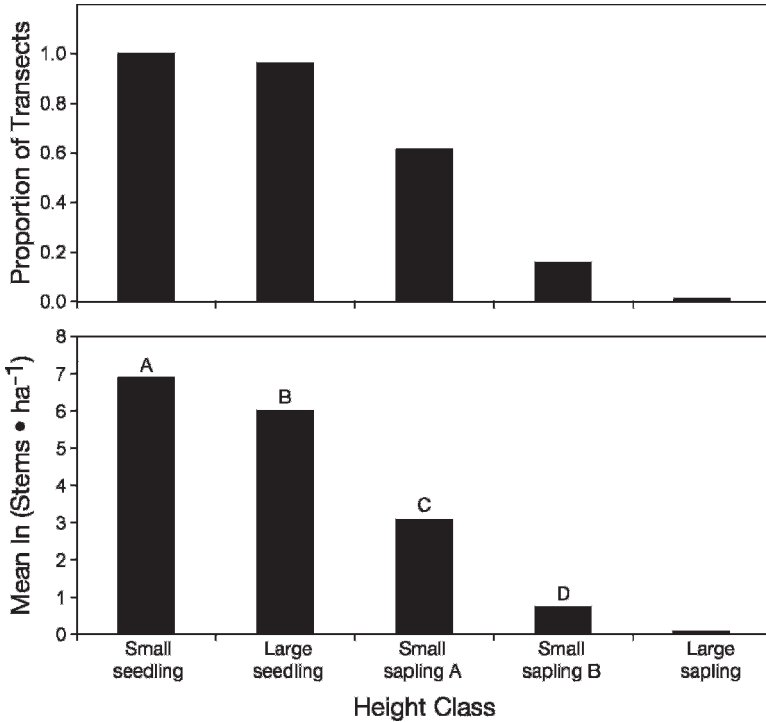


FIG. 2.—(A) Proportion of 100 m transects ($n = 83$) on which a given size class of cedar was observed. (B) Mean ln (density + 1) of cedar by height class. Different letters indicate significantly different means ($\alpha = 0.05$, permutation t -test with Holm adjustment). Only three large saplings were observed in the entire study and they were not considered in the statistical analyses

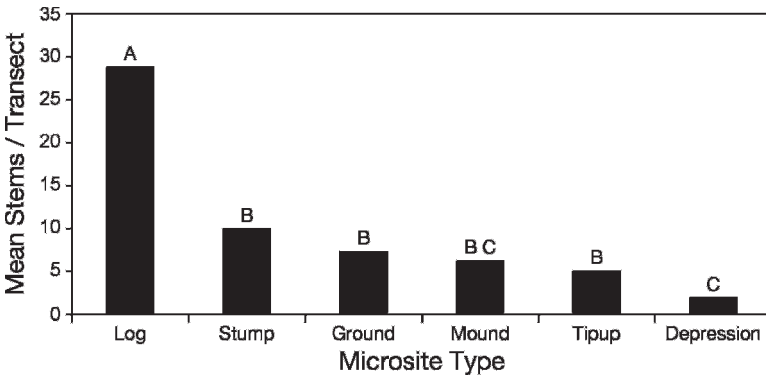


FIG. 3.—The mean number of seedlings per 200 m² transect ($n = 83$) on each microsite. The number of seedlings found on logs was significantly greater than the other locations ($\alpha = 0.05$, permutation t -test with Holm adjustment)

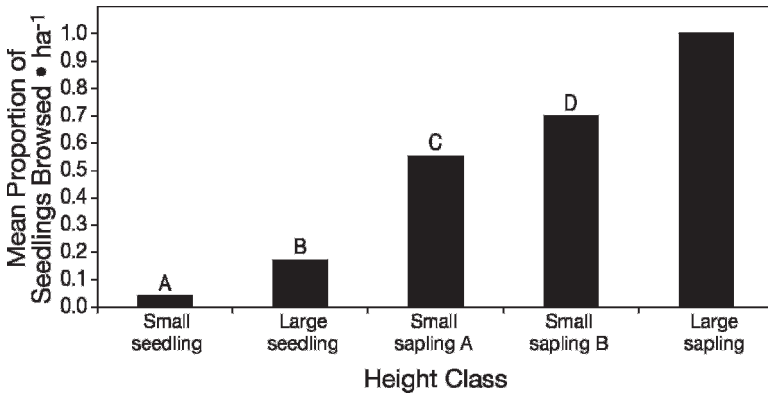


FIG. 4.—The mean proportion of seedlings browsed by size class. Bars with the same letter indicate no significant difference by a permutation *t*-test with a Holm adjustment ($\alpha = 0.05$)

discuss those with relative importance values greater than 0.33 (Table 2). The top ten models for each size class did not have significant within-site spatial structure ($P > 0.05$). Furthermore, no pattern of spatial autocorrelation was detected among stands in the semivariogram plots.

The most important variables for predicting small seedling density were two local factors. Both the basal area of mature cedar along the transect ($w_+ = 0.999$) and the distance of the transect to the nearest road ($w_+ = 0.73$) showed a positive relationship with the density of small seedlings. Predictive model fit, as estimated by R^2_{pred} , ranged between 0.06 and 0.14 for the top five models.

The density of large seedlings was positively related to the density of small seedlings ($w_+ = 1.00$) and the ratio of deciduous to coniferous forest surrounding the stand ($w_+ = 0.43$). A negative relationship was found with the basal area of cedar ($w_+ = 0.49$), closed canopy ($w_+ = 0.56$) and the edge density of forest surrounding the stand ($w_+ = 0.63$). The R^2_{pred} values of the top five models were relatively high (0.41 to 0.42); however, an investigation of the entire model set showed that much of that fit was related to the density of small seedlings.

Small sapling density showed a strong negative relationship to the density of closed canopy ($w_+ = 1.00$) and the edge to area ratio of the cedar stand ($w_+ = 0.73$). A strong positive relationship was found with the density of large seedlings ($w_+ = 0.98$) and the ratio

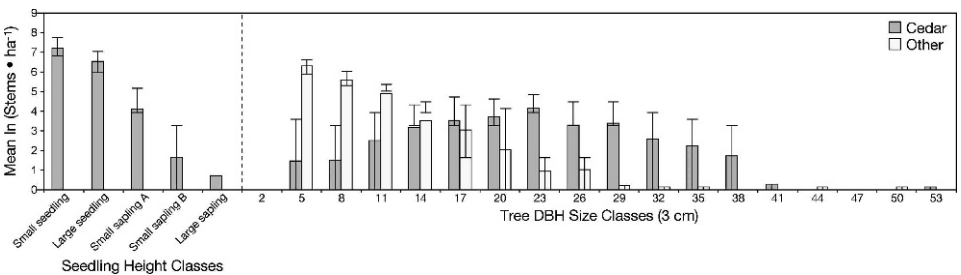


FIG. 5.—Mean ln (density + 1) of trees, saplings and seedlings pooled by stand ($n = 24$). Error bars represent the first and third quartiles

TABLE 2.—Results of top five regression models for each size class. The dependent variable refers to the $\ln(\text{seedlings} \cdot \text{ha}^{-1} + 1)$. The relative variable importance (w_i) and model averaged estimator ($\tilde{\beta}$) are calculated using all subset models

	Int	Cedar: BA	Dens S1	Dens S2	Closed canopy	Dist. roads	Edge: Area	Decid: Conif	Prop regen	Forest ED	R^2_{pred}	K	AIC _c	ΔAIC_c	w
Small	4.71	0.23			0	0.0016	0	0	0	0	0.144	5	250.7	0	0.16
seedlings	4.15	0.22			0	0.0016	0	0	0	1.021	0.058	6	252.5	1.85	0.064
	4.81	0.23			-0.29	0.0015	0	0	0	0	0.128	6	252.6	1.96	0.061
	4.95	0.22			0	0.0015	-0.0014	0	0	0	0.122	6	252.8	2.12	0.056
	4.69	0.23			0	0.0015	0	0.0059	0	0	0.066	6	252.9	2.25	0.053
$\tilde{\beta}$	4.84	0.22			-0.088	0.0011	-0.00058	0.0034	-0.71	0.34					
w_4		0.999			0.28	0.73	0.28	0.27	0.26	0.29					
Large	1.79	0	0.92		-0.97	0	0	0	0	-3.043	0.412	7	274.7	0	0.045
seedlings	1.47	-0.11	0.997		0	0	0	0	0	-2.82	0.416	6	274.9	0.23	0.040
	1.83	-0.083	0.98		-0.79	0	0	0	0	-2.88	0.411	7	275.2	0.45	0.036
	0.27	0	0.87		-1.050	0	0	0.036	0	0	0.411	7	275.3	0.60	0.033
	1.38	0	0.89		-1.021	0	0	0.024	0	-2.20	0.414	8	275.7	0.96	0.028
$\tilde{\beta}$	0.94	-0.046	0.93		-0.52	0.00015	0.00011	0.012	1.54	-1.83					
w_4		0.49	1.00		0.56	0.28	0.23	0.43	0.32	0.63					
Saplings	3.18	0		0.45	-3.70	0	-0.011	0.064	0	0	0.227	8	367.0	0	0.10
	2.71	0		0.45	-3.77	0	-0.011	0.075	11.55	0	0.208	9	367.7	0.75	0.069
	3.63	0		0.50	-3.64	0	-0.013	0	0	0	0.226	7	367.9	0.89	0.065
	1.39	0		0.46	-3.75	0	-0.010	0.082	0	2.94	0.206	9	368.4	1.41	0.050
	3.76	0		0.47	-3.86	-0.0013	-0.013	0.075	0	0	0.208	9	368.5	1.52	0.047
$\tilde{\beta}$	2.40	0.017		0.46	-3.87	-0.00021	-0.0088	0.061	3.29	0.70					
w_4		0.30		0.98	0.997	0.26	0.73	0.73	0.33	0.29					

of deciduous to coniferous forest in the surrounding landscape ($w_+ = 0.73$). Although the R^2_{pred} values for the top models for this size class (0.21 to 0.23) were not as high as those for the large seedlings, the importance of the variables was more evenly distributed.

DISCUSSION

Northern white cedar is not recruiting new stems into the canopy in the Great Divide District of the Chequamegon-Nicolet National Forest. Large saplings were essentially absent from the landscape with only three individuals recorded in this study. The small-sapling size class was also rare. As others have reported from Wisconsin and elsewhere, this lack of regeneration does not appear to be related to a deficient seed source or poor germination success (Blewett, 1976; Verme and Johnston, 1986; Heitzman *et al.*, 1997; Cornett *et al.*, 2000; Rooney *et al.*, 2002). Newly germinated seedlings were abundant in most stands; however, we see an exponential decline in density in the taller height classes. If cedar were effectively recruiting trees into the canopy, there would be an approximate linear decline in the $\ln(\text{density})$. In the stands we sampled, there was a severe departure from this trend, with balsam fir, black ash and other species dominating the smaller size class distributions (Fig. 5).

Initial establishment of seedlings is related to factors that can influence seed source and site suitability. The basal area of mature cedar was the single most important factor in explaining the density of small seedlings. Northern white cedar has limited seed dispersal capabilities (Johnston, 1977; Johnston, 1990), so a nearby concentration of mature trees is essential for initial seedling establishment (Heitzman *et al.*, 1997; Romme *et al.*, 1998; Heitzman *et al.*, 1999).

Substrate availability may be influencing seedling survival because most of our seedlings were found on decaying logs (Fig. 2). This trend is consistent with data from other cedar stands (Scott and Murphy, 1987; Rooney *et al.*, 2002). Logs may provide some benefits for germination (O'Hanlon-Manners and Kotanen, 2004); however, substrates such as raised mounds may yield better long term success (Rooney *et al.*, 2002). Whether log germination sites represent a mortality sink is unclear; however, the overall decline in abundance between size classes is so severe that no seedlings appear to reach the canopy or even subcanopy level.

The density of mature cedar and other canopy species may inhibit the success of seedlings by reducing light in the understory. We found that the densities of small saplings and large seedlings—and to a lesser extent, small seedlings—were negatively correlated with the proportion of transect sections with closed canopies. Large seedlings also showed a weak negative relationship to the basal-area of cedar, another indication that canopy density may affect growth and/or survival. Although Rooney *et al.* (2002) found that the amount of light was only significant for their smallest size class (similar in height to our large seedlings), our results are not surprising because northern white cedar is known to have a plastic growth response when canopy gaps are created by small-scale logging, windthrow or other disturbances (Scott and Murphy, 1987; Heitzman *et al.*, 1997).

Another local factor that played an important role in predicting seedling density was distance to roads. One explanation for finding more seedlings farther from roads is increased herbivory because the edges associated with road cuts can also act as refugia and corridors for numerous herbivores (Bellamy *et al.*, 2000; Cadenasso and Pickett, 2000). However, an abiotic effect may be more realistic because roads are known to impact the hydrology, water quality and biodiversity of wetlands (Ehrenfeld and Schneider, 1991; Findlay and Bourdages, 2000; Trombulak and Frissell, 2000). The hydrological effects may

be particularly important because benefits of drier microhabitats such as mounds and logs (Chimner and Hart, 1996) may be reduced if the local water table changes.

The ratio of deciduous to coniferous forest in the landscape showed a consistent, positive relationship with seedling and sapling densities and the strength of this relationship increased with size class. This pattern may be the result of herbivores altering their broad-scale habitat use in response to land-cover proportions. During the summer months, deer avoid landscapes with large amounts of coniferous forest, but show preference for clearcuts and other disturbed stands where they consume mostly herbaceous forbs (Lesage *et al.*, 2002; Plante *et al.*, 2004; Smith *et al.*, 2007). Thus, even though deer may be attracted to landscapes with more deciduous forest during the summer, their impact on young cedar is likely small. Deer prefer coniferous landscapes during winter (Morrison *et al.*, 2003), possibly because of the reduced snow depths associated with those stands (D'Eon, 2001). Furthermore, snowshoe hares also prefer coniferous cover and will actively avoid deciduous landscapes in the winter (Dolbeer and Clark, 1975; Wolff, 1980). The likely result of these habitat preferences is reduced browsing pressure on cedar stems growing in more isolated stands.

We found that the respective densities of large seedlings and small saplings were negatively related to the edge density of forest in the landscape and the cedar-stand edge to area ratio. We also detected a weak, positive response in large seedling and small sapling densities to proportion of recently logged stands in the landscape. In general, cervids respond positively to the amount of edge in the landscape, as well as overall heterogeneity of cover types (Alverson *et al.*, 1988; Kie *et al.*, 2002; Plante *et al.*, 2004). Deer feed extensively in and around clearcuts (Chang *et al.*, 1995) and logging activity can attract deer due to large amounts of slash and regrowth made available for browsing (Verme, 1973; Tierson *et al.*, 1985; Filipiak, 1994). Although greater proportions of high quality food in landscapes surrounding forested stands may reduce browsing intensity in the stands (Augustine and Jordan, 1998; Takada *et al.*, 2002), they also may attract more deer into the area while providing cover for smaller herbivores. This interaction between distance to high quality forage patches and the area of those patches in the landscape may result in unexpected browsing intensities. In a forest that is managed heavily for early successional stands, understanding this relationship may be critical if cedar is to be regenerated in the landscape.

Three of our four landscape covariates played important roles in predicting the density of the larger two size classes. Still, in all of our models local variables tended to be more important. Similar to the results of Rooney *et al.* (2002), one of the best predictors of the larger size classes was the density of the next smaller size class. The importance of this demographic momentum shows that there has been consistent recruitment within these small size classes. However, lacking a 20 to 30 y window without heavy browsing pressure, the existing cedar stands are not likely to produce viable recruitment into the large sapling and ultimately canopy size classes.

Our results contribute to the understanding of the factors explaining the lack of recruitment in northern white cedar stands. We demonstrate that broad-scale characteristics of the landscape explain portions of the variability in seedling and sapling density. Although there has been some debate in the literature regarding the utility of model averaging and AIC_c (Richards, 2005; Link and Barker, 2006), we feel that in combination with the R^2_{pred} statistic, this approach provides useful insights into the ecology of the system, and will aid in directing future experimental studies.

Manipulation of some of the factors considered in our study in conjunction with a moderate to severe reduction of the deer herd may create areas in the landscape where

cedar seedlings can escape browsing without the use of artificial herbivore exclosures. Experimental removal of deer social groups can help to create persistent areas of low deer density (McNulty *et al.*, 1997) and may be the best starting point for this recovery. However, whether these techniques will reduce deer densities below the 4 deer km⁻² deemed critical for cedar and other species (Alverson *et al.*, 1988), remains unknown. Although there are clearly other factors influencing the establishment and growth of cedar saplings, a reduction of local deer densities and a forest management regime that recognizes the importance of spatial pattern will increase the likelihood of cedar recovery in northern Wisconsin.

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