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Forest Ecology and Management 111 (1998) 211–224

Forest Ecology  
and  
Management

# Local and regional variation in hemlock seedling establishment in forests of the upper Great Lakes region, USA

Thomas P. Rooney<sup>\*</sup>, Donald M. Waller

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

Received 12 February 1998; accepted 11 May 1998

## Abstract

Successful tree regeneration requires both successful seedling establishment and subsequent survival and growth sufficient to ensure recruitment. We examined patterns of initial seedling establishment in randomly selected stands of eastern hemlock (*Tsuga canadensis*) distributed across northern Wisconsin and eastern Upper Michigan. In 1990, we counted all hemlock seedlings (defined as 4–29 cm tall) and sampled substrate conditions in two 7×7 m quadrats of 142 hemlock and hemlock–hardwood stands. In 1996, we resampled 109 of these stands more intensively using six 7×7 m quadrats. In 1997, we also intensively surveyed which substrate-supported hemlock seedlings in three 50 m<sup>2</sup> replicate areas from each of five stands. In 1990, we found no hemlock seedlings at 64 of the 142 stands sampled, and 46% of the stands had more than 100 hemlock seedlings ha<sup>-1</sup> (mean density=480±90 ha<sup>-1</sup>). In contrast, only 14 (13%) of the 109 stands resampled in 1996 had no seedlings and 66% had over 100 seedlings ha<sup>-1</sup> (mean density=840±200 ha<sup>-1</sup>). These results suggest that seedling establishment is patchy, causing the estimated frequency of successful establishment to depend strongly on the area sampled. Seedling abundance within sites was correlated between years, suggesting that site history may in part account for the abundance of seedlings. Analysis of variance to mean ratios reveals that seedlings are indeed strongly clumped at the 7×7 m scale or smaller. Such clumping probably results from the tendency for hemlock seedlings to occur most frequently on particular substrates (i.e. decaying wood). Hemlock seedlings occur less frequently in stands with high basal area of sugar maple but do not decline in stands with greater hemlock basal area, suggesting that maple litter may restrict local opportunities for seedling establishment. Seedling densities do not vary among habitat-types, and no other stand or regional variable significantly affected hemlock seedling density. These results suggest that ground surveys are needed to assess hemlock seedling abundance, and that such surveys should be based on quadrats of at least 100 m<sup>2</sup>. Successful hemlock regeneration should capitalize on local patches of existing hemlock seedlings where interference by hardwoods is minimal. Even high initial seedling establishment, however, may not guarantee regeneration in areas where high deer densities preclude recruitment into larger size classes. © 1998 Elsevier Science B.V.

**Keywords:** *Tsuga canadensis*; Seedling establishment; Regional variation; Natural regeneration; Great Lakes states

## 1. Introduction

Along with white pine and sugar maple, eastern hemlock (*Tsuga canadensis*) dominated mesic and

<sup>\*</sup>Corresponding author. Tel.: +1-608-265-2191; fax: +1-608-262-7509; e-mail: tprooney@students.wisc.edu

wet mesic pre-settlement forests in northern Wisconsin and upper Michigan (Curtis, 1959; Pastor and Brouchart, 1990). The life cycle of eastern hemlock has been summarized by Curtis (1959) and Mladenoff and Stearns (1993). Canopy trees produce a large seed crop every 2–3 years and moderately sized seed crops in intervening years (Hough, 1960). Seeds require stratification, and germinate on moist substrates (Curtis, 1959). Seedlings are highly susceptible to desiccation and are most likely to become established on substrates which provide a continuous moisture supply, such as moss beds or well-decayed nurse logs (Goder, 1961). Small seedlings (4–29 cm tall) are most abundant on coarse woody debris (Goder, 1961; Waller et al., 1996), and occur somewhat more abundantly in areas with higher light levels (Waller et al., 1996).

Extensive logging in the late 19th and early 20th century reduced the hemlock component by over 99% in the region (Eckstein, 1980). While not important commercially, its maintenance and restoration in the landscape are warranted because of its importance for wildlife (Howe and Mossman, 1996; Wydeven and Hay, 1996) and biodiversity (Thompson, 1990; Mladenoff et al., 1993; Crow et al., 1994). Although suitable habitat for hemlock occurs in many areas of northern Wisconsin and upper Michigan (Kotar et al., 1988), few of these suitable habitats are presently occupied.

Even though shade-tolerant, hemlock can perpetuate itself once established (Rogers, 1978; Eckstein, 1980; Frelich et al., 1993), seedling abundance beneath closed canopies is sparse in the upper Midwest. This lack of regeneration dates back to the early 20th century. In a survey of reproduction in unlogged mixed hardwoods in northern Wisconsin, Maissurow (1941) reported that hemlock seedlings were completely absent in over 99% of the 1722 milacre (approx. 4 m<sup>2</sup>) plots surveyed. In a study conducted in the Ottawa National Forest, Graham (1941) noted extensive hemlock reproduction in 1893 and again in 1940, with few seedlings occurring during the intervening years. In a survey of three old-growth hemlock–northern hardwood stands, Stearns (1951) found hemlock seedlings in only 10% of the seventy-five 16 m<sup>2</sup> plots surveyed. In contrast, a regionally extensive study of 142 hemlock stands conducted in the early 1990s revealed that some seedlings 4–300 cm tall were pre-

sent in nearly 80% of all the 98 m<sup>2</sup> plots surveyed (Waller et al., 1996). Since earlier studies did not define the threshold size of seedlings used for enumeration and because of differences in plot size, these studies are not directly comparable.

The fact that hemlock seedlings are so sparse yet hemlock often occurs in uneven-aged stands (Frelich and Lorimer, 1991) presents something of an enigma. The lack of seedlings cannot be attributed to poor seed production or low seed viability; hemlock and hemlock–hardwood stands typically produce millions of hemlock seeds per hectare and seed viability ranges from 25% to 27% (Fowells, 1965; Eckstein, 1980). Several hypotheses have been put forth to explain why hemlock seedlings are sparse in the upper Midwest. Hemlock seedlings tend to be abundant after light surface fires (Pubanz, 1996) and may even colonize sites after stand-replacing fires (Miles and Smith, 1960; Eckstein, 1980). This observation led some authors (e.g. Maissurow, 1941) to conclude hemlock is fire-dependent. While hemlock may benefit from fire, it is not fire-obligate, as indicated by the establishment of seedlings and saplings beneath unburned, closed-canopy stands throughout northern Wisconsin and upper Michigan (Waller et al., 1996). Others hypothesize that the availability of suitable substrates (Goder, 1961; Pastor and Mladenoff, 1992; Mladenoff and Stearns, 1993) or habitats (Hix and Barnes, 1984; Kotar, 1996; Kotar et al., 1988) limit seedling establishment. Several authors have also suggested that high levels of deer browsing could limit hemlock regeneration (Anderson and Loucks, 1979; Frelich and Lorimer, 1985; Alvenson et al., 1988).

Over the past decade, we have conducted a geographically extensive survey of naturally established hemlock seedlings in hemlock and hemlock–hardwood forests in northern Wisconsin and the upper peninsula of Michigan (Alvenson et al., 1988; Waller et al., 1996; Alvenson and Waller, 1997; Waller and Alvenson, 1997; Rooney and Waller, in review). We sought to identify those biotic and abiotic factors which could be used to explain regional variation in hemlock seedling abundance. Our studies reveal that the abundance of white-tailed deer accounts for much of the regional variation in the abundance of seedlings 30–300 cm tall, but not in the abundance of smaller (4–29 cm) hemlock seedlings. In this study, we analyze variation in the abundance of these smaller hemlock

seedlings within and among mature hemlock and hemlock–hardwood stands. We pose the following questions:

1. How does seedling abundance vary within and among stands?
2. How are seedlings distributed spatially within stands? Are densities uniformly low, or are there local patches where seedlings are abundant?
3. On what substrate-types are seedlings most abundant?
4. To what extent is seedling abundance influenced by stand-level and regional variables, such as canopy composition, habitat-type, and physiographic region?

## 2. Methods

### 2.1. Study sites

In the summer of 1990 Waller et al. (1996) established 142 study plots at random locations within existing hemlock and hemlock–hardwood stands distributed across northern Wisconsin and the western Upper Peninsula of Michigan (Fig. 1). These plots were 14×21 m and comprised six 7×7 quadrats. We selected 118 of our sites from a list of known hemlock stands that were stratified by ownership. We used a stratified random sampling procedure to select stands from this list of hemlock (> 50% hemlock basal area) and hemlock component (20–50% hemlock basal

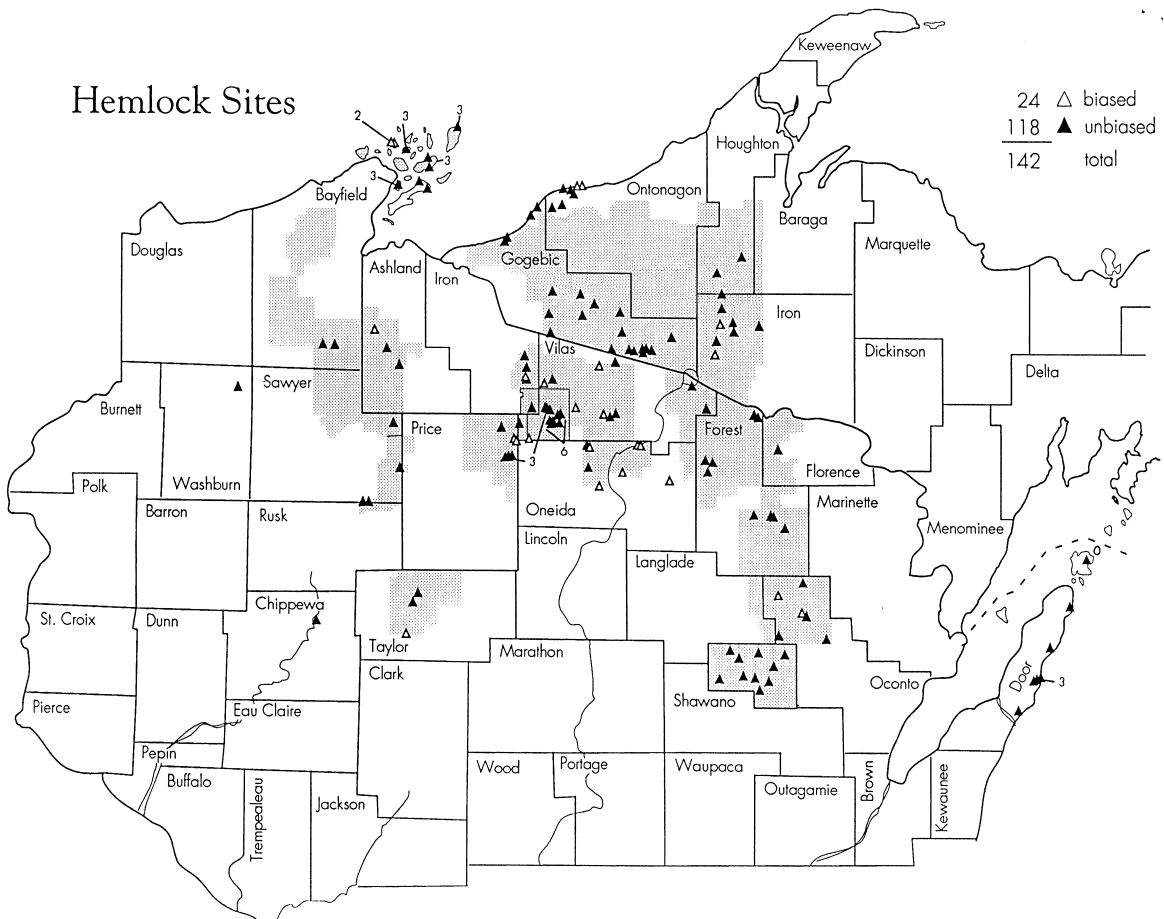


Fig. 1. Map of sampled study sites in northern Wisconsin and the western Upper Peninsula of Michigan.

area) stands provided by land management agencies. The list of stands covered a broad geographical area, and represented private lands, three national forests (Chequamegon, Nicolet, and Ottawa), two Indian reservations (Lac du Flambeau and Menominee), the Apostle Islands National Lakeshore, Porcupine Mountains Wilderness State Park, and Wisconsin state and county forest lands (additional details in Waller et al., 1996). An additional 24 sites were recommended to us by land managers on the basis abundant hemlock regeneration. These biased sites differed from the unbiased sites in the density of seedlings >30 cm tall, but were well within the range of natural variation for seedlings 4–29 cm tall. We, therefore, included these 24 sites in our analysis. We revisited as many of these sites as possible in 1996 ( $n=109$ ). We were able to relocate 77 of the plots established in 1990. At the 32 sites where we could not relocate our plot, we established a new plot as close as possible to where we thought our original plot was located.

## 2.2. Field methods

We examined a particular seedling size class rather than an age class for several reasons. First, mortality in plants is more often size-dependent than age-dependent, making size-based demographic studies more informative than those that are age-based (Harper, 1977; Caswell, 1989). Second, the relative importance of various biotic and abiotic factors affecting seedlings change as those seedlings grow larger. For example, Waller et al. (1996) report that white-tailed deer negatively affect hemlock seedlings >30 cm tall, but not smaller seedlings. Third, most sites had few seedlings that we did not feel justified in using the destructive sampling procedures that would be necessary for age determination. In 1996, we collected 25

hemlock seedlings between 10 and 100 cm tall from two sites where seedlings were abundant, and took them back to the lab. They were cross-sectioned and annual growth rings were counted. since seedling height should increase as a power function of age, we determined the least squares best fit regression line using:

$$\text{age} = (a)\text{height}^b$$

Regression of age against height was significant for hemlock seedlings (Fig. 2). When growing beneath a closed canopy, seedlings 4–9 cm are <2-years old, and 10–29 cm seedlings are between 2- and 11-years old.

All sites were visited in 1990, and 109 sites were revisited and resampled in 1996. In 1990, two of the six 7×7 quadrats were randomly selected, and all hemlocks 4–29 cm were counted and measured within these. In addition to counting hemlock seedlings, we identified the substrate upon which each seedling was growing: forest floor, raised mound (e.g. tip-up mound), or decaying wood (e.g. rotting log or stump). We also recorded basal area and species composition of all trees >2 cm dbh inside the 14×21 m plots. When we revisited sites in 1996, we modified our field protocol. Our first change involved counting hemlock seedlings in all six quadrats as opposed to only two, because increasing the area sampled increases the accuracy of the observation (Sokal and Rohlf, 1981). We also used Kotar et al.'s (1988) floristic-based habitat classification system to habitat-type our sites and characterize the relative nutrient and moisture availability of our sites (Table 1).

In 1997, we performed additional field surveys to determine the relative abundances of each substrate-type within hemlock stands. From our original 142 sites, we selected five representative sites for analysis. At each of the five sites, we established three replicate

Table 1

The moisture and nutrient regime for habitat-types which support hemlock and hemlock–hardwood stands in northern Wisconsin and western upper Michigan, based on Kotar et al. (1988)

Habitat-type	Soil moisture regime	Soil nutrient regime
<i>Tsuga–Maianthemum–Coptis</i>	Mesic to wet-mesic	Poor to medium
<i>Acer–Tsuga–Maianthemum</i>	Mesic	Medium
<i>Acer–Fagus–Dryopteris</i>	Mesic	Medium to rich
<i>Acer–Tsuga–Dryopteris</i>	Mesic	Medium to rich
<i>Acer–Viola–Osmorhiza</i>	Mesic	Rich to very rich

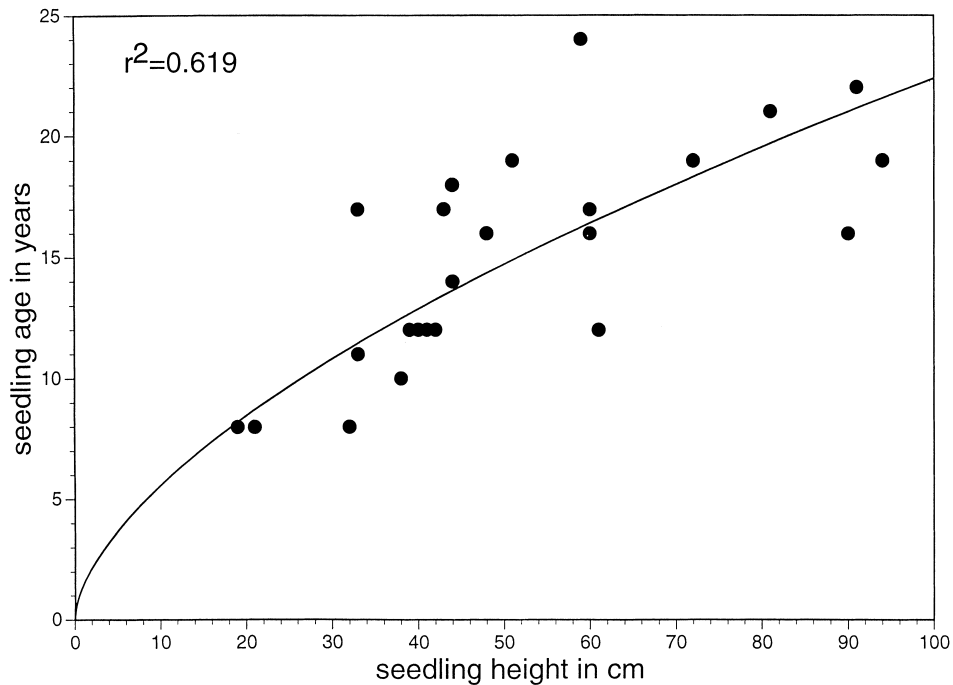


Fig. 2. Age–height relationship,  $Y=(1.39) X^{0.604}$ ;  $r^2=0.619$ ,  $p<0.001$ .

20×20 m plots, each 20–50 m apart. We determined the basal area of hemlock in each plot. Centered in each plot, we ran five 1×10 m belt transects, each separated by 1 m. We sampled the dominant substrate-type in 0.25 m<sup>2</sup> quadrats along one side of each transect, for a total of 40 quadrats per transect. To avoid confusion with the 7×7 quadrats, hereafter, we refer to these 0.25 m<sup>2</sup> quadrats as ‘micro-quadrats.’ In each micro-quadrat we counted all hemlock seedlings 4–9 cm tall and classified the substrate as either rotting wood, forest floor, or tip-up mound.

### 2.3. Data analysis

To determine the extent of hemlock seedling abundance, we counted the total number of hemlock seedlings 4–29 cm tall present in sampled quadrats in both 1990 and 1996. We converted the number of seedlings present in our quadrats (98 m<sup>2</sup> in 1990 and 294 m<sup>2</sup> in 1996) to the number of seedlings present per hectare. We also calculated a Pearson correlation coefficient to determine if the number of seedlings present in 1990 predicted the number present in 1996. We were unable to relocate 30% of our 1990 plots during the 1996 field

season, so for this analysis we only included those sites we did relocate ( $n=77$ ). Seedling abundances were naturally log-transformed prior to analysis to meet assumptions of normality.

We determined the spatial distribution of hemlock seedlings in each plot by counting the number of seedlings in each quadrat. We used an index of dispersion (Krebs, 1989) to determine if stems showed a uniform, random, or clumped-spatial pattern. This index takes the form:

$$I = (s^2/x)$$

where  $I$  is the index of dispersion,  $x$  is the mean number of seedlings per quadrat in a plot, and  $s^2$  is the variance. When  $I$  does not significantly differ from 1.0, the spatial pattern is random. If  $I$  is significantly less than 1, the pattern is uniform; if it is greater than 1, the pattern is clumped. To determine if  $I$  is significant, a  $\chi^2$ -test is used, where:

$$\chi^2 = I(n - 1)$$

where  $n$  is the sample size (total number of quadrats examined), and  $n-1$  is the degree of freedom (Krebs, 1989). We replicated this index of dispersion test

Table 2

Natural subdivisions of the northern highland deciduous coniferous forest and the Lake Michigan shoreland: Northern deciduous and conifer forest of Wisconsin, from Hole and Germain (1994)

Subdivision	Landform	Soils
Sugar maple–hemlock–yellow birch–white pine	Acidic outwash and till, moraines, drumlins, undulating to rolling landscape	Podzolized stony loams
Sugar maple–basswood–yellow birch–hemlock	Windblown silt cover, level to undulating	Slowly permeable silt loams
Sugar maple–basswood–yellow birch	Outwash sands, undulating	Podzolized-silt loams
Beech–sugar maple–hemlock	Calcareous till, undulating to rolling	Podzolized loams

across all quadrats in our study, and analyzed spatial patterns using a  $G$ -test for heterogeneity among plots using the  $\chi^2$  approximation to test statistical significance (Sokal and Rohlf, 1981).

Next, we examined how stand-level variables influence seedling abundance. Using 1990 data, we determined if hemlock seedlings showed positive or negative associations with particular substrates (decaying wood, raised mound, or forest floor) by performing a likelihood ratio test ( $G$ -test for goodness of fit). Our null hypothesis was that hemlock seedlings were equally distributed among three substrates. For 1990 data, seedlings were redefined as individuals 6–25 cm tall, because field workers placed hemlock stems into this size class category for substrate analysis. We used data from the 1997 field season to further examine the role of substrates in hemlock seedling establishment. At each of our five sites, we pooled data from three replicates, and determined the expected number of seedlings per substrate based on the relative abundance of each substrate. We performed a  $G$ -test for heterogeneity to determine the affinities of seedlings for each substrate within and between sites.

Using 1996 data, we also examined how hemlock and sugar maple basal area affected the abundance of hemlock seedlings using univariate regression analysis. To assess the influence of habitat-type (Kotar et al., 1988) on hemlock seedling abundance, we used one-way ANOVA with abundances naturally log-transformed to meet the assumption of homogeneous variances.

Hemlock is a component of Curtis' (1959) northern mesic forest-type of northern Wisconsin. There exist

natural divisions in the northern mesic forest where soils, bedrock geology, and landforms differ systematically. We examined 1996 hemlock seedling abundance in response to these natural divisions using Hole and Germain's (1994) Natural Divisions of Wisconsin. Hole and Germain recognized four subdivisions of which hemlock is a component (Table 2). We used one-way ANOVA to test for differences in regeneration abundance among the four subdivisions in which our stands were located, and a nested ANOVA (habitat-type within subdivision) to determine if habitat-type might be obscuring a larger pattern of seedling abundance. Only 63 of our study sites examined in 1996 occurred within the coverage area of Hole and Germain's (1994) map, so a subset of our sites was used for this analysis.

All data were analyzed using SYSTAT version 5.2.1.

### 3. Results

#### 3.1. Variation in seedling abundance among sites

In 1990, we recorded a total of 2363 hemlock seedling between 4 and 29 cm tall at our 142 sites. Sixty-four sites (44%) had no seedlings present, 8% had <100 seedlings  $\text{ha}^{-1}$ , and 48% had >100 seedlings  $\text{ha}^{-1}$ . Seedling densities ranged from 0 to 5000 seedlings  $\text{ha}^{-1}$ , and the mean density was  $480 \pm 90$  seedlings  $\text{ha}^{-1}$ . In 1996, we sampled an area three times larger than we did in 1990, but examined fewer sites. We recorded a total of 2699 hemlock seedlings between 4 and 29 cm tall among 109 sites. Fourteen

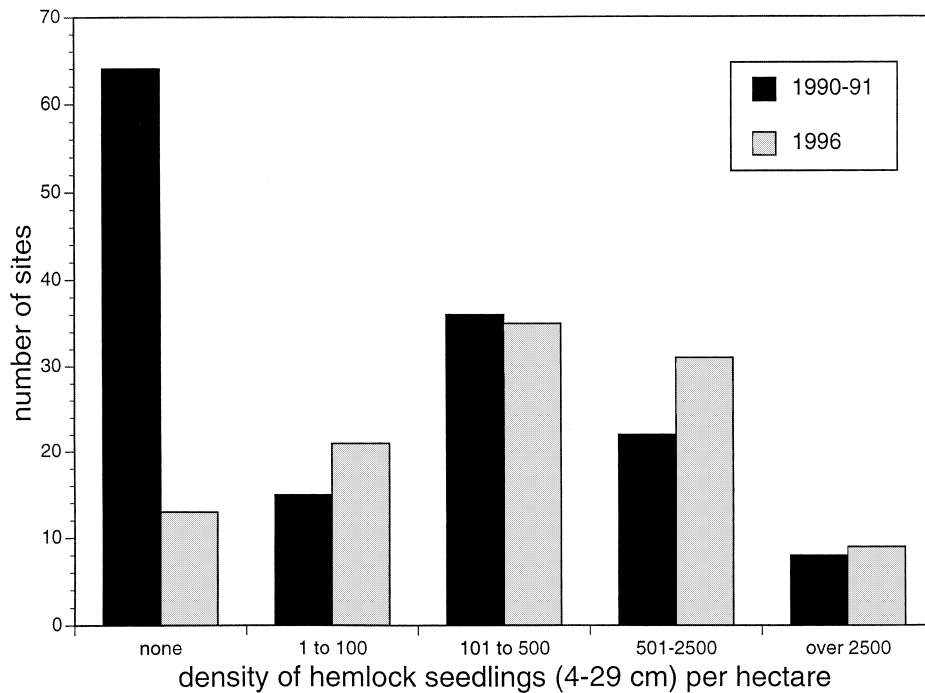


Fig. 3. Frequency histogram showing the number of sites containing various densities of hemlock seedlings in 1990 when two quadrats were surveyed, and in 1996, when six quadrates were surveyed.

sites (13%) had no seedling present, 21% had <100 seedlings  $\text{ha}^{-1}$ , and 66% had >100 stems  $\text{ha}^{-1}$ . Seedling density ranged from 0 to 20 400 stems  $\text{ha}^{-1}$ , and the mean density of hemlock seedlings across our 109 sites is  $840 \pm 200$  SE stems  $\text{ha}^{-1}$  (Fig. 3). The number of seedlings within plots in 1990 and 1996 was positively correlated (Pearson  $r=0.51$ ,  $\text{df}=75$ ,  $P<0.001$ ). Since there was 6-year interval between our observations and seedlings remain in the 4–29 cm size class for approximately 11 years, it is likely that some of the seedlings observed in 1990 were observed again in 1996. Others entered into the size class as new seedlings, whereas others left the size class and entered a larger one.

### 3.2. Spatial distribution of seedlings within sites

Within sites, seedlings are not distributed uniformly. Analysis of the spatial dispersion of seedlings within  $14 \times 21 \text{ m}^2$  plots reveals a strong tendency for seedlings to be clumped at  $7 \times 7 \text{ m}^2$  scale. Heterogeneity among sites is also significant, indicating that

Table 3

Index of dispersion test, replicated across each site ( $n=109$ ), for the spatial distribution of hemlock seedlings (4–29 cm tall) in 1996

Test	df	<i>I</i>	$\chi^2$
Pooled	5	348.4	1741.80 <sup>***</sup>
Heterogeneity	540	1.4	753.23 <sup>*</sup>
Total	545	4.5	2477.03 <sup>***</sup>

*I* scores significantly greater than 1 indicate a clumped distribution. <sup>\*</sup> $P<0.05$ , <sup>\*\*\*</sup> $P<0.001$

clumping was more extreme in some plots than others (Table 3). Additionally, as seedlings become more abundant, they also become more highly clumped (Fig. 4).

### 3.3. Substrate affinities

Hemlock seedlings are not evenly distributed among substrates. In 1990–91, there were significantly more seedlings on decaying wood and significantly less on raised mounds than would be expected if

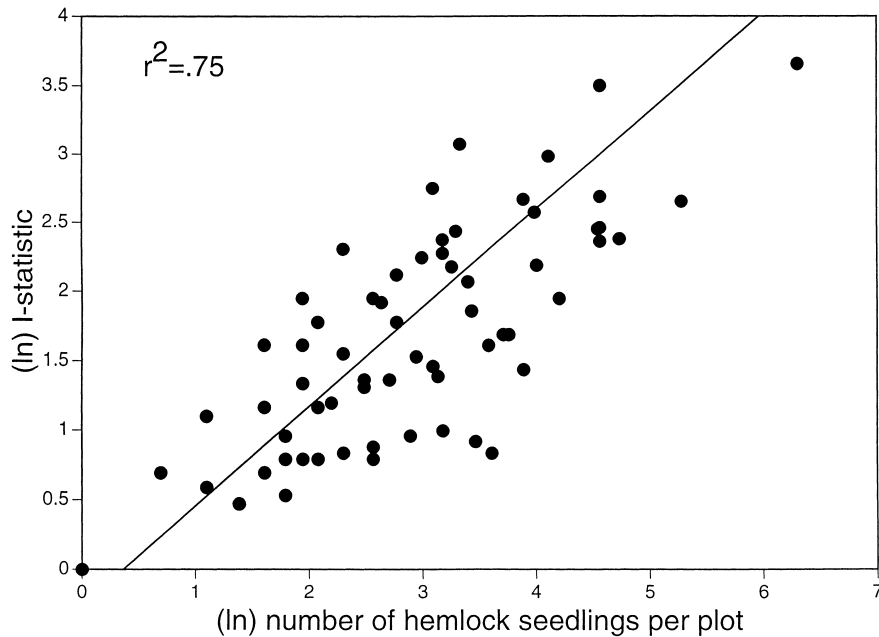


Fig. 4. Spatial clumping as measured by the index of dispersion ( $I$ ) as a function of hemlock seedlings per plot in 1996. Axes are natural log-transformed to meet assumptions of normality.  $r^2=0.75$ ,  $P<0.001$ .

seedlings were equally distributed among rotting woods, raised mounds, and the forest floor ( $G^2=152.21$ ,  $df=2$ ,  $P<0.001$ ). When the experiment was refined in 1997 in which the relative abundances of substrates were used to generate expected numbers of hemlock seedlings, observed seedlings are significantly positively associated with rotting wood and negatively associated with both raised mounds and the forest floor (Fig. 5; Table 4). The lack of heterogeneity among sites for seedling abundance on rotting wood indicates that rotting wood as an important factor promoting seedling establishment across all sites. In contrast, there is significant heterogeneity

among sites for the number of seedlings on the forest floor.

### 3.4. Stand and physiographic influences

Analyses at the stand level reveal the following patterns. When stratified by habitat-type, seedling abundance ranges from a mean density of  $1400 \pm 400$  SE stems  $ha^{-1}$  in *Tsuga-Maianthemum-Coptis* sites,  $300 \pm 100$  SE stems  $ha^{-1}$  in *Acer-Viola-Ozmorhiza* sites. However, differences in the abundance of hemlock seedlings across site classifications are not statistically significant (one-way ANOVA,

Table 4

The affinity of hemlock (4–9 cm) for rotting wood, raised mound, and forest floor substrates, as determined by the  $G$ -test for heterogeneity. Heterogeneity was not determined for seedlings on raised mound substrate due to excessive missing cells

Substrate association		Rotting wood (+)	Raised mound (–)	Forest floor (–)
Test	df			
Pooled	1	36.92***	5.33*	20.51***
Heterogeneity	4	3.70	—	11.17*
Total	5	40.62***	—	31.68***

\*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$ .

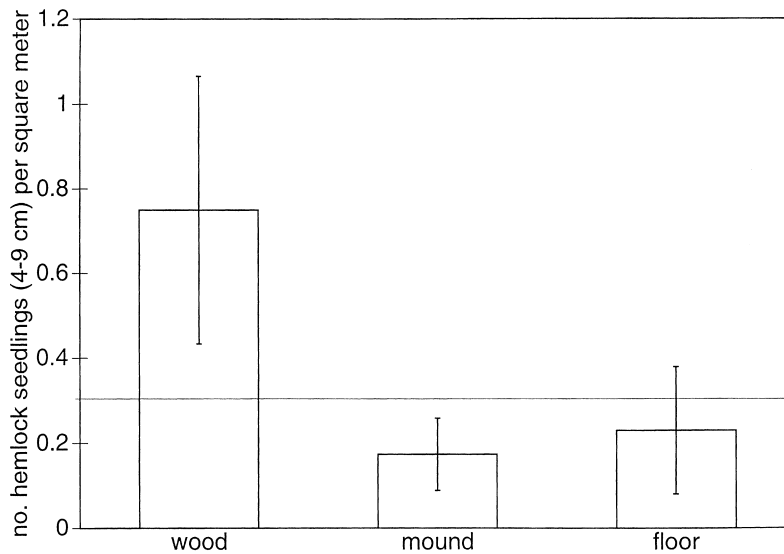


Fig. 5. The density of hemlock seedlings (4–9 cm) m<sup>-2</sup> on wood, mound, and forest floor substrates. Data from micro-quadrat study during 1997 field season. Error bars represent 1 SE, and the horizontal line at 0.3 indicates the expected density of seedlings for each substrate.

$F_{4,104}=1.38$ ,  $P=0.25$ ). In contrast, regression analysis reveals that seedling abundance declines somewhat as sugar maple basal area increases ( $F_{1, 76}=6.49$ ,  $r^2=0.08$ ,  $P=0.01$ ). Hemlock basal area had no statistically significant effect on hemlock seedling abundance. Our analysis of hemlock seedling abundance at the regional scale revealed no statistically significant patterns. The abundance of hemlock seedlings did not differ among natural regions (one-way ANOVA,  $F_{3,59}=0.72$ ,  $P<0.5$ ), even when variation due to habitat-type was controlled for (nested ANOVA,  $F_{3,16,43}=1.04$ ,  $P<0.4$ ).

#### 4. Discussion

##### 4.1. Variation in seedling abundance among sites

Hemlock seedling abundance varies widely within and among stands and over time throughout the region. In contrast to earlier studies, we found most sites had at least some seedlings present, and few had >2500 seedlings ha<sup>-1</sup> in either 1990 or 1996. In her 1993 field study of hemlock regeneration in the Nicolet National Forest, Nelson (1997) reported similar trends. Hemlock seedlings <30 cm tall were present in 93% of all sites she examined using two 7×7 quad-

rates. Seedling density was much higher than we report; it ranged from 0 to 70 000 seedlings ha<sup>-1</sup>, but only 7% of her 45 sites had >5000 seedlings ha<sup>-1</sup>. Both her study and ours indicate hemlock seedling abundance can be characterized as low but highly variable.

The interpretation of the positive correlation between seedling abundance in plots between 1990 and 1996 is not straightforward. The positive correlation could be due to high survivorship and low turnover between years. Alternatively, some sites may be consistently good or bad sites for seedling establishment, at least over this 6-year time period.

##### 4.2. Spatial distribution of seedlings within sites

Within stands, hemlock seedlings are patchy as revealed by significant clumping at the 7×7 m<sup>2</sup> scale. Since our 7×7 m<sup>2</sup> quadrats represent artificial boundaries and are internally heterogeneous with respect to light and substrates, the clumped seedlings we report here may be clumped at even finer scales than we detected. The typically clumped distribution of hemlock seedlings may account in part for some historic reports of poor hemlock regeneration. As quadrat size declines, they will be empty more frequently, as demonstrated by previous studies (Maissurow, 1941;

Stearns, 1951). Here, for example, we report that hemlock was absent from only 13% of our 294 m<sup>2</sup> plots, but if we treated each of our 7×7 quadrats as a separate plot seedlings would be absent from 51.3% of all plots. In 1990, hemlock was absent in 43.9% of our plots when only 98 m<sup>2</sup> was surveyed. When we plot the percentage of plots occupied by hemlock seedlings against the natural log of plot size using previously published data in Maissurow (1941) and Stearns (1951), and the percent absence values reported above, we find that plot size had a significant positive relationship on the probability of detecting hemlock regeneration, as expected ( $Y=0.21(\ln)PLOTSIZE$ ;  $df=3$ ;  $r^2=0.95$ ,  $P<0.01$ ). Thus, historic accounts of poor hemlock regeneration may be an artifact of a small quadrat size.

Clumping is a widely observed but poorly understood phenomenon in plant populations. Bergelson (1990) reports that the spatial clumping of common groundsel (*Senecio vulgaris*), an old-field perennial, is due to its spatially clumped regeneration niche: dead grass. The correlation between high hemlock seedling densities and greater clumping likewise could have been generated by a spatially clumped regeneration niche (sensu Grubb, 1977). Alternatively, Pielou (1977) shows that random deaths in a spatially clumped population reduces the index of dispersion as a linear function of the death rate, suggesting that sparser seedling densities should show less clumping regardless of substrate specificity. These two mechanisms are not necessarily mutually exclusive when we consider that seedlings will germinate on most substrates, but have substrate-specific establishment probabilities.

#### 4.3. Substrate affinities

Hemlock seedlings do not establish randomly with respect to substrate-type. Other investigators have reported that eastern hemlock seedlings occur most abundantly on decaying wood (Goder, 1961; Mladenoff and Stearns, 1993; Waller et al., 1996). In our analysis of the 1997 data, we adjusted seedling abundance to expected frequencies based on relative abundance of substrates, and found that there are more seedlings than would be expected on rotting wood, but less seedlings than would be expected on both the forest floor and on tip-up mounds. Thus, the

distribution of decaying wood in stands may help to account for the clumped distribution of regeneration. However, the presence of decaying wood does not automatically translate to the presence of hemlock regeneration. At some sites, decayed wood occupied 10–20% of the plot, yet they contained no regeneration. Rotting wood provides the most constant supply of moisture on the forest floor and alleviates competition with herbs and mosses, both of which could favor the initial establishment of hemlock seedlings (Harmon and Franklin, 1989; Mladenoff and Stearns, 1993). However, seedlings which establish on rotting wood may be less likely to form mycorrhizal connections than those that establish on the forest floor. In their study of western hemlock (*Tsuga heterophylla*), Christy et al. (1982) found that 71% of the seedlings established on the forest floor established mycorrhizal connections in the first year, compared to 20% of seedlings established on decayed logs. While the dependency of eastern hemlock on mycorrhizae is not known, western hemlock can survive up to 2 years without forming mycorrhizae, although seedling growth is greatly reduced (Christy et al., 1982). We can conclude that the presence of decayed wood in stands is important in the initial establishment of hemlock seedlings, but that their persistence may depend on making root contact with the forest floor.

#### 4.4. Stand and physiographic influences

Few of the stand-level characteristics we examined predict seedling abundance very well. For example, the habitat typing system of Kotar et al. (1988) appears to indicate where hemlock will and will not occur (Kotar, 1996), but was not a good predictor of seedling abundance in the stands we surveyed. The habitat-typing system attempts to identify areas where environmental variation is uniform enough such that similar plant communities will develop. However, soil properties show variation at smaller spatial scales than the habitat-type (Burrough, 1983). At some small spatial scales, there may be more environmental variation within individual sites than among sites of the same or different habitat-types. Since regeneration density is spatially clumped, it is likely that they are responding to variation in the environment at a finer scale than the habitat-type.

To our surprise, regeneration is uncorrelated with the basal area of mature hemlocks. The absence of such a pattern suggests three possibilities. First, mortality of individuals between the seed and established seedling stage is high. While seeds germinate in high numbers beneath a closed canopy, few survive more than a few weeks. Mladenoff (1990) did not find any hemlock seeds in the seed bank of a hemlock–hardwood stand in Wisconsin, indicating that seeds are either consumed by seed predators before they germinate, or newly germinated seedlings are killed by seedling predators, moisture stress, damping-off fungi, or some other agent (Eckstein, 1980; Ostfeld and Canham, 1993). Second, the influence of hemlock trees outside of the 14×21 m<sup>2</sup> plot was not determined. A large amount of seed could have entered some plots from dominant or co-dominant hemlock trees 5–10 m outside of plots (Ribbens et al., 1994), thereby obscuring the relationship between hemlock basal area and seedling abundance. Third, the stands we worked in had at a minimum 20% hemlock basal area. If we worked in stands with less or no hemlock, the correlation between basal area and seedlings abundance may have become significant.

The only stand-level property that significantly affected hemlock seedling establishment was sugar maple basal area, which depressed hemlock regeneration. In old-growth hemlock–northern hardwood forest, mature hemlock and sugar maple segregate to form nearly pure stands (Pastor and Brouschart, 1990; Frelich et al., 1993). Such aggregation patterns may reflect the negative effects each species has on the seedbed condition of the other (Mladenoff, 1987; Mladenoff and Stearns, 1993; Frelich et al., 1993). Increases in sugar maple basal area result in increased deciduous leaf litter deposition, negatively affecting hemlock seedbed conditions.

We detected no regional trends in the abundance of regeneration. Like habitat-type, Wisconsin's natural divisions indicate where hemlock regeneration will and will not occur. But there are no differences among regions, even when habitat-type was nested within regions to reduce residual variation. Nelson (1997) examined the effect of climate (temperature and precipitation) on hemlock seedling abundance, and found no effect. She found seedling densities to differ non-randomly among ecological land-types (tens of thousands of hectares), with the highest density of seed-

lings occurring on a landform characterized by well-drained sandy soils and swamp conifers. However, only three sites were sampled on this landform, and because data were analyzed using a  $\chi^2$ -test, the result may be an artifact of a single outlier site.

#### 4.5. Factors influencing hemlock seedling establishment

Hemlock seedlings are highly clumped, non-randomly associated with particular substrates, lack a correlation with hemlock basal area, and are not affected by different habitat-types or natural regions. They are small seeded, and thus, lack substantial endosperm reserves. All of these observations strongly suggest that variation in hemlock seedling establishment can best be attributed to its specific regeneration niche (Grubb, 1977), and less so to stand-level or larger-scale factors. Of course, natural division, habitat-type, and distance to seed source will determine if hemlock seedlings could occur, but seedling densities reflect the abundance and quality of the regeneration niche.

Beneath closed canopy hemlock and hemlock–hardwood forests, eastern hemlock seedlings reach their highest density on rotting wood. Similar results have been reported for western hemlock (Christy and Mack, 1984; Christy et al., 1982; Harmon and Franklin, 1989). Gray and Spies (1997) reported that western hemlock seedling establishment was highest on rotting wood and lower on mineral soil and leaf litter beneath closed canopy forest and small gaps. However, as gap size increased, seedling establishment on leaf litter and soil was not significantly different than establishment on rotting wood. Thus, the importance of rotting wood for hemlock seedlings appears context-dependent. The importance of particular substrates may also be important in different habitat-types. Hemlock seedlings might have higher densities on the forest floor in nutrient-poor *Tsuga-Maianthemum-Coptis* habitat-types where competition from herbs and other tree seedlings is minimal than in other more nutrient-rich habitat-types, where elevated rotted logs may alleviate competition. And while rotting wood may be eastern hemlock's regeneration niche in late-successional forest stands, other factors are probably important in earlier stages of succession. On one site, hemlock seedlings reached densities in

excess of 100 000 seeds ha<sup>-1</sup> following a prescribed burn which exposed mineral soil (Pubanz, 1996).

## 5. Conclusion

Hemlock seedling establishment appears to be governed predominantly by small-scale and local processes (see also Gray and Spies, 1997). Seedlings 4–29 cm show spatial aggregation, and seedlings 4–9 cm are most abundant on decayed wood and least abundant on the forest floor and tip-up mounds. Factors that varied among stands or across the region (except sugar maple basal area) appeared uncorrelated with hemlock regeneration.

From these observations, we offer the following management recommendations:

1. Since current site classification techniques (ECOMAP, 1993; Kotar, 1996; Diaz and Bell, 1997; Kimmins, 1997) do not provide a good indicator of how much regeneration will be present at a given site, site-specific surveys will need to be conducted to determine the extent of hemlock regeneration in stands. We expect that surveys may need to be completed for other species with very specific seedling establishment requirements.
2. Hemlock regeneration surveys should employ quadrats that are at least 100 m<sup>2</sup> in order to accurately detect seedling presence or absence.
3. Silvicultural operations designed to naturally regenerate hemlock should take the spatial distribution of natural seedlings into account. Eckstein (1980) suggests successful hemlock regeneration using even-aged silvicultural systems (including shelterwood) depends on the presence of >75 000 seedlings ha<sup>-1</sup>. Seedlings do not reach these densities, even after sites are shelterwood-cut and subsequently disk-scarified (Strong, 1996) or burned (Pubanz, 1996) to promote seedlings establishment. In most unmanaged stands, hemlock seedling abundance is simply sparse. Since hemlock has greater wildlife and biodiversity values than commercial value, silvicultural manipulations need not be heavy handed. Single-tree and group selection methods which take advantage of existing patches of seedlings will probably be more successful than treatments that ignore such patches.

Since white-tailed deer can eliminate seedlings >30 cm tall, seedling establishment does not readily translate to hemlock regeneration.

4. The occurrence and retention of coarse woody debris within uneven-aged stands appears to be important to ensure hemlock seedling establishment in future decades and centuries (see Tyrell and Crow, 1994). The north-facing side of large, newly-fallen logs contains a small moist microclimate extending 15 cm from the log which is favorable for hemlock seedling (Gray and Spies, 1997). As the log decays, it provides a suitable substrate for seedling establishment (Christy et al., 1982).

## Acknowledgements

We thank D. Reiter, P. Huff, and L. Warwoniwitz for facilitating access to many study sites, and Wis. Dept. of Natural Resources personnel for suggesting particular study sites. S. Solheim assisted with the field work, and K. Borgmann assisted with data entry. A. Bersch, J. Goodburn, and an anonymous reviewer provided helpful comments on an early draft of this paper. The U.W. Trout Lake Biological Station provided housing during field work. This study was financially supported by USDA Grant #93-00648 to DMW.

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