Current and Predicted Long-term Effects of Deer Browsing in Hemlock Forests in Michigan, USA

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ABSTRACT

Remnants of virgin hemlock Tsuga canadensis (L.) Carr. forest in the Porcupine Mountains, Michigan, USA, have experienced inadequate hemlock regeneration lasting several decades. White-tailed deer Odocoileus virginianus Zimmermann browsing seems to be the major cause of the observed decline of hemlock regeneration, rather than poor seedbed conditions or changing climate. In some areas, significant changes in the size-structure of the forest have already occurred, with a shift of dominance from hemlock to sugar maple Acer saccharum Marsh. taking place. A simulation of forest development is used to predict the changes in forest structure that will occur if no action is taken to control browsing. From this simulation it is estimated that in less than 150 years, hemlock will become only a minor component of the forest over large areas where it is currently the major dominant.

INTRODUCTION

Although mixed conifer-hardwood forests cover large areas of north-central and northeastern United States and adjacent Canada, forests of this type which remain in primeval condition exist only as a few isolated remnants. The most extensive of these remnants is within the Porcupine Mountains Wilderness State Park, Michigan (Braun, 1950). Unfortunately, the preservation of this area of mixed sugar maple Acer
saccharum Marsh. and hemlock Tsuga canadensis (L.) Carr. forest is problematic at the present time due to a lack of hemlock seedling and sapling recruitment in many areas.

Many of the hemlock stands in this region exhibit a diameter distribution (size-class versus frequency distribution) that is unimodal and in some cases bell-shaped. This type of diameter distribution is commonly considered to be demographically unbalanced, as a result of past disturbance to the stand. In contrast, a balanced diameter distribution for shade-tolerant species is usually descending monotonic in form with small trees most numerous (de Liocourt, 1898; Meyer and Stevenson, 1943; Hett and Loucks, 1976).

Several studies have shown that white-tailed deer Odocoileus virginianus Zimmermann browsing has a negative impact on forest regeneration, especially of hemlock (Graham, 1954; Stoeckler et al., 1957; Beals et al., 1960; Anderson & Loucks, 1979). White-tailed deer tend to yard up in hemlock stands during the winter because not only is hemlock foliage one of their preferred foods, but the evergreen canopy also intercepts snowfall and reduces windspeeds (Dahlberg & Guettinger, 1956). In addition, once browsed, hemlock seedlings are not able to resprout vigorously as are browsed seedlings of sugar maple, so that sugar maple reproduction is favoured in browsed areas (Anderson & Loucks, 1979). The result of overbrowsing by deer in mixed sugar maple-hemlock forests may be to alter overstorey species composition through the gradual removal of hemlock. Hemlock is otherwise capable of developing an all-aged population structure and maintaining itself indefinitely in the forests of this region (Hett & Loucks, 1976).

Deer populations in Upper Michigan are generally believed to have been quite low prior to logging operations which began about 1880, as well as during the following 40 years when extensive logging-slash fires greatly reduced available habitat. About 1920 fire control began to become effective, resulting in large areas of young hardwood forest becoming established and leading to an irruption in the deer population which peaked in 1940 (Leopold, 1943; Graham, 1954). The deer population has remained fairly high since then (Bartlett, 1950; McKee, 1982).

In addition to deer browsing there are other factors that influence the establishment of hemlock seedlings in the region which must be separated from the effects of white-tailed deer. It is well known that hemlock seedlings germinate and grow well on rotten logs (Goder, 1955) and that thick leaf litter inhibits their establishment (Davis & Hart, 1961).
Observations in hemlock stands in this region indicate that several methods of reducing litter thickness may stimulate hemlock seedling establishment. These include raking, light surface fires, and scarification (Eckstein, 1980). It has also been mentioned by some researchers that recent climatic events could prevent the successful establishment of hemlock seedlings due to summer droughts (Stearns, 1949). Hemlock seedlings require consistently high surface moisture during the first few years for survival. Thus, not all ecologists are in agreement that the scarcity of hemlock seedlings is due primarily to deer browsing (Eckstein, 1980).

Few studies dealing with the effects of browsing animals upon the forest have attempted to look at browsing in the context of long-term (> 100 year) changes in forest structure. The goal of this paper is to examine these long-term effects in the Porcupine Mountains Wilderness State Park with three main objectives in mind. The first is to estimate the current severity of deer browsing in the virgin forest and whether or not it is severe enough to prevent hemlock reproduction in some areas. The second is to determine whether or not deer browsing could be responsible for the observed unbalanced size-structure of the forest, a process that would take a minimum of several decades. The third objective is to predict the rate at which hemlock forest will be converted to sugar maple if the current low level of hemlock recruitment continues.

STUDY AREA

Porcupine Mountains Wilderness State Park is located at the western edge of the State of Michigan's Upper Peninsula (46°45' N, 89°45' E) along the south shore of Lake Superior. Forests in this area are part of the Superior Upland Section of the Hemlock-White Pine-Northern Hardwood Region of Braun (1950). Dominant tree species are hemlock and sugar maple, the former being the major dominant along the Lake Superior shore while the latter is the major dominant in upland forests a few km from the lake. Lesser amounts of yellow birch *Betula alleghaniensis* Britt., red maple *Acer rubrum* L. and basswood *Tilia americana* L. occur throughout the area. All other tree species are of local or sporadic occurrence. The study was confined to a large contiguous block of virgin forest of about 14500 ha which escaped any kind of logging.
Elevations range from 182 m on the surface of Lake Superior to about 600 m at 5 km south of the shore. Slopes in all of the study areas are gentle (5–15%) and mostly north in aspect. Soils are deep (> 1 m) and are of sandy loam, loam or silt loam texture.

The climate of the area is humid continental with annual precipitation averaging 81 cm. Summers are short and cool (mean July temperature 19°C). Winters are long and cold (mean January temperature −7°C). Large amounts of snow fall due to the effect of Lake Superior, especially inland where moist air that has blown over the lake is subjected to orographic uplift. The ground is snow-covered from the end of November until mid-April. Annual snowfall is about 2 m near the lake and up to 6 m inland (Eichenlaub, 1979). This heavy snowfall inland is an important factor related to deer browsing in winter. White-tailed deer have difficulty moving about in snow more than 0.6 m deep (Bartlett, 1950), so that movement of deer is hindered in the uplands during the winter. Deer therefore tend to congregate on a strip about 2–4 km wide along the Lake Superior shore and it is here that browsing is most severe. It is estimated that deer populations during the winter are about 2 km⁻² on the inland section and 10 km⁻² on the lakeshore section of the park (E. Harger, pers. comm.).

METHODS

Field methods

During the summer of 1982 three study areas were randomly located in the hemlock-dominated forest along Lake Superior, and three additional study areas were randomly located in the mixed sugar maple-hemlock forest in the interior. Within each study area a random 0.5 ha plot was selected for characterization of the size structure of the forest. On each plot the diameter of all stems > 2.5 cm dbh (diameter at 1.4 m) was measured and mapped on a coordinate grid system. All stems at least 1.4 m high but less than 2.5 cm dbh were tallied. Species and crown class of all trees > 1.4 m in height were noted. Since hemlock reproduction is of importance here, a special count of all hemlocks < 1.4 m but > 0.3 m in height was made on each plot in order to estimate the abundance of young hemlock reproduction. Hemlock seedlings < 1.4 m in height appear to have an average age of 30 years or less (Frellich, unpublished data). To use
hemlocks >1.4 m in height as an indication of abundance of reproduction would run the risk of including individuals that were established prior to the irruption of deer populations in the area and would not tell us whether or not deer are the cause of the decline in establishment of hemlock seedlings. At each of seven random points on each plot the nearest small (2.5–10.0 cm dbh), medium (10.1–35.0 cm dbh) and large (> 35.1 cm dbh) tree was cored for determination of age and growth rates. The location of the root crown of all fallen trees on the forest floor was mapped and the diameter and length of the associated log was noted as well as the direction of fall. Thickness of the L, F and H layers of the litter was also measured at 15 randomly located points on each plot. Canopy profiles were obtained on each plot by randomly selecting a 10.1 m wide strip that runs the length of the plot (70.7 m). On this strip the height to the base of the crown, to the widest part of the crown and to the top of each tree > 5.0 cm dbh was measured with a clinometer. The crown radius was also measured in the cardinal compass directions for each tree.

Finally, to estimate the current effects of deer browsing, ten circular 10 m² subplots were randomly located within each of the six large plots. On each of these subplots all available browse was tallied by species and by severity of damage. Browse is defined as woody stems between 0.3 and 2.1 m in height, since this is the range of heights accessible to deer (Bartlett, 1950; Beals et al., 1960). Severity of browsing on each available stem of browse was recorded as one of six categories according to the proportion of shoots which had been nipped off. These browsing categories are: none (0%), light (1–25%), moderately light (26–50%), moderately heavy (51–75%), heavy (> 75%) and total (stem killed by browsing).

Analysis of data on browsing severity

Severity of browsing in the study areas was estimated by calculating the percentage of sugar maple browse which showed some browsing damage, based on the data from the 60 circular subplots. Since hemlock saplings are scarce or absent on some plots, sugar maple is used as the indicator of browsing severity. The assumption is made that the severity of browsing on sugar maple also reflects the browsing pressure on hemlock. Since hemlock browse is preferred by deer over sugar maple, it is conceivable that heavy browsing of hemlock could exist while browsing of
sugar maple on the same site is low. However, our data suggest that this is not the case in the Porcupine Mountains. Whenever the proportion of browsed sugar maple stems on a study area is low, the number of hemlock seedlings (which are usually killed by one or two episodes of browsing), is high (see Results and Tables 2 and 3).

Significant differences in total litter thickness among the six plots was tested by analysis of variance. Homogeneous groups among the six plots were determined by the Newman–Keuls procedure. To calculate the surface area of rotten wood in each plot suitable for hemlock seedling establishment, Huber's formula for log volume (Avery, 1967) was modified so that it yields surface area instead of volume. Only moss-covered or well-rotted logs and stumps were counted since recently fallen solid wood does not provide a good seedbed for hemlock.

Assessing the relationship of browsing to the current unbalanced size-structure of hemlock

Current hemlock diameter distributions (Fig. 1) for the lakeshore study areas have an unbalanced or unimodal shape. The hemlock diameter distribution for the Big Carp River study area, on the other hand, is of the equilibrium descending monotonic form. If hemlock regeneration has been prevented by browsing since the deer population irrupted in the 1920s, would changes in the structure of the hemlock population be large enough to explain the unbalanced condition of the lakeshore study areas? A reasonable way to answer this question would be to use a computer simulation to project the size-structure of a balanced hemlock stand forward in time 60 years with no hemlock seedling establishment.

The method for projecting the diameter distribution forward in time used here is the same as that used for sugar maple in a previous study (Lorimer & Frelich, 1984). The basic procedure involves stand table projection (Husch et al., 1972) at 5-year intervals with 1 cm diameter classes. In this type of projection, size-dependent growth rates are used to predict the number of diameter classes that trees of various sizes would advance during each five-year period. Size-dependent mortality rates determine the proportion of the trees in each size-class that would die during each five-year period. Growth rates for hemlock were obtained from measurements of the previous five-year ring widths on the increment cores. An equation which predicts growth rates when given the diameter of a tree was fit by linear regression. This and all other regression
Fig. 1. Hemlock and sugar maple diameter distributions from two lakeshore study areas (Cardinal Creek and Union Bay) and from a near-equilibrium inland study area (Big Carp River). Lower right shows the hemlock diameter distribution from the Big Carp River stand projected ahead 60 years with no hemlock recruitment.

equations used in this paper are shown in Appendix 1. Mortality rates for hemlock were devised using the same methods described by Lorimer & Frelich (1984) for sugar maple. Field observations indicate that mortality rates are relatively high for small seedlings and saplings, low for medium-sized trees and moderate for larger trees in hemlock stands in the northeastern United States (G. R. Stephens, pers. comm., based on permanent plot data). Stephens' data indicate that small saplings about 4 cm in diameter have a ten-year mortality rate of about 6%. During the entire 20-year period of observation on Stephens' permanent plot, not one medium-sized tree (between 10.0 cm and 45.0 cm) died. This type of U-shaped diameter versus mortality rate function was also hypothesized by
Goff & West (1975) to explain observed diameter distributions in old growth hemlock forests of Menominee County, Wisconsin. Therefore, several different U-shaped mortality functions which are parallel but of different elevation were tried with the stand table projection. The mortality function selected for use in the simulation is one which gives a stand basal area and maximum diameter close to those observed in typical near-equilibrium hemlock stands on sites of similar quality. The ten-year mortality rates chosen for use are about 6% for small saplings (4 cm diameter), as low as 1.2% for medium-sized trees (30 cm diameter) and gradually rise to 2.5% for large trees (70 cm diameter).

Predicting the future effects of browsing

In old stands where hemlock saplings are lacking, other species of trees, especially sugar maple, are expected gradually to replace hemlock. Thus, gaps in the canopy of the Cardinal Creek study area have become completely dominated by hardwoods (Fig. 2). To predict the rate at which

![Fig. 2](image)

**Fig. 2.** Crown map of 0.5 ha plot on Cardinal Creek study area. Conifer crowns, which are almost all hemlock, are stippled. Open crowns are hardwoods. Note that recent gaps are completely dominated by hardwoods.
this replacement might occur, a gap dynamics model was developed which takes into account changes in the three-dimensional spatial relationships of a plot of forest land. The simulation was run for a 150-year period at ten-year intervals. At each interval the following steps are completed.

1) Expected mortality of existing trees is calculated. The same size-dependent mortality rates for hemlock used in the previous section of the paper are used here. For sugar maple the mortality rates from a previous study of the Porcupine Mountain stands (Lorimer & Frelich, 1984) are used. Ten-year mortality rates are about 54% for small saplings (4 cm diameter), 10% for medium-sized trees (30 cm diameter) and 35% for large trees (70 cm diameter). The same mortality rates are also used for other hardwood species such as yellow birch and red maple which occur in low density on our plots. Trees are killed randomly according to the specified mortality rate for their particular size-class.

2) Gaps are formed by the dying trees. The fall of dying trees is allowed to kill trees of smaller size which are in the path of the falling tree. The crown profile of the falling tree can be projected onto the plot map for the purpose of determining which trees are hit by the fall. The trunk of the falling tree is required to hit the middle 20% of the crown diameter of the other tree to cause mortality. In addition, trees with 50% or more of their crown area directly under the crown of the fallen tree can also be killed. In each iteration mortality is begun with the largest trees present on the plot in order to determine which of the smaller trees are killed by trees falling on them. Trees smaller than 15.0 cm dbh are considered too small to cause gaps. The total number of trees killed by the fall of other trees is not allowed to exceed that predicted by the mortality rates. When the simulation is actually run it is found that usually too few trees are killed by the fall of other trees as compared to the number of deaths predicted by the mortality rates. In this case, additional trees are removed from the forest as described in section 1 above.

For each of the 15 iterations one of eight possible directions of treefall is selected so that the probability of selection is proportional to the observed occurrence of treefalls in each azimuth sector. All trees which fall during a single iteration then fall in the same direction. Treefalls from the SW, W and NW
directions are most common, as would be expected since westerly winds dominate at this latitude. A wide buffer zone of mapped stem locations and measured heights is necessary to simulate gaps formed by trees which are outside the area of interest but which may fall into it and create a gap. A 20 m wide buffer zone is employed here.

(3) The gaps formed by individual tree mortality are filled with new sugar maple seedlings. The size of the gap is estimated by placing a dot grid over the map of the plot. The number of ten-year-old sugar maple trees which will fit in the gap can then be determined by dividing the gap size by the average crown area of a ten-year-old sugar maple. The new stems are placed at random locations within the gap. This procedure for filling the gaps seems reasonable in view of the fact that gaps that have already formed on the Cardinal Creek study area have been filled entirely with hardwoods (Fig. 2).

(4) Ten-year diameter growth is predicted for each of the surviving trees, based on the relationship between observed growth and tree size. Once this diameter growth prediction is completed, crown radius-diameter and height-diameter relationships are used to predict height and crown radius increments.

RESULTS

Severity of current browsing

The data obtained on the severity of current browsing clearly show the difference between the inland study areas and the lakeshore study areas where white-tailed deer yard up in the winter. On the inland study areas browsing frequency and intensity is light and hemlock seedlings are comparatively abundant, whereas on the lakeshore study areas browsing frequency and intensity is high and few or no hemlock seedlings are present (Tables 1 and 2). This lack of hemlock seedlings occurs despite the fact that the lakeshore study areas as a whole should have more input of hemlock seed as indicated by the greater basal area of hemlock on these study areas (Table 2). The few hemlock seedlings that do exist in the lakeshore study areas are nearly always browsed at or below the winter snow depth (Fig. 3).

Contingency table analysis reveals that there is a statistically significant
Deer grazing in hemlock forests

TABLE 1
Number of Sugar Maple Browse Stems in Each Browse Category by Study Area
(Category 1, not browsed; 2, light; 3, moderately light; 4, moderately heavy; 5, heavy and 6, total.)

<table>
<thead>
<tr>
<th>Study area</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Carp River</td>
<td>58</td>
<td>3</td>
<td>61</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scott Creek</td>
<td>19</td>
<td>1</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big Carp River</td>
<td>25</td>
<td>3</td>
<td>28</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Union Bay</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td>14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cardinal Creek</td>
<td>2</td>
<td>22</td>
<td>13</td>
<td>8</td>
<td>12</td>
<td>5</td>
<td>62</td>
</tr>
<tr>
<td>Speakers Creek</td>
<td>6</td>
<td>17</td>
<td>9</td>
<td>6</td>
<td>2</td>
<td>40</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 3. Hemlock seedlings are not common in the lakeshore hemlock forests, and where present, they are nearly always browsed at or below the winter snow line as shown here. (Pen in photo is 15 cm long.)
<table>
<thead>
<tr>
<th>Study area</th>
<th>Location</th>
<th>No. hemlock seedlings</th>
<th>% sm\textsuperscript{a} browsed</th>
<th>Duff thickness (cm)</th>
<th>Rotten wood (m\textsuperscript{2})</th>
<th>Basal area (m\textsuperscript{2})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Carp River</td>
<td>Inland</td>
<td>140</td>
<td>4.9</td>
<td>3.39 ± 0.55</td>
<td>203.4</td>
<td>27.4 11.8 9.6</td>
</tr>
<tr>
<td>Scott Creek</td>
<td>Inland</td>
<td>90</td>
<td>5.0</td>
<td>5.00 ± 1.31</td>
<td>0.0</td>
<td>24.0 8.4 8.6</td>
</tr>
<tr>
<td>Big Carp River</td>
<td>Inland</td>
<td>162</td>
<td>10.7</td>
<td>3.61 ± 1.73</td>
<td>0.0</td>
<td>25.2 29.4 2.2</td>
</tr>
<tr>
<td>Union Bay</td>
<td>Lakeshore</td>
<td>6</td>
<td>78.6</td>
<td>5.73 ± 2.08</td>
<td>23.6</td>
<td>10.6 41.4 5.2</td>
</tr>
<tr>
<td>Cardinal Creek</td>
<td>Lakeshore</td>
<td>0</td>
<td>96.8</td>
<td>3.89 ± 1.62</td>
<td>265.6</td>
<td>8.0 28.2 14.6</td>
</tr>
<tr>
<td>Speakers Creek</td>
<td>Lakeshore</td>
<td>0</td>
<td>85.0</td>
<td>7.86 ± 1.42</td>
<td>200.4</td>
<td>8.6 34.4 9.6</td>
</tr>
</tbody>
</table>

\textsuperscript{a} sm, sugar maple; hem, hemlock.

\textsuperscript{b} significantly thicker than the other plots.

95% confidence interval is shown.
interation between deer browsing and hemlock reproduction. Table 3 shows a two-way cross-classification of sugar maple browse from the 60 subplots on which all browse was tallied. The hypothesis that the proportion of browsed stems is independent of whether or not hemlock reproduction is present is readily rejected ($\chi^2 = 158.97$, 1 df).

Differences in litter thickness do not seem to explain the observed variation of hemlock reproduction on our study areas. Five of the six study areas have no statistically significant difference in mean litter thickness (Table 2). A Chi-square test easily confirms that the number of hemlock seedlings are not uniformly distributed among these five study areas, two of which have little and three of which have abundant hemlock reproduction. Litter thickness, in fact, does not appear to be a major limiting factor in hemlock seedling establishment because most seedlings and saplings are found on other microsites such as rotten wood or soil mounds created by windthrown trees. A survey of seedbed conditions under randomly selected hemlock seedlings on one interior site, for example, indicated that only 7% were growing on a leaf litter substrate, while 67% were found on soil mounds or rotten wood. Excavation around the bases of mature hemlock trees in two lakeshore plots (Cardinal Creek and Union Bay) showed that more than 75% apparently had a similar origin and can still be seen to be growing on soil mounds or rotten wood.

Although rotten wood is clearly an important microsite for hemlock
seedling establishment, hemlock seedlings may be abundant in some areas with no rotten wood if soil mounds are present and deer browsing is light (Scott Creek and Big Carp River, Table 2). Conversely, the occurrence of much rotten wood is not likely to result in successful seedling establishment if deer browsing is heavy (Cardinal Creek and Speakers Creek, Table 2). Thus deer browsing in this case appears to be overriding the seedbed conditions as a factor in establishment.

Relation of past browsing to the current unbalanced size-structure of hemlock

The expected effects of 60 years of heavy browsing on the diameter distribution of the near-equilibrium hemlock stand are shown in Fig. 1. The distribution is still highly positively skewed and resembles the current unbalanced diameter distribution at Union Bay (Fig. 1). The coefficients of skewness (Snedecor & Cochran, 1980) of the 60-year simulated diameter distribution from Big Carp River and the current diameter distribution at Union Bay are both significant at $\alpha = 0.05$ and of the same magnitude, indicating that exclusion of hemlock regeneration for 60 years in a stand initially near equilibrium could easily result in a skewed unimodal size-structure like that currently exhibited at Union Bay. The other two study areas with heavy deer browsing, Cardinal Creek and Speakers Creek, have near-normal diameter distributions for hemlock which are not significantly skewed, although there is a trend toward

<table>
<thead>
<tr>
<th>Study area</th>
<th>Coefficient</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Speakers Creek</td>
<td>0.322</td>
<td>102</td>
</tr>
<tr>
<td>Cardinal Creek</td>
<td>0.239</td>
<td>89</td>
</tr>
<tr>
<td>Union Bay</td>
<td>0.365*</td>
<td>193</td>
</tr>
<tr>
<td>Big Carp River (current)</td>
<td>1.018*</td>
<td>231</td>
</tr>
<tr>
<td>Big Carp River (60-year projection)</td>
<td>0.353*</td>
<td>193</td>
</tr>
</tbody>
</table>

* Significant positive skew $a = 0.05$. 
positive skewness (Table 4). Evidently regeneration has been excluded longer than 60 years on these plots, allowing them to develop a more unbalanced hemlock diameter distribution. Age data from the increment cores show that young hemlocks were becoming established periodically at Union Bay until 57 years ago. On the other hand, no hemlock trees younger than 110 years old were found at Cardinal Creek and only two hemlocks younger than 110 were found at Speakers Creek.

Thus, 60 years of heavy browsing is a sufficient explanation for the unbalanced structure of some stands but not others. Deer browsing cannot explain the current size-structure of stands like Cardinal Creek and Speakers Creek, but certainly deer have had a large effect here as well. It is evident from the map of Cardinal Creek study area that even fairly large recently formed gaps (lower left and upper right sections of Fig. 2) have been filled entirely with hardwoods rather than hemlock.

Predicted future effects of browsing

Canopy profiles of the current forest on a random transect of the Cardinal Creek stand as well as the simulated appearance of the forest 50, 100 and 150 years from now are shown in Fig. 4.

The current canopy profile shows a forest dominated by hemlock but with a few large sugar maples present as well. For the first 50-year period the relative proportion of hemlock in the canopy actually increases (Fig. 4B), even without input of new individual hemlocks. This is due to the fact that mortality rates for the older sugar maples in the current profile (Fig. 4A) are higher than mortality rates for hemlock. The demise of the hemlock canopy does not occur quickly because the smaller overtopped trees (currently in the 70-150 year age class) have very low mortality rates and are capable of expanding their crowns into some of the gaps created by the deaths of the large trees. After 100 years of simulation, however, the forest has reached a critical turning point. Large hemlocks continue to dominate the canopy (Fig. 4C) but they have now reached sizes and ages at which mortality rates begin to rise, setting the stage for a fairly rapid decline of the remaining hemlock canopy. In addition, several gaps have formed and sugar maple saplings, which will later dominate the canopy, are becoming abundant. After 150 years of simulation the hemlock canopy has largely disappeared. The canopy profile takes on the aspect of a dense young forest containing sugar maples of various ages with a few remnant hemlocks still present as canopy emergents (Fig. 4D).
Fig. 4. Current and projected canopy profiles 50, 100 and 150 years from now on a randomly chosen 70·7 × 10·1 m strip on the Cardinal Creek study area. Conifer crowns are stippled. Open crowns are hardwoods.
DISCUSSION

The causes of inadequate hemlock regeneration

Our conclusion, which is substantiated by the significance of the negative interaction between white-tailed deer browsing and hemlock reproduction, is that white-tailed deer browsing appears to be the major cause of the recent decline in hemlock reproduction in certain areas of the Porcupine Mountains. This conclusion is consistent with the results of other studies of the subject in this region. Anderson & Loucks (1979) and Goff (1967) found that hemlock reproduction was quite good in Menominee County, Wisconsin, an area where extensive deer hunting is allowed and deer populations are low. Rogers (1978) has surveyed a large portion of the range of hemlock in the northeastern United States and has found evidence that if seedbed conditions are good and deer populations are kept low, hemlock regenerates well.

Other important factors such as litter thickness and amount of rotten wood available for seedbeds, while they may have some influence on hemlock seedling establishment, do not seem to be limiting factors in the Porcupine Mountains. There is evidence in addition to the results of statistical analysis already presented which establishes this. The Big Carp River study area contains less rotten wood than any of the lakeshore study areas and its litter thickness is no different from two of the lakeshore study areas (Table 2). Yet excellent hemlock regeneration is present in the area while the lakeshore areas have little or none.

The hypothesis that climatic change has played a major role in preventing hemlock reproduction seems untenable in view of the fact that reproduction of all ages is abundant on some study areas. Climatic differences within the Porcupine Mountains cannot explain the observed disparities in abundance of hemlock reproduction because those study areas with the most favourable climate, those on the lakeshore, have the least abundant hemlock regeneration. Even though the inland study areas have a smaller component of hemlock in the larger size classes than the lakeshore areas, reproduction there is adequate to maintain the current population of hemlock.

Causes of unbalanced stand structure

There are no quantitative data available on whether or not deer browsing could have been a limiting factor to hemlock establishment more than 60
years ago, but there are other possible explanations for the long absence of hemlock regeneration on some of the study areas. Some of the study areas 60 years ago could have been recovering from a natural disturbance such as a heavy windstorm. A large blowdown of 1000 ha occurred in the park in 1953, and we have found evidence of earlier catastrophic disturbance in other parts of the park. The dense, even-aged cohorts resulting from such a disturbance clearly can prevent the establishment of an understory for several decades (Oliver, 1981). In such a stand very few hemlock seedlings would be present on the forest floor, even without heavy deer browsing. Roth (1898) noted that some hemlock stands in the Great Lakes region had very sparse understoreys long before the major irruption of the deer population. In addition there is evidence that hemlock reproduction occurs periodically at intervals of several decades during times when good seed crops coincide with favourable climate or with disturbances which create new openings in the forest canopy (Graham, 1941: Hough & Forbes, 1943).

The effects of severe deer browsing on mixed hemlock-sugar maple forests in this area depend on the state of the forest at the time the browsing begins. In stands that exhibit a unimodal diameter distribution due to past severe natural disturbance, there is little available browse in the understory. Thus, deer will not have an effect on the size-structure of the stand until it reaches an advanced age, in which case sugar maple will be the favoured species to invade new gaps because of its superior ability to resprout many times. On the other hand, if the stand in question has already begun to open up from mortality of old trees or is all-aged, the effects of heavy browsing will begin immediately. Small hemlocks occupying gaps will be killed by browsing and replaced with sugar maple. It has already been demonstrated that a size-structure like that in the Big Carp River valley could reasonably be converted to one like that of Union Bay by the 60 years of browsing that have already occurred.

Predicted future effects of browsing

It is apparent from the geographic distribution of deer browsing in the Porcupine Mountains that the preservation of the hemlock forest on a strip of land 2-4 km wide along Lake Superior, where deer concentrate in the winter, is most threatened. At the present time, hemlock seems capable of maintaining itself in the inland forests which experience only light summer browsing. It is unfortunate that the lakeshore stands are
generally those with the largest component of hemlock. If no action is taken to reduce deer browsing in these stands, the forest will eventually become like the sugar maple forest with scattered hemlocks, as is common in the interior of the Porcupine Mountains. The simulation summarized in Fig. 4 indicates that this process would take about 150 years. However, it should be realized that this is a conservative estimate of the rate of stand conversion to hardwoods. Severe storms, which occasionally hit the region, could easily remove many of the larger trees on one or more occasions during a 150-year period. Storms with sustained winds of 120 km h\(^{-1}\) have an expected recurrence of about 50 years in Upper Michigan (Thom, 1968). Storms of this magnitude could be expected to create small openings in old growth hardwood-hemlock forest (Stoeckler and Arbogast, 1955). Part of the Cardinal Creek study area has already been affected by a 1950 windstorm which is responsible for the gap filled with small hardwoods at the northeast corner of the crown map in Fig. 2. With continued heavy browsing by deer, this type of storm would simply accelerate the replacement of hemlock by sugar maple. Also, it should be noted that the random strip chosen for simulation currently has few gaps filled with sugar maple compared to the rest of the plot, parts of which are already dominated by young hardwoods.

There is likely to be some decline in the population of deer overwintering in the lakeshore area as hemlock disappears from the forest canopy. Several researchers have stated that cover provided by coniferous trees is the most important factor for winter survival of deer in the hemlock-hardwood forest region (Graham, 1954; Dahlberg & Guettenger, 1956). Whether this decline will be large enough to allow hemlock to regenerate, however, is doubtful. The unique situation in the Porcupine Mountains, with deeper snow and colder temperatures inland, will force many deer to overwinter along the lakeshore even without the cover provided by hemlock. This is already the case outside the park where extensive areas of the original hemlock forest have been converted to hardwoods by logging. Such lakeshore hardwood stands around the Porcupine Mountains are heavily used by deer during the winter (E. Harger, pers. comm.). Figure 4 indicates that a substantial number of hemlocks will remain in the canopy for about 100 years. Even if deer were forced by a lack of hemlock to move elsewhere 100 years from now, there would be a 160-year age gap in the hemlock population and the changes shown in Fig. 4 would be nearly complete. Fortunately, however, hemlock is such a long-lived species that in areas where the hemlock
canopy is still fully intact, the long-term changes depicted in Fig. 4D have barely begun to occur after 60 years of heavy browsing. It is thus still possible to alter the trend of species conversion in most hemlock stands by controlling the deer population.

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REFERENCES

Deer grazing in hemlock forests


(Appendix 1 follows)
APPENDIX 1

Regression Equations Used in Forest Development Simulations
(Diameter at 1·4 m is represented by symbol dbh.)

<table>
<thead>
<tr>
<th>Dependent variable and species</th>
<th>Equation</th>
<th>$R^2$ (%)</th>
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Tree height:
- Hemlock: $1·20 \text{dbh}^{739}$ 80·6
- Sugar maple: $3·49 \text{dbh}^{505}$ 76·4
- Yellow birch: $3·63 \text{dbh}^{461}$ 68·1
- Red maple: $4·18 \text{dbh}^{434}$ 76·5

Height to crown base:
- Hemlock: $0·56 \text{dbh}^{667}$ 70·1
- Sugar maple: $12·55 e^{-0·26/\text{dbh}}$ 55·2
- Yellow birch: $2·05 \text{dbh}^{429}$ 49·7
- Red maple: $2·29 \text{dbh}^{410}$ 48·0

Crown radius:
- Hemlock: $0·583 \text{dbh}^{489}$ 62·2
- Sugar maple: $1·39 + 0·065 5 \text{dbh}$ 73·3
- Yellow birch: $6·55 e^{-23·1/\text{dbh}}$ 77·6
- Red maple: $0·834 \text{dbh}^{405}$ 55·7

Five-year diameter growth:
- Hemlock: $-0·059 8 + 0·051 8 \text{dbh} - 0·000 6 \text{dbh}^2$ 15·3
- Sugar maple: $0·752 + 0·047 0 \text{dbh} - 0·000 6 \text{dbh}^2$ 18·0