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WHITE-TAIL DEER (*ODOCOILEUS VIRGINIANUS*) INFLUENCE ON STRUCTURE AND COMPOSITION OF *TSUGA CANADENSIS* FORESTS

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SUMMARY

(1) The effect of heavy and light deer browsing on the composition and structure of eastern hemlock forests was investigated in Wisconsin, United States.

(2) Sugar maple rapidly replaced hemlock when both were heavily browsed but reproduction in hemlock soon recovered upon removal of browsing.

(3) White-tailed deer have a substantial influence on the reproduction of hemlock, and on the potential of this species to replace itself in forests where hemlock is the dominant tree species.

INTRODUCTION

Eastern hemlock (*Tsuga canadensis* (L.) Carr) is a common dominant in the conifer-hardwood forest of central and northeastern United States, and is widely distributed throughout the conifer-hardwood forests of northern and eastern Wisconsin. In this area, hemlock saplings can tolerate long periods of suppression; for example, Stearns (1951) found saplings of 38 mm diameter that were 53-years-old. These suppressed saplings eventually achieve overstorey positions if canopy openings occur. However, little reproduction of hemlock occurs under dense stands of either hemlock or sugar maple (*Acer saccharum* Marsh.). Curtis (1959) concluded that hemlock would ultimately be replaced by sugar maple; he therefore assigned hemlock a climax adaptation value (CAV) of 8, and sugar maple a value of 10. On the other hand, Martin (1959) concluded that, in Algonquin Park, Ontario, Canada, hemlock was capable of replacing sugar maple and was therefore a climax species.

Numerous studies have shown that hemlock seedlings and saplings are browsed by white-tail deer (*Odocoileus virginianus* Zimmerman), particularly during the winter months when browse becomes scarce (Hosley & Ziebarth 1935; Swift 1948; Dahlberg & Guettinger 1956; Beals, Cottam & Vogl 1960).

Prior to 1800, deer occurred at high densities only in southern Wisconsin on prairies, oak savannahs and in scattered groves of oak trees (Curtis 1959). These areas burned frequently. Deer were less plentiful in northern Wisconsin forests. After logging in the late 1800s, white-tailed deer became more common in northern Wisconsin, though repeated severe wild fires briefly reduced suitable habitat for deer in the first two decades of the twentieth century. Legislation was passed to protect deer in the 1920s and second growth forests provided browse and cover for deer (Swift 1948; Dahlberg & Guettinger

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1956). As a result, deer populations increased and have remained high in northern forests. The effect of continuing deer browsing on forests has caused concern since 1940.

Hemlock is more severely damaged by browsing than is sugar maple. When the terminal shoots of hemlock are browsed, its potential for regrowth is greatly reduced. Sugar maple is browsed but it resprouts readily and, if it is not browsed for a few years, the terminal shoot reaches sufficient height to be out of the reach of deer.

As a result, sugar maple more commonly survives in the understorey of browsed forests than does hemlock. We conclude that the failure of hemlock to reproduce in Wisconsin forests, where it is the dominant tree species (Curtis 1959), is primarily due to deer browsing, rather than to the fact that hemlock is rapidly replaced by sugar maple in succession. Evidence from Canada supports this; all-aged stands of hemlock occur in many areas of Ontario (Hett & Loucks 1976), where wolves and hunting maintain the deer population at lower levels than in Wisconsin.

We have tested our hypothesis that deer restrict regeneration of hemlock in Wisconsin by studying the frequency distribution of the stem diameter of seedling and sapling populations of hemlock.

The study was carried out in the Flambeau Scientific Area (Sawyer County), and in forests of Menominee County. The forests of the Flambeau Scientific Area are dominated by an overstorey of mature hemlock; yellow birch (*Betula lutea* Michx.) and sugar maple are also abundant. The deer population in this area is 50 to 100 deer km^{-2} (Anonymous 1971). Seedlings of hemlock and yellow birch are infrequent but seedlings of sugar maple are common. The Menominee County forests are a mixture of types including pine, northern hardwoods, and hemlock-yellow birch-northern hardwoods. However, our work was limited to a single site where hemlock was dominant. The deer population in this county has been limited by over 100 years of unrestricted hunting, while the county was an Indian reservation. Surveys in the early 1960s indicated a population of between 5–12 deer km^{-2}, but the number of deer has increased to 37 km^{-2} since the reservation was terminated in 1961, and hunting restrictions were imposed (Anonymous 1971).

METHODS

An area of 62·7 ha within the Flambeau Scientific Area was fenced in 1969 to exclude deer. Five permanent study sites within this fenced area had been sampled in 1967 and were again sampled in 1973. These stands were selected, on the basis of soils and vegetation, to be similar to stands in Menominee County. The stands range from 0·4 to 0·8 ha in size; they have nearly level topography and a dominance of hemlock.

Sets of three nested circular quadrats were located at each of five randomly located sampling points in each stand. The largest circular quadrats (0·04 ha) were used to sample the trees, the intermediate quadrats (0·01 ha) were used to sample saplings, and the smallest quadrats (0·004 ha) were used to sample seedlings. Stems $\geqslant 90$ mm dbh were designated trees, those of $\geqslant 13$ mm < 90 mm dbh were designated saplings and those 15 cm tall and < 13 mm dbh were designated seedlings. Two small deer exclosures (0·04 ha) were established in the Flambeau Forest in 1961; these were sampled in 1967 and 1973. In these two exclosures a complete tally of the trees was made; two 0·01 ha circular quadrats were used to sample the saplings and seven plots (0·004 ha) were used to sample the seedlings. Data from the two exclosures were combined into a single sample. The tree basal area (m^2 ha^{-1}) and stem density (ha^{-1}) of each species was computed for all study sites.

Species Importance Values (Curtis & McIntosh 1951) for each stand were calculated, based on the sum of relative density and dominance (basal area) divided by 2. Thus Importance Values for all species in a stand sums to 100.

Seedlings, saplings, and trees in each hectare were grouped into size classes. Structural diagrams were prepared by plotting stems ha^{-1} (on a log scale) by size class. Seedlings constituted a single class (0 to 13 mm dbh, mean 6·5 mm) and so did the saplings (13 to 90 mm, mean 52 mm). Trees were grouped in size classes with intervals of 75 mm. The log number of trees (ha^{-1}), recorded in each size class, was plotted against mean stem diameter for that class.

Chi-square (Brandt and Snedecor's formula) was used to test the hypothesis that there was a homogeneous distribution of hemlock stems in various dbh size classes (Bailey 1959). For this analysis, data were divided into two groups. One group consisted of medium and large tree classes (mean $\geqslant 20$ cm) and the other consisted of the smallest tree class (mean, 13 cm) and the seedling and sapling classes. For the chi-square analysis, the number of stems sampled in each size class was used and not the log transformed data.

RESULTS

Hemlock was the leading dominant in all stands (Table 1), with a minimum importance value (I.V.) of 57·4 in stand (a), Flambeau Forest, and a maximum value of 86·2 in stand (b), Menominee County. Yellow birch was the second leading dominant in four stands and sugar maple in the remaining three. The maximum I.V. of sugar maple was 21 in stand (d) of the Flambeau Forest.

The stand basal areas were large (Table 2) and typical of old-growth forests, ranging from 30·0 to 52·0 $m^2\ ha^{-1}$. Tree density (Table 2) varied between 311 ha^{-1} for stand (d) in the Flambeau Forest and 558 ha^{-1}, for the Menominee County stand.

The relations between tree density and size class for hemlock, sugar maple, in the large exclosure of the Flambeau Scientific Area (Fig. 1), indicate that hemlock was the dominant species in the tree category (>90 mm), but it was essentially absent as seedlings (<13 mm) and saplings (13–90 mm). In contrast, sugar maple was of less importance as a tree, but it dominated the seedling and sapling layers. The smallest hemlock tree sampled in the Flambeau Forest area was 10 cm dbh. Until the establishment of the large deer exclosure in 1968, there were very few hemlock seedlings or saplings present. The few seedlings that were found were protected either by snow cover, logs or other cover. As these stems grew taller and protruded above the snow they were removed by browsing.

TABLE 1. Importance values of dominant species in Menominee county and Flambeau Scientific Area

Stand	*Tsuga canadensis*	*Betula lutea*	*Acer saccharum*	*Ulmus americana*	*Tilia americana*	*Pinus strobus*
Menominee County						
Stand (b)	86·2	8·3				1·1
Flambeau Scientific Area						
Stand (a)	57·4		15·6	11·1		
Stand (c) Small Exclosure	59·0	32·6	4·8			
Stand (d)	65·6	10·0	21·0			
Stand (e)	68·9	14·1	16·9			
Stand (f)	57·8	42·0			14·5	
Stand (g)	71·5	21·6	3·6			

TABLE 2. Tree basal area (m^2 ha^{-1}) and density (ha^{-1}) in forests of Menominee County and the Flambeau Scientific Area

Stand	Basal Area (m^2 ha^{-1})	Density (ha^{-1})
Menominee County		
Stand (b)	37	558
Flambeau Scientific Area		
Stand (a)	30	400
Stand (c) Small Exclosure	36	395
Stand (d)	39	311
Stand (e)	46	336
Stand (f)	41	438
Stand (g)	52	410

Only the hemlock population in Menominee County (Fig. 1(b)) had a structural diagram characteristic of an all-age population. The Flambeau Forest stands had no saplings, and few seedlings; only the 12-year exclosure (Fig. 1(c)) had sufficient seedlings of hemlock to be able to maintain itself.

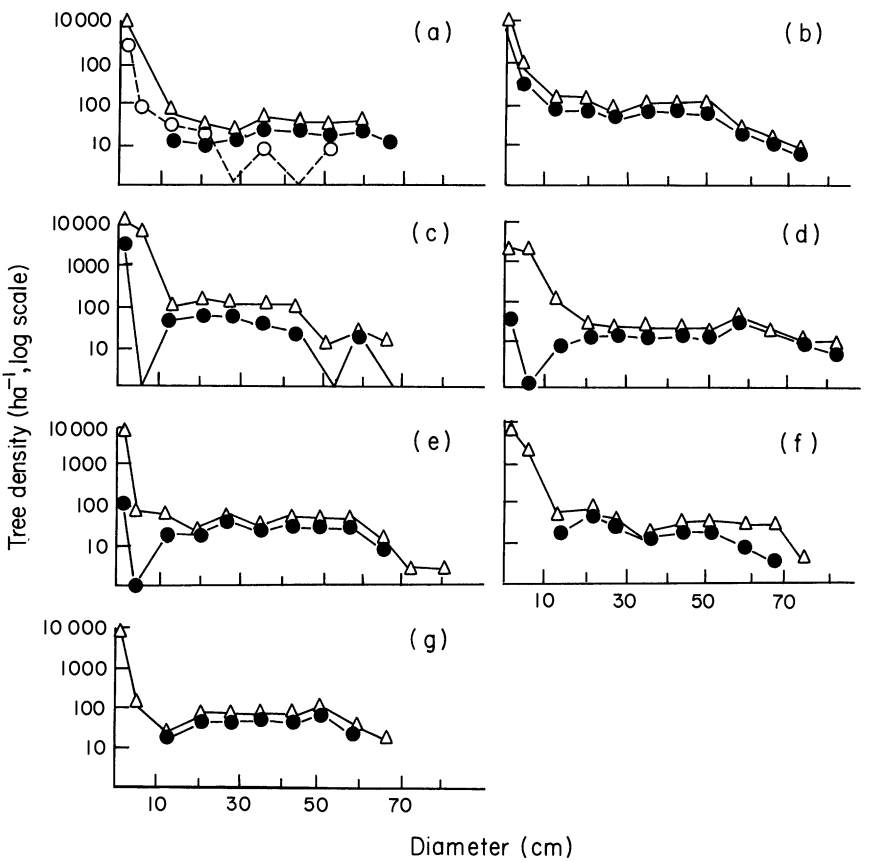

FIG. 1. The relation between $\log_{10}$ number of stems (ha^{-1}) and stem diameter (cm) for hemlock (●), sugar maple (○), and all trees (△) in an area exclosed in 1961 (c), in five areas exclosed in 1969 (a & d–g), and in an area in Menominee Co. (b). For clarity, sugar maple is shown for only stand (a), though this relationship is similar to that in other stands in the Flambeau area.

Tests for a homogeneous distribution of hemlock stems indicated that, in the medium and large size classes, there was generally a homogeneous distribution of hemlock stems (Table 3). Two stands in the Flambeau Forest (Fig. 1(f) and (g)) were exceptions to this generalization. They had a small number of large stems of hemlock, resulting in a significant departure from a homogeneous distribution. Large stems (class mean $\geqslant 58$ cm) do not usually occur in high density and this could be the reason for their under-representation in these two samples. If the size classes with means < 58 cm are considered, there are no significant departures from a homogeneous distribution for the medium and large size tree classes. This occurs in spite of the apparent deficiency of the smallest trees classes of hemlock in several stands in the Flambeau Forest (Fig. 1(a), (d), (f)).

TABLE 3. Chi-square test for homogeneous distribution of hemlock stems in two groups of stems

Stand	Group 1 [seedling, sapling, smallest tree class ($d.f. = 2$)]		Group 2 [tree classes means $\geqslant 20$ cm]		
	X^2	P	X^2	$d.f.$	P
Menominee County					
Stand (b)	40·2	$P < 0{\cdot}001$	8·3	7	NS
Flambeau Scientific Area					
Stand (a)	56·0	$P < 0{\cdot}001$	7·4	6	NS
Stand (c) Small Exclosure	180·8	$P < 0{\cdot}001$	4·8	6	NS
Stand (d)	8·4	$P < 0{\cdot}01$	6·5	8	NS
Stand (e)	32·2	$P < 0{\cdot}001$	13·7	8	NS
Stand (f)	53·5	$P < 0{\cdot}001$	16·3	7	$P < 0{\cdot}05$
Stand (g)	162·0	$P < 0{\cdot}001$	14·1	6	$P < 0{\cdot}05$

In contrast, there was a significant departure from a homogeneous distribution of stems in the smallest tree and seedling and sapling classes for all stands, including the Menominee County Stand (Table 3). For the Menominee County Stand, this significant departure from homogeneity resulted from the high proportion of hemlock seedlings (9188 hemlock and 11 856 total stems ha^{-1}), compared to a relatively smaller proportion of hemlock stems in the sapling (356 hemlock and 968 total stems ha^{-1}) and small tree (69·2 hemlock and 158 total stems ha^{-1}) classes. However, for the Flambeau Forest stands, the lack of hemlock seedlings, saplings, or both accounted for the significant departure from a homogeneous distribution.

DISCUSSION

The results from the analyses of the homogeneity of distribution of hemlock stems, within size classes of the two groups, suggests that in the past hemlock successfully reproduced in the Flambeau Forest. That is, there was a relatively constant proportion of hemlock stems in all sizes classes. However, in the recent past, the reproductive success of this species was diminished.

Hemlock is sufficiently shade tolerant, so that seedlings are abundant in other areas where hemlock is the dominant tree species (McIntosh 1972). With reduced deer browsing, hemlock would probably have reproduced in the Flambeau sites, just as it has in the Menominee County stand. Sugar maple could move into the stand slowly and perhaps

gain in dominance, but the importance of hemlock should be expected to remain high in the Flambeau stands.

Hemlock is well represented in all size classes, in the Flambeau stands, with the exception that there are few seedlings, saplings, and the smallest trees. In the 12-year-old exclosure, seedlings of hemlock were several hundred times more abundant, but there was still an absence of saplings, indicating that seedlings failed to establish prior to exclosure. The increase in the number of seedlings, that occurred after protection, has not yet reached the sapling classes. Hemlock in stands (d) and (e), which were protected for 4 years at the time they were sampled, already show signs of limited reproductive success.

These results, together with those of DeBoer (1947), Swift (1948), Beals *et al.* (1960), and Ross, Bray & Marshall (1970) show that high white-tailed deer population have a substantial impact on the reproduction of some trees, and on the long-term species composition of Lake States Region Forests (Wisconsin, Michigan, Minnesota). This study considered the role of deer in reducing the reproduction only of hemlock-dominated forests. However, other evergreen trees such as white cedar (*Thuja occidentalis* L.), white, red, and jack pines (*Pinus strobus* L., *P. resinosa* Ait. and *P. banksiana* Lamb.), and balsam fir (*Abies balsamea* (L.) Mill.) also suffer deer damage. We suggest that, if the wildlife components are to be maintained in equilibrium over long periods of time, wildlife should not be favoured to the detriment of important understory tree species such as hemlock. Liberalization of hunting regulations in these areas may be the only feasible means of preventing change in tree species composition and further degradation of wildlife habitat.

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REFERENCES

Anonymous. (1971). Annual deer census. Wisconsin Department of Natural Resources, Madison, Wisconsin.

Bailey, N. T. J. (1959). *Statistical Methods in Biology*, The English University Press Ltd., London.

Beals, E., Cottam, G. & Vogl, R. (1960). Influence of deer on vegetation of the Apostle Island, Wisconsin. *Journal of Wildlife Management*, **24,** 66–80.

Curtis, J. T. (1959). *The Vegetation of Wisconsin.* University of Wisconsin Press, Madison, Wisconsin.

Curtis, J. T. & McIntosh, R. P. (1951). An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, **32,** 476–496.

Dahlberg, B. L. & Guettinger, R. G. (1956). *The White-tail Deer in Wisconsin.* Wisconsin Conservation Department, Madison.

DeBoer, S. G. (1947). The damage to forest reproduction survey. *Wisconsin Conservation Bulletin*, **12,** 1–23.

Hett, J. & Loucks, O. (1976). Age structure models of balsam fir and eastern hemlock. *Journal of Ecology* **64,** 1029–1044.

Hosley, N. W. & Ziebarth, R. K. (1935). Some winter relations of the white-tailed deer to the forests in north central Massachusetts. *Ecology*, **26,** 535–553.

Martin, N. D. (1959). An analysis of forest succession of Algonquin Park, Ontario. *Ecological Monographs*, **29,** 196–218.

McIntosh, R. P. (1972). Forests of the Catskill Mountains, New York. *Ecological Monographs*, **42,** 143–161.

Ross, B., Bray, J. & Marshall, W. (1970). Effect of long term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. *Ecology*, **51**, 1088–1093.

Stearns, F. (1951). The composition of sugar maple–hemlock–yellow birch association in northern Wisconsin. *Ecology*, **32**, 245–265.

Swift, E. (1948). Wisconsin's deer damage forest reproduction survey—final report. *Wisconsin Conservation Department Publication*, **347**.

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