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).

TABLE 2

Attributes of the Six Study Areas

(Seedling density, area of rotten wood and basal areas are per hectare)

Study area	*Location*	*No. hemlock seedlings*	*% sm[a] browsed*	*Duff thickness (cm)*	*Rotten wood (m^2)*	*Basal area (m^2)*		
						sm[a]	*hem[a]*	*All other*
Little Carp River	Inland	140	4·9	3·39 ± 0·55	203·4	27·4	11·8	9·6
Scott Creek	Inland	90	5·0	5·00 ± 1·31	0·0	24·0	8·4	8·6
Big Carp River	Inland	162	10·7	3·61 ± 1·73	0·0	25·2	29·4	2·2
Union Bay	Lakeshore	6	78·6	5·73 ± 2·08	23·6	10·6	41·4	5·2
Cardinal Creek	Lakeshore	0	96·8	3·89 ± 1·62	265·6	8·0	28·2	14·6
Speakers Creek	Lakeshore	0	85·0	[b]7·86 ± 1·42	200·4	8·6	34·4	9·6

[a] sm, sugar maple; hem, hemlock.
[b] significantly thicker than the other plots.
95% confidence interval is shown.

TABLE 3

Cross-classification of Sugar Maple Browse as to whether Each Stem was Browsed or Unbrowsed and whether Each was on a Study Area With or Without Abundant Hemlock Reproduction

(Browsed stems are those in categories 2-6 of Table 1. Study areas with abundant hemlock reproduction are the inland study areas, as designated in Table 2.)

	Hemlock reproduction present	*No hemlock reproduction present*
Maple browsed	7	105
Maple unbrowsed	102	11

$\chi^2 = 158{\cdot}97$, 1 df.

interaction 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 (7: = 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 saplings 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 a = 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 4
Coefficients of Skewness for Hemlock Diameter Distributions

Study area	*Coefficient*	*n*
Speakers Creek	0·322	102
Cardinal Creek	0·239	89
Union Bay	0·365[a]	193
Big Carp River (current)	1·018[a]	231
Big Carp River (60-year projection)	0·353[a]	193

[a] Significant positive skew a = 0·05.