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Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests

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Summary

1 Efforts to understand and forecast long-term forest dynamics are often hindered by limited data on mortality rates and longevity of trees in older stands. In this study, mortality data were analysed from 11-year permanent plot records in 10 tracts of hemlock-hardwood forest with little past human disturbance in the upper Great Lakes region, USA.

2 We compared tree size-mortality trends in mature stands (canopy trees mostly 100–170 years old) with those in true old-growth stands (canopy trees mostly 200–350 years old). Stem sections were also cut from 71 recently fallen trees to determine average and maximum longevity for canopy trees of each species.

3 All five mature stands had descending monotonic size-mortality trends for shade-tolerant species, with low rates of mortality (generally much less than 1% per year) for trees > 18 cm d.b.h. In contrast, all five old-growth stands had U-shaped mortality functions, with annual mortality rates of 1.5–2.9% for trees > 66 cm d.b.h. These size-mortality trends are biologically consistent with 'rotated sigmoid' size distributions observed for major species, although mortality rates were nearly size-invariant for trees between 18 and 66 cm d.b.h.

4 Both late-successional and gap-phase species had fairly high mortality rates for saplings (2–10 cm d.b.h.) of 25–34% over the 11-year period, which suggests that size distributions with moderately steep negative slopes are needed to compensate for mortality and ensure population sustainability.

5 Average age at time of death for canopy trees was 216 years for sugar maple (*Acer saccharum*) and 301 years for hemlock (*Tsuga canadensis*), suggesting that the biological transition from mature to old-growth forest probably doesn't occur on these sites until a stand age of about 180–250 years.

Key-words: forest models, old-growth definitions, population sustainability, tree life tables

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Introduction

Tree mortality plays a major role in promoting the distinctive structure of old-growth forest and thus providing unique habitat for certain species of animals and plants. Mortality rates in old-growth stands (i.e. stands relatively undisturbed by humans and which have numerous old trees; Hunter 1989) affect stand structure, maximum size and age of trees, formation rates of snags, logs and canopy gaps, and development of multilayered vegetation (Tyrrell & Crow 1994a, 1994b; Tyrrell *et al.* 1998). Differences in mortality rates among species are also considered to be key life-history attributes that influence long-term changes in forest composition, structure and sustainability (Harcombe 1987). Pacala *et al.* (1996), for example, used the 5-year survivorship of 1-cm d.b.h. saplings under conditions of 1% full sunlight as a measure of the ability of a species to persist in the understorey. In their trials with the SORTIE model, they found that the dominant species late in succession were invariably those with low mortality rates in the understorey. Data on average and maximum longevity of canopy trees are also important for establishing historic baseline values that can be compared with forests invaded by exotic pathogens (e.g. Orwig & Foster 2000).

In forecasting long-term change in forests, it is often desirable to utilize data on how mortality changes with tree size or age; i.e. the mortality component of life-table data (Harcombe 1987). However, because long-term

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data on tree mortality and longevity are rare, modellers have often had either to make simple assumptions about mortality trends or else use indirect evidence. In the JABOWA model (Botkin *et al.* 1972), a baseline mortality rate was established by assuming that 2% of a cohort would survive to reach the maximum age of the species. Growth-dependent mortality was modelled by assuming an annual mortality rate of 37% for any tree that grew less than 0.1 mm in diameter per year.

Another approach has been to estimate size-related mortality rates indirectly from static measures of forest structure. The diameter distribution in such cases is essentially treated as a survivorship curve that requires an assumption that the stand is close to a steady-state condition (see review in Harcombe 1987). Several different mathematical functions, however, have been proposed as providing the best fit to steady-state diameter distributions, including the negative exponential (de Liocourt 1898; Meyer & Stephenson 1943; Leak 1996), the negative power function (Hett & Loucks 1976) and a 'rotated sigmoid' distribution that can be approximated by polynomial functions of the logarithm of tree density vs. diameter class (Goff & West 1975). Each of these three functions implies different underlying size-related mortality trends: size-invariant mortality in the negative exponential, continually declining mortality with increasing size in the power function, and a 'U-shaped' trend with minimum mortality in the middle size classes in the case of the rotated sigmoid.

Direct monitoring of mortality on permanent plots is needed for unambiguous evidence on mortality-size trends in old-growth stands and for the development of improved models. In recent years a large amount of data has become available from permanent plots in managed and unmanaged second-growth forest in eastern North America, both at individual research sites (Christensen 1977; Runkle 2000) and from a regional network of forest inventory plots (Buchman 1983; Teck & Hilt 1990). Harcombe (1987) has summarized much of the earlier evidence, especially relating to Buchman's work in the midwestern United States of America (USA), to show that mortality rate in most second-growth stands shows a monotonically declining trend to very low levels for medium and large trees. Whether these trends would also apply to old-growth forests is less clear. Most regional studies based on inventory plots have comparatively few old trees or stands in the database. For example, the largest size class (53 cm d.b.h.) analysed in Buchman's (1983) analysis is more comparable with the mean diameter of overstorey trees in old-growth temperate hardwoods. Based on permanent plot records in several old stands, Runkle (2000) recently reported greater mortality for larger trees, while Woods (2000) found no clear trend.

In this paper we utilize 11-year permanent plot records to document size-mortality trends from 10 tracts of mature and old-growth hemlock-hardwood forest in the upper Great Lakes region, USA. Specific questions include: (i) Do these stands have descending monotonic or U-shaped size-mortality trends, and do these trends differ in mature vs. old-growth stands? (ii) Do mortality rates for a given size class differ in the two developmental stages? (iii) What are the average and maximum longevities of canopy trees in late-successional hardwood forests?

Methods

STAND AND SITE CHARACTERISTICS

Ten study sites were located in mixed hemlock-hardwood forest on mesic sites in western upper Michigan and north-eastern Wisconsin. A randomly located 0.5-ha permanent plot (70.7 × 70.7 m) had been established at each of the sites in 1981–82 as part of a larger study on forest dynamics and natural disturbance regimes (Frelich & Lorimer 1991). The stands, eight of which were located in areas of primary forest within the Porcupine Mountains Wilderness State Park, were selected to cover a wide range of developmental stages on mesic sites dominated by sugar maple (*Acer saccharum* Marsh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.) and yellow birch (*Betula alleghaniensis* Britt.). These three species together make up 87% of the mean basal area of each stand, although usually either hemlock or sugar maple is dominant within a particular stand. The 10 stands are all located on level to gently sloping terrain with loam or sandy loam soils. The two habitat types represented (*Acer-Tsuga-Dryopteris* and *Tsuga-Maianthemum*, with one site intermediate between *Acer-Tsuga-Dryopteris* and *Acer-Viola-Osmorhiza*) are considered above average in moisture-nutrient availability and productivity compared with all habitat types in the region (Coffman *et al.* 1980; Fassnacht & Gower 1997). However, because different stand ages cannot be found on sites with identical environmental characteristics, all 10 stands were initially analysed as independent cases and subsequently pooled within a forest type-developmental stage category only if no substantial differences in mean mortality or size-mortality trend were found.

Based on the stand structural criteria of Frelich & Lorimer (1991) that were developed for use in similar multi-aged temperate deciduous stands on good sites, four stands are classified as mature and five as old growth. One stand, heavily damaged by a windstorm in 1953, was classified as a pole stand but also has mature trees that survived the disturbance. Its mortality rates and size-mortality trends were similar to other mature stands and it was therefore grouped with them for analysis. In the structural classification, mature and old-growth stands must both have at least two-thirds of the canopy space occupied by crowns of trees > 26 cm d.b.h. (canopy space measured as the sum of projection areas of the portion of tree crowns exposed to direct skylight). In mature stands, the sum of exposed crown projection area for large trees (> 46 cm d.b.h.) is less than the sum for mature trees (26.0–45.9 cm d.b.h.), whereas in old-growth stands this ratio is > 1.0. For all 10 mature and old-growth stands combined, the threshold d.b.h. for mature trees corresponds to a mean age of 130 years for sugar maple and 160 years for hemlock. The corresponding mean age for the large-tree threshold is 200 and 210 years, respectively. Most of the mature stands are broadly uneven-aged, reflecting a long history of variable-intensity disturbance typical in this region, and have trees much older than most second-growth stands in the region. They differ from old-growth stands in having had one to several episodes of moderate disturbance in the 19th and early 20th centuries that cumulatively removed 30–50% of the canopy trees (Frelich & Lorimer 1991). Canopy trees in the mature stands typically range from 100 to 170 years in age, with scattered trees > 200 years. A previous study of gap formation in these stands verified that in spite of the prevalence of 100–170-year-old trees in the mature stands, gap sizes and gap formation rates are much lower than in the true old-growth stands (Dahir & Lorimer 1996).

The five maple-dominated stands (one pole, one mature and three old growth) are located in the interior of the Porcupine Mountains State Park, in Sub-subsection IX.6.1 (Gogebic-Penokee Iron Range) of the ecological landscape classification of Albert (1995). The Precambrian bedrock is predominantly volcanic andesites and felsites, as well as sandstone, siltstone, shale and conglomerate (Dorr & Eschman 1970). The soils are classified as Porcupine loam (Veatch *et al.* 1921).

One mature and two old-growth hemlock-dominated stands are also located in the Porcupine Mountains, on lacustrine sediments deposited under glacial Lake Duluth. They are located in Subsection IX.8 (Lake Superior Lake Plain) of Albert's 1995 landscape classification on Ontonagon fine sandy loam and Porcupine loam, respectively. Because mature hemlock stands are not common in the Porcupine Mountains or in the nearby Sylvania Wilderness, the remaining two sites were located in natural areas in adjacent north-eastern Wisconsin. These two stands, at the Plum Lake Scientific Area and the Kemp Natural Resources Station, occur on the Pence-Padus soils series, an inclusion of sandy loam surface soil within a region of pitted outwash (Subsection IX.5 in Albert's (1995) classification).

The climate in the region is humid continental with average temperatures in upper Michigan ranging from –7.8 °C in January to about 19.2 °C in July, and in northern Wisconsin from –12.3 °C in January to about 19.5 °C in July. In both areas, mean annual precipitation ranges from 90 to 97 cm, 70% of which falls between April and September. Two recent periods of subnormal growing season moisture occurred from 1976 to 1978 and from 1986 to 1988. Winters are generally long and cold with snowfall averaging over 32 cm per month from November through March.

FIELD METHODS

Species, diameter at breast height (d.b.h.), crown class and map coordinates had been recorded for all trees > 2 cm d.b.h. when each 0.5-ha plot was established. Crown classes (dominant-codominant, intermediate, overtopped and suppressed) follow the definitions of Smith (1986). In eight of the plots, one or two 10.1 × 70.7-m transects had also been randomly selected for more detailed measurements of tree heights and crown radii (measured for each tree in four cardinal directions from stem to crown edge).

The plots were re-censused in 1991–93. Diameter at breast height and crown class were recorded for all trees that had been at least 2 cm d.b.h. in 1981–82 and the identities noted of all trees that had subsequently died. Mortality of saplings 2–4 cm d.b.h. was determined only on the transects. Crown radii were re-measured for all trees > 5 cm d.b.h. on the transects. On four of the transects, measurements were also made of the radii of the 'exposed crown', i.e. the portion exposed to direct skylight and not overtopped by branches of neighbouring trees.

On 13 of the transects, all living trees that had been > 10 cm d.b.h. in 1981 were cored in 1992 to determine tree ages. Trees > 15 cm d.b.h. were cored at a height of 1.0 m to reduce the chances of encountering heart rot, and trees 10–15 cm d.b.h. were cored at a height of 0.3 m.

Cross-sectional wedges were cut from trees of late-successional species that died on the Porcupine Mountains 0.5-ha plots during the 11-year period to determine the total age at the time of death. Of the 80 dead trees > 15 cm d.b.h., eight were so visibly rotted in the field that no sample was taken. Wedges were cut as close to the base of the tree as possible, but often had to be taken above breast height to avoid heart rot. Heights at which wedges were cut averaged 3.4 m and ranged from 0.4 to 12.2 m. Eleven samples collected in the field were later discarded because decay was too far advanced for accurate ring counts.

LABORATORY AND ANALYTICAL METHODS

Analysis of increment cores and wedges

Each wedge was cut with a bandsaw into a rectangular section along a clear radius that included the pith. Increment cores and wedge sections were sanded and the surface or a portion of the surface then shaved with a razor blade. Ring widths were measured under a binocular microscope with stage micrometer. If the pith was missing on a sample, the distance to pith was estimated from a pithfinder template based on the curvature of the rings (Applequist 1958). This distance was then divided by the mean ring width of the innermost 10 rings on the sample to estimate the number of missing rings. The number of years required for saplings to reach core or wedge height was estimated using the height–age regressions of hemlock and sugar maple saplings (combined sample of understorey and gap saplings) from Frelich (1986). These equations indicated a mean correction factor of 8 years for a 1.0-m sample height in sugar maple and 16 years for hemlock. Core and wedge samples were cross-dated using a master chronology based on hemlock and sugar maple canopy trees with no periods of severe or prolonged suppression (Lorimer *et al.* 1999).

Calculation of mortality rates and competition variables

Annual rates of mortality were calculated from observed 10- or 11-year rates using a negative compound interest formula (Hamilton & Edwards 1976):

$$M = 1 - \{(N_t/N_o)^{1/t}\}$$

where M = annual mortality rate, N_t = number of surviving trees at re-measurement time t (t = 10 or 11 years), and N_o = number of trees at plot establishment.

Several measures were computed as a means of investigating possible differences in competition levels among individual trees in mature and old-growth stands. Relative diameter, defined as the ratio of the d.b.h. of an individual tree to the mean diameter of all canopy trees (dominant-codominant crown classes) in the stand, was used to provide a simple measure of the relative status for a given tree size among stands of different developmental stages. Exposed crown projection areas of trees on the transects were calculated by summing the areas of the four quarter-ellipses defined by the four exposed crown radii of each tree measured in the field.

Relative diameter by itself can serve as a simple index of competition but does not take into account variation in stand density or crowding. We derived measures of crowding from empirical stand density charts for northern hardwoods and hemlock-hardwoods in the Great Lakes region (Tubbs 1977). These charts are similar to self-thinning diagrams (Westoby 1984; Osawa & Sugita 1989) and show regional average and maximum observed stand basal area values for stands with a given mean tree diameter. We used the regional average basal area values as a standard for comparison in a competition index as maximum values were not available for all species combinations (Tubbs 1977). We developed a simple competition index that integrates stand density and relative tree size into a single index:

$$CI = \frac{B_D / \overline{B_D}}{R_i}$$

where CI = competition index, B_D = observed plot basal area for stand of mean tree diameter D, $\overline{B_D}$ = average regional stand basal area for stands of mean tree diameter D, and R_i = relative diameter of a tree of size class i on sample plot.

In this formulation, a CI of 1.0 can be expected for canopy trees of average size in stands of average density. Values of CI exceed 1.0 for canopy trees in dense stands or for trees of below-average relative size. Values are < 1.0 for large canopy trees or those in low-density stands.

Differences in mortality rates of trees in mature vs. old-growth stands were evaluated statistically for three broad size classes (2–25.9 cm, 26–49.9 cm and > 50 cm d.b.h.), with the stand as the experimental unit (n = 10). Each size class was subdivided into three subclasses of width 8 cm. Because the smaller trees within each 24-cm size class were usually much more numerous than larger trees, the mortality figure used for the statistical test in each stand and size class was the mean mortality for the three 8-cm subclasses, to avoid giving undue weight to small trees. Statistical comparisons between mature and old-growth stands for the 2–26-cm and 26–50-cm classes were made using t-tests. Because of the disproportionately greater number of trees > 50 cm d.b.h. in the old-growth stands, and differences in distribution of stand-level mortality rates between the two stand stages, the non-parametric Wilcoxon rank-sum test was used for evaluating differences in mortality between mature and old-growth stands for the largest size class. t-Tests were also used to evaluate differences in diameters and mean competition levels among trees in each of the three broad size classes.

Results

MORTALITY TRENDS BY SIZE CLASS AND SPECIES

The shape of the size-mortality trend for all shade-tolerant species combined was descending monotonic for all five mature stands but asymmetrically U-shaped for all five old-growth stands (Fig. 1). In the mature stands, the observed 11-year mortality rate was 40% for the smallest diameter class (2–10 cm d.b.h.) and declined to 4% or less in the medium and large size classes. In the old-growth stands, on the other hand, 11-year mortality declined from about 35% in the smallest diameter class to 4% in the 46-cm class, and then rose again to about 20% in the classes > 66 cm d.b.h.

Hemlock and sugar maple, when examined separately on each site, also followed these patterns in most cases. The main exception was that medium-sized sugar maple trees in mature hemlock-dominated stands were unusually old for their size because of slow growth, and their relatively high mortality resulted in a more erratic size-mortality trend on those sites. Data from mature stands are therefore presented according to dominant species (Tables 1 and 2) but are pooled for all old-growth stands (Table 3).

Mortality rates were relatively low for medium-sized trees of shade-tolerant species, typically < 1% annually, regardless of the particular species or stand developmental stage. Nevertheless, while mortality rates were low for both sugar maple and hemlock, differences between the two species were large enough to influence mean longevity. Hemlock typically had lower mortality rates than sugar maple in size classes > 18 cm d.b.h. In many size classes, including all trees > 58 cm d.b.h. in the old-growth stands, sugar maple mortality rates were approximately double or triple those of hemlock (Tables 1 and 3).

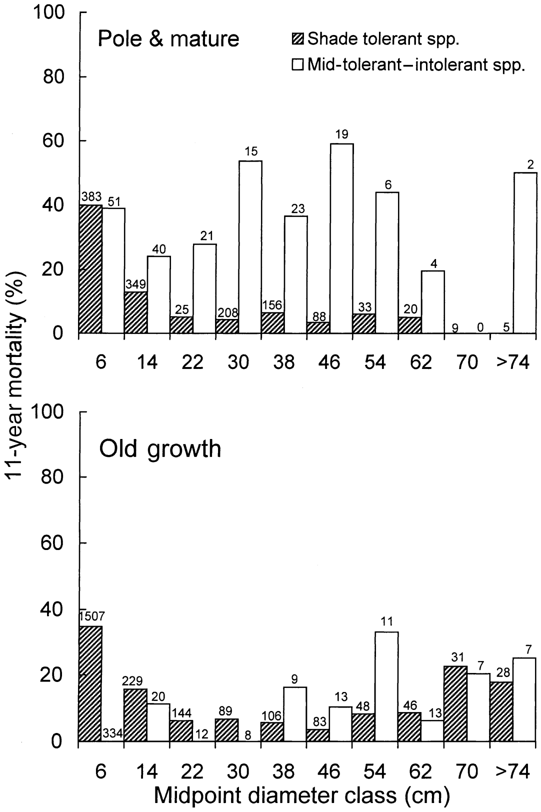

Fig. 1 Observed 11-year mortality rates by size class for shade-tolerant species (shaded bars) and mid-tolerant–intolerant species (clear bars) in mature and old-growth stands. Numbers above each bar indicate sample size (number of living trees at the beginning of the measurement interval in 1981). The tolerant species group includes *Acer saccharum*, *Tsuga canadensis*, *Acer rubrum*, *Tilia americana* and *Thuja occidentalis*. The mid-tolerant–intolerant group includes *Betula alleghaniensis*, *Betula papyrifera*, *Quercus rubra*, *Fraxinus pennsylvanica* and *Ulmus americana*.

Mid-tolerant and intolerant tree species (*Betula alleghaniensis*, *Betula papyrifera* Marsh., *Quercus rubra* L., *Fraxinus americana* L. and *Ulmus americana* L.) were a relatively small component of most stands but as a group had very high mortality rates, with 11-year rates of 40–60% in many size classes (Fig. 1). Paper birch (*Betula papyrifera*), which was present only in the Plum Lake mature hemlock stand and was probably more than 100 years old, had 74% mortality across all size classes. Yellow birch, although normally a common gap-phase component of late successional stands in this region, also had mortality rates that appear to be too high for the existing canopy population to be sustained, with a number of medium and large size classes losing more than 40% of the trees to mortality (Tables 1 and 3).

DIFFERENCES IN MORTALITY RATES AMONG MATURE AND OLD-GROWTH STANDS

Significant differences in mortality rates between mature and old-growth stands occurred only for the larger size class (> 50 cm d.b.h.) in sugar maple and all shade-tolerant species combined (Table 4). In both hemlock and hardwood dominated stands, mortality rates of 50–74-cm d.b.h. trees were about four times higher in old-growth than in the mature stands (11-year rates of 13% vs. 3%, respectively). In other size classes, however, mortality rates were fairly similar between mature and old-growth stands (Fig. 1, Tables 1 and 3). Thus we could find no evidence that mortality rates were consistently higher or lower across all size classes in old-growth forest. Rather, mortality trends differed significantly only for the larger size classes where the U-shaped trend in old-growth forests and the descending monotonic trend in mature stands began to diverge (Fig. 1).

Mean diameter for trees > 15 cm d.b.h. differed significantly between mature (31.7 cm) and old-growth stands (42.2 cm, $t = -3.787$, 9 d.f., $P = 0.005$). Thus, while a tree 30 cm d.b.h. is close to an average sized canopy tree in the mature stands, it has a relative diameter of only 0.71 in the old-growth stands. Likewise, a 40-cm d.b.h. tree is slightly below average in size in an old-growth stand but has a relative diameter of 1.26 in a mature stand. Evaluation of mean competition measures for

Table 1 11-year and annual mortality rates for the principal species in the three mature hemlock-dominated stands. N refers to the number of living trees at the beginning of the measurement interval

	Sugar maple			Hemlock			Yellow birch		
Midpoint dbh class (cm)	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N
6	34.8	3.8	46	23.6	2.4	55	–	–	0
14	13.3	1.3	75	13.2	1.3	144	0.0	0.0	2
22	11.1	1.1	45	3.5	0.3	114	0.0	0.0	1
30	15.4	1.5	26	1.9	0.2	106	66.7	9.5	9
38	25.0	2.6	20	2.4	0.2	83	28.6	3.0	7
46	11.1	1.1	9	3.4	0.3	58	44.4	5.2	9
54	0.0	0.0	3	6.3	0.6	16	100.0	100.0	2
62	0.0	0.0	2	0.0	0.0	9	50.0	6.1	2
70	0.0	0.0	1	0.0	0.0	7	–	–	0
> 74	–	–	0	0.0	0.0	4	100.0	100.0	1
Total			227			596			33

Table 2 11-year and annual mortality rates for principal species in the two mature stands dominated by maple

	Sugar maple			Hemlock			Yellow birch		
Midpoint dbh class (cm)	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N
6	44.2	5.2	276	–	–	0	66.7	9.5	3
14	9.6	0.9	94	0.0	0.0	2	23.8	2.4	21
22	0.0	0.0	67	0.0	0.0	3	0.0	0.0	3
30	2.2	0.2	45	0.0	0.0	4	0.0	0.0	4
38	0.0	0.0	25	0.0	0.0	10	0.0	0.0	2
46	0.0	0.0	10	0.0	0.0	4	–	–	0
54	0.0	0.0	5	14.3	1.4	7	0.0	0.0	2
62	0.0	0.0	7	0.0	0.0	1	–	–	0
70	0.0	0.0	1	–	–	0	–	–	0
> 74	0.0	0.0	1	–	–	0	–	–	0
Total			531			31			35

Table 3 11-year and annual mortality rates for the principal species in the five old-growth stands

	Sugar maple			Hemlock			Yellow birch		
Midpoint dbh class (cm)	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N	11-year mortality (%)	Annual mortality (%)	N
6	34.3	3.7	1411	34.0	3.7	64	29.4	3.1	229
14	15.0	1.5	160	17.4	1.7	46	18.2	1.8	11
22	4.4	0.4	68	3.3	0.3	60	0.0	0.0	9
30	12.5	1.2	40	2.6	0.2	39	0.0	0.0	7
38	10.9	1.0	46	3.9	0.4	51	22.2	2.3	9
46	4.3	0.4	47	0.0	0.0	27	9.1	0.9	11
54	7.4	0.7	27	5.3	0.5	19	40.0	4.5	10
62	15.0	1.5	20	4.3	0.4	23	20.0	2.0	10
70	26.3	2.7	19	16.7	1.6	12	42.9	5.0	7
> 74	20.0	2.0	10	27.8	2.9	18	42.9	5.0	7
Total			1848			359			310

Table 4 Comparison of mean mortality rates for trees in each of three broad size classes in mature and old growth stands

Size class (cm)	Number of trees		11-year mortality (%)		T-test			Wilcoxon rank sum	
	Mature	Old growth	Mature	Old growth	T-statistic	MSE	*P*-value	Sum of scores	*P*-value
Sugar maple									
2–25.9	603	1639	14.0	16.4	0.26	0.010	0.622		
26–49.9	135	133	11.2	7.0	0.14	0.034	0.714		
> 50	20	76	0.0	22.0				10	0.015
Hemlock									
2–25.9	318	170	8.3	29.0	1.72	0.086	0.231		
26–49.9	265	117	2.0	1.2	0.56	0.013	0.479		
> 50	44	72	2.5	11.2				14	0.171
All tolerant species*									
2–25.9	1079	1996	13.8	18.6	1.45	0.008	0.263		
26–49.9	502	281	6.4	5.2	0.00	0.022	0.967		
> 50	77	157	2.8	17.0				15	0.012

*Includes sugar maple, hemlock, basswood, red maple, and white cedar.

individual trees in each of the three broad size classes revealed consistently higher values for trees in old-growth stands, especially when a stand density term and relative diameter were combined in a single index (Table 5). These results suggest that trees of all sizes are growing under greater competitive stress in old-growth forests, but no actual evidence of higher mortality rates in old growth was found for trees < 50 cm d.b.h.

Although the number of trees per hectare > 50 cm d.b.h. was 70% higher in old-growth than in

Table 5 Comparative mean values of two competition measures for trees in each of the three broad size classes in mature and old-growth stands

	Relative diameter						Relative basal area/relative diameter			
	Mean value						Mean value			
Size class (cm)	Mature	N	Old growth	N	T-statistic	*P*	Mature	Old growth	T-statistic	*P*
Sugar maple										
0–26	0.41	5	0.18	5	5.47	< 0.001	2.13	9.71	−7.5	< 0.001
26–50	1.07	5	0.93	5	1.75	0.118	0.94	1.48	−2.8	0.020
> 50	1.92	4	1.52	5	2.10	0.074	0.53	0.93	−3.49	0.010
Hemlock										
0–26	0.46	4	0.35	5	1.97	0.090	2.47	6.34	−2.59	0.036
26–50	1.07	4	0.85	5	4.95	0.013	0.89	1.51	−5.43	0.001
> 50	1.67	4	1.54	5	1.60	0.154	0.59	0.85	−6.02	0.0005
All tolerant species*										
0–26	0.47	5	0.22	5	5.68	< 0.001	2.19	8.14	−8.15	< 0.001
26–50	1.13	5	0.90	5	2.85	0.021	0.81	1.51	−4.05	0.004
> 50	1.94	5	1.52	5	1.69	0.130	0.48	0.88	−3.63	0.007

*Includes sugar maple, hemlock, basswood, red maple, and white cedar.

mature stands, trees in the 50–74-cm d.b.h. class were well represented in both forest stages. In old-growth stands, 148 trees of hemlock and sugar maple > 50 cm were initially present, and 9.4% of these died over the 11-year period. In mature stands, 64 trees of hemlocks and maples were initially present in this size class, and only 3.1% died. The old-growth stands did have a higher proportion of very large trees: 40% of the trees in the 50–74-cm size class were > 66 cm d.b.h., compared with 22% in the mature stands. This might account for the observed higher mortality of large trees in old growth since the mortality curve becomes noticeably steeper beyond a size of 66 cm d.b.h. (Fig. 1) and many such trees are probably approaching senescence. It is likely that large trees in the mature stands were somewhat younger on average than trees of comparable sizes in the old-growth stands. However, the largest trees that died during the 11-year period in old-growth stands had relatively small exposed crown areas compared with the mean crown area of all trees in the same d.b.h. class (Fig. 2). This suggests that competitive stress was probably also an influential factor in the death of large trees during the observation period.

LONGEVITY OF SUGAR MAPLE AND HEMLOCK CANOPY TREES

Trees that died in the five old-growth stands were considered the best indicators of average and maximum longevity of canopy trees as mature stands had relatively few trees > 250 years old. The size of canopy trees (gapmakers) that died during the 11-year period spanned a wide range from 10 to 80 cm d.b.h. but averaged 49 cm d.b.h. for all species combined ($n = 56$). Mean d.b.h. at the time of death for sugar maple (43 cm) was slightly lower than the mean for all species, while yellow birch (59 cm) and hemlock (65 cm) were higher. Age estimates were obtained from 34 of the 52 gapmakers of these three species, with yellow birch having the largest number that could not be aged. Mean observed age at time of death was 210 years for sugar maple, 193 years for yellow birch and 328 years for hemlock. These estimates are similar to those obtained from a sample of disks from dead maple and hemlock trees cut on the same sites in 1983 (mean of 206 years for sugar maple and 277 years for hemlock; data base of Lorimer & Frelich 1989).

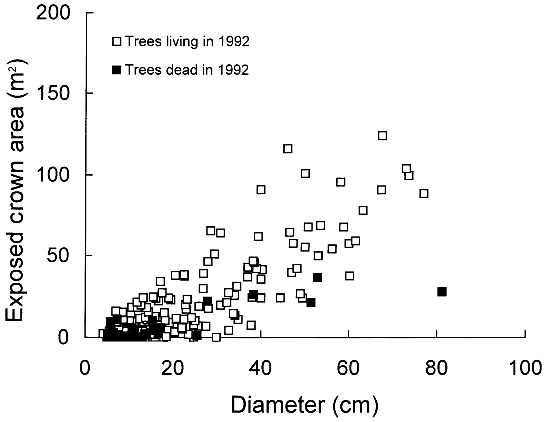

Fig. 2 Living-dead status of trees on the transects in 1992, plotted in relation to exposed crown area of each tree at the beginning of the measurement interval in 1981. Note that trees which died had a smaller than average exposed crown area for their size, suggesting competition-induced mortality.

We feel that the best unbiased estimates of average canopy tree longevity are obtained by: (i) combining the 1983 and 1992 data sets to increase sample size; (ii) taking the mean d.b.h. of all gapmakers at the time of death, including those that could not be aged; (iii) fitting a regression of age at time of death vs. d.b.h for the subsample that could be aged (Fig. 3); and (iv) using the regression to predict mean age at time of death from the unbiased sample of mean gapmaker d.b.h. This

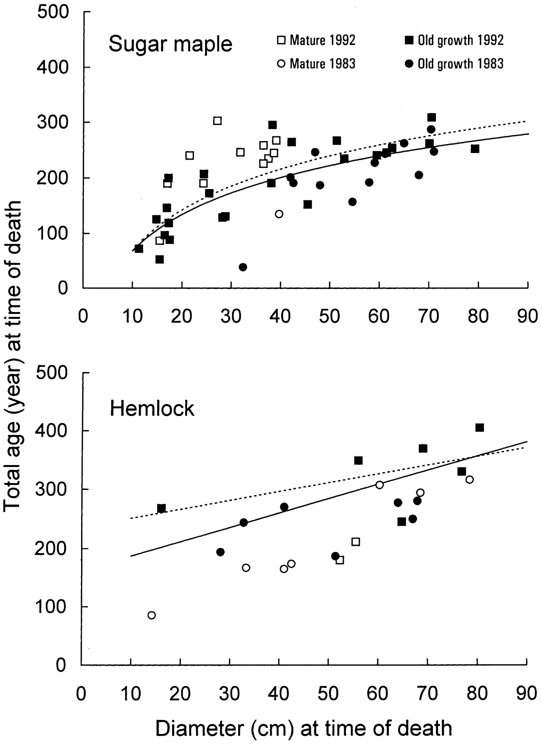

Fig. 3 Total age of individual canopy gapmaker trees at the time of death, plotted in relation to their d.b.h. Circles represent data collected in 1983 (from Lorimer & Frelich 1989) and squares represent data collected in 1992 (this study). Regression lines shown were fit to the data from old-growth stands only (black symbols). Dotted lines show the regression for the 1992 old-growth data only, while solid lines show the regressions for the combined 1983 and 1992 old-growth data.

procedure resulted in estimates for mean age at time of death of 216 years for sugar maple ($n = 40$, mean gapmaker d.b.h. = 46.8 cm) and 301 years for hemlock ($n = 17$, mean gapmaker d.b.h. = 56.8 cm).

Maximum estimated ages based both on cores from living trees and wedges from dead trees suggest that sugar maple may often reach or exceed an age of 300 years (Fig. 3). The oldest sugar maple in our sample (a dead tree 40 cm d.b.h. in an old-growth hemlock stand) had 318 observed rings and an estimated total age of 328 years. Maximum ages of hemlock were greater than in sugar maple. Two dead hemlocks sampled in 1992 were 405 and 369 years old (observed number of rings 340 and 319, respectively), and one dead hemlock sampled in 1983 was 513 years old (observed number of rings 509). These three old hemlocks were all unusually large for these sites, ranging in size from 69 to 80 cm d.b.h. The oldest yellow birch was 342 years old (316 observed rings, d.b.h = 74 cm). We found no evidence from increment cores of living trees that the live-tree population included trees older than these.

Although mortality of canopy trees was limited on the mature plots from 1981 to 1992, the trees that did die were fairly old. Most of the mortality of sugar maple in mature stands occurred in hemlock-dominated stands. These dead sugar maples had a mean d.b.h. of 30 cm but were unusually old for their size, averaging 219 years ($n = 12$). The number of dead hemlock trees in 1992 in mature stands was too limited for analysis, but when combined with the dead trees from the 1983 data, they averaged 50 cm d.b.h and 211 years of age ($n = 9$). The oldest dead trees on mature plots approached an age of *c.* 300 years for both sugar maple and hemlock (Fig. 3).

Discussion

CHANGES IN MORTALITY-SIZE TRENDS WITH STAND AGE

The data from these 11-year permanent plot records support the hypothesis that there is a fundamental difference in the shape of the size-mortality trend in mature and old-growth forests. As has been reported for mature deciduous forests elsewhere (Harcombe 1987), shade-tolerant species in the five mature stands in this study had descending size-mortality trends. There was little mortality in the medium and large size classes, even though many of the larger trees were more than 200 years old. The five old-growth stands, in contrast, all had asymmetric U-shaped mortality trends. A sharp increase in mortality rates was most clearly evident for trees > 66 cm d.b.h., with 11-year mortality rates increasing from *c.* 10% to 20% at that point. These findings of a U-shaped size-mortality trend are consistent with higher mortality rates among large vs. medium-sized trees reported by Runkle (2000) in several mesic old-growth stands. Complete U-shaped mortality functions have also been reported in several studies of individual old-growth stands (Parker *et al.* 1985; Platt *et al.* 1988; Nakashizuka *et al.* 1992).

Underlying causes of increased mortality of larger trees are not well known (Loehle 1988), especially the relative importance of biomechanical and biotic factors. Larger trees are more susceptible than medium-sized trees to windthrow during storms (King 1986; Canham *et al.* 2001), probably caused by several factors such as increased winds at greater heights, more exposed crowns, and increased heartwood decay in older trees (Hepting & Hedgecock 1937; Norden 1954; Stillwell 1955; King 1986). However, in this study it was not clear that susceptibility to stem breakage or uprooting during storms were the most important factors in determining longevity. *Tsuga canadensis* had a much greater lifespan and mean d.b.h. at time of death than *Acer saccharum*, despite greater susceptibility of *Tsuga* to windthrow during storms (Canham *et al.* 2001) and its greater sensitivity to drought (Fowells 1965). While it is not clear that tissue senescence in trees occurs in the same sense as in animals (Loehle 1988), it is possible that older individuals are less able to ward off major pathogens such as *Armillaria* root rot disease, and that differential resistance among species influences longevity.

The U-shaped size-mortality trends are biologically consistent with the observed size distributions of all-aged stands of sugar maple, approaching a rotated sigmoid curve on a graph of logarithm of tree density vs. diameter class on these similar sites. Size distributions have a steep negative slope from 5 to 20 cm d.b.h., then show a markedly shallower decline from 20 to 65 cm d.b.h., and finally have a precipitous decline beyond 65 cm d.b.h. (Lorimer & Frelich 1984; Goodburn & Lorimer 1999). Abrupt changes in the slope of the size distributions mirror the abrupt decline in mortality rate between 18 and 20 cm d.b.h. and the steep increase in mortality rates beyond 65 cm d.b.h. (Fig. 1, this study). Overall, our findings support the mechanistic link between mortality rates and size distributions hypothesized by Goff & West (1975). However, in our data mortality rates were nearly constant over a surprisingly wide range of tree sizes (Fig. 1), which may explain why the negative exponential distribution often provides a reasonable fit to size distributions between the limits of 15–65 cm d.b.h. (cf. Leak 1996).

Annual mortality rates for sugar maple in mature hardwood stands in this study are comparable with the very low rates of 0.2–0.4% reported by Buchman (1983) for second-growth hardwood stands of similar age. However, in the old-growth stands in our study, mortality rates for sugar maple were two–four times higher than rates recorded for comparable size classes in Buchman's second-growth stands. Field competition measures based on stand density and relative tree size suggest that competitive stress may be higher for all size classes of trees in old-growth forest. This might explain the higher mortality rates compared with Buchman's (1983) analysis, but statistically higher mortality rates in old growth were documented only for trees > 50 cm d.b.h. The lack of significant differences among the small and medium size classes may simply be a consequence of high variability in sugar maple mortality between the hemlock- and maple-dominated mature stands (Tables 1 and 2). However, it is also likely that the gap structure of uneven-aged forests that exposes many sapling and pole trees to direct skylight mitigates the effect of higher stocking levels in old growth.

The baseline mortality rate assumed in the JABOWA-FORET models is 4.0/AGEMAX, where AGEMAX is the maximum age commonly attained by the species (Shugart 1984). Using the maximum ages observed in our stands, the mean annual mortality rate for mature trees in JABOWA would be approximately 1.2% for sugar maple and 0.78% for hemlock. These compare reasonably well with observed mortality of 0.96% for sugar maple and 0.49% for hemlock in the 14–62-cm diameter classes. JABOWA also adds a growth-dependent mortality rate for trees with an annual diameter growth rate < 0.1 mm that makes the size-mortality trend U-shaped (Urban & Shugart 1992). SORTIE has a more sophisticated method than JABOWA for estimating sapling mortality rates based on site-specific data, and the SORTIE mortality functions clearly mimic the steep decline in mortality rates as saplings increase in size (Kobe *et al.* 1995). However, JABOWA would provide better predictions of mature and large tree mortality in our stands because the JABOWA baseline mortality functions are inherently coupled to species longevity. The current version of SORTIE assigns 1% annual mortality to all mature and old canopy trees regardless of size or species (Pacala *et al.* 1996). An overall 1% annual gap formation rate is often reported in temperate deciduous forests (Runkle 1985), but our data raise the possibility of important variations among species and perhaps among regions. Even though sugar maple and hemlock are both considered long-lived, late-successional species, average and maximum longevity for hemlock were 40–55% longer than those of sugar maple (see similar findings in Woods 2000). Annual mortality rate averaged only 0.3% for hemlocks with 18–66 cm d.b.h., and the overall annual gap formation rate in hemlock-dominated old-growth forest was only 0.58%.

MORTALITY RATES AND POPULATION SUSTAINABILITY

Large differences in mortality rates between shade-tolerant species and mid-tolerant–intolerant species were observed in this study. The high mortality rates in the mid-tolerant–intolerant group appear to have varied causes. The severe 1988 drought was followed by dramatic and widespread mortality of paper birch and yellow birch, known simply as 'birch dieback', throughout northern Wisconsin and upper Michigan that was similar to an earlier episode between 1932 and 1955 (Prey *et al.* 1988; Erdmann 1990; Houston 1992). High mortality of American elm was probably a consequence of Dutch elm disease, which is caused by an introduced pathogen for which the trees have little resistance (Boyce 1961). The observed mortality rates for the mid-tolerant–intolerant group are clearly not typical of long-term historic averages and are too high for the canopy populations to be sustained at current levels.

However, the mortality rates for shade-tolerant species that heavily dominate these forests are similar to the long-term norm. A reconstruction of 50 years of canopy gap formation in these stands indicated that the overall gap formation rate during the 11-year permanent plot survey was close to the mean for the entire 50-year period (Dahir & Lorimer 1996). The gap turnover time (inverse of annual gap formation rate) during that decade was also similar to the mean canopy–tree residence time (defined as mean time from first release in a gap to the time of death) as determined from independent analysis of radial increment patterns from dead trees.

The question of whether present population levels of these species are sustainable over the long-term, however, also depends in part on the rate of new sapling recruitment. The mortality data in this study provide some insight into the common but puzzling question of whether populations of a dominant shade-tolerant or mid-tolerant species are sustainable if the density of saplings is relatively low, either within a specific stand or on the landscape as whole. In these forests, hemlock and yellow birch are the two prominent examples of late-successional species that often have deficient recruitment (Eyre & Zillgitt 1953; Waller *et al.* 1995; Woods 2000). Species with a low density of seedlings and saplings could conceivably have stable populations provided that mortality rates of the young trees are correspondingly low (O'Hara 1996). Yellow birch in the present study area is a classic 'gap-phase species' that normally has few saplings under a closed canopy but which colonizes large treefall gaps (White *et al.* 1985; Erdmann 1990). Even if the size distributions of yellow birch are rather 'flat', which was the case for 73% of the 70 stands studied by Lorimer & Frelich (1998), the populations might be sustainable if yellow birch saplings outgrow competitors in gaps and have low mortality. However, the data in this study indicate that mortality rates for small trees were not, in fact, low for either yellow birch, hemlock or sugar maple. All three species had similar and substantial 11-year mortality rates of 29–34% for the 6-cm d.b.h. class and 15–18% for the 14-cm size class, similar to the findings of Woods (2000). These high mortality rates raise doubts about the sustainability of 'flat' diameter distributions for both shade-tolerant and gap-phase species. About 20% of the stands studied by Lorimer & Frelich (1998) had substantial cohorts of young yellow birches that established after partial canopy removal by wind, fire and other means. This suggests that the species may rely more heavily on infrequent, episodic recruitment after partial stand destruction than on the scattered treefall gaps that occur in most decades.

AVERAGE LONGEVITY OF CANOPY TREES AND OLD-GROWTH DEFINITIONS

Previous knowledge of canopy tree longevity has largely been restricted to anecodotal observations of exceptionally old trees (e.g. Burns & Honkala 1990) and on age ranges of living trees in old-growth stands. Analysis of ages at time of death can provide more precise estimates of longevity, analogous to life expectancy statistics in life tables (e.g. Selvin 1991). In both the mature and old-growth stands in this study, best estimates of the mean age of canopy trees at the time of death in old-growth forests were about 215 years for sugar maple and 300 years for hemlock. These average ages at time of death are one-half to two-thirds of the maximum observed ages in our sample (328 years for sugar maple and 513 years for hemlock), which agree well with one of the possible criteria for old growth suggested by Hunter (1989).

A suitable general definition for old-growth forest would ideally link typical old-growth structural features (sizeable canopy gaps, large snags and logs, and multi-layered vegetation) with the population dynamic processes that produce these features. If we assume that the transition from mature to old-growth forest does not occur until there is significant mortality of dominant canopy trees from old age, wind, disease, etc., our data suggest that the transition to old growth probably does not occur on these sites until the relatively advanced age of 180–250 years. These estimates for a biological age threshold for old-growth forest agree with the early JABOWA predictions by Bormann & Likens (1979) based on expected patterns of biomass accumulation and losses from mortality, but are much higher than the criteria of 100–150 years often used by land managers for inventorying old growth on public lands (e.g. Rusterholz 1996; Schmidt *et al.* 1996). Four stands classified as 'mature' in this study were dominated by relatively old canopy trees 100–170 years of age, and trees older than 200 years occupied up to 25–33% of the canopy space. Canopy gaps in these stands, however, were small and comparatively infrequent. While these mature stands are old enough to meet many of the operational definitions of old growth, the dynamics of these stands are more similar to those of second-growth mature stands < 100 years old, and they might best be characterized as 'late aggradation' stands in the scheme of Bormann & Likens (1979). Further long-term field observations might resolve whether stands dominated by 100–170-year-old trees are still indeed increasing in total biomass despite their relatively advanced ages, and whether the habitat and wildlife value of such stands is comparable with that of true old growth forests.

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