The age structure of a striped maple population

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Cohort and population age structure analysis showed that, after the initially high mortality rates of the 1st year (87.5%), striped maple seedlings (*Acer pensylvanicum* L.) underwent practically no mortality until the age of 15. Annual mortality was up (3.8%) between the ages of 16 and 40, then dropped to a lower level (1.6%). Mortality was age dependent and generally density independent. The survivorship curve agrees well with a pattern that could be expected of a species whose strategy is gap phase replacement.

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L'analyse de la structure d'âge des populations et des groupes d'*Acer pensylvanicum* L. a révélé qu'après un taux élevé de mortalité au cours de la première année (87.5%), les semis de cette espèce n'ont connu pratiquement aucune mortalité jusqu'à l'âge de 15 ans. La mortalité annuelle s'élevait jusqu'à 3.8% entre 16 et 40 ans pour diminuer subséquemment à un plus bas niveau (1.6%). La mortalité est fonction de l'âge et généralement pas de la densité. La courbe de survie correspond bien à celle dont on peut s'attendre d'une espèce colonisant les trouées.

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Introduction

The age structure of a population is the sum of the many factors that affect natality and mortality. It is a reflection of the species' life history. As such, an examination of age structure, in a survivorship curve or other form, can identify age-specific events that change mortality, and this can lead to a better understanding of the species' strategy for dealing with these events.

Deevey (1947) described three types of survivorship curves (population age distributions) of which the Type III or inverse-J curve is usually associated with tree species. Type III curves have been considered to fit a negative exponential model, a mathematical function based on a constant mortality rate (Harper 1967). Hett (1971) showed that, for sugar maple (*Acer saccharum* Marsh.), the inverse-J curve was better described by a power function model, a function based on a mortality rate that decreased with age.

In the northern hardwood forests of New England, the striped maple (*A. pensylvanicum* L.) population appears to have two basic forms: a small, slow growing or suppressed seedling form carpeting the forest floor and a large tree form growing in small forest gaps. The majority of the population is in the seedling form (Wilson and Fischer 1977; Hibbs 1978; Hibbs and Fischer 1979).

Leak (1974) reported an inverse-J relationship between density and age of striped maple in a virgin stand in central New Hampshire, but this description of the age structure of striped maple appears inadequate in light of several aspects of its life history, including the dimorphism in plant size and its gap phase replacement (Bray 1956) life cycle (Hibbs and Fischer 1979). The objectives of this study were, therefore, to determine the age structure of a striped maple population, interpret it in terms of the parameters influencing mortality, and finally, restate the age structure as a function of the underlying pattern or species' strategy.

Although it reproduces most often sexually, striped maple can reproduce vegetatively by layering and basal sprouting. Plants produced this way, however, constitute a small portion of the population. In general, vegetative reproduction of striped maple can be considered a means of surviving suppression and not a means of population increase (Hibbs and Fischer 1979).

Study Area

Data were collected from four state forests in western Massachusetts, U.S.A.: Daughters of the American Revolution (Goshen), Hawley-Savoy, Monroe, and Mt. Toby, areas that ranged in elevation from 75 to 700 m. Northern hardwood forests had covered these areas for at least 200 years and there had been almost no logging in them since about 1900. They were little affected by the hurricane of

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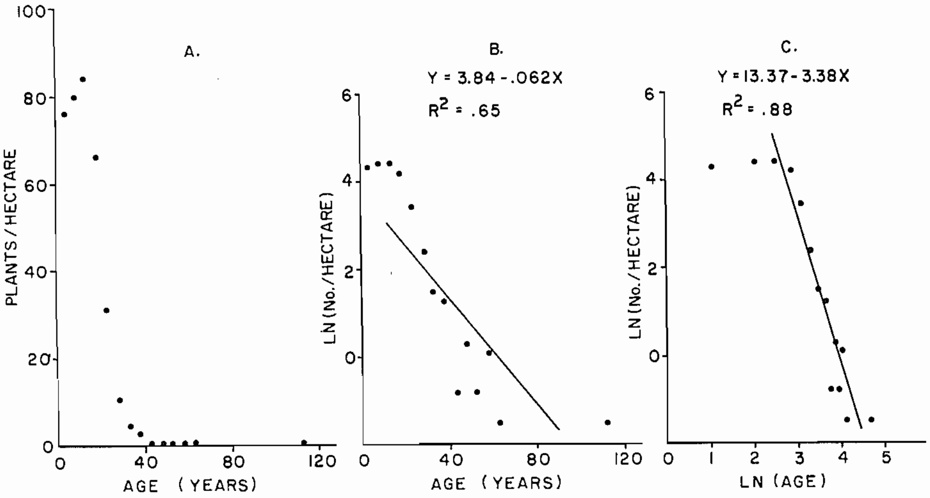

FIG. 1. The survivorship of striped maple. (A) Age distribution. (B) Negative exponential model. (C) Power function model. Regression was done with the youngest two age-classes omitted for (B) and (C).

1938. The few areas that had been recently logged were not surveyed and there had been no other major disturbance since the land was purchased by the State between 1910 and 1925.

Methods

Sampling points were located at 60-m intervals on 11.2 km of the transects lines in the four study areas. The ages of the 10 striped maple plants closest to each point and within a 13.7 m radius circle were determined by bud scale scar or ring counts. First-year seedlings were not included because the sampling was done over a period of high mortality among these seedlings. A total of 1617 trees were aged. Depending on stem diameter, plants as old as 40 years could be aged by counting bud scale scars. The age of almost any tree can be found by ring counts, but counting scars is quick and can be done in the field. A correlation of 0.994 was found between ring counts and scar counts in a sample population of 42 plants between the ages of 5 and 34, the age range over which there was most overlap in aging methods. Most errors in aging came either from inability to see annual rings well or from years missed by not taking stem sections close enough to the ground. Younger (smaller) trees are probably aged more accurately than older, with errors rarely more than 2 years. Total plant age for layered and sprouting plants was used.

Regression analysis used the BMDP statistical programs (Dixon 1975). The trees were grouped into 5-year age-classes (1–5, 6–10, etc.) and the midpoint of each class used in analysis.

The mortality of four natural populations of 20 1st-year seedlings each on Mt. Toby State Forest was followed for 1 year. The populations were under the parent tree(s) in northern hardwood, northern hardwood – hemlock, and hemlock forests.

Results

Equating a population age structure curve with a survivorship curve carries the implicit assumption that reproduction and mortality have been relatively constant over the span of ages studied, and this assumption is usually considered to be met if the habitat of the population has been consistent for a period sufficient to allow the population to equilibrate. There were three reasons for believing this to have been true for this striped maple population. First, the forest type had remained unchanged for a long time and there had been no major disturbances in the recent forest history. Second, although the age distribution found for striped maple (Fig. 1A) might be interpreted to imply that some event took place 35–45 years ago which brought about a lasting change in the reproduction of striped maple, I could identify no such phenomenon that could have covered such a large area, lasted so long, and have had such a marked effect on striped maple dynamics. Finally, the results of this study fit well into the larger picture of the life cycle and strategy of striped maple (Hibbs 1978; Hibbs and Fischer 1979). If the results of this study had not related to what else was known about striped maple, this might have been evidence that the original assumption was incorrect. That they do relate was secondary evidence, at least, that the assumption was correct. I have, therefore, called the population age structure described in Fig. 1A a survivorship curve.

The survivorship curve of striped maple after the 1st year had the inverse-J form commonly associated with other tree species as well as with many other plant and animal species (Fig. 1A). The curve had, however, an unusual feature. There was no apparent decrease in density with age for the first 15 years. In fact, the curve showed a slight increase, an increase which was not significantly different from a horizontal line when single year age-classes were considered. That is to say, there was enough year to year variation in age-class size for the first 15 years that the increase was only apparent, not real. There was a small decrease in density between 15 and 20 years of age.

The remainder of this survivorship curve had the inverse-J form and could be treated separately (Figs. 1B, 1C). From the age of 15 or 20, density decreased rapidly to near zero by the age of 40. The methods of Hett (1971) were used to analyze this decrease.

Regression on the J-shaped portion of the survivorship curve indicated that the power function model ($r^2 = 0.88$) better represented the survivorship than did the negative exponential model ($r^2 = 0.65$). The youngest two age-classes (1–10 years) were not included in the regression because they came from the period when the population showed little mortality and, therefore, appeared to represent a different function where different life history processes were operating. The survivorship curve of striped maple after the age of 10 would be described as:

$$Y = (6.4 \times 10^5)X^{-3.38}$$

where Y is the density of plants per hectare of age X years. The mortality rate after age 15 was high, 3.90 plants/ha per year by age 20, but decreased with increasing age, reaching 1.16 plants/ha per year by age 50.

The J-shaped portion of the survivorship curve could be subdivided into two phases that are visually apparent in Fig. 1A. The first phase, between the ages of 15 and 40, was a period of high mortality in which very few plants survived. The second phase, after age 40, included the population of plants that had survived the period of high mortality and were then subject to a low mortality rate.

The entire survivorship curve, therefore, had three phases: an early phase of low mortality, a middle phase of high mortality, and a final phase of reduced mortality. Simple mean mortality rates for these periods (1–15 years, 16–40 years, and 51–100 years) were near 0, 2.61, and 0.04 plants/ha per year or approximately 0, 3.8, and 1.6% of the population per year, respectively.

In four populations of 20 1st-year seedlings, total mortality the 1st year was high, averaging 87.5%, with most mortality occurring between the middle of May and early July (Fig. 2). The population under northern hardwoods had the least mortality (65%). Seedling mortality could be attributed to three causes. Seedlings either (*i*) disappeared, indicating that they had been eaten, (*ii*) wilted and died, apparently having dehydrated or been infected by damping-off fungus, or (*iii*) died during the winter.

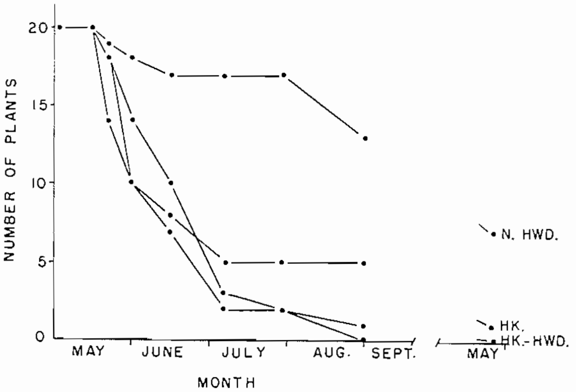

FIG. 2. Survivorship of striped maple seedlings in four natural populations of 20 seedlings each. The forest type is listed on the right.

Discussion

The survivorship pattern of striped maple produced by the synthesis of the cohort and the population age structure studies contains two periods of high mortality, year 1 and years 16–40, and two periods of low mortality, years 2–15 and over 40. This mortality is summarized in a life table (Table 1). The low mortality of plants 2–15 years old is an unusual feature for survivorship curves, being found only in a few other species (Deevey 1947).

The causes of mortality are different in each step of the life cycle of striped maple and correspond well with different phases of its life history. Mortality of 1st-year seedlings appears to be dependent on predation and the nature of the seedbed. Some of this mortality might be caused by genetic load (death attributable to genetic causes) (Franklin 1972). The mortality of plants 2–15 years old, although there may have been some variation in the size of input into each age-class, is low but certainly not nonexistent. Because these seedlings would be small, this low mortality suggests, as Wilson and Fischer (1977) found, that the seedlings are tolerant of shading. The mortality of plants 16–40 years old is the death of the shaded, unreleased plants that have grown too large to be supported in the low understory light levels. Their photosynthesis to respiration ratio has dropped below one (P:R < 1). The life expectancy of plants 40 years old or more

TABLE 1. Life table for a hypothetical striped maple population of 10 000 plants (after Harper 1977)*

Age-classes (years)	Length of period, D_x (years)	Survivorship at start of period, l_x (no.)	Mortality during period, d_x (no./period)	Mean mortality rate for period, m_x (no./year)	Life expectancy* at start of period, e_x (years)	Probable causes of death
0–1	1	10 000	8750	8750	4.1	43% eaten† 16% winter kill 41% other
2–15	14	1 250	Low	Low	28.2	Little mortality
16–40	25	1 250	1205	48	14.2	P:R < 1
41–100	60	45	43	0.7	33.6	Crown closure Physical damage
100+	—	2	—	Low	—	

*Life expectancy was found by assuming a constant mortality rate throughout a time period and a maximum age of 200 years.
†Details in text.

is greater than that of any other age group (Table 1). These trees are the small portion of the original population that is growing in forest gaps. The causes of mortality in this phase of the life cycle are the closure of the overstory canopy or random events like wind-throw.

Most of the mortality, in contrast with the usually stated case (Harper 1967), appears to be independent of the density of striped maple. First-year seedlings are spaced many plant diameters apart and so are not likely to be competing with each other. The increase in mortality for 16- to 40-year-old plants is sudden and precipitous and, therefore, not easily explained by intraspecific competition. In addition, most of the mortality throughout the life cycle can be attributed to specific causes external to the species: predation, interspecific shading, and accident.

The fitting of the power function to the survivorship curve indicates that mortality is age dependent, and this lends further support to the density independent mortality hypothesis. The mortality of striped maple is regulated by age-specific events, by the relationship between plant age and the creation and closure of forest gaps. If an opening is made, the already present plants will survive past the age of 20. Later, as the opening closes, the plants growing within it will die. There is some opportunity for density dependent mortality if several striped maple plants are released within the same small opening.

The gap phase replacement strategy of striped maple has imposed characteristic mortality rates on the population and has produced its apparent dimorphism in plant size. The high mortality of 1st-year seedlings is simply a reflection of the tenuous life of fragile seedlings. Mortality rates for the rest of the life cycle carry a clear imprint of the necessities of a gap phase replacement life cycle. The low mortality of plants 2–15 years old produces a population of suppressed plants: the carpet of seedlings scattered over the forest floor. These plants are stored in a manner analogous to the buried seed of pin cherry (Marks 1974). They are stored in anticipation of possible canopy disturbances that will provide the needed growing space to complete their life cycle. In New England, one source of canopy disturbance, windfall, averages 1–3/ha per year (Henry and Swan 1974; Lyford and McLean 1966; Stephens 1956). The high mortality in the next age-class (16–40 years) is the death of plants that have not been released by a canopy opening. The plants that are released and growing in gaps are the second major form in the population. These plants have a long life expectancy, primarily regulated by the closure of the opening in which they are growing. The continual cycle of gap creation and closure causes the release, growth, reproduction, mortality, and eventual reestablishment of the striped maple population and produces the survivorship pattern characteristic of this gap phase replacement species.

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