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HABITAT REQUIREMENTS AND GROWTH OF STRIPED MAPLE (*ACER PENSYLVANICUM* L.)[1]

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Abstract. Surveys of distribution and habitat characteristics, growth patterns, and growth in recently logged areas of striped maple (*Acer pensylvanicum* L.) were made in western Massachusetts, USA. Highest densities at a given altitude were found on mesic sites on middle and upper slopes. Density increased with increasing slope and altitude but was not affected by aspect or light conditions. Ninety percent of the striped maples were found in the northern hardwood-hemlock forest type although the type covered only 52% of the study area. Optimum height growth occurred at intermediate light intensities, on higher and more northerly slopes, and on mesic sites. Half of the plants in the nonlogged areas were growing <3 cm/yr in height. In logged areas, 75% of the plants present before overstory removal were released by removal, but most subsequent new seedlings were suppressed. The distribution and growth patterns of striped maple suggest that it is a gap-phase replacement species that utilizes temporary forest openings for growing space.

Key words: Acer pensylvanicum; *gap-phase replacement; habitat requirements; northern hardwoods; tree growth.*

INTRODUCTION

The regeneration of mature forests through reproduction in small forest openings, sometimes called gap-phase replacement, has been extensively studied in tropical forests (Whitmore 1975) but has only recently received much attention in temperate forests. In the eastern United States, there are several studies of the distribution and general characteristics of forest openings (Gysel 1951, Skeen 1976, Robertson et al. 1978, Roman et al. 1978, Runkle 1978, Wallace and Dunn 1978) but most of the existing information on the relationship between individual species and openings was collected by silviculturists interested in uneven-aged forest management, e.g., Frothingham (1915), United States Forest Service (1950), Eyre and Zillgitt (1953), Gilbert and Jensen (1958). These studies, because of the practical interests of the investigators, are limited in scope and have dealt primarily with overstory species.

This paper reports on the distribution, density, and growth of striped maple (*Acer pensylvanicum* L.) in the forests of western Massachusetts, roughly the center of its north-south range, and considers this information in terms of life history strategy and forest dynamics. In addition to its information on forest dynamics, this report has some special interest because the focus, striped maple, is an understory tree.

Striped maple appears to be a gap-phase species which responds to the increased light in small forest openings (Wilson and Fischer 1977). It occurs extensively throughout northeastern North America, extending north to the Gaspé Peninsula, west to Minnesota, and, at higher elevations, as far south as Georgia (Sargent 1933, Hosie 1969). In the White Mountains of New Hampshire, striped maple had the third highest density in a virgin northern hardwood stand, the Bowl, and the sixth highest density in an old-growth northern hardwood stand (Leak 1973).

Striped maple occurs in many forest types. Braun (1950) listed it in the mixed mesophytic, oak-chestnut, and hemlock-white pine-northern hardwood forest regions, while Kuchler (1964) placed it in the mixed mesophytic and northern hardwood types. Raup (1938) associated striped maple with the white oak-hickory, chestnut-oak, red oak, mixed hardwoods, and hemlock-hardwood types in New York State. According to Brown (1938) and Hosie (1969), striped maple occurs on moist soils in deep valleys, on cool, moist, shaded north-facing slopes, and on acid soils (Wherry 1957). Whittaker (1956) found striped maple at middle elevations (400–1700 m) and on mesic sites in the Great Smoky Mountains. In the Green Mountains of Vermont, Siccama (1974) found striped maple over the altitude range of 550–850 m. It reached its highest densities, however, below 750 m in northern hardwood

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stands. At Hubbard Brook, New Hampshire, striped maple was found over the entire watershed (W-6), from 550 to 800 m (Bormann et al. 1970). In a Tennessee study of cove hardwoods, northern hardwoods, spruce-fir, hemlock, and closed oak forests, Woods and Shanks (1959) found striped maple in 18 of 35 stands.

Methods

Field surveys were made in six state forests in the Berkshire Range: Cadwell, Daughters of the American Revolution (DAR; Goshen), Hawley-Savoy, Monroe, Mt. Toby, and Wendell; and in one isolated mountain range just east of the Connecticut River, the Holyoke Range. These forests represent most of the variety of forest conditions in western Massachusetts and range in altitude from 75 to 700 m.

The first survey, designed to evaluate habitat preference of striped maple, used a regular sampling scheme of nested circular plots spaced 60 m apart on transects in Cadwell and Mt. Toby State Forests and 121 m apart at the other sites. The lines ran north-south and covered sites of all aspects. End points of lines, usually located at roads, were chosen for convenience. Each plot consisted of two concentric circles. The larger circle (0.06 ha) was used to characterize past agricultural use (yes, no) and fire history (yes, no, fire date), and to measure local aspect, slope angle, slope position (Bowersox and Ward 1972), exposure (Fralish and Loucks 1975), forest type (Society of American Foresters 1954), number of tree stories, crown closure (visual estimate), presence or absence of rock outcrops, presence or absence of visible stones, gap size (measured in one-quarter heights of the surrounding trees), side light (nearness of canopy opening), and average canopy tree height. Slope position is a five-point scale indicating sites from the bottom (0) to the top (5) of slopes, and exposure is a five-point scale combining aspect, slope, and slope position. Indications of past agricultural use were stone walls, plow layers, and lack of windthrow mounds. Total number, number of suppressed, and number of released striped maple plants in the 0.06-ha circle were recorded using a logarithmic scale (0, 1, 2, 3, for 0, 1–10, 11–100, 101–1000 plants per plot, respectively). Suppressed plants were defined as those producing only one leaf pair from each bud in the year of the survey (Wilson and Fischer 1977).

In the smaller circle (0.01 ha), we counted the number of mounds, cut tree stumps, and individuals of each overstory species. Basal area of trees >7.6 cm dbh was estimated using a 2.3 factor prism, and O and A soil horizon depths were measured. Altitude and regional aspect were obtained from United States Geological Survey topographic maps. On plots that contained no striped maple, only historical factors, regional and local aspects, slope, slope position, exposure, and forest type were recorded. A total of 1047 plots was measured, 557 with and 490 without striped maple.

Striped maple growth was studied in a second survey limited to state forests in the northern hardwood zone of western Massachusetts (DAR, Hawley-Savoy, Monroe, and Mt. Toby State Forests), where striped maple was found to occur in the highest densities. Using a 60-m sampling interval, a total of 186 sample plots was taken on a subset of lines used in the first survey. A subset of the total list of variables was recorded, including altitude, regional and local aspects, slope, slope position, basal area, forest type, crown closure, number of tree stories, overstory tree height, and total number of striped maple (actual density, not classes). In addition, the total height, diameter above butt swell (1–10 cm above ground surface), and age of the 10 striped maple plants closest to plot center and within the 0.06-ha plot were measured. Age was determined by counting terminal bud scars or annual rings. In a population of 42 trees between the ages of 5 and 34 yr, the range in which there was a choice of aging methods, there was a correlation of .99 between the ages obtained by counting terminal bud scale scars and annual rings. Average annual height growth was determined by dividing total height by total age.

To evaluate the response of striped maple to release and logging, sampling in a third survey included all cuts <10 yr old on the Hawley-Savoy and DAR State Forests. Each cut area was overlain with a 60 × 60 m grid, and 159 circular sample plots (0.06 ha) were located at the intersections on the grid. The same list of variables as in the second survey was used, excluding number of mounds, agricultural and fire history, rock outcrops, rockiness, and side light. In addition, the number of striped maples (actual density) present before the cut and becoming established after the cut was determined by aging the plants. These two groups were further subdivided into suppressed and released plants.

The data were analyzed using the BMDP series of statistical programs (Dixon 1975). Analysis of variance was used for discontinuous variables and correlation analysis for continuous variables. Discriminant analysis supported the results of ANOVA in the habitat survey where striped maple density classes were used. Regression did not improve on the correlation analysis used in the growth and cut area studies where density and growth were recorded as continuous variables. Principal component analysis rarely produced interpretable factors and, when it did, no information not already present in the correlation matrices was added. Hence, in this paper, only results from the more simple or common analytic method are presented.

Aspect was transformed with the equation $A' = 1 + \sin(A + 45)$ so that values ranged from 0.0 (southwest) to 2.0 (northeast) (Beers et al. 1966). A modified importance value was calculated as the sum of relative basal area and relative density.

TABLE 1. Mean values of site variables in each striped maple density class. Only variables that show a significant effect ($P = .05$) of striped maple density in ANOVA are included, listed in order of decreasing significance.

Variable	Number of plots	Striped maple density classes (plants per hectare) 0	1–107	108–1667	>1668
Altitude (m)	1047	247	306	380	443
Slope (°)	1047	8.0	14.0	15.6	14.9
Slope position*	1047	2.7	3.1	3.3	3.3
Number of mounds†	557	...	0.9	1.0	1.4
Number of tree stories	557	...	1.2	1.3	1.4
Overstory tree height (m)	557	...	16.8	17.5	18.1
Crown closure (%)	557	...	76.8	76.8	72.0
Northern red oak I.V.‡	557	...	166.6	109.4	43.9
American beech B.A.§	557	...	3.5	9.1	15.3
Paper birch B.A.§	557	...	5.8	7.6	9.7
Hemlock I.V.‡	557	...	103.8	86.2	57.0

* Five-point scale, 0 at bottom.
† This variable and those below it measured only on those plots with striped maple.
‡ Importance value (I.V.) = relative basal area + relative density.
§ Absolute basal area (m^2/ha).

TABLE 2. The incidence of forest types and of striped maple within types.

Forest type*	Fraction of study area (%)	Fraction of striped maple plants (%)	Frequency of striped maple† (%)	Density of striped maple (plants per hectare)
Northern hardwood-hemlock	52	90	79	1351
Northern red oak	25	3	24	99
Oak-hickory	8	3	28	247
White pine	8	2	18	180
Spruce-fir	2	<0.5	65	180
Shrub or field	4	<0.5	16	82
Other	1	<0.5		

* The aspen-birch-pin cherry, northern conifer swamp, and red pine types are omitted from this summary because they constituted so few sample sites. Types after Society of American Foresters (1954).
† 0.06-ha plots.

RESULTS

Habitat preference

Density of striped maple increased with altitude and slope (Table 1), and was higher on slopes and ridges (positions 3–5) than in valley bottoms and lower slopes (positions 1–2).[3] The effect of disturbance is apparent in the significant increase in number of mounds, the decrease in crown closure and the increase in paper birch with increasing striped maple density. The positive relationship of striped maple with beech and the negative relationship with northern red oak suggests an affinity with the northern hardwoods forest (see also Table 2). The negative relationship with hemlock suggests that striped maple is not associated with that phase of the northern hardwood-hemlock forest type.

The relationship between forest type and the distribution of striped maple is undoubtedly confounded by the relationship between forest type and altitude. One forest type map (Society of American Foresters 1955) places spruce-fir forest on the highest part of our study area, northern hardwood-hemlock on the broad middle range, and transition hardwoods (red oak, oak-hickory) at the lowest end. It appears, therefore, that within the study area, striped maple and the northern hardwood forest have roughly coincident ranges. Striped maple was not often found in other forest types or at altitudes above or below this range.

[3] For four pages of site variable correlation matrices, see National Auxiliary Publications Service documents #03525. For a copy of this document, contact the senior author, or order from ASIS/NAPS, Microfiche Publications, Box 3513, Grand Central Station, New York, New York 10017 USA.

The negative relationship between striped maple density and red oak (*Quercus rubra* L.) (Table 1) and the low density of striped maple in the northern red oak, oak-hickory, and white pine types (Table 2) (species and types that tend to occur on drier sites), all point to a mesic site requirement for the striped maple. Whittaker (1956) also found striped maple on mesic sites in the Great Smoky Mountains, with none present in the moister, lower hemlock forests. Contrary to the statements of Brown (1938) and Hosie (1969), we found that striped maple was more common on slopes and ridges than in valley bottoms, and that density did not appear related to aspect or understory light levels, as indicated by the lack of significant relationship with regional and local aspect, overstory basal area, opening size, and nearby openings.

Size and age relationships

The relationship between plant height and age illustrates the variety of growth patterns and growth rates of striped maple (Fig. 1). The slope of line A is the maximum sustained annual growth rate of striped maple, 27.2 cm/yr for up to 45 yr. The slope of line B is the minimum sustained rate of growth, 1.0 cm/yr for up to 35 yr. After 35 yr, plants had either been released or had died. This mortality is denoted by the change in numbers on each age class, these numbers representing the population age distribution (Hibbs 1979). Plants released after prolonged suppression grew at a minimum rate of 22.9 cm/yr (line C), almost the same rate as those which had never been suppressed (line A). From this figure, it appears that most of the plants are small, with those under 20 yr old averaging <1 m tall.

Suppression and release

We used two measures of growth: suppression and height growth. Suppressed plants are, by definition,

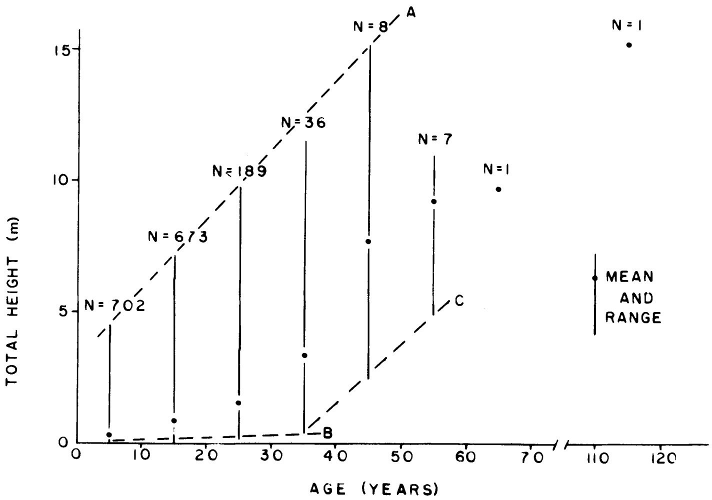

FIG. 1. Relationship of plant height to age. Ten-year age class means and ranges are indicated.

slow growing (one leaf pair per year) but a released plant could be slow growing (a few short internodes) or fast growing. In general, however, released plants grew faster than suppressed ones. In the habitat preference survey, we found an overall average of 335 suppressed and 403 released striped maple plants per hectare. Thirty-nine plants per hectare had been released but were suppressed at the time of survey. Suppressed plants tended to be found with beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), and released plants tended to be found with sugar maple (*Acer saccharum* Marsh.) (Table 3A). Disturbance as indicated by windfall mounds also appears to play a role in the creation or maintenance of suppressed populations, perhaps by representing sites of past reproduction. Several variables (e.g., paper birch, *Betula papyrifera* Marsh.) appear correlated with overall striped maple density (suppressed plus released plants).

The role of light in governing suppression is supported by the correlations of number of suppressed plants with crown closure, years since cut, residual basal area, number of stumps, canopy height, and organic horizon depth (Table 3A, B), all variables that affect or are reflections of understory light intensity. These six variables are intercorrelated, and principal component analysis grouped the first five together in one factor. The most consistent interpretation of the interrelationship and of the factor is that the variables all affect understory light levels.

Striped maple plants present before overstory removal tended to be released by cutting the overstory and those germinating after cutting tended to be suppressed (Table 4) (P = .01, G test of independence, Sokal and Rohlf 1969). In addition this indicates that most plants are capable of release, in spite of ages as high as 35 yr (Fig. 1).

Growth rate

The mean growth rate (total height over total age) of the 1617 striped maple plants measured was 2.87 cm/yr and ranged from 0.76 to 72.14 cm/yr. After logging, the mean growth rate of the 1322 plants measured

TABLE 3. Coefficient of correlation between site variables and the number of suppressed and released striped maple plants. Correlations significant at the .05 level. A. Habitat survey. The first three variables are those that appear correlated with overall striped maple density. N = 557. B. Plants which survived recent logging. N = 159.

	Coefficient of correlation	
Variable	Suppressed plants	Released plants
A.		
Paper birch B.A.*	.15	.18
Northern red oak I.V.†	−.14	−.19
Altitude	.10	.23
Crown closure (%)	.10	−.16
Organic horizon depth	.11	...
Sugar maple B.A.*	...	.11
Number of mounds	.10	...
Yellow birch I.V.†	.10	...
Regional aspect	−.10	...
Hemlock I.V.†	...	−.10
Canopy height	...	.09
B.		
Crown closure (%)	.30	...
Years since cut	.25	...
Residual basal area	.25	...
Number of stumps	−.22	...
Canopy height	.22	...
Organic horizon depth	.20	...
Slope	−.16	...
Local aspect	−.16	...

* Absolute basal area (m^2/ha).

† Importance value (I.V.) = relative basal area + relative density.

TABLE 4. The density of suppressed and released striped maple plants of pre- and post-cut origin in recently logged areas.

Plant condition	Density (plants per hectare) Pre-cut origin	Post-cut origin
Suppressed	171	203
Released	1174	47

in recently cut areas was 20.3 cm/yr, ranging from 1.0 to 107.4 cm/yr.

In recently cut areas, the highest growth rates for striped maple were found at residual stand basal areas of 4.7–9.2 m^2/ha. Growth rate decreased as basal area increased or decreased from this range (Fig. 2). Lack of light in deep shade clearly limits growth. The limiting effect of full sun, also seen by Hosier (1974), Leak and Solomon (1975), and Wilson and Fischer (1977), is not well understood. We did note, however, that open-grown striped maples had misshapen leaves and were generally multistemmed in contrast to the usual single stem of forest-grown plants. The light conditions provided by stands in this optimal density range would correspond to those found under very thin canopies or in small canopy openings.

Variables affecting understory light which affected suppression (Table 3) appear again in an analysis of annual growth rates (Table 5). In addition, growth rates prior to overstory cutting are correlated with later growth, perhaps a reflection of site differences. Under similar light conditions, plants on better sites grow faster than those on poorer sites. Striped maple height growth also increased from the bottom to the top of slopes and, in spite of a small increase in basal area, height growth increased with altitude (Table 5).

DISCUSSION

In western Massachusetts, striped maple occurred at highest densities at the higher altitudes and on the steeper slopes in the northern hardwood forest of the Berkshire Range, and at lower densities in the Connecticut River Valley and hills to the east where both altitude and slope were less. The density and distribution of striped maple did not seem to be influenced by aspect or understory light conditions although the growth rate was largely controlled by light conditions.

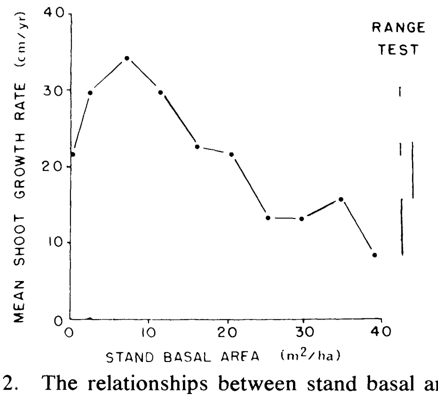

FIG. 2. The relationships between stand basal area and mean shoot growth rate of striped maple in recently logged areas. Using Duncan's new multiple range test (Steel and Torrie 1960), growth values spanned by the same vertical bar on the right of the figure are not significantly different (P = .05. N = 1322).

TABLE 5. Coefficients of correlation between mean annual shoot growth (cut area) or the log of mean annual shoot growth (uncut area); N = 159 and 186, respectively. Correlations significant at the .05 level.

Variable	Coefficient of correlation Cut area	Uncut area
Previous growth	.39	...
Number of tree stories	−.38	...
Number of mounds	−.32	−.18
Crown closure (%)	−.30	−.28
Residual basal area	−.27	−.16
Slope position	.17	.21
Altitude	.17	...
O horizon depth	.16	...

Associations with canopy disturbance and adaptations to a gap-dependent life cycle are found in many aspects of the distribution and growth of striped maple. The total density of striped maple increased with the number of windthrow mounds; thus, in some way, general density increases near mounds must be related to past canopy disturbances resulting from windthrow. Presumably, gaps are more common in older forests due to both tree senescence and extended exposure to disturbance, and the density of striped maple did increase with stand age as indicated by the positive correlation with tree height (an approximation of age) and striped maple's association with the northern hardwood forest type. This type is at the end of the common New England sere: old field to white pine and/or grey birch to northern hardwoods, and is the type in which striped maple was most abundant. The density of suppressed plants also increased with windthrow mound density and is part of the same disturbance-related phenomenon. These plants may represent past reproduction, now awaiting release, near old disturbances. Finally, growth rates decreased with increasing mound density. This may simply be stating the obvious, that the suppressed plants, in this instance associated with mounds, are slow growing.

The growth pattern of striped maple is unusual, although a similar pattern has been described for sugar maple (Bourdo 1968). Most of the striped maple individuals are small, slow-growing plants, seedlings that persist on the forest floor for up to 35 yr. If released, these plants can grow rapidly at rates of up to 1 m/yr. A striking difference between the growth patterns of striped and sugar maple is that, while sugar maple grows into the surrounding canopy and reproduces there, striped maple does not. With a maximum height of ≈15 m, striped maple will rarely join the forest canopy. Rather, it reproduces under it and probably at a younger age than larger species like sugar maple.

The relationship between height growth of striped maple and understory light is strongly indicative of a gap-phase strategy. Not only did growth increase with increases in light as reflected in the different measures of overstory density, but growth declined if understory light levels became too high. Wilson and Fischer (1977) found maximum seasonal height growth of striped maple at 32–58% of solar radiation in the open, this range presumably corresponding to the maximum growth found at 4.7–9.2 m^2/ha of basal area in the field measurement. This pattern of light response appears to indicate that striped maple is best adapted to growing under thin canopies and in small forest openings.

Different phases in the life cycle of striped maple (suppressed plants, released plants) are associated with different major northern hardwood species (Table 3), but the reasons for this are not clear. Sugar maple, as a competitor in small openings (Gilbert and Jensen 1958, Leak and Wilson 1958, Bourdo 1968) might be expected to be found with released plants. Yellow birch, however, also utilizes forest openings for regeneration (Eyre and Zillgitt 1953, Gilbert and Jensen 1958, Leak and Wilson 1958, Forcier 1975) and is found more commonly with suppressed striped maple plants. The relationship with beech is difficult to judge because of the changing role of beech in forest dynamics brought about by the beech scale-*Nectria* disease.

The life cycle of striped maple can be summarized as follows: most plants in the population are suppressed seedlings stored on the forest floor in anticipation of eventual release resulting from canopy disturbance. Upon release, plants can respond with rapid height growth, with growth at its maximum in small openings and under thin canopies. Reproduction generally takes place under the canopy and the striped maple plants are eventually overtopped by competing regeneration or by closure of the canopy overhead.

Yellow birch and sugar maple are two species that commonly co-occur with striped maple and all three species exhibit some gap-phase related behavior. To understand more fully the position of striped maple in the northern hardwood forest, it is necessary to understand the relationships between these species. To facilitate this comparison we will use a framework provided by Whitmore (1975) for the comparison of gap-related strategies of tropical trees. He divided species into four classes:

a) those species whose seedlings both establish and grow up under high forest;
b) those which establish and grow up under high forest but show some signs of benefiting from gaps;
c) those which establish mainly in high forest but definitely require gaps to grow up; and
d) those which establish mainly or entirely in gaps and only grow up in gaps.

While few, if any, temperate tree species fall into the first category, we think that the other categories can provide useful distinctions.

Yellow birch becomes established in openings and requires them for growth (category d). It grows best with side shade and in openings of ≈0.01–0.03 ha (Frothingham 1915, United States Forest Service 1950, Eyre and Zillgitt 1953, Gilbert and Jensen 1958, Leak and Wilson 1958, Forcier 1975, Roman et al. 1978). Sugar maple becomes established in forests but grows in openings (category c). It becomes established better in partial shade than full sun (United States Forest Service 1965) and grows best in the partial shade of small (<0.01 ha) forest openings (United States Forest Service 1950, Gysel 1951, Gilbert and Jensen 1958, Leak and Wilson 1958, Bourdo 1968). Forcier (1975), however, implies that sugar maple can grow up under and through yellow birch canopies. In either case, the prime points of differentiation between these species are that they have different requirements for establishment, and that yellow birch utilizes slightly larger openings than sugar maple.

Striped maple falls easily into category c, along with sugar maple. It becomes established under a canopy and grows up in openings. An ecological question to answer, then, is how can these two species with the same apparent strategy be distinguished from each other ecologically? A difference between sugar maple and yellow birch lies in the size of opening utilized, and the same distinction may be employed to differentiate between sugar and striped maple. Sugar maple is a large tree that can dominate a large area of the forest when mature. Sugar maple requires, therefore, an opening large enough to accommodate its size and large enough to remain open overhead until it reaches the canopy. Striped maple never becomes large; consequently, it does not require much lateral growing space. Moreover, it rarely gets tall enough to reach the canopy. Striped maple appears, therefore, to utilize smaller openings than sugar maple. By maintaining a population of stored seedlings, responding rapidly to release, growing well in partial shade, and reaching maturity at relatively small sizes, striped maple can efficiently utilize small, even temporary openings. These openings would not be available to a species that needs to reach the canopy before beginning to reproduce.

The above discussion provides a glimpse of a much larger and very important process in forest dynamics. Yellow birch, sugar maple, and striped maple are examples of species that appear to utilize different portions of the spectrum of sizes of forest openings. Openings can range from large ones colonized by pioneer species (not usually considered gaps) to small ones. Pin cherry (*Prunus pensylvanica* L.) requires openings of at least 0.1 ha (Marks 1974) while striped maple appears to utilize some of the smaller openings. Even smaller ones may be utilized by ephemeral species. The result is a changing array of species adapted to different opening sizes within a mature forest. Given this variety of possible opening sizes and associated species, it becomes easier to understand the mosaic type of forest structure discussed by Horn (1974) and Williamson (1975) and the role of striped maple in this structure.

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