
Sexual and Vegetative Reproduction of Striped Maple (Acer pensylvanicum L.)
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Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.)

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HIBBS, D. E. (Univ. Mass., Amherst, Mass. 01003) and FISCHER, B. C. (Purdue Univ., West Lafayette, Ind. 47907). Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). Bull. Torrey Bot. Club 106: 222–227. 1979.—Striped maple (*Acer pensylvanicum* L.) may reproduce sexually and vegetatively. Many aspects of both processes appear to be adaptations to the unpredictable occurrence, variable duration, and wide spacing of forest gaps. Flowering appeared to be initiated by a decline in plant growth brought about by crown closure. Further deterioration in growth conditions and plant health caused a sex change from male to female. Striped maple was primarily dioecious with a ratio of approximately 81 male: 15 female, but 4% of the population was monoecious. Seed dispersal was localized but appeared to offer the opportunity for wide dispersal. Layering and basal sprouting appeared to be means by which smaller and larger plants, respectively, cope with suppression caused by crown closure.

The life history of striped maple (*Acer pensylvanicum* L.) presents an unusual set of conditions and constraints within which reproduction must take place. Striped maple is an understory tree which maintains a population of slow growing plants "stored" on the forest floor, plants that can

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rapidly respond to release as a result of canopy disturbance. These stored seedlings undergo little mortality for about 20 years. When forest openings are formed, the stored seedlings must grow rapidly, reproduce, and disseminate seed to maintain the dispersed, stored seedling population (Wilson and Fischer 1977; Hibbs 1978).

Little is known about reproduction of striped maple. We could find no reports of vegetative reproduction although we have observed both layering and basal sprouting. Vegetative reproduction is found, however, in red maple (*A. rubrum* L.), vine maple (*A. circinatum* Pursh), and mountain maple (*A. spicatum* Lam.) (Wilson 1968; Anderson 1969; Post 1969). The reports on sexual reproduction of striped maple are confusing and somewhat contradictory. Striped maple has been characterized as both monoecious (Hosie 1969) and dioecious (Brown 1938). De Jong (1976), looking at garden grown specimens in Europe, found examples of dioecy and monoecy. The monoecious trees had male, female, and sometimes, complete flowers. In a sample of eight trees followed for 6 years, he found some sex changes, with the plants usually single-sexed, but also monoecious at some time in the period. De Jong found that the natural populations represented in European herbaria contained few monoecious individuals and that, on these few trees, male flowers occurred higher in the tree than female flowers.

The objective of this study was to describe the reproductive habits of striped maple and to characterize them in terms of the species life history. Because the literature is unclear about the importance and process of both sexual and vegetative reproduction, there is value in studying a species that employs such a wide range of reproductive tactics. In addition, it is important to understand how these tactics are adapted to a life cycle that appears to utilize the light resource of small forest openings.

Methods. The study areas were located in five state forests (Cadwell, Hawley-Savoy, Monroe, Mt. Toby, and Wendell) and one isolated mountain range (the Holyoke Range), representing most of the forest situations in western Massachusetts. These study areas covered the altitude range of 75 to 100 m. We used a regular sampling scheme of circular plots (0.06 ha) spaced 60 (Cadwell and Mt. Toby) or 121 m apart on transect lines originally located on USGS topographic maps.

Within each plot the number of striped maple plants that had been suppressed, released, or resuppressed, or had flowered were counted. Suppressed plants (usually seedlings) were those which produced only one leaf pair in the summer of the survey and resuppressed plants (usually larger plants) were those that had been released in the past (two or more leaf pairs per year) but were suppressed at the time of the survey. Because flowers are often produced by terminal buds, frequent forking of the upper, smaller branches less than 10 years old was considered to be an indication of recent flowering. This branching pattern was rarely observed on trees known to be nonflowering.

The density of plants with a given characteristic in each plot was used to calculate correlation coefficients. Densities ranged from 0 to over a thousand stems per plot with an average density of 49 plants per plot (810 plants per ha). Only the 557 plots with striped maple on them were used in analysis ($N = 557$).

The stems from one unusually large sprouting stump were dissected and aged to determine the extent to which sprouting could prolong life. The original stem was dead, so an assumed overlap of ten years between this stem and the oldest sprouts was used to calculate total tree age. An overlap figure of ten years was used because no living stems were observed in the course of the study to have sprouts over ten years old.

Flowering habits were studied in populations in the Holyoke Range and Mt. Toby State Forest. We found three kinds of flowers on striped maple plants and classified them as functionally male, female, or complete (after de Jong 1976). Population sex ratios were determined by inspection of flowers on each tree in two sample populations ($N = 69$ on the Holyoke Range, $N = 243$ on Mt. Toby). Trees were either male or female or had flowers of both sexes. The vertical position on the tree of flowers of each sex was noted for plants in the latter category. In the spring of 1976, members of a flowering population of 243 trees in the Mt. Toby State Forest were sexed and tagged for later identification. In the fall of

Table 1. Sex of striped maple plants in two populations of flowering trees.

		Plant sex		
Population	N	Male %	Male and female %	Female %
1	69	81	3	16
2	243	82	5	13

1976, trees with seed were identified as a double-check on the spring census. The following spring (1977), the sex of each flowering tree was determined again and its health noted. Unhealthy trees had discolored bark and few or wilted leaves. Bark damage on upper or south-facing stem surfaces, not of animal origin, and similar in appearance to sunscald was recorded as scald. The height of each tree was recorded and, at the end of the study, a subsample of 48 trees was collected for aging by ring count.

The dispersal of seed (samaras) was measured using traps and litter sampling. The traps, horizontal meter-square wooden frames with a plastic bottom, were placed at 10 m intervals to a distance of 60 m in four directions from the seed source. Litter sampling for seed was done in the spring by carefully removing the litter from meter-square samples starting at the base of the seed tree and proceeding in 10 m intervals in four directions to a distance of 30 m.

Viability of 6,000 seed from a single source was tested. Seed was wrapped in damp paper towels, enclosed in a jar, and stored in the dark for six months at 5 C.

The nomenclature follows Fernald (1950) except for *Acer circinatum* Pursh which follows Van Dersal (1938).

Results. VEGETATIVE REPRODUCTION. Layered plants arose where branches, stems or whole plants had been bent to the ground and buried in litter. In general, plants that were layered had been spindly and under 3 m in height. Layering produced one to 30 new stems, depending on the number of branches involved. An average of 24 stems per ha, 3% of the striped maple population were produced by layering.

Plants with basal sprouts were generally the larger plants and produced from one to 20 sprouts from the lower 20 cm of the stem. No root sprouts were found. Eight percent of the striped maple plants (65 plants per ha) had basal sprouts. Sprouting seemed to be followed by the death of the main stem within 10 years.

One large sprouting stump was approximately 110 years old. The original stem was approximately 75 years old and had been dead for many years. There were two succeeding generations of sprouts, one aged 40 to 45 years and a second 22 to 26 years old. While this plant was unusual in its size and age, it is an example of the extent to which sprouting can extend the life of a striped maple plant.

SEXUAL REPRODUCTION. Seven percent of the population (52 plants/ha) showed evidence of flowering in the past 10 years. The density of flowering plants was poorly correlated with the densities of suppressed ($r = 0.25$) and resuppressed ($r = 0.33$) plants and not significantly correlated with the density of released plants ($P = 0.05$; Snedecor and Cochran 1976). Among the 48 flowering stems aged on Mt. Toby and 40 from other study areas, most were over 4 m tall and 30 years old. The youngest was 11 years old, and the smallest was 1 m tall.

Male and female flowers were similar in overall size and structure. Male flowers had well developed stamens and anthers (2.5 to 4.0 mm long) but lacked a pistil. Female flowers had well developed pistils and ovaries and had anthers and stamens less than 1 mm long. The anthers in female flowers did not open to release pollen. Complete flowers (less than 0.1% of the total) had fully developed and apparently functional pistils, stamens, and anthers.

Flowers were produced in terminal and lateral racemes. Inflorescences, with only rare exceptions, were single-sexed. Terminal flowering gave rise to a fork in the branch.

In two populations of flowering trees,

Table 2. The number of healthy and unhealthy, scalded and unscalded striped maple trees separated by plant sex in a population of flowering striped maple trees on Mt. Toby State Forest.

	Sex	
Plant condition	Female	Male
Healthy	8	164
Unhealthy	14	6
No scald	3	105
Scald	19	65

most of the individuals had male flowers, some had female flowers, and a few had flowers of both sexes (Table 1). In these few monoecious trees, flowers of different sexes were found in the same raceme, in different racemes on the same branch, on different branches, and on different main stems of the same plant. Most of these bisexual plants had a number of female flowers on a primarily male plant, and the female flowers were generally limited to partially broken or otherwise injured stems. Complete flowers were found in racemes with both male and female flowers. There was no apparent vertical stratification of male and female flowers on trees from 1 to 10 m tall.

Flower sex had no significant relationship with plant height or age, but did have a highly significant relationship with health and scald (Table 2). Females were significantly less healthy than males (P = 0.01, G-test of independence, Sokal and Rohlf 1969). In some portions of the study area, there was a high incidence of sunscald or similar appearing injury, and, in the flowering study, female plants tended to have scald (P = 0.01).

In a flowering population on Mt. Toby State Forest, 24 of 243 plants changed sex from 1 year to the next (Fig. 1). Changes were from male to bisexual (seven plants), male to female (eight plants), and bisexual to female (six plants). Three plants changed sex in the opposite direction. There was, therefore, a net directional change from male to female with the possibility of an intermediate step of plants with flowers of both sexes. In addition, two-thirds of the plants identified as female the first year had died by the second year.

Seed production ranged from approximately ten seeds per plant to several thousand. One 7 m tree produced 3,700 seeds, and the density of seed collected in seed traps around this tree dropped from 13.75 seeds per m^2 at 10 m to 1.25 seeds per m^2 at 60 m. The degree of dispersal around a second tree (about 2,000 seeds) measured by litter sampling was less. We found 55 seeds per m^2 at 0 m and 0.75 seed per m^2 at 10 and 30 m. Some seed was observed on the trees until about the time of flowering the following spring. In the viability test, 88% of the seed germinated.

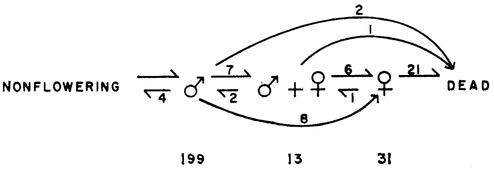

Fig. 1. Sex changes in one year in a population of 243 flowering striped maple trees.

Discussion. Vegetative reproduction. For some woody plant species, vine maple (*Acer circinatum* Pursh), mountain maple (*A. spicatum* Lam.), and hazelnut (*Corylus cornuta* Marsh.), vegetative reproduction is an important means of increasing population size (Anderson 1969; Post 1969; Tappeiner 1971). This does not appear to be true for striped maple although the species is quite able to both layer and produce basal sprouts. Plants produced by layering constituted only three percent of the population. Basal sprouting, while occasionally producing large sprout clumps, accounted for only 8% of the population.

If the vegetative reproduction of striped maple is thought of in terms of the species' life history, its function becomes apparent. In a forest understory, there must be situations in which growth conditions are not optimal but are sufficient for some growth. If these conditions occur beneath thin canopies or small canopy openings, the light resource that they represent will likely soon be lost. In these situations, vegetative reproduction allows a plant to have its biomass reduced and to await future canopy disturbances. Basal sprouting, as in the case of the one sprouting stump we investigated in detail, is a means by which large plants can respond to resuppression. In a similar fashion, layering is a method by which smaller plants that have been resuppressed can reduce their biomass and survive until growing conditions improve. Auclair and Cottam (1971) discussed a process of dying back and resprouting in black cherry (*Prunus serotina* Ehrh.), pointing out that basal sprouting allowed a plant to survive suppression and be in better condition for later release. A similar process occurs in white oak (*Quercus alba* L.) seedlings (Merz and Boyce 1956). Most oak "seedlings" (74%) were, in fact, sprouts with real ages up to 37 years.

Sexual reproduction. In general, the flowering striped maples were the larger plants. The average height for the whole population was under 1 m (Hibbs 1978) while the average height for a flowering plant was over 4 m. We found, however, that small (1 m tall) or young (11 years) plants could flower. Flowering plants also appear to have been the resuppressed plants. They were not released plants, and it is unlikely that they were suppressed plants because most suppressed plants were seedlings.

Because resuppression would occur when the opening in which a tree was growing began to close overhead, it may be that flowering is brought on by crown closure. Complete crown closure would eventually kill the tree. If this is so, these flowering stems would be near the end of their life cycle and in a reproductive phase for the short period before their biomass became too large to be supported by the diminishing light levels.

While striped maple has been described as both monoecious (Hosie 1969) and dioecious (de Jong 1976; Brown 1938), it is —together with *Acer negundo* L.—one of the few dioecious maple species. Most maples are dichogamous or duodichogamous (de Jong 1976). A few individual striped maple plants had flowers of both sexes. Nevertheless, with rare exceptions, a given flower was either functionally male or female. This is in agreement with de Jong (1976) who reported finding most striped maple trees to have either only male or only female flowers. This is also in general agreement with the statement of Wright (1953) that structurally, but never functionally, perfect flowers can be found in *Acer*.

In both populations of flowering trees, most of the individuals had male flowers. This condition presumably extends to the general population. H. Michaels (personal communication) has found a male biased sex ratio in *A. rubrum.* The skewed sex ratio may be an adaptation by striped maple to the wide spacing of forest openings (more pollen to cover large areas) or, alternatively, it may allow younger (smaller) plants to produce pollen with little reduction of vegetative growth and older, more mature trees to produce seed as vegetative growth slows.

Striped maple can change flower sex from year-to-year, and, in one population at least, the net change is strongly directional from male to female. If sex has some relationship with plant health, and the annual death of two-thirds of the female population seems to support this relationship, then it is likely that some internal nutritional or hormonal balance regulates sex change. This change, related to plant health and, therefore, probably to a deterioration in growing conditions, may indicate that sex change is regulated by progressive crown closure. This sequence of male to female potentially allows each plant to produce pollen early in the reproductive cycle and seed shortly before death.

Changing sex and the keying of sex change to crown closure appear to be adaptations of this species for growth in forest gaps. If there are only 52 flowering trees per ha and about 80% of them are male, then the density of female, seed producing trees is low. Changing sex, however, allows each tree to produce seed while previously having produced pollen. The further adaptation of keying sex change to progressive crown closure insures that trees from each gap will produce seed. In this way, seed is produced in as many locations as possible in the first step toward producing the dispersed stored population of plants necessary to repeat the life cycle.

Seed from scattered seed-bearing trees is concentrated in a 30 or 40 m radius circle around the parent tree, but can travel more than 60 m. Seed that falls from the tree in the winter has the potential to be blown on top of the snow for considerable distances. This distance might correspond to the maximum dispersal of 4 km for an unspecified maple species reported by Pijl (1972). With an average spacing of about 14 m (52 plants per ha) between flowering plants and remembering that most of these will eventually produce seed, it is apparent that seed dispersal is adequate to cover the distances needed to colonize most sites within a forest. When flowering trees are clustered together in openings, the actual distance between points of reproduction may be greater than 14 m. Using the 3,700 seeds per tree as a rough and perhaps higher than average estimate of production and a viability of around 88%, the 10 female trees per ha will produce 32.600 viable seeds per ha per year, a number that would seem adequate to insure restocking of the seedling population.

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With the last steps of seed production and dispersal, the sexual reproduction cycle is complete. Within this cycle and within the vegetative reproduction processes are found many apparent adaptations to the creation and closure of gaps in the forest canopy. The sexual cycle includes a male biased sex ratio, directional changes of plant sex, and possible keying of the flowering process to gap dynamics. Through the sexual cycle the dispersed seedling population is maintained. By layering and sprouting, false starts under poor growth conditions do not necessarily have fatal results. Together, these two reproductive processes enable striped maple to successfully reproduce as a forest understory tree.

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Comments on *Cuscuta*—For collectors and curators

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AUSTIN, DANIEL F. (Dept. Biol. Sci., Florida Atlantic Univ., Boca Raton, Florida 33431). Comments on *Cuscuta*—for collectors and curators. Bull. Torrey Bot. Club 106: 227–228. 1979.—Study of *Cuscuta* for almost a decade has led to certain ideas about how specimens should be prepared. It is recommended that material without mature flowers not be collected unless in fruit; that fertile host plants be collected; and, that specimens be mounted within packets.

Over the past few years (1969–1978) it has been my task to attempt determinations of a great many collections of *Cuscuta*. These parasitic members of the Convolvulaceae have had no thorough systematic examination since studies of George Englemann in the late 1800's (cf. Englemann 1859) and T. G. Yuncker in the early

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