

Aceraceae C Maple family

Acer L.

maple

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Growth habit, occurrence, and use. Maples C members of the genus *Acer* C are deciduous (rarely evergreen) trees; there are 148 species (de Jong 1976; Van Gelderen and others 1994). The majority of species originate in central and eastern Asia, China, and Japan (de Jong 1976; Van Gelderen and others 1994; Vertrees 1987). There are several taxonomic treatments available for the genus. Vertrees (1987) and Van Gelderen and others (1994) should be consulted for a discussion and comparison of the different classifications. Van Gelderen and others (1994) recognize 16 sections, some of which are further divided into 2 to 3 series. The publications by De Jong (1976), Van Gelderen and others (1994), and Vertrees (1987) are filled with interesting information and are wonderful reference books for the genus *Acer*.

Based on the classification of Van Gelderen and others (1994), there are 9 species in the United States and Canada (tables 1 and 2). In addition, there are 8 species closely related to sugar maple C these include black maple, Florida maple, bigtooth maple, and whitebark maple C as well as a number of subspecies for others. Van Gelderen and others (1994) actually classify the 4 species mentioned above as subspecies of sugar maple. Eight of the 16 sections of the genus are represented in North America (Van Gelderen 1994). Additionally, a number of species (table 1) have been introduced for use as ornamentals (Burns and Honkala 1990; Dirr 1990; Dirr and Heuser 1987; Fischer 1990; Van Gelderen and others 1994; Vertrees 1987). The native species range in size from trees that dominate forest canopies to medium to tall understory shrubs or small trees (table 2). Boxelder has been introduced into Alaska, where it survives and reproduces; however, it does dieback periodically under extreme winter temperatures (Viereck 1997).

The native maples all regenerate vegetatively by basal sprouting, but the ability to do so varies among species and with plant age (Burns and Honkala 1990; Fischer 1990). Vine, Rocky Mountain, striped, and mountain maples frequently layer, giving them the potential to develop relatively complex clones of varying size and morphology (Hibbs and Fischer 1979; O'Dea and others 1995; Post 1969; Zasada and others 1992).

Some species of maple are important sources of firewood, pulpwood, high-quality lumber, and veneer (Alden 1995; Burns and Honkala 1990). Four species have been used to produce maple sugar and syrup C sugar, black, red (Jones 1832; USDA FS 1982), and bigleaf maple. Sugar maple is the most important of these species because it has the highest sugar content. In the western United States, bigleaf maple produces adequate quantities of sap, but its sugar content is low compared to the sap of sugar and red maples, and the flow is erratic (Burns and Honkala 1990). Maples are very

important for wildlife, providing browse and cover for a variety of mammals, important sites for cavity-nesting birds, and food for seed-eating mammals and birds (Burns and Honkala 1990). Maples are also important substrates for various lichens and mosses. Their occurrence on mountain slopes makes them useful in the protection of watersheds. Boxelder is an important species for shelterbelt planting.

Many of the maples have ornamental value because of their attractive foliage or interesting crown shape, flowers, or fruit; native and introduced maple varieties with desirable features such as a particular foliage color or attractive bark have been propagated specifically for ornamental use (Dirr 1990). For an interesting discussion of variation in form and leaf morphology in Japanese maples, see the wonderfully written and illustrated book by Vertrees (1987).

Flowering and fruiting. There is substantial variation within the genus in terms of gender of trees. Some species—for example sugar, black, and bigleaf maples—are monoecious with flowers that appear perfect but are functionally either male or female. In the monoecious species, the functionally male and female flowers often occur in different parts of the crown (Burns and Honkala 1990; De Jong 1976).

Other species—for example boxelder and red, striped, silver, and bigtooth maples—are primarily dioecious, but some individual trees are monoecious to varying degrees. In natural populations of red maple, the sex ratio tends to be male-biased. The ratio may vary somewhat between geographic areas within the species range. Sex ratio was also found to be highly skewed to males in red maples just beginning to flower. Change of sexual expression does occur in these dioecious species but only in a small percentage of the population. Variation in sex expression was related to site conditions in boxelder (Freeman and others 1976), but the relationship of gender to site has not been well-established for all species. There do not appear to be consistent differences in growth rate between males and females. Sakai and Oden (1983) reported that monoecious silver maples were larger than dioecious trees and exhibited a different size distribution pattern. Male boxelder trees showed no growth advantage over females despite the increased amount of carbon needed for fruit production (Willson 1986). However, it was observed that female trees that were previously male had a higher mortality rate than trees that were consistently male or trees that were previously female (Barker and others 1982; De Jong 1976; Hibbs and Fischer 1979; Primack and McCall 1986; Sakai 1990b; Sakai and Oden 1983; Townsend and others 1982).

Flowering and pollination occur in spring and early summer (table 3). Dichogamy (male and female parts in the same flower or different flowers on the same tree mature at different times) is common in maples and has been described for sugar maple and other species (De Jong 1976; Gabriel 1968). Insect and wind pollination both occur, but the relative importance of each differs among species (De Jong 1976; Gabriel 1968; Gabriel and Garrett 1984).

The fruit is composed of 2 fused samaras (a term used interchangeably with seed here), which eventually separate on shedding, leaving a small, persistent pedicel on the tree. The fused samaras may be roughly identical in appearance or differ in physical size; both samaras may or may not contain viable embryos (Abbott 1974; Greene and Johnson 1992). Parthenocarpic development occurs but differs in the strength of expression among species; this phenomena may explain size differences in paired samaras (De Jong 1976). Samara pairs may occur singly or in clusters of 10 or more. The fruits of the maples vary widely in shape, length of wings, and angle of divergence of the fused samaras (figure 1) (Carl and Snow 1971; De Jong 1976; Greene and Johnson 1992; Sipe and

Linnerooth 1995). Each filled samara typically contains a single seed without endosperm (figure 2). However, polyembryony has been observed in sugar and bigleaf maples (Carl and Yawney 1972; Zasada 1996). Maple seeds turn from green or rose to yellowish or reddish brown when ripe; the color of mature samaras can vary among species. Pericarps have a dry, wrinkled appearance when fully mature (Albenskii and Nikitin 1956; Anonymous 1960; Carl and Snow 1971; Harris 1976; Rehder 1940; Sargent 1965; Vertrees 1987).

The embryo with associated seedcoats is contained within the pericarp (figure 2). The surface of the pericarp is usually glabrous (except that of bigleaf maple, which has dense, reddish brown pubescence). The pericarp can be extremely hard (particularly when it has dried out) and difficult to cut open. Development of the samara in black maple has been described in detail by Peck and Lersten (1991). Both the pericarp and seedcoat have been identified as causes of dormancy. The cavity (locule) in which the embryo occurs may have concave or convex walls. There are 2 types of embryo folding: (a) incumbent folding, in which the hypocotyl is against the back of one cotyledon, and (b) accumbent folding, in which the hypocotyl is against the edges of the folded cotyledons. Of the native maples, vine and sugar maples are classified as incumbent and the others (except bigtooth maple, which was not classified) are accumbent. The cotyledons may be green while still in the pericarp (Carl and Yawney 1972; De Jong 1976; Dirr and Heuser 1987; Olson and Gabriel 1974; Peck and Lersten 1991; Vertrees 1987).

During the maturation process, the pericarp and wing change color as seed biochemistry, anatomy, and moisture content change (Carl and Yawney 1966; Peck and Lersten 1991; Vertrees 1987). Both anatomical and physiological studies indicate that green samaras photosynthesize, thus contributing to the carbon balance and growth of the fruit (Bazzaz and others 1979; Peck and Lersten 1991).

The native species can be divided into 2 groups based on timing of seed dispersal (table 3) (Burns and Honkala 1990). Silver and red maples release samaras in late spring and early summer, whereas the other species disperse theirs in late summer and fall. The summer-dispersing species appear to release seeds over a period of about 1 month (Bjorkbom 1979). The fall-dispersing species release samaras in a more protracted manner, usually over 2 months or more (Bjorkbom 1979; Garrett and Graber 1995; Graber and Leak 1992). In sugar maples, seedfall has been observed in every month of the year, but seeds dispersed during the summer months are usually empty (Garrett and Graber 1995). Bigleaf maples in western Oregon and Washington may retain seeds through March.

The mechanics of samara flight following release from the tree have been studied in considerable detail (Green 1980; Greene and Johnson 1990, 1992; Guries and Nordheim 1984; Matlack 1987; McCutchen 1977; Norberg 1973; Peroni 1994; Sipe and Linnerooth 1995). The remainder of this paragraph briefly summarizes the main points of these papers. Maple seeds spin when they fall. There are 2 components to flight—the initial free-fall before spinning and the spinning itself. Depending on species, the initial phase covers a distance of 0.4 to 0.8 m. The terminal velocity attained during spinning varies from 0.8 to 1.3 m/sec and is related to the size of the seed. Within an individual species, descent rate of individual samaras varied from 0.6 to 1.7 m/sec depending on seed size and shape. These are the main factors determining how far seeds will fly during primary dispersal under different wind conditions. In relatively strong winds, the free-fall phase may not occur. Wind conditions for early summer dispersal of red and silver maples may

differ substantially from those of fall dispersal of seeds because the fully developed canopy can affect within-stand wind conditions. Secondary dispersal after flying may occur over a fairly long distance if seeds fall into moving water or a short distance if seeds are cached by rodents or moved by rainwater or snowmelt.

The maximum dispersal distance for maple seeds is reported to be at least 100 m under open conditions as might occur in a large gap or clearcut (Burns and Honkala 1990). Dispersal distance and patterns of seed rain will vary within stands due to tree distribution and stand microclimate. For example, seed rain around an individual red maple within a hemlockBhardwood forest dropped from 340 seeds/m² (range, 200 to 450/m²) at the base of the tree to about 50/m² (range, 0 to 100/m²) at 10 m from the base (Ferrari 1993). The large variation in seed rain at each distance indicates that microclimate, location of seeds within the tree crown, and other factors create a relatively heterogeneous pattern of seed deposition.

The weight of maple seeds varies substantially among species (table 4) (Green 1980; Guries and Nordheim 1984). Some examples of within-species variation in seed weight are given below. The average dry weight of sugar maple seeds varied from 0.09 to 0.03 g in a collection from across the eastern United States; the heaviest seeds were from New England area and the lightest from the southern part of the range (Gabriel 1978). In the central Oregon Coast Range, the dry weight of bigleaf maple samaras varied from 0.25 to 0.65 g; embryo dry weight accounted for 30 to 40% of total samara weight (Zasada 1996). Sipe and Linnerooth (1995) found that average weight of silver maple seeds varied from 0.10 to 0.16 g. Peroni (1994) found that the dry weight of red maple samaras from 10 North Carolina seed sources varied from 0.013 to 0.016 g. Townsend (1972) reported a 2- to 3-fold variation in red maple fruit weight for seeds collected throughout the species-range.

Seed production can vary significantly among years for a single stand or between stands in a given year in quantity, quality, biomass, and seed weight as a percentage of total litterfall (Bjorkbom 1979; Bjorkbom and others 1979; Burns and Honkala 1990; Chandler 1938; Curtis 1959; Garrett and Graber 1995; Godman and Mattson 1976; Graber and Leak 1992; Grisez 1975; Pregitzer and Burton 1991; Sakai 1990). Although separated geographically and conducted in stands differing in composition, seed production studies over 11 to 12 years in Wisconsin and New Hampshire reported similar results. In Wisconsin, the quantity of sugar maple seedfall in a pure stand of sugar maple varied from 0.1 to 13 million seeds/ha and percentage of filled seeds from 3 to 50% during a 12-year period. Seed production exceeded 2.5 million seeds/ha in 5 of 12 years (Curtis 1959). In a mixed hardwood stand in New Hampshire in which sugar maple made up 69% of the basal area, production varied from 0.2 to 11.9 million seeds/ha; viability was generally related to size of the seed crop and ranged from 0 to 48%. Seed production exceeded 2.5 million seeds/ha in 6 of 11 years (Graber and Leak 1992). In northern Wisconsin, good or better seed years occurred every other year in red maples over a 21-year period and every third year for sugar maples over a 26-year period (Godman and Mattson 1976). In a gradient study of sugar maple stands from southern Michigan to the Upper Peninsula, production of reproductive litter (seeds and flower parts) varied by a factor of 2 and 4 for 2 seed years. The southern stands were more productive one year, whereas the northern stands were more productive the other year (Pregitzer and Burton 1991). Flower and seed crops in red and sugar maples were related and the former could be used to predict seed crops (Bjorkbom 1979; Grisez 1975). Fertilization has been shown to alter seed production in maples (Bjorkbom

1979; Chandler 1938). Long and others (1997) reported that liming affected seed crop size but not periodicity in sugar maple in Allegheny hardwood forests. They also reported that good sugar maple seed crops occurred the year after a June-July period with a relatively severe drought index (that is, when plants were subjected to a high level of moisture stress).

Most studies of seed production are conducted in pure stands or those with a majority of the stems of the desired species. However the availability of seeds when species make up only a minor component of the stand is of interest when estimating seeds available for further colonization. An example of this is provided for a New Hampshire sugar maple-yellow birch-beech stand (Graber and Leak 1992). In this study covering 11 years, the total production of red and striped maples, both minor components, was 0.6 (0% viability) and 0.5 million seeds/ha (40% viability), respectively (Graber and Leak 1992). Seed quality of species present in low number may be limited by pollination. Ferrari (1993) provided information on production and dispersal of seeds from an isolated red maple in a hemlock-hardwood forest in upper Michigan.

Abbott (1974) and Grisez (1975) found that seed production in red and sugar maples was related to dbh. The following listing provides some indication of this relationship for red maple (Abbott 1974):

Tree dbh (cm)	Seeds/tree (thousands)
5	11.9
12	54.3
20	91.4
31	955.8

Reductions in the potential seed crop can result from biotic and abiotic factors. The strong summer winds and rain associated with thunderstorms in the northern hardwood forests often litter the forest floor with immature seeds and flower parts. Post-zygotic abortion occurring soon after fertilization was the primary cause of empty seeds; in addition, insects affected the quality of more than 10% of seedfall (Graber and Leak 1992). Furuta (1990) found that aphid infestations had an adverse effect on seed production in the Japanese maple *A. palmatum* subsp. *amoenum* (Carr.) H. Hara. Carl and Snow (1971) suggest that heavy aphid infestations affect seed production in sugar maple. Experimental defoliation reduced seed production in striped maples during the year of defoliation but not in the following year (Marquis 1988). Once seeds have been dispersed, seed predation by small mammals can greatly reduce the seed pool before germination (Fried and others 1988; Graber and Leak 1992; Myster and Pickett 1993; Tappeiner and Zasada 1993; Von Althen 1974).

Collection of fruits. Minimum seed-bearing age differs among species. Intervals between mast years vary by species, but some seeds are usually produced every year (table 3) (Burns and Honkala 1990). Seeds may be picked from standing trees or collected by shaking or whipping the trees and collecting the samaras on sheets of canvas or plastic spread on the ground. Samaras may also be collected from trees recently felled in logging operations. Samaras from species such as boxelder and vine, sugar, bigleaf, silver, and Norway maples can be gathered from lawns and pavements and from the surface of water in pools and streams. After collection, leaves and other debris can be removed by hand, screening, or fanning. The following weights were reported (Olson

and Gabriel 1974) for samaras:

Species	Weight/volume of samaras	
	kg/hl	lb/bu
vine maple	15.3	11.9
bigleaf maple	5.9	4.6
sugar maple	13.1	10.2

Seed collection for most species occurs when the samaras are fully ripened and the wing and pericarp have turned tan or brown in color (Carl 1982a; Carl and Yawney 1966). However, for maples that are difficult to germinate such as vine maple, striped maple, and the Japanese maples it is recommended that seeds be collected before they have dried completely, when the wing has turned brown but the pericarp is still green (Dirr and Heuser 1987; Vertrees 1975, 1987).

Although the seeds of most maples are glabrous, those of bigleaf maple are often densely pubescent. The pubescence may irritate the skin and cause some respiratory tract congestion when airborne. Individuals who might be sensitive to this material should use rubber gloves and a face mask.

Extraction and storage of seeds. Maple seeds are generally not extracted from the fruits (samaras) after collection, except when seeds are used in research on seed dormancy or lots of particularly valuable seeds that are difficult to germinate. De-winging reduces weight (wings account for about 15 to 20% of samara weight (Greene and Johnson 1992; Sipe and Linnerooth 1995)) and bulk for storage. The separation of filled and empty samaras for sugar maple can be accomplished on small lots by floating the samaras in n-pentane (filled seeds sink). This practice had no apparent effect on long-term seed viability (Carl 1976, 1982a; Carl and Yawney 1966). Removal of empty samaras, which can be done readily on a gravity table, improves seed handling, storage, sowing, and control of seedbed density.

After dispersal, maple seeds (with the exception of silver maple seeds and some red maple seeds) lie dormant in the forest floor for at least 3 to 5 months before germinating (Fried and others 1988; Houle and Payette 1991; Marquis 1975; Sakai 1990b; Tappeiner and Zasada 1993; Wilson and others 1979). Sugar and bigleaf maples usually germinate fully in the spring and summer after dispersal. Seeds of vine, striped, red, and mountain maples and the Japanese maples may lie dormant for 1 to 2 or more growing seasons before germinating (Marquis 1975; Peroni 1995; Sakai 1990b; Tappeiner and Zasada 1993; Vertrees 1987; Wilson and others 1979). In the southern United States, however, one test has indicated that seeds of red maple will maintain viability only for a few months when buried in the litter (Bonner 1996). Thus, with the exception of silver maple and possibly red maple seeds in some areas, seeds of all maples are stored naturally in the forest floor for varying lengths of time.

The critical factors in seed storage are temperature and seed moisture content. The moisture content of samaras depends on the stage of seed development and species. Beginning in late August, the moisture content of sugar maple seeds declined from about 160% (dry weight basis) to between 30 to 40% at dispersal (Carl and Snow 1971). The moisture content of sycamore maple seeds decreased from 750% (100 days after flowering) to 125% (200 days after flowering). Moisture content at dispersal for other species has been reported to be 7 to 50% for bigleaf maples (Zasada

and others 1990); 80 to 100% for silver maples (Becwar and others 1983; Pukacka 1989), 30 to 35% for Norway maples (Hong and Ellis 1990), and 125 to 130% for sycamore maple (Hong and Ellis 1990).

Moisture content for seed storage falls into 2 groups—seeds that can be stored at relatively low moisture contents (orthodox seeds) and those that must be stored at relatively high moisture contents (recalcitrant seeds). Silver and sycamore maple are clearly recalcitrant (Becwar and others 1982, 1983; Bonner 1996; Dickie and others 1991; Hong and Ellis 1990; Pukacka 1989). Seeds of these species can be stored for about a year (Bonner 1996), and seed moisture content should be maintained at about 80% (dry weight) (Dickie and others 1991; Pukacka 1989).

Orthodox seeds can be stored for longer times and at lower moisture contents than recalcitrant seeds. Viability of sugar maple seeds did not decrease over a 54-month storage period when seeds were stored in sealed containers at a moisture content of 10% (dry weight) and a temperature range of –10 to 7 °C. Similarly, viability did not decrease significantly at 17% moisture content and –10 °C. Seeds stored in open containers at the same temperature lost viability more rapidly than those in sealed containers (Yawney and Carl 1974). Sugar maple seed moisture content can be reduced slowly from 100% (dry weight basis) at the time of collection to 20% with little effect on viability (Carl and Yawney 1966). Under stress conditions (seeds maintained at 52 °C), longevity of Norway maple seeds increased linearly as seed moisture content declined from 23 to 7% (fresh weight); seeds died when dried to moisture contents of 4 and 2.5% (Dickie and others 1991). Viability of bigleaf maple seeds declined from 73 to 62% when they were stored for 1 year in sealed containers at 1 °C and at a moisture content of 16% (dry weight); viability was reduced from 73 to 12% when seeds were stored at –10 °C (Zasada and others 1990).

It was previously believed that bigleaf maple seeds could not be stored for even short periods (Olson and Gabriel 1974). Based on recent work by Zasada and co-workers (Zasada 1992, 1996; Zasada and others 1990) in the central Oregon Coast Range, an important consideration in storing these seeds seems to be collecting them before autumn rains begin, when the seeds are at their lowest water content. When collected at this time, some seedlots have moisture contents of 7 to 15% (dry weight basis), whereas seeds collected at other times have moisture contents of 25 to 35%. Once autumn rains begin, seeds attached to the tree increase in moisture content and, if they stay on the tree, can germinate under the right conditions. Although more work is required to determine the optimum storage conditions, the limited data suggest that seeds collected at the lowest moisture content behave more like orthodox seeds whereas those collected after autumn rains have increased moisture contents and some characteristics similar to recalcitrant seeds. The pubescent pericarp may play an important role in the moisture content of samaras.

For the other native maples, the fact that they remain viable for 1 year or more in the forest floor or nursery bed suggests that they could be stored for extended periods. Temperatures of 1 to 3 °C and seed moisture contents when dispersed should retain viability for several years.

Pregermination treatment and germination. Germination is epigeal for most species (figure 3), but silver maple and *A. tataricum* L. exhibit hypogeal germination (Burns and Honkala 1990; De Jong 1976; Harris 1976).

Under field conditions, maple germination falls into 3 general types, with red maple exhibiting a combination of 2 types. The first general pattern includes the 2 late spring/early summer seed dispersers (table 3)—red and silver maples—which is the best example. All seeds of this species must

germinate before they dry below a moisture content of about 30% (fresh weight) or they die (Pukacka 1989). In red maples, the percentage of non-dormant seeds varies with the seed source and among trees in a given geographic area; indeed, this species shares some characteristics with the second type of germination (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Marquis 1975; Peroni 1995; Wang and Haddon 1978).

The second pattern is typified by sugar and bigleaf maples. Seeds are dispersed in the fall and early winter, stratify during winter and spring, and germinate as soon as temperature thresholds are reached. Both can germinate at constant temperatures just above freezing. In the relatively mild climate of western Oregon, bigleaf maple germinants begin to appear in late January. Bigleaf maple seeds that remain on the tree until late February or March can germinate on the tree (Zasada 1992; Zasada and others 1990). Sugar maple seeds have been observed to germinate under the snow in the spring (Godman and others 1990).

The third pattern has been observed in vine and striped maples (Tappeiner and Zasada 1993; Wilson and others 1979) and may occur in Rocky Mountain and mountain maples. Japanese and paperbark maples and other maples from Asia also exhibit this pattern (Dirr and Heuser 1987; Vertrees 1987). Seeds are dispersed as in the second pattern, but germination occurs over several years. In Massachusetts, less than 1 and 25% of striped maple seeds germinated, respectively, in the first and second years after sowing at the time of natural seedfall (Wilson and others 1979); in coastal Oregon 70 to 80% of vine maple seeds germinated in the second growing season after fall sowing, with the remainder germinating in the first and third growing seasons (Tappeiner and Zasada 1993). Delayed germination of vine maple has also been observed in nursery beds (Vertrees 1975; Zasada 1996). Vertrees (1987) observed that Japanese maple germinants appeared over a 5-year period after a single sowing.

Methods for testing germination and pre-sowing treatments in nurseries are related in general to the germination patterns described above (tables 5 and 6). Silver maple seeds are not dormant (Pukacka 1989). Some red maple seeds may germinate without stratification, but stratification is necessary for seeds from some populations (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Peroni 1995; Wang and Haddon 1978). The group represented by sugar and bigleaf maples requires 30 to 90 days of stratification. Germination paper, sand, perlite, and sphagnum moss were all suitable stratification media for sugar maple seeds (Carl and Yawney 1966). Seeds will germinate completely at stratification temperatures. To assure that seeds have been stratified long enough, it may be advisable to wait until the first germinants appear before moving them to warmer temperatures to increase germination rate or sowing in the nursery. The optimum temperature for stratification in general is 0 to 3 °C, but some species will germinate well after stratification at temperatures up to 10 °C (Nikolaeva 1967).

The species that exhibit delayed germination are, under field conditions, exposed to warm and cold conditions and thus a warm period of incubation followed by cold stratification may stimulate germination. These species may also germinate better after a treatment that physically breaks the seed pericarp and testae (tables 5 and 6). Soaking seeds in warm water for 1 to 2 days is often recommended when they are completely dried out and the seedcoat has become very hard (Browse 1990; Dirr and Heuser 1987; Vertrees 1987). Seed testing rules recommend tetrazolium testing and excised embryo tests for the more difficult-to-germinate species (ISTA 1993).

Optimum temperatures for germination are not clearly defined. Although most species have

their best germination at higher temperatures within the optimum range (table 6), this is not always the case. Studies with red and striped maples have shown that, for seeds from some sources, germination is faster at lower than at higher temperatures (Farmer and Cunningham 1981; Farmer and Goelz 1984; Wilson and others 1979).

Germination occurs on a wide variety of substrates and a full range of light conditions (Burns and Honkala 1990; Fischer 1990; Olson and Gabriel 1974). Under field conditions, germination often occurs in association with leaf litter and other organic substrates on relatively undisturbed seedbeds. Germination paper, sand, perlite, and sphagnum moss support good germination in controlled environments. Red maple was shown to be more sensitive to the acidity of a substrate than sugar maple (Raynal and others 1982).

The morphological and physiological basis for seed dormancy in maples varies among species and includes pericarp-and-seed-coat-imposed dormancy and embryo dormancy (Farmer 1996; Young and Young 1992). The type of dormancy may change as seeds mature. There may be little relationship between dormancy of the mature seed and that of a seed with a fully developed embryo that is not yet mature in a biochemical sense (Thomas and others 1973). Thus for some species it may be best to collect and sow immature seeds as suggested by Vertrees (1975, 1987) for vine and Japanese maples and more generally by Dirr and Heuser (1987) for species with the third germination pattern mentioned above. The type of dormancy imposed by the pericarp and seedcoat (such as that in vine and striped maples) may be released by removing the pericarp and all or part of the testae (figure 2) or by physically breaking the pericarp without actually removing the embryo (table 5) (Wilson and others 1979). Some of the delayed field germination described above is caused by the impenetrability of the seedcoat after embryo dormancy has been released (Dirr and Heuser 1987; Wilson and others 1979).

Nursery practice. Maple seedlings can be produced as container stock or as bareroot seedlings. Bareroot seedlings seem to be the most common when all species of maples are considered. Presowing treatment and sowing time are based on the characteristics of the seed being sown, convenience, and experience. Cutting tests or x-radiography to determine the presence of embryos are advised for some of the introduced species because poor seed quality is common (Dirr and Heuser 1987; Hutchinson 1971; Vertrees 1987). The information reviewed above on dormancy and germination pattern suggest a number of options for sowing. The least amount of seed handling is required when seeds are sown immediately after collection and allowed to stratify naturally before germination. Silver and red maple seeds are sown after collection in late spring, whereas seeds of other maples are sown in the fall when they are mature and the nursery beds mulched (Harris 1976; Olson and Gabriel 1974; Yawney 1968). If stratification requirements are not satisfied with this method or if secondary dormancy is imposed, there may be a substantial number of seeds that do not germinate in the first growing season. Treatment of seeds may result in more uniform germination. For example, Webb (1974) proposed soaking sugar maple seeds for 24 hours before stratification to promote more uniform germination.

For difficult species such as vine and striped maples, which germinate over a several-year period, it has been recommended that seedcoats be either physically broken to promote more uniform germination or soaked in warm water, or given both treatments to reduce the amount of seed not germinating during the first growing season (Browse 1990; Olson and Gabriel 1974; Vertrees 1975, 1987). Vertrees (1987) describes several sowing methods for Japanese maples. The choice of a

method depends on degree of maturity, length of time seeds have been stored and the time desired for sowing. It is also recommended that nurserybeds in which these seeds are sown be maintained for several years so that late germinating seeds are not destroyed; this is particularly true when seed supplies are limited.

Maple seeds are usually sown 0.6 to 2.5 cm (3/8 to 1 in) deep, either broadcast or using drills. Seedbed densities from 158 to 1,520/m² (15 to 144/ft²) have been recommended (Carl 1982b; Olson and Gabriel 1974; Vertrees 1987; Yawney 1968). Densities in the range of 158 to 320/m² (15 to 30/ft²) appear most satisfactory for the production of vigorous seedlings. In some instances, seedbeds require treatment with repellents against birds and mice and treatment with fungicides to prevent damping off (Olson and Gabriel 1974; Vertrees 1987). Shade is recommended during the period of seedling establishment (Olson and Gabriel 1974). Sometimes maple seedlings are large enough to plant as 1+0 stock, but frequently 2+0 or even 2+2 stock is needed to ensure satisfactory results. In general, the larger the planting stock, the better the survival.

Container seedling production is less common than bareroot production, but is used by some producers (Tinus 1978). Container seedlings grown in a greenhouse will usually be larger than those grown outdoors in containers or in a nursery bed (Wood and Hancock 1981). Container production would probably be best achieved with stratified seeds that are just beginning to germinate; this can be easily achieved for species like bigleaf and sugar maples that germinate during stratification. Various sizes and types of containers can be used. One producer uses a container that is 4 cm (1.6 in) in diameter and 15 cm (6 in) deep to produce 30- to 40-cm-high (12- to 16-in-high) stock in 1 growing cycle. These seedlings can be outplanted or transplanted to nursery beds or larger containers for production of larger stock for ornamental purposes.

Artificial sowing in field situations is an alternative to planting seedlings. Successful germination and early growth have been demonstrated for bigleaf maple and vine maple under a variety of forest conditions (Fried and others 1988; Tappeiner and Zasada 1993) and red maple (Brown and others 1983). One drawback to sowing under forested conditions is heavy seed predation by various small mammals.

Desirable maple genotypes can also be propagated vegetatively by rooting stem cuttings and various types of layering (Dirr 1990; Dirr and Heuser 1987; O'Dea and others 1995; Post 1969; Vertrees 1987; Yawney 1984; Yawney and Donnelly 1981, 1982). Methods for rooting and overwintering cuttings before outplanting are available for sugar maple (Yawney and Donnelly 1982) and Japanese maples (Dirr and Heuser 1987; Vertrees 1987).

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Figure 1 *Acer*, maple: samaras, $\times 1$.

Figure 2 *Acer circinatum*, vine maple: longitudinal section of a seed showing bent embryo, $\times 7$.
On drying the seed shrinks, leaving space between the seedcoat and the pericarp.

Figure 3 *Acer platanoides*, Norway maple: seedling development at 1, 3, 7, and 19 days after germination, $\times 2$.

Table 1 *Acer*, maple: nomenclature, occurrence, and uses

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>A. circinatum</i> Pursh	vine maple, mountain maple	SW British Columbia to N California E side of Cascades W to Pacific Coast
<i>A. ginnala</i> Maxim.	Amur maple, Siberian maple	NE Asia; introduced to N & central Great Plains
<i>A. glabrum</i> var. <i>glabrum</i> Torr.	Rocky Mountain maple, dwarf maple, mountain maple	SE Alaska, S to S California, E to S New Mexico, N to Black Hills, South Dakota
<i>A. grandidentatum</i> Nutt.	bigtooth maple, sugar maple	SE Idaho, S to SE Arizona, E to S New Mexico & northern Mexico, N to W Wyoming
<i>A. griseum</i> (Franch.) Pax	paperbark maple	Central China & Japan
<i>A. macrophyllum</i> Pursh	bigleaf maple, broadleaf maple, Oregon maple	Pacific Coast from W British Columbia S to S California
<i>A. negundo</i> L. <i>Negundo aceroides</i> (L.) Moench.	boxelder, ashleaf maple, California boxelder	Throughout most of US & prairie provinces of Canada*
<i>A. palmatum</i> Thunb.	Japanese maple	Japan, China, & Korea
<i>A. pensylvanicum</i> L. <i>A. striatum</i> DuRoi.	striped maple, moosewood	Nova Scotia, W to Michigan S to Ohio, E to S New England, mtns of N Georgia
<i>A. platanoides</i> L.	Norway maple	Europe & the Caucasus; introduced to central & E US
<i>A. pseudoplatanus</i> L.	planetree maple, sycamore maple	Europe & W Asia; introduced to central & E US
<i>A. rubrum</i> L. <i>A. carolinianum</i> Walt.	red maple, soft maple, swamp maple	Throughout E US & southern Canada from SE Manitoba & E Texas to Atlantic Coast
<i>A. saccharinum</i> L. <i>A. dasycarpum</i> Ehrh.	silver maple, river maple, soft maple	New Brunswick, S to NE Florida NW to E Oklahoma, N to central Minnesota
<i>A. saccharum</i> Marsh. <i>A. saccharophorum</i> K. Koch	sugar maple, rock maple, hard maple	New Brunswick, S to central Georgia, W to E Texas, N to SE Manitoba
<i>A. spicatum</i> Lam.	mountain maple	Newfoundland, S to New Jersey, W to Iowa, N to Saskatchewan, S in Appalachian Mtns to N Georgia

Sources: De Jong (1976), Dirr (1990), Fischer (1990), Olson and Gabriel (1974), Rehder (1940), Van Gelderen and others (1994), Vertrees (1987), Viereck and Little (1972).

* Introduced into subarctic interior Alaska, where it forms a small tree and produces viable seeds (Viereck 1996).

Table 2 *Acer*, maple: height, seed-bearing age, and seed crop frequency

Species	Height (m) at maturity	Year first cultivated	Minimum seed-bearing age (yrs)	Interval between large seed crops (yrs)
<i>A. circinatum</i>	9	1826	C	1B2
<i>A. ginnala</i>	6	1860	5	1
<i>A. glabrum</i> var. <i>glabrum</i>	9	1882	C	1B3
<i>A. griseum</i>	8	1901	C	C
<i>A. macrophyllum</i>	35	1812	10	1
<i>A. negundo</i>	23	1688	C	1
<i>A. palmatum</i>	6	1820	C	C
<i>A. pensylvanicum</i>	11	1755	C	C
<i>A. platanoides</i>	31	Long ago	C	1
<i>A. pseudoplatanus</i>	31	Long ago	C	1
<i>A. rubrum</i>	28	1656	4	1
<i>A. saccharinum</i>	28	1725	11	1
<i>A. saccharum</i>	31	Long ago	22	3B7
<i>A. spicatum</i>	9	1750	C	C

Sources: Burns and Honkala (1990), Dirr (1990), De Jong (1976), Olson and Gabriel (1974), Vertrees (1987).

Note: *A. rubrum*, *A. negundo*, *A. pensylvanicum*, and *A. saccharinum* are dioecious to varying degrees. The other species are monoecious, but male and female flowers may occur in different parts of the tree.

Table 3 *Acer*, maple: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
<i>A. circinatum</i>	MarBJune	SeptBOct	OctBNov
<i>A. ginnala</i>	AprBJune	AugBSept	SeptBJan
<i>A. glabrum</i> var. <i>glabrum</i>	AprBJune	AugBOct	SeptBFeb
<i>A. macrophyllum</i>	AprBMay	SeptBOct	OctBMar
<i>A. negundo</i>	MarBMay	AugBOct	SeptBMar
<i>A. palmatum</i>	MayBJune	AugBSept	SeptBOct
<i>A. pensylvanicum</i>	MayBJune	SeptBOct	OctBFeb
<i>A. platanoides</i>	AprBJune	SeptBOct	OctBNov
<i>A. pseudoplatanus</i>	AprBJune	AugBOct	SeptBNov
<i>A. rubrum</i>	MarBMay	AprBJune	AprBJuly
<i>A. saccharinum</i>	FebBMay	AprBJune	AprBJune
<i>A. saccharum</i>	MarBMay	SeptBOct	OctBDec
<i>A. spicatum</i>	MayBJune	SeptBOct	OctBDec

Sources: Dirr (1990), Burns and Honkala (1990), Olson and Gabriel (1974).

Table 4C *Acer*, maple: seed yield data

Species	Cleaned seeds/weight		Average	
	Range		/kg	/lb
	/kg	/lb	/kg	/lb
<i>A. circinatum</i>	7,710B12,220	3,490B5,530	10,210	4,620
<i>A. ginnala</i>	22,980B44,640	10,400B20,200	37,570	17,000
<i>A. glabrum</i> var. <i>glabrum</i>	17,280B44,860	7,820B20,300	29,680	13,430
<i>A. macrophyllum</i>	5,970B8,840	2,700B4,000	7,180	3,250
<i>A. negundo</i>	18,120B45,080	8,200B20,400	29,610	13,400
<i>A. pennsylvanicum</i>	21,430B34,400	9,700B15,600	24,530	11,100
<i>A. platanoides</i>	2,810B10,300	1,270B4,660	6,320	2,860
<i>A. pseudoplatanus</i>	6,480B15,910	2,930B7,200	11,290	5,110
<i>A. rubrum</i>	28,070B84,420	12,700B38,200	50,520	22,860
<i>A. saccharinum</i>	1,990B7,070	900B3,200	3,930	1,780
<i>A. saccharum</i>	7,070B20,110	3,200B9,100	15,540	7,030
<i>A. spicatum</i>	33,810B60,330	15,300B27,800	48,910	22,130

Source: Olson and Gabriel (1974).

Table 5C *Acer*, maple: warm and cold stratification treatments for internal dormancy

Species	Warm period		Cold period	
	Temp. (°C)	Duration (days)	Temp. (°C)	Duration (days)
<i>A. circinatum</i> *	20B30H	30B60	3	90B180
<i>A. ginnala</i> *	20B30H	30B60	5	90B150
<i>A. glabrum</i>	20B30H	180	3B5	180
<i>A. macrophyllum</i>	C	C	1B5	40B60
<i>A. negundo</i> *	C	C	5	60B90
<i>A. palmatum</i> (dry seeds)	warm water ^l	1B2	1B8	60B120
<i>A. palmatum</i> (fresh seeds)	C	C	1B8	60B120
<i>A. pennsylvanicum</i>	C	C	5	90B120
<i>A. platanoides</i>	C	C	5	90B120
<i>A. pseudoplatanus</i>	C	C	1B5	40B900
<i>A. rubrum</i> ¹	C	C	3	60B90
<i>A. saccharinum</i>	C	C	C	0
<i>A. saccharum</i>	C	C	1B5	40B90
<i>A. spicatum</i>	C	C	5	90B120

Sources: Browse (1990), Dirr and Heuser (1987), Harris (1976), Olson and Gabriel (1974), Vertrees (1987).

Note: Even after standard pretreatment, seedlots of *A. griseum* may require 2 to 3 years for complete germination.

* Mechanical rupture of the pericarp may improve germination. This is necessary in *A. negundo* when seeds are very dry; a warm soak as for *A. palmatum* may suffice.

H The benefit of warm incubation prior to stratification is not well-documented. Seeds may go through at least 1 warm/cold cycle before germinating under field conditions.

l Water temperature at start of incubation is 40 to 50 °C and allowed to cool gradually. Some recommend a 21 °C incubation period following warm water treatment and a 90-day stratification period.

¹ Requirement for stratification is highly variable. In all seedlots, some seeds will germinate without stratification.

Table 6C *Acer*, maple: germination test conditions and results for stratified seed

Species	Germination test conditions			Germination rate		Total germination (%)
	Temp. (°C)		Duration (days)	Amount (%)	Time (days)	
	Day	Night				
<i>A. circinatum</i>	30	20	38	12	10	19
<i>A. ginnala</i>	30	20	38	50	10	52
<i>A. glabrum</i>	10B16	10B16	C	40	30	C
<i>A. macrophyllum</i> *						
Source 1	2B3	2B3	120	15B66	60B90	100
Source 2	2B3	2B3	120	0B13	60–90	100
Source 3	2B3	2B3	120	8B92	60B90	100
<i>A. negundo</i>	C	C	24B60	14B67	14B48	24B96
<i>A. pensylvanicum</i> H	5	5	90	C	C	82
	23	23	60	C	C	76
<i>A. platanoides</i>	4B10	4B10	C	C	C	30B81
<i>A. pseudoplatanus</i>	C	C	C	24B37	20B97	50B71
<i>A. rubrum</i> l						
Low elevation (U)	15	5	C	C	C	55
Low elevation (S)	15	5	C	C	C	89
High elevation (U)	15	5	C	C	C	13
High elevation (S)	15	5	C	C	C	54
<i>A. saccharinum</i>	30	30	5B18	72B91	3B13	94B97
<i>A. saccharum</i>	2B3	2B3	90	80	75	95
<i>A. spicatum</i>	C	C	C	32	31	34

Sources: Olson and Gabriel (1974), Farmer and Goelz (1984), Farmer and Cunningham (1981), Vertrees (1987).

Notes: Germination rate indicates the number of seeds germinating in the time specified and total germination all of the seeds germinating in the test. The length of germination tests are not same for all species.

Seeds of *A. griseum* and *A. palmatum* are very difficult to germinate and seed quality is usually poor. Cutting tests are recommended to determine potential viability. Tetrazolium tests could be used to determine if seeds are alive; knowing this one can sow and wait several years for seeds to germinate. Because the delay in germination appears related to a very hard pericarp, removing the pericarp can improve germination.

* Seed sources from central Oregon Coast Range. Germination rate greatly increased when seeds moved to 20 to 25 °C when germination in stratification begins (Zasada 1996).

H Germination of seeds with testa removed over radicles. Seeds with testae did not germinate at 23 °C even after 5 months of stratification, whereas seeds kept at 5 °C germinated completely after 6 months (Wilson and others 1979).

l Seed sources from Tennessee, total germination at higher temperatures was lower than shown here (Farmer and Cunningham 1981). Similar trends were observed with red maple from Ontario (Farmer and Goelz 1984). U = stratified seeds, S = unstratified seeds.