Rosaceae—Rose family

Crataegus L.

hawthorn, haw, thorn, thorn-apple

F. Todd Lasseigne and Frank A. Blazich

Mr. Lasseigne is assistant director of the J.C. Raulston Arboretum; Dr. Blazich is professor of plant propagation and tissue culture at North Carolina State University's Department of Horticultural Science, Raleigh, North Carolina.

Growth habit, occurrence, and uses. The genus *Crataegus* is a complex group of trees and shrubs native to northern temperate zones (Mabberley 1997), mostly between latitudes 30E and 50E N (Phipps 1983). Although most species can attain tree-sized proportions, hawthorns in general do not form large trees or exist as canopy dominants in forests (Little 1980a&b). Some species are decidedly shrubby, whereas others can grow to heights of 12 m (table 1). There are about 250 currently recognized species, most native to the New World (about 200 species), and the remainder (about 50 species) native to the Old World (Christensen 1992; Phipps and others 1990). Species native to the United States, as well as those that have been introduced and naturalized and some of those grown horticulturally, are included herein (table 1).

Historically, the taxonomy of the hawthorn genus has been rife with disagreement and confusion. The circumscriptions of species have varied widely, and authors of various floristic treatments have misidentified species that occur in regions treated in their works (Phipps 1998c). The genus has vexed so many authors that early experts on the group termed the situation "the *Crataegus* problem" (Eggleston 1910; Palmer 1932). Nearly 1,500 "species" were described in North America alone, mostly by W. W. Ashe, C. D. Beadle, and C. S. Sargent, from the 1890's through the 1910's (Christensen 1992; Phipps 1988; Phipps and others 1990; Robertson 1974). Palmer later reduced the number of species of hawthorns, such that only 20 to 100 were recognized, a range followed by subsequent authors (Phipps 1988). Recently, taxonomists have taken a middle approach, recognizing 100 to 200 species in North America (Kartesz 1994a&b; Phipps and others 1990), a larger number than that accepted in treatments of 20 to 30 years ago. Two primary references—Kartesz (1994a) and Phipps and others (1990)—offer the most complete survey of North American hawthorns (excluding Mexico).

Crataegus belongs to the subfamily Maloideae in the Rosaceae, a natural group of complex genera with the ability to interbreed freely (or hybridize), as they all possess the basal chromosome number of 17 (Phipps and others 1991; Robertson 1974; Robertson and others 1991). Authors have long regarded hybridization and apomixis as potential explanatory factors for the speciation phenomenon existing in hawthorns (Phipps 1988; Radford and others 1968; Vines 1960). Robertson (1974) related empirically derived data that implicated apomixis and hybridization as causes of the variation found within the genus. Specifically, he cited (1) widespread occurrence of pollen sterility; (2) cytological proof of triploidy or polyploidy in >75% of plants observed; (3) similarity between offspring produced from triploid or pollensterile plants and parental plants; and (4) the ability of flowers that have stigmas removed at anthesis to set fruit.

Many authors allude to the existence of putative hybrids in New World hawthorns (Elias 1987; Harlow and others 1996; Jacobson 1996; Kartesz 1994a&b; Knees and Warwick 1995; LHBH 1976; Little 1980a&b; Phipps 1984; Vines 1960). However, despite widespread documentation of hybrid species complexes existing in Eurasia (Christensen 1992), few scientifically verified examples of hybrid species in North American hawthorns are known (Phipps 1998a). Several recent studies now demonstrate unequivocal proof that both apomixis and polyploidy are implicated in the complex variation seen in this genus in North America (Dickinson 1985; Muniyamma and Phipps 1979a&b, 1984, 1985; Phipps 1984). Apomixis and hybridization are also known in other Rosaceous genera, including *Alchemilla* L. (lady's-mantle), *Cotoneaster* Medik., *Potentilla* L. (cinquefoil), and *Rubus* L. (blackberries and raspberries) (Mabberley 1997).

Around the world, hawthorns are used for a wide range of purposes. Many hawthorn species are grown for their edible fruits in Asia, Central America, and various Mediterranean countries (Everett 1981; Guo and Jiao 1955; Mabberley 1997; Usher 1974). The fruits of some species contain higher concentrations of vitamin C than do oranges (*Citrus* L.) (Morton 1981).

In recent years, cultivation of mayhaws native to the southeastern United States—including eastern, western, and rufous mayhaws—has increased (Bush and others 1991; Payne and Krewer 1990; Payne and others 1990). Mayhaws are atypical among the hawthorns in their early flowering period (from late February through mid-March) and their early fruit ripening dates (May) (table 2) (Payne and Krewer 1990). At least 12 cultivars have been selected for improved fruit size, yield, and ease of harvest, and these are grown for production of jellies, juices, preserves, and wine. Vitamin contents are comparable to those found in manzanilla (*C. mexicana* DC.) (Payne and others 1990), a species used for medicinal purposes in Central America (Morton 1981). However, until propagation, production, and harvest techniques are improved, limited supplies of fruits derived from orchard-grown plants will necessitate further collection of fruit from native stands (Bush and others 1991). Other North American *Crataegus* species cultivated for fruit production are black, yellow, and downy hawthorns (Mabberley 1997; Usher 1974).

Many hawthorn taxa are grown in North America and Europe solely as ornamental plants because their small stature, brilliant flowers in spring, and brightly colored fruits in fall (Bean 1970; Christensen 1992; Dirr 1998; Everett 1981; Flint 1997; Griffiths 1994; Jacobson 1996; Knees and Warwick 1995; Krüssmann 1984; Mabberley 1997). In the United States, the most commonly encountered hawthorn taxa in cultivation include Washington,'Winter King', cockspur, plumleaf, and Lavalle hawthorns (*C.* H *lavallei* Henriq. ex Lav.) (Bir 1992; Dirr 1998; Everett 1981; Flint 1997). One caution, however, is necessary with regard to cultivated hawthorns. Because only a partial understanding of the taxonomy of native populations of hawthorns now exists, especially in North America, it is likely that identities of many cultivated hawthorns may be either incorrect or imprecisely defined.

Hawthorns are important for wildlife. They offer good nesting sites for birds because of their dense branching and their thorns, which deter predators (Martin and others 1961). Fruits of many species are consumed by songbirds, game birds, small mammals, and ungulates (Shrauder 1977). Hawthorns are recommended commonly by professionals as landscaping and shelterbelt plants that can attract wildlife (Bir 1992; Elias 1987; Foote and Jones 1989; Morgenson 1999; Petrides 1988).

Flowering and fruiting. Flowers always appear after leaf emergence and are borne either in flat-topped inflorescences termed corymbs or in globular inflorescences termed umbels (Phipps 1988). Flower color is usually white, but rarely, pink-flowered variants are found in horticultural selections. From 1 to 25 flowers can be produced per inflorescence (Christensen 1992; Phipps 1988). Flowers usually contain 5 petals and 5 to 20 stamens and have a fetid odor in many species.

Hawthorn fruits are known as pomes, although the seeds and their bony endocarps are termed pyrenes, or nutlets (figure 1). Between 1 and 5 pyrenes are produced in each pome. Although most species produce flowers in spring and fruits in fall, mayhaws are notable for their early flowering and fruit ripening period. Some species drop fruits in autumn, and others have fruits that persist through winter. Timing of these events is important to horticulturists and wildlife and game managers (table 2).

Collection of fruits; seed extraction, cleaning, and storage. Mature fruits of most hawthorn species are collected readily from the ground in autumn, whereas fruits of species that tend to hold their fruits through the winter must be hand-picked from the trees (Brinkman 1974). Harvested fruits can be macerated to separate the seeds from the fleshy pericarp (Munson 1986). The macerated pericarp material can be removed by water flotation, and the seeds should then be air-dried. Seed yield data are available for only a few species, and there is considerable variability among them (table 3).

As an alternative to macerating the fruits and subsequently storing the seeds, fermenting freshly collected, undried fruits of western mayhaw for 4 or 8 days yielded 93% germination. However, fermentation periods greater than 8 days adversely affected seed germination (Baker 1991). Most other reports stated that acid scarification and/or cold stratification are obligatory to enhance seed germination. Fermentation treatments may prove extremely beneficial in reducing the time required to produce seedlings of hawthorns. However, further research on a wide range of hawthorns is needed before making general conclusions about the usefulness of such treatments.

After extracting, cleaning, and drying, the seeds should be stored under refrigerated conditions (Dirr and Heuser 1987; Hartmann and others 1997). All indications are that hawthorn seeds are orthodox in storage behavior, but reports on long-term seed viability during storage do not all agree. Dirr and Heuser (1987) stated that seeds of hawthorns, in general, can remain viable for 2 to 3 years in cold storage. St. John (1982), however, noted decreased seed viability in oneseed, cockspur, plumleaf, and scarlet hawthorns after storage for 2 years and recommended that seeds be stored for no more than 1 year. Bir (1992) found decreases in seed viability of Washington hawthorn after cold storage for 1 year. However, Christensen (1992) observed that under natural conditions, seeds of Eurasian species may require from 2 to 6 years to germinate.

Pregermination treatments and germination tests. Seeds of many hawthorns exhibit double dormancy (Hartmann and others 1997). Therefore, pregermination treatments usually consist of acid scarification followed by a period of cold stratification (Brinkman 1974; Hartmann and others 1997). Many authors also recommend periods of warm stratification for selected species (Brinkman 1974; Dirr and Heuser 1987; Morgenson 1999; St. John 1982;

Young and Young 1992). Brinkman (1974) stated that "all" seeds of the hawthorns exhibit embryo dormancy, therefore requiring cold stratification. This is reflected in the general recommendation by Hartmann and others (1997) that, following acid scarification, seeds should be stratified for 5 months at 4 EC. However, Kosykh (1972) reported that acid scarification and cold stratification for 6 months did not enhance germination of several species of hawthorns occurring in the Russian Crimea. In *C. mexicana* DC., cold stratification failed to enhance germination in seeds that were pretreated with a 1- or 3-minute hot-water soak at 80 EC (Felipe Isaac and others 1989). The fermentation work by Baker (1991) with western mayhaw also demonstrated high germination percentages without pretreating the seeds via acid scarification or cold stratification. Phipps (1998a) commented that hawthorns native to warm temperate climates possessed only endocarp dormancy, whereas those species native to regions with colder climates displayed embryo dormancy in addition to endocarp dormancy. In a large and geographically widely distributed genus such as hawthorn, these different observations are not surprising.

Differences in endocarp thickness have been noted by several authors. Endocarp thickness in oneseed hawthorn varies not only among individual trees, but also over years (St. John 1982). Some species (for example, Washington hawthorn) lack thickened endocarps and can germinate without acid scarification (Bir 1992; Brinkman 1974; Dirr and Heuser 1987; Hartmann and others 1997). In contrast, other hawthorns exhibit highly thickened endocarps (up to 0.5 cm) and require up to 7 to 8 hours of acid scarification (Dirr and Heuser 1987) before other germination pretreatments can be imposed. Table 4 summarizes pregermination treatments that have been tested on various species of *Crataegus*.

Tipton and Pedroza (1986) studied germination requirements of Tracy hawthorn and failed to achieve germination > 54% in seeds pretreated with acid scarification for up to 4.5 hours, in combination with other pretreatments (see table 4). They speculated that a combination of longer durations of acid scarification (for example, > 4.5 hours), lower germination chamber temperatures (for example, < 16EC), shorter durations of warm stratification (for example, 0 to 60 days), and longer durations of cold stratification (for example, 100 to 322 days) might improve germination in this species. The low germination percentages observed may have been due to embryo decay caused by excessively long periods of warm stratification or high temperatures in the germination chamber, in combination with incomplete modification of the endocarp due to an inadequate duration of acid scarification. Interestingly, some seeds germinated during cold stratification before being placed into the germination chambers.

Morgenson (1999) noted differential responses of 3 hawthorn to acid scarification, as well as warm and cold stratification pretreatments. Specifically, he found that although 2 hours of acid scarification did not enhance seed germination of Arnold ('Homestead') and downy hawthorns, some beneficial effects on seed germination in fireberry hawthorn were noted, especially in combination with warm and cold stratification pretreatments. Germination of both Arnold ('Homestead') and downy hawthorn seeds was optimized under a 60-day warm and 120-day (or more) cold stratification regime, with 37 and 51% germination occurring, respectively. For fireberry hawthorns, 90 to 120 days of warm stratification, followed by 120 to 180 days of cold stratificationn resulted in 18 to 27% germination. In all 3 species tested, extreme radicle elongation was observed in some treatments, for example, in all 120-day cold stratification combination treatments for fireberry hawthorns, and in some 60 and 120-day cold stratification combination treatments for Arnold ('Homestead') and downy hawthorns.

In *C. azarolus* L., cold stratification treatments reduced abscisic acid (ABA) content in seeds, especially during the first 20 days, but only yielded 24% germination (Qrunfleh 1991). Work in England with oneseed, cockspur, plumleaf, and scarlet hawthorns resulted in as much as 80% germination (see table 4 for pregermination treatments) (St. John 1982). Using alternating 3-month periods of warm stratification at 21EC and cold stratification at 4 EC, seeds of oneseed hawthorn exhibited 31% germination after a warm-cold cycle and 55% after a cold-warm-cold-warm-cold cycle (Deno 1993). Utilizing these alternating cold-warm regimes with Washington hawthorn, 50% germination was attained with a warm-cold scheme, and 51% germination occurred with cold stratification only (Deno 1993). This latter result for Washington hawthorn agreed with data reported by Brinkman (1974). Studying seeds of downy hawthorn sown into old-field vegetation patches, Burton and Bazzaz (1991) noted a negative correlation between germination percentage and the quantity of plant litter on the soil surface. This suggested that seed germination in downy hawthorn may be inhibited by the presence of organic acids or allelochemicals released by decaying organic matter.

Official seed testing prescriptions are in place for only 2 species. AOSA (1993) recommends 2 hours of soaking in concentrated sulfuric acid, followed by 90 days of incubation at room temperature and then 120 days of moist prechilling for downy hawthorn. Germination should then be tested on moist blotters or creped paper at 20/30 EC for 14 days. For oneseed hawthorn, ISTA (1993) prescribes 90 days of incubation at 25 EC, followed by 9 months of moist prechilling at 3 to 5 EC. Germination is to be tested in sand at 20/30 EC for 28 days. Both organizations also allow tetrazolium staining to determine viability as an alternative to actual tests. For all hawthorn species, ISTA (1996) recommends cutting transversely one-third from the distal end of the seeds, then incubating for 20 to 24 hours in a 1% solution at 30 EC. The embryos must be excised for evaluation. Maximum unstained tissue is one-third the distal end and the radicle tip. Some germination test results are summarized in table 5.

Because hawthorns produce apomictic seeds, reports have appeared on clonal production of plants by seed propagation (Hartmann and others 1997). In western mayhaw, this phenomenon occurs widely because of the production of nucellar embryos and may be exploitable for production of superior clones (Payne and Krewer 1990; Payne and others 1990). Further study of apomixis in *Crataegus* is needed.

Nursery practice. Hawthorns are produced in nurseries utilizing both sexual and asexual propagation techniques. In horticulture, sexual propagation of hawthorns (via seeds) is important for production of large numbers of rootstocks, to which superior, clonal scions (often cultivars) are budded (Bush and others 1991; Dirr and Heuser 1987). In particular, this is necessary for rapid build-up of clonal orchards of desirable species of hawthorns (such as those with potential pomological interest), for which there are limited scion material and little knowledge of vegetative propagation by stem cuttings. Western mayhaw is a good example of such a species (Bush and others 1991). Brinkman (1974) recommended that if controlled seed pretreatment regimes (such as stored refrigerated conditions) are not used by nurseries, seeds should be sown in early fall (versus spring) to satisfy any potential requirements for cold stratification. This may be an adequate generalization for many hawthorns, although it is important to note the aforementioned exceptions for those species (for example, those from warm temperate climates) that will germinate either in shorter time periods without the cumbersome waiting periods involved in cold stratification or through innovative seed pretreatment techniques such as fermentation.

Research on vegetative propagation of hawthorns by stem cuttings is limited. Dirr and Heuser (1987) reported previous efforts as being “rarely successful,” whereas Dirr (1998) and Hartmann and others (1997) make no mention of stem cutting propagation. However, 35% rooting was achieved utilizing softwood stem cuttings of 2 cultivars of western mayhaw—‘Super Spur’ and ‘T.O. Super Berry’—treated with 8,000 ppm of the potassium (K) salt of indolebutyric acid (IBA) in combination with 2,000 ppm of the K salt of naphthalene acetic acid (NAA) (Payne and Krewer 1990). Hardwood stem cuttings of this species (no clone specified) exhibited poor rooting, with callus visible 12 weeks after sticking cuttings, and ultimately only 10% rooting occurring (Bush and others 1991). However, softwood stem cuttings taken from new growth in mid-spring (in Calhoun, Louisiana) rooted in percentages >80% in 8 weeks under intermittent mist. No differences in rooting occurred for cuttings treated with talc formulations of 0, 3,000, or 8,000 ppm IBA (Bush and others 1991). Clearly, these latter results suggest potential for developing readily producible clonal hawthorns by stem cuttings. If so, this could reduce the importance of seed-propagated hawthorns.

Vegetative propagation of hawthorns by grafting and budding is used widely in the horticulture industry. T-budding is one of the most viable vegetative propagation procedures employed for a wide range of cultivars of hawthorns (Dirr and Heuser 1987; Hartmann and others 1997). Root-grafting is also mentioned (Hartmann and others 1997) but rarely practiced. In the United States, Washington hawthorn is the “universal” rootstock, due to the fact that (a) seedlings are commonly available (because seeds of this hawthorn species germinate more easily than those of other species) and (b) bark-slippage occurs over a long season (late summer to early fall) (Dirr and Heuser 1987). Cultivars budded onto Washington hawthorn can be expected to grow 0.9 to 1.2 m in the growing season following budding (Dirr and Heuser 1987). Cultivars of European species (for example, English and oneseed hawthorns) should be budded onto rootstocks of European species, whereas hawthorns native to North America should be budded onto rootstocks of North American species (Dirr and Heuser 1987; Hartmann and others 1997). Aside from these constraints, T-budded hawthorns appear to be highly compatible across many species.

Several grafting procedures are employed (rather than budding procedures) in production of plants of mayhaw. Cleft grafts for larger rootstocks or whip-and-tongue grafts for small diameter rootstocks are used widely in late winter (Payne and Krewer 1990). In Louisiana, cleft grafting is the most popular grafting method used for western mayhaw (Bush and others 1991). Other species, such as parsley, cockspur, Washington, and yellow hawthorns, also can be used as rootstocks for mayhaws (in particular, western mayhaw) due to graft compatibility (Payne and Krewer 1990).

Brinkman (1974) called for additional trials on hawthorns to acquire more knowledge on seed biology. However, little comprehensive research has been conducted in the intervening 25 years on this subject. Much work remains to be done before a comprehensive understanding of propagation of hawthorns will be possible.

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Figure 1—*Crataegus,* hawthorn: cleaned pyrenes (nutlets) of selected species, H 4.

Figure 2—*Crataegus,* hawthorn: longitudinal section through a pyrene (nutlet) of a species, H 8.

Table 1—*Crataegus,* hawthorn: nomenclature, occurrence, and heights at maturity

Scientific name & synonyms	Common name	Occurrence	Height at maturity (m)
***C. aestivalis* (Walt.) Torr. & Gray** *C. cerasoides* Sarg. *C. luculenta* Sarg. *C. maloides* Sarg.	**eastern mayhaw**, shining, may, or apple hawthorn	N Florida & SE Alabama, N to E North Carolina	3–12
***C. anomala* Sarg. (pro sp.)** *C. arnoldiana Sarg.*	**Arnold hawthorn**, anomalous hawthorn	Quebec & New England, S to New York	5–10
***C. berberifolia* Torr. & Gray**	**barberry hawthorn,** bigtree hawthorn	Virginia to Kansas, S to Georgia & Texas	6–15
***C. brachyacantha* Sarg. & Engelm.**	**blueberry hawthorn**, blue haw	Arkansas to Oklahoma, S to Mississippi & Texas; Georgia also	2–7
***C. brainerdii* Sarg.**	**Brainerd hawthorn**	Quebec to Michigan, S to New England, North Carolina & Ohio	4–6
***C. calpodendron* (Ehrh.) Medik.** *C. calpodendron* var. *hispidula* (Sarg.) Palmer *C. fontanesiana* (Spach) Steud. *C. hispidula* Sarg. *C. tomentosa* L.	**pear hawthorn,** sugar or black hawthorn	Ontario to Minnesota & Kansas, S to Georgia & Texas	4–6
***C. chrysocarpa* Ashe** *C. brunetiana* Sarg. *C. doddsi* Ramalay *C. faxonii* Sarg. *C. praecoqua* Sarg. *C. praecox* Sarg.	**fireberry hawthorn,** roundleaf or golden-fruit hawthorn	Newfoundland to British Columbia, S to North Carolina& New Mexico	5–10
***C. coccinoides* Ashe**	**Kansas hawthorn,** Eggert thorn	Indiana to Kansas, s to Arkansas & Oklahoma	4–7
***C. crus-galli* L.** *C. acutifolia* Sarg. *C. bushii* Sarg. *C. canby* Sarg. *C. cherokeensis* Sarg. *C. regalis* Beadle *C. salicifolia* Medik.	**cockspur hawthorn,** Newcastle thorn, & hog-apple	Quebec to Michigan & Kansas, S to Florida & Texas	5–10
***C. dilatata* Sarg.**	**broadleaf hawthorn,**	Quebec to Michigan, S to	4–8

C. conspecta Sarg. *C. locuples* Sarg.	& apple-leaf hawthorn	New York, Kentucky, & Missouri	
***C. douglasii* Lindl.** *C. columbiana* Howell	**black hawthorn,** Douglas or western black hawthorn, & black thornberry	Alaska to S California, Ontario to Dakotas, S to Michigan & Nevada	7–12
***C. erythropoda* Ashe** *C. cerrona* A. Nelson	**cerro** & chocolate hawthorn	Wyoming to Washington, S to New Mexico & Arizona	2–6
***C. flabellata* (Spach) Kirchn.** *C. densiflora* Sarg. *C. grayana* Egglest.	**fanleaf hawthorn**	Maine to Quebec to Michigan, S to Florida & Louisiana	4–6
***C. flava* Ait.** *C. aprica* Beadle *C. cullasagensis* Ashe	**yellow hawthorn**, yellow or summer haw, hoghaw, sunny hawthorn	Maryland & West Virginia, S to Florida & Mississippi	5–8
***C. greggiana* Egglest**	**Gregg hawthorn**	Texas & NE Mexico	3–6
***C. harbisonii* Beadle**	**Harbison hawthorn**	Tennessee, S to Georgia & Alabama	3–8
***C. intricata* Lange**	**thicket hawthorn,** entangled or Allegheny hawthorn	New England to Michigan to Missouri, S to Florida & Alabama	1–7
***C. lacrimata* Small**	**Pensacola hawthorn,** weeping or sandhill hawthorn	Florida	3–6
***C. laevigata* (Poir.) DC.** *C. oxyacantha* L., in part *C. oxycanthoides* Thuill.	**English hawthorn,** English midland or English woodland hawthorn, may, whitethorn	Central & W Europe	2–4
***C. marshallii* Egglest** *C. apiifolia* (Marshs.) Michaux.	**parsley hawthorn,** parsley haw, parsely-leaf thorn	Virginia to Illinois, S to Florida & Texas	2–8
***C. mollis* Scheele** *C. albicans* Ashe *C. arkansana* Sarg. *C. brachyphylla* Beadle *C. coccinea* var. *mollis* Torr. & Gray *C. invisa* Sarg.	**downy hawthorn,** summer hawthorn, Texas hawthorn, red haw, turkey-apple	Ontario to the Dakotas, S to Alabama & Texas	6–12
***C. monogyna* Jacq.** *C. oxyacantha* L. ssp. *monogyna* (Jacq.) Rouy & Camus	**oneseed hawthorn,** single-seed or common hawthorn, may, quickthorn	Europe, N Africa, & W Asia	5–12
***C. nitida* (Engelm.) Sarg.** *C. viridis* var. *nitida* Engelm.	**shining hawthorn,** glossy hawthorn, & shining thorn	Ohio to Illinois, S to Arkansas	7–12
***C. opaca* Hook. & Arn.** *C. nudiflora* Nutt. ex Torr. & Gray	**western mayhaw**, apple haw, may, or riverflat hawthorn	W Florida to Texas, N to Arkansas	6–10

***C. pedicellata* Sarg.** *C. aulica* Sarg. *C. caesa* Ashe *C. coccinea* L. in part	**scarlet hawthorn** & Ontario hawthorn	Maine to Michigan, S to Virginia & Illinois; South Carolina & Florida also	4–8
***C. persimilis* Sarg.** *C. laetifica* Sarg. *C. prunifolia* Pers.	**plumleaf hawthorn**	New York to Ontario, S to Pennsylvania & Ohio	7–10
***C. phaenopyrum* (L. f.) Medik.** *C. cordata* (Mill.) Ait. *C. populifolia* Walt. *C. youngii* Sarg.	**Washington hawthorn**, Virginia hawthorn, Washington thorn, hedge thorn, red haw	New Jersey to Missouri, S to Florida, Mississippi & Louisiana	7–10
***C. piperi* Britt.** *C. columbiana* auct. *C. columbiana* var. *columbiana* T.J. Howell *C. columbiana* Howell var. *piperi* (Britt.) Egglest.	**Columbia hawthorn,** Piper hawthorn	British Columbia, S to Idaho & Oregon	4–6
***C. pruinosa* (Wendl. f.) K. Koch** *C. formosa* Sarg. *C. georgiana* Sarg. *C. porteri* Britt. *C. leiophylla* Sarg. *C. rugosa* (Ashe) Kruschke	**frosted hawthorn,** waxy-fruited hawthorn	Newfoundland to Wisconsin, S to West Virginia & Oklahoma	2–8
***C. pulcherrima* Ashe** *C. flava* Ait. not auctt. *C. opima* Beadle *C. robur* Beadle	**beautiful hawthorn**	Florida to Mississippi	4–8
***C. punctata* Jacq.** *C. fastosa* Sarg. *C. punctata* var. *aurea* Ait. *C. verruculosa* Sarg.	**dotted hawthorn,** flat-topped, thicket, or large-fruited hawthorn	Quebec to Minnesota & Iowa, S to Georgia & Arkansas	5–10
***C. reverchonii* Sarg.**	**Reverchon hawthorn**	Missouri to Kansas, S to Arkansas & Texas	1–8
***C. rufula* Sarg.**	**rufous mayhaw**	N Florida, SW Georgia, & SE Alabama	3–9
***C. saligna* Greene**	**willow hawthorn**	Colorado	4–6
***C. sanguinea* Pall.**	**Siberian hawthorn**	E Russia & Siberia, S to Mongolia & China	5–8
***C. spathulata* Michx.** *C. microcarpa* Lindl.	**littlehip hawthorn,** small-fruited, or pasture hawthorn	Virginia to Missouri, S to Florida to Texas	5–8
***C. succulenta* Schrad. ex Link**	**fleshy hawthorn,** longspine or	Nova Scotia to Montana, S to	5–8

C. florifera Sarg. *C. laxiflora* Sarg.	succulent hawthorn	North Carolina & Utah	
***C. tracyi* Ashe ex Egglest** *C. montivaga* Sarg.	**Tracy hawthorn** & mountain hawthorn	Texas & NE Mexico	3–5
***C. triflora* Chapman**	**three-flower hawthorn**	Tennessee, S to Georgia & Louisiana	4–6
***C. uniflora* Müenchh.** *C. bisculcata* Ashe *C. choriophylla* Sarg. *C. dawsoniana* Sarg. *C. gregalis* Beadle	**dwarf haw,** one-flowered hawthorn, & dwarf thorn	New York to Missouri, S to Florida & Texas	½–4
***C. viridis* L.** *C. amicalis* Sarg. *C. ingens* Beadle	**green hawthorn**, southern or tall hawthorn, green haw, green or southern haw	New York to Missouri, S to Florida & Texas	5–12

Sources: Beadle (1913), Brinkman (1974), Dirr (1998), Flint (1997), Foote and Jones (1989), Griffiths (1994), GRIN (1999), Jacobson (1996), Little (1980a, b), Palmer (1988, 1995, 1998a & b), Phipps and O'Kennon (1988), Sargent (1933), Strausbaugh and Core (1978), Tidestrom (1933), Vines (1960), Wasson (2001),Weakley (2002)..

Table 2—*Crataegus,* hawthorn: phenology of flowering and fruiting, and color of ripe fruit

Scientific name	Flowering dates	Fruit ripening dates	Color of ripe fruit*
C. aestivalis	Mar	—	Lustrous, scarlet
C. anomala	May	—	Bright crimson
C. berberifolia	Mar–Apr	Oct	Orange with red face
C. brachyacantha	Apr–May	Aug	Bright blue with white wax
C. brainerdii	May–June	Sept–Oct	Red
C. calpodendron	May–June	Sept–Oct	Orange-red to red
C. chrysocarpa	May–June	Aug–Sept	Yellow to orange to crimson
C. coccinoides	May	Oct	Glossy, dark crimson
C. crus-galli	June	Oct	Dull red
C. dilatata	May	Sept	Scarlet with dark spots
C. douglasii	May	Aug–Sept	Lustrous, black to chestnut-brown
C. erythropoda	Apr–May	Oct	Red to wine purple, brown, or black
C. flabellata	May	Sept	Crimson
C. flava	Apr	Oct	Dark orange- brown or yellow
C. greggiana	Apr	Oct–Nov	Bright red
C. harbisonii	May	Oct	Bright red or orange-red
C. intricata	May–June	Oct	Greenish or reddish brown
C. lacrimata	Apr	Aug	Dull yellow or orange or red
C. laevigata	Apr–May	Sept–Oct	Deep red
C. marshallii	Apr–May	Oct	Bright scarlet
C. mollis	May	Aug–Sept	Scarlet with large dark dots
C. monogyna	May	Sept–Oct	Bright red
C. nitida	May	Oct	Dull red covered with white wax
C. opaca	Feb–Mar	May	Lustrous scarlet with pale dots
C. pedicellata	May	Sept	Glossy, scarlet
C. persimilis	May–June	Oct	Bright red
C. phaenopyrum	May	Sept–Oct	Lustrous scarlet
C. piperi	May–June	Aug–Sept	Salmon-orange to scarlet
C. pruinosa	May–June	Oct–Nov	Dark purple-red
C. pulcherrima	Apr–May	Sept–Oct	Red
C. punctata	May–June	Sept–Oct	Dull red or bright yellow
C. reverchonii	May	Oct	Shiny or dull red
C. rufula	Mar–Apr	June–July	Red
C. saligna	May	Oct	Red to blue-black
C. sanguinea†	May	Aug–Sept	Bright red
C. spathulata	Apr–May	Sept–Oct	Red
C. succulenta	May–June	Sept–Oct	Bright red
C. tracyi	Apr–May	Sept–Oct	Orange-red
C. triflora	May	Oct	Red, hairy
C. uniflora	Apr–May	Sept–Oct	Yellow to dull red to brown
C. viridis	Apr–May	Sept–Oct	Bright red, orange-red, yellow

Sources: Brinkman (1974), Dirr (1998), Everett (1981), Flint (1997), Foote and Jones (1989), Jacobson (1996), Little (1980a b), Phipps (1988a).

* Color of ripe fruit is highly arbitrary and varies in interpretation amoung authors due to lack of standardization. Accurate determinations of fruit color cannot be ascertained from herbarium specimens.

† Plants growing in Boston, Massachusetts, not in native habitat.

Table 3—*Crataegus,* hawthorn: seed yield data

Species	Provenance	Seed wt/fruit wt kg/kg	Seed wt/fruit wt lb/ 100 lb	Average cleaned seeds/wt /kg	Average cleaned seeds/wt /lb	Samples
C. chrysocarpa	South Dakota	—	—	21,500	10,750	1
C. douglasii	Washington Idaho, Oregon	0.15	15.2	45,200	22,600	6
C. phaenopyrum	—	—	—	59,600	29,800	1
C. punctata	Minnesota	0.11	11.3	9,400	4,700	2
C. sanguinea	Russia	0.15	15.0	—	—	—
C. succulenta	—	—	—	41,200	20,600	1

Source: Brinkman (1974).

Table 4—*Crataegus,* hawthorn: pregermination treatments

		Stratification treatments			
		Warm period		Cold period	
Species	Scarification* (hr)	Temp (EC)	Duration (days)	Temp (EC)	Duration (days)
C. anomala	4.5	—	—		
	0	21–27	30–90	2–9	90–180
C. crus-galli	2–3	21–25	21	Low†	21–135
	0	21	120	7	135
C. douglasii	0.5–3	—	—	5	84–112
C. mollis	2	25	90	5	120
	0	30	21	10	180
C. monogyna	—	25	90	3–5	270
	0.5–2	20	14–28	2–4	70–84
C. pedicellata	2	20	28	2–4	84
C. persimilis	4	20	14–28	2-4	70–84
C. phaenopyrum	0	—	—	5–10	135
C. punctata	0	21	120	5	135
C. sanguinea	2	21–25	21	5	21
	0	20–25	30	4–7	—
C. succulenta	0.5	—	—	4	110–140
C. tracyi	0, 0.5, 2.5, 4.5	21–27	0, 20, 60, 120	4	0, 20, 100

Sources: Brinkman (1974), Felipe Isaac and others (1989), Qrunfleh (1991), St John (1982), Tipton and Pedroza (1986), Young and Young (1992).

* Immersion time in sulfuric acid (H_2SO_4).

† Outdoor winter temperatures.

Table 5—*Crataegus,* hawthorn: germination test conditions and results

	Germination test conditions*					
		Temp (EC)			Germination	
Scientific name	Medium	Day	Night	Duration (days)	Avg (%)	Samples
C. anomala	Soil	8	2	180	35	1
C. crus-galli	Soil	21	21	21	73	1
C. douglasii	Peat or sand	21	21	35–45	30†	6
C. mollis	Soil	21	21	—	42–50	3
C. phaenopyrum	Soil	21	21	—	71	2
	Peat	5	5	135	92	1
C. punctata	Peat	21	21	21	60	1
C. sanguinea	Peat	21	21	21	73	1
	Peat	4	7	30	50	2
C. succulenta	Soil	—	—	—	35–40	2
C. tracyi ‡	Germination blotters	16	16	28	0	2

Sources: Brinkman (1974), Tipton and Pedroza (1986).

* Light provided $8 hours per day. For each species, seeds were pretreated as shown in table 4.

† Sound seed . 45% of total seeds sown.

‡ 16/8 hour light/dark cycle used.