Fagaceae—Beech family

Quercus L.

oak

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Growth habit, occurrence, and use. The oaks—members of the genus *Quercus*—include numerous species of deciduous and evergreen trees and shrubs and make up the single most economically important genus of hardwoods in North America. *Quercus* is also the largest genus of trees native to the United States (Little 1979) and has recently been designated as the "national tree" by the National Arbor Day Foundation. About 500 species are widely distributed throughout the temperate regions of the Northern Hemisphere in both the Eastern and Western Hemispheres as well as southward through Central America to the mountains of Colombia and through Turkey to Pakistan (Sargent 1965). There are about 58 tree and 10 shrub species native to the United States, 104 species in Mexico, and another 30 in Central America and Colombia. At least 70 hybrids have been described, and there are probably many more (Little 1979). Information on hybrids and genetic variation has been summarized for 25 species in Burns and Honkala (1990).

Oaks are divided into 2 subgenera: *Lepidobalanus* (white oaks) and *Erythrobalanus* (black oaks). These subgenera differ in several ways, but most importantly for seed considerations, they differ in time required for fruit maturation, chemical composition of their stored food reserves, and degree of dormancy. In this book, 48 taxa are considered (table 1). Oaks are valuable for a very wide range of products and uses: construction timber, furniture, interior trim, and flooring; watershed protection, wildlife habitat and food, and ornamental plantings; as well as tannins and other extractives and cork. Consequently, many oak species are widely planted for a variety of purposes. For additional information on growth habit, uses, ecology, and silviculture of individual oak species, consult Burns and Honkala (1990).

Flowering and fruiting. Flowering is monoecious. The staminate flowers are borne in clustered aments (catkins) and the pistillate flowers in solitary (or in 2- to many-flowered) spikes in the spring (February to May) before or coincident with emergence of the leaves. Staminate flowers develop primarily from leaf axils of the previous year and range in length from 3 to 35 cm, depending on the species. Pistillate flowers develop from axils of leaves of the current year. The fruit is a nut, commonly called an acorn (figure 1). Acorns of white oaks mature in the year of flowering, whereas acorns of black oaks mature at the end of the second year after flowering (Sargent 1965). Acorns are 1-seeded, or rarely 2-seeded, and occur singly or in clusters of 2 to 5. They are subglobose to oblong, short-pointed at the apex, and partially enclosed by a scaly cup (the modified involucre) at their base. Removal of the cup discloses a circular scar that is often useful in judging acorn maturity. Acorns range in size from 6 mm in length and diameter for willow oak to 50 mm in length and 38 mm in diameter for bur oak (Sargent 1965). Fruits ripen and seeds disperse in the autumn, from late August to early December (Olson 1974; Radford and others 1964; Sargent 1965). The embryo has 2 fleshy cotyledons, and there is no endosperm (figure 2). Acorns are generally green when immature and turn yellow, brown, or black when ripe.

The oaks vary widely in initiation of seed bearing and frequency of large crops (table 2). Acorn production by coppice shoots of chestnut oak only 3 and 7 years old indicates that seed production may start earlier on trees of sprout origin, although coppice sprouts of scarlet and black oaks of comparable ages did not bear seeds (Sharik and others 1983). Environmental factors—such as late spring freezes (Neilson and Wullstein 1980), high humidity during pollination (Wolgast and Stout 1977), or summer droughts (Johnson 1994)—will reduce the acorn crop, but some inherent periodicity seems to exist in many species. Most species produce good crops ("mast years") 1 year out of 3 or 4 (Beck 1977; Christisen and Kearby 1984; Downs and McQuilkin 1944; Goodrum and others 1971). Sork and others (1993) reported good acorn crops in Missouri every 2, 3, and 4 years for black, white, and northern red oaks, respectively. In central California, a study of acorn production in

Figure 1— *Quercus*, oak: acorns of **(top row, left to right)** *Q. alba*, white oak; *Q. falcata*, southern red oak; *Q. kelloggii*, California black oak; *Q. lyrata*, overcup oak. **(second row, left to right)** *Q. macrocarpa*, bur oak; *Q. marilandica*, blackjack oak; *Q. michauxii*, swamp chestnut oak. **(third row, left to right)** *Q. muehlenbergii*, chinkapin oak; *Q. nigra*, water oak; *Q. pagoda*, cherrybark oak; *Q. phellos*, willow oak. **(fourth row, left to right)**, *Q. rubra*, northern red oak; *Q. shumardii*, Shumard oak; *Q. sinuata*, Durand oak; *Q. stellata*, post oak. **(bottom row, left to right)**, *Q. texana*, Nuttall oak; *Q. velutina*, black oak; *Q. wislizeni*, interior live oak.

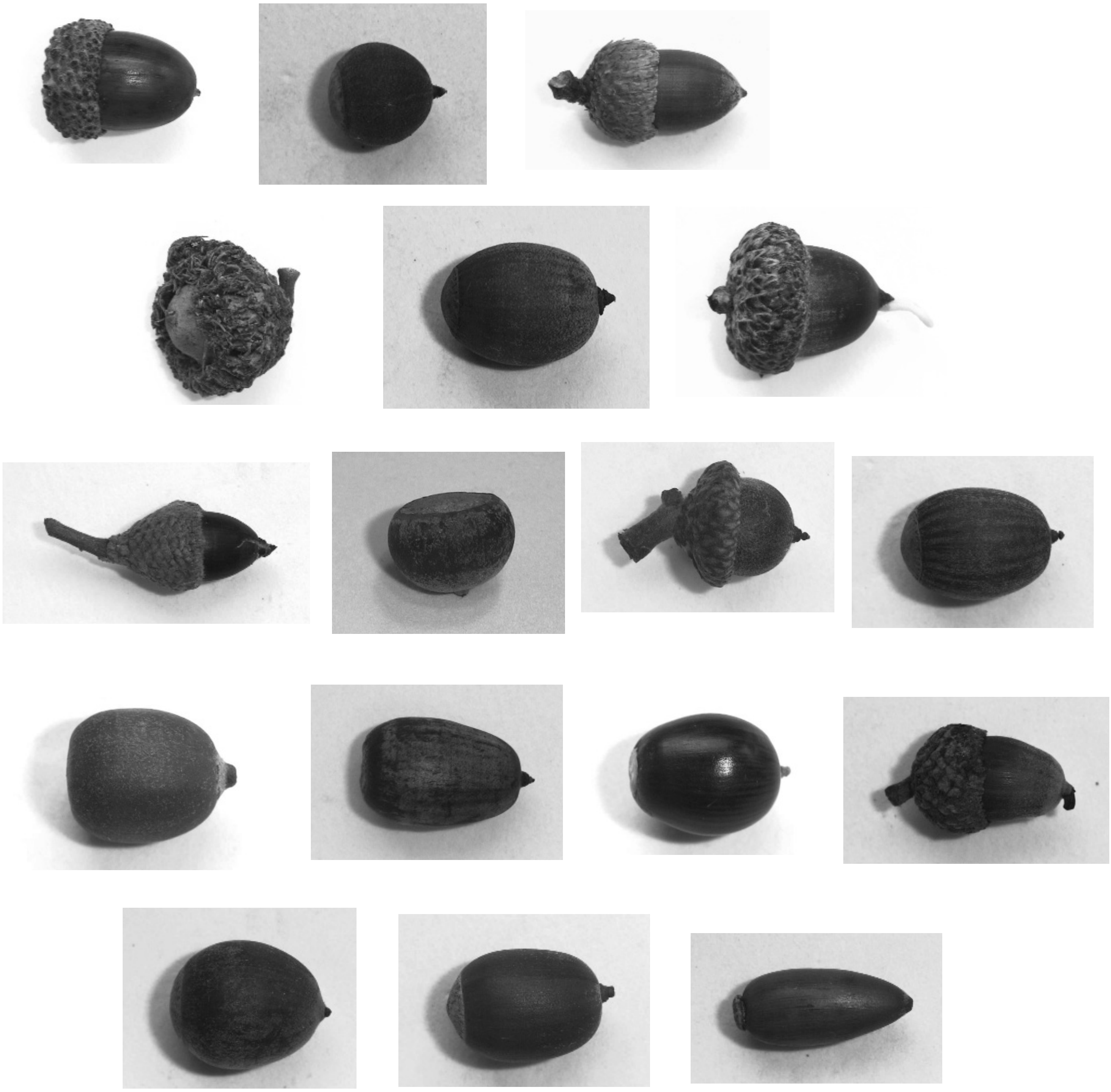


Table 1—*Quercus,* oak: nomenclature and occurrence

Scientific name & synonym(s)	Group*	Common names	Occurrence
Q. *acutissima* Carr.	white	**sawtooth oak**	E Asia & Japan; introduced to E US
Q. *agrifolia* Née	black	**California live oak,** coast live oak; *encina*	Coastal ranges from central to S California
Q. *alba* L.	white	**white oak,** fork-leaf white & stave oaks	SW Maine to N Wisconsin; S to N Florida & E Texas
Q. *arizonica* Sarg.	white	**Arizona white oak,** Arizona oak; *roble*	SW Texas to New Mexico, Arizona, & N Mexico at 1,500–3,000 m
Q. *bicolor* Willd.	white	**swamp white oak,** cow oak	SW Maine to N Wisconsin S to Tennessee & Missouri
Q. *cerris* L.	white	**European turkey oak,** turkey oak	S Europe to W Asia; introduced to central US
Q. *chrysolepis* Liebm.	white	**canyon live oak,** canyon, maul, goldcup, & live oaks	Mtns of SW Oregon, S to S California & N Mexico; local in mtns. of Nevada & Arizona
Q. *coccinea* Muenchh.	black	**scarlet oak,** black & Spanish oaks	SE Maine to Michigan; S to Georgia, & S Alabama & Missouri
Q. *douglasii* Hook. & Arn.	white	**blue oak,** California blue, iron, & mountain white oaks	Foothills of Sierra Nevada & coastal ranges of California
Q. *dumosa* Nutt.	white	**California scrub oak**, scrub oak	Coast Ranges & offshore islands of California & Baja California
Q. *ellipsoidalis* E. J. Hill	black	**northern pin oak,** black, jack, & Hill oaks	Michigan to SW North Dakota; S to Iowa & NW Ohio
Q. *emoryi* Torr.	black	**Emory oak,** black oak, *bellota, roble negro*	Mtns of Trans-Pecos Texas, SW New Mexico, SE & central Arizona, & N Mexico
Q. *falcata* Michx. *Q. triloba* Michx.	black	**southern red oak,** Spanish & red oaks	SE New York to S Missouri; S to N Florida & SE Texas
Q. *gambelii* Nutt. *Q. vreelandii* Rydb. *Q. utahensis* (A. DC.) Rydb.	white	**Gambel oak,** Rocky Mtn. white & Utah white oaks; *encino*	Colorado and Wyoming, W to Utah & S to Arizona, New Mexico, Texas, & NW Oklahoma
Q. *garryana* Dougl. ex Hook.	white	**Oregon white oak,** Garry, post, Oregon, Brewer, & shin oaks	British Columbia; S in mtns to central California
Q. *grisea* Liebm.	white	**gray oak**	SW Texas to New Mexico, Arizona, & N Mexico
Q. *ilicifolia* Wangenh.	black	**bear oak,** scrub oak	S Maine, W to New York; S to West Virginia, SW Virginia, & W North Carolina
Q. *imbricaria* Michx.	black	**shingle oak,** laurel oak	Pennsylvania, S to S Michigan; North Carolina & Arkansas; local in Louisiana & Alabama
Q. *incana* Bartr.	black	**bluejack oak,** sandjack, bluejack, shin, & turkey oaks	Coastal plain from Virginia to central Florida; W to Louisiana, E Texas, Oklahoma, & Arkansas
Q. *kelloggii* Newb.	black	**California black oak,** black & Kellogg oaks	SW Oregon; S through Coast Ranges & Sierra Nevada to S California
Q. *laevis* Walt. *Q. catesbaei* Michx.	black	**turkey oak,** scrub & Catesby oaks	Coastal plain from SE Virginia to central Florida, & W to Louisiana
Q. *laurifolia* Michx.	black	**laurel oak,** Darlington, water, swamp, laurel, & diamond-leaf oaks	Coastal plain from SE Virginia to S Florida; W to E Texas & S Arkansas
Q. *lobata* Née	white	**California white oak,** valley, valley white, weeping, & water oaks; *roble*	Valleys & foothills in California; also Santa Cruz & Santa Catalina Islands
Q. *lyrata* Walt.	white	**overcup oak,** swamp post, water white, & swamp white oaks	Coastal plain from Delaware to Florida; W to E Texas & SW Indiana
Q. *macrocarpa* Michx.	white	**bur oak,** mossycup, blue oak, mossy-overcup, & scrub oaks	S New Brunswick & Manitoba; S to Tennessee & SE Texas

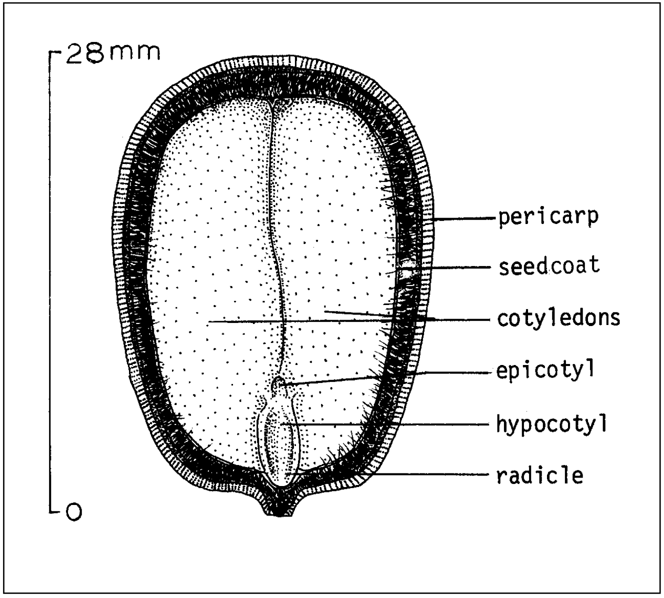
Table 1—*Quercus,* oak: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Group*	Common names	Occurrence
***Q. marilandica* Muenchh.**	black	**blackjack oak,** barren & jack oaks; blackjack	New York, W to Ohio, Iowa, & Oklahoma; S to Texas & NW Florida
***Q. michauxii* Nutt.** *Q. prinus* L.	white	**swamp chestnut oak**, cow & basket oaks	Coastal plain from New Jersey to N Florida; W to E Texas; N in Mississippi Valley to S Illinois & Indiana
***Q. muehlenbergii* Engelm.**	white	**chinkapin oak**, rock, yellow, chestnut, yellow chestnut, & rock chestnut oaks	W Vermont & New York to Minnesota & SE Nebraska; S to NW Florida & central Texas
***Q. nigra* L.**	black	**water oak,** possum oak	Coastal plain from New Jersey to S Florida, W & spotted oaks to E Texas, & N in Mississippi Valley to SE Oklahoma
***Q. pagoda* Raf.** *Q. falcata* var *pagodaefolia* Ell.	black	**cherrybark oak,** bottomland red, Elliott, & swamp red oaks	SE New Jersey to E Oklahoma; S to N Florida & E Texas
***Q. palustris* Muenchh.**	black	**pin oak,** swamp, water, Spanish, & swamp Spanish oaks	Massachusetts & Vermont to S Michigan; S to NE Oklahoma, Tennessee, & central North Carolina
***Q. petraea* (Mattusch) Liebl.** *Q. sessiliflora* Salisb.	white	**durmast oak**, sessile oak	Europe & W Asia; planted in central & NE US
***Q. phellos* L.**	black	**willow oak**, pin, peach, & swamp willow oaks	Coastal plain from New Jersey to N Florida; W to E Texas & S Illinois
***Q. prinus* L.** *Q. montana* Willd.	white	**chestnut oak,** rock chestnut, rock, & tanbark oaks	SW Maine & S Ontario; S to central Georgia & NW Mississippi
***Q. robur* L.**	white	**English oak**, pedunculate oak	Europe, N Africa, & W Asia; naturalized in SE Canada & NE US
***Q. rubra* L.** *Q. borealis* Michx.f.	black	**northern red oak**, red, common red, eastern red, & gray oaks	Cape Breton Island & Nova Scotia; W to Ontario & S to eastern Oklahoma & Georgia
***Q. shumardii* Buckl.**	black	**Shumard oak,** spotted, Schneck, swamp red, & Shumard red oaks	Coastal plain, mostly, from North Carolina to N Florida; W to central Texas, Kansas, & S Illinois
***Q. sinuata* Walt.** *Q. durandii* Buckl.	white	**Durand oak,** Durand white, bluff, & bastard oaks	Coastal Plain from North Carolina to N Florida & W to Texas, Oklahoma, & NE Mexico
***Q. stellata* Wangenh.**	white	**post oak,** iron oak	SE Massachusetts to SE Iowa, & S to central Florida & Texas
***Q. suber* L.**	white	**cork oak**	SW Europe & N Africa; planted in California
***Q. texana* Buckl.** *Q. nuttallii* Palmer	black	**Nuttall oak**, red, Red River, & pin oak	Gulf coastal plain from Alabama to SE Texas; N in Mississippi Valley to SE Missouri
***Q. turbinella* Greene**	white	**shrub live oak,** turbinella & scrub oaks; *encino*	SW Colorado & Utah; S to S California, Arizona, & northern Mexico
***Q. turbinella* var. *ajoensis* (C.H. Muller) Little**	white	**shrub live oak,** Ajo oak	SW Arizona & N Mexico
***Q. vaccinifolia* Kellog**	white	**huckleberry oak**	SW Oregon to central California
***Q. variabilis* Bl.** *Q. chinensis* Bge.[not Abel] *Q. serrata* Carruth. [not Thunb.]	black	**oriental oak**	N China, Korea, & Japan; planted in central & NE US
***Q. velutina* Lam.**	black	**black oak**, yellow, smooth-bark, quercitron, & yellow-bark oak; *quercitron*	SW Maine to SE Minnesota; S to N Florida & E Texas
***Q. virginiana* P. Mill.**	white	**live oak**, Virginia live oak; *encino*	Coastal plain from SE Virginia to S Florida (including Florida Keys); W to S Texas
***Q. wislizenii* A. DC.**	black	**interior live oak**, highland live & Sierra live oaks	Foothills of Sierra Nevada & Coast Ranges in California, S to Mexico

Sources: Little (1979), Olson (1974), Sargent (1965).

* White oaks belong to subgenus *Lepidobalanus;* black oaks belong to subgenus *Erythrobalanus*.

Figure 2—*Quercus rubra,* northern red oak: longitudinal section through a seed.



valley, blue, and California black oaks and canyon live and coast live oaks (Koenig and others 1994) found no mast production patterns at the population level. Crop failures did occur frequently but they were probably more related to lack of pollination and fertilization success than to inherent patterns. Cecich (1993) concluded that most of the potential seedcrop in oaks in Missouri is lost when pistillate flowers abort between the time of pollination and fertilization. Really good crops of California black oak acorns were found to occur only every 8 years or so (McDonald 1992). The following yield averages on an area basis have been reported: 3.2 to 1,620 kg/ha (2.9 to 1,448 lb/ac) for white oak in Illinois (Johnson 1975); 208 kg/ha (186 lb/ac) for southern Appalachian oaks (Beck 1977); and 560 kg/ha (500 lb/ac) for Oregon white oak in California (Stein 1990).

Collection and cleaning of acorns. Collecting acorns of high quality requires an awareness of the indices of acorn maturity. Natural dissemination from the tree is a sure sign of maturity, of course, but collections are often made before this time to reduce losses to deer, rodents, and other predators that quickly eat fallen acorns. Good indices of maturity for most species are (1) change in pericarp color from green to yellow, brown, or black; (2) a cup scar colored pink, lemon, orange, or white; and (3) cups that slip easily from the acorns without resistance (Bonner and Vozzo 1987; Lotti 1959). Ripe acorns may be collected from August to December from the ground or they can be shaken from trees onto canvas or plastic sheets after ripening. Mechanical tree shakers can be very effective with oaks where the terrain or stand conditions permit it. Collecting acorns from downed trees in logging operations also can be successful if the trees were cut after the acorns matured. Acorns should be collected from the ground within a few days after dispersal to avoid losses to predators, desiccation of the acorns, and early germination of the non-dormant species (primarily the white oaks). California black oak also requires prompt collection because mold often infects fallen acorns (McDonald 1990).

To avoid desiccation, which can quickly reduce acorn quality, acorns should be floated in water after collection, preferably at the end of each collection day. This action will maintain high moisture contents and permit removal of trash and unsound acorns. Sound acorns will sink and the other material will float. For acorns collected from the ground, moisture conditions at time of collection can affect the flotation process. If the ground is very dry, many good acorns may float initially, and the lot may have to stay in the water overnight to allow sound acorns enough time to take up moisture and sink. In contrast, when the ground is wet, many unsound acorns may be heavy enough to sink in water, and a few hours of drying at ambient temperature can help the separation. Water flotation is never 100% effective, but common sense and attention to detail will enable collectors to make dramatic improvements in the quality of their acorns. Another way to allow for different acorn moisture conditions may be to use salt solutions to change the density of the water. In a test with water oak and willow oak (Johnson 1983), 230 g of salt/liter of water for unsaturated acorns and 285 g/liter for saturated acorns, led to recovery of up to 11% more good acorns. The acorns were not in the salt solutions long enough to take up the chemical, and a quick rinse after recovery removed surface salt. In the dry climate of California, acorns of blue oak dry so quickly that collection directly from the tree may be the only way to ensure seed quality (McCreary and Koukoura 1990). A loss of only 10% acorn moisture resulted in almost 40% less germination for blue oak.

Data on acorn size and weight are summarized in table 3. For many years, nurseries did little sizing of acorns, but now that is changing, at least in the South. Numerous nurseries now size acorns with screens or other devices (Bonner and Vozzo 1987) to gain in uniformity of germination and bed density. Positive correlations between acorn size and leaf area have been reported for northern red, chestnut, white, and bear oaks (Farmer 1980) and also between acorn size and shoot growth for English and durmast oaks (Kleinschmit and Svolba 1979).

In years when light crops are produced, the percentage of acorns that are infested with insect larvae will be large,

Table 2—*Quercus,* oak: height, seed-bearing age, and seedcrop frequency

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
Q. acutissima	15	1862	5	—
Q. agrifolia	23	1849	15	—
Q. alba	30	1724	20	4–10
Q. arizonica	12	—	—	—
Q. bicolor	30	1800	20	3–5
Q. cerris	30	1735	—	—
Q. chrysolepis	30	1877	20	2–4
Q. coccinea	30	1691	20	3–5
Q. douglasii	18	—	—	2–3
Q. dumosa	6	—	—	—
Q. ellipsoidalis	21	1902	—	2–4
Q. emoryi	18	—	—	—
Q. falcata	27	1763	25	1–2
Q. gambelii	15	—	—	—
Q. garryana	21	1873	—	2–3
Q. grisea	20	—	—	—
Q. ilicifolia	6	1800	—	—
Q. imbricaria	21	1724	25	2–4
Q. incana	12	—	—	—
Q. kelloggii	26	1878	30	2–3
Q. laevis	9	1834	—	1–2
Q. laurifolia	27	1786	15	1
Q. lobata	30	1874	—	2–3
Q. lyrata	24	1786	25	3–4
Q. macrocarpa	30	1811	35	2–3
Q. marilandica	15	—	—	—
Q. michauxii	30	1737	20	3–5
Q. muehlenbergii	24	1822	—	—
Q. nigra	24	1723	20	1–2
Q. pagoda	34	1904	25	1–2
Q. palustris	24	1770	20	1–2
Q. petraea	30	Long	40	5–7
Q. phellos	30	1723	20	1
Q. prinus	24	1688	20	2–3
Q. robur	34	Long	20	2–4
Q. rubra	30	1724	25	3–5
Q. shumardii	34	1907	25	2–3
Q. sinuata	23	—	—	—
Q. stellata	18	1819	25	2–3
Q. suber	24	1699	12	2–4
Q. texana	30	1923	5	3–4
Q. turbinella	3	—	—	3–5
Q. vaccinifolia	1	1895	—	—
Q. variabilis	24	1861	—	2
Q. velutina	27	1905	20	2–3
Q. virginiana	18	1739	—	1
Q. wislizenii	18	1874	—	5–7

Sources: Burns and Honkala (1990), Olson (1974), Sargent (1965), Smith (1993), Sork and others (1993), Vines (1960).

and flotation offers a simple way to remove these damaged acorns. The major insect pests of acorns in the United States are the acorn weevils (*Curculio* spp.), filbertworms (*Melissopus latiferranus* Walsingham), and acorn moths (*Valentinia* spp.) (Baker 1972; Gibson 1972, 1982; Oliver and Chapin 1984; Vozzo 1984). A cynipid wasp that causes galls on acorns of European turkey oak and English oak is a major pest in Europe, causing 30 to 50% losses of the acorn crop each year in the United Kingdom (Collins and others 1983). Prevention of infestation is not possible, so infested acorns must be removed from the lots. Some collectors kill the larvae of acorn weevils by immersing the acorns in hot water (48 °C) for 40 minutes (Olson 1974). This temperature is dangerously close to conditions that will damage the

Table 3—*Quercus,* oak: seed yield data

	Seed weight/ fruit vol		Cleaned seeds/weight				
			Range		Average		
Species	**kg/hl**	**lb/bu**	**/kg**	**/lb**	**/kg**	**/lb**	**Samples**
Q. acutissima	—	—	210–245	95–110	85	187	2
Q. agrifolia	—	—	—	—	200	440	1
Q. alba	58–129	45–100	155–465	70–210	98	215	23
Q. bicolor	—	—	200–385	90–175	265	120	3
Q. cerris	—	—	130–320	60–145	240	110	4
Q. chrysolepis	—	—	110–310	50–150	—	—	—
Q. coccinea	39–77	30–60	230–890	105–405	520	235	4
Q. douglasii	—	—	120–330	55–180	220	100	4
Q. dumosa	—	—	—	—	220	100	1
Q. ellipsoidalis	—	—	450–640	205–290	540	245	11
Q. falcata	42–64	33–50	705–1,730	320–785	1,190	540	9
Q. garryana	50	39	165–220	75–100	185	85	3
Q. ilicifolia	—	—	—	—	1545	700	1
Q. imbricaria	—	—	695–1,750	315–795	915	415	11
Q. incana	—	—	500–1,500	225–680	—	—	—
Q. kelloggii	—	—	115–325	52–145	210	95	49
Q. laevis	—	—	—	—	870	395	1
Q. laurifolia	—	—	860–1,520	90–690	1,235	560	3
Q. lobata	—	—	165–525	75–237	285	130	4
Q. lyrata	—	—	285–340	130–154	265	120	6
Q. macrocarpa	39–45	30–35	90–300	40–135	165	75	8
Q. michauxii	51–80	40–62	75–430	35–195	125	55	35
Q. muehlenbergii	60–66	47–51	580–1,145	265–520	870	395	4
Q. nigra	57–72	44–56	510–1,545	230–700	640	290	226
Q. pagoda	—	—	925–1,640	420–745	690	312	41
Q. palustris	—	—	705–1,190	320–540	475	220	33
Q. petraea	—	—	130–650	60–295	375	170	9
Q. phellos	59–60	46–47	600–1,530	270–695	835	380	183
Q. prinus	—	—	120–430	55–195	220	100	5
Q. robur	—	—	200–495	90–225	285	130	10
Q. rubra	28–134	22–104	165–565	75–255	235	105	55
Q. shumardii	64	50	170–280	80–130	220	100	27
Q. sinuata	53	47	—	—	6,400	290	1
Q. stellata	69	54	440–1,400	200–635	840	380	9
Q. suber	—	—	110–220	50–100	165	75	13
Q. texana	67	52	125–315	55–145	220	100	83
Q. turbinella	—	—	660–770	300–350	715	325	2
Q. vaccinifolia	33	26	1630–2,910	740–1,320	2,270	1,030	2
Q. variabilis	—	—	165–275	75–125	230	105	12
Q. velutina	53–63	41–49	275–882	125–400	540	245	7
Q. virginiana	71	55	530–1,125	240–510	775	350	4
Q. wislizenii	36	28	100–152	100–150	275	125	3

Sources: Burns and Honkala (1990), Olson (1974), Toumey and Korstian (1942), Van Dersal (1938).

acorns, however, so caution must be used. In a study with live oak, germination and seedling growth dropped dramatically after hot water treatments of 7.5 to 60 minutes (Crocker and others 1988). Because none of these insects attacks other acorns during storage, the infestation cannot spread. Only in cases of exporting acorns to other countries where seed health regulations require treatment would this treatment be completely justified.

Storage. Acorns are recalcitrant seeds; they cannot tolerate desiccation below a rather high minimum moisture content and are therefore very difficult to store. Oaks are by far the most commercially important group of recalcitrant species in the temperate zone. The lethal moisture contents vary by species, but range from 15 to 20% in black oaks and 25 to 30% in white oaks. Most species of the black oak group can be stored for 3 years by maintaining high acorn moisture levels (above 30%) and storing just above freezing (1 to 3 °C) in containers that allow some gas exchange with the surrounding atmosphere (Bonner 1973; Bonner and Vozzo 1987; Suszka and Tylkowski 1982). Most species will germinate in storage under these conditions, but pre-sprouting does not prevent sowing or production of plantable seedlings (Bonner 1982). White oak acorns can be stored in a similar fashion, but safe moisture levels are 45 to 50%. White oaks germinate in storage much more readily than black oaks, and do not survive as well. As a practical matter, storage of white oak acorns for more than 6 months is seldom attempted in this country. Acorns of English oak have been successfully stored for 3 years in Europe by lowering the moisture levels slightly and mixing them with dry sawdust or peat (Suszka and Tylkowski 1980). Acorns of the same species are routinely stored for 3 years in Denmark also by lowering the moisture content slightly and storing the acorns right at freezing in open containers with no medium. In the case of another white oak, partial drying of California scrub oak acorns significantly improved viability retention over 8 months (Plumb and McDonald 1981). The partial drying may be beneficial because it reduces the incidence of fungi on the surface of the acorns.

Acorns can be stored in plastic bags, drums, or even boxes as long as the containers are not completely sealed and the acorns do not get too dry. Some European species can be stored by immersion in water (Jones 1958), and Nuttall oak has been successfully stored overwinter submerged in water at 3 to 5 °C (Johnson 1979). If drums or boxes are used, it is wise to insert a plastic bag liner. Respiration is rapid in seeds with high moisture levels, and oxygen will be depleted and carbon dioxide increased dramatically in just a few weeks. Plastic bags at least 4 mils thick are useful for storage; tops should be loosely folded over, not sealed. There is some evidence that white oaks should be stored in thinner bags (1.75 mils) because of their greater requirement for oxygen (Rink and Williams 1984). Most species can actually tolerate temperatures a few degrees below freezing (Suszka and Tylkowski 1980), but storage below –5 °C is usually fatal.

Pregermination treatment. Acorns of the white oak group generally have little or no dormancy and will germinate almost immediately after falling. These species should usually be planted in the fall. They will quickly put down radicles, but epicotyl dormancy occurs in some species and prevents shoot growth until the following spring. Epicotyl dormancy has been noted in English oak (Wigston 1987) and in eastern and southern white and chestnut oaks (Farmer 1977). White oaks in the warmer climate of California—coast and canyon live oaks, and blue, California scrub, and valley oaks—apparently do not have epicotyl dormancy (Matsuda and McBride 1989). Acorns of bur oak from the northern portion of its range actually require 60 days of cold, moist stratification for prompt germination (Tinus 1980). Acorns of the black oak group exhibit variable dormancy that is apparently imposed by the pericarp, the embryo, or both (Hopper and others 1985; Jones and Brown 1966; Peterson 1983), and stratification is usually recommended before spring-sowing or certain types of germination tests. Epicotyl dormancy has been reported in at least 1 black oak species—bear oak (Allen and Farmer 1977). If proper procedures are followed for storage of black oak acorns, the storage conditions will also serve to complete the stratification requirement, and additional treatment is not necessary (Bonner and Vozzo 1987). If additional stratification is needed, imbibed acorns should be held for 4 to 12 weeks at temperatures of 2 to 5 °C. The acorns may be mixed with peat or other media, but this is not necessary. Most managers stratify in plastic bags without medium, turning the bags each week or so to prevent pooling of excess moisture in the bags (Bonner and Vozzo 1987). Acorns of the black oak group sown in the fall or early winter need not be stratified before to sowing.

Germination tests. In the standard official laboratory test procedure for all oaks, the acorns should be soaked in water for 48 hours; then a third of the acorn at the cup scar end should be cut off and the pericarp removed from the top half and placed on thick, moist blotters at alternating temperatures of 20 to 30 °C (ISTA 1993). No other pretreatments are necessary, and germination should be complete within 14 days. Germination can also be tested with intact acorns in sand, peat, or other media in greenhouse flats. In such tests, stratification may be necessary for black oak species (table 4). Germination is hypogeal (figure 3) and is generally complete in 3 to 5 weeks. Rapid estimates of viability can also be made with cutting tests, radiography, or tetrazolium staining (Belcher and Vozzo 1979; Bonner and Vozzo 1987). Cutting tests are reliable on freshly collected acorns, and radiography is very good for quick determination of insect infestation. Tetrazolium staining can also provide information on seed vigor, but acorn chemistry and morphology present some problems in this test (Bonner 1984).

Nursery practice. Numerous research studies have shown that success in planting oaks depends on production of vigorous seedlings through low sowing densities and undercutting in the beds (Schultz and Thompson 1990). Container production in greenhouses is also practiced for a few species (Tinus 1980). Fall-sowing acorns is preferable to spring-sowing in many instances if weather allows bed preparation in the fall. Fall-sowing eliminates the need for a large storage capacity for acorns and avoids the problems of fungi and early germination in storage. One disadvantage to

Table 4—*Quercus,* oak: germination test conditions and results

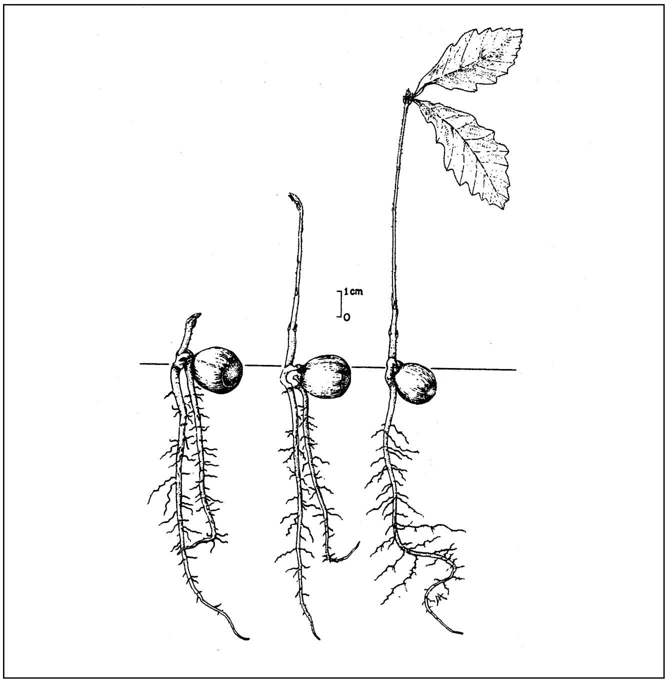
	Cold stratification	Germination test conditions				Germinative rate		Germination	
			Temp (°C)						
Species	**(days)**	**Medium**	**Day**	**Night**	**Day**	**Avg (%)**	**Days**	**(%)**	**Samples**
Q. acutissima	—	—	—	—	—	—	—	98	1
Q. agrifolia	0	—	—	—	15–40	—	—	73	1
Q. alba	0	Kimpac	30	20	30–98	39–93	10–41	50–99	21
Q. bicolor	0	Sand	21–35	10–16	60–240	65–95	80–120	78–98	3
Q. cerris	0	Germinator	22	20	30	—	—	33–76	3
Q. chrysolepis	0–60	Peat/loam	30	20	56–60	—	—	56–75	2
Q. coccinea	30–60	Kimpac	30	20	30–60	97	16	94–99	7
Q. douglasii	0	Sand	30	20	30	—	—	70–72	4
Q. durmosa	30–90	Sand	30	20	28	—	—	80–90	3
Q. ellipsoidalis	60–90	Sand	30	21	30–60	80–93	18–26	95	5
Q. falcata	30–90	Sand	23–27	23–27	30–57	62–74	22–36	75–100	8
Q. gambelii	14	—	—	—	—	92	15	92	1
Q. garryana	0	Loam	30	21	90	—	—	77–100	4
Q. ilicifolia	60–120	Sand/perlite	30	20	36–81	—	—	86–94	12
Q. imbricaria	30–60	Sand	24	16	30	—	—	28–66	2
Q. kelloggii	30–45	Sand	30	21	30–40	—	—	95	1
Q. laevis	60–90	Sand	27	23	7	—	—	82	2
Q. laurifolia	0	Soil			108	—	—	50	1
	14–90	Sand	27	23	30–90	—	—	45–92	6
Q. lyrata	0	Sand	21–35	10–16	160	82	100	84	1
	42	Sand	27	23	128	—	—	82	4
Q. macrocarpa	30–60	Sand	30	20	40	28-85	25-45	45	11
Q. marilandica	90	—	—	—	—	—	—	91	1
Q. michauxii	0	Soil	32	21	50–84	23–48	40–60	49	2
	30	Soil	32	21	50	86	22	98	1
Q. muehlenbergii	0	Kimpac	30	20	45	95	8	98	4
Q. nigra	30–60	Sand/peat, Kimpac	30–32	20–21	52–73	54–80	31–73	60–94	12
Q. pagoda	60–120	Sand/perlite	30	20	30–40	85–90	21–38	86–98	11
Q. petraea	0	Sand	30	20	30	—	—	65–74	7
Q. phellos	30–90	Soil, Kimpac	32	21	45–100	41	55	67	4
	0	Soil	32	21	90	83	47	89	1
Q. prinus	0	Sand	27	18	60	72–78	40	82	3
Q. robur	0	Sand	25	16	30–60	—	—	81	4
Q. rubra	30–45	Sand	30	20	40–60	39–85	13–42	58	11
	70	Sand/peat	20	20	20	80	10	100	1
Q. shumardii	60–120	Soil, Kimpac	32	21	29–50	53–66	21–28	72–82	3
Q. sinuata	0	Kimpac	30	20	30	81	21	87	4
Q. stellata	0	Sand, Kimpac	30	20	45–60	42–93	10–45	54–98	7
Q. suber	0	Sand	27	27	20–30	—	—	73-100	5
Q. texana	60–90	Soil	32	21	58–87	—	—	60–69	20
Q. turbinella		Sand	38	5	—	—	—	95	2
Q. vaccinifolia	0	Loam	23	19	180	38	30	43	1
Q. variabilis	0	Sand	25		28	55	28		2
Q. velutina	30–60	Sand	27	18	30–50	—	—	47	5
Q. virginiana	0	Kimpac	30	20	—	92	8	97	4
Q. wislizenii	30–60	Sand/peat	30	20	69	—	—	75	1

Sources: Dirr and Heuser (1987), Korstian (1927), Larsen (1963), Olson (1974), Swingle (1939).

fall-sowing in the southern part of the country is that mild winters may not completely satisfy the stratification requirement of dormant black oaks, and germination in the spring may be slow and erratic. Another disadvantage is prolonged exposure to predators, such as grackles (*Quiscaluis spp.*) and blue jays (*Cyanocitta cristata*), that dig up acorns from the beds. If spring-sowing is used (very common in the South), the acorns should be stratified.

Acorns should be drilled in rows 20 to 30 cm (8 to 12 in) apart and covered with 6 to 25 mm ($^1/_4$ to 1 in) of firmed soil. The planting depth should at least be equal to the average acorn diameter. Desirable seedbed densities are 100 to

Figure 3—*Quercus macrocarpa*, bur oak: seedling growth 1, 5, and 12 days after germination



160 seedlings/m^2 (10 to 15/ft^2) (Williams and Hanks 1976), or less. For cherrybark oak, a study of bed densities from 43 to 108/m^2 (4 to 10/ft^2) showed that the lowest density produced more plantable seedlings per weight of seed, even though nursery costs were approximately 20% higher (Barham 1980). Another study with this same species found that 86/m^2 (8/ft^2) produced the greatest number of plantable seedlings (Hodges 1996). Fall-sown beds should be mulched with sawdust, ground corncobs, burlap, straw, or similar materials. Where high winds may blow the mulch, some sort of anchoring device, such as bird netting, must be used. Mulches reduce erosion and frost heaving and provide some protection against rodents and birds. In the spring, after frost danger is past, the straw and hay mulches should be removed, but sawdust can remain on the beds. Partial shade has been found to improve germination of Nuttall (Johnson 1967) and cherrybark oaks (Hodges 1996) but is not commonly used for other oaks. The common planting stock for oaks is a 1+0 seedling.

Oaks can also be direct-seeded in the field but must be covered to control predation by animals. Spot-seeding at depths of 2 to 5 cm (1 to 2 in) have been successful for bur, chestnut, white and pin oaks in Kentucky (Cunningham and Wittwer 1984); white, northern red, and black oaks in Tennessee (Mignery 1975); and cherrybark, Nuttall, sawtooth, Shumard, and water oaks in Mississippi (Francis and Johnson 1985; Johnson 1984; Johnson and Krinard 1985). Rapid germination will also reduce losses to rodents and birds, so acorns direct-seeded in the spring should be stratified. In recent years, large areas have been seeded to oaks in the Mississippi River floodplain in Mississippi and Louisiana. Results have been mixed; some operations have been successful and others have not, but the reasons for failure have not always been understood. In these sites, control of competing vegetation is often necessary in the first few years.

Oaks in general are extremely difficult to propagate vegetatively on a commercial scale, although a few successes have been reported. Grafting and budding have been somewhat successful for ornamental selections (Dirr and Heuser 1987), and some advances have been made in tissue culture of certain oaks (Chalupa 1990; Gingas 1991).

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Rhamnaceae—Buckthorn family

Rhamnus L.

buckthorn

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Growth habit, occurrence, and use. Until recently, the buckthorn genus—*Rhamnus*—and the closely related genus *Frangula* have been treated as the single genus *Rhamnus* consisting of more than 125 species of evergreen or deciduous shrubs and trees with alternate branches and simple leaves with prominent pinnate veins (Hickman 1993). Kartesz and Gandhi (1994), however, used floral morphology and leaf venation, as well as anatomical features of xylem vessels to support segregation of *Frangula*. Under their treatment, *Rhamnus* spp. have winter buds protected with bud scales and arcuate leaf nerves. Both *Rhamnus* and *Frangula* are native to the temperate regions of North America, Europe, and Asia, and also occur in the Neotropics and southern Africa as shrubs and trees up to 1.5 m dbh and over 60 m tall (Johnston and Johnston 1978; Krüssmann 1985). The common name buckthorn, which is shared by both genera, may have arisen in Europe, where some of the species are thorny (Mozingo 1987; USDA 1937). *Rhamnus* is the Latinized form of the ancient Greek name for the genus. At least 14 species and subspecies are distributed within the United States (table 1) (USDA NRCS 2001).

European buckthorn, native to Europe and temperate Asia and widely naturalized in the northeastern United States, is a common old-field invader (Gill and Marks 1991) that grows to about 4 m in height with branches that may end in sharp thorns. The bark yields yellow and saffron-colored dyes. The black fruits have been collected for over a thousand years as the source of a strong cathartic and laxative that is so potent that its purgative properties may be retained in the flesh of animals that have consumed the fruit (Mozingo 1987).

Alder buckthorn has perhaps the broadest distribution of all the species native to North America. The specific epithet refers to its similarity to alder (*Alnus*) in leaf shape. The leaves are deciduous, and the wood has been used as a source of the finest charcoal for gunpowder (Everett 1982). It grows to a height of 1.5 m on moist mountain slopes and streambanks.

Spiny, hollyleaf, and island redberries are evergreen shrubs or small trees of California chaparral. The fruits of spiny and hollyleaf redberries may be preferred browse of deer (*Odocoileus* spp.) (Conrad 1987).

Alder buckthorn and European buckthorn are alternate hosts for crown rust—*Puccinia coronata* Corda.—which causes yellow leaf spot in the aecial stage. Economic damage by crown rust is confined to heavy damage in fields of oats grown in close proximity to hedges and fence-rows of buckthorns (Ziller 1974).

The dates of earliest known cultivation of species native to North America includes 1778 for alder buckthorn and the mid-1800's for spiny redberry (Krüssmann 1985).

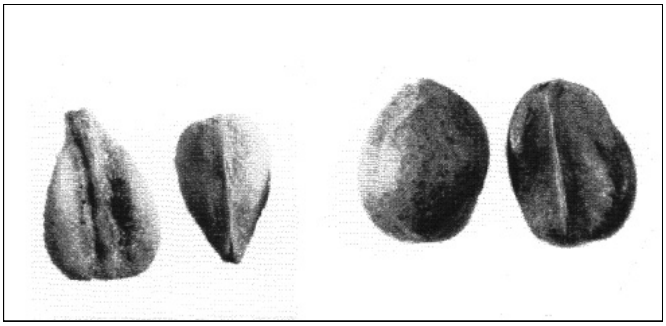
Flowering and fruiting. The inconspicuous flowers are either perfect or imperfect and are borne in small axillary racemes, fascicles, or occasionally reduced to single flowers in alder buckthorn and spiny, hollyleaf, and island redberries. The shallow to deeply campanulate hypanthium is rimmed with 4 deltoid, thin and spreading sepals, with the upper part of the hypanthium falling after maturity and the lower part remaining around the developing fruit (Hitchcock and others 1961; Kartesz and Gandhi 1994). White to greenish white petals are equal to the sepals in number and alternating, or lacking. There are 4 stamens, and the anthers are shorter than filaments. The ovary has 2 to 4 cells. Flowers are unisexual in spiny, hollyleaf, and island redberries; alder buckthorn and European buckthorn plants may be dioecious. Flowers appear in the spring and fruits ripen several weeks to months later (Hubbard 1974).

Fruits are drupaceous, the berrylike pulpy mesocarp embedding several free 1-seeded stones (figure 1) (Johnston and Johnston 1978). Fruits are 6 to 8 mm in diameter; they are generally black in alder buckthorn and red in spiny, hollyleaf, and island redberries. Spiny, hollyleaf, and island redberries have 2 stones per fruit; alder buckthorn has 3 stones per fruit; and European buckthorn has 3 or 4 stones per fruit (figure 2). Stones are grooved on the outside (Kartesz and Gandhi 1994). Dispersal is mostly by birds.

Table 1—*Rhamnus,* buckthorn: nomenclature and occurrence

Scientific names & synonym(s)	Common name(s)	Occurrence
R. alnifolia **L'Hér.**	**alder buckthorn**	Transcontinental in S Canada, Maine to Virginia, Tennessee, W to Utah, California
R. arguta **Maxim**.	—	Introduced in Indiana
R. cathartica **L.**	**European buckthorn,** waythorn, common buckthorn	Europe & Asia; naturalized from Nova Scotia, Maine, S to Virginia, W to Montana, Wyoming, Utah, & California
R. crocea **Nutt.** *R. pilosa* (Trel.) Abrams	**spiny redberry,** redberry buckthorn	California to Baja California Sur, Arizona, & New Mexico
R. davurica **Pallas**	**Dahurian buckthorn**	Siberia to N China; introduced in Rhode Island, Pennsylvania, North Carolina, E to North Dakota, Nebraska
R. davurica **Pallas ssp. *nipponica* (Makino) Kartesz & Gandhi**	**Dahurian buckthorn**	Introduced in Rhode Island
R. ilicifolia **Kellogg** *R. crocea* Nutt. ssp. *ilicifolia* (Kellogg) C.B. Wolf *R. crocea* Nutt. var. *ilicifolia* (Kellogg) Greene	**hollyleaf redberry**	Oregon, California, Nevada, & Arizona
R. japonica **Maxim.**	**Japanese buckthorn**	Japan: introduced in Illinois
R. lanceolate **Pursh ssp. *glabrata* (Gleason) Kartesz & Gandhi** *R. lanceolata* Pursh var. *glabrata* Gleason	**lanceleaf buckthorn**	Virginia, Ohio, Tennessee, Alabama, W to South Dakota, Arkansas, Texas
R. lanceolate **Pursh ssp. *lanceolata***	**lanceleaf buckthorn**	Pennsylvania, Virginiana, W to Wisconsin, Indiana, Missouri, Tennessee, Alabama
R. pirifolia **Greene** *R. crocea* Nutt. var. *pirifolia* (Greene) Little *R. crocea* Nutt. ssp. *pirifolia* (Greene) C.B. Wolf	**island redberry**	S California to Mexico
R. serrata **Humb. & Bonpl. ex J.A. Schultes** *R. fasciculata* Greene *R. smithii* Greene ssp. *fasciculata* (Greene) C.B. Wolf	**sawleaf buckthorn**	Arizona, New Mexico, Texas
R. smithii **Greene** *R. smithii* Greene ssp. *typica* C.B. Wolf	**Smith buckthorn**	Colorado & New Mexico
R. utilis **Dcne.**	**Chinese buckthorn**	E China; introduced in Michigan & Illinois

Figure 1—*Rhamnus*, buckthorn: cleaned seeds of *R. alnifolia*, alder buckthorn (**left**) and *R. davurica*, Dahurian buckthorn (**right**).



Good seedcrops for all species are likely to occur in most years. Regeneration of spiny and hollyleaf redberries is primarily by stump-sprouting after fire (Conrad 1987; Keeley 1981).

The reproductive biology of a few non-North American species has been investigated, including (1) the obligatory re-sprouting of *R. palaestina* Boiss. in Israel (Naveh 1974); (2) population sex ratio, flowering phenology, and between-sex differences in reproductive allocation in Italian buckthorn (*R. alaternus* L.), a dioecious shrub of the Mediterranean region (Guitián 1995a); (3) the population sex ratio, pollen-to-ovule ratio, and flowering and fruiting phenology in *R. legionensis* Rothm., a dioecious shrub restricted to limestone areas in the León Province of northwest Spain (Guitian 1995b); and (4) the partitioning of dry mass and nitrogen between flesh and stone in European buckthorn (Lee and others 1991).

Collection, extraction, and storage. Fruits can be collected from the shrubs and trees when ripe, although collection timed to occur about 2 weeks before the fruit is fully ripe may limit losses to birds (Hubbard 1974). Fruits can be

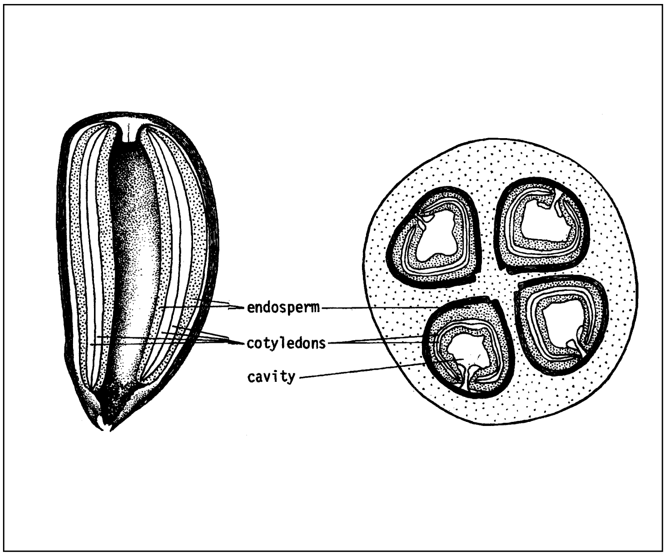


Figure 2—*Rhamnus cathartica*, European buckthorn: longitudinal section through a seed (**left**) and transverse section (**right**) through 4 seeds in a fruit.

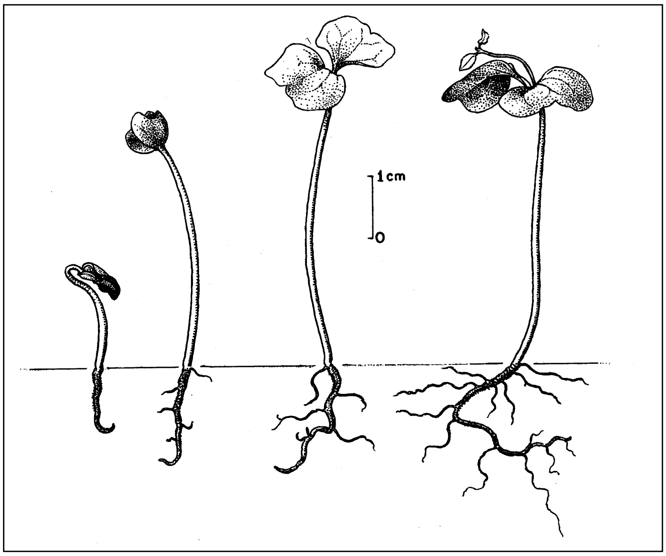


Figure 3—*Rhamnus cathartica*, European buckthorn: seedling development at 1, 4, 19, and 28 days after germination.

run through a macerator with water soon after collection; full seeds can then be cleaned of other material by repeated decantation. Data on yield of seeds are scant and based on limited samples; yields are about 105 seeds/g (2,975 seeds/oz) for spiny redberry (Keeley 1987) and 95 seeds/g (2,690 seeds/oz) for European buckthorn (Lee and others 1991).

Seed storage guidelines have not been developed for buckthorn species, but it appears that seeds can be stored adequately for several years if they are kept in sealed containers at low temperatures (Hubbard 1974).

Pregermination treatment. Considerable variability seems to exist in the need for pregermination treatments of buckthorn seed. Fresh seeds of alder buckthorn and spiny redberry apparently have no innate germination requirements (Hubbard 1974; Keeley 1987). During laboratory tests involving 1 month of stratification at 5 °C, however, more than 75% of the total germination occurred after 7 days of incubation at 23 °C in the dark. Germination increased to 90% when seeds were incubated with an initial heat treatment of 100 °C for 5 minutes and seeds were placed on soil containing 0.5 g powdered charred wood (charate) of the chaparral shrub chamise or greasewood—*Adenostoma fasciculatum* Hook. & Arn.—a treatment designed to simulate conditions after a chaparral fire (Keeley 1987). Seeds of spiny redberry germinated best after 1 month of cold stratification followed by an initial heating treatment of 100 °C for 5 minutes and incubation at 23 °C in charate-enriched soil under a 12-hour photoperiod of 350 μmol/m^2/sec. Seeds germinated slowly, with more than 75% of the total germination delayed until a second cycle of stratification and incubation (Keeley 1987). Seeds of European buckthorn have been stratified for 2 to 3 months in moist peat at 5 °C (Dirr 1990). Soaking European buckthorn seeds in concentrated sulfuric acid treatment for 20 minutes to break dormancy was found to be harmful (Hubbard 1974).

There are no officially prescribed germination tests procedures for buckthorns. Viability tests by tetrazolium staining have been suggested for European species (Enescu 1991). Seeds should be soaked in water for 24 hours, cracked open in a vise, then re-soaked overnight. Staining should take place in a 1% tetrazolium solution for 24 hours at 30 °C (Dirr 1990). To be considered viable, the embryos must be completely stained, with the exception of the extreme third of the distal ends of the radicle and cotyledons.

Nursery and field practice. Detailed nursery techniques have not been developed for most buckthorn species. The available information suggests that for most of the species, the seeds should be sown in the spring at a depth of 10 to 40 mm (0.4 to 1.6 in) after they have been treated to break dormancy (Hubbard 1974). Germination is epigeal with thin, usually curved cotyledons (figure 3) (Kartesz and Gandhi 1994). Some buckthorns also are propagated by layering and by cuttings or by grafting (Hubbard 1974).

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Ericaceae—Heath family

Rhododendron L.

rhododendron and azalea

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Occurrence. The genus rhododendron—*Rhododendron* L.—is indigenous mainly to the Northern Hemisphere, with large concentrations in the mountain ranges of China, Tibet, and upper Burma as well as in Japan and the eastern United States. Plants are found commonly in regions with highly organic soils, high rainfall, high humidity, and a temperate climate (Cox 1990). Species range from tiny, prostrate, alpine shrubs only 5 cm tall to trees with enormous leaves that reach heights of 24 m (Leach 1961). Species native to North America are listed in table 1.

Growth habit. There are over 900 species of rhododendrons and numerous cultivars (Davidian 1992). They include many of the most spectacular flowering trees and shrubs and are one of the most important and diverse groups of ornamental plants in cultivation (Dirr and Heuser 1987). The genus comprises both rhododendrons and azaleas. General characteristics are listed in table 2; however, these distinct characters are now known to be part of a continuum of gradation. Therefore, there are no clear delineations between azaleas and rhododendrons.

Uses. Besides their aesthetic appeal, rhododendrons in the wild provide erosion control for steep watersheds and protection for wildlife. In addition, some Himalayan species have been utilized for medicinal purposes, as a tea substitute, or for incense (Cox 1990). Under cultivation, the species are recognized as one of the most important plants available due to their attractive foliage and extremely showy flowers. For landscaping, rhododendrons are unsurpassed with their variations in form, flower color, texture, and leaf morphology. Those with larger leaves should be planted in a woodland or similar setting. Rosebay rhododendron is ideal as a woodland shrub or for tall evergreen backgrounds, but its texture is much too coarse and its stature entirely too large for home foundation plantings. Catawba rhododendron and its western relative, west coast rhododendron, are also well suited for woodland plantings, although in cooler climates Catawba rhododendron occurs often in full sun. Catawba rhododendron also has been used as a parent in many breeding programs to provide cold-hardy cultivars for the northeastern United States (LHBH 1976). Piedmont rhododendron can endure temperatures to –32 °C and flowers later in the year, when there is not much floral color from other shrubs (Leach 1961). It is also among the most heat tolerant of all rhododendrons. Piedmont rhododendron grows too tall for foundation plantings but is useful as a robust, evergreen background shrub that tolerates shade. Carolina rhododendron is one of most useful and adaptable of all rhododendrons, thriving on a wide variety of sites and exposures (Leach 1961). It is well suited as a foundation planting due to its moderate size and growth habit. Chapmans' rhododendron is suited for lowland southern gardens, probably the only evergreen rhododendron that is truly heat resistant and easy to grow in the Deep South (Leach 1961). Deciduous, dwarf, small-flowering species of azaleas should be mass planted, as no other shrubs can provide such intense color in a mass planting (Hillier Nurseries 1994).

Geographic races and hybrids. Rhododendrons in the wild are quite variable. A single species may have numerous varieties and forms, and some of the deviations are extreme (Leach 1961). In addition, natural introgression among species is common, so species tend to merge with one another. Within a species, the environmental conditions present in northern locations or at high elevations can dwarf species normally attaining much larger proportions when grown in the more favorable environmental conditions present in more-southern or lower-elevation sites. At higher altitudes, leaves of various species diminish in size, which helps them to resist the drying effects of strong winds (Leach 1961).

Cultivated rhododendrons and azaleas may be species, but frequently they are cultivars of well-known hybrids. Hybrids usually result from controlled pollinations in attempts to produce plants possessing desirable characteristics of both parents. A selected hybrid is known as a clone,

Table 1—*Rhododendron*, rhododendron and azalea: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
Evergreen Rhododendrons		
***R. carolinianum* Rehd.**	**Carolina rhododendron,** Carolina azalea	Higher slopes of Blue Ridge Mtns
***R. catawbiense* Michx.**	**Catawba rhododendron,** Catawba rosebay, mountain rosebay, purple laurel,	Mtns of West Virginia & Virginia to Georgia & Alabama
***R. chapmannii* A. Gray** *R. minus* var. *chapmanii* (A. Gray) Duncan & Pullen	**Chapman's rhododendron**	Sandy coastal plain of NW Florida
***R. macrophyllum* D. Don ex G. Don** *R. californicum* Hook. *R. washintonianum* Hort. ex Zab.	**west coast rhododendron,** California rosebay, Pacific rhododendron	Pacific Coast from British Columbia to central California
***R. maximum* L.** *R. maximum* var. *roseum* Pursh *R. ashleyi* Coker	**rosebay rhododendron,** rosebay, great laurel rhododendron	Ontario & Nova Scotia S along Appalachian Mtns to Georgia & Alabama
***R. minus* Michx.** *R. cuthbertii* Small; *R. punctatum* Andr.	**piedmont rhododendron**	Piedmont & lower mtn elevations of Tennessee & North Carolina to Alabama
Deciduous Rhododendrons		
***R. alabamense* Rehd.** *Azalea alabamensis* (Rehd.) Small	**Alabama azalea**	Alabama
***R. albiflorum* Hook.** *Azalea albiflora* (Hook.) O. Kuntze *Azaleastrum albiflorum* (Hook.) Rydb.	**Cascade azalea**	Rocky Mtns of British Columbia & Alberta to Oregon & Colorado
***R. arborescens* (Pursh) Torr.** *Azalea arborescens* Pursh	**smooth azalea,** sweet azalea	Pennsylvania to Georgia & Alabama
***R. atlanticum* (Ashe) Rehd.** *Azalea atlantica* Ashe.	**coast azalea,** dwarf azalea	Delaware to South Carolina
***R. austrinum* (Small) Rehd.** *Azalea austrina* Small	**Florida flame azalea,** orange azalea	Florida to SE Mississippi
***R. calendulaceum* (Michx.) Torr.** *Azalea calendulacea* Michx. *Azalea lutea* auct. non L.	**flame azalea,** yellow azalea	SW Pennsylvania & Ohio to Georgia
***R. camtschaticum* Pallas** *Therorhodion camtschaticum* (Pallas) Small	**Kamchatka rhododendron**	NE Asia, Alaska to British Columbia
***R. canadense* (L.) Torr.** *Azalea canadensis* (L.) O. Kuntze *Rhodora canadensis* L.	**rhodora**	Newfoundland to Pennsylvania
***R. canescens* (Michx.) Sweet** *Azalea canescens* Michx. *R. candidum* (Small) Rehd.	**Florida pinxter**, hoary azalea, mountain azalea	North Carolina to Florida & Texas
***R. cumberlandense* E.L. Braun** *R. bakeri* auct. non (Lemm. & McKay) Hume	**Cumberland rhododendron**	Kentucky & West Virginia to North Carolina, Georgia, & Alabama
***R. flammeum* (Michx.) Sarg.** *R. speciosum* (Willd.) Sweet *Azalea speciosa* Willd.	**Oconee azalea,** Piedmont azalea	South Carolina & Georgia
***R. lapponicum* (L.) Wahlenb.** *Azalea lapponica L.*	**Lapland rhododendron,** Lapland rosebay	Mtns of N Europe, N Asia, & N North America
***R. oblongifolium* (Small) Millais** *Azalea oblongifolia Small*	**Texas azalea**	Arkansas, SE Texas, & E Oklahoma
***R. occidentale* (Torr. & A. Gray ex Torr.) A. Gray**	**western azalea**	S Oregon to S California

or cultivar, and does not come true from seed. Thus, vegetative propagation is essential, as seed propagation results in inevitable variation among individuals. Generally, hybrids are more adaptable because they possess a combination of those genes required by their parents to withstand the environments where they originated. As a group, hybrids flower at an earlier age and more regularly year after year than their original parents (Leach 1961). However, every improvement in flower size or color is often accompanied by a loss in some other trait, such as foliage characteristics or disease resistance.

Table 1—*Rhododendron*, rhododendron and azalea: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. periclymenoides* (Michx.) Shinners** *R. nudiflorum* (L.) Torr. *Azalea nudiflora* L. *R. periclymenoides* var. *eglandulosum* Seymour *R. nudiflorum* var. *glandiferum* (Porter) Rehd.	**pinxterbloom,** pinxter flower, honeysuckle, pink azalea	Maine to South Carolina & Tennessee
***R. prinophyllum* (Small) Millais** *R. roseum* (Loisel.) Rehd. *R. nudiflorum* var. *roseum* (Loisel.) Wieg. *Azalea prinophylla* Small	**rose-shell azalea,** early azalea, piedmont azalea, mayflower azalea	S Quebec, through New England to Virginia & W as far as Missouri
***R. prunifolium* (Small) Millais** *Azalea prunifolia* Small	**plumleaf azalea,** plum-leaved azalea	Georgia & Alabama
***R. vaseyi* A. Gray** *Azalea vaseyi* (A. Gray) Rehd. *Biltia vaseyi* (A. Gray) Small	**pink-shell azalea**	North Carolina
***R. viscosum* (L.) Torr.** *Azalea viscosa* L. *R. serrulatum* (Small) Millias *Azalea serrulatum* Small *R. viscosum* var. *aemulans* Rehd. *R. viscosum* var. *glaucum* (Michx.) A. Gray *R. viscosum* var. *montanum* Rehd. *R. viscosum* var. *nitidum* (Pursh) A. Gray *R. viscosum* var. *serrulatum* (Small) Ahles *R. viscosum* var. *tomentosum* Rehd. *R. coryi* Shinners	**swamp azalea,** white swamp azalea, swamp honeysuckle, clammy azalea, hammock-sweet azalea	Swamps from Maine to Florida & Louisiana

Source: LHBH (1976).

Table 2—*Rhododendron*, rhododendron and azalea: general distinguishing characteristics

Plant part	Rhododendrons	Azaleas
Leaves		
Duration	Evergreen	Deciduous
Texture	Coriaceous	Membranous
Abaxial surface	Scaly or punctate	Pubescent
Margin	Entire	Ciliate or ciliolate
Flowers		
Corolla	Campanulate	Funnelform
Stamens	10 or more	5
Ovary	Scaly or tomentose	Setose

Source: LHBH (1976).

Hybrids began to appear about 1825, with most of the early ones derived from Catawba and rosebay rhododendrons, tree rhododendron (*R. arboreum* Sm.), Caucasian rhododendron (*R. caucasicum* Pall.), and *R. ponticum* L., indigenous to the United States, the Himalayas, Caucasus, and Turkey, respectively. Most of these early hybrids possessed ample foliage, firm and full flower trusses, and the ability to withstand exposure to freezing temperatures, and hence are often referred to as the "hardy hybrids." They are suited for landscape plantings in cold climates, and many are ideal as informal hedges or screens (Hillier Nurseries 1994). With the exploration of China and the eastern Himalayas during the first part of the 20th century, many new species were discovered and included in breeding programs. These newer hybrids show even greater variation in foliage, flower color, and growth habit (Hillier Nurseries 1994).

Two examples of hybrids that are planted widely throughout the southeastern United States are the Indian and Kurume azaleas. In fact, the Indian hybrid azaleas are likely the most popular of all flowering evergreen shrubs. They are derived primarily from Sims azalea (*R. simsii* Planch.) and macranthum azalea [*R. indicum* (L.) Sweet]—which, despite its specific epithet, is native to southern Japan not India. These hybrids are confused often with the parent species macranthum azalea, as they are sometimes sold as varieties or cultivars of *R. indicum* (LHBH 1976). Indian hybrids are broad mounding shrubs that are 2.5 to 3.0 m tall and usually grow dense in full sunlight and open and airy in the shade. They are utilized in the landscape as accent plants, for screening, and in mass groupings. The large showy flowers are 5 to 9 cm across, blooming in May with colors ranging from white, to pink, magenta, and orange-red (Odenwald and Turner 1987). Indian azaleas are grown also as large-flowered greenhouse azaleas.

Kurume azaleas are derived primarily from Hiryu azalea—*R. obtusum* (Lindl.) Planch.—also indigenous to Japan. These low-mounding, fine-textured hybrids are slow growers with relatively small, single or "hose-in-hose" double flowers in a variety of colors (Odenwald and Turner 1987). Many selections are available and they are planted widely in the southern United States, even though they are very site-specific and temperamental shrubs.

Flowering and fruiting. The perfect, showy flowers appear from March to August (table 3). Flower colors vary widely, with white, pink, and purple predominating. Flowers are pollinated by bees (Gibson 1901) and to a lesser extent by birds (Cox 1990). Fruits are oblong, 5-valved, dehiscent capsules that generally ripen during autumn (figure 1). When mature, capsules turn from green to brown, at which time they split along the sides, releasing minute seeds (figures 2–4). Capsules of rosebay rhododendron contain about 400 viable seeds/capsule (Romancier 1970).

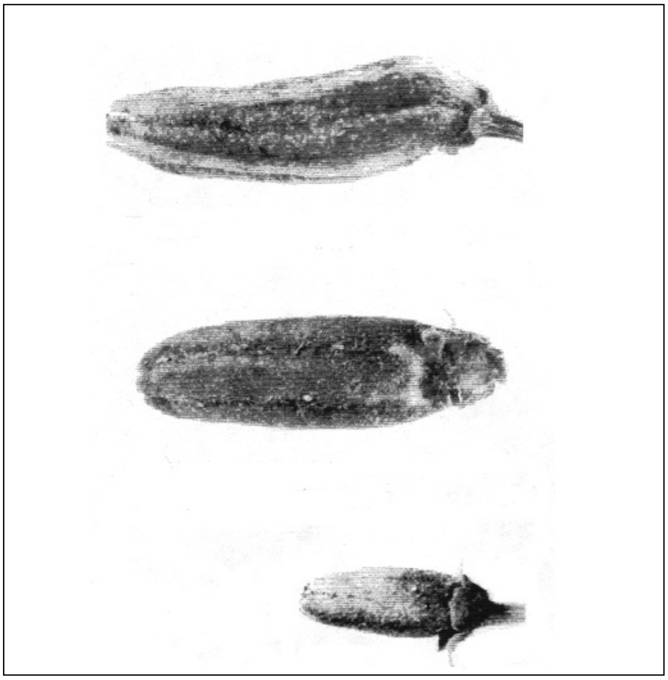
Collection of fruits, seed extraction, and cleaning. In general, capsules should be observed closely from mid-September onward and collected as they start to turn from green to brown (Bowers 1960). Fruits are dehiscent and if capsules are not collected before they open, most of the seeds will be lost. However, capsules can be picked green and then opened in gentle heat as long as their seeds are fully developed. Capsules may be air-dried at about 21 °C for 2 to 4 weeks (Blazich and others 1991; Malek and others 1989) or oven-dried for 12 to 24 hours at 35 °C (Dirr and Heuser 1987). Many capsules will split open during drying,

Table 3—*Rhododendron*, rhododendron and azalea: growth habit and flowering

Species	Growth habit & maximum height	Flowering	Flower color
Evergreen Rhododendrons			
R. carolinianum	Compact shrub; to 1.8 m	May	Pink, mauve, white
R. catawbiense	Spreading, rounded in the open; generally wider than tall to 3 m, sometimes small tree to 6 m	May–June	Magenta, pink, white, red
R. chapmanii	Shrub to 1.8 m	May	Rose
R. macrophyllum	Open tree-like shrub; often erect to 3–9 m	May–June	Purplish rose, white
R. maximum	Shrub in cultivation; to 4.6 m (sometimes to 12 m in the wild)	June–July	White, pink, purplish red
R. minus	2.8 m	June	Rose, white
Deciduous Rhododendrons			
R. alabamense	Low stoloniferous shrub; to 0.6–2.4 m	Apr–May	White
R. albiflorum	Erect shrub; from 0.9–2.1 m	June–July	Creamy white, yellow
R. arborescens	From low spreading bushes in open to tall and leggy in shade; up to 6 m	June–July	White
R. atlanticum	Stoloniferous shrub, forms branching sprays when well established; 0.3–1.5 m	May	White, pink
R. austrinum	Stiff and upright; from 3.0–3.6 m	Apr	Yellow-orange
R. calendulaceum	Stiff and upright; to 3.6 m	May–June	Yellow, orange, scarlet, pink
R. camtschaticum	Very small shrub; to 0.2 m	May	Reddish purple
R. canadense	Much branched shrub; to 0.9 m	Apr	Rose-purple, white
R. canescens	Sparingly branched shrub; to 4.6 m	Apr–May	Pink, white
R. cumberlandense	Low and twiggy, often stoloniferous shrub; to 2.4 m but rarely over 1.8 m	June–July	Yellow, orange, scarlet
R. flammeum	Mounding form; to 2.5 m	May	Scarlet, orange, yellow
R. lapponicum	Dwarf, procumbent shrub; to 0.3 m	Apr	Purple
R. oblongifolium	Upright, somewhat stoloniferous shrub; to 1.8 m	June	White, pink
R. occidentale	Rounded, occasionally upright or low shrub; to 1.0–4.6 m	Apr–Aug	White, pink, pale yellow
R. periclymenoides	Usually tall, vigorous and much- branched shrub; to 2.7 m & up to 4.5 m in wild	May	Pale pink, rose, reddish, white
R. prinophyllum	Upright, well branched shrub; to 2.5 m	May	Pink, white, rosy red
R. prunifolium	Tall, rounded-topped; up to 3.6 or 5.5 m in wild	July–Aug	Yellow, orange, scarlet
R. vaseyi	Upright shrub to 3.6 m	Apr–May	White, pink, crimson
R. viscosum	Form various: large & upright to dwarf, small tree; from 3–6 m, rounded or straggly shrub, stoloniferous form to 4.6 m	July–Oct	White, pink

Sources: Davidian (1992), Leach (1961), LHBH (1976).

Figure 1—*Rhododendron*, rhododendron: capsules with styles removed of *R. catawbiense*, Catawba rhododendron (**top**); *R. macrophyllum*, west coast rhododendron (**center**); and *R. maximum*, rosebay rhododendron (**bottom**).



whereas others may require crushing. Seeds should be cleaned well to remove chaff and broken pieces of capsules by shaking through various sized sieves. Seeds should then be graded further by removal of abnormal, damaged, or undersized seeds.

Rhododendrons normally produce copious amounts of seeds (Cox 1990; Romancier 1970); however, viable seeds are not always available on a yearly basis. Seeds are extremely small and size can vary greatly among species (Arocha and others 1999; Blazich and others 1991, 1993; Glenn and others 1998; Olson 1974) and among provenances within a species (Rowe and others 1994a). However, small differences in moisture content can cause wide variability in estimates of the number of seeds per given weight (table 4).

Storage. There is little information on proper storage techniques for maintaining long-term viability in the rhododendrons, but the evidence available suggests that the seeds of this genus are orthodox in storage behavior.

Seeds of rhododendrons with a moisture content of 4 to 9% will remain viable about 2 years at room temperature (Bowers 1960; Olson 1974). However, at room temperature,

Figure 2—*Rhododendron*, rhododendron: seeds of *R. calendulaceum*, flame azalea (**upper left**); *R. carolinianum*, Carolina rhododendron (**upper right**); *R. catawbiense*, Catawba rhododendron (**center**); *R. chapmanii*, Chapman's rhododendron (**lower left**); and *R. maximum*, rosebay rhododendron (**lower right**).

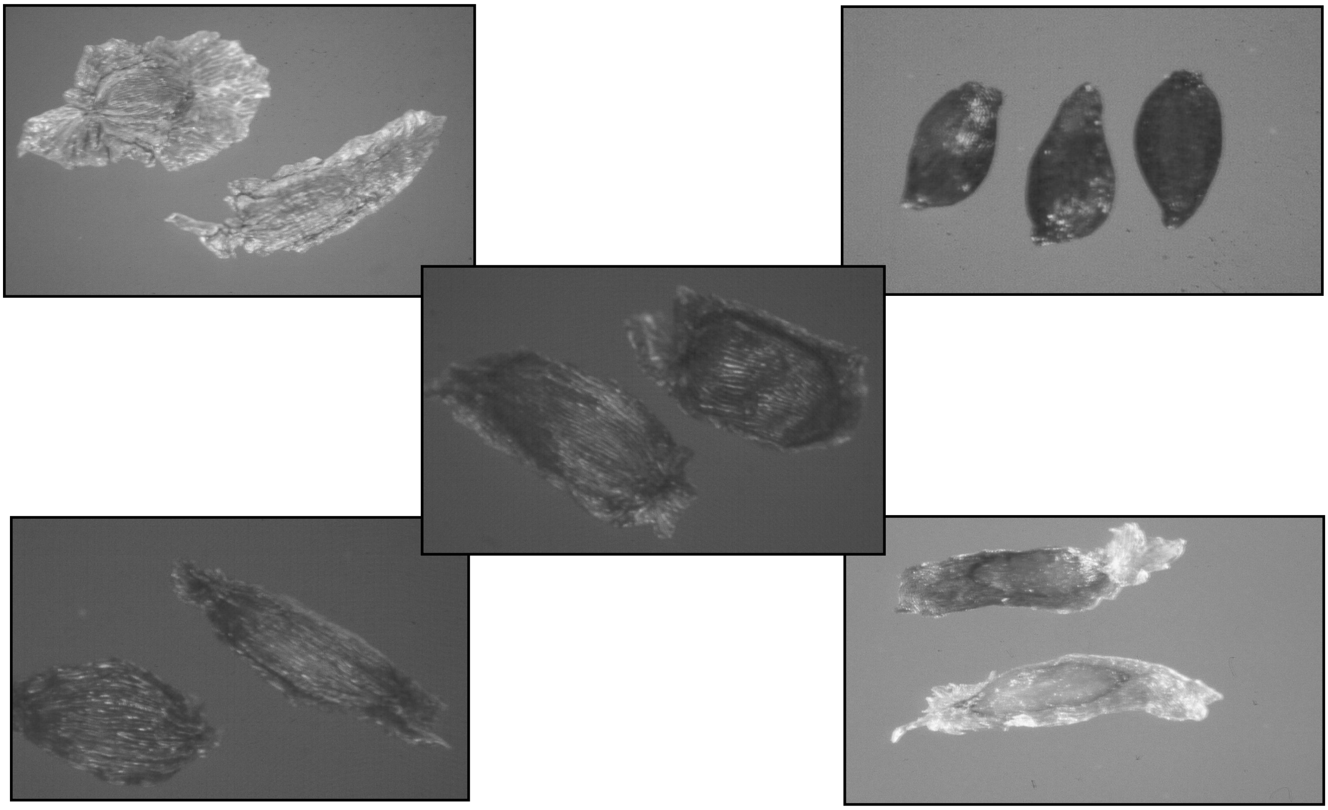


Figure 3—*Rhododendron macrophyllum*, west coast rhododendron: seeds in external view (**top left**), longitudinal section (**center**), and cross section (**bottom right**).

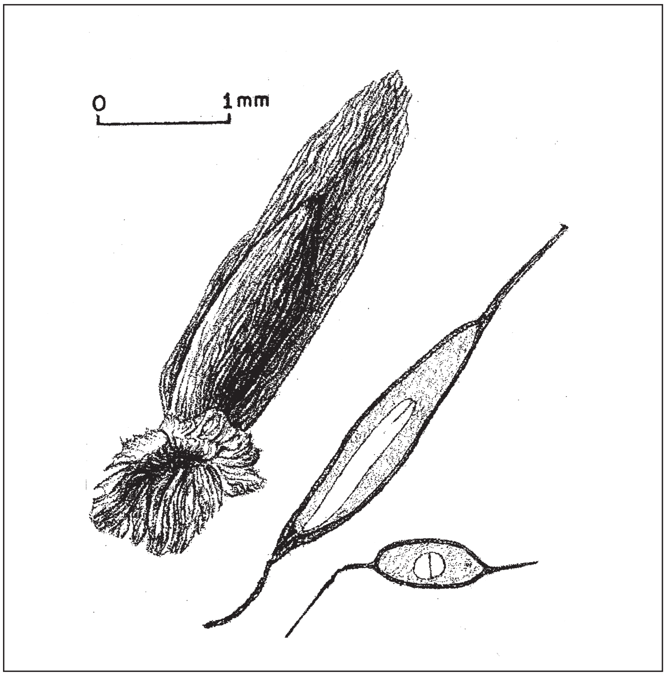
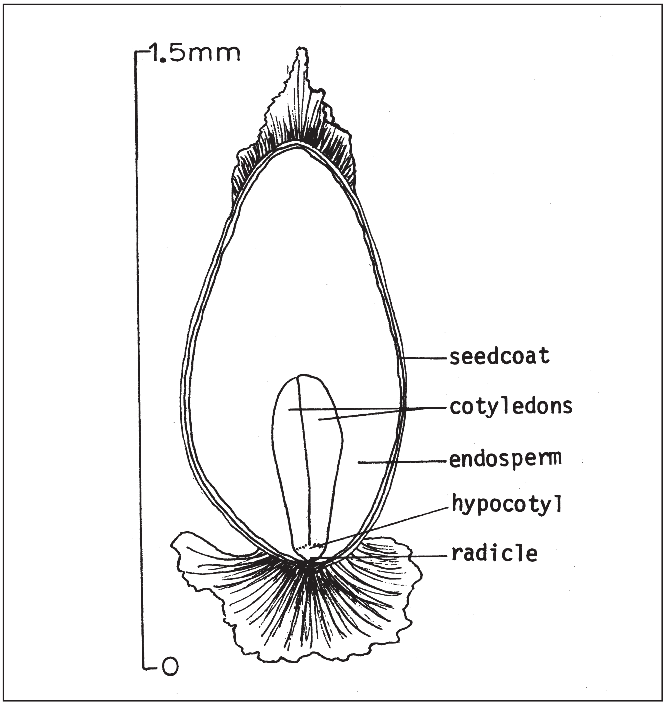


Figure 4—*Rhododendron maximum*, rosebay rhododendron: seed in longitudinal section.



seeds lose their viability at a rate of 50% a year, and those that retain their ability to germinate will sprout more slowly (Leach 1961). For Catawba and rosebay rhododendrons, Glenn and others (1998) compared seed germination under storage conditions analogous to storage in a home freezer at –18 °C, a refrigerator at 4 °C, and at room temperature (23 °C). Seed viability remained unchanged after 5 years of storage at –18 °C and 4 °C, which strongly suggests that viability for even longer periods is possible. Thus, long-term seed storage of Catawba and rosebay rhododendrons is possible, provided seeds are first dried to moisture contents of 5 to 7% and then stored in sealed containers at –18 or 4 °C. Room temperature storage (about 23 °C) should be avoided, as viability is lost rapidly (Glenn and others 1995). In the same study, Glenn and others (1998) also included seeds of Carolina rhododendron that were stored for only 4 years. After these 4 years at –18 or 4 °C, viability remained unchanged. Although viability decreased with storage at 23 °C, the decrease was not as dramatic as that observed for seedlots of Catawba and rosebay rhododendrons at the same temperature.

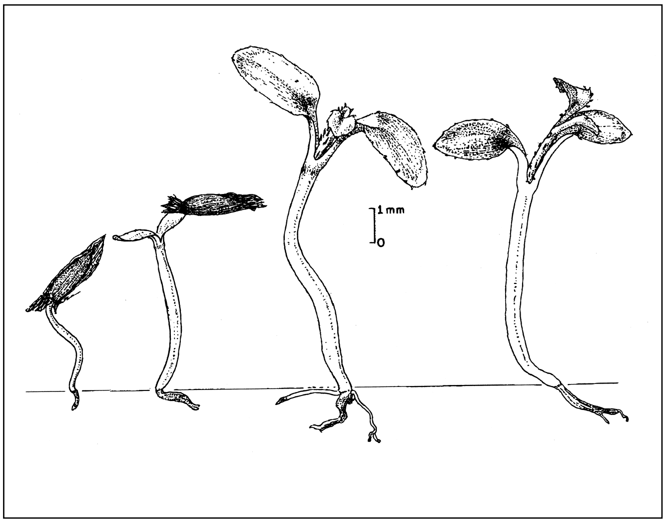
Pretreatment and germination tests. Mature seeds of rhododendrons possess no dormancy and will germinate shortly after sowing (Fordham 1960; Romancier 1970). Official testing rules prescribe a 21-day test on the top of moist blotter paper at 8 hours of daylight at 30° C and 16 hours of night at 20° C or a constant of 25° C with 8 hours of light daily (AOSA 1993). Germination is epigeal (figure 5). Several 30-day germination tests have been conducted for various species at a constant temperature of 25 °C or an alternating 8/16 hour thermoperiod of 25/15°C in combination with photoperiods ranging from total darkness to 24 hours. During these tests, light was provided by cool-white fluorescent lamps that provided an approximate photosynthetic photon flux (400 to 700 nm) of 28 μmol/m^2/sec (2.2 klux). Species tested included flame azalea (Malek and others 1989) and Carolina (Blazich and others 1993), rosebay (Blazich and others 1991), and Catawba rhododendrons (Blazich and others 1991; Rowe and others 1994a). In all species tested except one, seeds required light to germinate. In addition, an alternating thermoperiod enhanced germination when light was limiting. These results agree partially with the work of Cho and others (1981), who also reported that seeds of 5 species of rhododendron native to Korea—macranthum azalea, *R. indicum* (L.); Sweet; Japanese azalea, *R. japonicum* A. Gray Suring; *R. mucronulatum* Turcz*;* royal azalea, *R. schlippenbachii* Maxim.; and yodogawa azalea, *R. yedoense* Maxim. ex Regel—did not germinate in darkness at a constant temperature but did germinate in darkness when subjected to an alternating temperature. In addition, germination sometimes is inhibited by long photoperiods. For equivalent photoperiods, inhibition (when present) will be more pronounced at 25/15 °C than at 25 °C because an alternating temperature can substitute partially

Table 4—*Rhododendron*, rhododendron and azalea: variation in seed size among species and seed source

Species	Seed source	Elevation (m)	Seed moisture content (%)	Cleaned seeds/wt /g	Cleaned seeds/wt /oz
R. calendulaceum	Watauga Co., North Carolina	1,400	6	4,350	122,000
R. carolinianum	Henderson Co., North Carolina	720	6	29,460	825,000
	Burke Co., North Carolina	1,100	4	23,930	670,000
R. catawbiense	Buncombe Co., North Carolina	1,860	7	6,070	170,000
	Buncombe Co., North Carolina	1,860	6	6,070	170,000
	Yancey Co., North Carolina	1,954	10	6,780	190,000
	Johnston Co., North Carolina	67	9	5,700	160,000
	Cherokee Co., Georgia	320	7	5,000	140,000
R. chapmanii	Gadsden-Liberty Cos., Florida	—	5.5	29,100	815,000
R. macrophyllum	Oregon	—	—	4,460	125,000
R. maximum	Avery, Co., North Carolina	950	6	11,790	330,000
	Avery, Co., North Carolina	950	5	11,430	320,000

Sources: Arocha and others (1999), Blazich and others (1991, 1993), Glenn and others (1998), Malek and others (1989, 1990), Olson (1974), Rowe and others (1994a).

Figure 5—*Rhododendron macrophyllum*, west coast rhododendron: seedling development at 1, 9, 40, and 60 days after germination.



for the light requirement for some species (Toole and others 1955). However, this inhibition usually dissipates by the end of 30 days of germination (Blazich and others 1991, 1993; Rowe and others 1994a).

A test of seeds of flame azalea collected from the Blue Ridge Mountains of western North Carolina demonstrated that (at a constant temperature of 25 °C) increasing photoperiods increased germination, with maximum germination (85%) occurring by day 12 under continuous light (Malek and others 1989). An 8/16-hour thermoperiod of 25/15 °C enhanced germination when light was limiting. Maximum germination of 84 to 91% was reached by day 24 for all photoperiods ≥ $^1/_2$ hour, although at photoperiods ≥ 4 hours, comparable germination was noted at day 18 (Malek and others 1989). Similar results were reported for seeds of Carolina rhododendron collected in Henderson County, North Carolina, except that cumulative germination was lower (Blazich and others 1993).

Seeds of rosebay rhododendron collected in Avery County, North Carolina, also required light for germination regardless of temperature. At 25 °C, increasing photoperiods increased germination, with 79 and 81% germination occurring by day 21 for the 12- and 24-hour photoperiods, respectively. The alternating temperature again enhanced germination when light was limiting. At the alternating thermoperiod, germination of 92 to 97% was reached by day 21 for photoperiods ≥ 4 hours (Blazich and others 1991).

Rowe and others (1994a) also found that seeds of Catawba rhododendron have an obligate light requirement for germination. In contrast, Blazich and others (1991), reported that without light, seeds of Catawba rhododendron collected in Buncombe County, North Carolina, germinated in the dark. However, germination at 25 °C was low (5%), with moderate germination (64%) occurring at 25/15 °C. At both thermoperiods, germination > 95% was attained by day 15 for photoperiods of $^1/_2$ to 12 hours. This suggests that the germination response of Catawba rhododendron in darkness may vary, depending on the provenance or on the environmental conditions under which the seeds developed. The work of Glenn and others (1998) has suggested that the light requirement does not disappear during dry storage.

In addition, Rowe and others (1994a) compared germination in seeds from 3 provenances of Catawba rhododendron—Johnston County, North Carolina (elevation 67 m); Cherokee County, Georgia (elevation 320 m); and Yancey County, North Carolina (elevation 1,954 m)—representing diverse geographical and altitudinal distributions. Generally, light and temperature requirements for germination of seeds from all provenances were similar. Regardless of temperature, seeds required light for germination, and daily photoperiods as short as $^1/_2$ hour maximized germination. The major difference in germination response among provenances was related to seed vigor. Seeds from the Yancey County (higher-elevation) provenance germinated at a faster rate with greater cumulative germination than seeds from lower elevation provenances.

In studying effects of irradiance on seed germination of rosebay rhododendron, Romancier (1970) provided a range of irradiance levels to seeds during 16-hr photoperiods at 22 °C. He reported zero germination in total darkness but found no significant differences in germination with light intensities ranging from 1.6 $\mu mol/m^2/sec$ (0.13 klux or 12 foot-candles) to 21.9 $\mu mol/m^2/sec$ (1.72 klux or 160 foot-candles), indicating that very low levels of irradiance will stimulate germination. All seeds, including those in total darkness, had been exposed to light before the test began, so it is during the period following imbibition that light is essential. Glenn and others (1999) reported that dormancy was induced in seeds of Catawba and rosebay rhododendrons by not subjecting seeds immediately to light following inbibition. However, the degree of dormancy varied depending on (a) the length of time imbibed seeds were maintained in darkness and (b) the temperature at which the dark treatments were imposed and the seeds were germinated.

Nursery practice and seedling care. Rhododendrons may be propagated by seeds, stem cuttings (Dirr and Heuser 1987; Hartmann and others 2002), layering (Wells 1985), grafting (Wells 1985), and micropropagation (tissue culture) (Anderson 1984; McCown and Lloyd 1983). Commercially, plants usually are propagated by stem cuttings, although rooting ability is genotype specific. Procedures developed for micropropagation are currently being used with great success. Nevertheless, seed propagation is still practiced to develop new hybrids, raise understocks for grafting, and propagate wild species.

Seeds should be sown in January or as early as local conditions will allow. This is important to allow maximum growth the first year. The longer the growing period before mid-July (when growth normally ceases), the larger the seedlings will be at the end of the first season (Leach 1961). Many materials have been used as a germination medium, including vermiculite, perlite, sawdust, peat, and various soil mixes. Flats filled with peat moss and sand or perlite mixtures topped with 6 mm ($^1/_4$ in) of slightly firmed shredded sphagnum moss work well (Wells 1985). Many propagators are convinced that a medium consisting solely of shredded sphagnum moss provides the best results (Leach 1961; Wells 1985). Sphagnum moss is naturally acidic, retains water, and inhibits fungal organisms responsible for damping-off.

Seeds should be sown sparingly. Because of the need for light and their small size, seeds should not be covered with medium. Flats can then be placed in a greenhouse with moderate heat (24 °C), preferably under intermittent mist. Covering flats with glass or plastic may be advisable if mist is not available. Most seeds germinate in 1 to 3 weeks. In an additional 4 to 8 weeks, small seedlings will have 2 to 4 true leaves in addition to the cotyledons (Anderson and Anderson 1994). The time of germination and the first few weeks thereafter are critical. Seedlings must be shaded from direct sunlight, and the surface of the medium should never be allowed to become dry, not even briefly. Some growers sow about 1,000 seeds in a standard flat measuring 36 × 51 × 10 cm (14 × 20 × 4 in) and then transplant seedlings when they are still very small. Others sow them more sparsely and wait until the plants are about 2.5 cm (1 in) tall before transplanting.

In about 6 months, seedlings will be large enough to be transplanted. During the critical transplanting stage, young seedlings are carefully teased out from the sphagnum. The root system will separate easily if an underlying sand and peat mixture is used. Then, seedlings are transplanted into prepared flats containing an acidic medium (pH 4.0 to 5.5), taking care not to bury the cotyledons. Commercial growers usually put 108 seedlings into a standard flat filled with sterilized medium (Leach 1961). Flats may then be placed back in the greenhouse under shade, where they will remain for 9 months. Overwintering is seldom a problem in a greenhouse as long as plants are prevented from freezing. During seedling growth, plants may be fertilized with about 180 ppm N from a 15-45-5 ($N:P_2O_5:K_2O$) water-soluble fertilizer also containing 200 ppm calcium chloride ($CaCl_2$) and 75 ppm magnesium sulfate ($MgSO_4$). In addition, terminal growth often is pinched back to produce bushier plants. With flame azalea, Malek and others (1992a) reported that lateral shoot development in seedlings could be stimulated by either manual or chemical pinching. Generally, the number of lateral shoots increased with the leaf stage at which manual pinching was imposed. The highest number of shoots resulted by removing the terminal 2 nodes at the 16-leaf stage. Both pinched and nonpinched plants treated with dikegulac—2,3:4,6 bis-O-(1-methylethylidene) α-L-xylo-2-hexulofuranosonic acid—produced more lateral shoots than manual pinching alone. The number of shoots increased linearly with increasing concentrations of dikegulac over a range of 0 to 4,000 ppm, whereas responses to 4,000, 6,000, and 8,000 ppm were comparable. However, considerable reduction in leaf, stem, and root dry weights occurred with increasing concentration. This research also demonstrated that pinching seedlings manually prior to dikegulac treatment did not result in significantly greater numbers of lateral shoots compared to dikegulac treatment of nonpinched plants.

In spring, 1-year-old seedlings are removed from the flats, graded, and planted into pots or prepared beds to grow 1 or 2 more years before planting in permanent locations. They can be placed outdoors to harden off when the chance of killing frost has past, but they must not be exposed to direct sunlight. When plants of Catawba rhododendron were grown in controlled-environment growth chambers under long days at 16 different day/night temperature combinations, Rowe and others (1994b) found that a day/night cycle of 22/22 °C to 26/22 °C was optimal for seedling growth, whereas cycles ranging from 30/22 °C to 26/22 °C optimized net photosynthesis (Rowe and others 1994c). Similar results were reported for flame azalea (Malek and others 1992b). Throughout propagation and subsequent culture, plants should be examined frequently for insect and disease problems. Rhododendrons can be raised successfully with proper handling of the tender and delicate young seedlings by using a porous, well-drained acidic medium high in organic matter, and by maintaining ample moisture at all times.

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Rosaceae—Rose family

Rhodotypos scandens (Thunb.) Makino

jetbead

Paul O. Rudolf and Peyton W. Owston

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Synonyms. *R. tetrapetalus* (Sieb.) Makino

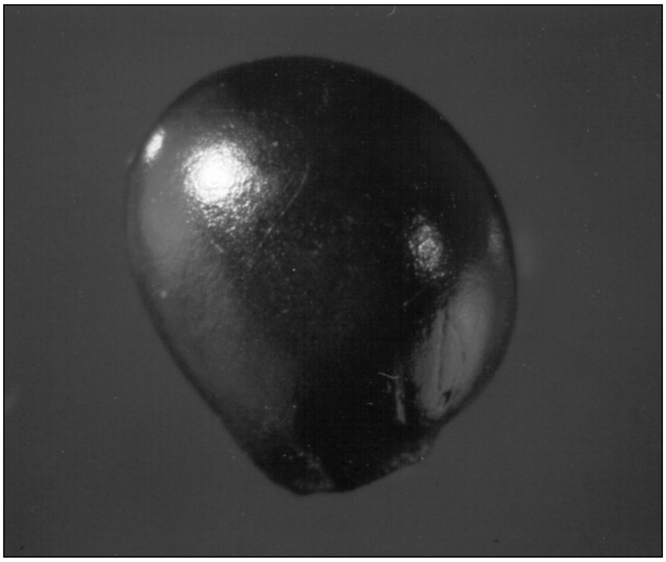
Growth habit, occurrence, and use. The only member of the genus *Rhodotypos* introduced to any extent in the United States is jetbead—*R. scandens* (Thunb.) Makino. Native to Japan and central China, jetbead is an upright, spreading, deciduous shrub usually 1 to 2 m tall; it reaches 5.5 m in Japan. It was introduced into cultivation chiefly for ornamental purposes in 1966 (Ohwi 1965; Rehder 1940) and is now considered invasive.

Flowering and fruiting. The showy, white, perfect flowers are 2.5 to 5 cm across and bloom from April to June (Ohwi 1965; Rehder 1940). Jetbead fruits are shiny, black, dry drupes, obliquely ellipsoid in shape (figure 1). They ripen in October or November and persist on the plant well into the winter; each contains 1 small stubby ellipsoidal stone (seed) about 6 mm long, dull tan in color, and characteristically sculpted in the manner of leaf venation, with the "midrib" extending around the longest periphery (figure 2) (Rehder 1940; Wyman 1947).

Collection of fruits, and extraction and storage of seeds. The fruits can be collected from the bushes by hand or flailed onto canvas from October to midwinter (Rudolf 1974). Extraction of stones from the fruits may not be necessary. In one sample, the number of cleaned seeds per weight was 11,488/kg (5,210/lb); purity was 89% and soundness 86% (Rudolf 1974). Seeds of this species are orthodox and can be stored air-dry in open containers at 1 to 10 °C for up to 9 months without loss of viability. Storage in sealed containers and in a vacuum at various humidities did not improve results (Flemion 1933).

Pregermination treatments. The seeds exhibit a combined dormancy that can be overcome by stratification in moist peat for 30 days at 25 to 30 °C, followed by 90 days of stratification at 5 °C (Barton 1961; Flemion 1933). Partially after-ripened seeds subjected to high temperature go into secondary dormancy (Flemion 1933).

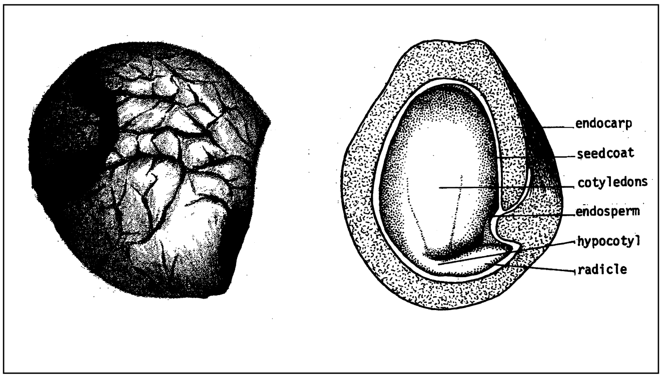
Figure 1—*Rhodotypos scandens*, jetbead: fruit.



Germination tests. Germination tests can be made in sand flats at temperatures of 20 °C (night) and 30 °C (day) for 90 days. In 3 tests, 81% (range 72 to 86%) of stratified seeds germinated, whereas only 16% of untreated seeds germinated (Flemion 1933; Rudolf 1974).

Nursery practice. Seeds should be sown in the fall in mulched or board-covered cold frames. A sowing depth of 12 mm ($^1/_2$ in) is suggested. Some germination will take place the second year (Flemion 1933). Slightly green (immature) seeds sown in the fall are reported to germinate in 1 year (Dirr and Heuser 1987). Presumably, stratified seeds could be sown in the spring. In a planting test of slightly green seeds collected in August and sown immediately, 100% germination was seen the next spring (Titus 1940). Stem cuttings of jetbead can be rooted any time that the plants have leaves, but June and July are best. A mistbed or shaded plastic tent is recommended (Dirr and Heuser 1987).

Figure 2—*Rhodotypos scandens*, jetbead: cleaned seed (**left**) and longitudinal section through a seed (**right**).



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Anacardiaceae–Sumac family

Rhus L.

sumac

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Growth habit, occurrence, and use. The genus sumac—*Rhus* L.—consists of about 150 species of deciduous or evergreen shrubs, trees, and vines indigenous to temperate and subtropical regions of both hemispheres (LHBH 1976; Rehder 1990; RHS 1994). They occur frequently as pioneer species on disturbed sites and abandoned fields and along woodland borders. However, they are intolerant of shade and cannot compete with invading trees (Gill and Healy 1974). Sumacs are tolerant of poor, sandy, or rocky soils, and of soil moisture regimes ranging from dry to wet. For example, smooth sumac is adaptable to sites ranging from nearly bare rock to sand to heavy clay, and tolerates soil pH from acidic to slightly alkaline (Johnson and others 1966). Species native to North America are listed in table 1.

Three species of the genus *Toxicodendron*—poison-oak, *Toxicodendron diversilobum* (Torr. & Gray) Greene; poison-ivy, *T. radicans* (L.) Kuntze; and poison-sumac, *T. vernix* (L.) Kuntze—also are included because they are referred to frequently as *R. diversiloba* Torr. & Gray, *R. radicans* L., and *R. vernix* L., respectively. Laurel-sumac—*Malosma laurina* (Nutt.) Nutt. ex Abrams), until recently known as *Rhus laurina* Nutt.—is also included for the same reason.

Members of the sumac genus are shrubs, vines, or trees with alternate, simple, or featherlike (pinnate) compound leaves. Winter buds are minute, naked (without scales), and covered with dense hairs. Sumacs are fast growing and usually short-lived plants. Roots of sumac can spread more than 16 m in each direction, forming an extensive root network near the surface (Duncan 1935).

Sumacs are valuable for erosion control because of proliferation of rhizomes that results in an extensive root system. The species is ideally suited for roadside plantings, revegetation of areas of eroded or depleted soils, range reclamation and mine spoils restoration, and other conservation plantings (Brinkman 1974; Humphrey 1983). Some are grown as ornamentals for their pinnate foliage; persistent terminal showy fruits; and brilliant red, orange, or yellow fall color. This is especially true of the cutleaf staghorn sumac —*R. hirta* (L.) Sudworth 'Laciniata'— with its deeply cut, bright green leaves in summer; brilliant orange-red fall color; and twisted, exotic forms in winter (Cross 1988). Sumacs are recommended as ornamental shrubs for dry and open sites, but cultivation is easy in any garden soil.

Species of sumac also provide wildlife with habitat and an important source of food. Their thicket-forming growth provides excellent cover for birds and animals. The fruits, produced in large quantities each year, are eaten by over 30 species of birds, as well as rodents and other mammals. The twigs and leaves are browsed by deer (*Odocoileus* spp.), moose (*Alces americana*), and mountain sheep (*Ovis* spp.) (Elias 1989; Strauss 1988). The wood is soft, weak, and of no commercial value (Elias 1989). However, skunkbush was once used by Native Americans for food, as a tobacco substitute, and for making baskets. In addition, some species can be processed to yield tannin and lacquer (LHBH 1976).

Geographic races and hybrids. There is some disagreement among taxonomists as to the classification of genera (*Rhus* vs. *Toxicodendron*) and particular species. For example, prairie sumac is often considered to be a variety or race of shining sumac (Elias 1989). In addition, natural hybridization occurs in the wild (Johnson and others 1966).

Flowering and fruiting. Plants are dioecious (flowers imperfect, one sex) or polygamous (flowers imperfect and perfect, both sexes). Flowers are small and rather inconspicuous and are borne in terminal or axillary clusters in the spring (table 2). They are pollinated by bees. Fruits are small, hairy, berry-like drupes, rounded to egg-shaped, containing a single nutlet or seed without endosperm (figures 1–3) (Brinkman 1974; Elias 1989). In most species, fruits form a dense cluster and ripen in the fall and may persist on the plant through winter. Seeds are spread primarily by birds and small mammals (Brinkman 1974). Sumacs generally produce copious quantities of seeds with some seeds produced nearly every year.

Table 1—*Rhus,* sumac; *Toxicodendron,* poison-ivy, etc.; *Malosma,* laurel-sumac: nomenclature and occurrence

Scientific names & synonym(s)	Common name(s)	Occurrence
***R. aromatica* Ait.** *R. canadensis* Marsh.	**fragrant sumac,** lemon sumac, sweet-scented sumac	Vermont & Ontario to Minnesota, S to Florida & Louisiana
***R. choriophyllum* Woot. & Standl.**	**Mearns sumac**	S New Mexico & Arizona & adjacent Mexico
***R. copallina* L.**	**shining sumac,** winged sumac, mountain sumac, wing-rib sumac, dwarf sumac	Maine & Ontario to Minnesota, S to Florida & Texas
***R. glabra* L.** *Schmaltzia glabra* Small *R. borealis* Greene	**smooth sumac,** scarlet sumac	Maine to British Columbia, S to Florida & Arizona
***R. hirta* (L.) Sudworth** *R. typhina* L.	**staghorn sumac,** velvet sumac	Quebec to Ontario, S to Georgia, Indiana, & Iowa
***R. integrifolia* (Nutt.) Benth. & Hook. f. ex Brewer & S. Wats.**	**lemonade sumac,** sourberry, lemonade berry	S California & Baja California
***R. kearneyi* Barkl.**	**Kearney sumac**	Arizona & N Baja California
***R. lanceolata* (Gray) Britt.** *R. copallina* var. *lanceolata* Gray	**prairie sumac**	S Oklahoma & E Texas to S New Mexico & adjacent Mexico
***R. michauxii* Sarg.** *Schmaltzia michauxii* M. Small	**false poison sumac**	North Carolina to Georgia
***R. microphylla* Engelm. ex Gray**	**desert sumac,** scrub sumac, small-leaf sumac	SW US & adjacent Mexico
***R. ovata* S. Wats.** *R. ovata* var. *traskiae* Barkl.	**sugarbush,** sugar sumac	Arizona, S California, N Baja California
***R. trilobata* Nutt.** *Schmaltzia anisophylla* Greene *S. trilobata* var. *anisophylla* (Greene) Barkl.	**skunkbush,** ill-scented sumac	Illinois to Washington, California, & Texas
***R. virens* Lindheimer ex Gray**	**evergreen sumac,** tobacco sumac, lentisco	SW US
RELATED TAXA		
***Toxicodendron diversilobum* (Torr. & Gray) Greene** *R. diversiloba* Torr. & Gray *R. toxicodendron* ssp. *diversilobum* Torr. & A. Gray) Engl.	**poison-oak**	British Columbia to Baja California
***T. radicans* ssp. *radicans* (L.) Kuntze** *R. radicans* L.; *R. toxicodendron* L.	**poison-ivy**	Nova Scotia to Florida, W to Minnesota, Nebraska, & Arkansas
***T. vernix* (L.) Kuntze** *R. vernix* L.	**poison-sumac,** swamp sumac, poison elder	Swamps, Maine to Minnesota, S to Florida & Louisiana
***Malosma laurina* (Nutt.) Nutt. ex Abrams** *R. laurina* Nutt.	**laurel-sumac**	S California, Baja California

Sources: Elias (1989), LHBH (1976), Rehder (1990), RHS (1994).

Collection of fruits, seed extraction, and cleaning. Fruit clusters, which may be picked by hand as soon as they are ripe, are often available until late in the year. If collected early, fruits of smooth sumac and staghorn sumac, which occur in very dense clusters, may need additional drying and should be spread out in shallow layers for drying. However, fruits usually will be dry enough to process if they are collected in late fall or early winter (Brinkman 1974). Hybrid clumps often are found where smooth sumac and staghorn sumac occur near each other (Johnson and others 1966). These hybrid clumps may have seed-stalk heads that appear normal, but most seeds therein are generally empty, with the few full seeds usually infertile. Care must be taken to avoid such hybrid clumps. Even seeds of nonhybrid clumps should be checked carefully before collection to make certain that an excessive amount of empty seeds are not present. An estimate of the amount of empty seeds can be determined by crushing a small sample with a pair of pliers (Johnson and others 1966).

Dried fruit clusters can be separated into individual fruits by rubbing or beating the clusters in canvas sacks, followed by screening to remove debris (Brinkman 1974). Seeds can then be cleaned by running them through a macerator with water to remove remaining pieces of seedcoats

Table 2—*Rhus,* sumac; *Toxicodendron,* poison ivy, etc.; *Malosma,* laurel-sumac: growth habit, flowers, and fruits

Speicies	Growth habit & max height	Flowers	Fruits
R. aromatica	Shrub to 2.5 m	Yellowish, in clustered spikes 5–20 cm long, forming short panicles that appear before leaves	Red, hairy, 6 mm across; early summer, persist into early winter
R. choriophylla	Shrub or small tree to 5 m with an open irregular crown	Tiny, in dense branched clusters 5–6 cm long & wide from July–August	Red, hairy, 6-8 mm across
R. copallina	Shrub or small tree to 6 m	Greenish, in dense terminal panicles	Red, hairy; late summer, persist into winter
R. glabra	Shrub or tree to 6 m	Green, in dense panicles 10–25 cm long	Scarlet, hairy; summer
R. hirta	Shrub or tree to 9 m, twigs densely pubescent	Greenish in dense, terminal panicles 10–20 cm long	Crimson, densely hairy; late summer, persist on plant into winter
R. integrifolia	Evergreen shrub or tree to 9 m	White or pinkish in pubescent panicles	Dark red, hairy; spring
R. kearneyi	Large shrub or tree to 5 m	White in short, crowded clusters at tips of branchlets	Reddish, hairy
R. lanceolata	Thicket-forming shrub or small tree to 10 m	Yellowish-green to white in dense clusters at end of branchlets in July or August	Dark red, hairy; September or October
R. michauxii	Low stoloniferous shrub to 1 m	Greenish-yellow in panicles 10–20 cm long	Scarlet, densely hairy, in dense panicles
R. microphylla	Shrub, to 2 m, rarely treelike to 5 m	White in heads or spikes	Globose, to 0.1 cm diameter, orange-red
R. ovata	Evergreen shrub to 3 m, rarely a tree to 4.5 m	Light yellow, in short dense spikes	Dark red, hairy; spring
R. trilobata	Shrub to 2 m	Greenish, in clustered spikes, appearing before leaves	Red, hairy; spring
R. virens	Shrub	White to 4 cm long in terminal panicles	—
Related Taxa			
T. diversilobum	Shrub to 2.5 m, sometimes climbing	Greenish, in axillary panicles	Whitish
T. radicans ssp. *radicans*	Trailing or climbing vine, shrub, or rarely a tree	Greenish white in panicles 3–6 cm long	Whitish, berrylike 5–6 mm across, in axillary clusters; early summer, persisting into winter
T. vernix	Shrub or small tree to 9 m	Greenish, in slender panicles 8–20 cm long	Greenish white in pendent axillary panicles to 20 cm long; pedicles persist through winter
M. laurina	Shrub, 3–6 m	Greenish white, in dense panicles 5–10 cm long	Whitish; early summer

Sources: Elias (1989), LHBH (1976), Rehder (1990), RHS (1994).

and empty seeds. Such thorough cleaning is seldom practiced except for skunkbush; seeds of other species are sown with pieces of the fruit wall still attached (Brinkman 1974). Trials have shown that about 99% of the empty seeds of smooth sumac can be removed by flotation, as empty seeds float and filled ones sink (Johnson and others 1966). However, the flotation method of separating empty seeds is not always successful with seeds of staghorn sumac (Brinkman 1974). Number of seeds per unit weight and seed yields vary among species (table 3).

Storage. Seeds of sumac are orthodox in storage behavior and can be stored over winter and possibly for years without special treatment (Dirr and Heuser 1987). Seeds of smooth sumac stored at room temperature for 10 years still exhibited over 60% germination, suggesting that controlled storage conditions are not required. Seeds of shining sumac have even survived 5 years of burial in the soil in Louisiana (Haywood 1994). However, Farmer and others (1982) recommend storing dried seeds of smooth sumac and shining sumac in sealed glass containers at 3 °C. Seeds of other species should be stored under a temperature range from 0 to 5 °C.

Pregermination treatments. Seeds of sumac need to be scarified in concentrated sulfuric acid for 1 to 6 hours, depending upon the species—then either fall-planted out-of-doors or stratified for approximately 2 months at about 4 °C before planting (Hartmann and others 2002). Farmer and others (1982) reported that without scarification, < 5%

Figure 1—*Rhus,* sumac: fruits of *R. triblobata,* skunkbush (**left**) and *R. hirta,* staghorn sumac (**right**).

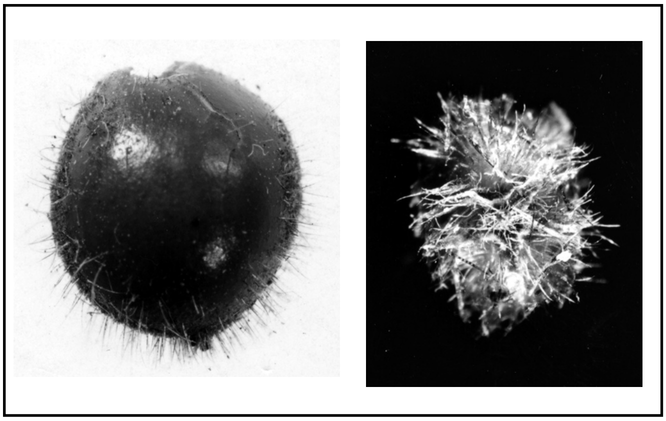


Figure 2—*Rhus,* sumac; *Malosma,* laurel-sumac: nutlets (seeds) of *R. glabra*, smooth sumac (**upper left**); *R. integrifolia,* lemonade sumac (**upper right**); *M. laurina*, laurel-sumac (**middle left**); *R. ovata*, sugarbush (**middle right**); *R. triblobata,* skunkbush (**bottom left**); *R. hirta*, staghorn sumac (**bottom right**).

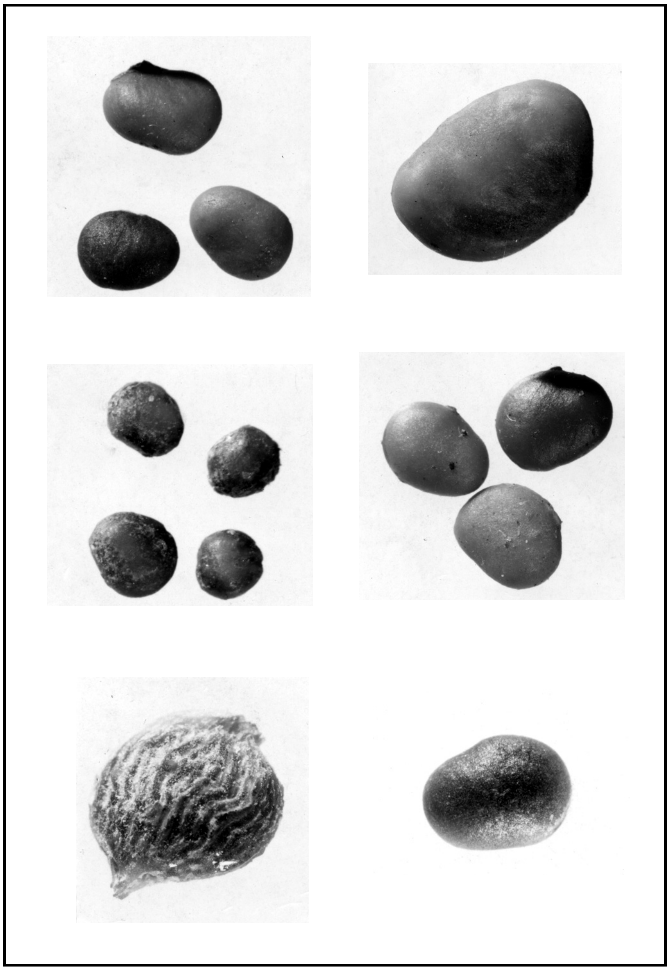
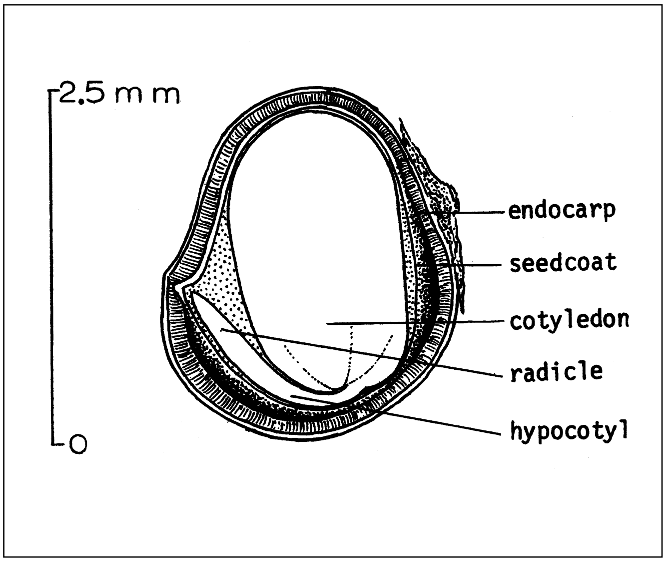


Figure 3—*Rhus hirta*, staghorn sumac: longitudinal section of a seed.



of seeds of smooth sumac germinated, but 3 to 4 hours of scarification in concentrated sulfuric acid promoted an average of 58% germination. Even after 20 years, without scarification, 3% of the seeds receiving no acid treatment germinated. However, there was a gradual increase in the number of decayed seeds with increasing durations of scarification (Farmer and others 1982).

In other species such as fragrant sumac and skunkbush, seed dormancy is caused by both a hard seedcoat and a dormant embryo, thus requiring both scarification and stratification for optimum germination (Heit 1967). These 2 treatments must be performed in proper sequence for spring-sown seeds, but the moist prechilling treatment is not necessary for fall-sown seeds. Scarification with sulfuric acid for about 1 hour followed by cold stratification at 1 to 4 °C for 1 to 3 months is recommended for seeds of fragrant sumac. Skunkbush requires 1.5 to 2 hours of scarification and 1 month or slightly longer of moist prechilling for maximum germination (Heit 1967; Weber and others 1982). Seeds of evergreen sumac need to be acid-scarified with concentrated sulfuric acid for 50 minutes and then cold-stratified for 73 days (Hubbard 1986; Tipton 1992).

High temperatures also are effective in removing seedcoat dormancy, a phenomenon that occurs naturally during wildfires. Germination of prairie sumac increases after seeds are exposed to fire (Rasmussen and Wright 1988). High temperatures scarified seeds of prairie sumac when temperatures reached 76 °C in wet environments or 82 °C in dry environments. Heat ruptures the seedcoats and waxy cuticle, enabling seeds to imbibe water. Heat generated on or near the soil surface by fire (82 °C) is sufficient to scarify seeds

Table 3—*Rhus,* sumac; *Malosma,* laurel-sumac: seed yield data

	Fruits (x1,000)/wt		Cleaned seeds (x1,000)/weight				
			Range		Average		
Species	**/kg**	**/lb**	**/kg**	**/lb**	**/kg**	**/lb**	**Samples**
R. copallina	—	—	81.4–173.8	37.0–79.0	125.4	57.0	4
R. glabra	50.6–105.6	23.0–48.0	52.8–277.2	24.0–126.0	107.8	49.0	28
R. hirta	66.0	30.0	107.1–148.7	48.7–67.6	117.3	53.3	5
R. integrifolia	6.6	3.0	15.0–17.6	6.8–8.0	16.7	7.6	2
R. ovata	37.4	17.0	41.1–57.2	18.7–26.0	—	—	2
R. trilobata	15.4–19.8	7.0–9.0	23.3–66.0	10.6–30.0	44.7	20.3	9
M. laurina	198.0	90.0	—	—	285.1	129.6	1

Source: Brinkman (1974).

(Rasmussen and Wright 1988). In seeds of nutgall tree, or Chinese gall, or nutgall tree—*R. chinensis* Mill., a species native to China that is often referred to incorrectly as *R. javanica* L.—a temperature of 55 ± 7.4 °C was successful in overcoming the impermeable seedcoat (Washitani 1988). With increasing temperature, shorter exposures became sufficient to render seeds permeable, but temperatures > 75 °C damaged seeds and resulted in lower germination. The most favorable regimes among those tested were temperatures of 65 to 75 °C for durations of 30 to 120 minutes, which frequently occur on denuded ground during the midday hours of clear spring and summer days (Washitani 1988).

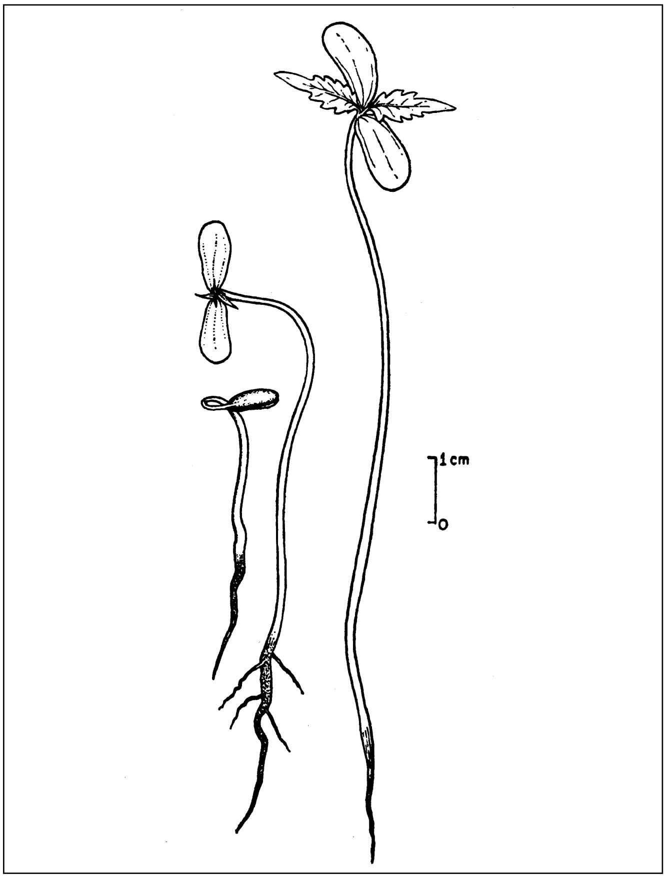
Other scarification treatments include hot water and mechanical scarification. A 2-minute submersion in boiling water was the most effective of timed heat treatments for seeds of smooth sumac (Johnson and others 1966). Germination of seeds of prairie sumac scarified with sulfuric acid was greatest when they were soaked for 60 minutes but was less than that of seeds that were mechanically scarified or treated with wet heat at 94 or 97 °C (Rasmussen and Wright 1988).

The degree of seedcoat hardness and embryo dormancy varies within and among seedlots for most species (Hartmann and others 2002; Krugman and others 1974). Seed sources also must be considered when determining scarification and stratification pretreatments. This is true for sumacs, as individual seedlots and seed sources vary in their acid treatment requirements to remove seedcoat dormancy (Heit 1967). Test averages alone are not a good representation of germination potential because of wide family differences and a significant family by treatment interaction (Farmer and others 1982). For example, germination of individual clonal seedlots of smooth sumac ranged from 25 to 75% (Farmer and others 1982). Family differences in germination are apparently based on variable susceptibility of individual seeds to scarification (Farmer and others 1982). The duration of scarification and stratification should be determined for each seedlot.

Germination tests. Light and temperature influence germination, which is epigeal (figure 4). When seeds were subjected to total darkness, the percentage germination of seedlots of smooth sumac (Brinkman 1974) and prairie sumac (Rasmussen and Wright 1988) were reduced. Heit (1967) also stressed the importance of germination in the presence of light. Likewise, temperature also is important. Evergreen sumac germinated at temperatures ranging from 21 to 30 °C (Tipton 1992), similar to that reported for other sumacs (Brinkman 1974). Final percentage germination declined with increasing temperature from a predicted maximum of 52% at 21 °C, whereas maximum germination rate increased with temperature to a predicted maximum of 69% germination at 31 °C. These results demonstrate that under low temperatures, germination would be delayed and slow, but eventually yield more seedlings. Under high temperatures, germination would also be delayed, but relatively rapid, yet it would yield few seedlings (Tipton 1992). In studies with alternating day/night temperatures, percentage germination of smooth sumac and shining sumac seedlots was significantly greater when they were subjected to an alternating temperature (16/8 hours) of 20/10 °C than at 15/5 °C or 30/20 °C. Germination rate was also affected—germination was completed within 10 days at 20/10 °C and 30/20 °C but took 20 days at 15/5 °C (Farmer and others 1982). Maximum germination of prairie sumac occurred when seeds were subjected to alternating temperatures of 20/10 °C with a short-day light cycle of 8 hours of light and 16 hours of darkness (Rasmussen and Wright 1988).

Gibberellins and ethylene or ethephon (2-chloroethyl phosphonic acid) are known to overcome dormancy in seeds of some species by completely or partially substituting for the moist-prechilling requirement (Hartmann and others 2002; Norton 1985). This was true for seeds of staghorn sumac, as germination after 30 days was higher for seeds

Figure 4—*Rhus hirta*, staghorn sumac: seedling development at 2, 4, and 17 days after germination.



incubated for 24 hours in 100 mg/liter gibberellic acid (GA) (26% germination) than 0, 1, 10, or 1000 mg/liter GA (19, 22, 24, and 22% germination, respectively). When seeds were stratified at 4 °C for 0, 10, 20, or 30 days, percentage germination increased with the length of the stratification period to a maximum of 48%. However, combining infusion of GA into seeds with cold stratification did not further enhance germination if the stratification period exceeded 10 days (Norton 1986, 1987). In contrast, promotion of germination due to ethephon was demonstrated only after 20 or 30 days of stratification, whereas no effect was observed in the absence of a cold treatment (Norton 1985). A combination of ethephon treatment at 200 mg/liter for 24 hours followed by 30 days of cold treatment at 4 °C increased germination to 60%.

Soil pH has some influence on germination. Once prairie sumac seeds were scarified, germination occurred under a wide range of pH (4 to 10), but highest germination occurred at a pH of 10 (Rasmussen and Wright 1988). In nature, soil pH increases for a short time following fire. Increased pH is attributed to ash deposition on burned areas. Fire enhances these conditions, thus aiding establishment following burning. Furthermore, seedling emergence and root growth of staghorn sumac were inhibited by simulated acid rain (Lee and Weber 1979), which tended to lower soil pH.

In addition, exudates from leaves of sumac (identified as miasmins and saprolins) inhibit germination and seedling growth of a number of other plants (Matveev and others 1975). Water-soluble extracts from leaves of shining sumac had an adverse effect on germination and radicle growth of loblolly pine—*Pinus taeda* L.—which suggests that shining sumac, a common shrub on southern pine sites, may interfere with regeneration of loblolly pine from seeds (Smith 1990). Furthermore, extracts from seeds of skunkbush inhibited growth of brome—*Bromus* L. spp.—either by killing newly germinated seeds or by reducing coleoptile growth by 30% compared to the control (Hampton and Singh 1979).

Nursery practice and seedling care. Sumacs can be propagated from seeds, by rooting stem cuttings (Hartmann and others 2002; Tipton 1990), or by field-planting root cuttings in early spring (Cross 1982, 1988; Jonsson and Zak 1975; Hartmann and others 2002). Although sumacs are heavy seed producers, commercially they are usually propagated vegetatively by root cuttings (Cross 1988; Jonsson and Zak 1975).

When propagating by seeds, the ideal sowing time depends on the species. Seeds that do not require stratification, such as those of shining, smooth, and staghorn sumacs, are sown best in the spring after a scarification treatment. Seeds scarified in sulfuric acid should be rinsed thoroughly with running water prior to sowing. Species that exhibit double dormancy, such as fragrant and skunkbush, can be either subjected to scarification and stratification and planted in spring or they can be scarified and sown in the fall, thus allowing winter temperatures to provide moist prechilling naturally (Dirr and Heuser 1987). In general, seeds should be sown at least 1.3 linear cm (1/2 in) deep at a rate of about 82 viable seeds/linear m (25/ft) (Brinkman 1974). However, depth of planting from 0 to 6 cm (0 to 2.4 in) did not affect percentage emergence of seeds of prairie sumac (Rasmussen and Wright 1988).

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Grossulariaceae—Currant family

Ribes L.

currant, gooseberry

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Growth habit, occurrence, and use. The currant and gooseberry genus—*Ribes*— includes about 150 species of deciduous, (rarely) evergreen, shrubs that grow in the colder and temperate parts of North America, Europe, Asia, and South America. The unarmed species are commonly called currants; the prickly species are gooseberries. Of the more important species for which seed data are available, 16 are native to the United States and 1 was introduced from Europe (table 1). These species generally occur as rather low-growing shrubs, although 3 species can attain heights of 3 to 4 m (table 2).

Six of the more showy species—alpine, American black, golden, wax, clove, and winter currants—are cultivated for their colorful fruit, attractive flowers, and ornamental foliage. Berries are made into jam, jelly, pie, juice, and syrup. All native species are valuable as food and cover for wildlifeand many provide browse for livestock (Plummer and others 1968). Golden and clove currants have been used in shelterbelt plantings in the prairie–plains and intermountain regions. The former also has been widely planted for erosion control (Pfister 1974). Golden, wax, white-stem, and gooseberry currants are valued as ornamentals in the United States and Canada (Barnes 1986). Currants are shade tolerant (Quick 1954). Many species regenerate vegetatively as well as from seed (Dittberner and Olson 1983; Wasser 1982). Most are rhizomatous (Lotan and others 1981). Seeds of currants remain viable in soil for long periods of time (Lyon and Stickney 1976).

Germination is stimulated by disturbances such as fire (Lotan and others 1981; Morgan and Neuenschwander 1985; Young 1983). Consequently, currants are common pioneer species on hot burns occurring on xeric sites (Hopkins and Kovalchik 1983). However, their seedcoats are relatively thin and may be destroyed by severe fires. Moist mineral soil with high amounts of humus provides a good seedbed for currants. Seeds are often introduced to the seedbank by birds and mammals that cannot digest the seeds (Lyon and Stickney 1984). Moss and Wellner (1953) suggested that, in the northern Rocky Mountains, seeds are also directly deposited simply by falling to the ground below parent plants. Seeds remain viable in the soil for long periods of time (Lyon and Stickney 1976). Moss and Wellner (1953) found soil-borne seeds of prickly currant more than 200 years old.

Many species serve as alternate hosts to white pine blister rust—*Cronartium ribicola* J.C. Fischer—a disease that has severely affected forest ecology and forest management practices (Ketcham and others 1968). Wax currant has also been shown to produce allelopathic effects (Heisey 1982).

Geographic races. Nine of the species listed (table 1) have recognized varieties; these species are pasture, Sierra, and Missouri gooseberries, and alpine, clove, winter, wax, Hudson Bay, and sticky currants. Distinctions in the first 5 species are not clearly related to geographic races, whereas the last 4 species contain geographic races (Hitchcock and others 1955; Rehder 1940; Steyermark 1963).

Flowering and fruiting. Flowers are bisexual (dioecious in alpine currant), usually small and greenish, but yellow to red in some species (Rehder 1940). The flowers are borne singly or in few- to many-flowered racemes from April to June (table 3). Flowers are often wind-pollinated (Quick 1954). Fruit is a green, many-seeded, glandular or smooth berry 6 to 13 mm in diameter (figure 1) that ripens in early to late summer. Mature fruits are red in some species, from purple to black in others, and occasionally red, yellow, or black within a species (table 4). Bees are very important to pollination of some European currants (Blasse and Hofman 1988). A mature seed (figure 2) is filled with a large endosperm containing a minute, rounded embryo (figure 3). Seeds are dispersed almost entirely by birds and mammals during the summer and fall.

The earliest seedcrops produced by Sierra gooseberry and prickly and sticky currants are borne when the plants are 3 to 5 years old. Good seedcrops are borne at intervals

Table 1—*Ribes,* currant, gooseberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. alpinum* L.** *R. opulifolium* L.	**alpine currant**	Europe to Siberia
***R. americanum* P. Mill.** *R. floridum* L'Herit.	**American black currant**	Nova Scotia to Alberta, S to Virginia & New Mexico
***R. aureum* Pursh** *Chrysobotrya aurea* (Pursh) Rydb. *R. flavum* Colla; *R. tenuiflorum* Lindl.	**golden currant,** slender golden currant, flowering currant	E Washington to Saskatchewan & South Dakota, S to California & New Mexico
***R. aureum* var. *villosum* DC.** *R. odoratum* H. Wendl. *Chrysobotrya odorata* (Wendl.) Rydb.	**clove currant,** buffalo currant	South Dakota & Minnesota, S to Missouri, W Texas, & Arkansas
***R. cereum* Dougl.** *R. churchii* A. Nels & Kenn. *R. inebrians* Lindl.; *R. pumilum* Nutt.	**wax currant,** squaw currant	British Columbia to central Montana, S to northern Mexico
***R. cynosbati* L.** *Grossularia cynosbati* (L.) Mill. *R. gracile* Michx.	**pasture gooseberry,** eastern prickly gooseberry	Nova Scota to Alberta, S to Virginia, Nebraska, & New Mexico
***R. hudsonianum* Richards.** *R. petiolare* Dougl.	**Hudson Bay currant,** wild black currant, northern black currant	Alaska to Hudson Bay, S to N California, Utah, Wyoming, & Minnesota
***R. inerme* Rydb.** *Grossularia inermis* (Rydb.) Cov. & Britt. *R. divaricatum* Dougl. var. *inerme* (Rydb.) McMinn *R. purpusii* Koehne ex Blank.	**white-stem gooseberry**	British Columbia to Montana, S to California & New Mexico
***R. lacustre* (Pers.) Poir.** *Limnobotrya lacustris* Rydb. *R. echinatum* Dougl.; *R. grossulariodes* Michx. *R. parvulum* Rydb.	**prickly currant,** swamp gooseberry, swamp black currant	Alaska to Newfoundland, S to California, South Dakota, & Pennsylvania
***R. missouriense* Nutt.** *Grossularia missouriensis* (Nutt). Cov. & Britt. *R. gracile* Pursh, not Michx.	**Missouri gooseberry**	Minnesota to Connecticut, S to Tennessee, Arkansas, & Kansas
***R. montigenum* McClatchie** *Limnobotrya montigena* McClatchie Rydb. *R. lacustre* var. *molle* Gray. *R. lentum* Cov. & Rose; *R. molle* Howell	**gooseberry currant,** alpine prickly currant, mountain gooseberry	British Columbia to Montana, S to S California & New Mexico
***R. nevadense* Kellogg** *R. ascendens* Eastw.; *R. grantii* Heller	**Sierra currant**	S Oregon, N California, & W Nevada
***R. oxyacanthoides* ssp. *irriguum* (Dougl.) Sinnott** *R. irriguum* Dougl. *R. divaricatum* var. *irriguum* (Dougl.) Gray *Grossularia irrigua* (Dougl.) Cov. & Britt.	**Idaho gooseberry,** inland black gooseberry	British Columbia, S to NE Oregon & E to W Montana
***R. roezlii* Regel** *Grossularia roezlii* (Regel) Cov. & Britt. *R. amictum* Greene; *R. aridum* Greene *R. urlsonianum* Greene	**Sierra gooseberry**	California & Nevada
***R. rotundifolium* Michx.** *Grossularia rotundifolia* (Michx.) Cov. & Britt. *R. triflorum* Willd.	**roundleaf gooseberry,** Appalachian gooseberry	Massachusetts to New York S to North Carolina
***R. sanguineum* Pursh** *Calobotrya sanguinea* (Pursh) Spach *Coreosma sanguinea* (Pursh) Spach *R. glutinosum* Benth.	**winter currant,** red flowering currant, Oregon currant, blood currant	W British Columbia, S to California
***R. viscosissimum* Pursh** *Coreosma viscosissima* (Pursh) Spach *R. halli* Jancz.	**sticky currant**	British Columbia to Montana, S to California & N Arizona

Source: Pfister (1974).

Table 2—*Ribes,* currant, gooseberry: growth habit, height at maturity and year of first cultivation

Species	Growth habit	Height at maturity (m)	Year first cultivated
R. alpinum	Dense, unarmed shrub	0.9–2.4	1588
R. americanum	Unarmed shrub	0.6–1.8	1727
R. aureum	Unarmed shrub	0.9–3.0	1806
R. aureum var. *villosum*	Unarmed shrub	0.9–3.0	1812
R. cereum	Unarmed shrub	0.3–1.5	1827
R. cynosbati	Prickly shrub	1.5	1759
R. hudsonianum	Unarmed shrub	0.3–1.8	1899
R. inerme	Prickly shrub	0.9–2.1	1899
R. lacustre	Prickly shrub	0.3–1.8	1812
R. missouriense	Prickly shrub	0.3–1.8	1907
R. montigenum	Low, very prickly shrub	0.3–0.9	1905
R. nevadense	Unarmed shrub	0.9–1.8	1907
R. oxyacanthoides spp. *irriguum*	Prickly shrub	0.3–2.4	1920
R. roezlii	Prickly shrub	0.6–1.5	1899
R. rotundifolium	Low, prickly shrub	0.9	1809
R. sanguineum	Unarmed shrub	0.9–3.6	1818
R. viscosissimum	Hardy, unarmed shrub	0.3–1.8	1827

Source: Pfister (1974).

Table 3—*Ribes,* currant, gooseberry: phenology of flowering and fruiting

Species	Location	Fruit ripening	Flowering
R. alpinum	Europe	Apr–May	July–Aug
R. americanum	—	Apr–June	June–Sept
R. aureum	—	Apr–May	June–July
R. aureum var.*villosum*	Wyoming	Late May	Late Aug
	Kansas	Mid–Apr	June
	—	Apr–June	June–Aug
R. cereum	—	Apr–June	Aug
R. cynosbati	—	Apr–early June	Late July–Sept
R. hudsonianum	—	May–July	—
R. inerme	—	May–June	—
R. lacustre	—	Apr–July	Aug
R. missouriense	—	Apr–May	June–Sept
R. montigenum	—	Late June–July	Aug–Sept
R. nevadense	—	May–July	—
R. oxyacanthoides ssp. *irriguum*	—	Apr–June	—
R. roezlii	—	May–June	—
R. rotundifolium	—	Apr–May	July–Sept
R. sanguineum	Oregon	Apr–May	July–Aug
	—	Mar–June	—
R. viscosissimum	—	May–June	Aug–Sept

Sources: Fernald (1950), Hitchcock and others (1955), Krüssmann (1960–1962), Loiseau (1945), Munz and Keck (1965), NBV (1946), Petrides (1955), Pfister (1974), Rehder (1940), Stephens (1969), Steyermark (1963), Symonds (1963), Wyman (1949).

of 2 to 3 years (Moss and Wellner 1953; Quick 1954). Clove currant, however, produces good crops annually (Pfister 1974).

Seed collection and extraction. The fruits should be picked or stripped from the branches as soon as they are ripe to preclude loss to birds. Unless the seeds are to be extracted immediately, fruits should be spread out in shallow layers to prevent overheating (Pfister 1974). Berries of alpine currant are often allowed to ferment in piles for a few days prior to extraction (NBV 1946). Maceration and washing are used to separate the seeds from the pulp. Dried fruits should first be soaked in water before cleaning. Small quantities of berries can be cleaned in a kitchen blender. The berries are covered with water and ground in the blender for 15 to 45 seconds. After the seeds have separated from the pulp, additional water is added to allow the sound seeds to settle. The pulp,

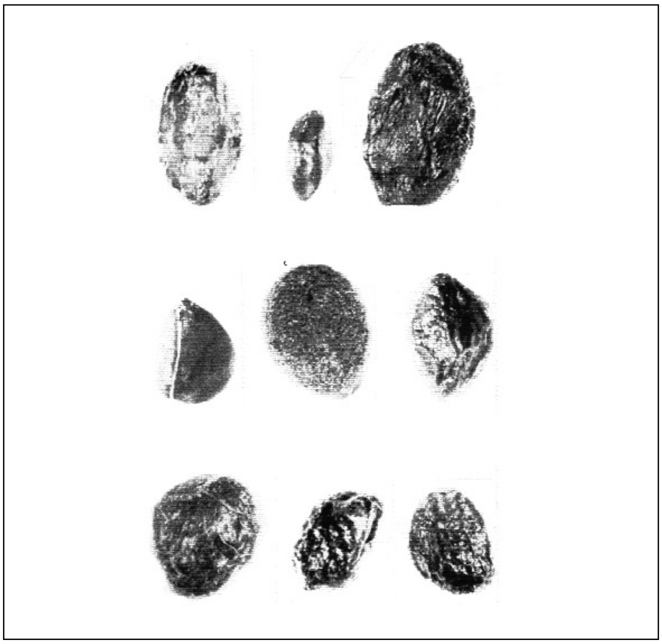
Table 4—*Ribes,* currant, gooseberry: fruit characteristics and seed storage conditions for air-dried seeds

	Fruit characteristics			Storage conditions		
Species	**Surface**	**Diam (cm)**	**Ripe color**	**Temp (°C)**	**Duration (yr)**	**Viability at end (%)**
R. alpinum	Glabrous	—	Scarlet	—	—	—
R. americanum	Glabrous	0.6	Black	6	4	38
R. aureum	Glabrous	0.6	Red, black, or yellow	21	17	89
R. aureum var. *villosum*	Smooth	1.0	Black, golden, or reddish brown	21	17	32
R. cereum	Glandular	0.6	Dull to bright red	21	27	4
R. cynosbati	Glandular	—	Reddish purple	21	7	8
R. hudsonianum	Smooth	1.0	Black	21	17	40
R. inerme	Smooth	0.6	Reddish purple	21	11	80
R. lacustre	Glandular	0.6	Purple to black	—	—	—
R. missouriense	Smooth	1.3	Purple to black	—	—	—
R. montigenum	Glandular	0.6	Red	—	—	—
R. nevadense	Glandular	—	Blue to black	Soil	4	81
	Glandular	—	Blue to black	21	4	88
R. oxyacanthoides ssp. *irriguum*	Smooth	1.0	Bluish purple	—	—	—
R. roezlii	Glandular	1.3	Purple or deep reddish brown	Soil	13	82
	Glandular	1.3	Purple or deep reddish brown	2	12	45
R. rotundifolium	Smooth	0.6	Purple	—	—	—
R. sanguimeum	Glandular	1.0	Blue to black	—	—	—
R. viscosissimum	Glandular	1.3	Black	21	17	23
	—	—	—	21	22	7

Sources: Hitchcock (1955), Jepson (1925), Ketchum and others (1968), Munz (1965), Pfister (1974), Quick (1945, 1947, 1954), Rehder (1940), Stephens (1969).

Figure 1—*Ribes*, currant, gooseberry: berries of *R. cereum*, wax currant (**upper left**); *R. cynosbati*, pasture gooseberry (**upper right**); *R. lacustre*, prickly currant (**middle left)**; *R. montigenum*, gooseberry currant (**middle right**); *R. sanguineum*, winter currant (**bottom left**); *R. viscosissimum*, sticky currant (**bottom right**).

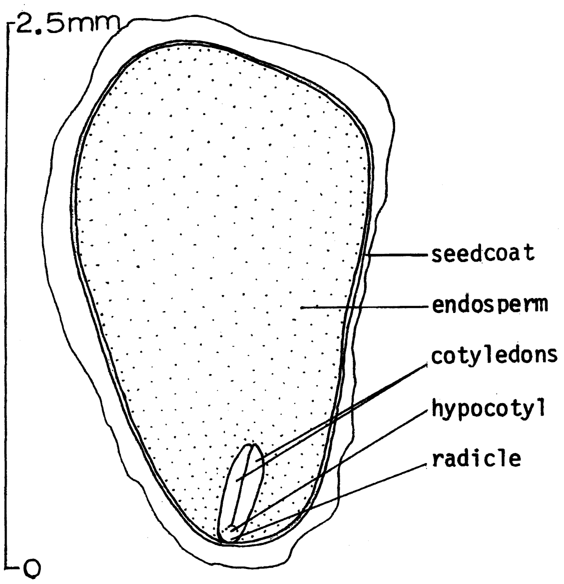
Figure 2—*Ribes*, currant, gooseberry: seeds of *R. cereum*, wax currant (**upper left**); *R. hudsonianum*, Hudson Bay currant (**upper center**); *R. oxyacanthoides* ssp. irriguum, Idaho gooseberry (**upper right**); *R. lacustre*, prickly currant (**center left**); *R. montigenum*, gooseberry currant (**center middle**); *R. nevadense*, Sierra currant (**center right**); *R. roezli*, Sierra gooseberry (**bottom left**); *R. sanguineum,* winter currant (**bottom center**); *R. viscosissimum*, sticky currant (**bottom right**).



empty seeds, and excess water can then be decanted. Seeds may be washed using a funnel lined with filter paper and then dried on the filter paper (Morrow and others 1954). Munson (1986) recommends replacing the blades in a food-processing blender or milkshake blender with a short length of plastic or rubber hose to extract the seeds. Data on the numbers of cleaned seeds per weight are listed in table 5.

Seed yields from 45 kg (100 lb) of berries was 1.8 kg (4 lb) for golden currant, 3.6 kg (8 lb) for clove currant, and 1.8 kg (4 lb) for winter currant (Pfister 1974). One liter of berries from winter currant weighs about 0.5 kg (1 bu weighs about 40 lb). Each prickly currant plant produces around 50 to 75 berries, and each berry has 8 seeds (Moss and Wellner 1953).

Figure 3—*Ribes missouriense*, Missouri gooseberry: longitudinal section through a seed.



Storage. Currant seeds are orthodox and remain viable for long periods when stored in sealed containers at a low moisture content. Temperature is evidently not critical. Samples of Sierra gooseberry seeds buried in soil in inverted open containers for 13 years exhibited 70 to 94% viability (Quick 1947b). Seeds of several species stored dry at room temperature also maintained high viability for periods up to 17 years (table 4).

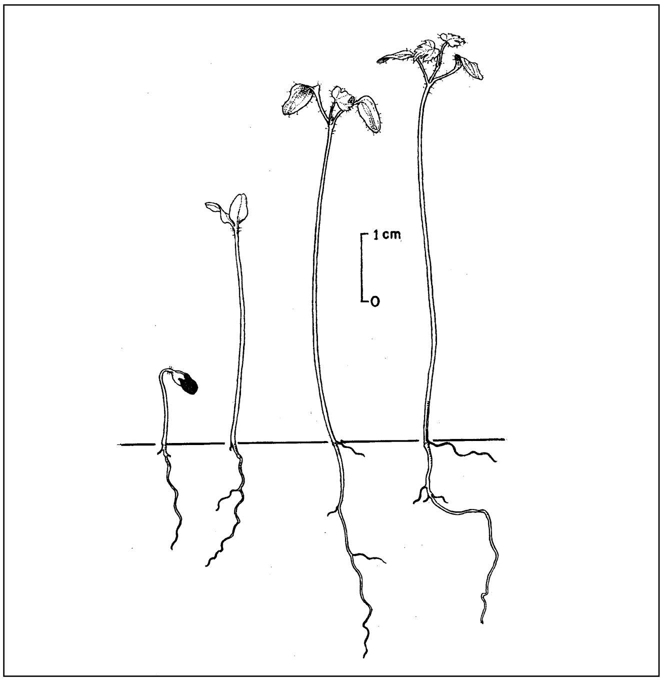
Germination. In nature, currant seeds normally germinate in spring following dispersal, although some seeds may remain dormant for many years (Moss and Wellner 1953; Quick 1954). The best seedbed appears to be mineral soil well supplied with humus. Germination is epigeal (figure 4). In the laboratory, seeds are slow to germinate except for those of Hudson Bay currant and roundleaf gooseberry. Most species require at least 1 stratification period of fairly long duration to break embryo dormancy (Rudolf 1949). Stidham and others (1980) achieved good germination of golden currant after 10 weeks of wet chilling in distilled water. Impermeable seedcoats also appear to be involved in dormancy of some seedlots of clove and American black currants (Pfister 1974). Germination rate and total can be increased by wet prechilling in sand, peat, or vermiculite or in a mixture of these media. Seed losses from damping-off fungi can be prevented by applying 646 mg of copper

Table 5—*Ribes,* currant, gooseberry: seed yield data

		Cleaned seeds (x1,000)/weight				
	Place	Range		Average		
Species	collected	/kg	/lb	/kg	/lb	Samples
R. americanum	—	544–741	247–336	690	313	4
R. aureum	—	441–628	200–285	514	233	4
R. aureum var. *villosum*	North Dakota	234–395	106–179	368	167	8
R. cereum	California	443–624	201–283	553	251	5
R. cynosbati	—	417–487	189–221	452	205	2
R. hudsonianum	Idaho	1,389–2,703	630–1,226	2,127	965	12
R. inerme	Idaho & California	780–877	354–398	807	366	5
R. lacustre	California	—	—	1,135	515	1
R. missouriense	—	344–370	156–168	357	162	2
R. montigenum	Utah	—	—	313	142	1
R. nevadense	California	650–935	295–424	862	391	10
R. roezlii	California	388–650	176–295	520	236	10+
R. sanguineum	Oregon	—	—	626	284	1
R. viscosissimum	Idaho & California	562–769	255–344	657	298	5

Sources: Pfister (1974), Quick (1936, 1954).

Figure 4—*Ribes missouriense*, Missouri gooseberry: seedling development at 2, 7, 23, and 44 days after germination.



oxalate per 100 cm^2 of culture surface (Quick 1941). Optimal temperature and duration of stratification vary by species and, to a lesser degree, between seedlots within a species. For most species, a second wet chilling and a repeat germination test are necessary to obtain complete germination of viable seed (table 6). The dormancy irregularity within a seedlot provides a natural adaptive advantage: some seeds germinate immediately and some remain dormant in the forest soil until conditions are optimal for germination and development. Many methods of breaking dormancy have been tried on various species, including acid treatment of seedcoat, warm incubation, freeze-and-thaw, and stratification with alternating temperatures (Quick 1939a&b, 1940, 1941, 1943, 1945, 1947a&b). For most species these treatments offer little advantage over normal wet chilling. A lower temperature can improve germination and reduce wet-chilling requirements (Fivaz 1931; Pfister 1974). Stidham and others (1980) used potassium nitrate to improve early germination of golden currant. Most tests were conducted in a greenhouse using sand flats moistened with Hoagland's nutrient solution (Quick 1941). Some species showed considerable germination capacity without wet chilling when

Table 6—*Ribes,* currant, gooseberry: pregermination treatments and germination test results

	Pregermination treatment		**Germination under test conditions***	**Germination**	
Species	**Temp (°C)**	**Days**	**(%)**	**capacity† (%)**	**Samples**
R. alpinum	0 to 10	90+	80	—	10
R. americanum	–2 to 2	90–120	68	76	39
R. aureum	–2 to 2	60	60	63	19
R. aureum var. *villosum*	20/0 (D/N)	120	94	98	3
R. cereum	–2 to 0	120–150	61	72	61
R. cynosbati	–2 to 5	90–150	69	72	19
R. hudsonianum	NP	NP	57	85	116
	0 to 2	90–120	69	76	42
R. inerme	0	120–200	60	74	54
R. lacustre	0	120–200	48	61	64
R. missouriense	–2 to 5	90+	73	—	3
R. montigenum	0	200–300	53	—	6
	0	120–150	8	33	15
R. nevadense	0	120	78	87	43
R. oxyacanthoides ssp. *irriguum*	0 to 5	90	79	81	11
R. roezlii	0	100–150	80	87	200
R. rotundifolia	–2 to 0	90+	80	81	10
R. sanguineum	0–2	100–140	61	64	55
R. viscosissimum	–2 to 0	140	58	67	88

Sources: NBV (1946), Pfister (1974), Quick (1939, 1940, 1941, 1943, 1945, 1947).

Note: D/N = day/night, NP = no pretreatment.

* Virtually all of the tested seeds were stratified and germinated in sand moistened with nutrient solution. The germination tests were conducted under greenhouse conditions for periods of 30 to 40 days.

† Germination capacity was determined by retrial stratification and a repeat germination test with conditions about the same as used initially.

investigators alternated diurnal temperatures (25 and 5 or 10 °C)—for example, prickly currant (Miller 1931), clove currant (Quick 1941), roundleaf gooseberry (Fivaz 1931), and sticky currant (Miller 1931). For these tests, 5 minutes of soaking in 2 to 10% sulfuric acid solution improved germination of prickly and sticky currant seeds (Miller 1931). Each species has its own unique germination characteristics, so that no procedure is best for all species. Additional work is needed to fully understand the dormancy mechanisms in the Ribes genus.

Nursery practice. Currant seeds are normally sown in fall, although they can be stratified and sown in spring. Few tests have been conducted to determine which species can be sown in spring without stratification; Hudson Bay currant may be one of these (table 6). Fall-sowing is recommended, especially if seedcoat dormancy is present (Heit 1968). However, Sierra gooseberry seeds must be dried before they are sown because fresh seeds will not germinate, even after stratification (Quick 1939). If fall-sowing is not possible, the seeds should be stratified before spring-sowing using the procedures summarized in table 6. Seeds should be sown at a rate of 646 to 860/m^2 (60 to 80/ft^2) (NBV 1946) or 130 viable seeds/m of row (40/ft) and covered to a depth of 3 to 6 mm ($^1/_8$ to $^1/_4$ in) (Pfister 1974). Seeds of Sierra gooseberry and wax and Sierra currants may be covered up to 1.3 cm (1/2 in) (Quick 1939a, 1940).

The only reported experience in nursery stock production is for clove currant (Pfister 1974). Seedbeds are fall-sown, mulched to a depth of 5 to 8 cm (2 to 3 in) and covered with snow fence. About 20,000 seedlings are produced per kilogram of seeds (9,000/lb) and the normal outplanting age is 2 years. Most species can be propagated readily from hardwood cuttings taken in autumn (Pfister 1974).

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Fabaceae—Pea family

Robinia L.

locust

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Growth habit, occurrence, and use. The locust genus—*Robinia*—includes 9 species, with 8 varieties native to the United States and Canada (BONAP 1996). Four species, 6 varieties, and 4 hybrids are considered here (table 1). Most of these species are shrubs and a few are deciduous trees. Black locust is a medium-sized tree 12 to 18 m high with a maximum of 30 m (Roach 1965). It reaches its best development in the Appalachian region and has been widely planted in the Western Hemisphere and Europe. The rapid growth of black locust on good sites, its nitrogen-fixing ability, and the durability of its wood (especially for fence posts) makes black locust one of the most valuable species in the genus. Bristly locust and its variety Kelsey locust are low shrubs, 0.6 to 3 m high (Fernald 1950). They are useful for erosion control because of prolific root sprouting. Growth of locust species is very good on calcareous soils, but bristly locust will grow also on strip mine spoils, where acid soils have pH values as low as 4.0. Bristly locust is a triploid and Kelsey locust is a diploid (Whitaker 1934). New Mexican locust is a small tree, 3 to 7.5 m high (Wooten 1913).

Flowering and fruiting. The perfect flowers occur in racemes originating in the axils of leaves of the current year; they appear in the spring and early summer (Radford and others 1964; Sargent 1965). Flowers are pollinated by insects, especially bees (Robertson 1928). The fruit, a legume (figure 1), ripens in the autumn and contains 4 to 10 dark brown to black seeds about 4.8 to 6 mm long (figure 2) (Olson 1974; Small 1933). When they ripen, the legumes (pods) become brown and open on the tree, releasing the seeds. Black locust begins seed-bearing at about 6 years of age and produces good crops every 1 to 2 years (Little and DeLisle 1962; Olson 1974). Seeds contain no endosperm (figure 3).

Collection, cleaning, and storage. Ripe seeds should be collected before the legumes open. Legumes can be picked from the trees by hand or flailed or stripped onto canvas or plastic sheets from late August throughout the winter (table 2). The legumes should be spread out to air-dry until they are brittle to facilitate breaking them open. Alternatively, they can be dried in a forced-air seed or cone drier if a faster result is needed or if natural drying conditions are too humid. Once the legumes are brittle, they can be threshed by flailing them in a bag or by running them through a macerator or brush machine (chapter 3). Chaff and light seeds can be removed by fanning or flotation in water. Legumes of New Mexican locust should be collected soon after ripening, because they open rapidly once ripening is complete (Olson 1974). Seed weights are similar among the locusts (table 3). Soundness and purity of seedlots is high. Seedlot purities of 97% and soundness of 90 to 99% have been obtained (Olson 1974). Locust seeds are orthodox in storage behavior. In prolonged storage, dry seeds retain their viability for 10 years or more if placed in closed containers at 0 to 4.5 °C. For periods of 3 to 4 years, open storage in a cool, dry place can be practiced (Olson 1974). Seeds can be stored dry and sown within a year (Wyman 1953).

Pregermination treatment. Dormancy in untreated seeds of locust is entirely due to impermeable seedcoats. Prompt germination can be induced by proper scarification. Several methods have been devised for this. The most well-developed treatment, with concentrated sulfuric acid, has been used on both New Mexican (Cox and Klett 1984) and black locusts (Brown 1973; Chapman 1936; Meginnis 1937; Olson 1974, Singh and others 1991). Myatt (1991) reports a much-refined acid scarification procedure. First the seeds are sized in a 2-screen cleaner using a 3.2-mm (#8) round-hole top screen and a 2.8-mm (#7) round-hole bottom screen. Larger seeds were found to require a shorter acid treatment than do small seeds. By treating the sizes separately, fewer of the seeds remain impermeable and fewer are damaged by too-long a treatment. Large seeds are treated for 45 to 60 minutes, medium seeds from 60 to 75 minutes, and small seeds from 75 to 90 minutes. Seeds are first wet with

Table 1—*Robinia,* locust: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R.* × *ambiqua* Poir. (pro sp)** *R.* × *ambique* var. *bella-rosea* (G. Nicholson) Rehder *R.* × *dubia* Foucault	**locust**	North Carolina
***R. hispida* L.** *R. pallida* Ashe *R. speciosa* Ashe *R. grandiflora* auct. non Ashe nec L. nec Schneid.	**bristly locust**	Nova Scotia & Maine S to Florida, W to Ontario, Minnesota, & Texas
***R. hispida* var. *fertilis* (Ashe) Clausen** *R. fertilis* Ashe *R. grandiflora* Ashe *R. pedunculata* Ashe	**bristly locust**	Connecticut S to North Carolina, W to Iowa
***R. hispida* var. *kelseyi* (Colwell ex Hutchinson) Isely** R. kelsyi Cowell ex Hutchinson	**Kelsey locust**	Kentucky, Tennessee, North & South Carolina; also New Jersey
***R. hispida* var. *nana* (Ell.) DC.** *R. elliottii* (Chapman) Ashe ex Small *R. nana* Ell.	**bristly locust**	S Appalachian Mtns of Alabama, Georgia, North & South Carolina, Kentucky, & Tennessee
***R. hispida* var. *rosea* Pursh** *R. albicans* Ashe *R. boyntonii* Ashe *R. leucantha* Rehd.	**mossy locust,** bristly locust	S Appalachian Mtns of Alabama, Georgia, North & South Carolina, Kentucky, & Tennessee
R. x holdtii Beissn. *R.* x *coloradensis* Dode	**Holdt locust**	Colorado, Utah, & Wyoming
R. x longiloba Ashe (pro sp.)	**locust**	North & South Carolina
***R. x margarettiae* Ashe (pro sp.)** *R. x salvinii* Rehd.	**Margarett locust**	New Brunswick & Nova Scotia S to Georgia, W to Ontario & Ohio
R. neomexicana Gray *R. luxurians* (Dieck) Schneid. ex Tarouca & Schneid. *R. neomexicana* var. *luxurians* (Gray) Dieck *R. neomexicana* var. *subvelutina* (Gray) (Rydb.) Kearney & Peebles	**New Mexican locust**	Wyoming S to New Mexico & Texas, W to California
***R. neomexicana* var. *rusbyi* (Woot. & Standl.) Martin & Hutchins ex Peabody** *R. breviloba* Rydb. *R. rusbyi* Woot. & Standl.	**Rusby locust**	Arizona & New Mexico
***R. pseudoacacia* L.** *R. pseudoacacia* var. *rectissima* (L.) Raber	**black locust**	Nova Scotia & New Brunswick S to Florida, W to Washington & California
***R. viscosa* Vent.**	**clammy locust**	Nova Scotia & New Brunswick S to Georgia, W to Ontario, Wisconsin, & Tennessee
***R. viscosa* var. *hartwegii* (Koehne) Ashe** *R. hartwegii* Koehne	**Hartweg locust**	Georgia & North & South Carolina

Source: BONAP (1996).

water in a leak-proof plastic tub. The concentrated sulfuric acid is added at a rate of 720 ml/4.5 kg of seeds. This amount of seeds is easily worked. A small amount of additional water is added to allow the seeds to be stirred with a wooden slat during the treatment. Stirring should be almost constant to evenly distribute the acid and thus prevent burning of individual seeds. At the end of the prescribed time in the acid, the seeds should be rinsed thoroughly in running water, then next soaked overnight in water. Those that have been successfully scarified will swell. Air-drying the treated seeds just enough to surface-dry them will allow the swollen seeds to be screened from the non-swollen seeds using the 2-screen machine. The top screen for this second screening would be about a 4-mm (#10) round-hole screen. The non-swollen seeds can be retreated in acid for 45 to 60 minutes using the same procedure as with the full lot. Swollen seeds are now ready for planting. They may be temporarily placed in a cooler for a few days until planted. If only 1 cycle of

Figure 1—*Robinia*, locust: legumes (pods) of *R. hispida* var. *rosea*, mossy locust (**left**); *R. hispidus* var. *fertilis*, bristly locust (**top center**); *R. neomexicana*, New Mexican locust (**bottom center**); *R. pseudoacacia*, black locust (**right**).

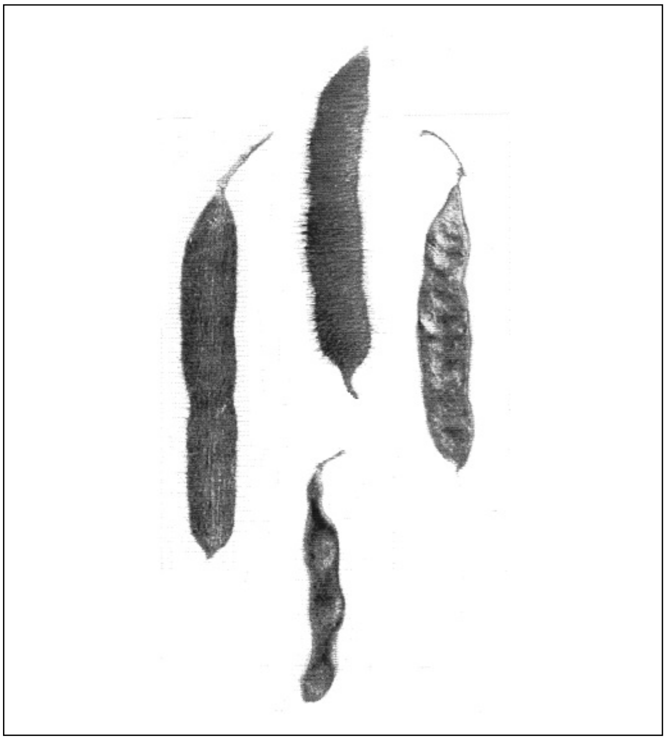
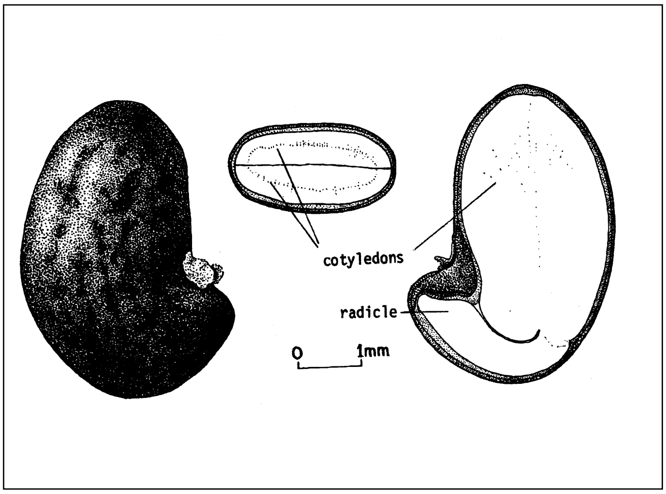
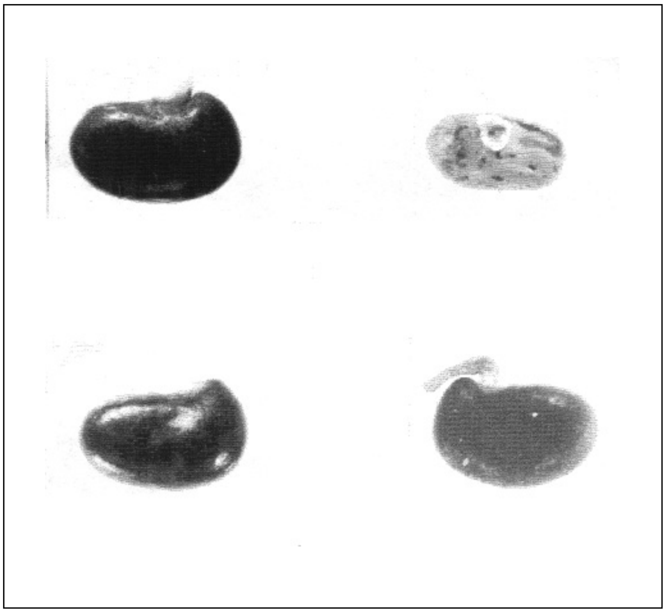


Figure 3—*Robinia pseudoacacia*, black locust: exterior (**left**) and longitudinal (**right**), and cross (**center**) sections of a seed.



acid is planned, a test sample should be run to determine the length of soak. Here small seed samples are soaked in acid for progressively longer intervals until a majority of the seeds are swollen following the water soak. Predetermined soaking times have varied from 10 to 120 minutes (Heit 1967; Meginnis 1937). Acid scarification is hazardous, so wearing adequate protective clothing—face shield and rubber gloves, boots, and apron—is mandatory.

Figure 2—*Robinia*, locust: seeds of *R. hispidus* var. fertilis, bristly locust (**top left**); *R. hispida* var. *rosea*, mossy locust (**top right**); *R. neomexicana*, New Mexican locust (**bottom left**); and *R. pseudoacacia*, black locust (**bottom left**).



A second widely used method is hot water treatment (Singh and others 1991; Wilson 1944). This procedure can be done by bringing a container of water to a boil, removing it from the heat, and pouring in the seeds. The water and seeds are then allowed to cool overnight. Although not practiced, it is reasonable to assume that the sizing of the seeds described above for acid would allow for a more complete scarification. Burning a hole in the seedcoat with a heated needle, nicking the seedcoat with a clipper, and heat shock (alternate boiling and cold water dips) have also been tried (Singh and others 1991). The nicking was as effective as the acid, burning less effective, and heat shock, even with multiple cycles of hot and cold, was still less effective.

Germination tests. Germination tests on scarified seeds may be made with any conventional medium. After 10 to 40 days at diurnally alternating temperatures of 30 °C in the day and 20 °C at night, germination capacities of several species of locust ranged from 10 to 93% (Olson 1974). Light is not required for germination (Heit 1968; Meginnis 1937). Germination capacity depends primarily on the effectiveness of the scarification treatment in making the seedcoat permeable to water without damaging the embryo (Meginnis 1937). For seeds used in a germination test, mechanical scarification with a needle, razor blade, or clipper can be done rapidly and without the hazards of handling acid. Acid-treated seeds have also been found to mold much more easily than mechanically treated seeds in germination tests at the USDA Forest Service's National Seed Laboratory (Karrfalt 1990).

Table 2—*Robinia,* locust: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
R. hispida	May–June	July–Sept	—
R. hispida var. *fertilis*	Early June	Sept	Oct–Nov
R. neomexicana	—	Sept	Sept–Oct
R. pseudoacacia	—	Sept–Oct	Sept–Apr

Sources: Olson (1974), Radford and others (1964), Sargent (1965).

Table 3—*Robinia,* locust: seed yield data

	Seed yield/fruit weight		Cleaned seeds/weight	
Species	**/45.4 kg**	**/100 lb**	**/kg**	**/lb**
R. hispida var. *fertilis*	—	—	50,715	23,000
R. hispida	—	—	61,080	27,700
R. neomexicana	9	20	47,630	21,600
R. pseudoacacia	6.8–15	15–33	52,920	24,000*

Sources: Sargent (1965), Small (1933), Swingle (1939).

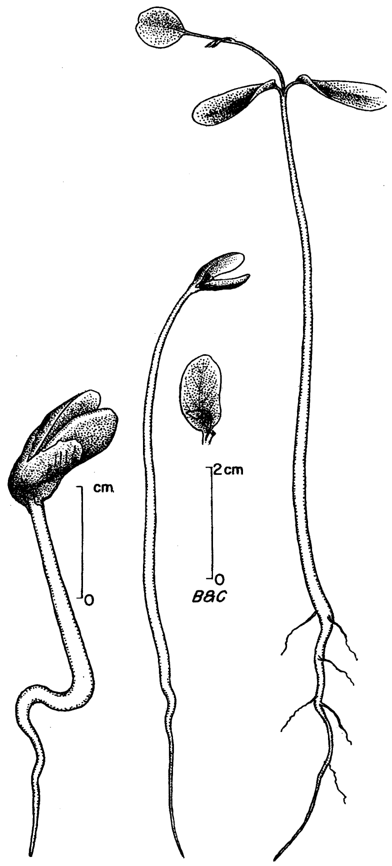
* Range was 16,000 to 35,000 seeds/lb.

For official germination testing, the Association of Official Seed Analysts (AOSA 1993) prescribe a pretreatment of a 1-hour soak in concentrated sulfuric acid, then chilling for 21 days at 20 °C. International rules (ISTA 1993) prescribe either scarification of the seeds at the cotyledon end or soaks in sulfuric acid until the surface of the seedcoats are pitted. Germination is then carried out at alternating temperatures of 20/30 °C for 14 days.

Nursery practice. Locust seeds may be drilled in rows 15 to 20 cm (6 to 8 in) apart at a rate of 65 to 100 seeds/m (20 to 30/ft), or broadcast in fertile soil from March to May. Seeds should be covered with about 6 mm ($^1/_4$ in) of soil, sand, or a mixture of sand and sawdust (McWilliams 1970; Olson 1974). Seeds should be treated with a nitrogen inoculant, especially if the seedbeds have been fumigated. Mulching is not mandatory, but a light straw mulch has been used advantageously in the culture of bristly locust in New York (McWilliams 1970). Germination is epigeal (figure 4). Seedlings of locust have large roots, and raising nursery beds 15 to 20 cm (6 to 8 in) facilitates lifting. One-year-old seedlings can be planted successfully on most fertile soils. Chaney and Kozlowski (1974) found that the addition of anti-transpirants to the nursery soil before sowing would reduce germination but had the potential to improve the growth and water balance of the surviving seedlings.

Direct seeding. Locust is often used in revegetating disturbed sites such as road cuts and strip mines. It is important in such areas to cover the seeds with about 6 mm

Figure 4—*Robinia pseudoacacia*, black locust: seedling development after 1, 3, and 8 days of germination.



($^1/_4$ in) of soil, as in the nursery. Brown (1973) reported a 10- to 60-fold improvement in germination from covering the seeds planted on West Virginia mine spoils. Brown also found (1973) that soil compaction from grading the sites and herbaceous competition resulted in poorer conditions for germination and seedling establishment. Salinity can also be a problem along highways and in dry countries where irrigation must be practiced in agroforestry applications. Under salinity levels of 0.05 to 0.80%, black locust germination was reduced and occurred more slowly (Bangash 1977; Bicknell and Smith 1975).

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Rosaceae—Rose family

Rosa L.

rose, briar

Susan E. Meyer

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Growth habit, occurrence, and uses. The genus *Rosa* is found primarily in the North Temperate Zone and includes about 200 species, with perhaps 20 that are native to the United States (table 1). Another 12 to 15 rose species have been introduced for horticultural purposes and are naturalized to varying degrees. The nomenclature of the genus is in a state of flux, making it difficult to number the species with precision. The roses are erect, clambering, or climbing shrubs with alternate, stipulate, pinnately compound leaves that have serrate leaflets. The plants are usually armed with prickles or thorns. Many species are capable of clonal growth from underground rootstocks and tend to form thickets. Usually found in the more moist but sunny parts of the landscape, wild roses provide valuable cover and food for wildlife, especially the birds and mammals that eat their hips and act as seed dispersers (Gill and Pogge 1974). Wild roses are also utilized as browse by many wild and domestic ungulates. Rose hips are an excellent source of vitamin C and may also be consumed by humans (Densmore and Zasada 1977). Rose oil extracted from the fragrant petals is an important constituent of perfume. The principal use of roses has clearly been in ornamental horticulture, and most of the species treated here have been in cultivation for many years (Gill and Pogge 1974).

Many roses are pioneer species that colonize disturbances naturally. The thicket-forming species especially have potential for watershed stabilization and reclamation of disturbed sites. If roses are to be used for these purposes, it is greatly preferable to utilize species native to the region rather than exotics, which can become serious pests. An

Table 1—*Rosa,* rose: scientific names and geographic distribution for 12 species native or naturalized in the United States

Scientific name	Common name(s)	Geographic distribution
R. acicularis **Lindl.**	**prickly rose**	Circumboreal, S in North America to Utah, New Mexico, Nebraska, & New York
R. blanda **Ait.**	**meadow rose,** smooth rose	E North America, S to Missouri & Nebraska
R. californica **Cham. & Schlecht.**	**California rose**	S Oregon, S to Baja California
R. canina **L.**	**dog rose**	Introduced from Europe; locally escaping in E North America
R. eglanteria **L.**	**sweetbriar rose,** eglantine	Introduced from Europe; naturalized in the Pacific NW & in E North America
R. gymnocarpa **Nutt.**	**baldhip rose,** dwarf rose	Pacific NW S to central California & E to Montana & Idaho
R. multiflora **Thunb. ex Murr.**	**multiflora rose,** Japanese rose	Introduced from Japan; widely naturalized in E North America
R. nutkana **K. Presl.**	**Nootka rose**	Alaska S to California, Utah, & Colorado
R. rugosa **Thunb.**	**rugosa rose,** hedgerow rose	Introduced from E Asia; naturalized in E & mid-W North America
R. setigera **Michx.**	**prairie rose,** climbing rose	Mid-W United States S to Texas; naturalized in E North America
R. wichuraiana **Crépin.**	**wichura rose,** memorial rose	Introduced from E Asia; locally escaping in E North America
R. woodsii **Lindl.**	**Woods rose**	Widely distributed in W & mid-W North America

Source: Gill and Pogge (1974).

example is the multiflora rose, a Japanese species that was widely promoted as a "living fence" in a previous era (Anderson and Edminster 1954). It has invaded thousands of acres of unimproved pastureland in the eastern United States and is now the target of a large and expensive control program (Mays and Kok 1988).

Flowering and fruiting. The large, perfect flowers are usually borne singly or in groups of 2 or 3, though some species (for example, wichura, multiflora, and prairie roses) have flat-topped inflorescences with few to many flowers. The flowers generally appear in late spring or early summer and are insect-pollinated. They are perigynous, with the 5 sepals, 5 to many petals, and many stamens inserted on the edge of the hypanthium and the many pistils borne within its cup. In fruit, the hypanthium enlarges to become the fleshy, berrylike hip (figure 1), and the pistils become single-seeded achenes (figures 2 and 3). The achene wall is usually hard, bony, and resistant to damage.

The fruits may ripen from late summer to fall, but they usually persist on the plants through the winter, presumably as an enticement to dispersers. The hips are often brightly colored in hues of orange, red, and purple that are attractive to birds. Those that have not been taken by spring are pushed off by the newly developing flowers of the next season. Once on the ground, the hips disintegrate quickly.

Figure 1—*Rosa*, rose: fruits (hips) of *R. eglanteria*, sweetbriar rose (**top**); *R. multiflora*, multiflora rose (**bottom left**); *R. nutkana*, Nootka rose (**bottom center**); and *R. setigera*, prairie rose (**bottom right**).

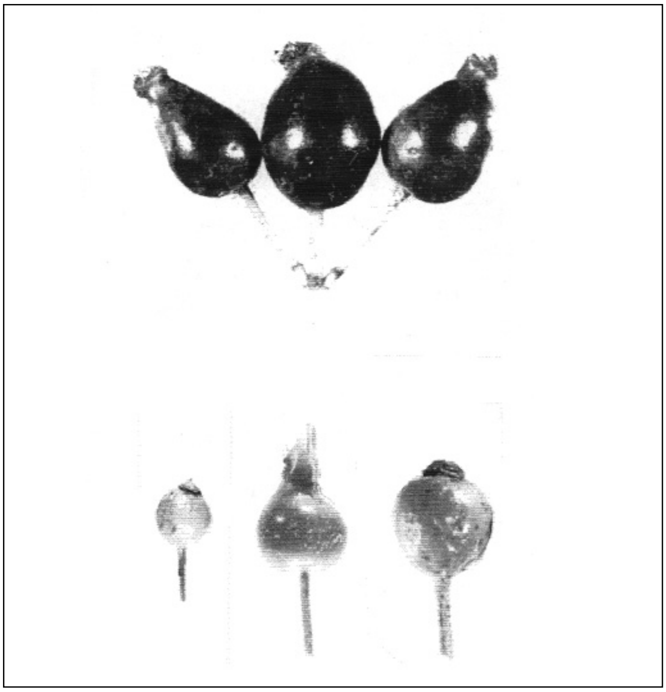
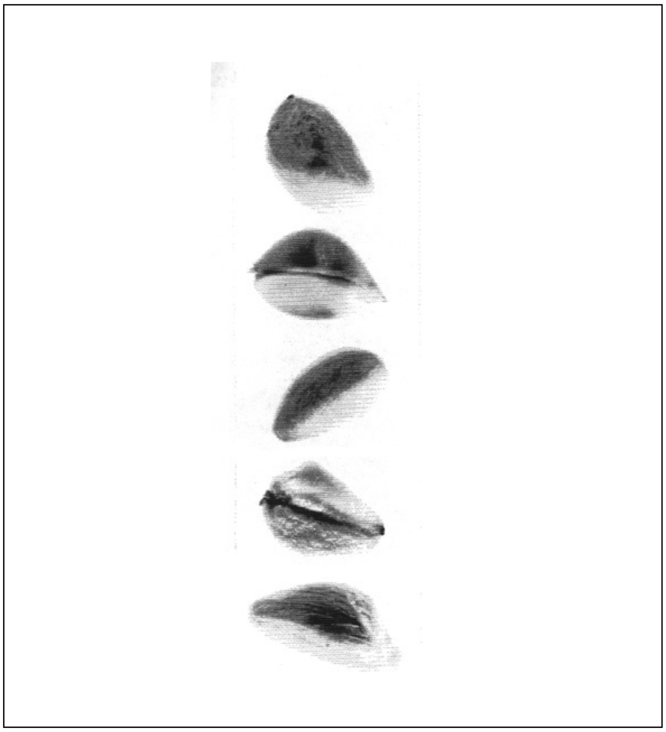


Figure 2—*Rosa*, rose: seeds (achenes) of *R. eglanteria*, sweetbriar rose (**top**); *R. gymnocarpa*, baldhip rose (**second**); *R. multiflora*, multiflora rose (**third**); *R. nutkana*, Nootka rose (**fourth**); and *R. setigera,* prairie rose (**bottom**).



Chalcid wasps of the genus *Megastigmus* (Torymidae) are important predispersal consumers of rose seeds (Mays and Kok 1988; Nalepa 1989). These wasps emerge as adults in spring and oviposit through the hip wall into the ovules of newly developing achenes. Their larvae develop by consuming the seeds over the summer, overwinter as late-instar larvae, pupate in early spring, and emerge as adults in time to repeat the life cycle. Chalcid infestations of 50 to 60% are common (Semeniuk and Stewart 1964; Svejda 1968) and infestations as high as 90% have been reported (Nalepa 1989). Achenes containing chalcid larvae appear normal in size and density and cannot be distinguished by inspection from viable achenes. The native chalcid *M. nigrovariegatus* Ashmead and the light form of the introduced rose seed chalcid *(M. aculeatus* Hoffmeyer) attack most if not all species of rose, whereas the dark form is apparently specific to multiflora rose and is being utilized in biocontrol programs (Mays and Kok 1988; Nalepa 1989).

Seed collection, cleaning, and storage. Rose hips may be collected by hand-stripping or by beating them into containers any time after the seeds are fully ripe. Ripeness is signaled by a change in the color of the hips from green to orange, red, or purple. If not processed right away, the hips should either be refrigerated or spread out to dry, as otherwise they can overheat and the seeds become damaged. The hips should be soaked in water if they have been allowed to dry prior to processing, then macerated using a macerator or similar device. Small lots can be macerated by rubbing the hips through screens. The achenes may be separated from the pulp by flotation or the material may be dried and the achenes cleaned out using a fanning mill. Achene weights vary from 5 to 17 mg (1.8^{-4} to 6.0^{-4} oz) and they number 59,530 to 185,220/kg (27,000 to 84,000/lb), depending on species and seedlot (table 2). Rose seeds may have a limited storage life, with some loss of viability in laboratory or warehouse dry storage after as little as 2 to 3 years (Crocker and Barton 1931; Gill and Pogge 1974), but they are almost certainly orthodox in storage behavior. Seeds of Woods rose have been reported to retain viability in open warehouse storage for 15 years (Stevens and others 1981). Sealed storage of air-dried seeds at low temperature is recommended (Gill and Pogge 1974).

Germination and seed testing. Rose seeds are normally dormant at maturity and require some form of pretreatment in order to germinate. Release from dormancy is a complex process that may involve changes at the pericarp, testa, and embryo levels. The degree of dormancy and the principal level of dormancy control varies among species, cultivars, seedlots, and even among hips within a single bush. Because the achenes have a thick, hard pericarp and do not swell when placed in water, it is often assumed that they are water-impermeable. Work by Svejda (1972) and others has shown that this is not the case. The achenes do take up water, although the mechanical restriction presented by the pericarp can sometimes prevent full imbibition. Tincker and Wisley (1935) showed, for 10 rose species, that cracking the pericarp alone did not remove dormancy. The importance of including treatments that weaken the pericarp in efforts to remove rose seed dormancy depends on the species and the particular lot. In nursery propagation of the rootstock rose *R. dumetorum* (*R. corymbifera*) 'Laxa', sulfuric acid treatment before warm plus cold stratification improves germination (Roberts and Shardlow 1979). The acid scarification can be eliminated and the warm stratification period shortened if the achenes are warm-stratified with compost activator (Cullum and others 1990). The role of these treatments is apparently to weaken the pericarp along

Figure 3—*Rosa setigera*, prairie rose: longitudinal section through a seed.

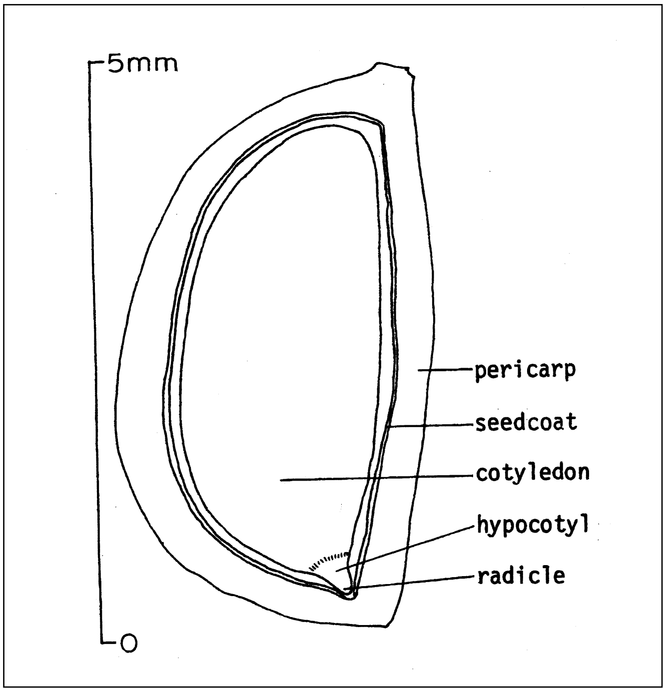


Table 2—*Rosa*, rose: achene weight data

Species	Mean weight mg	Mean weight oz	Achenes/weight /kg	Achenes/weight /lb
R. acicularis	25–28	0.9–1.0	35,940–40,130	16,300–18,200
R. blanda	9–12	0.3–0.4	81,580–116,860	37,000–53,000
R. californica	4	0.1	224,910	102,000
R. canina	13 (8–17)	0.5 (0.3–0.6)	59,530–119,070	27,000–54,000
R. eglanteria	15	0.5	68,355	31,000
R. gymnocarpa	16	0.6	61,740	28,000
R. multiflora	6–9	0.2–0.3	110,250–180,810	50,000–82,000
R. nutkana	8–15	0.3–0.5	66,150–132,300	30,000–60,000
R. rugosa	6–9	0.2–0.3	114,660–163,170	52,000–74,000
R. setigera	9	0.3	110,250	50,000
R. wichuriana	5	0.2	185,220	84,000
R. woodsii	9 (7–13)	0.3 (0.2–0.5)	77,170–143,320	35,000–65,000

Sources: Belcher (1985), Gill and Pogge (1974), Mirov and Kraebel (1939).

the sutures, whether with acid or through microbial digestion. Responsiveness to warm plus cold stratification can also be increased in *R. dumetorum* 'Laxa' by vacuum-infiltrating the achenes with growth hormones such as gibberellic acid or benzyladenine (Foster and Wright 1983), which suggests that something other than simple mechanical restriction may be involved. Similarly, in the relatively non-dormant multiflora rose, the achenes may be induced to germinate without chilling either by treatment with macerating enzymes that weaken pericarp sutures or by leaching with activated charcoal to remove inhibitors from the incubation solution (Yambe and Takeno 1992; Yambe and others 1992). By using macerating enzymes to remove dormancy, these workers were able to demonstrate a phytochrome-mediated light requirement for germination in this species (Yambe and others 1995). Acid scarification (but not mechanical scarification) is reported to substitute for warm pretreatment in the cultivated rose *R. gallica* L. (Svejda 1968).

Chilling is the treatment most often applied to remove rose seed dormancy, and the achenes of most species will germinate eventually if chilled for long enough periods. For some species, periods of cold stratification corresponding to a single winter in the field are sufficient, as in prairie, multiflora, and wichura roses (table 3). Achenes of these species may show increased dormancy if the chilling period is preceded or interrupted by periods of incubation at warmer temperatures (Semeniuk and Stewart 1962; Stewart and Semeniuk 1965). Interruption of chilling with warm incubation resulted in secondary dormancy induction only if the temperature of warm incubation was too high. If the seeds were held below this 'compensating' temperature, no change in dormancy resulted, and the seeds could accumulate the effects of chilling across warm interruptions. Seeds whose chilling requirements had just barely been met germinated best at relatively low incubation temperatures, whereas those that had been in chilling for longer than necessary either eventually germinated in chilling or could germinate at a wide range of temperatures, including those above the compensating temperature. Semeniuk and others (1963) showed that, for prairie rose, the effect of the warm pretreatment

Table 3—*Rosa*, rose: stratification requirements

	Warm stratification		Cold stratification			
Species	**Days**	**Temp (°C)**	**Days**	**Temp (°C)**	**Germination temp (°C)**	**Incubation (%)**
R. acicularis	—	—	365	5	5	57*
	118	25	90	5	20, 10/20	90*
R. blanda	—	—	90	5	13, 18	7†
	—	—	270	5	13, 18	53†
R. californica	—	—	90	5	—	62
R. canina	60	20	60	4	—	47
	90	20	150	4	—	34
R. eglanteria	—	—	570	5	5	24
	—	—	450	5	5	40
R. gymnocarpa	—	—	90	5	—	43
R. multiflora	—	—	90	5	15–18	45
	—	—	180	5	15–18	60
	—	—	120	5	5	72
R. nutkana	—	—	365	4.5	4.5	65
	—	—	128	4.5	18.5	48
	128	18.5	128	4.5	18.5	72
R. rugosa	—	—	90	3	20–29	32
	60	20	90	3	20–29	60
	—	—	210	4	20	85
R. setigera	—	—	120	5	15–18	90
	—	—	90	4.4	18.3	48
R. wichuriana	—	—	60	5	15–18	75
	—	—	45	5	18.3	76
R. woodsii	—	—	120	3	—	0
	60	20	90	3	—	49

Sources: Crocker and Barton (1931), Densmore and Zasada (1977), Gill and Pogge (1974), McTavish (1986), Mirov and Kraebel (1939), Rowley (1956), Semeniuk and Stewart (1962, 1964, 1966), Stewart and Semeniuk (1965), Svejda (1968), Tillberg (1983), Tinker and Wisley (1935).

* Based on total viable seeds.

† Total viability known to be about 55%; all other percentages based on total seeds, viability unknown.

above the compensating temperature was to induce secondary dormancy at the embryo level. Interestingly, this dormancy could be alleviated only by chilling whole achenes; chilling the embryos did not alleviate their dormancy.

Other species, such as prickly, Nootka, and Woods roses, show much increased germination percentages in response to chilling periods corresponding to a single winter if the chilling period is preceded by a period of warm incubation (table 3). This requirement for warm incubation before chilling would effectively postpone seedling emergence in the field until the second spring after seed production (Densmore and Zasada 1977). The temperature and duration of the warm treatment is sometimes important. In rugosa rose, a warm pretreatment of 60 days at 20 °C before 90 days of chilling at 3 °C increased germination over chilling alone, but longer periods resulted in decreased germination (Svejda 1968). The effect of warm pretreatment on chilling response has been formally documented for only a few rose species, but it is likely that high-viability lots of any species that show minimal germination after 6 months of chilling would be benefitted by a warm pretreatment.

Exactly what changes take place in rose seeds during warm pretreatment or chilling is not known. In many cases, the warm pretreatment seems to have effects at the seed level rather than simply providing an opportunity for pericarp weakening (Densmore and Zasada 1977). Hormonal balance has been implicated in the imposition of dormancy in rose seeds by several workers. Substances leached from dormant rose achenes or obtained from them by grinding have been shown to suppress germination of otherwise non-dormant excised rose embryos (Jackson and Blundell 1963, 1965; Svejda and Poapst 1972). Excised seeds with physically disrupted testas showed much lower germination than embryos with testas removed, suggesting that inhibitors leaching from the testa suppressed germination (Jackson and Blundell 1963). Other workers have shown that, although inhibitory substances are present in dormant achenes and may disappear during dormancy loss, their removal alone is not sufficient to induce germination (Julin-Tegelman 1983; Tillberg 1983).

Variation in dormancy-breaking requirements both within and among lots of any rose species make it difficult to predict effective treatments. One of the causes of this variation has been quite well-studied in cultivated tea roses, and the results probably apply to wild species as well. Von Abrams and Hand (1956) were the first to demonstrate that seeds of a given cultivar matured in the field at warmer temperatures were less dormant (that is, had a shorter chilling requirement) than seeds matured at cooler temperatures. This result has been confirmed by De Vries and Dubois (1987), who also found that warmer maturation temperatures were associated with higher hip set and higher numbers of achenes per hip. Gudin and others (1990) examined the relationship of maturation temperature with developmental rate, endocarp thickness, and dormancy status. They also looked at the effect of the pollen parent in controlled crosses. They found that achenes matured at cooler spring temperatures had slower development, thicker endocarps, and higher levels of dormancy than those matured at warmer summer temperatures. Pollen parent also had an effect on both dormancy and endocarp thickness, presumably through its effect on developmental rate. These workers concluded that the higher dormancy associated with lower maturation temperature was mediated through endocarp thickness, but slow development could also have effects at the testa or embryo level. For example, Jackson and Blundell (1963) reported that excised embryos of rugosa rose grown in Wales were non-dormant, whereas Svejda (1972) and Julin-Tegelman (1983), working with lots grown in Canada and Sweden, reported that excised embryos of this species required 3 to 4 weeks of chilling to become germinable.

Another source of variation in dormancy status for rose achenes is a consequence of the post-maturation environment. Semeniuk and Stewart (1960, 1966) showed for several species that achenes from hips that had overwintered on the bush were more dormant than achenes from those same bushes collected and tested in the fall or stored dry and tested along with the field-overwintered achenes. This effect has also been noted by other workers (Jackson and Blundell 1963; Roberts and Shardlow 1979). It is probably best to collect rose hips soon after they reach maturity and to clean the collections immediately if seed dormancy status is an issue.

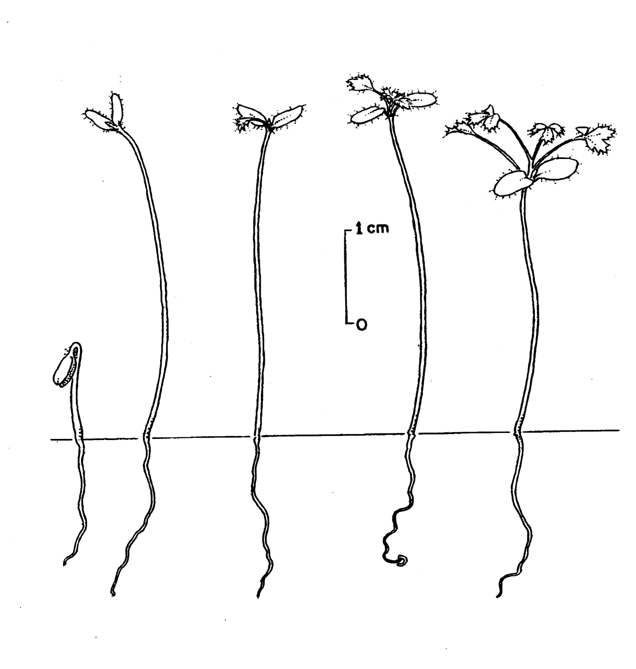
Because of the wide variation in dormancy-breaking requirements within each species, quality evaluations of rose seeds are usually carried out using tetrazolium staining (Gill and Pogge 1974). The achenes are first soaked in water for 24 hours. Firm pressure with a knife on the suture or a tap with a small hammer is used to split open the pericarp. The testa is then scratched or clipped at the cotyledon end and the seed is immersed in 1% tetrazolium chloride for 6 hours at room temperature. The testa is slit along the side and the embryo, which fills the seed cavity, is squeezed or teased out for evaluation (Belcher 1985). The excised embryo method may also be used, although it has little advantage over tetrazolium staining (Gill and Pogge 1974). For purposes of determining fill and chalcid infestation levels, x-radiography is suitable (Belcher 1985).

The preferred method in official testing is also tetrazolium staining (ISTA 1993), although stratification for 28 days at 3 to 5 °C is suggested for multiflora rose (AOSA 1993). For other rose species, the international rules (ISTA 1993) suggest an alternate method of 12 months of stratification, followed by germination in sand at 20 °C for 70 days. Germination is epigeal (figure 4).

Field seeding and nursery practice. Woods rose has been fall-seeded as a part of mixes for revegetation of deer winter ranges in pinyon-juniper and mountain brush communities of the Intermountain West (Plummer and others 1968). It is recommended for areas with more than 300 mm of annual precipitation, and should be broadcast-seeded or drilled with other small-seeded shrubs at rates of 0.5 to 1 kg/ha (0.45 to 0.9 lb/ac). It reportedly is relatively easy to establish from seeds and persists very well after initial establishment. Other native rose species could probably also be direct-seeded successfully in wildland settings.

Planting rose seeds in a nursery setting may be carried out in fall for outdoor cold stratification or in summer for warm followed by cold stratification. Seedlings will emerge the following spring. For spring plantings, the achenes must be appropriately stratified or otherwise pretreated prior to planting. Recommended planting depth is 5 to 10 mm (1/5 to 2/5 in), depending on seed size. Bareroot plants may be produced successfully as 1+0 stock, and container stock can be produced by 3 to 5 months after germination (Landis and Simonich 1984; Shaw 1984). Roses are also readily propagated from cuttings.

Figure 4—*Rosa blanda*, meadow rose: seedling development at 1, 3, 6, 26, and 41 days after germination.



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Arecaceae—Palm family

Roystonea O.F. Cook

royal palm

Kristina F. Connor and John K. Francis

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Synonyms. *Oreodoxa regia* (H.B.K.) for Cuban royal palm; *Roystonea elata* (Bartr.) F. Harper for Florida royal palm. Note that Little (1979) states that the Cuban royal palm has been united with the Florida royal palm, *R. elata*. However, all articles written before and some articles written after 1979 do not unite these 2 species.

Growth habit, occurrence, and use. There are 2 noteworthy species of *Roystonea* palms grown in the United States and its territories (table 1). Puerto Rico royal palm is native to Puerto Rico and Vieques, St. Croix in the U.S. Virgin Islands, and possibly Tortola in the British Virgin Islands (Francis 1992; Little and Wadsworth 1964). It has possibly naturalized in the British Virgin Islands and in St. Thomas and St. John in the U.S. Virgin Islands (Francis 1992). The smooth gray trunk with its swollen base and the gracefully drooping fronds are a common sight in the island cities. Its ability to withstand a polluted atmosphere and to grow well on either moist, well-drained soils or nutrient-deprived fill dirt enhances its value as a landscape plant. Francis (1992) reports heights of 26.4 m and diameters of 25 to 70 cm in Puerto Rico. Maximum age is 80 to 110 years, and flowering can begin as early as the seventh year. Little and Wadsworth (1964) and Braun (1983) note heights reaching only 18 m and diameters of 30 to 61 cm for the species, whereas LHBH (1977) reports heights reaching at least 15 m. Because of its ability to withstand hurricane-force winds, it is able to become dominant in the forest canopy despite its short stature (Francis 1992). In addition to its importance as an ornamental, the palm's lumber is widely used in rural construction, the leaves as a roof thatch, the flowers as an important nectar source for honey bees (*Apis mellifera* L.), and the fruits as a fat-rich food source for birds (Francis 1992; Little and Wadsworth 1964). The tree apparently has no serious insect pests, but the lumber is susceptible to attack by the dry-wood termite *Cryptotermes brevis* (Walker) (Francis 1992; Little and Wadsworth 1964; Wolcott 1946).

Cuban royal palm is a native of Cuba that is now naturalized in Hawaii (Neal 1965) and in Collier, Dade, and Monroe Counties in Florida (Little 1979; West and Arnold 1952). Like its relative, it too is a widely planted ornamental. There is some variation in reported height growth for the species: Neal (1965) noted heights reaching only 15 to 21 m in Hawaii, but West and Arnold (1952) reported heights of 24 to 34.5 m and diameters up to 61 cm in Florida. LHBH (1977) lists maximum heights of at least 23 m.

Both species grow in the subtropical moist and subtropical wet life zones (Holdridge 1967). Moore (1973) describes other species of royal palm growing on the eastern coast of Mexico, Guatemala, and Honduras, and in Venezuela. Their upper trunks are encased in a green column of leaf sheaths 1 to 3 m long. The pinnate leaves have short petioles, and a sheath and blade 2.4 to 3.7 m long. In Puerto Rico royal palm, the youngest leaflet projects as a spire above the oth-

Table 1— *Roystonea,* royal palm: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***R. borinquena* O.F. Cook**	**Puerto Rico royal palm**	Puerto Rico & Vieques; St. Croix, U.S. Virgin Islands; Tortola, British Virgin Islands
***R. elata* (Bartr.) F. Harper** *R. regia* (H.B.K.) O.F. Cook *Oreodoxa regia* (H.B.K.)	**Cuban royal palm,** Florida royal palm	Cuba; naturalized in S Florida & Hawaii

Sources: Francis (1992), Little (1979), Little and Wadsworth (1964), Neal (1965), West and Arnold (1952).

ers (Little and Wadsworth 1964), and pinnae grow from the rachis in 2 planes (LHBH 1977). Pinnae grow in several planes along the rachis of each Cuban royal palm leaf. Little and Wadsworth (1964) contend that another characteristic distinguishing Puerto Rico royal palm from Cuban royal palm is that the latter lacks the swollen trunk of the former; however, both West and Arnold (1952) and Neal (1965) report the swollen base—and Neal (1965) and Braun (1983) the swollen middle trunk—in Cuban royal palm.

Flowers and fruits. Flowers of both species develop from buds formed at the base of the leaves. Whitish male and female flowers form on the same panicle, with male flowers of each tree opening and falling before the female flowers to prevent self-fertilization. Generally, each female flower forms between 2 male flowers on the panicle (Francis 1992; Little and Wadsworth 1964). The male flowers have 3 small broad sepals and 3 blunt-pointed petals; the females have 3 small broad sepals and a tubular corolla (Little and Wadsworth 1964).

In Puerto Rico royal palm, the twice-branched drooping panicles develop from large narrow buds. The panicles develop inside a dark brown sheath that is 0.9 to 1.5 m long (Francis 1992; Little and Wadsworth 1964). According to LHBH (1977) and Braun (1983), one feature that distinguishes this species from the Cuban royal palm is the presence of scales on the axes bearing the flowers (rachillae). The length of the inflorescence also seems to differ, with that of Puerto Rico royal palm reaching up to 1 m (Little and Wadsworth 1964) and that of Cuban royal palm reaching only 60 to 80 cm (Braun 1983; West and Arnold 1952). The panicle of Puerto Rico royal palm bears stalkless male flowers measuring 13 mm across, smaller female flowers, and, eventually, greenish yellow fruits that are 13 mm long and about 10 mm in diameter (Little and Wadsworth 1964). Fruits (figure 1) ripen to a brownish purple color and contain 1 light brown elliptic seed that is 8 mm long, hard, and oily (figures 2 and 3). Flowers can occur throughout the year.

Figure 1—*Roystonea borinquena*, Puerto Rico royal palm: fruit.

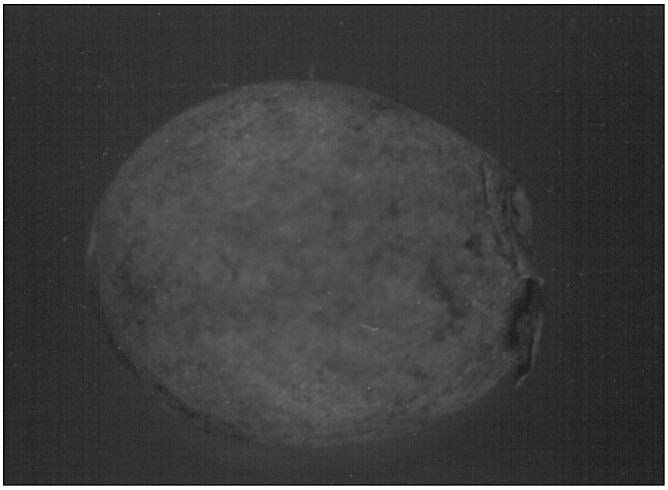


Figure 2—*Roystonea borinquena*, Puerto Rico royal palm: seeds.

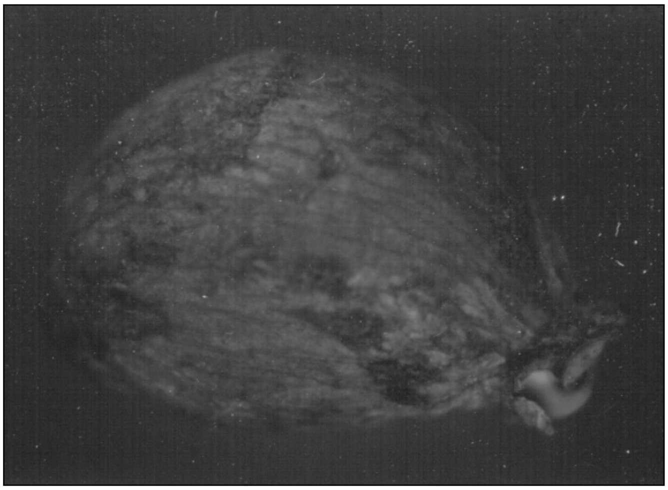
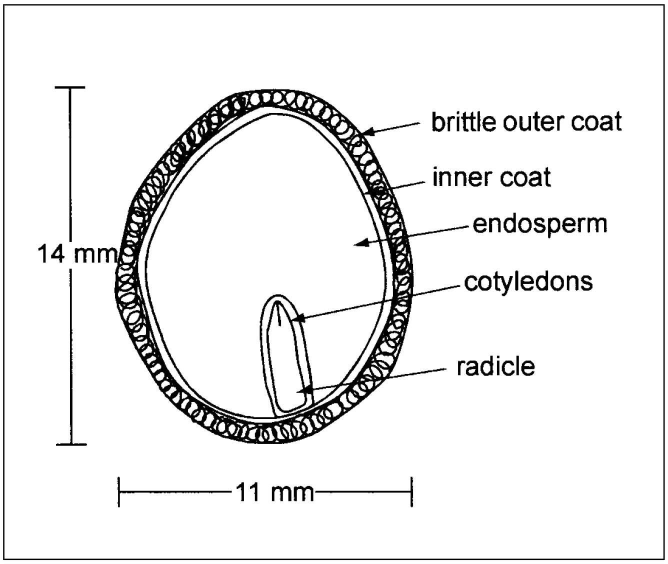


Figure 3—*Roystonea borinquena*, Puerto Rico royal palm: longitudinal section through a seed.



The Cuban royal palm bears white, fragrant flowers on a many-branched panicle. Male flowers measure 6 mm across and the violet-purple fruits are smooth, ovate, and measure 13 mm in length. Each fruit bears a single light brown, thin seed that is embedded in brown fibrous flesh (Neal 1965; West and Arnold 1952). The seeds contain oil that may be sold commercially (Moscoso 1945).

Collection, storage, and germination. Francis (1992) reports that, in a survey of 100 Puerto Rico royal palm trees, 35% bore no fruit whereas others produced massive quantities of fruit and seeds (6,000 to 12,000/tree). Seeds are commonly dispersed by water, birds, rodents, and domestic animals but are easily collected for propagation on the ground beneath open-grown trees. Francis and Rodriguez (1993) estimate an average of 2,980 seeds/kg (1,352/lb). Seeds can be stored for 1 to 2 months in sealed containers at room temperature and for longer periods of time under refrigeration. Seeds sown in trays of sand with no pretreatment and kept at ambient temperatures (24 to 30 °C) averaged 80% germination after 14 days. Germination is hypogeous (Francis 1992) and may take up to 2 months after sowing. The radicle emerges first, the shoot about 3 weeks later. Under natural conditions, germination of both species may not begin for 50 to 60 days and may not be completed for an additional 100 days (Braun 1983). Broschat and Donselman (1988) found that soaking Cuban royal palm seeds in 1,000 ppm GA_3 solution for 48 hours slightly increased the rate of germination but also resulted in abnormally elongated seedlings. The best results were obtained if seeds were cleaned and then germinated at temperatures between 30 to 35 °C. They also determined that the best method for long-term storage for Cuban royal palm was to place clean, half-ripe to ripe seeds (air-dried at 80 to 90% relative humidity and treated with a fungicide, for example, thiram) in tightly sealed polyethylene containers held at room temperature (23 °C). The seeds of royal palm may be intermediate in their storage behavior. Ellis and others (1991) put forth the idea that seeds of the Cuban royal palm are not truly orthodox nor recalcitrant. Apparently, drying the seeds to a low moisture content or storing them below 0 °C may result in damage.

Nursery practices. Puerto Rican royal palm seedlings kept in full sunlight averaged 30 cm (12 in) in height after 6 months and 90 cm (36 in) after 15 months; they can be grown to heights of 1.5 m (60 in) or more in 4-liter (1-gal) containers (Francis 1992). Even large trees can be dug up with a backhoe and transplanted. Survival is high as long as they are braced and watered frequently. High mortality results if young trees with only a few basal leaves or short trunks are moved without a protective ball of earth and left without shade and water (Francis 1992).

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Rosaceae—Rose family

Rubus L.

blackberry, raspberry

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Growth habit, occurrence and use. *Rubus* is a large and complex genus with 12 subgenera. The 2 largest subgenera and those most important in North America are *Eubatus* (blackberries) and *Idaeobatus* (raspberries). There are about 200 species in *Idaeobatus* and perhaps as many as 1,000 or more in *Eubatus* (Fernald 1950; Jennings 1988). There are 3 other subgenera—*Chamaemorus* (cloudberries), *Cyclatis* (Arctic berries), and *Anoplobatus* (flowering raspberries)—that include 1 or more North American species. Blackberries are distinguished from raspberries by the presence of a core or torus that fills the center of the berry when it is removed from the plant; the ripe fruits of raspberries have no core and are shaped like a thimble when removed from the plant. Most species are native to the cool, temperate regions of the Northern Hemisphere; a few are found in the tropics and the Southern Hemisphere (Jennings 1988). The occurrence, general uses, and growth form of some species common in North America are listed in tables 1 and 2.

Although more than 1 species may occur on a given site within a specific geographic area, each species has a specific site-type on which it achieves best development. For example, in Wisconsin there are 6 *Rubus* spp. (Curtis 1959). Allegheny blackberry, trailing raspberry (*R. pubescens* Raf.), and red raspberry are the most widespread and occur together on some sites, but the maximum presence for each is in southern dry, northern wet-mesic, and boreal forests, respectively. The other 3 species—swamp dewberry, blackcap raspberry, and thimbleberry—attain maximum presence in northern dry, southern dry-mesic, and boreal forest types, respectively (Curtis 1959). Most species occur on relatively similar sites throughout their ranges. However, thimbleberry occurs on very different sites over its natural range. For example, in western Oregon it occurs in areas generally free of frost, whereas in Wisconsin and northern Michigan, maximum presence is in areas receiving significant amounts of snow and having prolonged winter air-temperatures well below freezing. Species distribution for various geographic regions can be found in works by Hickman (1993), MacKinnon and others (1992), Meades and Moores (1994), USDA Forest Service (1993), and Viereck and Little (1972), as well as in other regional flora and site classification manuals.

Rubus spp. are a major fruit crop in the North Temperate Zone in Europe and North America; this is their dominant use. Because the primary product is a fruit, there has been a large amount of research focusing on factors limiting fruit production, and thus directly and indirectly seed production. In this chapter, we can only briefly summarize the available literature; a more complete discussion can be found in Ourecky (1978), Moore and Janick (1983), and Jennings (1988). Jennings (1988) provides a very thorough discussion of *Rubus* breeding and cultivation.

The many growth forms of the various species, and the wide range of site conditions on which they occur, make the species useful in reclamation, revegetation, and erosion control projects. Because of the stout spines on some species, dense stands make good barriers to restricted areas as well as providing cover and food for many animal species. Stems and leaves are browsed by a large number of animals. Palatability varies among species and seasons of the year and by site conditions for a species. The fruits are eaten by animals ranging in size from insects to birds to small mammals to the Alaska brown bear (*Ursus middendorfii*). Fruit and bark of the roots and stems have medicinal properties and were used by Native Americans to cure a variety of ailments (Coladonato 1990a&b; Krochmal and others 1969; MacKinnon and others 1992; Meeker and others 1993; Snow and Snow 1988; Tirmenstein 1990a–f). Salmonberry was introduced in Great Britain and has become a weed problem in lowland forests and plantations (Paterson 1996).

Rubus spp. native to North America and some naturalized exotic species can be found at all stages of forest succession (table 1). The most impressive communities in terms

Table 1—*Rubus,* blackberry, raspberry: nomenclature and occurrence

Scientific name & synonym(s)	Common names	Occurrence
SUBGENUS: *Eubatus* (blackberries)		
R. allegheniensis Porter	**Allegheny blackberry,** sow-teat blackberry	New Brunswick to Minnesota, S to Missouri, Arkansas, E to North Carolina
***R. canadensis* L.** *R. millspaughii* Britt. *R. randii* (Bailey) Rydb. *R. amabilis* Blanchard	**smooth blackberry,** thornless blackberry, mountain blackberry	Newfoundland to Ontario & Minnesota, S to Tennessee & Georgia
***R. hispidus* L.** *R. obovalis* Michx. *R. sempervirens* Bigel.	**swamp dewberry**, running blackberry	Prince Edward Island to Ontario, S to Wisconsin, E to Maryland & mtns of North Carolina
***R. laciniatus* Willd.** *R. fruticosus* var. *laciniatus* West. *R. vulgaris* Weihe & Nees	**cutleaf blackberry**, evergreen blackberry	Old-World origin; escaped from cultivation in Massachusetts to Michigan & S; also W of Cascade Mtns from British Columbia to California
***R. procerus* P.J. Müll. & Boulay**	**Himalayan blackberry**	Europe; naturalized from Delaware to Virginia, S British Columbia to California W of Cascade Mtns
***R. ursinus* Cham. & Schlect**. *R. macropetalus* Dougl. ex Hook	**trailing blackberry**, Pacific blackberry	British Columbia to California & Idaho
SUBGENUS: *Idaeobatus* (raspberries)		
***R. idaeus* L.**	**red raspberry**	Present in all states (but SE US, Texas, & Oklahoma) & all provinces of Canada
***R. occidentalis* L.**	**blackcap raspberry**, black raspberry, thimbleberry	New Brunswick to Minnesota, S to Colorado, E to Georgia
***R. spectabilis* Pursh** *R. stenopetalus* Cham.	**salmonberry**	SE Alaska to Idaho & California; becoming naturalized in Great Britain
SUBGENUS: *Chamaemorus* (cloudberry)		
***R. chamaemorus* L.**	**cloudberry**, bake-apple	Alaska, New England, & all Canada
SUBGENUS: *Anoplobatus* (flowering raspberries)		
***R. odoratus* L.** *Rubacer odoratus* (L.) Rydb.	**fragrant thimbleberry,** flowering raspberry, purple-flowering raspberry	S Quebec to Ontario S to Michigan & E to Georgia
***R. parviflorus* Nutt.**	**thimbleberry**, western thimbleberry	SE Alaska to California, New Mexico, Dakotas to N Great Lakes area
SUBGENUS: *Cyclatis* (Arctic berries)		
***R. arcticus* L.**	**nangoon berry,** arctic bramble, wineberry	North America from Alaska to Labrador & Newfoundland; also Minnesota

Sources: Brinkman (1974), Curtis (1959), Fernald (1950), Hickman (1993), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

of sheer abundance and site domination are found after major disturbances such as forest harvesting and fire and on abandoned agricultural land and along roadsides, where light, water, and nutrients are readily available. These stands originate from soil seedbanks, with subsequent clonal development (as in the case of red raspberry in north temperate and boreal forests) or from vegetative reproduction (as in salmonberry in the coastal forests of the Pacific Northwest) (Lautenschlager 1991; Ruth 1970; Tappeiner and others 1991; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994) (figures 1 and 2). Dense stands can prevent or greatly delay establishment of trees and other species (Tappeiner and others 1991; Lautenschlager 1990). Trailing raspberry in north temperate forests, cloudberry and nagoonberry in boreal forests and tundra, and five-leaf bramble (*R. pedatus* Sm.) in coastal forests of the Pacific Northwest and Alaska are perennials with a low or trailing growth form and are present in understory plant communities in mature and old growth forests (Coladonato M 1990a&b; Graber and Thompson 1978; Tappeiner and Alaback 1989; Mackinnon and others 1992; Maxwell 1990; Maxwell and others 1993; Meeker and others 1993; Meidinger and Pojar 1991; Piroznikov 1983; Tirmenstein 1990a–f; Viereck and Little 1972; Viereck and others 1992; Whitney 1978).

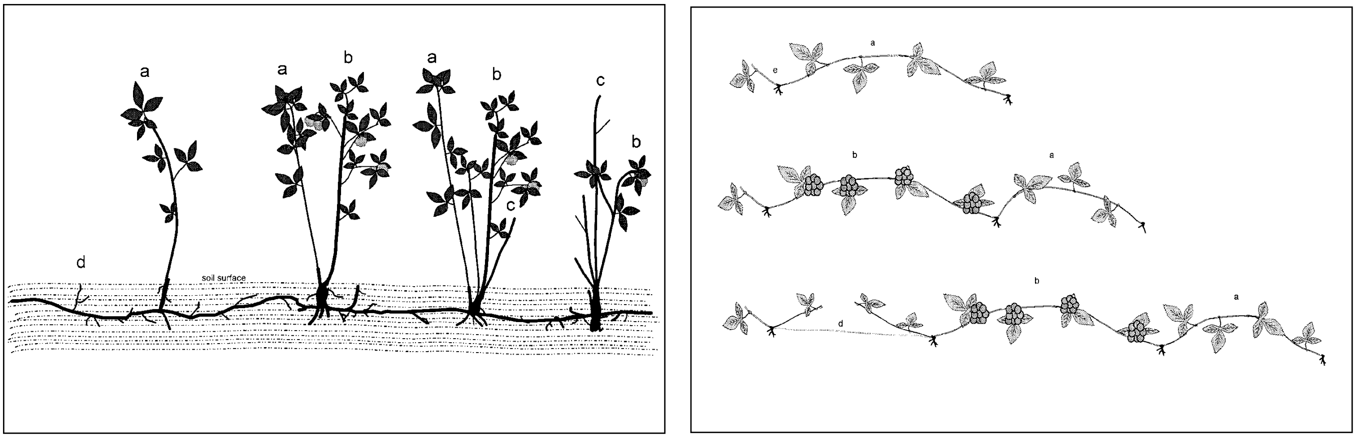
Rubus spp. collectively have one of the most versatile systems for reproduction, colonization, and species maintenance among woody plants. In addition to sexual reproduction, asexual reproduction (apomixis) is well-developed in most species. Asexual reproduction also includes all forms of vegetative reproduction and agamospory (formation of

Table 2—*Rubus,* blackberry, raspberry: height or length at maturity and fruit ripeness criteria

Species	Growth habit	Height or length at maturity (m)	Year first cultivated	Fruit ripeness criteria Preripe	Ripe
SUBGENUS: ***Eubatus***					
R. allegheniensis	Shrub	1.8	1905	Red, hard	Black-purple
R. canadensis	Shrub	2.8	1727	Red, hard	Black, soft
R. hispidus	Vine	1.8–2.5	—	Red, hard	Reddish purple to black
R. laciniatus	Vine	2.8–4.6	1770	Dull red	Black, sweet, shining
R. procerus	Vine	6.2–9.2	1890	Red, hard	Black, soft
R. ursinus	Vine	4.6–6.2	—	Red, hard	Black, shining, soft
SUBGENUS: ***Idaeobatus***					
R. idaeus	Shrub	2.2	—	Pink, hard	Red, sweet
R. occidentalis	Shrub	1.5–2.2	1696	Bright red, hard	Purple-black, soft
R. spectabilis	Shrub	2.8–4.6	1827	Pink, hard	Orange or red, soft
SUBGENUS: ***Chamaemorus***					
R. chamaemorus	Perennial forb, below-ground rhizome	0.1–0.2	—	Red, hard	Orange, soft
SUBGENUS: ***Anoplobatus***					
R. odoratus	Shrub	1.8	1635	Pink, hard	Red, soft
R. parviflorus	Shrub	0.5–2.5	—	Pink, hard	Red, soft

Sources: Brinkman (1974), Fernald (1950), Jennings (1988), MacKinnon and others (1992), Viereck and Little (1972).

Figure 1—*Rubus*, blackberry, raspberry: general structure of ramets in populations with different growth habits. Diagram (**left**) for species—in this case red raspberry, a biennial cane species—in which clone development occurs in the soil by development of root (for example, red raspberry) or rhizome (for example, salmonberry) systems. Diagram (**right**) for species in which clones expand by layering of above ground stems (for example, trailing raspberry). KEY: **a** = primocanes, **b** = florocanes, **c** = dead canes, **d** = part of stem or root system that is either dead or non-flowering. (Drawings are based on observations by Whitney (1982, 1986), Suzuki (1987, 1989, 1990), and the authors.)



seeds without sexual reproduction) (Grant 1981; Richards 1986). These various modes of reproduction affect the frequency and distribution of genotypes in natural populations; sexually reproducing species have more genotypes than those where apomixis is common (Nybom and Schaal 1990).

Although a detailed description of all aspects of vegetative reproduction is beyond our scope, a general knowledge of these characteristics is necessary to understand spatial and temporal variation in fruit and seed production. There are 3 basic types of clone development, each producing ramets with different life expectancies and flowering potential. These are layering, development from roots or rhizomes, and basal sprouting (figures 1 and 2). The longevity of ramets within a clone varies from 1 growing season to 15 years or more, depending on the species and site conditions (Jennings 1988; Rantala 1976; Ryynanen 1973; Suzuki 1987, 1989, 1990; Tappeiner and others 1991, 2001; Whitney 1978, 1982, 1986; Zasada and others 1992, 1994). Salmonberry has relatively long-lived ramets developing from rhizomes, whereas red raspberry ramets are biennial and produced from a spreading root system. Even in red raspberry, however, ramets may be produced by basal sprouting from one point on the root system, giving that physical position a life-span of more than 2 years (figure 1). Yet another pattern is that of cloudberry, an herbaceous, perennial species with a well-developed rhizome system from which leaves and flowers are produced annually (Jennings 1988; Rantala 1976; Rynnanen 1973). Clonal expansion in other species, for example trailing raspberry and Himalaya blackberry, occurs by layering at the tip or other nodes (figure 1) (Jennings 1988; Whitney 1978, 1986).

Although most species are deciduous, several are evergreen—for example, cutleaf blackberry and Himalayan blackberry, both exotic species that have become naturalized in the western United States. Stems of some species lack spines or bristles whereas others are very well-armed. Dense thickets of Himalayan blackberry and Allegheny blackberry can be very difficult and painful (!) to walk through. The density of spines for a given species can vary with site conditions (Zasada 1996) and the genes controlling spine production are known (Jennings 1988).

Humans have a mixed relationship with *Rubus* spp. On the one hand, they provide a highly edible and nutritious fruit in cultivation and in native plant communities. On the other hand, they can be competitors for growing space, often retarding or (in the extreme case) preventing the establishment of commercially valuable trees. In this case, significant measures are taken to reduce their density and biomass. An understanding of seed production, seed longevity, germination, and seedling establishment is necessary for benefitting from all of the values of these plants while minimizing their development on sites where their presence may prevent achieving management goals.

Geographic races. The genetics of *Rubus* is complex because of the presence of sexual and asexual reproduction. This appears to be particularly true in the *Eubatu*s subgenus, where hybrids with varying degrees of sterility are produced sexually. Sterility is to a significant degree dependent on ploidy levels and these range from 2 to 7x (x = 7). Once produced, these hybrids reproduce asexually by vegetative reproduction and agamospermy. The subgenus *Idaeobatus* is predominantly diploid and sexual reproduction is most common. Crossability among species within both subgenera has been studied (Brainerd and Peitersen 1920; Grant 1981; Jennings 1988; Peitersen 1921).

Flowering and fruiting. Most *Rubus* species are monoecious, but there are dioecious species—for example, cloudberry (Agren and others 1986) and other Arctic spp. (Jennings 1988). Flowering occurs during the spring or summer and rarely in the fall (table 3). Flowers normally have 5 sepals and petals. Size of the flowers varies with subgenus, and *Anoplobatus* flowers generally are the largest.

Pollination by insects is common, and pollinators have been identified for some species—for example, cloudberry (Hippa and Koponen (1976), salmonberry (Barber 1976), and red raspberry (Whitney 1978). *Rubus* flowers produce large quantities of nectar, thus attracting insects (Jennings 1988). In blackberries, self-pollination is often adequate to provide the stimulus necessary for asexual seed production, but a mixture of self-pollination and cross-pollination often occurs. Fertilization occurs about 1 day after pollination (Jennings 1988; Nybom 1985, 1986, 1988; Ourecky 1975).

Pollen can be collected and stored for use at a later time. Maintenance of viability during storage varies with temperature and humidity, and species (Otterbacher and others 1983; Ourecky 1975; Perry and Moore 1985). Perry and Moore (1985) concluded that pollen should be collected every few days to assure that pollen is fresh for crossing and that if pollen must be stored, then subfreezing temperatures (–5 to –40 °C) and low humidities provided the best conditions. Nybom (1985) described methods for assessing pollen viability in subgenus Rubus.

A raspberry or blackberry fruit is an aggregate of small, usually succulent drupelets (figure 3), that each contain a single hard-pitted pyrene or nutlet (figure 4). [The words “nutlet” and “seed” can be used interchangeably, but we

Table 3—*Rubus,* blackberry, raspberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
SUBGENUS: *Eubatus*				
R. allegheniensis	—	May–July	Aug–Sept	Aug–Sept
R. canadensis	—	June–July	July–Sept	July–Sept
R. laciniatus	NE US	June–Aug	July–Oct	Sept–Oct
R. hispidus	—	June–early Sept	Mid-Aug–Oct	Aug–Oct
R. procerus	Washington	June–Aug	Aug–Sept	—
R. ursinus	Pacific Coast	June–July	Aug–Sept	Oct–Nov
SUBGENUS: *Idaeobatus*				
R. idaeus	Rangewide	Late May–July	Late June–Oct	July–Oct
R. occidentalis	—	Apr–June	June–Aug	June–Aug
R. spectabilis	Alaska	May–June	June–Aug	June–Aug
	Oregon–Washington	Apr–May	May–July	June–July
SUBGENUS: *Chamaemorus*				
R. chamaemorus	Boreal North America	June–July	July–Aug	Aug–Sept
SUBGENUS: *Anoplobatus*				
R. odoratus	—	June–Sept	July–Sept	July–Sept
R. parviflorus	Pacific Northwest	May–June	June–July	July–Aug

Sources: Barber (1976), Brinkman (1974), Coladonato (1990a), Hippa and Koponen (1976), Viereck and Little (1972), Whitney (1978).

Table 4—*Rubus,* blackberry, raspberry: fruit weight and number of seeds/fruit

Species	Fresh fruit weight (g)	Seeds/fruit		Source
		Avg	Range	
R. spectabilis	—	62	28–128	W Oregon
		40	17–65	SE Alaska
R. parviflorus	—	190	127–246	W Oregon
R. idaeus	1.3 (0.8–2.4)	36	28–47	British Columbia & N Alberta
General (N = 8 cv)	—	63	27–103	Norway
Restricted pollination	—	13	—	Norway
Open-pollination	—	32	—	Norway
R. arcticus	0.37–1.09	25	10–35	Finland
R. chamaemorus				
Full light	—	11	7–13	Sweden
Shade	—	14	10–16	Sweden
Hand-pollination	—	11	—	Sweden
Open-pollination	—	8	—	Sweden
No defoliation	—	8	—	Sweden
50% defoliation	—	8	—	Sweden
General	2.5	18	—	Finland
General	—	10	3–18	Alaska
Rubus subgen. *Eubatus*	1.2–6.8	56	27–83	Arkansas

Sources: Ågren (1989), Moore and others (1974a), Nybom (1986), Rantala (1976), Redalen (1977), Ryynänen (1973), Staniforth and Sidhu (1984), Suzuki (1990), Van Adrichem (1972), Willson (1996), Whitney (1978), Zasada (1996).

have used seed.] Each drupelet is a complete fruit, a miniature version of a cherry or plum (which are drupe-type fruits). Each aggregate fruit is the product of 1 flower and the number of drupelets per aggregate varies with species, pollination success, and environmental conditions (figure 3 and table 4). Ripening occurs 30 to 36 days and 40 to 70 days after pollination in raspberries and blackberries, respectively. Drupelets within an aggregate fruit ripen uniformly, but there can be considerable variation among fruits. Three phases of development are recognized: rapid fruit growth following pollination, slow growth as the seed develops, and a final period of rapid growth before the fruit is fully mature (Jennings 1988). In natural populations, the interaction between microclimate and genetic variation in flowering and fruit ripening usually spreads the timing of aggregate maturation over a period of several weeks or more.

Figure 2—*Rubus*, blackberry, raspberry: red raspberry clone showing distribution of ramets (**circles**) as they were in a clone excavated on an upland site in central Alaska. This plant was about 5-years-old and originated from seed. Red raspberry clones develop by expansion of the root system. Salmonberry, thimbleberry, cloudberry, and other species may develop clones with similar ramet distribution, but clone expansion occurs by the growth of rhizomes. Ramet longevity in these latter species is also different.

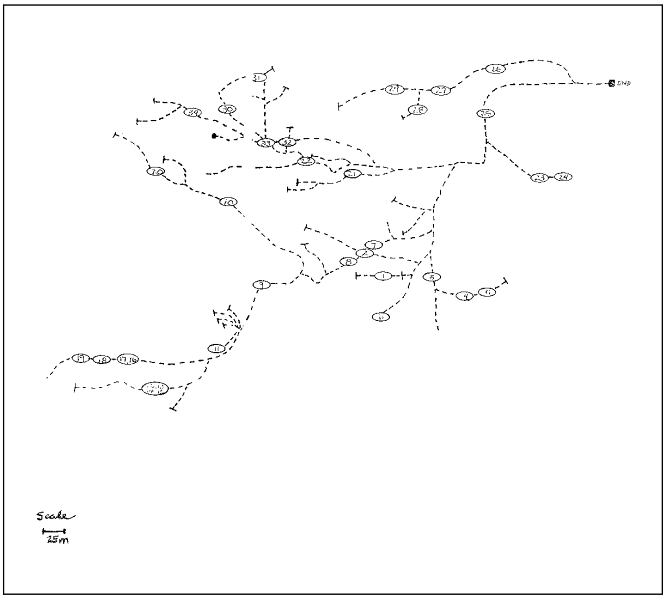
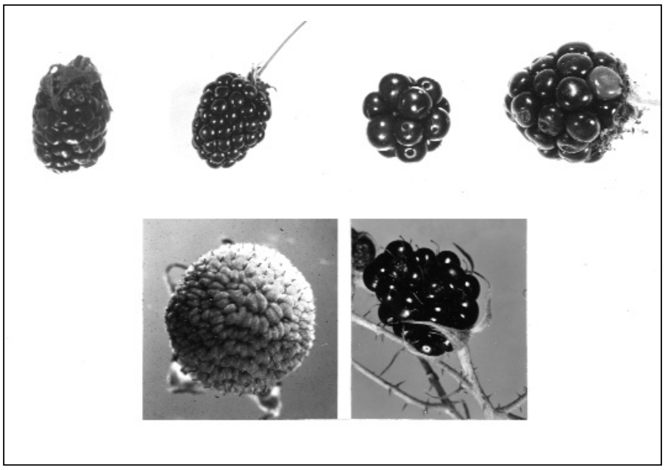


Figure 3—*Rubus*, blackberry, raspberry: fruits of *R. alleghensis*, Allegheny blackberry (**upper far left**); *R. canadensis*, smooth blackberry (**upper middle left**); *R. hispidus*, swamp dewberry (**upper middle right**); *R. procerus*, Himalayan blackberry (**upper far right**); *R. parviflorus*, thimbleberry (**lower left**); and *R. ursinus*, trailing blackberry (**lower right**).



The breeding system in *Rubus* is often described as versatile because seeds are formed sexually and asexually. The relative importance of these two types of seeds varies within and among subgenera and species and may differ within a plant depending on the pollen source. In the *Idaeobatus* group, seeds are normally formed sexually. In *Eubatus* species, seeds are produced sexually and asexually (Jennings 1975; Nybom 1985, 1986, 1988). In most cases, pollen is required to produce seed asexually, but the embryo is not produced by the fusion of male and female gametes (pseudogamy). Parthenogenesis (seed formation without pollination) occurs in some species. Seeds of both sexual and asexual origin may be present in the same fruit (Jennings 1975; Nybom 1985, 1986, 1988).

The abscission layer that develops as the fruit ripens differs in raspberries and blackberries. Fruits may drop from the plant or be removed by various animal species. The number of drupelets or entire aggregates removed at any one time depends on the size of the fruit and the size and eating habits of the animal (Snow and Snow 1988). Seeds are usually deposited with other materials in the feces. Large animals such as the grizzly bear (*Ursus arctos*), may deposit 50,000 to 100,000 salmonberry seeds in a single pile of feces. Seeds may be secondarily consumed or moved from the feces piles by small rodents and birds. Brunner and others (1976), Jordano (1984), Gervais (1996), and Traveset and Willson (1997, 1998) discuss other aspects related to selection and dispersal of *Rubus* seeds by animals. The amount of fruit removed has been found to vary from near 100 to 40% and will depend on habitat type and type of animal feeding on the fruits (Jordano 1982; Snow and Snow 1988). In British Columbia, forest silvicultural practices are being altered in coastal riparian areas to provide for adequate fruit production by salmonberry and other species that are important food sources for grizzly bear (McLennan and Johnson 1993).

Although fruit consumption is often viewed as a loss of seeds, in *Rubus* spp. consumption of seeds is important to the reproductive biology of the plant. Several examples are described below. Dispersal of seeds away from parent plants depends on animals. The distribution of seeds in space and time depends on the size and eating habits of the animal (for example, bears deposit large quantities of seeds in one place, whereas small birds deposit only a few seeds at a time), and the movement habits of the animal following feeding. Seeds that pass through the digestive tract of animals receive varying degrees of scarification (for example, salmonberry seeds in bear feces may have had the fleshy fruit wall completely removed or be little affected, as evidenced by the presence of complete fruit aggregates) and as a result have potentially different germination patterns. Deposition in feces of differing composition and chemistry affects the germination substrate, and physical and chemical environment available for seedling establishment. If animals are feeding simultaneously on fruits of different plants, fecal deposits may affect competitive and other interactions between *Rubus* spp. and other genera.

Good seedcrops occur nearly every year. Environmental factors affect the amount of flowering and fruit production. In northern Wisconsin, red raspberry crop failures may occur in clearcut areas as a result of severe frosts in mid- to late June, whereas in adjacent areas with 50 to 75% canopy cover, frost may have little effect (Zasada 1996). There are a host of fungi, bacteria, viruses, and insects that affect fruit production in domesticated cultivars and varieties (Jennings 1988; Mason and others 1981; Ourecky 1975).

Flowering occurs on perennial stems (salmonberry), biennial canes (red raspberry), and flower buds produced annually from rhizomes (cloudberry) (figures 1 and 2). Because of the importance of biennial caned species for fruit production, considerable information exists (Jennings 1988; Ourecky 1975; Whitney 1978; Zasada 1996). Briefly, the first-year vegetative canes in red raspberry are termed "primocanes." During the second growing season, they flower ("florocanes"), produce a fruit crop, and die. Within a natural stand of red raspberry, primocanes usually outnumber florocanes by a factor of 2 or more (Whitney 1978, 1982, 1986; Zasada 1996). Primocanes do produce flowers on occasion, and this trait has been developed into a fall-producing cultivar (Prive and others 1993a&b).

The rate of node production is about constant in primocanes. Node density, and thus density of potential flower buds, is determined by the rate of internode elongation. Flower bud initiation occurs at about the time that canes become dormant and may continue in the spring after a period of dormancy. Nodes can have primary, secondary, and tertiary flower buds; the secondary and tertiary buds develop if the primary bud is damaged or dies (Hudson 1959; Jennings 1988).

In florocanes, there is little or no height growth. Fruiting laterals develop from the nodes. The number and distribution of fruiting laterals is dependent on genotype, node position, and microclimate. Fruit production per lateral may vary from 10 to 100 in domestic cultivars of raspberry and blackberry (Jennings 1988).

Primocanes and florocanes may compete for resources, and fruiting may be reduced on individual florocanes. Similarly, in the absence of florocanes more primocanes are produced. Clones vary considerably in the effects of this interaction on fruiting (Crandall and others 1974; Waister and others 1977). Vegetative characteristics of salmonberry and red raspberry stems are affected by light and other resource availability in forest stands where they commonly grow (Lautenschlager 1990; Tappeiner and others 1991; Zasada 1996).

Collection of fruits. During the maturation process, fruits change from green to their characteristic color (table 2). Although all species have a characteristic fruit color when ripe, there can be variation among genotypes. For example, in salmonberry, there are 2 mature fruit color polymorphisms—red and orange. The orange form is generally more common in the southern part (that is, Oregon) of the range, and the red form in the northern part (southeastern Alaska) of the range, although clones with red and orange fruits intermingle in both areas (Gervais 1996). The red fruit form passes through an orange stage on the path to maturation (Gervais 1996; Traveset and Willson 1998), but at maturity there is a distinct and easily observed difference in color. The amount of variation in fruit color may also vary among sites and geographic areas. Thus, to use fruit color as an index of maturity, one needs to know the color variation that occurs in a species. Although fruits are usually collected when they are fully ripe, Ourecky (1975) suggested that fully developed green fruits contain well-developed seeds and could be picked in that condition. Another index of ripeness is the ease with which fruits can be picked as a result of the development of the abscission layer. Fruits in natural populations will be available for picking over a period of several weeks to a months because of the variation in maturation due to the effect of genotype and microclimate on flowering and fruit development. Because of the importance of fruits as animal food, it may be important to closely monitor an area in order to collect adequate quantities before animals take them (Snow and Snow 1988). For salmonberry, it has been shown that the red-fruited form may be preferred to the orange-fruited type in some cases and may vary by species of birds and mammals (Traveset and Willson 1998).

Rubus fruits are usually picked by hand, but machines have been developed to mechanically harvest commercial crops (Ourecky 1975). They can also be picked after they have dropped from the plant. The number of seeds per fruit varies considerably among species (table 4). Within a species, seeds per fruit may also vary by a factor of 2 or more depending on microclimate, pollination, and genetic variability. Seed weight also varies considerably among and within species (table 4). For example, in *R. ulmifolius*

Table 5—*Rubus*, blackberry, raspberry: seed yield data

		Seed wt/fruit wt		Seeds (x1,000)/weight			
	Place	**Seed wt/fruit wt**		**Range**		**Average**	
Species	**collected**	**g/kg**	**lb/100 lb**	**/kg**	**/lb**	**/kg**	**/lb**
SUBGENUS: *Eubatus*							
R. allegheniensis	—	40	4	370–724	168–329	574	262
R. canadensis	—	40	4	458–495	208–225	476	216
R. hispidus		—	—	282–513	128–233	408	185
R. laciniatus	Washington	7	0.7	—	—	301	137
R. procerus	—	—	—	—	—	323	147
R. ursinus	Washington	58	5.8	—	—	845	384
Rubus (general European)*	Sweden	—	—	359–869	163–395	480	219
SUBGENUS: *Idaeobatus*							
R. idaeus	Minnesota	30	3	667–845	303–384	722	328
	British Columbia/Alberta	46	4.6	469–794	213–397	632	288
R. occidentalis	Minnesota	30–80	3-8	629–845	286–384	735	334
R. spectabilis	Oregon 1	—	—	251–528	115–240	354	162
	Oregon 2	—	—	189–321	87–146	240	109
	Oregon 3	—	—	270–45	123–157	316	144
	Oregon 4	—	—	216–298	98–135	265	120
	Alaska	—	—	—	—	315	143
SUBGENUS: *Chamaemorus*							
R. chamaemorus	Sweden/Finland	59	(5.9)	—	—	122	56
	Alaska	—	—	80–101	37–45	90	40
SUBGENUS: *Anoplobatus*							
R. odoratus	Pennsylvania	—	—	—	—	1,085	493
R. parviflorus	Oregon	—	—	357–806	162–367	611	278
	Washington	—	—	719–1201	327–546	20	418
SUBGENUS: *Cyclatis*							
R. arcticus	Sweden/Finland	76	(7.6)	—	—	980	446

Sources: Brinkman (1974), Lautenschlager (1990), Nybom (1980), Rantala (1976), Zasada (1996).

* Seeds of 20 species in Sweden.

Schott., the individual seed weight with the highest frequency was 2 to 2.5 mg, whereas weights ranged from 1 to 5 mg (Jordano 1984).

Extraction and storage of seeds. Seeds may be extracted by macerating the fruits in water then floating off or screening out the pulp and empty seeds (Brinkman 1974). Because of the high strength of the endocarp (figure 5), maceration does not damage the seeds (Rose 1919). Small lots of fruit may be covered with water and macerated in a blender until the pulp and fiber are separated (Morrow and others 1954). Additional water is then added, the sound seeds allowed to settle, and the pulp and empty seeds decanted. Several changes of water will yield cleaner seeds. Seed yield data are presented in tables 4 and 5.

The cleaned seeds should be dried before storage. Clark and Moore (1993) reported that seeds from raspberry cultivars germinated well after storage for 26 years at 4 to 5 °C.

Rubus seeds can be present in the forest floor of many forest types in North America (Barber 1976; Graber and Thompson 1978; Granstrom 1982; Maxwell 1990; McGee 1988; Moore and Wein 1977; Peterson and Carson 1996; Piroznikov 1983; Quick 1956; Ruth 1970; Whitney 1978; Yokohama and Suzuki 1986; Zasada 1996) long after the species has disappeared from the site. The longevity of seeds in the forest floor is believed to be on the order of decades to a century or more, indicating that seeds can be stored for long periods of times under seasonally alternating temperature and moisture conditions.

Understanding longevity of seeds in the forest floor is complicated for at least 2 reasons. First, Graber and Thompson (1978) found that 6,000 to 7,000 viable *Rubus* seeds/ha (2,400 to 2,800/ac) were deposited annually in northern hardwood forests in New England, making it difficult to determine the age of the seed population. Second, few controlled experiments have been conducted to demonstrate seed longevity in the soil; Granstom (1987) reported that artificially buried seeds remain viable for at least 5 years.

Germination. Raspberry and blackberry seeds are described as having deep dormancy caused by one or more of the following: impermeable seedcoat (endocarp), mechan-

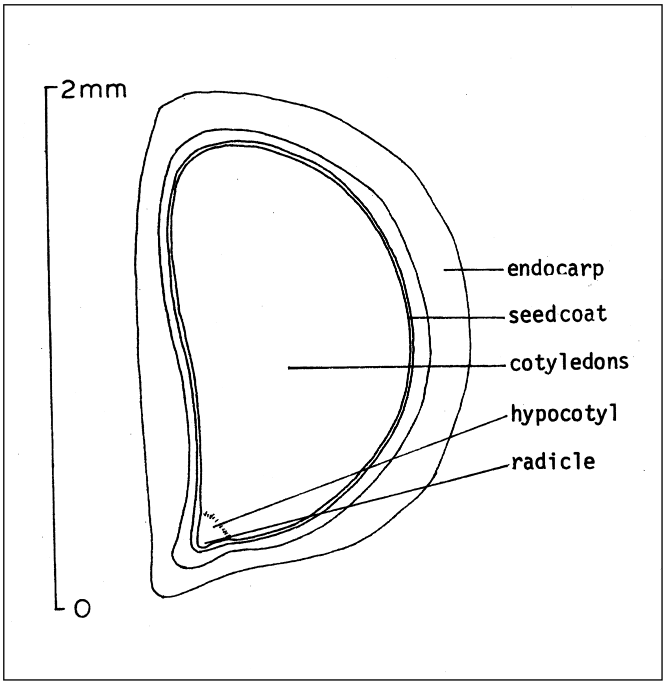
Figure 4—*Rubus*, blackberry, raspberry: nutlets (seeds) of *R. alleghensis*, Allegheny blackberry (**upper far left**); *R. canadensis*, smooth blackberry (**upper middle left**); *R. hispidus*, swamp dewberry (**upper middle right**); *R. lacinatus*, cutleaf blackberry (**upper far right**); *R. ursinus*, trailing blackberry (**lower far left**); *R. occidentalis*, blackcap raspberry (**lower middle left**); *R. odoratus*, fragrant thimbleberry (**lower center**); *R. procerus*, Himalayan blackberry (**lower middle right**); *R. spectabilis*, salmonberry (**lower far right)**.

ical resistance of the seedcoat to growth, chemical inhibitors in the seedcoat and endocarp and the presence of a dormant embryo (Jennings 1988; Nybom 1980; Ourecky 1975). Under natural conditions, dormancy is broken by a combination of factors, including exposure to freeze-thaw cycles, diurnal and annual changes in temperature, cycles of wetting and drying of the seedcoat, passage thru the digestive system of animals, and activity of fungi and insects on the seedcoat. A given cohort of seeds germinates over a period of 2 to 3 or more years under field conditions, with some seeds apparently lying dormant for decades. The germination pattern will vary by species, microclimate, and condition of seeds when dispersed, among other factors (Barnes 1985; Dale and Jarvis 1983; Krefting and Roe 1949; Maxwell 1990; Nybom 1980; Tappeiner and Zasada 1993). It is commonly believed that passage through the digestive tract of an animal speeds germination. However, the importance of this treatment appears to be dependent on the species and the type of animal passing the seeds (Barber 1976; Lautenschlager 1990).

There may be an interaction between the way in which seeds are handled and dried and the type of dormancy seeds exhibit. For example, Dale and Jarvis (1983) indicate that raspberry seeds that do not undergo a prolonged period of drying germinate better that those that are dried. Rantala (1976), however, indicates that some species may germinate better after prolonged drying. The point is that dormancy may be manageable to some degree for some species during the handling process. Depth of dormancy may also be affected by the temperature at which fruits develop (Dale and Jarvis 1983).

The list of treatments used to improve overall germination and rate of germination is comprehensive to say the least. These have included the following by themselves or in various combinations: chemical scarification with sulfuric acid or sodium hypochlorite (either used alone or both sequentially); mechanical scarification by removing part of the endocarp, seedcoat, and endosperm; hormone treatment (gibberellic acid); warm temperature incubation; immersion in boiling water; cold stratification; incubation in oxygenated water; treatment with nitrate; and recovery of seeds from feces of various animals (Barber 1976, 1978; Brinkman 1974; Campbell and others 1988; Dale and Jarvis 1983; Galletta and others 1989; Jennings 1988; Ke and others 1985; Lautenschlager 1990; Lundergan and Carlisi 1984; Maxwell 1990; Moore and others 1974a&b; Nesme 1985; Nybom 1980; Ourecky 1975; Rantala 1976; Rose 1919; Scott and Ink 1957; Traveset and Willson 1998; Warr and others 1979). In spite of the efforts to improve the uniformity of germination, results are highly variable within and among species and no standard method seems to be available for germination of species in the genus.

Figure 5—*Rubus canadensis*, smooth blackberry: longitudinal section of a seed.



Some form of sulfuric acid treatment followed by cold stratification is a common treatment prior to germination. Sulfuric acid significantly changes the structure and thickness of the endocarp and the weight of the seed (Lautenschlager 1990; Moore and others 1974b). Some important considerations for acid treatment mentioned in the above references are listed below:

- The seed surface should be dry, otherwise the reaction between water and acid will result in temperatures lethal to the embryo.
- Raspberry seeds should be treated for no more than 15 to 20 minutes, whereas blackberry seeds require up to several hours. Seeds should be stirred frequently during treatment.
- It may be necessary to immerse the container with seeds and acid in an ice bath to keep the temperature at safe levels for the embryo.
- Seeds should be thoroughly washed following treatment to remove acid. Although some seeds will germinate with acid treatment alone (which essentially removes the seedcoat as a barrier) (Nesme 1985), 60 to 120 days of cold stratification seems to improve germination for some species.

Various concentrations of sodium or calcium hypochlorite can be used as an alternative to sulfuric acid (Campbell and others 1988; Galletta and others 1989). Sometimes calcium hydroxide is used in combination with the hypochlorite. Hypochlorites also significantly alter the endocarp but

Table 6—*Rubus,* blackberry, raspberry: germination results

Species or variety & source	Germination temp (°C)	Total germination (%)	Time to 50% germination
*R. idaeus**	10	69 (18–94)	28 days
	20	93 (84–96)	6 days
	30	60 (40–88)	33 days
R. idaeus† 'Glen Cova'			
No stratification	—	48	—
Stratification	—	53	—
R. idaeus‡			
Bear feces			
Acid scarification	21	6	—
No scarification	21	0	—
Coyote feces			
Acid scarification	21	10	—
No scarification	21	0	—
Fresh seed			
Acid scarification	21	8	—
No scar.ification	21	0	—
R. spectabilis§			
Fresh seeds			
Acid scarification	21–28	0	—
Scarification & 2-mon stratification	21–28	0	—
Scarification & 4-mon stratification	21–28	62	—
Scarification & 6-mon stratification	21–28	81	—
Bird feces			
No stratification	21–28	0	—
4-mon stratification	21–28	25	—
6-mon stratification	21–28	73	—
Coyote feces			
6-mon stratification	21–28	6	—
*R. chamemorus*II			
3–5-mon stratification	Variable	<1	—
6–9-mon stratification	Variable	3–10	—
10–13-mon stratification	Variable	30–31	—

Sources: Barber (1996), Dale and Jarvis (1983), Lautenschlager (1990), Lundergan and Carlisr (1984); Moore and others (1974); Nesme (1985), Rantala (1976).

* Seeds were treated as follows: surface sterilized in 1% sodium hypochlorite (NaClO) for 10 minutes, nicked to expose radicle; soaked for 3 min in 1% NaClO, and incubated in the dark for 1 year.

† Seeds were extracted and air-dried, treated for 20 minutes with sulfuric acid and 7 days with calcium hypochlorite; stratified at 5 °C or unstratified. Fruits were collected 43 days after anthesis. Seeds were from fruits collected earlier or later differed in germination response.

‡ Seeds were from natural populations in Maine; they were stratified for 2 to 6 months after acid treatment; tests were conducted for 30 days.

§ Fresh seeds from Washington state populations; stratified at 2 to 5 °C.

II Seeds stratified at 1 °C and germinated monthly in a mist propagation chamber.

do not carbonize it as does sulfuric acid. Duration of the treatment is several days as opposed to minutes or several hours for sulfuric acid. Solutions of 12 to 15% appeared to work best for raspberry but were not as effective with blackberries (Galletta and others 1989). Seeds should be thoroughly washed after treatment.

Plant breeders often excise embryos or "nick" the endocarp of individual seeds to improve germination when seed supply is limited or when seeds from particularly valuable controlled crosses are being grown (Ke and others 1985; Nesme 1985; Warr and others 1979). This is generally not possible for large seedlots.

The effectiveness of the cold stratification treatment depends on the stratification temperature and the length of stratification (Rantala 1976). The optimum temperature may differ among species. Cloudberry, for example, seems to germinate better following stratification at 1 °C than at 4 °C. Rantala (1976) and Barber (1976) have demonstrated the value of stratifying seeds for 6 months or more for cloudberry and salmonberry, respectively.

Seed quality can be can be estimated from cutting tests and x-radiography (Nesme 1985). Seeds that sink when placed in water contained what appeared to be viable embryos, and a general separation of high from low-quality seeds is possible in this way (Lautenschlager 1990; Nybom 1980).

Germination following the above described treatments that attempt to alter the condition of the seedcoat and eliminate inhibitors or other conditions by cold stratification is highly variable among species and within species. In table 6 are listed a few examples of the variation in germination that may be encountered in seeds collected from natural populations and from varieties produced for fruit production. Generally, treatments that mechanically remove the endocarp improve germination above the values in table 6. Rate of germination is generally slow; in tests conducted out-of-doors and allowed to run for a year or more, germination will commonly occur over at least 1 or 2 growing seasons for many species (Barnes 1985; Nybom 1980; Tappeiner and Zasada 1993; Traveset and Willson 1997, 1998). Graber and Thompson (1978) concluded that seeds are most likely to germinate after being in the soil at least 5 years. It seems safe to conclude that many of the tests that are conducted do not stratify seeds long enough to remove the impediment to germination. Brinkman (1974) provides general germination information for several other species.

The examples shown in table 6 were generally conducted in a constant temperature environment. For some species, diurnally fluctuating temperatures result in better germination than constant temperatures (Campbell and others 1988).

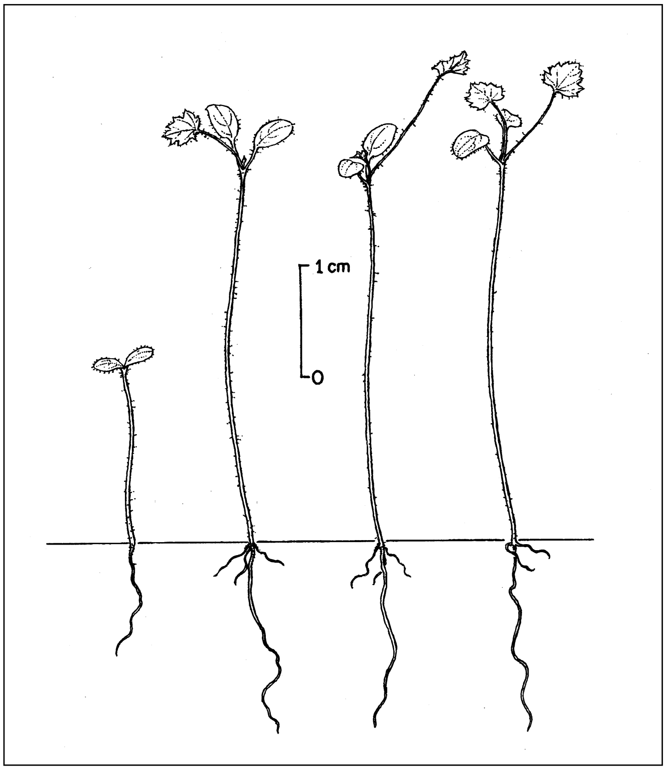
Light appears to improve germination in many species (Nybom 1980; Ourecky 1975). However, some species (for example, red raspberry, cloudberry, and salmonberry) do not require light to germinate (Warr and others 1979; Lautenschlager 1990).

Germination is epigeal (figure 6). Cotyledons are normally 2, but Nybom (1980) observed that seedlings with more than 2 cotyledons were fairly common and that treatments increasing germination increased cotyledon number. Polyembryony has been reported in cloudberry (Rantala 1976).

Nursery practice. The best germination usually follows sowing of scarified seeds in the late summer or early fall (Wroblowna 1949), although spring-sowing scarified and stratified seeds is also recommended (Heit 1967). Seeds should be sown in drills and covered with 3 to 5 mm ($^1/_8$ to $^3/_8$ in) of soil (Brinkman 1974). Mulching over winter reduces drying and soil-freezing (Hill and Beattie 1956).

Barnes (1985) recommends the following schedule for production of *R. deliciosus* Torr. from seed: gather seeds in late summer, clean and store them at near freezing; sow from October–December in unfertilized sand beds and cover with sand; wet down and firm soil over seeds; once

Figure 6—*Rubus occidentalis*, blackcap raspberry: seedling development at 1, 13, 22, and 36 days after germination.



seeds have germinated and reached a height of 5 to 7 cm (2 to 3 in) transplant to deep 15 cm (6 in) pots to promote both lateral and vertical root development. Fall-sowing produces better results than spring-sowing of stratified seeds. Seeds germinate over several growing seasons and the beds are usually not resown for at least 2 seasons in order to get better return of seedlings from sown seeds.

Ourecky (1975) found that full-sized green fruits can be collected cleaned, treated, and sown. Moist vermiculite and finely shredded sphagnum are both good planting media. Seeds should not be covered with more than 2 to 8 mm ($^1/_{10}$ to $^3/_{10}$ in) of the medium. As soon as the second true leaf appears (figure 6), seedlings can be transplanted to individual containers.

Vegetative propagation—by tip-layering, rooting suckers, and crown division and by taking leaf-bud and stem cuttings—is used to increase availability of desirable varieties (Ourecky 1975). Salmonberry can be established in coastal Oregon under field conditions with little post-planting care from crowns or rhizome cuttings if planted in the winter during the wet season (Maxwell 1990).

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