

Arctostaphylos Adans.

manzanita

Susan E. Meyer

Dr. Meyer is a research ecologist at the USDA Forest Service's Rocky Mountain Station, Shrub Sciences Laboratory, Provo, Utah.

Growth habit, occurrence, and uses. The shrub genus *Arctostaphylos*, or manzanita, comprises about 50 species, 90% of which are endemic to California and adjacent areas (Munz and Keck 1959). Three species—greenleaf manzanita, Mexican manzanita, and rosybract manzanita—are widely distributed in the southwestern United States and Mexico. One species—bearberry or kinnickinnick—is circumboreal in distribution (table 1). The manzanita habit varies from mat-forming (bearberry) to nearly arborescent (bigberry manzanita). About a quarter of the species have subterranean burls that generate new sprouts both after fire and throughout the long life of the plant (Keeley 1992; Wells 1969). The leaves of manzanitas are leathery, entire, and evergreen. They are major components of chaparral and are also common understory species in montane coniferous forest types, especially ponderosa (*Pinus ponderosa* Dougl. ex Laws.) and Jeffrey (*P. jeffreyi* Grev. & Balf.) pines. They are most abundant in the fire-prone vegetation of regions with dry summers.

The manzanitas are moderately important as winter browse plants for wild ungulates but are less important for domestic livestock (Berg 1974). They are used principally after fire, when new shoots or seedlings are produced in abundance. The fruits are used by bears (*Ursus* spp.), grouse (*Dendragapus* spp), and coyotes (*Canis latrans*) (Belcher 1985; Kauffmann and Martin 1991) and the seeds are taken by various rodents (Keeley and Hays 1976). The sprouting species are particularly important for watershed protection after fire, and many species could be used in revegetation for erosion control. Manzanitas also have great potential for use as ornamentals. Their smooth red bark; interesting, twisted growth forms; and bright evergreen leaves make them attractive year-round. Bearberry has found wide acceptance as a versatile groundcover (Dirr 1983) and has also been used medicinally (Belcher 1985).

Flowering and fruiting. Small urn-shaped white to pink perfect flowers appear on the plants from early winter through spring. The bud primordia are formed the previous year, and flowering and fruiting intensity is positively correlated with the previous year's precipitation (Keeley 1977). The flowers are pollinated by insects, principally bees and flies (Fulton and Carpenter 1979). Obligately seeding species (that is, those unable to sprout after fire) may have a higher investment in pollinator attraction than sprouting species, as evidenced as higher flower density and nectar production (Fulton and Carpenter 1979). They may also be more likely to be self-fertile and to have higher seed-set overall as measured by the incidence of inviable or unfilled seeds (Keeley and Zedler 1978). Many of the sprouting species are tetraploids, and Kelly and Parker (1991) report that lower

seed set may be associated with polyploidy rather than the sprouting habit per se.

Fruits ripen about 2 months after full-flowering, generally from June to September, depending on elevation. The fruits are drupe-like, with a hard, bony endocarp enclosing multiple seeds, a mealy mesocarp, and a thin exocarp (figure 1). Each seed is borne in a nutlet-like section. Ripe fruits may persist on the plant for several months but eventually fall. They may be dispersed by birds or mammals, especially coyotes (Kauffman and Martin 1991). The nutlets themselves may be dispersed by scatter-hoarding rodents, but rodents most often consume the seeds *in situ* and thus act solely as seed predators (Keeley 1977).

The nutlets may break apart at maturity or remain variously fused. In some species (for example, bigberry manzanita) the nutlets are completely coalesced, whereas in most species, including Eastwood and greenleaf manzanitas, the stone breaks irregularly into 1- to several-seeded-segments. The endocarp wall surrounding each seed is usually thick, hard, resinous, and impervious (figure 2). The wall has a channel (periole) at the basal or micropylar end. This channel is plugged with tissue that is not as hard as the endocarp itself. When the seed germinates, the radicle and hypocotyl are forced out through this periole (Berg 1974). The endocarp wall is thought to have a protective function, especially with regard to heat damage during fire. Seeds surrounded by very thick endocarps or contained within fused nutlets are apparently more likely to survive fire than those borne singly or with thinner endocarps (Keeley 1977). The testa itself is thin and membranous, and the well-developed straight or curved embryo is embedded in abundant endosperm (Berg 1974).

Seed collection, cleaning and storage. Good seed crops are produced on average every 2 to 3 years, usually the year following a year of high precipitation (Keeley 1977). The fruits range from pink or red to black when ripe, depending on species. They may be hand-stripped or picked up off the ground. Seed fill is often low, and considerable insect damage may be evident (Keeley and Hays 1976). Fill may be checked in the field by cutting the fruits transversely, preferably before the endocarp hardens (Berg 1974). Kelly and Parker (1991) reported a mean set (percentage of ovules forming seeds) of 62% for 14 California species, with a range from 50 to 80%.

To clean manzanita seeds, the fruits should be soaked in water, then macerated by hand or in a Dybvig machine to separate the pulp from the stones. The pulp may be removed by flotation, or the material may be dried, after which nutlets may be separated from the dried pulp using screens or a fanning mill (Berg 1974). Seedlots may be cleaned to high purity (Belcher 1985). Representative seed unit weights are given in table 2. Seed unit weights are highly variable even within a seedlot because a seed unit may be single or multiple-seeded, depending on the degree of coalescence of the nutlets.

Manzanita seeds form persistent seed banks and are apparently long-lived under field conditions (Kelly and Parker 1990). There is little information on longevity in warehouse storage, but it is probable that seedlots would maintain viability over periods of 10 years or more.

Germination and seed testing. In natural stands, new seedlings (figure 3) of most species of manzanita grow only after fire, and the seeds of these species are considered to be refractory, that is, germinating only in response to fire-related environmental cues (Keeley 1991, 1995). But unlike the refractory seeds of most chaparral shrubs, manzanita seeds apparently do not become germinable through heat shock (Kauffman and Martin 1991; Keeley 1987a). There is evidence that charate leached from incompletely burned wood can trigger manzanita seed germination, but the maximum

percentages attained using recently collected seeds were not high (13% for Eastwood manzanita and 19% for greenleaf manzanita (Keeley 1987a, 1991). It is probable that, under field conditions, the seeds change in some way following dispersal, perhaps through dry-afterripening at the embryo level, that renders them more responsive to the charate stimulus. Parker and Kelly (1989) report that hoary manzanita seeds retrieved from the soil seed bank germinated readily in response to charate, whereas hand-harvested seeds less than 1 year old did not. In spite of the massive endocarp, manzanita nutlets are permeable to water, and the enclosed seeds are capable of imbibition without any pretreatment, at least in greenleaf manzanita (Meyer 1997). This explains how charate rather than heat shock could trigger germination. Presumably the charate stimulus enters the seed through the periole.

Even though manzanitas form persistent seed banks, there is evidence that these seed banks turn over fairly quickly, as there was no net gain in size of the seed bank in the absence of fire over 10 years for 2 chaparral species (bigberry and Eastwood manzanitas), even in the face of massive inputs (Keeley 1987b). Most of the seed loss appears to be due to rodent predation rather than germination or loss of viability (Keeley and Hays 1976). This suggests that the seeds available for seedling recruitment after fire probably belong mostly to recently produced cohorts.

Even though manzanita nutlets are water-permeable, most reports on germination describe the seeds as hard-seeded, and the traditional pretreatment is sulfuric acid scarification for 3 to 15 hours (Belcher 1985; Berg 1974; Carlson and Sharp 1975; Emery 1988). Because the periole is much weaker than the endocarp wall, acid can enter there and damage the embryo long before the endocarp wall is stripped away, so care must be taken to remove the seeds before this damage occurs (Belcher 1985; Berg 1974). Coalesced nutlets generally require more time in acid than solitary nutlets, perhaps because the perioles, which are on the inner face of each nutlet, are better-protected when the nutlets are coalesced. Chaparral species such as bigberry and Eastwood manzanitas may be rendered immediately germinable by acid scarification, although reported percentages are low—3 to 8% (Berg 1974). Populations of greenleaf manzanita required both acid scarification (2 to 4 hours) and subsequent chilling for 60 days (Berg 1974) and 90 days (Carlson and Sharp 1975). Final germination percentages were 20 to 50%. Bearberry has been reported to respond to warm plus cold stratification following a 3- to 6-hour acid treatment—60 to 120 days at 25 °C, followed by 60 to 90 days at 5 °C (Berg 1974). Final germination percentages ranged from 30 to 60%. Belcher (1985) reported that warm plus cold stratification of bearberry resulted in 40 to 60% germination without acid scarification, but that acid scarification for 3 hours could be substituted for warm stratification. In bearberry, even excised embryos were dormant prior to chilling (Giersbach 1937).

Emery (1988) reported that a fire treatment (burning 3 to 4 inches of pine straw or excelsior over the planted seeds) in fall resulted in some emergence the following spring for many species of manzanitas, but the mechanism of dormancy loss under these conditions was not further explored. Charate could have been the stimulus responsible for this effect. It would be worth experimenting with charate as a germination stimulant in a nursery propagation setting.

Formal seed quality evaluation in manzanita is rendered difficult by the lack of reliable germination tests and by the thick endocarp. Tetrazolium staining requires excision of the seed from the endocarp by twisting it open along the suture or by cutting the nutlet off-center longitudinally, procedures difficult to carry out without damage (Belcher 1985). A seed unit may contain multiple seeds, only 1 of which has to be viable for the seed unit to be considered viable. For seedlots that

have not been incorrectly handled (for example, stored at high moisture content) or stored for long periods, a cut test to determine fill is probably the best way to get a quick idea of total viability.

Field seeding and nursery practice. It will probably continue to be very difficult to obtain manzanita from direct seeding until there is a much better understanding of factors controlling release from dormancy. The absence of manzanita seedlings in unburned chaparral (Keeley 1992) coupled with the regular appearance of thousands of manzanita seedlings per hectare following fire, as reported by Keeley (1977), strongly suggests that a successful seeding prescription would include a seed pretreatment simulating fire-related germination cues. The sulfuric acid-stratification treatments described above and the fire treatment of Emery (1988) are currently the only published procedures for nursery seed propagation. The manzanitas are much more easily propagated from cuttings than from seed, and in practice most nursery propagation is probably accomplished in this way (Berg 1974; Emery 1988).

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Figure 1 *Arctostaphylos*, manzanita: fruits (drupes) and seeds (nutlets or stones), all $\times 3$. *A. glauca*, bigberry manzanita: bottom (left) and top (right) views of a fruit. *A. glandulosa*, Eastwood manzanita: fruit and coalesced nutlets. *A. patula*, greenleaf manzanita: fruit (left) and partially coalesced nutlets plus 2 separated nutlets (right).

Figure 2 *Arctostaphylos uva-ursi*, bearberry: longitudinal section through a nutlet, $\times 12$.

Figure 3 *Arctostaphylos patula*, greenleaf manzanita: seedling at 1 month, actual size.

Table 1 *Arctostaphylos*, manzanita: habitat requirements and geographic distribution

					Scientific name Common name Habitat Distribution
<i>A. canescens</i> Eastw.	hoary manzanita	Shrubby, without burl	ponderosa pine forest, chaparral	N California to Oregon	
<i>A. glandulosa</i> Eastw.	Eastwood manzanita	Shrubby, with burl	ponderosa pine forest, chaparral	California to Oregon	
<i>A. glauca</i> Lindl.	bigberry manzanita	Shrubby or treelike, without burl	Chaparral, joshua tree woodland	S California to Baja California	
<i>A. patula</i> Greene	greenleaf manzanita	Shrubby, with burl	Ponderosa pine forest	California to Oregon, Arizona, & Colorado	
<i>A. pungens</i> Kunth	Mexican manzanita, pointleaf manzanita	Shrubby, without burl	Ponderosa pine forest, chaparral, pinyon-juniper woodland	S California, E to Utah & Texas & S into Mexico	
<i>A. pringlei</i> Parry	rosybract manzanita, Pringle manzanita	Shrubby, without burl desert shrubland	Ponderosa pine forest, chaparral, mixed warm	S California, S to Baja California & E to Arizona & SW Utah	
<i>A. uva-ursi</i> (L.) Spreng.	bearberry, kinnickinnick	Mat forming, without burl	Coniferous forest mostly at high elevation	Circumboreal, S to California, New Mexico, Illinois, & Georgia	

Source: Munz and Keck (1959).

Table 2C *Arctostaphylos*, manzanita: seed weights and filled seed percentages

Species	Seed unit	No. of seeds/weight		Filled seed (%)	Sample
		/kg	/lb		
<i>A. glandulosa</i>	1B2 seeded	66,150B97,020	30,000B44,000	C	2
<i>A. glandulosa</i>	1B3 seeded	55,125	25,000	58	2
<i>A. glauca</i>	entire stone	990B1,760	450-800	83	5
<i>A. patula</i>	variable	36,690B55,125	18,000B25,000	C	1+
<i>A. patula</i>	1-seeded	44,100	20,000	85	1
<i>A. uva-ursi</i>	1-seeded	59,535B90,405	27,000B41,000	C	3+

Sources: Belcher (1985), Berg (1974), Keeley (1977, 1991), Keeley and Hayes (1976) Meyer (unpublished data).