

Asteraceae—Aster family

Artemisia L.

sagebrush

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Growth habit, occurrence, and use. Sagebrush—*Artemisia* L.—species are probably the most common shrubs in western North America. Big sagebrush alone occupies an estimated 60 million ha as a landscape dominant or codominant in the semiarid interior, and related species of the subgenus *Tridentatae* are estimated to occupy an additional 50 million ha (Beetle 1960; McArthur and Stevens in press). Sagebrush-dominated vegetation occurs mostly under semiarid climatic regimes characterized by cold winters and predominantly winter precipitation. The genus is circum-boreal in distribution and consists of about 400 species of mostly evergreen shrubs, subshrubs, and herbaceous perennials.

The 20 or so shrubby sagebrush species in the United States differ widely in their growth form, ecology, distribution, and abundance (table 1). Big, black, silver, and low sagebrushes are widely distributed, polymorphic species of relatively broad ecological amplitude, whereas most of the remaining species are either more geographically restricted or more specialized in their habitat requirements. The subshrub fringed sagebrush, common and widespread in both the Old and New Worlds, may be the most widely distributed sagebrush taxon. Sand sagebrush is an important species on sandy soils on the Great Plains and in the Southwest, whereas the summer-deciduous subshrub bud-sage is the principal sagebrush species of salt desert shrub vegetation in the Great Basin.

Because of their status as regional dominants, sagebrush species—especially those of the subgenus *Tridentatae*—have been the object of a great deal of study (McArthur and Welch 1986). Many have long been regarded as undesirable plants by the ranching industry because of their perceived low palatability to livestock and propensity for increase under conditions of abusive grazing. However, they provide a principal source of browse on winter ranges for both wild and domestic ungulates, and undoubtedly are central to the habitat requirements of many other wildlife species.

Most sagebrush species rely on seeds for regeneration and have neither the ability to resprout following burning—with notable exceptions (McArthur and others 2004)—nor a long-lived soil seedbank (Young and Evans 1975, 1989; Meyer 1990). Invasion by exotic annual grasses and the associated increase in fire frequency has resulted in loss of big sagebrush over vast acreages of its former area of dominance (Billings 1990; D'Antonio and Vitousek 1992). This loss has led to a realization of the importance of the shrub overstory for maintaining the integrity of the ecosystem and also to a renewed interest in seed propagation of sagebrush species (Meyer 1994). Sagebrush has been seeded as part of big-game winter-range rehabilitation and mined-land reclamation efforts for over 30 years, so there is a considerable fount of knowledge to draw upon (Plummer and others 1968).

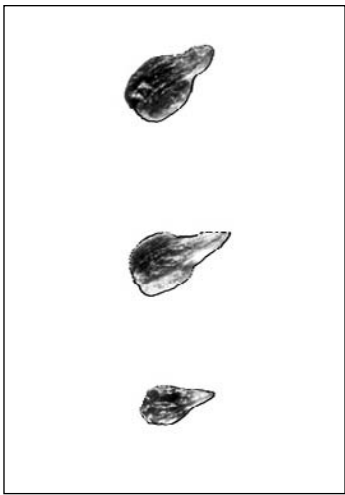
Subspecies and ecotypes. The more complex sagebrush species are made up of series of subspecies that are morphologically and ecologically distinct. In addition, many sagebrush taxa have been shown through common garden studies to be made up of numerous ecotypes that result from adaptation to local conditions through the process of natural selection (McArthur and others 1979). Such site-specific adaptation may be reflected in traits such as frost or drought hardiness, growth rate, competitive ability, flowering time, and seed germination regulation (McArthur and Welch 1982; Meyer and Monsen 1990). This means that the use of seed from locally adapted or at least habitat-matched populations is important to successful long-term restoration of these species.

An alternative to using adaptedness as the principal criterion for ecotype selection has been to identify native germplasms with desirable traits such as high winter-forage-quality for wild ungulates (for example, Welch and others 1986). Their use is recommended in artificial seedings with specific management objectives on sites that fall within their range of adaptation.

Table 1— <i>Artemisia</i> , sagebrush: distribution and ecology of principal shrubby species in the United States			
Scientific name	Common names(s)	Distribution	Habitat
SUBGENUS <i>TRIDENTATAE</i>			
<i>A. arbuscula</i> Nutt.	low sagebrush	Widely distributed, mostly intermountain	Shallow, rocky soils in mtns
<i>A. bigelovii</i> Gray	Bigelow sagebrush, rimrock sagebrush	SW deserts	Shallow rocky soils at middle to low elevations bottoms or
<i>A. cana</i> Pursh	silver sagebrush	NW Great Plains, N intermountain region & N Sierras	Deep sandy soils in valley snow catchment basins in mtns
<i>A. nova</i> A. Nels.	black sagebrush	Widely distributed, mostly intermountain	Shallow soils over bedrock at middle to low elevations region
<i>A. pygmaea</i> Gray	pygmy sagebrush	Utah & adjacent parts of Nevada & Colorado	Fine-textured calcareous soils at low elevations
<i>A. rigida</i> (Nutt.) Gray	stiff sagebrush, scabland sagebrush	Columbia Plateau, E Washington & Oregon	Shallow rocky soils over basalt at low elevations
<i>A. tridentata</i> Nutt.	big sagebrush	Widely distributed, W North America	Wide ecological amplitude
<i>A.t. ssp. tridentata</i> Nutt.	basin big sagebrush	See species	Mostly on deep well-drained soils of valley bottoms
<i>A.t. ssp. vaseyana</i> (Rydb.) Beetle	mountain big sagebrush, Vasey sagebrush	See species	Mostly on coarse soils at middle to high elevations benchlands
<i>A.t. ssp. wyomingensis</i> Beetle & Young	Wyoming big sagebrush	See species	On coarse to fine soils of at middle to low elevation
<i>A. tripartita</i> Rydb.	threetip sagebrush	Columbia Plateau E into Wyoming	Deep to shallow mostly volcanic soils at low elevations
OTHER SUBGENERA			
<i>A. filifolia</i> Torr.	sand sagebrush, old man sagebrush	W Great Plains & SW deserts	Sandy soils at low to middle elevations
<i>A. frigida</i> Willd.	fringed sagebrush	W North America to central Asia	Very wide ecological amplitude
<i>A. spinescens</i> D.C. Eat. <i>Picrothamnus desertorum</i> Nutt.	budsage	Widely distributed, mostly N intermountain region	Semiarid bottoms, benches, & foothills, salt desert shrublands

Flowering and fruiting. Most North American sagebrush species flower in late summer or autumn and ripen fruit from September through December. Seeds of high-elevation populations generally ripen earlier than those of low-elevation populations. Budsage, which flowers in March or April and sets seed in May or June before entering summer dormancy, is a major exception. The tiny yellowish or brownish flowers are wind-pollinated and are borne in groups of about 2 to 70 (depending on species) in small heads enclosed in overlapping bracts with thin, dry margins. The numerous heads are arranged in spikelike or open panicles that occur terminally on the branches of current-season growth. Each fertile floret within a head may develop into a small, 1-seeded fruit (achene) that lacks any special appendages for dispersal (figure 1). The pericarp of the achene is papery and membranous, whereas the seedcoat of the enclosed seed is firmer and somewhat shiny. The endosperm is reduced to a membrane fused to the inner wall of the seedcoat, whereas the embryo is well-developed and fills the interior of the seed. Mucilaginous nerves on

Figure 1—*Artemisia*, sagebrush: achenes (cleaned seeds) of *A. arbuscula*, low sagebrush (**top**); *A. nova*, black sagebrush (**middle**); and *A. tridentata*, big sagebrush (**bottom**).



the exterior of the pericarp may aid in adhesion to the soil surface during radicle penetration (Walton and others 1986). The hypocotyl hairs that develop as a first manifestation of germination have been shown to have a similar function (Young and Martens 1991).

The fruits fall or are shaken from the plant by wind within a few weeks of maturation. The potential yearly seed production of a single plant of big sagebrush is prodigious, on the order of hundreds of thousands of seeds (Welch and others 1990). However, many factors operate to restrict seed production in wildland stands, including excessive browsing (Fairchild 1991; Wagstaff and Welch 1991), intraspecific competition (Fairchild 1991; Young and others 1989), insect and disease attack (Welch and Nelson 1995), and cycles of dry years (Young and others 1989). Sagebrush in field cultivation for seed production yields harvestable crops within 2 years of establishment and generally produces high yields yearly (Welch and others 1990). Wildland stands vary in the consistency and quality of their seedcrops, depending on the factors listed above and also on the taxon under consideration and on site quality factors. An alternative to field cultivation for needed ecotypes that produce minimal numbers of seeds in the wild is management of wildland stands through thinning or protection from browsing to maximize seed production.

Seed collection, cleaning, and storage. Sagebrush seeds (actually, the 1-seeded achenes) are collected by beating or stripping them into shoulder hoppers, baskets, or bags. They are much more easily harvested by beating when dry than wet. Usually there is considerable among-bush variation in ripening date within a population. Harvesting too late may result in a high proportion of half-filled and aborted fruits.

Purity on a dry-weight basis before cleaning is often 10% or less. Passage through a barley de-bearder serves to break up the inflorescences to release the seeds; hammer-milling is less desirable, as it tends to make the material ball-up and may damage the seeds (McArthur and others 2004). Screening and fanning can then be used to remove sticks and other debris, resulting in lot purities of 50% or more. This cleaning procedure may strip many of the seeds of their membranous pericarps, but this has no effect on viability or storage life, although it may reduce seed dormancy or light requirement somewhat (Meyer and others 1990; Welch 1995). Sagebrush seeds are not easily damaged in cleaning equipment because of their small size (Welch 1995). Advantages to cleaning to relatively high purities include improved accuracy in quality evaluation; reduced shipping, handling, and storage costs; better regulation of

moisture content during storage; and better metered flow through seeding devices (Welch 1995). On the other hand, sagebrush seeds are so small that lots at high purity must be diluted with a carrier in order to achieve realistic seeding rates. Seed size varies substantially among species and also among populations within species (table 2). Seeding rates should take seed size and therefore seed number per unit weight into account.

Sagebrush seeds are not long-lived in warehouse storage. Seedlots commonly hold full viability for 2 or 3 years (Stevens and others 1981). Seedlots of initial low quality lose viability more quickly than high-quality lots. Careful attention to moisture content (6 to 8% is optimal) and storage at relatively low temperatures (<10 °C) can extend storage life to 5 years and possibly longer. Because of late ripening dates, almost all sagebrush seed is held at least 1 year (until the following autumn) before planting.

Germination. We have good information on seed germination patterns for only a few species of sagebrush, but evidence indicates that this information may be broadly applicable to other species (Meyer and Monsen 1991, 1992; Meyer and others 1990). Variation in germination response is generally related to climatic variation at collection site rather than to specific or subspecific identity. Timing mechanisms are keyed to a pattern of winter or early spring germination and early spring emergence for all species examined so far. Sagebrush seeds are characterized by relatively low levels of dormancy at dispersal but may be more or less strongly light-requiring or slow to germinate. Both dormancy and light requirement are removed through moist chilling (stratification), so that most seeds become germinable during winter. After-ripening in storage also tends to reduce dormancy or light requirement. In the studies of big sagebrush germination ecophysiology cited above, patterns of variation in dormancy, light requirement, and germination rate were shown to be linked to collection site habitat. Seeds of populations from montane habitats with long, snowy winters tend to be dormant, light-requiring, or slow to germinate at autumn temperatures. These traits protect them from autumn germination, a risk for seeds dispersed in early autumn into relatively mesic environments. Seeds of populations from habitats with short, mild winters and hot, dry springs are dispersed later. They tend to be nondormant, not light-requiring, and quick to germinate, which facilitates germination during winter, when conditions are most favorable on warm desert fringe sites.

Germination under winter snowcover conditions is also keyed to habitat. Seeds of montane populations may take 20 weeks or more to germinate under conditions simulating

snowcover in the field, whereas those of warm desert fringe populations may do so in as little as 1 week. Seeds of montane populations can also sense and respond with increased germination rates to the shift from dark to light in the cold that results from thinning snow cover in the early spring. These habitat-correlated patterns apparently hold for black, silver, and low sagebrushes as well as for big sagebrush, based on preliminary data (table 3). Germination under snowcover seems to be a common pattern for sagebrush, ensuring emergence in very early spring just as the snow is melting (Meyer 1990; Meyer and Monsen 1990; Monsen and Meyer 1990).

Most big sagebrush seeds germinate during the winter and spring following the autumn of their production. They have no apparent mechanisms for seed bank carryover from year to year, and studies on *in situ* seed banks have failed to detect any substantial carryover (Young and Evans 1975, 1989). The tiny fraction of seeds that sometimes carries over (Hassan and West 1986) is probably made up of buried seeds whose light requirement has not yet been overcome because of inadequate chilling (Meyer and others 1990). The observation that sagebrush seeds germinate over a broad range of temperatures (see for example, Bai and Romo 1994; McDonough and Harniss 1974; Weldon and

Table 2— <i>Artemisia</i> , sagebrush: seed data (pure live seeds)				
Species	Cleaned seeds (million)/weight			
	Mean		Range	
	/kg	/lb	/kg	/lb
<i>A. arbuscula</i>	1.81	0.82	1.13–2.15	0.15–0.98
<i>A. bigelovii</i>	5.54	2.52	—	—
<i>A. cana</i>	2.87	1.30	1.81–4.90	0.82–2.23
<i>A. nova</i>	2.03	0.92	2.00–2.12	0.91–0.96
<i>A. pygmaea</i>	1.04	0.47	—	—
<i>A. rigida</i>	1.10	0.50	—	—
<i>A. tridentata</i>				
spp. <i>tridentata</i>	5.26*	2.38*	4.25–5.67*	1.93–2.58*
spp. <i>vaseyana</i>	4.30	1.95	4.23–4.36	1.92–1.98
spp. <i>wyomingensis</i>	4.72	2.14	4.00–5.42	1.82–2.46
<i>A. tripartita</i>	4.87	2.21	—	—
<i>A. filifolia</i>	3.20	1.45	—	—
<i>A. frigida</i>	10.0	4.55	—	—
<i>A. spinescens</i>	3.06	1.39	2.25–3.70	1.02–1.68
Sources: Belcher (1985), Deitschman (1974), McArthur and others 2004, Meyer (1990). * Subspecies not distinguished.				

Table 3— <i>Artemisia</i> , sagebrush: germination data							
Species	Germination percentage* on day 14 at 15 °C				Days to 50% germination at 1 °C (light)		
	Mean		Range		Mean	Range	Lots #
	Light	Dark	Light	Dark			
<i>A. arbuscula</i>	100	—	—	—	38.2	38	1
<i>A. bigelovii</i>	100	—	—	—	—	—	1
<i>A. cana</i> ,	100	81.5	100	75–88	56.0	54–58	2
<i>A. nova</i>	92.3	21.2	75–100	3–57	47.6	17–80	5
<i>A. tridentata</i>							
ssp. <i>tridentata</i>	94.6	18.6	84–100	0–46	54.0	27–95	5
ssp. <i>vaseyatia</i>	85	12.2	64–94	0–24	49.2	16–98	5
ssp. <i>wyomingensis</i>	98.4	13.4	94–100	2–46	55.2	18–98	5
<i>A. filifolia</i>	100	—	—	—	—	—	1
<i>A. spinescens</i>	92.7	72.6	87–98	52–93	45.5	38–53	2
Sources: All data from Meyer (1990) except for <i>A. tridentata</i> lots stored 4 months (Meyer and others 1990). * Expressed as percentage of viable seeds.							

others 1959; Wilson 1982) probably stems from the fact that sagebrush seeds have no need for protection from germination at summer temperature, as they almost never encounter summer regimes. Budsage, a species with seeds that ripen in early summer but do not germinate until the following early spring, shows strong germination suppression at summer temperatures (Meyer and Kitchen 1997).

Germination testing for sagebrush species is a relatively straightforward process. We recommend a 21-day test at 15 or 20 °C with light as the standard for big sagebrush and black sagebrush, with a 2-week chill (stratification) for more dormant lots (AOSA 1993; Meyer and others 1988a, 1988b). Because many dormant sagebrush seeds will not germinate in response to a short chilling, the viability of ungerminated seeds should be evaluated with tetrazolium.

Tetrazolium staining also represents an alternative to the germination test for evaluating the viability of sagebrush seeds. The fruits are pierced with a needle through the center of the cotyledon region of the embryo (figure 2) and immersed in buffered 1% tetrazolium chloride solution for 6 hours at 25 °C. The pericarp and seedcoat are then slit with a needle at the cotyledon end, and the embryos are squeezed out. Embryos stained a uniform bright red may be classed as viable.

The principal source of inconsistent results in sagebrush seed testing comes from decisions made during the purity evaluation. The inclusion of non-viable half-filled and aborted fruits in the pure seed fraction has little effect on the value for percentage purity but can affect the viability per-

centage considerably. In research, we routinely exclude such fruits and only occasionally encounter recently collected or properly stored lots whose viability is less than 90%. The seed analyst has a more difficult problem and we hope that the advent of better cleaning procedures for sagebrush seeds will help to make these difficulties unnecessary.

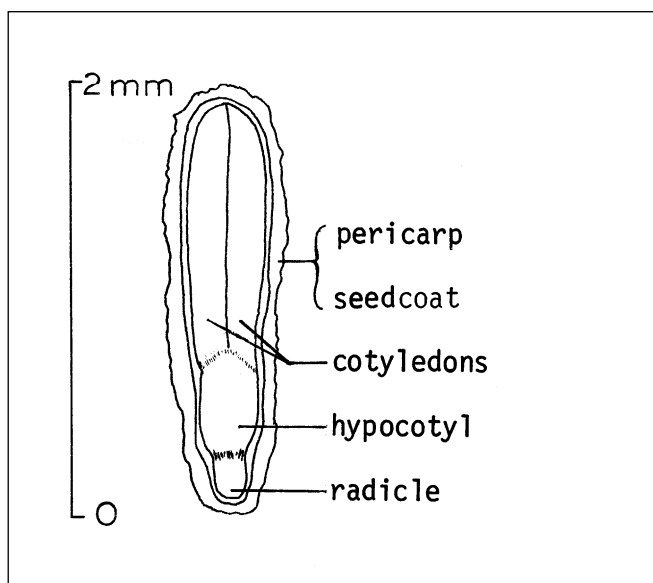
Nursery and field practice. Many species of sagebrush have been successfully grown both as container and as bareroot stock (Long 1986; McArthur and others 2004; Welch and others 1986). In addition, the practice of transplanting wildlings has been particularly successful with sagebrush (McArthur and others 2004). Planting is best carried out in early spring, when moisture conditions are favorable. Container stock requires careful hardening (Long 1986).

Sagebrush species are among the few native shrubs that can be reliably established by direct seeding. Seedling recruitment is regularly observed on small-scale disturbances in wildland stands where competition from adult plants and from weedy understory species is not too severe. Artificial seeding should mimic natural processes of dispersal. Seeding in late fall or onto snow in winter is most successful; spring-seeding is not recommended. Seeding rates that result in an average of 50 to 100 seeds/m² (5 to 9/ft²) usually result in adequate stands. This corresponds to a rate of 0.1 to 0.2 kg/ha (1.5 to 3 oz/ac) on a pure live seed (PLS) basis for a lot that averages 4 million seeds/kg (113,400/oz). The seeds should be planted at or near the surface of a firm but not compacted seedbed. Because of their small size, drilling or broadcasting seeds into a loose, sloughing seedbed may bury them too deeply for successful emergence (Jacobsen and Welch 1987; Monsen and Meyer 1990).

Sagebrush plants are generally quite long-lived, and successful recruitment from seeds every year is not necessary for perpetuation of the stand. On drier sites, winter snowfall may be inadequate for successful emergence and establishment in a typical year, especially on the bare, windswept surfaces of artificial seedings. Small-scale use of snow-fencing has been shown to enhance sagebrush stand establishment under such marginal conditions (Monsen and others 1992). Once nuclear stands are established, the shrubs themselves may act as both seed sources and living snow entrapment structures. It is common to see newly establishing seedlings spread out on the leeward side of an adult plant, where drifting snow accumulates.

Sagebrush species have been successfully seeded onto drastic disturbance sites such as mine- waste rock dumps, but adding topsoil (even minimally) often greatly enhances

Figure 2—*Artemisia nova*, black sagebrush: longitudinal section through an achene.



success, perhaps through re-inoculation with essential symbionts such as mycorrhizae (Monsen and Richardson 1984). Fertilization per se usually favors herbaceous competitors over the shrub seedlings and is not generally recommended.

Reports on seedling competitiveness in sagebrush are somewhat contradictory. In the era of sagebrush control on rangelands, managers often remarked on the ability of sagebrush to reestablish in perennial forage grass plantings (Pechanec and others 1944). Follow-up moisture in the summer appears to facilitate shrub seedling survival in competition with perennial grasses. Success in mixed seedings may be enhanced by separating the seeds spatially, for example,

in separate drop boxes on the seeding implement, or by interseeding into scalps (McArthur and others 2004).

Sagebrush seedlings in the presence of strong exotic annual grass competition have almost universally been failures (Monsen 1995). It may be that, in order to restore big sagebrush–bunchgrass communities on many sites now dominated by exotic annuals like cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* (L.) Nevski), seeding and establishment of the native perennial understory is a necessary prerequisite to successful establishment of sagebrush. More-expensive weed-control measures are often not an option on the large acreages involved.

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