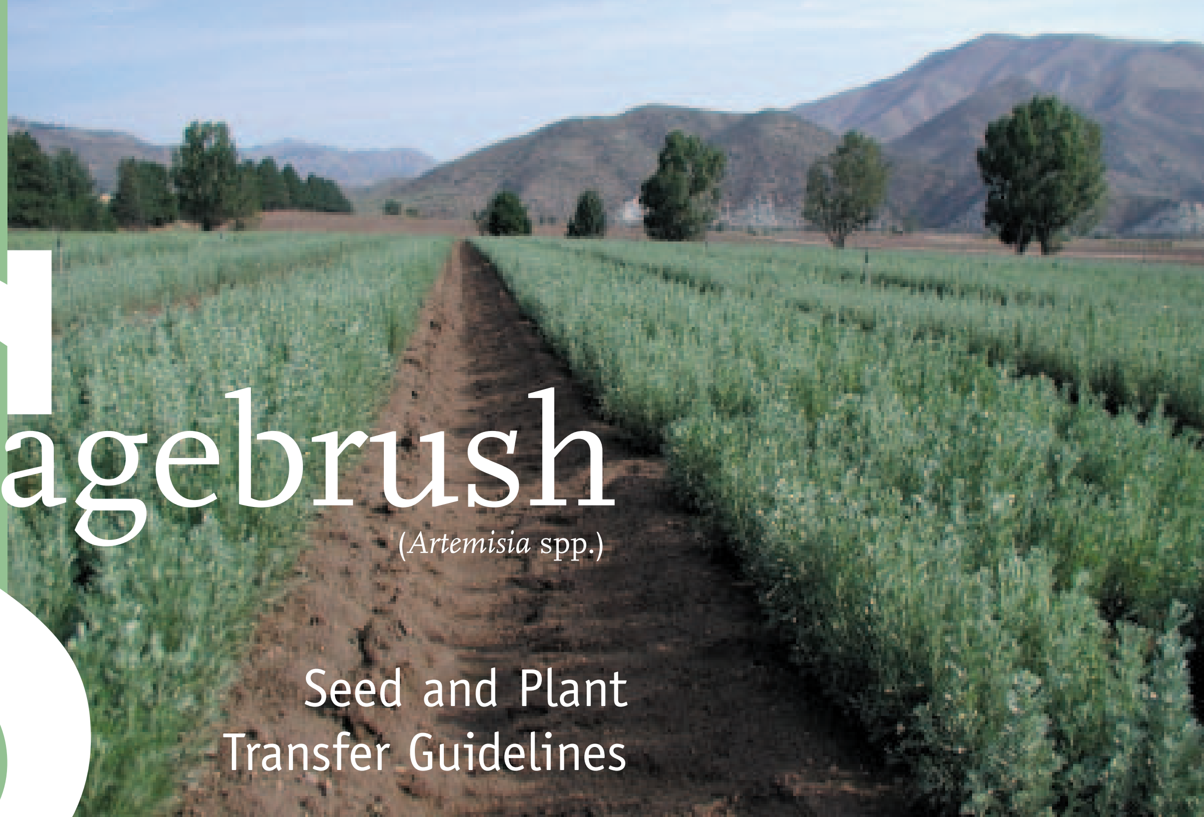
Sagebrush

(*Artemisia* spp.)

Seed and Plant Transfer Guidelines



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ABSTRACT

Seed and plant transfer guidelines are offered for 11 species of sagebrush (*Artemisia arbuscula, A. bigelovii, A. cana, A. rothrockii, A. longiloba, A. argillosa, A. rigida, A. nova, A. tripartita, A. pygmaea,* and *A. tridentata*). These species constitute the true sagebrushes of the subgenus *Tridentatae* of *Artemisia*. The geographic distribution of each species serves as the geographic boundary for the 11 seed zones, with the additional restriction that seeds should not be moved farther than 483 km (300 mi) to their target planting site, and if less than 483 km, not outside of their native distribution. For *A. tridentata*, seed transfer should ensure that subspecies are planted with respect to moisture and elevational gradients. For all other species, no additional transfer guidelines are proposed based on changes in elevation, but when local data suggest moisture gradients and ranges of elevation in excess of 458 m (1500 ft), conservative guidelines could further restrict seed transfer up 153 m (500 ft) in elevation, or down 305 m (1000 ft) in elevation, from the origin collection area. Correctly applied, seed and plant transfer guidelines minimize the risk of planting maladapted stock, increasing the survival and reproductive success to achieve restoration, rehabilitation, reclamation, and wildlife habitat improvement objectives.

KEY WORDS

seed zones, adaptive traits, elevation gradients, ecotypes, ploidy, hybridization

NOMENCLATURE

USDA NRCS (2004)

Species of sagebrush have long been recognized as having an important ecological role on rangelands over much of the West. Sagebrush provides desirable browse and cover for livestock and wildlife, soil cover and stabilization, mining reclamation, medicinal purposes, and can play a pivotal role in fire relations. The degree of desirability of sagebrush depends upon the species and in some cases, the subspecies and varieties that are present (White and Currie 1984; McArthur and Stevens 2004).

This paper presents seed transfer guidelines for 11 species of sagebrush based on patterns of genetic variation and taxonomy that were published previously (McArthur and Plummer 1978; McArthur and others 1979, 1981; McArthur 1983; McArthur and Sanderson 1999a). Where data are lacking for some species, conservative transfer zones inferred from neighboring sagebrush species are recommended using additional information from planting, transplanting, and chemical variation data.

A crop of 1 + 0 bareroot sagebrush growing at the USDA Forest Service Lucky Peak Nursery near Boise, Idaho. Photo by Clark Fleege, USDA Forest Service

TABLE 1

Genetic structure of sources of variation within a species.

SPECIES
SUBSPECIES
VARIETY
RACE
PROVENANCE [a]
FAMILY
INDIVIDUAL
CLONE

[a] Provenance (Seed Source, Stand, Metapopulation)

OVERVIEW OF THE ROLE OF SEED TRANSFER

Restoration, range rehabilitation, livestock forage, and wildlife habitat improvement carries the risk that planted shrubs will not be adapted to the environment in which they are planted. This risk can be minimized by limiting the distance that seeds and plants are moved from their origin both geographically and by elevation. These geographic and elevation limits known as seed transfer guidelines should be based on genetic differentiation of populations for traits reflecting adaptation to natural environments. Examples of adaptive traits in sagebrush species are drought resistance, reduced winter injury or cold hardiness, recovery from browsing (also chemical defense against herbivory), insect resistance, growth habit, root system development, response to fire, and allelopathy. Patterns of genetic variation in adaptive traits are based on the genetics, environment, and interaction of genetics and that environment for each species.

Seed transfer guidelines are within-species genetic management. Within-species management deals with management at the population or stand level (sometimes metapopulation) source of variation in the context of genetic structure for each species (Table 1). A common description of this source of variation applied to seed transfer guidelines is the seed zone. In other woody plants in the Intermountain West, mainly conifers, changes in elevation gradients may account for as much if not more of the observed patterns of genetic variation in adaptive traits (Rehfeldt 1991) and should be given consideration in developing seed transfer guidelines for woody plants. A model for shrub seed transfer zones, in the form of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt. [Chenopodiaceae]), was recently published by Sanderson and McArthur (2004). Restoration, rehabilitation, riparian, and wildlife improvement programs, working together with natural genetic systems, will reinforce the adaptation of populations to natural environments, maintain genetic diversity, and support long-term genetic conservation.

Populations of some species are characterized as having a specialist adaptive strategy if they are adapted to a relatively small segment of an environmental gradient, have most of their genetic variability among populations, or have a small or narrow geographic distribution. Conversely, populations of some species are characterized as having a generalist adaptive strategy if they are broadly adapted to an environmental gradient, have most of their genetic variability within populations, or generally have a large geographic distribution. Common-garden studies or transplantation experiments can help clarify whether species exhibit specialist or generalist adaptive strategies. When overall growth and morphology remain consistent with the source origin then a specialist adaptive strategy is inferred. Likewise, when populations of a species adjust to a common environment, by not rigidly upholding the characteristics of their source origin growth and morphology (exhibit plasticity), then a generalist adaptive strategy is assumed. Based on geography and available genetic data, *A. arbuscula*, *A. cana*, *A. nova*, and *A. tridentata* would be considered as having a generalist adaptive strategy. The more geographically restricted species, *A. bigelovii*, *A. longiloba*, *A. rigida*, *A. tripartita*, and *A. rothrockii* are likely to have a more intermediate to specialist adaptive strategy.

Choice of Species

The first, often-ignored step in seed transfer is choosing the appropriate species. Species distribution maps (Figures 1 to 6), forest and rangeland cover types, habitat typing, and ecological maps serve as useful tools for matching appropriate species to a particular planting site. Seed or plant material for a particular geographic location is determined by individual species' distributions (*Artemisia arbuscula, A. bigelovii, A. cana, A. rothrockii, A. longiloba, A. argillosa, A. rigida, A. nova, A. tripartita, A. pygmaea*, and *A. tridentata*) (Figures 1 to 6; Table 2). When determining species mix, if more than a single species occurs in a geographic location, it is more important to match a species to its native environment, than to choose a subspecies of big sagebrush for wildlife or livestock preferred forage. Sharp environmental gradients sort out sagebrush taxa on landscapes. For example, reciprocal transplant experiments have demonstrated the relative fitness of basin and mountain big sagebrush and their hybrids in a single small watershed (Wang and others 1997).

Definition of a Seed Zone

The geographic distribution of each sagebrush species serves as the geographic boundary for each seed zone, with the additional restriction that seed or plants should not be moved farther than 483 km (300 mi) to its target planting site, and if less than 483 km, plant material should not be moved outside of its native distribution. These relatively generous distances are justified by the wind-pollinated nature of the group wherein genetic makeup is often quite similar among populations of the same taxa. For example, some Wyoming big sagebrush individual plants have genetic markers more in common with distant populations (McArthur and others 1998) than with local populations. Based on these designations, seed zone nomenclature for data management and seedlot identity control can correspond to the four- or five-digit code in the National List of Scientific Plant Names found in the PLANTS database (USDA NRCS 2004) (for example, the seed zone code for *Artemisia arbuscula* = ARAR8).

The USGS Water Resources Council HUC third field drainage (accounting unit) may also be a useful seed zone boundary for those administering seed zones (nurseries, seed warehouses), particularly for universal naming conventions and ease of database management. This third field drainage unit is typically smaller in size than most of the *Artemisia* species' distributions and is, therefore, a more conservative seed zone boundary. The fourth field drainage (cataloging

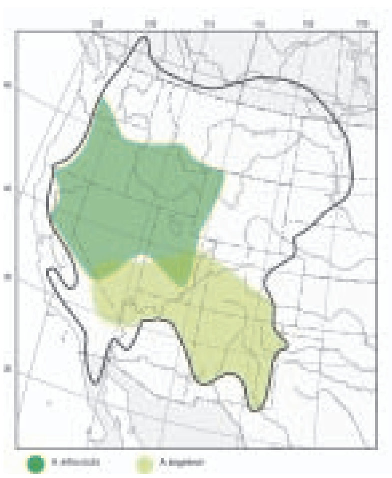

Figure 1. Distribution ranges of *Artemisia arbuscula* and *A. bigelovii*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

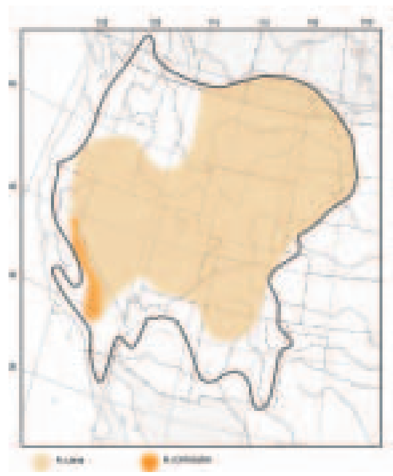

Figure 2. Distribution ranges of *Artemisia cana* and *A. rothrockii*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

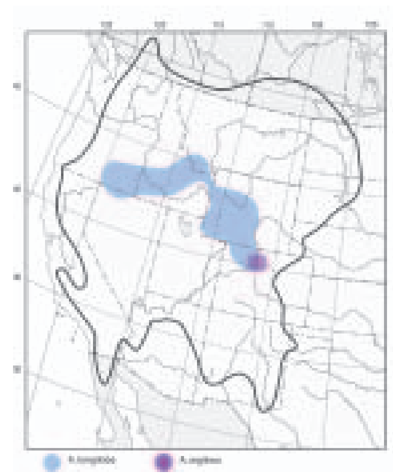

Figure 3. Distribution ranges of *Artemisia longiloba* and *A. argillosa*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

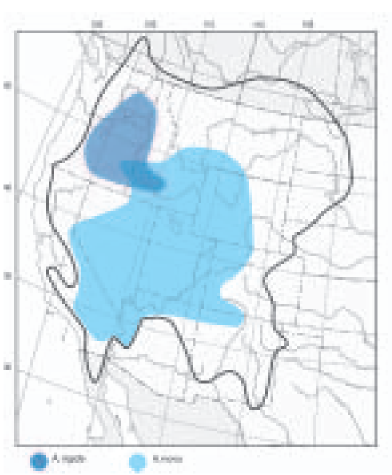

Figure 4. Distribution ranges of *Artemisia rigida* and *A. nova*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

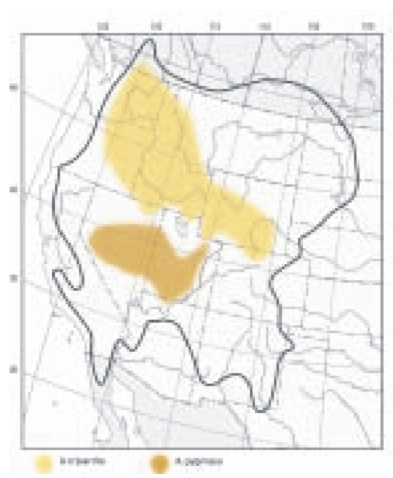

Figure 5. Distribution ranges of *Artemisia tripartita* and *A. pygmaea*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

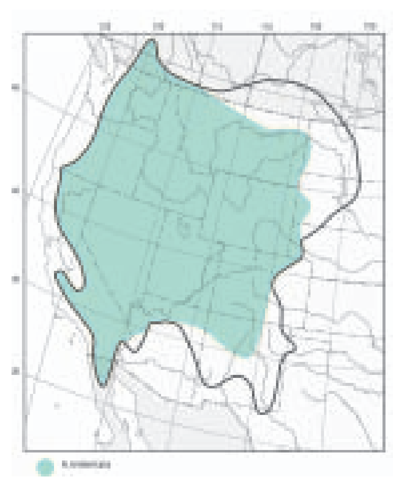

Figure 6. Distribution range of *Artemisia tridentata*. The bold line is the distributional limit of the subgenus *Tridentatae* (McArthur and Plummer 1978).

TABLE 2

Subgenus *Tridentatae* species with site adaptations and generalized distributions. [a]

Species	Subspecies	Common name(s)	Site adaptation	Distribution	Range of elevation m (ft)	Chromosome counts (ploidy) [b]
A. arbuscula	*arbuscula*	Low sagebrush	Dry, sterile, rocky, often shallow alkaline, clay soils	W Wyoming to SC Washington and N California	700 to 3780 (2300 to 12 400)	2x, 4x
	longicaulis	Lahonton low sagebrush	Dry, sterile, rocky, often shallow alkaline, clay soils in the vicinity of old Lake Lahonton	NW Nevada and neighboring Oregon and California	1050 to 2000 (3445 to 6560)	6x
	thermophila	Hot springs low sagebrush	Spring-flooded, summer-dry soils	W Wyoming, N Utah, and E Idaho	1800 to 2500 (5900 to 8200)	2x
A. argillosa		Coaltown sagebrush	Alkaline spoil material	Jackson County, Colorado	2400 to 2600 (7870 to 8530)	4x
A. bigelovii		Bigelow sagebrush	Rocky, sandy soils	Four Corners area extending to NE Utah, SE California, and W Texas	915 to 2440 (3000 to 8000)	2x, 4x, 8x
A. cana	*bolanderi*	Bolander silver sagebrush	Alkaline basins	E Oregon, W Nevada, and N California	1525 to 3350 (5000 to 11 000)	2x
	cana	Plains silver sagebrush	Loamy to sandy soils of river bottoms	E of Continental Divide, Alberta and Manitoba to Colorado, possibly in Sevier County, Utah	1525 to 3350 (5000 to 11 000)	4x, 8x
	viscidula	Mountain silver sagebrush	Mountain areas along streams and in areas of heavy snow pack	W of Continental Divide, Montana and Oregon to Arizona and New Mexico	305 to 3050 (1000 to 10 000)	2x, 4x
A. longiloba		Alkali sagebrush	Heavy soils derived from alkaline shales or on lighter, limey soils	SW Montana, NW Colorado, W Wyoming, N Utah, S Idaho, N Nevada, and E Oregon	1680 to 2440 (5500 to 8000)	2x, 4x
A. nova	*nova*	Black sagebrush	Dry, shallow, stony soils; some affinity for calcareous soils	SE Oregon to SC Montana to S California and NW New Mexico	625 to 2990 (2050 to 9800)	2x, 4x
	duchesnicola	Duchesne black sagebrush	Reddish clay soils of Duchesne River Formation	NE Utah	1700 to 1800 (5575 to 5900)	6x [c]
A. pygmaea		Pygmy sagebrush	Desert calcareous soils	C Nevada and NE Utah to N Arizona	1220 to 1830 (4000 to 6000)	2x
A. rigida		Stiff sagebrush	Rocky scablands	E Oregon, WC Idaho, and E Washington	230 to 2130 (755 to 7000)	2x, 4x
A. rothrockii		Rothrock sagebrush	Deep soils along forest margins at high elevations in Sierra Nevada and outliers	California and Nevada	1000 to 4000 (3280 to 13 120)	4x, 6x

Species	Subspecies	Common name(s)	Site adaptation	Distribution	Range of elevation m (ft)	Chromosome counts (ploidy) [b]
A. tridentata	*spiciformis* [d]	Snowbank big sagebrush	High mountain areas or associated with *A. cana* ssp. *viscidula* but in slightly drier areas	Wyoming, Idaho, Colorado, and Utah	2075 to 3050 (6800 to 10 000)	2x, 4x
	tridentata	Basin big sagebrush	Deep, dry, fertile soils of valleys and foothills	British Columbia and Montana to New Mexico and Baja California	610 to 2140 (2000 to 7020)	2x, 4x
	vaseyana	Mountain big sagebrush	Deep, well-drained soils often with summer moisture available in mountains and foothills	British Columiba and Montana to S California and N New Mexico	780 to 3100 (2560 to 10 170)	2x, 4x
	wyomingensis	Wyoming big sagebrush	Shallower, well-drained, hottest soils. Utah: often underlain by a caliche or silica layer in valleys and foothills	North Dakota and Washington to Arizona and New Mexico	1520 to 2150 (2500 to 7260)	2x, 4x
	xericensis	Xeric big sagebrush	Basaltic and granitic soils	WC Idaho	1520 to 2140 (2500 to 7260)	4x
A. tripartita	*rupicola*	Wyoming threetip sagebrush	Rocky knolls	Wyoming	1100 to 2300 (3390 to 7085)	2x
	tripartita	Tall threetip sagebrush	Moderate-to-deep, well-drained soils	E Washington and W Montana to N Nevada and N Utah	1100 to 2300 (3390 to 7085)	2x, 4x

[a] General sources: Beetle (1960), Winward (1970), McArthur and Plummer (1978), Winward (1980), Harvey (1981), McArthur (1983, 1994), Winward and McArthur (1995).

[b] See McArthur and Sanderson (1999a) for details except for *A. arbuscula* ssp. *thermophila* and *A. tripartita* ssp. *rupicola*, which were recently determined to be diploid (2x) by McArthur and Sanderson (unpublished).

[c] *Artemisia nova* var. *duchesnicola* (Welsh and Goodrich 1995) was recently determined by McArthur, Sanderson, and Goodrich (unpublished data) to be hexaploid (6x).

[d] Described as a separate species (Rydberg 1916) or as a form of *A. tridentata* ssp. *vaseyana* (Beetle 1959).

unit) has formerly been recommended as a seed zone for some USDA Forest Service Native Plants Programs (USDA Forest Service 1995). Though overly conservative and not representative of the more generalist and intermediate adaptive strategies of *Artemisia* spp., this sub-basin cataloguing unit is a useful tool for developing seed collection strategies to ensure that broad genetic samples are collected over time and to further minimize the negative consequences of depleting a local seed source by over-collecting in one or more years.

Whether using the species geographic boundary or the USGS Water Resources Council HUC third field drainage as the seed zone boundary, federal, state, and local agencies and conservation organizations should adopt a consist format among participants. As additional research takes an in-depth look at more populations within a species and specifically addresses the objective of developing seed transfer guidelines, seed zone designations and seed transfer guidelines may be updated to reflect newer findings.

Choice of Subspecies

Varying species and subspecies may have very different seed transfer guidelines within a watershed depending on the microhabitat. After choosing the appropriate seed zone and species mix, choice of an appropriate subspecies is the next critical step in seed transfer (Table 2), particularly for *A. tridentata*. Basin big sagebrush (ssp. *tridentata*) is recommended for foothills and valley floors with deep, seasonally dry soils. Mountain big sagebrush (ssp. *vaseyana*) is appropriate for foothills and mountain areas with deep soils—usually with summer moisture events. Wyoming big sagebrush (ssp. *wyomingensis*) is a good choice for foothills, plains, and mountain basins with shallow, rocky soils, or if caliche is present. Timberline or snow-

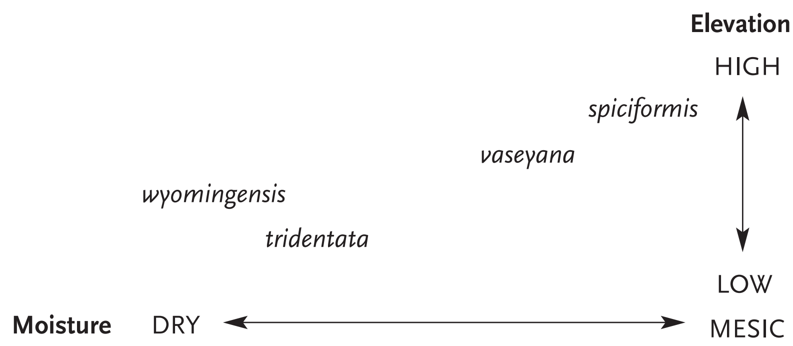

Figure 7. Artemisa tridentata subspecies occurrence by moisture and elevational gradients (McArthur 1983).

bank big sagebrush (ssp. *spiciformis*) is suited to high mountain areas. Xeric big sagebrush (ssp. *xericensis*) is suitable for dry slopes and draws in southwestern Idaho where it is a restricted endemic. Within a given drainage as many as three subspecies may be needed for planting, depending upon moisture gradients and elevation (Figure 7).

OTHER FACTORS GUIDING SEED TRANSFER

Ploidy Levels

Polyploidy is an important mechanism in the differentiation and adaptation of *Artemisia* species in general and *Tridentatae* species in particular. Polyploidy can influence fertility and plant vigor. Polyploidy may mask the interpretation of adaptive traits inherited in a quantitative fashion and could be more significant than geographic source or seed zone. Mixed ploidy matings can represent outbreeding depression (matings among genetically different populations resulting in progeny with less fitness) and sterility because of unbalanced meiotic segregation. In general, polyploids have higher heterozygosity than diploids (McArthur 1989; Cronn and Wendel 2003).

Tridentatae species not only exhibit broad general polyploidy patterns but also patterns that are evident at ecotonal interfaces and within populations. Ploidy levels may also be an adaptive strategy. Hagerup (1932) suggested that polyploids were better adapted to extreme ecological environments than were their diploid relatives. This seems to be the case with the sagebrushes and some other western North American shrub complexes (Sanderson and others 1989; McArthur and Sanderson 1999a). Autopolyploidy, the form of polyploidy in the *Tridentatae* (McArthur and others 1981), alters cytologic, biochemical, genetic, and physiological, and developmental characters, which may provide tolerance beyond limits of diploid progenitors (Levin 1983). In contrast to the norm in herbaceous plants, where plant size and growth rate in polyploids are typically larger than diploids, *Artemisia* spp. show a contrasting phenomenon; the polyploids are smaller. This is believed to occur in these woody plants as a result of increased cellulose as ploidy levels increase, thus metabolism and growth are retarded, lowering growth rates and increasing drought tolerance.

Phylogenetic and cytological studies reveal multiple ploidy levels among the 11 species of sagebrush (Table 2). The genus has 2 principal base chromosome numbers x = 8 and x = 9. However, x = 9 is by far the most common and is the base number for the sagebrushes of North America (= subgenus *Tridentatae*) (Vallès and McArthur 2001). Polyploidy is common, 2x to 8x in North American sagebrush and up to 12x for the genus. Polyploidy also exists within populations (McArthur and Sanderson 1999a). When drought tolerance is critical for planting success and capturing a site, ploidy level should be given consideration for seed source choices. For example, Wyoming big sagebrush (*A. tridentata* ssp. *wyomingeneis*) is tetraploid (4x) and is adapted to drier sites than are the predominately diploid basin and mountain big sagebrushes.

Introgression and Interspecific Hybridization

In the case of seed transfer, interspecific hybridization is viewed as a naturally occurring process leading to increased diversity and the promotion of speciation over time. Some researchers and practitioners recommend the avoidance of all hybrid zones for seed collection both for restoration and revegetation projects. These naturally occurring hybrid zones, however, have allowed *A. tridentata* to be widely adaptable. Hybrid zones are suitable for seed collection for restoration, as hybridization contributes to the versatility of *Artemisia* spp. (McArthur and Sanderson 1999b).

Even if seed transfer guidelines prohibited the sampling and planting of hybrid areas, it must be acknowledged that hybridization is a naturally occurring process and will continue on its own regardless of management direction and perhaps will even be promoted as the increasing urban interface contains nonlocal sagebrush species in landscape settings. Hybrid areas should be sampled for seed collection and actively restored within the context of a target watershed.

Cronn and Wendell (2003) call for a multidisciplinary approach to investigating the extent of hybridization in evolutionary biology, as inferences concerning the frequency and importance of hybridization are always underestimated. In the meantime, practical guidelines for seed and plant movement are still needed. They should be reasonable but not unduly limiting until introgression and interspecific hybridization are more fully understood.

Both polyploidization and hybridization have shaped the differentiation and patterns of genetic variation in the *Tridentatae* (McArthur and others 1988; McArthur and Sanderson 1999a). Hybrid zones are likely the source for differentiation of new genetic combinations that were able to exploit new habitats as climates changed in the Pliocene and Pleistocene epochs and that will be able to adopt to new habitats during predicted changes in the near future (Neilson and Drapek 1998).

Elevation Movement

When local conditions contain moisture gradients and ranges of elevation in excess of 458 m (1500 ft), conservative guidelines further restrict seed transfer up 153 m (500 ft) in elevation, or down 305 m (1000 ft) in elevation, from the origin collection area for all species except *A. tridentata* (Figure 7). Seeds from western shrub species show ecotypic differences in seed germination. Rapid germination under snow pack in high mountain environments from low elevation or warm desert seed sources may lead toward decreased seedling survival and an increase in damage due to frost and damping-off (Meyer 1990). Germination patterns in big sagebrush populations are dependent on habitat; movement of seed for rehabilitation or restoration plantings would be better served by using seed from similar habitats to ensure initial germination success (Meyer and others 1990; Meyer and Monsen 1992).

Drought Tolerance

In addition to ploidy level, choose a drought-tolerant ecotype such as upland Wyoming big sagebrush, which is more drought hardy than basin big sagebrush, which is adapted to deeper soils. Basin big sagebrush is a prolific seed producer and its seed is readily available, but planting basin big sagebrush on uplands sites is risky. Wyoming big sagebrush is also the subspecies of choice for droughty, mineralized, or coal-mined reclamation lands.

When Local Sources Are Not Available

In experiments where wild seedlings of several accessions of *A. tridentata* ssp. *tridentata*, *A. nova*, *A. cana*, and *A. bigelovii* were transplanted from one area to another, the results of Plummer and others (1968) and Plummer (1977) suggest that if seeds must be brought in from some distance, it is best to get them from a harsher climate or more northerly location.

Managing Genetic Diversity through Collections

For all species, collect from at least 30 unrelated plants, separated by a minimum of 30 m (100 ft) in distance. An equal number of seeds should be collected per plant. Each seed lot should not span more than 92 m (300 ft), nor should the collection area exceed 0.5 km (1640 ft), to optimize its transfer capabilities.

SUMMARY

Seed transfer guidelines first call for the selection of appropriate species and sometimes an associated species mix for a target planting location based on the geographic distribution or seed zone for each species. Within each species, additional considerations are offered for appropriate subspecies based on elevation and moisture gradients for *A. tridentata.* Elevation transfers are more liberal for moving seed sources down in elevation than up in elevation. Specific ecotypes or ploidy level may also be useful for droughty areas and mineral soils for choosing particular seed sources. Though some species are more consistent seed producers, adopting these seed transfer guidelines, partnered with monitoring the frequency of seed crops (every 1 to 4 y), will benefit seed procurement activities, management of genetic diversity, and encouraging successful planting programs.

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