ADAPTATION AND SUCCESS OF BIG SAGEBRUSH AND RUBBER RABBITBRUSH ON DISTURBED SITES[1]

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Abstract: Restoration or reclamation of many disturbed sites in the western United States requires the use of the widespread native shrubs big sagebrush (*Artemisia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*). Each of these species is taxonomically complex with numerous subspecies and populations that are adapted to specific habitats. Although big sagebrush is a competitive species, it is ordinarily late seral in niche, particularly in the secondary successional processes of disturbed sites. In contrast, the common rubber rabbitbrush subspecies are early seral. The two species often grow together and are compatible in space and time in secondary succession processes. Matching the habitats of seed source and restoration or rehabilitation areas is a wise management practice. Two case studies on successful long term (33 and 16 years) big sagebrush and rubber rabbitbrush disturbed site restoration are reviewed.

Additional Key Words: *Artemisia tridentata, Chrysothamnus nauseosus,* site restoration, rehabilitation.

Introduction

Big sagebrush (*Artemisia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*) are two of the most widespread and common shrubs in the Western United States (McArthur and Welch 1986, McArthur and Stevens in press). For much of the history of rangeland rehabilitation plantings in the Western United States these species were not used because they were considered range weeds. A common objective in rangeland rehabilitation plantings was to replace them with more desirable forage plants. The changing attitude in respect to the use of these plants based on their competitiveness and widespread adaptation was championed by A. Perry Plummer, among others (Plummer et al. 1968, McArthur 1992, Monsen and McArthur in press). Both species are native and both include a wide array of taxonomic and genetic variation (McArthur et al. 1979, Utah State University 1979, Johnson 1983, McArthur 1983, Weber et al. 1985, McArthur and Welch 1986, McArthur and Stevens in press, McArthur and Tausch in press, and references cited therein). The ubiquitous presence of sagebrush on western rangelands is illustrated by an observation by Passey et al. (1982) who noted in a wide-ranging, comprehensive study, that "sagebrush species or subspecies have been observed and evaluated on ... several hundred tracts ... One or more species of sagebrush were present on every area examined except where there was unmistakable evidence of recent burning, tillage, or mechanical or chemical treatment. Many of these observations were made on rangelands where the plant community was judged to be in near-climax condition. Some areas, in fact, had no evidence of use or disturbance of any kind except by native fauna." Rabbitbrush, likewise, is widely distributed and common in the Western United States (Hall and Clements 1923, Weber et al. 1985).

The purpose of this paper is to review the systematics, adaptation, and ecological establishment attributes of big sagebrush and rubber rabbitbrush and to present some case studies of their use and performance in reclamation plantings.

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Systematics and General Distribution of Big Sagebrush and Rubber Rabbitbrush

Big Sagebrush

Big sagebrush is the central species of a complex (or group) of species that share many characteristics (Beetle 1960, McArthur et al. 1981). This group of about 25 taxa including eleven species (*A. arbuscula, A. argillosa, A. bigelovii, A. cana, A. longiloba, A. nova, A. pygmaea, A. rigida, A. rothrockii, A. tridentata, A. tripartita*) and more than a dozen subspecific entities (Beetle 1960, McArthur 1983) comprises the subgenus *Tridentatae* of *Artemisia* (McArthur et al. 1981, Shultz 1986). We use the term *Tridentatae* as being synonymous with true sagebrush. Not all woody *Artemisias* belong to the *Tridentatae*. Non-*Tridentatae* examples include bud sage (*A. spinescens*), sand sage (*A. filifolia*), and fringed sage (*A. frigida*) (McArthur and Stevens in press). The *Tridentatae* are woody, North American plants with glabrous receptacles and homogamous, perfect-flowered heads composed of disc flowers with the exception of Bigelow sagebrush (*A. bigelovii)*. Bigelow sagebrush has floral heads that usually also include a ray flower or two (McArthur et al. 1979, McArthur 1983). Although several other *Tridentatae* species are geographically widespread and taxonomically differentiated, e.g., low sagebrush (*A. arbuscula*), silver sagebrush (*A. cana*), black sagebrush (*A. nova*), threetip sagebrush (*A. tripartita*), big sagebrush is clearly the preeminent species of *Tridentatae*. Big sagebrush covers almost all of the geographical distributional range of the subgenus and contributes most of the large, landscape dominant populations of sagebrush (Beetle 1960, McArthur and Plummer 1978)--silver sagebrush extends the range somewhat to the northeast and Bigelow sagebrush somewhat to the southeast..

Big sagebrush includes five subspecies: basin big sagebrush (*A. tridentata* ssp. *tridentata*), mountain big sagebrush (*A. t.* ssp. *vaseyana*), Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), spicate big sagebrush (*A. t.* ssp. *spicata*), and xeric big sagebrush (*A. t.* ssp. *xericensis*) (Goodrich et al. 1985, Rosentreter and Kelsey 1991, McArthur 1994). The latter two are limited in distribution to high elevation snowbank habitats in northern Utah, eastern Idaho, western Wyoming and Western Colorado (spicate big sagebrush) and basaltic foothills of west central Idaho (xeric big sagebrush). The three common subspecies (basin, mountain, and Wyoming big sagebrush) are widely distributed within the overall big sagebrush distribution range from southern British Columbia and Saskatchewan to northern Baja California and western Texas (McArthur and Plummer 1978, McArthur 1983). The three common subspecies are characterized as follows (McArthur 1983, Stevens 1987, McArthur and Stevens in press, and references therein):

Habitat-------------------------------------	Basin big sagebrush, foothills and valley floors, deep seasonally dry soils; mountain big sagebrush, foothills and mountains, deep soils; Wyoming big sagebrush, foothills, plains, and mountain basins, shallow, rocky soils, sometimes with caliche.
Common height---------------------------	Basin big sagebrush, 0.9 to 4 m; mountain big sagebrush, 0.5 to 1.5 m; Wyoming big sagebrush, 0.5 to 0.9 m.
Seedling growth rates---------------------	Basin big sagebrush, highest aerial with longest sustained root growth; mountain big sagebrush, intermediate aerial with slowest root growth rate; Wyoming big sagebrush, both aerial and root growth are fast initially then slow down.
Shrub shape--------------------------------	Basin big sagebrush, uneven topped; mountain big sagebrush, usually even topped; Wyoming big sagebrush, usually uneven topped but somewhat round.
Position of flower stalks------------------	Basin big sagebrush, throughout crown; mountain big sagebrush, above crown; Wyoming big sagebrush, throughout crown.
Flowers per head---------------------------	Basin big sagebrush, 3 to 6; mountain big sagebrush, 4 to 8; Wyoming big sagebrush, 3 to 8.
Flower and seed phenology--------------	Basin big sagebrush, late; mountain big sagebrush, early; Wyoming big sagebrush, late-intermediate.
Leaf shape----------------------------------	Basin big sagebrush, narrowly cuneate, mountain big sagebrush, cuneate to spatulate, Wyoming big sagebrush, cuneate.
Ultraviolet visible coumarins------------	Basin big sagebrush, trace; mountain big sagebrush, abundant; Wyoming big sagebrush, trace, but often more than basin big sagebrush.

Tendency to layer-------------------------	Basin big sagebrush, none; mountain big sagebrush, slight; Wyoming big sagebrush, none.
Palatability to deer and sheep----------	Basin big sagebrush, low; mountain big sagebrush, usually highest; Wyoming big sagebrush, often highest for sheep, sometimes high for deer.
Protein content----------------------------	Basin big sagebrush, high; mountain big sagebrush, low; Wyoming big sagebrush, low.
Seed germination prior to stratification	Basin big sagebrush, high; mountain big sagebrush, low; Wyoming big sagebrush, intermediate.
Effect of fire on seed germination-----	Basin big sagebrush, negative; mountain big sagebrush, positive; Wyoming big germination sagebrush, neutral.
Ploidy level----------------------------------	Basin big sagebrush, mostly diploid, occasionally tetraploid; mountain big sagebrush, mostly diploid, some tetraploids; Wyoming big sagebrush, always tetraploid.

Rubber Rabbitbrush

The rabbitbrushes (*Chrysothamnus*) include 16 species and some 50 taxa in all including subspecies (Anderson 1986, McArthur and Meyer 1987, McArthur and Stevens in press). The genus is wholly shrubby and is endemic to western North America. Rubber rabbitbrush is the most taxonomically complex species in the genus with 25 subspecies. It is also the most common and widely distributed rabbitbrush. Under the right conditions, rubber and other chemicals might be extracted for industrial use (Hegerhorst et al. 1987). Rubber rabbitbrush and Parry rabbitbrush (*C. parryi*) differ from the other species, e.g., low rabbitbrush (*C. viscidiflorus*), spreading rabbitbrush (*C. linifolius*), Greene rabbitbrush (*C. greenei*), dwarf rabbitbrush (*C. depressus*), desert rabbitbrush (*C. paniculatus*), by having tomentose stems with densely compacted hairs. Rubber rabbitbrush differs from Parry rabbitbrush by its more obtuse floral involucral bracts and by its larger more course (0.3 to 2.0 m high versus 0.2 to 0.6 m) structure (Anderson 1986, McArthur and Meyer 1987).

Several of the rubber rabbitbrush subspecies, in common with other species in the genus, are early seral in nature, i.e., they invade and establish on disturbed sites. Four rubber rabbitbrush subspecies, in particular, are widespread, common, and early seral: white rubber rabbitbrush (*C. nauseosus* ssp. *albicaulis* and *C. n.* ssp. *hololeucus*), threadleaf rubber rabbitbrush (*C. n.* ssp. *consimilis*), and green rubber rabbitbrush (*C. n.* ssp. *graveolens*) (McArthur et al. 1979, Anderson 1986, Hegerhorst et al. 1987). The two subspecies referred to as white rubber rabbitbrush, differ in that *C. n.* ssp. *albicaulis* has longer corolla lobes and styles and is more of an upland taxon surrounding the Great Basin whereas *C. n.* ssp. *hololeucus* has a distribution centered on the Great Basin, Colorado Plateau, and Snake River Plains--Anderson 1986, McArthur and Stevens in press. Other subspecies of particular note include the sandy habitat specialists (*C. n.* ssp. *arenarius*, *C. n.* ssp. *bigelovii*, *C. n.* ssp. *nitidus*, *C. n.* ssp. *turbinatus*), the montane subspecies, *C. n.* ssp. *salicifolius*, the northern plains, badlands subspecies, *C. n.* ssp. *nauseosus*, and subspecies adapted to desert habitats of rocky outcrops, uplands, or shale barrens (*C. n.* ssp. *iridis*, *C. n.* ssp. *junceus*, *C. n.* ssp. *leiospermus*) (Anderson 1986, Meyer in press). The four common, widespread, early seral subspecies are characterized as follows::

Habitat---------------------------------------	White rubber rabbitbrush, plains, basins, foothills, and mountains on better drained soils; threadleaf rubber rabbitbrush, plains, basins, and foothills usually on heavier and more saline soils; green rubber rabbitbrush, foothills and mountains on better drained soils.
Size---	White rubber rabbitbrush, mature plants are 0.6 to 2 m tall; threadleaf rubber rabbitbrush, 0.8 to 3 m; green rubber rabbitbrush, 0.6 to 2 m.
Stems and leaves---------------------------	White rubber rabbitbrush, leaves and stems covered with white, dense, tomentum, leaves narrow (<3 mm); threadleaf rubber rabbitbrush, green or yellow-green tomentum, leaves thread-like (<1 mm); green rubber rabbitbrush, green, yellow-green, or gray-green tomentum, leaves broader (1 to 3 mm).
Nutritive quality and palatability--------	White rubber rabbitbrush, generally more palatable to browsing animals; threadleaf rubber rabbitbrush, generally least palatable; green rubber

rabbitbrush, intermediate in palatability; nutritive quality varies more by individual population than by subspecies.

Adaptation, Ecology, and Establishment

Both big sagebrush and rubber rabbitbrush are widely and broadly adapted, especially when individual subspecies and populations are considered. The two species often occur together. Big sagebrush, however, is late seral and the common rubber rabbitbrush subspecies are early seral. So, rubber rabbitbrush is much more apparent when disturbances have occurred but gives way to big sagebrush dominance in time as vegetative communities mature. The two species are ecologically compatible in time and space.

Big Sagebrush

Big sagebrush is the most widespread and common shrub of western North America. It grows on a variety of soil types and with a wide array of other plant species including trees, other shrubs, grasses, and forbs. Usually it is the dominant plant in the less disturbed communities were it grows. However, in addition to occurring in large continuous stands, big sagebrush subspecies and populations also occur in complex mosaics with other vegetation types (McArthur 1983). The distribution of big sagebrush subspecies is along interactive moisture and elevational gradients. As moisture increases Wyoming big sagebrush gives way to basin big sagebrush and basin big sagebrush subsequently gives way to mountain big sagebrush; as elevation increases basin big sagebrush gives way to Wyoming big sagebrush which in turn gives way to mountain big sagebrush. In some situations, there is introgression and hybridization between the subspecies as well as other sagebrush taxa (McArthur et al. 1979, 1988b, McArthur 1994). Since Euro-American settlement, big sagebrush populations have expanded and thickened in some areas within their broad original geographic range in response to some activities, e.g., livestock grazing. In other areas and circumstances, e.g., intensive agriculture and pastoralism and urban development, populations have been thinned or extirpated (Johnson 1986). A serious problem with the overall sagebrush ecosystem is the invasion of exotic annuals, e.g. cheatgrass (*Bromus tectorum*), that are adapted to a much shorter fire cycle than is sagebrush, in general, two or three years versus 50 or more years. Frequent fires have resulted from the population build up of these exotic annuals and large areas of big sagebrush have burnt off and are not capable of rapid self-renewal although efforts to restore them are underway (McArthur et al. 1990, Monsen and Kitchen 1994 and references cited therein).

Big sagebrush plants may produce hundreds of thousands of seeds annually (McArthur et al. 1988b, Welch et al. 1990). Seed production, however, can be greatly reduced by heavy browsing (Wagstaff and Welch 1991). Seeds are shed during the October to December period. Given a suitable seedbed, seeds have germination patterns that are generally correlated with moisture and temperature habitat attributes (Meyer 1994). Dormancy is limited to seeds from cold sites, usually mountain big sagebrush populations. Germination almost always occurs by early spring. Differential timing of germination between fall and spring among big sagebrush populations and subspecies have to do with responses to conditions likely to be encountered by seeds between the time of dispersal and the optimum germination time for a particular habitat (Meyer 1994). Seeds from cold winter sites have either dormancy (montane Mountain big sagebrush populations) or light requirements (Wyoming big sagebrush) so that they do not prematurely germinate (Meyer and Monsen 1992). Seeds from populations of big sagebrush at mild winter sites are dispersed in early winter. Seeds from all subspecies on these milder sites are non-dormant and have rapid germination rates at near-freezing temperatures (Meyer et al. 1990, Meyer and Monsen 1992). We believe, on these sites early emergence is an advantage so that early melting snow pack conditions can be effectively used even during the winter period. However, unusually cold winter weather can be damaging or fatal to seedlings in mild winter habitats as can unusually cold spring weather or extended dry, hot summer periods in any sagebrush habitat (McArthur et al. 1988a, Meyer 1994). An example of stress induced by the summer heat is an ongoing experiment on sagebrush hybrid zone dynamics (Freeman et al. 1991, in press, Graham et al. in press, McArthur unpublished). In these experiments nearly a hundred small plots were seeded in a reciprocal manner throughout the hybrid zone and parental population study sites after the 1992 seed crop matured. Those small plots were still nice seedbeds after the 1993 seed crop matured. The artificially seeded experimental plants established well during the spring and summer of 1994 and many continue to do well. Naturally recruiting seedlings established in plots in the late winter and spring of 1994 but *not one* of the dozens of 1994 seedlings survived the summer. The difference between the two years was that during 1993, but not during 1994, timely spring and summer rains came which allowed the 1992 cohort, but not the 1993 cohort, to survive and grow. Meyer and Monsen (1990) in a small plot field germination experiment using two Wyoming and three mountain big sagebrush populations in three sites (Wyoming big sagebrush, pinyon-juniper, and mountain brush) demonstrated that successful establishment of the big sagebrush seedlings was related to habitat characteristics at the site of seed origin.

The ideal big sagebrush seedbed is one that is open from immediate established plant competition and is firm but irregular. Big sagebrush can be established in mixed seedings so long as it is surface or near surface seeded and the seeding simulates natural conditions, i.e., is performed in the late fall or winter. Big sagebrush readily transplants provided that stock is relatively dormant and there is adequate soil moisture (fall and early spring) (McArthur et al. 1979, Stevens 1994, McArthur and Stevens in press).

Life history strategy differences among the three principal big sagebrush subspecies were suggested by Bonham et al. (1991). We believe the Bonham et al. (1991) strategies have merit but that they should be interpreted within the overall late seral niche of big sagebrush, in general. Based on the classification system of Grime (1977), Bonham et al. (1991) concluded that:

1) basin big sagebrush demonstrates a colonization strategy as it is a prolific seed producer and would be able to spread and occupy open disturbances;
2) that mountain big sagebrush should be more competitive as it produces a moderate seed crop each year investing more energy into competitive vegetative growth;
3) that Wyoming big sagebrush manifests a strategy designed to tolerate abiotic stress through sporadic seed production. During periods of stress resources are directed to sustain vegetative growth but with less stress more resources are directed to seed production.

These factors obviously influence natural regeneration of disturbed shrublands. When artificial seedings are conducted on fresh mine disturbances these regulatory factors may be relatively less important. Other factors are important as well. Cundell (1977) reported that topsoil microbiota such as vesicular arbuscular mycorrhizae and free-living nitrogen fixers are important for big sagebrush recruitment. Wicklow-Howard (1994) reported that revegetation of severely disturbed lands indicate the presence of mycorrhiza improves survival and growth of host species.

Rubber Rabbitbrush

Rubber rabbitbrush grows best in openings within salt desert shrub, sagebrush, pinyon-juniper, and ponderosa pine communities in sandy, gravelly, or clay-alkaline soils. It is a vigorous early invader of disturbed sites such as roadcuts and heavily grazed rangelands.. On sites where big sagebrush has been destroyed by fire, insects, vehicular traffic, or sustained heavy grazing, rubber rabbitbrush will increase and often become the dominant vegetation (McArthur and Stevens in press). Common rubber rabbitbrush subspecies sometimes grow in mixed stands but little gene exchange occurs between taxa. Where these subspecies grow in mixed stands, the best ecological interpretation is that of a clinal situation. Each subspecies has a preferred habitat but those habitats broadly overlap. For example, white rubber rabbitbrush and threadleaf rubber rabbitbrush often grow together but careful observation shows that white rubber rabbitbrush occupies coarser soils and foothills, whereas threadleaf rubber rabbitbrush prefers heavier soils and bottomlands. The subspecies overlap not only because the habitats overlap but also because they are adapted to establish rapidly on disturbed habitats and their achenes disseminate over relatively long distances.. Therefore ecotonal lines between the subspecies are indistinct (McArthur and Meyer 1987).

Rubber rabbitbrush, like big sagebrush, is ordinarily a prolific seed producer and also produces seed in the fall period. In contrast to big sagebrush, however rubber rabbitbrush seeds are awned and aerially mobile so their seeds disperse much further from the source plant. Seeds from montane populations sometimes exhibit dormancy but lower elevation plants do not. Seed germination patterns most likely represent an integration of genetic and environmental factors (Meyer and McArthur 1987, Meyer et al. 1989). Like big sagebrush the preferred source for seeding rubber rabbitbrush is to match the site to be planted with a seed source as ecologically closely as possible (Meyer et al. 1989). As early seral plants, common rubber rabbitbrush subspecies are well adapted to colonize disturbed habitats, particularly mine wastes and related disturbances. Plants germinate and establish more successfully if the achenes are in contact with the soil and partially buried. In natural situations, the papus of the achene acts as a parachute positioning and anchoring the achene in an upright position which is the optimal position for successful establishment (Stevens et al.1986). Rubber rabbitbrush establishes readily from transplanting in the fall or preferably in the spring to avoid frost heaving if the transplants are dormant, there is adequate soil moisture, and the plants are small ($\leq$ 25 cm) (Stevens 1994, McArthur and Stevens in press).

Case Studies

Two case studies are presented that report on the long term success of seeding big sagebrush and rubber rabbitbrush on disturbed sites. Direct seeding of these species has ranged from poor to excellent in other reported studies, e.g., Van Epps and McKell 1980, Colbert and Colbert 1983, Young et al. 1984, Meyer and Monsen 1990, Monsen and Meyer 1990. Results from these two sites may help to explain the role of both shrubs in rehabilitation projects.

Four-way Exclosure Study

This study, located at the Utah Division of Wildlife Resources Fountain Green Wildlife Management area 8 km north of Fountain Green, Utah, was begin in 1962 as a joint Intermountain Research Station and Utah Division of Wildlife Resources venture. The experimental plots consists of five square areas, each 45.7 m on a side (Stevens 1986). The five areas together have a total area of just larger than a ha (10,442 m^2). The areas were chained to remove pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*) in the fall of 1962. Seeded species included basin big sagebrush and rubber rabbitbrush in a mixture with grasses, forbs, and other shrubs. The seed source for basin big sagebrush was from the pre-treated site and for rubber rabbitbrush was from nearby. Only a few site indigenous plants of both species survived the initial chaining treatment. The five treatment areas were fenced in such a way that one area received no rabbit, deer or cattle use, a second area received deer use only, a third area received only rabbit use, a fourth area received rabbit and deer use, and a fifth area received rabbit, deer and cattle use. All shrubs were mapped, recorded, and measured in 1964, 1973, and 1984. Visual observations have been made more frequently up to 1995. Percent cover of all herbaceous and woody species and production of herbs have also been recorded about every 5 years and are on file at the Great Basin Experimental Range in Ephraim, Utah. Both basin big sagebrush and rubber rabbitbrush have performed well at the site.

There were 52 basin big sagebrush plants at the time of initial post treatment evaluation in 1964. Three of these were mature (> 51 cm high) plants that survived the chaining, 48 were immature (13 - 51 cm high), and there was one seedling (< 13 cm high). In our judgement many of the immature and seedling plants were established after the 1962 seeding. Since big sagebrush plants do not remain viable in the seedbank (Meyer 1994) and the treatment was prior to maturation of current year seed production on the site, we presume that most, perhaps all, of these younger plants came from the seeding. Over time, basin big sagebrush plants have continued to recruit from seed produced by these initial plants so that by 1973 there were 2,018 plants (2% seedlings, 54% immature plants, 44% mature plants). By 1984 the total number of plants had been reduced to 1,646 (5% seedlings, 14% immature plants, 81% mature plants). In 1995 mature plants continue to dominate the site but the other age classes are also present. Cattle grazing on herbaceous plants apparently tilted the competitive balance in favor of basin big sagebrush so that shrub numbers continued to increase longer than in the other treatments where sagebrush numbers began to decline after 1973 (Stevens 1986).

The initial post treatment evaluation in 1964 revealed only nine immature and one mature rabbitbrush (no seedlings). The immature plants probably came from the direct seeding but could have recruited from the margins of the treatment. By 1973 there were 576 plants (9% seedlings, 69% immature plants, 22% mature plants) and by 1984 the number was 371 plants (18% seedlings, 60% immature plants, 22% mature plants). There may have been some replacement of early seral white rubber rabbitbrush by late seral basin big sagebrush. However both species apparently benefited from cattle grazing. In the area where cattle grazed and the competitive herbaceous plants, crested (*Agropyron cristatum*) and intermediate (*Thinopyrun intermedium)* wheatgrasses, were suppressed, rabbitbrush as well as sagebrush continued as more substantive parts of the plant community. By 1995 rubber rabbitbrush has continued to decline where there is a strong understory of crested and intermediate wheatgrasses.

Beacon Pit Mine Experiments

The Beacon Pit Mine is an inactive barite mine about 24 km southeast of Battle Mountain, Nevada. Two studies at this site contribute information about the establishment of big sagebrush and rubber rabbitbrush on disturbed sites. Monsen and Richardson (1984) reported the results of seeding establishment of several shrubs (including Wyoming big sagebrush and white rubber rabbitbrush) and forbs on topsoiled and non-topsoiled areas. Monsen and Meyer (1990) reported on the seeding and establishment of site indigenous Wyoming big sagebrush as part of a widespread, five mine site, big sagebrush establishment study where fresh topsoil was applied. We visited the site in 1994 and noted the condition of the seedings at that time as well.

In the earlier study (Monsen and Richardson 1984), both Wyoming big sagebrush (Blaine Co., Idaho) and white rubber rabbitbrush (Ada Co., Idaho) established well on topsoiled treatments but only the white rubber rabbitbrush established on the non-topsoiled treatments. This seeding took place in December 1979. The later seeding (November 1987) turned out to have propitious timing in that there was a substantive snow pack during the 1987-88 winter and all the treatments had high numbers of seed germination and seedling establishment of big sagebrush. In contrast, the other four mine sites of the study had dry winters and little success in sagebrush seedling establishment occurred (Monsen and Meyer 1990). However, broadcast seeding on a firm seedbed resulted in better spatial seed dispersion and survival of emerged seedlings than drilling or harrowing in broadcast seed. Our 1994 observations indicated that Wyoming big sagebrush that established in both sets of experiments (1979 and 1987) continues to persist and aid in natural community development. The white rubber rabbitbrush seeded in 1979 behaved as early seral in that it established, matured and is declining in importance. We point out that site indigenous white rubber rabbitbrush has also been important in community development by invading disturbances, stabilizing those disturbed sites and waning in importance as other shrubs, notably Wyoming big sagebrush, have attained coverage and maturity. In the non-topsoiled portion of this study an area was seeded to grass and forbs only, the plantings failed, and the site was colonized by white rubber rabbitbrush within four years. Ten years after the initial seeding size class distribution for both rubber rabbitbrush and big sagebrush was determined (Meyer and Monsen 1990). Sixty percent of all white rubber rabbitbrush were classified as adults (height > 30 cm), and less than one percent were seedlings (< 10cm). Approximately 70 percent of the Wyoming big sagebrush plants were classified as adults (> 39 cm). This indicates that rubber rabbitbrush performed as an early colonizer, yet after initial invasion site conditions were ameliorated, permitting subsequent invasion of Wyoming big sagebrush. Meyer and Monsen (1990) concluded that rubber rabbitbrush plants collected fine textured wind-blown soil and organic material which improved seedbed conditions for sagebrush establishment. Once sagebrush plants became established species composition shifted to big sagebrush dominance.

Big sagebrush and rubber rabbitbrush perform somewhat differently in secondary succession on disturbed native rangelands and, as demonstrated in these case history studies, mine wastes. Meyer (1994) discussed the selection pressures of different habitats with life history strategies of big sagebrush. A number of factors influence establishment and subsequent importance of both species in newly created communities.

Synthesis

The primary factors that influence shrub establishment in developing communities are differences in population adaptation; seed germination and establishment requirements; and biotic and abiotic influences on plant establishment. Differences in establishment patterns between big sagebrush and rubber rabbitbrush influence their occurrence in restoration of disturbed sites.

In reestablishing either shrub by seed it is important to plant correct subspecies and to match the collection site and the area to be planted. Although between population differences exist among subspecies of both big sagebrush and rubber rabbitbrush, big sagebrush is less adaptive to infertile soils and disturbances than is rubber rabbitbrush. Big sagebrush may be more sensitive to topsoil microbiota (Cundell 1977). Rubber rabbitbrush will generally establish earlier than will big sagebrush on raw mine disturbances. Big sagebrush is less tolerant of infertile sites than is big sagebrush. Seed germination patterns and seedbed requirements of both shrubs regulates natural recruitment and planting success (Meyer et al. 1989, 1990; Meyer and Monsen 1990, 1991, 1992). Seed maturation and dispersal occurs at the most appropriate period to facilitate natural recruitment in undisturbed shrublands. In contrast, artificial seeding of mine disturbances may occur at dates that are less conducive to seedling establishment. Although seedling establishment of both shrubs may suffer if planted at the wrong season, seedbed requirements of big sagebrush is extremely critical. Big sagebrush seeds are small and require surface or near surface planting. Seeds do not germinate well on gravely or coarse textured soils. In contrast, rubber rabbitbrush seeds attach and germinate well on rough surfaces (Stevens et al. 1986). Big sagebrush seeds are light dependent. Meyer (1994) reported light limits seed germination of big sagebrush populations that occur on cold winter sites. Such seed does not germinate in early fall or mid winter because of light or cold dormancy. In addition, seed germination is controlled by snowpack. Seeds collected form montane sites germinate slowly at near-freezing temperatures, especially in the dark, yet germination rates accelerate when snow levels thin and becomes translucent (Monsen and Meyer 1990, Monsen et al. 1992). These conditions allow seeds to germinate just before or just as snow melts. Monsen and others (1992) demonstrated the importance of snow cover for sagebrush seedling emergence on mine sites by erecting snow fences to trap and hold snow. Snow fence treatments on a site with average winter precipitation increased seedling establishment by six fold over control areas. On a below average precipitation site no sagebrush seedling appeared without snow fencing. McArthur and others noted the importance of and relationship of snow cover in seedling establishment in their hybrid zone studies (Freeman et al. 1991, in press, Graham et al. in press, McArthur unpublished) as well.

Snow entrapment and timing of seeding on mine disturbances is critical to big sagebrush germination and establishment. Open mine sites collect and retain less snow cover than undisturbed shrub stands. Rapid and prolonged drying of soil surfaces is detrimental to big sagebrush seedling survival (McArthur et al. 1988a) but so detrimental to rubber rabbitbrush.

Both big sagebrush and rubber rabbitbrush seedlings can be suppressed by weedy herbs and sod forming perennials (Bleak and Miller 1955, Young and Evans 1989). Another factor is that high seed densities often naturally occur for big sagebrush creating intense competition among big sagebrush seedlings. Monsen and Meyer (1990) found survival of emerged big sagebrush was significantly higher in seeding treatments with greater seed dispersion. Rubber rabbitbrush seedlings appear more competitive with herbaceous species than does big sagebrush. Rubber rabbitbrush plants frequently invade weedy sites and open areas in perennial grass stands. Rubber rabbitbrush plants are able to establish with newly seeded communities on mine sites, and thus become a major component of early developing communities. Big sagebrush often takes longer to establish but establishes well in the presence of established rubber rabbitbrush.

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