GERMINATION AND ESTABLISHMENT ECOLOGY OF BIG SAGEBRUSH: IMPLICATIONS FOR COMMUNITY RESTORATION

Susan E. Meyer

ABSTRACT

Big sagebrush (Artemisia tridentata) *seedling recruitment is limited by seed production and dispersal in space and time, by genetic constraints of specific ecotypes, and by environmental factors that include weather, microsite attributes, soil microbiota, herbivory, and inter- and intraspecific competition. Establishing this species from seed on degraded wildlands requires use of site-adapted ecotypes, manipulation of seedbed conditions to provide favorable microsites, and reduction of early competition from both annual grass weeds and seeded species.*

INTRODUCTION

Big sagebrush (*Artemisia tridentata*) is the regionally dominant shrub on millions of acres of steppe shrub-grassland in the Intermountain West (West 1983). Abusive grazing practices have resulted in the depletion of native perennial bunchgrasses from the shrub-grassland understory over large areas, opening the way for establishment of annual grass weeds such as cheatgrass (*Bromus tectorum*) (Billings 1990). This in turn has set the stage for massive conversion through repeated cycles of wildfire to annual grasslands dominated by exotic species (D'Antonio and Vitousek 1992).

Any effort to restore shrub steppe plant communities now dominated by exotic annual grasses to the structurally complex and species-rich communities that existed in presettlement times must include ecologically sound and effective techniques for reestablishing big sagebrush through direct seeding. By examining factors that affect big sagebrush recruitment in wildland stands as well as in artificial seedings, this paper provides a synthesis of the information currently available to address sagebrush-related restoration problems in shrub-steppe ecosystems.

FACTORS LIMITING RECRUITMENT

Seed Production and Seed Bank Dynamics—The potential annual achene (dry single-seeded fruit hereafter referred to as a seed) production of a single big sagebrush plant may be in the range of 500,000 seeds (Welch and others 1990). But many factors operate to limit production. First, there are genetic constraints at the subspecies and population level (Young and others 1989). Basin big sagebrush (ssp. *tridentata*) plants are potentially larger and more floriferous than those of mountain big sagebrush (ssp. *vaseyana*). Wyoming big sagebrush (ssp. *wyomingensis*) plants are smallest and least floriferous (McArthur and Welch 1982).

Site differences and between-year differences in resource availability (especially water) also play a role in seed production (Young and others 1989). Basin big sagebrush populations in bottoms that receive run-on moisture often set large seed crops every year. Xeric upland Wyoming big sagebush stands may set very little seed except in wet years. High-elevation mountain big sagebrush stands usually set seed every year, but seed production per plant is not necessarily high.

Intraspecific competition within a stand may also affect flowering intensity and seed set, especially in dry years. Young and others (1989) found that big sagebrush individuals in weeded, spaced plantings set more seed than plants of in situ populations at five arid sites in northwestern Nevada. Seed production was one to two orders of magnitude lower in the Nevada plantings than in a seed orchard on a mountain big sagebrush site in northern Utah (Welch and others 1990).

Because it is partially self-fertile, isolated plants of big sagebrush can set seed in the absence of any nearby source of pollen (McArthur and others 1988). Thus seed set is probably not strongly pollen-limited in this wind-pollinated species even in years when flowering is sparse. Seed production variation between individuals is also seen in field cultivation where resource limitation is not a factor (Welch and others 1990).

Plant disease can affect flowering or seed set. Stem rust fungi may reduce seed yield in field cultivation and probably play a similar role in native stands (Nelson 1992). Insect predispersal seed predators and herbivores like thrips that feed on flower parts may also reduce effective seed set. Disease or parasitic insect agents responsible for gradual dieback and ultimate death of individual plants may lower whole-plant vigor so that flowering is reduced or eliminated, resulting in senescent or decadent stands.

Excessive browsing by ungulates can have a major effect on seed stalk production. This impact may be especially great for remnant individuals on heavily used mule deer winter ranges. On a mountain big sagebrush site near Hobble Creek, UT, protection from browsing for a

single winter resulted in a 20-fold increase in number of seed stalks the following fall, and successive years of protection resulted in a progressive increase in seed production for 6 years (Wagstaff and Welch 1990, 1991).

Seed Dispersal in Space and Time—Sagebrush seeds are very small (average weight 0.018 g/100 seeds for ssp. *tridentata*, 0.025 g/100 seeds for ssp. *vaseyana* and *wyomingensis*; Meyer and others 1987). They are dispersed by wind over some distance, even though they possess no special adaptations for wind dispersal. Maximum reported dispersal distances are in the range of 30 m, but most seeds (85-90 percent) fall within 1 m of the canopy edge (Wagstaff and Welch 1990; Young and Evans 1989a). Seedling recruitment studies showing concentrations of seedlings farther out from the mother plant on the windward side illustrated the effect of wind direction in dispersal (Wagstaff and Welch 1990). Mueggler (1956), Frischknecht and Bleak (1957), and Johnson and Payne (1968) all emphasized the ineffectiveness of long-distance dispersal by wind as a means of recolonization on large forage grass seedings or burns. The importance of residual plants not killed at the time of treatment as a source of seeds for reinvasion of forage grass seedings by big sagebrush has been clearly established (Frischknecht and Bleak 1957; Johnson and Payne 1968).

Most big sagebrush seeds produced in a given autumn are gone from the soil seed bank by late spring of the following year (Young and Evans 1989a). Seed retrieval and emergence studies have shown that the great majority of seeds are lost from the seed bank through germination in winter or spring (Meyer 1990; Young and Evans 1989a). Postdispersal loss to rodents appears minimal, possibly because of small seed size (Latourette and others 1971).

A small fraction of big sagebrush seeds may sometimes persist over the summer following dispersal, as evidenced by second-year emergence in artificial seedings (Monsen and Richardson 1986; Welch 1993) and the presence of small quantities of seeds in summer seed bank samples. Hassan and West (1986) found a small fraction of viable big sagebrush seeds in seed bank samples even after a summer burn, lending credence to the conclusion of Mueggler (1956) that postburn establishment was from an in situ seed bank. Young and others (1989) were unable to detect viable seeds in postburn seed bank samples but reported seedling establishment at very low densities (1 plant/1,000 m²) on the burn.

Neither Hassan and West (1986) nor Young and Evans (1975) detected a winter peak in seed numbers, presumably because seed production was very low or absent on site in the years of sampling in their studies. In a later study, Young and Evans (1989a) found that seed bank numbers peaked in January a few weeks after the initiation of dispersal.

The fraction of seed that enters the persistent seed bank is probably much less than 1 percent, but given the sometimes prodigious seed production, this tiny fraction is potentially significant. Because of the germination ecology of the species, persistence over more than a single summer is extremely unlikely. Big sagebrush seed is relatively short-lived in warehouse storage, a characteristic often associated with formation of transient or only weakly persistent soil seed banks (Stevens and others 1981).

Another contributor to loss from the effective seed bank is dispersal to microsites where successful emergence is impossible, as into the deep duff under juniper trees. Because of their small size and limited reserves, placement of seeds at depths exceeding 5 mm during artificial seeding probably effectively removes them from the seed bank (Jacobson and Welch 1987). Natural processes such as freeze-thaw and wet-dry cycles may also sometimes result in deep burial.

SEEDLING ESTABLISHMENT AND SURVIVAL

Genetic Factors—There are major genetically based differences among subspecies and ecotypes of big sagebrush with regard to both seed germination and seedling establishment traits. These differences are correlated with the selection pressures of different habitats and with a variable life history strategy.

Using a community composition approach, Bonham and others (1991) found evidence to support the idea that the three major subspecies represent different life history strategies in spite of their basic similarity in habit and reproductive biology. Using the classification system of Grime (1977, 1984), they determined that for populations in the Piceance Basin of western Colorado, basin big sagebrush should have a more ruderal or colonizing strategy, mountain big sagebrush should have a more competition-based strategy, and Wyoming big sagebrush should have a strategy based on the ability to tolerate abiotic stress. The prolific seed production and smaller seeds of basin big sagebrush do seem to be the attributes of a colonizing taxon. The regular, but not necessarily large, seed production of mountain big sagebrush could be based on the predictable need to invest a high proportion of energy into vegetative growth in the face of competition. The sporadic seed production of Wyoming big sagebrush populations could be interpreted to mean that resources fluctuate unpredictably. In high-stress years, all resources are needed to maintain vegetative growth; in low-stress years the extra may be allocated to sexual reproduction.

Growth rates of the three subspecies also tend to support this life history strategy interpretation. Mountain big sagebrush growth rates are faster than those of Wyoming big sagebrush but slower than those of basin big sagebrush when even-aged plants are grown in a common garden setting (McArthur and Welch 1982). These differences in growth rates parallel differences in absolute size at maturity.

Growth rate differences are present even in the early seedling stages. Welch and colleagues (Booth and others 1990; Welch and Jacobson 1988) found that Wyoming big sagebrush seedlings had the lowest maximum growth rates and reached this maximum earliest. Their relatively rapid early shoot growth was accompanied by more rapid root elongation than in the other two subspecies. The seedlings showed no further increase in shoot height after 15 weeks in the greenhouse, even though resources were not limiting. This seedling strategy appears to be

an adaptation for sites that dry quickly in the spring, xeric upland sites where abiotic drought stress is the most serious threat to seedlings.

Basin big sagebrush seedlings had the most rapid shoot growth rate at 7 weeks and continued to have a positive growth rate for the full 24 weeks of the experiment, reaching heights three times the heights of Wyoming big sagebrush seedlings. But their rate of early root elongation was less than that of Wyoming big sagebrush. They invested in shoot growth at the expense of root growth at least in the early stages and showed a highly plastic response to the continued availability of resources. This strategy appears to be an adaptation to relatively resource-rich and frequently disturbed environments such as floodplains, where opportunistic growth patterns permit continued growth as long as conditions remain favorable, increasing the probability of seed production early in life. Floodplain sites would also dry out more slowly, allowing the seedlings to harden gradually.

Mountain big sagebrush seedlings showed a third pattern of growth. Early root elongation was slowest and root length at 24 weeks was least of the three subspecies; shoot growth rate was intermediate. This seedling strategy appears to be an adaptation to relatively mesic but densely vegetated sites, where competition may be for some belowground resource other than water. Maximum root length may not be as important as root proliferation in the shallow soil layers where nutrients are concentrated. Shoot growth rate must be fast enough to permit survival in an environment that could become light limited in summer, but there is no advantage to an extremely plastic response in an environment where resources are predictably limited.

These seedling studies (Booth and others 1990; Welch and Jacobson 1988) described differences at the subspecies level; each subspecies was represented by four to five accessions from throughout the range. While between-population differences within a subspecies were not discussed, one can infer from the experimental error structure that these differences must have been minimal. Harniss and McDonough (1975), in work with a single accession of each subspecies, failed to detect any subspecies difference, possibly because of small container size and overwatering (Welch 1993).

Patterns of variation in big sagebrush seed germination traits, on the other hand, are much more strongly correlated with habitat attributes at the population level than they are with subspecies identity (Meyer and Monsen 1991, 1992; Meyer and others 1990; Young and Evans 1989b). Big sagebrush seed germination biology at the species and subspecies level has been characterized by several workers (Harniss and McDonough 1976; McDonough and Harniss 1974a,b; Payne 1957; Weldon and others 1959; Young and Evans 1991). The seeds are usually nondormant at harvest though they often require light. Primary dormancy that is removed by moist chilling has been reported mostly for montane populations of mountain big sagebrush (McDonough and Harniss 1974b; Meyer and Monsen 1991). The light requirement of nondormant seeds may be removed through chilling or dry-afterripening (Meyer and others 1990). The seeds germinate over a wide array of temperatures, including many

in the higher range. As pointed out by Young and Evans (1991), germination of big sagebrush seeds by early spring is virtually certain in this fall-seeding species, so that germination response at higher temperatures is largely irrelevant ecologically. Differences among subspecies and ecotypes that are ecologically relevant have to do with responses to conditions likely to be encountered by the seeds between the time of dispersal and the optimum time for germination in a given habitat.

The mortality risk to seedlings when autumn-produced seeds germinate prior to spring is likely to vary as a function of climate. Seeds from populations at cold winter sites are produced early in the fall and require mechanisms to reduce the probability of germination under both fall and early winter conditions. Mechanisms to limit autumn germination include dormancy that is not removed by short moist chilling, slow germination (requiring more than 10 days to reach 50 percent) at autumn temperatures, and a light requirement that limits germination under the more favorable moisture regime of the shallow subsurface. These mechanisms are found in high-elevation mountain big sagebrush populations, on sites where autumn storms are the norm (Meyer and Monsen 1991, 1992; Meyer and others 1990). High-elevation Wyoming big sagebrush seeds lack dormancy and slow rate mechanisms but have a light requirement; their sites are generally autumn-dry, so surface emergence is unlikely (Meyer and Monsen 1992; Meyer and others 1990).

The likelihood of germination during winter at montane sites is controlled by germination behavior under snowpack. Germination rate at near-freezing temperatures is slow (more than 100 days required to reach 50 percent) in seeds from long-winter sites for all three subspecies, especially in the dark (Meyer and Monsen 1991, 1992; Meyer and others 1990). Its rate accelerates when the snow thins enough to become translucent, signaling the approach of the optimum time for emergence. In this way germination takes place just before or just as the snow is melting.

The germination timing scenario for big sagebrush seeds at mild winter, warm desert fringe sites is quite different. Seeds are dispersed in early winter. Winter conditions are optimal for seedling establishment; early emergence is an advantage in a habitat where snowpack does not persist and the risk of early spring drought exceeds risks associated with freezing. Seeds from all subspecies on these kinds of sites are nondormant and have rapid germination rates at both cool and near-freezing temperatures (Meyer and Monsen 1992). Fifty percent may germinate under near-freezing conditions in as few as 10 days. They also tend to be less light requiring (Meyer and others 1990).

These studies with seeds from 70 populations of big sagebrush from a wide geographic range show that germination regulation functions predictively to time germination to immediately precede or coincide with conditions that are optimal for seedling establishment. Field emergence studies indicate that most emergence takes place immediately in the wake of spring snowmelt (Meyer and Monsen 1990b; Wagstaff and Welch 1990; Young and others 1990).

Emergence studies may not be able to demonstrate that between-population differences in germination traits are related to different fitness consequences at a particular site in a given year (Meyer and Monsen 1990a,b; Young and others 1990). Risks to seedlings are stochastic in nature; sometimes the weather events that germination timing mechanisms have evolved to contravene may not take place. And the optimization of timing does not by any means guarantee success every year, even on the native site.

Big sagebrush seeds have no clear mechanism for between-year carryover of any major seed fraction, but a few seeds may retain their light requirement even after chilling (Meyer and others 1990). Shallowly buried seeds with a light requirement probably account for the small amount of carryover that sometimes takes place.

Environmental Factors—Even though ecotypes of big sagebrush have seed germination and seedling growth patterns that are site-adapted to maximize the chances of seedling establishment, the vast majority of sagebrush seedlings that emerge are not recruited into the population. Many environmental factors, both abiotic and biotic, act to restrict recruitment.

A primary factor in seedling mortality is undoubtedly the weather. Any weather event or sequence that pushes seedling-zone environmental conditions beyond the range of tolerance can cause mortality. Newly emerged seedlings are remarkably frost tolerant, as they must be to survive emergence in the very early spring, but late spring frosts, when the seedlings are no longer hardy, may be a significant cause of mortality (Meyer and Monsen 1990a). Many seedling deaths attributed to frost may actually be a result of damping-off diseases or mechanical damage associated with frost heaving.

Drought is a principal cause of seedling mortality. Again, timing is important. Especially on xeric Wyoming big sagebrush sites, seedlings must be able to survive summer drought to establish, regardless of the year. But they need sufficient time to become drought hardy. Early or protracted drought can cause mortality. Sagebrush seedlings established on mine sites where there is little competition may have remarkably high first-year survival rates through summer drought periods (Monsen and Meyer 1990; Monsen and Richardson 1986).

Another key weather variable is amount and timing of winter snowfall. In a seeding experiment on a series of semiarid mine sites, a single late-winter snowfall made the difference between zero emergence at one site and emergence as high as 80 percent of seeds sown at another similar site (Monsen and Meyer 1990). It appears that emergence is rarely achieved except when winter snow cover is present. Early spring watering on part of the unsuccessful seeding did not result in emergence, and there was no emergence the following year, which had adequate winter snowpack.

Artificial big sagebrush seedings on large disturbances such as burns sometimes fail even when natural recruitment takes place in adjacent native stands (Monsen 1992). This is true even when good seedbed conditions are created and competition is controlled. It may be that extra snow accumulation in the lee of adult shrubs

accounts for much of the difference in recruitment success (Sturges and Tabler 1981).

Monsen and others (1992) tested the idea of enhancing big sagebrush establishment using snow harvesting. The study, which was carried out at three semiarid mine sites, included a factorial combination of snowfencing and crimped straw mulch treatments. Seedling emergence was increased by a factor of six in the snowfence treatments at a site with average winter precipitation; up to 60 percent of sown seed emerged. At a site with record high winter precipitation, there was no effect from either snowfencing or mulch, and emergence averaged 30 percent of sown seed. At a site with below-average precipitation, maximum emergence (10 percent of sown seed) was observed in snowfencing treatments with or without straw mulch, with a lower percentage (7 percent) on the straw mulch only treatment. On this site there was no emergence at all without some form of snow harvesting. These results strongly suggest that snow harvesting, whether by in situ vegetation or by structures, can increase big sagebrush emergence in years of average or below-average winter precipitation. It also supports the idea that successful emergence is dependent on snow cover.

Because they are surface or near-surface emerging, big sagebrush seeds are very sensitive to microsite conditions. The pericarp wall that is somewhat gelatinous when wet and the hypocotyl hairs help fix the germinating seed to the surface and permit the radicle to penetrate the soil (Young and Martens 1991).

Young and others (1990) showed, through the use of an elaborate experimental design that involved reciprocal soil transport among five sites on an elevational gradient, that soil surface characteristics are sometimes as important as winter precipitation for big sagebrush seedling emergence. The best soil for emergence was one that combined silts and clays in the top 2-mm fraction with a high gravel content; more uniformly sandy granitic soils were generally not as favorable. The authors hypothesized that the surface characteristics of the most favorable soil, which was from a site at the extreme dry end for big sagebrush, might be the key factors that made establishment possible on this site. Surface characteristics changed during the course of the winter, and surface features when the plots were broadcast seeded in the fall had more effect on emergence than spring surface features. The idea of a gravel mulch to improve water relations for establishment was also supported in an earlier study, where a surface mulch of glass marbles also increased emergence (Young and Evans 1986).

Application of topsoil often improves seedling success on semiarid mine spoils. In a study at the Beacon Pit Mine in central Nevada, Monsen and Richardson (1984) seeded shrubs, grasses, and forbs onto a rock waste dump with and without topsoil. Most species established better on topsoiled sites, but big sagebrush results were unequivocal—no seedlings established unless topsoil was present. In a no-topsoil area that was seeded to grasses and forbs only, the seeding failed, and the area was subsequently colonized by rubber rabbitbrush (*Chrysothamnus nauseosus*). Ten years after the initial seeding, size class distributions for rubber rabbitbrush and big sagebrush

were obtained from this area (Meyer and Monsen 1990b). Over 60 percent of the rubber rabbitbrush individuals were in adult size classes (height >30 cm), and less than 1 percent were <10 cm. About 70 percent of the big sagebrush plants, on the other hand, were in the <30-cm size classes. This suggests that, after initial invasion by rubber rabbitbrush, site conditions were ameliorated, permitting subsequent colonization by big sagebrush. The rabbitbrush plants formed coppices of finer textured windborne material and organic matter, improving the seedbed microenvironment for sagebrush emergence and establishment. The presence of topsoil microbiota, such as vesicular arbuscular mycorrhizae and free-living nitrogen fixers, may also be important for big sagebrush recruitment (Cundell 1977).

Probably the most-researched aspect of big sagebrush seedling recruitment is the role of interplant competition. Few of these studies have taken place in established big sagebrush stands, however. Within-species competition is probably important in restricting seedling recruitment in closed stands, though the interaction may be as much between adults at the flowering and seed production stage as between adults and seedlings. Stand thinning using chaining resulted in an exponential increase in seed production by surviving Wyoming big sagebrush plants under drought conditions in a pinyon-juniper woodland in eastern Utah (Davis 1992).

Reichenberger and Pyke (1990) reported on a study using hollow tubes of varying depth to give establishing seedlings varying degrees of protection from matrix vegetation root competition. They found that establishing Wyoming big sagebrush seedlings on a dry site and mountain big sagebrush seedlings on a more mesic site were both more negatively impacted by competition from a matrix of adult big sagebrush plants than by competition from either native bluebunch wheatgrass or introduced crested wheatgrass vegetation. Owens and Norton (1989) found that postseedling juvenile survival was a function both of initial plant size and gap size. Shelter from the canopy of an adult individual increased survival as long as gap size was large.

Because of high seed densities and synchronous germination, intense competition between big sagebrush seedlings probably accounts for much of the initial mortality as the soil dries out in late spring. In a study with different pieces of seeding equipment on a mine disturbance, Monsen and Meyer (1990) found that survival of emerged seedlings was significantly higher in seeding treatments that resulted in greater spatial dispersion of seeds. This suggests that a major cause of mortality was intraspecific mortality or self-thinning in treatments where seedlings tended to be more closely spaced. Owens and Norton (1990) found that cohort density up to 30 individuals/m² had no effect on survival rates for postseedling juveniles, perhaps because initial self-thinning had already taken place. Mortality was concentrated in the smaller size classes, however.

Most of the work on interspecific competition effects on big sagebrush establishment was undertaken to understand how to prevent establishment. The useful life of a forage grass seeding on sagebrush range is determined in part by the rate of reestablishment of the eradicated

shrub species (Blaisdell 1949; Pechanec and others 1944). A great deal of useful knowledge about big sagebrush establishment ecology was generated.

One of the first generalizations to emerge was that if eradication took place too late in the fall, the effect was to plant big sagebrush along with the seeded grass species (Bleak and Miller 1955; Frischknecht and Bleak 1957; Johnson and Payne 1968). This showed that big sagebrush (basin big sagebrush in most of these cases) could establish along with crested wheatgrass in years when late-season precipitation was above average. Once the crested wheatgrass was well established, it could effectively exclude further big sagebrush recruitment even in the face of seed production by residual plants. If the crested wheatgrass stand was thin because of poor initial emergence or heavily grazed, sagebrush recruitment would continue.

In their study in Ruby Valley, NV, Frischknecht and Bleak (1957) found that seeded bluebunch wheatgrass stands in good condition were more likely to permit big sagebrush recruitment than crested wheatgrass stands in similar condition. This result parallels the experimental results of Reichenberger and Pyke (1990) at Curlew Valley, the Wyoming big sagebrush site. At the mountain big sagebrush site, however, their experimental results indicated that competition from bluebunch wheatgrass was more severe than from crested wheatgrass, although both had a significant negative effect on survival.

Johnson and Payne (1968) found no relationship between grass density and sagebrush reestablishment rates on a series of forage grass seedings in southwestern Montana. They gave no indication of grazing intensity. Date of treatment and presence of residual plants not initially killed were the main factors affecting seedling recruitment. They found increased recruitment rates on finer textured (silty) soils and on more mesic northwest slopes in some cases.

Owens and Norton (1990) found that juvenile survival was higher in short-duration grazing pastures than under continuous spring grazing. Richardson and others (1986) compared grazed and ungrazed treatments 7 years after seeding mountain big sagebrush with grasses and forbs on a mid-elevation mine site in southeastern Idaho. They found significantly lower big sagebrush plant densities in the grazed treatment, an effect they attributed at least partially to trampling.

Richardson and others (1986) also examined the effect of different grass mix seeding rates on shrub establishment. Mountain big sagebrush was better able to establish in competition with a mix dominated by crested and intermediate wheatgrass than was antelope bitterbrush, but was unable to establish when grass mix seeding rates exceeded 12 lb/acre. Recruitment increased dramatically when shrubs were seeded alone.

The effect of exotic annual grasses such as cheatgrass in limiting field recruitment of big sagebrush (and most other native shrubs) has been observed countless times, but few quantitative studies have documented this effect. Young and Evans (1989a) reported no new recruitment of big sagebrush over a 4-year period at five sites with cheatgrass-dominated understories in northwestern Nevada, in spite of the fact that some emergence took

place every year. Wagstaff and Welch (1990) carried out an experimental study that examined the effects of tillage and protection from browsing on natural recruitment of mountain big sagebrush around remnant maternal plants on heavily disturbed mule deer winter range on the Wasatch Front. They found that no tillage and early till-age treatments resulted in a total lack of recruitment, while late fall tillage (after cheatgrass emergence) re-sulted in seedling densities that were directly correlated with maternal plant seedstalk production. Seedling sur-vival through the first summer was very high. These studies, as well as numerous observations from through-out the cheatgrass problem area in the Intermountain West, demonstrate the futility of seeding big sagebrush onto cheatgrass-infested wildlands without some strategy for cheatgrass control.

IMPLICATIONS FOR COMMUNITY RESTORATION

Some argue the feasibility or even the desirability of restoring semiarid shrub-grasslands that have been con-verted to exotic annual grassland. It is true that the mil-lions of acres in the Intermountain West that have under-gone this conversion or are on the brink of conversion through wildfire present a daunting spectacle to the restorationist. Any method that is likely to be used over an area of significant size must be inexpensive on a per-acre basis. This limits the practical options to direct seeding.

In reestablishing big sagebrush from seed, the first choice is of a source of seed to plant. It is of paramount importance not only to plant the correct subspecies, the same one that was native onsite predisturbance, but also to match seed collection site and seeding site habitat characteristics as closely as possible. This means collec-tion of the seed from a known wildland stand, preferably one not far from the seeding site. On large disturbances, onsite collection of seed is usually not possible, but it might be possible to collect from remnant plants and use the seed to start a seed production field (Welch and others 1990). Another possibility is to manage wildland stands in situ to increase seed production, perhaps through stand thinning.

The seed should be spot checked for quality prior to large-scale harvest, harvested when fully ripe, carefully cleaned (excessive heat or handling can damage the seed), and stored under cold dry conditions (<10 °C, 6-8 percent moisture content) until use. Purity of commercial lots of big sagebrush seed averages 10 to 20 percent. Because of its small size, it is usually seeded with a carrier, so clean-ing to any higher purity may not be cost-effective or nec-essary. Viability of recently harvested seed should be in the 85 to 95 percent range. Properly stored seed should remain viable for at least 5 years if it was initially of high viability. Viability should be rechecked with a germina-tion test immediately before seeding to determine seeding rates on a pure live seed (PLS) basis. Seeding rates in the range of 0.25 to 0.5 lb/acre PLS are appropriate.

Big sagebrush seed should be surface planted or planted with very light coverage on a firm (not hard or compacted) seedbed. Broadcast seeding is usually as effective as any other method. Site preparation or planting methods that create a loose, sloughing seedbed should be avoided, as they can result in poor soil-seed contact or planting too deep. But some surface roughness to create a variety of microsites is encouraged. Sagebrush seed should not be drill seeded.

The best season for planting is late fall, just before the first winter snowfall, when big sagebrush would naturally be dispersing onsite. Broadcast seeding onto snow in win-ter may be very successful. Spring seeding should be avoided.

If the sagebrush is to be seeded in a mix with other spe-cies, it may be helpful to separate different components, as in different drop boxes on the seeder, especially if the mix includes fast-growing perennial grass species. This may be less necessary when seeding with native grasses rather than introduced forage grasses bred for rapid seed-ling growth rate. Seeding rates for the more competitive species should be kept relatively low, especially if spatial segregation is not possible, as in aerial broadcast seeding.

Soil fertility may affect the outcome of a seeding. Higher fertility favors faster growing species more plastic in their response to nutrient supply. Shrub seedlings have more opportunity to obtain the water they need to survive the first summer when low fertility keeps competing seedlings smaller.

No truly satisfactory method for controlling weed com-petition on large-scale big sagebrush plantings has been developed. Methods currently in use include summer burning while weed seed heads are still on the plants, till-age or herbicide treatment after fall greenup, and scalp-ing to remove weed seed-infested soil from the immediate vicinity of the planted seeds. These methods may or may not create a good seedbed for big sagebrush.

Not all weeds are equally damaging to big sagebrush seedling survival. Russian thistle (*Salsola pestifer*) can actually act as a nurse plant. Annual grasses such as cheatgrass inevitably have a negative effect, as mentioned earlier.

Another more long-term strategy for big sagebrush es-tablishment is the idea of first establishing early seral species, such as squirreltail (*Elymus elymoides*, formerly *Sitanion hystrix*), that appear to be better able to compete with exotic annual grasses. Once early seral natives take hold and dominate the site, big sagebrush could then be seeded along with late-seral understory species.

The use of snow harvesting techniques to increase odds of big sagebrush establishment may be justified if the site is in a precipitation zone where winter snowpack is un-likely to be sufficient without manipulation. The sage-brush could be spot-seeded near snow-trapping structures or in topographic positions where extra snow is likely to accumulate naturally. Once a small stand is established, the shrubs themselves will act as snow traps and seed sources that enhance shrub recruitment downwind in sub-sequent years. As long as the matrix vegetation is made up of species that permit some recuitment, and other fac-tors such as browsing by deer are not limiting, the shrub population should continue to extend itself through time. Other possibilities are seedbed manipulation such as contour furrowing to increase snow accumulation or an

annual cover crop (preferably one not capable of persisting on the site) to create snow-trapping stubble.

The art and science of ecological restoration are still in their infancy. But much of the information acquired over the last 80 years in the name of range improvement can be utilized and reinterpreted in the light of a new set of public land management goals that place the health and diversity of natural ecosystems at the top of the list of priorities. The opportunity and responsibility we have to take part in this redirection of research efforts is truly exciting and challenging.

ACKNOWLEDGMENTS

REFERENCES

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In: Woodell, G. M., ed. The earth in transition: patterns and processes of biological impoverishment. Cambridge, UK: Cambridge University Press: 301-322.

Blaisdell, J. P. 1949. Competition between sagebrush seedlings and reseeded grasses. Ecology. 30: 512-519.

Bleak, A. L.; Miller, W. G. 1955. Sagebrush seedling production as related to time of mechanical eradication. Journal of Range Management. 8: 66-69.

Bonham, C. D.; Cottrell, T. R.; Mitchell, J. E. 1991. Inferences for life history strategies of *Artemisia tridentata* subspecies. Journal of Vegetation Science. 2: 339-344.

Booth, G. D.; Welch, B. L.; Jacobson, T. L. C. 1990. Seedling growth rate of 3 subspecies of big sagebrush. Journal of Range Management. 43: 432-436.

Cundell, A. M. 1977. The role of microorganisms in the revegetation of strip-mined land in the Western United States. Journal of Range Management. 30: 299-305.

D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 23: 63-87.

Davis, J. N. 1992. [Personal communication]. Provo, UT: Utah Division of Wildlife Resources, Shrub Sciences Laboratory.

Frischknecht, N. C.; Bleak, A. T. 1957. Encroachment of big sagebrush on seeded range in north-eastern Nevada. Journal of Range Management. 10: 165-170.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist. 111: 1169-1194.

Grime, J. P. 1984. The ecology of species, families, and communities of the contemporary British flora. New Phytologist. 98: 15-33.

Harniss, R. O.; McDonough, W. T. 1975. Seedling growth of three big sagebrush subspecies under controlled temperature regimens. Journal of Range Management. 28: 243-244.

Harniss, R. O.; McDonough, W. T. 1976. Yearly variation in germination of three subspecies of big sagebrush. Journal of Range Management. 29: 167-168.

Hassan, M. A.; West, N. E. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology. 67: 269-272.

Jacobson, T. L. C.; Welch, B. L. 1987. Planting depth of 'Hobble Creek' mountain big sagebrush seed. Great Basin Naturalist. 47: 497-499.

Johnson, J. R.; Payne, G. F. 1968. Sagebrush reinvasion as affected by some environmental influences. Journal of Range Management. 21: 209-213.

Latourrette, J. E.; Young, J. A.; Evans, R. A. 1971. Seed dispersal in relation to rodent activities in seral big sagebrush communities. Journal of Range Management. 24: 118-120.

McArthur, E. D.; Welch, B. L. 1982. Growth rate differences among big sagebrush (*Artemisia tridentata*) accessions and subspecies. Journal of Range Management. 35: 396-401.

McArthur, E. D.; Welch, B. L.; Sanderson, S. L. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268-276.

McDonough, W. T.; Harniss, R. O. 1974a. Effects of temperature on germination in three subspecies of big sagebrush. Journal of Range Management. 27: 204-205.

McDonough, W. T.; Harniss, R. O. 1974b. Seed dormancy in *Artemisia tridentata* Nutt. ssp. *vaseyana* Rydb. Northwest Science. 48: 17-20.

Meyer, S. E. 1990. Seed source differences in germination under snowpack in northern Utah. In: Fifth Billings symposium on disturbed land rehabilitation; Vol. I; Hardrock waste, analytical, and revegetation. Reclamation Research Unit Publ. 9003. Bozeman, MT: Montana State University: 184-191.

Meyer, S. E.; Kitchen, S. G.; Wilson, G. R.; Stevens, R. 1987. Supporting evidence for the proposed rule for *Artemisia tridentata*, big sagebrush. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Meyer, S. E.; Monsen, S. B. 1990a. Seed germination and establishment ecology of big sagebrush and rubber rabbitbrush, and its relationship to artificial seeding success. Unpublished report on file at: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Meyer, S. E.; Monsen, S. B. 1990b. Seed source differences in initial establishment for big sagebrush and rubber rabbitbrush. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT- 276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 200-208.

Meyer, S. E.; Monsen, S. B. 1991. Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seed germination patterns. Ecology. 72: 739-742.

Meyer, S. E.; Monsen, S. B. 1992. Big sagebrush germination patterns: subspecies and population differences. Journal of Range Management. 45: 87-93.

Meyer, S. E.; Monsen, S. B.; McArthur, E. D. 1990. Germination response of *Artemisia tridentata* (Asteraceae) to light and chill: patterns of between-population variation. Botanical Gazette: 151: 176-183.

Monsen, S. B. 1992. [Personal communication]. Provo, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory.

Monsen, S. B.; Meyer, S. E. 1990. Seeding equipment effects on establishment of big sagebrush on mine disturbances. In: Fifth Billings symposium on disturbed land rehabilitation; Vol. I; Hardrock waste, analytical, and revegetation. Reclamation Research Unit Publ. 9003. Bozeman, MT: Montana State University: 192-199.

Monsen, S. B.; Meyer, S. E.; Carlson, S. L. 1992. Sagebrush establishment enhanced by snowfencing. In: Rangeland Technology Equipment Council 1992 annual report. Washington, DC: U.S. Department of Agriculture, Forest Service, Technology and Development Program 2200-Range: 6-8.

Monsen, S. B.; Richardson, B. Z. 1986. Seeding shrubs with herbs on a semiarid minesite with and without topsoil. In: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., eds. Proceedings—symposium on the biology of *Atriplex* and related chenopods. Gen. Tech. Rep. INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 298-305.

Mueggler, W. F. 1956. Is sagebrush seed residual in soil or is it windborne? Res. Note 35. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 10 p.

Nelson, D. L. 1993. [Personal communication]. Provo, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory.

Owens, M. K.; Norton, B. E. 1989. The impact of 'available space' on *Artemisia tridentata* seedling dynamics. Vegetatio. 82: 155-162.

Owens, M. K.; Norton, B. E. 1990. Survival of juvenile basin big sagebrush under different grazing regimes. Journal of Range Management. 43: 132-135.

Payne, G. F. 1957. Some germination studies of *Artemisia tridentata*. Montana Academy of Science Proceedings. 17: 41-42.

Pechanec, J. F.; Plummer, A. P.; Robertson, J. H.; Hull, A. C. 1944. Eradication of big sagebrush (*Artemisia tridentata*). Res. Pap. 10. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 23 p.

Reichenberger, G.; Pyke, D. A. 1990. Impact of early root competition on fitness components of four semiarid species. Oecologia. 85: 159-166.

Richardson, B. Z.; Monsen, S. B.; Bowers, D. M. 1986. Interseeding selected shrubs and herbs on mine disturbances in southeastern Idaho. In: McArthur, E. D.; Welch, B. L., eds. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 134-139.

Stevens, R.; Jorgensen, K. R.; Davis, J. N. 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Naturalist. 41: 274-277.

Sturges, D. L.; Tabler, R. D. 1981. Management of blowing snow on sagebrush rangelands. Journal of Soil and Water Conservation. 36: 287-292.

Wagstaff, F. J.; Welch, B. L. 1990. Rejuvenation of mountain big sagebrush on mule deer winter ranges using onsite plants as a seed source. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 171-174.

Wagstaff, F. L.; Welch, B. L. 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal of Range Management. 44: 72-74.

Welch, B. L.; Jacobson, T. L. C. 1988. Root growth of *Artemisia tridentata*. Journal of Range Management. 41: 332-334.

Welch, B. L.; Wagstaff, F. J.; Jorgensen, G. L. 1990. 'Hobble Creek' mountain big sagebrush seed production. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 167-170.

Weldon, L. W.; Bohmont, D. W.; Alley, H. P. 1959. The interrelation of three environmental factors affecting germination of sagebrush seed. McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Journal of Range Management. 12: 236-238.

West, N. E. 1983. Temperate deserts and semideserts. Ecosystems of the world, 5. Amsterdam: Elsevier Scientific Publishing Company.

Young, J. A.; Evans, R. A. 1975. Germinability of seed reserves in a big sagebrush community. Weed Science. 23: 358-364.

Young, J. A.; Evans, R. A. 1986. Seedling establishment of five sources of big sagebrush in reciprocal gardens. In: McArthur, E. D.; Welch, B. L., eds. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 370-374.

Young, J. A.; Evans, R. A. 1989a. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. Weed Science. 37: 201-206.

Young, J. A.; Evans, R. A. 1989b. Reciprocal common garden studies of the germination of seeds of big sagebrush (*Artemisia tridentata*). Weed Science. 37: 319-325.

Young, J. A.; Evans, R. A. 1991. Temperature profiles for germination of big sagebrush seeds from native stands. Journal of Range Management. 44: 385-389.

Young, J. A.; Evans, R. A.; Palmquist, D. E. 1989. Big sagebrush (*Artemisia tridentata*) seed production. Weed Science. 37: 47-53.

Young, J. A.; Evans, R. A.; Palmquist, D. E. 1990. Soil surface characteristics and emergence of big sagebrush seedlings. Journal of Range Management. 43: 358-366.

Young, J. A.; Martens, E. 1991. Importance of hypocotyl hairs in germination of *Artemisia* seeds. Journal of Range Management. 44: 438-442.