THE ADAPTATION OF HIGH ELEVATION PLANTS TO LOW ELEVATION GROWTH¹

Richard Dunne²

Abstract. From 1999 to 2002 we gathered seed from 19 perennial species deemed critical for roadside revegetation of the Beartooth highway in Wyoming and Montana, 40 miles northeast of the east entrance to Yellowstone. Collection elevations ranged between 2,895 and 3,322 meters during mid August to early September as seed ripened. In 2001 and 2002 we transplanted 38,000 tubelings for seed production at a farm in the Big Horn Basin of Wyoming with an elevation of 1,230 meters. After four years of production the field grow-out was cancelled due to poor results. 13 species exhibited premature anthesis, which lead to poor seed production or early mortality. Nine species exhibited difficulty adapting to heavy clay soils or very sandy soils. Nine species exhibited traits rendering mechanized seed harvest impossible or prohibitively expensive. Two species were highly susceptible to predators. In all, only four species exhibited favorable attributes for commercial seed production while an additional three could be made commercially viable with further work. Twelve species were considered very unlikely for commercial availability. The successful species, (Achillea millefolium, Penstemon procerus, Poa nevadensis, Stipa nelsonii), where usually minor components of the source landscape, dominated by grasses, (Deschampsia cespitosa, Danthonia intermedia, Phleum alpinum, Poa alpina). Results indicate a need for a collection and trials of many populations to develop broadly adapted cultivars for high elevation mining use in North America.

Additional Key Words: native plant propagation, commercial seed production, high elevation revegetation, ecoregion seed production.

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Introduction and Background

In 1999 we began an effort to produce seed from high elevation sources in anticipation of reconstruction of a segment of the Beartooth Highway over Beartooth Pass straddling the Wyoming/Montana border near Yellowstone National Park. The arctic/alpine flora of the Beartooth Plateau has been recognized as containing species found nowhere else in the continental United States, (Fertig 2001). Given the pristine condition and unique flora in areas to be disturbed by highway construction, the Federal Highway Administration, ERO Resources, Denver, CO, and Wind River Seed, Manderson, WY, teamed up to implement a seed growout experiment of key species in an effort to mitigate construction impacts in the alpine areas. The seed was collected from areas near and/or adjacent to the proposed roadway reconstruction site, then established in tubelings by Bitterroot Native Growers, Corvallis MT, and transplanted into seed production fields in the Big Horn Basin of Wyoming. Most selected species had never been evaluated for seed production, but a few had been tried by the Plant Materials Centers at Bridger, Mt, and Meeker, CO with mixed success, (personal communication Mark Majerus, Steve Parr).

While generating much valuable information about high elevation species, and some successes in seed production, this project revealed that, under the given conditions, it would not be possible to generate the seed need to revegetate the disturbed sites. It can serve as a warning of the dangers of trying to do full scale seed production without first doing basic research and development. At present, several federally funded programs in Oregon and Colorado aim to establish local source, untested plant materials, directly into seed production fields of private producers without benefit of prior scientific evaluation of suitability for such purpose. This paper should serve as a cautionary example of the importance of conducting programs only after scientific research supports such efforts.

Table 1 lists the perennial species collected between 1999 and 2002 for growout. Most species were selected for their apparent ability to establish on disturbed sites and others were chosen simply because they were common and making seed during the drought which spanned the collection period. We sought species from talus slopes and cut and fill slopes reinvaded by natives following the original construction in the 1930’s. Several species had been tested in various on site experimental plantings by ERO Resources, and others had been tested at nearby high elevation sites by Dr. Ray Brown in his work to establish vegetative cover for mine spoils at Lulu and Daisy Pass above Cooke City, Montana, (Brown et al. 2003).
Table 1. Species Collected and Elevations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common name</th>
<th>Elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em></td>
<td>Western yarrow</td>
<td>2,677m. (8,700 ft.)</td>
</tr>
<tr>
<td><em>Agoseris glauca</em></td>
<td>False dandelion</td>
<td>2,770m. (9,000 ft.)</td>
</tr>
<tr>
<td><em>Anaphalis margaritacea</em></td>
<td>Pearly everlasting</td>
<td>2,923m. (9,500 ft.)</td>
</tr>
<tr>
<td><em>Aster foliacius</em></td>
<td>Leafybract aster</td>
<td>2,923m. (9,500 ft.)</td>
</tr>
<tr>
<td><em>Carex nigricans</em></td>
<td>Black alpine sedge</td>
<td>3,015m. (9,800 ft.)</td>
</tr>
<tr>
<td><em>Carex paysonis</em></td>
<td>Payson’s sedge</td>
<td>2,985m. (9,700 ft.)</td>
</tr>
<tr>
<td><em>Danthonia intermedia</em></td>
<td>Intermediate oatgrass</td>
<td>2,985m. (9,700 ft.)</td>
</tr>
<tr>
<td><em>Deschampsia cespitosa</em></td>
<td>Tufted hairgrass</td>
<td>3,262m. (10,600 ft.)</td>
</tr>
<tr>
<td><em>Elymus glaucus</em></td>
<td>Blue wildrye</td>
<td>2,770m. (9,000 ft.)</td>
</tr>
<tr>
<td><em>Elymus scribneri</em></td>
<td>Scribner’s wheatgrass</td>
<td>3,323m. (10,800 ft.)</td>
</tr>
<tr>
<td><em>Festuca ovina</em></td>
<td>Sheep fescue</td>
<td>3,077m. (10,000 ft.)</td>
</tr>
<tr>
<td><em>Penstemon procerus</em></td>
<td>Little flowered penstemon</td>
<td>3,015m. (9,800 ft.)</td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>Silverleaf phacelia</td>
<td>2,985m. (9,700 ft.)</td>
</tr>
<tr>
<td><em>Phleum alpinum</em></td>
<td>Alpine timothy</td>
<td>3,015m. (9,800 ft.)</td>
</tr>
<tr>
<td><em>Poa alpina</em></td>
<td>Alpine bluegrass</td>
<td>3,323m. (10,800 ft.)</td>
</tr>
<tr>
<td><em>Poa nevadensis</em></td>
<td>Nevada bluegrass</td>
<td>2,770m. (9,000 ft.)</td>
</tr>
<tr>
<td><em>Polemonium viscosum</em></td>
<td>Sky pilot</td>
<td>3,262m. (10,600 ft.)</td>
</tr>
<tr>
<td><em>Potentilla diversifolia</em></td>
<td>Varileaf cinquefoil</td>
<td>3,262m. (10,600 ft.)</td>
</tr>
<tr>
<td><em>Stipa nelsonii</em></td>
<td>Needlegrass</td>
<td>3,015m. (9,800 ft.)</td>
</tr>
</tbody>
</table>

In the three years of collecting on the Beartooth Plateau, seed ripening dates varied by as much as two weeks depending upon summer heat and precipitation. Seed ripening in the Beartooths occurred as early as August 1 for lower elevation sheep fescue and intermediate oatgrass while higher elevation populations of these species seeded out 2-3 weeks later. Seed ripening for blue wildrye and pearly everlasting occurred in mid August while the rest of the species seeded out in early September (Table 2). Collections were hampered by frequent moisture, including snow, low temperatures and high winds. In some years silverleaf phacelia, Scribner’s wheatgrass, alpine bluegrass and alpine timothy may not have been fully mature by the time snow fell in early September because seed would not separate from the plant rachis or receptacle on the last feasible seed collecting day before winter snow-in.

Given the constant wind, frequent cold and wet weather, prospect of ongoing drought inhibiting seed production, high cost of collecting such low-stature seed in the wild, and the small quantities of seed available, it was decided to use the collected seed for farm growout and seed increase. Three species, (alpine timothy, tufted hairgrass, and alpine bluegrass), were grown out in 7 cubic inch Ray Leach cells by Bitterroot Restoration, and transplanted into farmland in early May 2001. The same species were direct seeded at the same time into a sandy clay loam. The remainder of the species were planted in 2002.
The project design chose containerized transplanting seedlings established in a greenhouse to compare against the results of direct-seeding. Though it dramatically raised the cost, greenhouse production allowed us to treat seed before planting, to break seed dormancy, (Copeland, 1976). Issues associated with unknown seed such as no direct knowledge of seeding depth, seedling damp-off, diseases, and weed control were avoided by transplanting. Indeed, some seed germinated poorly or not at all even after pre-treatment, showing that high seed dormancy was present in several species, (silverleaf phacelia, sky pilot, varleaf cinquefoil).

The farm, located 72 miles south and 112 miles east from the Beartooth Plateau at an elevation of 1220 meters represented a drop of between 5447 ft. to 6830 ft. from seed collection areas. Soils are Lostwells series grading from clay-loam to very sandy clay loam. Plots were furrow irrigated. An unusually hot spring, in which temperatures soared into the mid 90s by May 5, turned into a hot and dry summer.

**Results**

I will not discuss the results of each species, but only those representing general themes which emerged during the project. Direct seeded 2001 trials failed quickly when seeds planted on May 1 emerged around May 10 into 95 degree heat. The tufted hairgrass and alpine timothy transplants established well initially, but the alpine bluegrass began to fail immediately, with 97% mortality by summer’s end. I speculate that the roots of the alpine bluegrass were unable to meet the evapotranspiration needs of the plants and lacked the energy to invade the surrounding soil. The alpine timothy suffered 30% mortality throughout the summer, before going dormant in fall 2001. The tufted hairgrass prospered, establishing two-inch crowns by summer’s end.

In 2002, the alpine timothy and tufted hairgrass greened up in mid-March. By late April both species were in anthesis, with seed for the tufted hairgrass maturing by June 5.

Due to the summer heat, the mature tufted hairgrass seed shattered quickly, reducing our yield greatly. The alpine timothy matured on June 10th. Unlike the tufted hairgrass, which after harvest went into a period of vegetative quiescence, the alpine timothy continued to make seed over a three month period. By the end of the summer 95% of the alpine timothy had died. Prolonged flowering may have reduced the root growth necessary for continued good health and exhausted the root reserves of the plants.

In spring of 2003, only six of the original 4900 alpine timothy plants remained. Soils were a factor in the mortality of this species. The soil in this irrigated field graded from a clay loam at the top of the irrigated field through a transitional sandy clay loam to a sandy loam at the bottom of the field. Mortality was higher and earlier in the clay loam and sandy loam, with the bulk of seed being produced in the middle transition zone. This pattern was repeated in a subsequent direct seeding trial conducted in the same soil type in 2002.

The tufted hairgrass appeared to be equally adapted to all three soil types. In 2002 plants greened up early and made seed in early June. In 2003, the same development pattern of early green up, anthesis and maturation occurred. By year’s end, the dense crowns of tufted hairgrass were 8” in diameter with hundreds of fine leaves, living and dead, in each crown. In spring 2004, the stand exhibited 30% winter mortality, with the remaining survivors having few live leaves within large, dense, decrepit crowns, the field was abandoned. Since irrigation water is cut off by Oct 1, a warm, dry fall and winter may have contributed to its decline, as well as too many other species in this test.
Table 2. Comparison of Seed Maturation Dates for Beartooth Collections.

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed Harvest Wild</th>
<th>Seed Harvest Farm</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em></td>
<td>8/15</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Agoseris glauca</em></td>
<td>8/30</td>
<td>7/15-freeze</td>
</tr>
<tr>
<td><em>Anaphalis margaritacea</em></td>
<td>8/30</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Aster foliacius</em></td>
<td>8/30</td>
<td>6/30-freeze</td>
</tr>
<tr>
<td><em>Carex nigricans</em></td>
<td>8/20</td>
<td>na</td>
</tr>
<tr>
<td><em>Carex paysonis</em></td>
<td>8/30</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Danthonia intermedia</em></td>
<td>8/15</td>
<td>na</td>
</tr>
<tr>
<td><em>Deschampsia cespitosa</em></td>
<td>8/30</td>
<td>6/05</td>
</tr>
<tr>
<td><em>Elymus glaucus</em></td>
<td>8/15</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Elymus scribneri</em></td>
<td>9/05</td>
<td>7/01-freeze</td>
</tr>
<tr>
<td><em>Festuca ovina</em></td>
<td>8/15</td>
<td>6/15</td>
</tr>
<tr>
<td><em>Penstemon procerus</em></td>
<td>8/15</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Phacelia hastata</em></td>
<td>9/05</td>
<td>na</td>
</tr>
<tr>
<td><em>Phleum alpinum</em></td>
<td>9/05</td>
<td>6/10</td>
</tr>
<tr>
<td><em>Poa alpina</em></td>
<td>9/05</td>
<td>7/10</td>
</tr>
<tr>
<td><em>Poa nevadensis</em></td>
<td>8/15</td>
<td>7/15</td>
</tr>
<tr>
<td><em>Polemonium viscosum</em></td>
<td>8/10</td>
<td>na</td>
</tr>
<tr>
<td><em>Potentilla diversifolia</em></td>
<td>8/30</td>
<td>6/15</td>
</tr>
<tr>
<td><em>Stipa nelsonii</em></td>
<td>8/20</td>
<td>7/01</td>
</tr>
</tbody>
</table>

In this and subsequent direct-seeded trials of tufted hairgrass, another general theme emerged. Seed stalks tended to be much shorter than those found in native habitat. On the Beartooth Plateau, seed stalks were 8” to 16” long, whereas at the farm, stalks tended to rises between 4” and 8”. I speculate that high temperatures reduced the maturation period and growth, both in length of seed stalks and in number of seed stalks per plant. The effect was observed in subsequent trials of alpine bluegrass in which seed stalks did not rise above the leaf canopy. Other species with short seed stalks were leafybract aster, pearly everlasting and sheep fescue.

Initial direct seeding of tufted hairgrass, alpine timothy and alpine bluegrass in spring of 2001 resulted in poor germination due to an error in soil type choices and unusually hot May weather. Planting into sandy clay loam, high heat and wind struck during our initial irrigation resulting in poor seed germination. Those seeds which did germinate struggled to prosper in soil that dried quickly and had limited capillary capacity to bring moisture in from water furrows. The seeding was abandoned. In direct seeding in fall of 2001, all three species established good stands except at the very clayey tops and very sandy bottoms of the fields.
Direct seeding showed no increased vigor of the tufted hairgrass over the transplants from the previous year. Alpine timothy and alpine bluegrass grew with good vigor, over wintered well and produced seed in 2003. As with the earlier transplants, alpine timothy continued to make seed throughout the summer of 2003. The alpine bluegrass made copious seed, but the seed heads were shorter than the leaf lengths, averaging less than 2 1/4 inches off the ground, rendering mechanized harvest impossible. During mid summer, the bluegrass was attacked by an unknown predator, resulting in high mortality. The continuously flowering alpine timothy went into the very dry and warm winter of 2003 with no signs of distress, but 90% mortality was clear by spring of 2004.

Another theme of note was the production of empty, non-viable seed, from blue wildrye, leafybract aster and pearly everlasting. Extreme heat during flowering is presumed to be the cause of poor seed in these species.

Other species were so small, that though they grew well, their stature presented insurmountable harvesting difficulties. In the cases of Scribner’s wheatgrass and cinquefoil, seed production expansion was ruled out because of low height, (less than 1 ½ inch) Fig. 1.

Figure 1. Growth habit of Scribner’s wheatgrass

Some species developed too slowly to be practical for seed production. The cinquefoil and Payson’s sedge developed very slowly and were just beginning to make small amounts of seed in year three, 2004. Commercial production of such species requires greater productivity of the land very high prices.
Some species, in spite of appearing to thrive, didn’t make enough seed to warrant continuation. Needlegrass and false dandelion fit this category. Both species have persisted well, but the needlegrass made only one pound of seed per 1000 plants. Also, because of the high seed dormancy of needlegrass, it may not lend itself to direct seeding to improve yield per acre, (the minimum transplant space between plants was 1 ½ ft). The false dandelion spreading rhizomatosely, produced very few flowers. In three years, single plants became 1 meter clusters, consisting of up to thirty plants, with occasional single seed stalks on plants. What makes this species desirable for soil stabilization, its rhizomatousness, may render it unsuitable for seed production.

Two species were highly susceptible to predators, the alpine bluegrass to an unknown bug and the false dandelion, whose flowers attracted deer. Intermediate oatgrass and black alpine sedge failed to survive repeated attempts to establish them.

The winter of 2004 killed a large number of species in the test. Interestingly, while sheep fescue and Scribner’s wheatgrass transplants from 2001 and 2002 died, transplants of these species planted in 2003 survived the winter of 2004 unharmed. This, and the rapid decline of other species, is further evidence that cumulative stresses related to climate, soils and water reduced life expectancy. Such stresses are common in agricultural areas and must be considered when evaluating the seed production potential of species.

There were successful results also. The vigor and stature of some species increased under hotter, more fertile conditions. Western yarrow, little flowered penstemon, (Fig. 2) Scribner’s wheatgrass, and needlegrass all showed increased stature, vigor or seed production. Nevada bluegrass, little flowered penstemon, western yarrow and possibly blue wildrye appear to be successful, long term seed producers at lower elevations.

Figure 2. Little flowered penstemon

Table 3 summarizes the results by species where E denotes excellent attributes, M denotes modest attributes and P represents poor attributes related to the column headings. The column headings represent significant factors affecting suitability for seed production. “Survival and Vigor” represent morbidity and an ocular judgment of the fitness of survivors. “Climate” and “Soils” are an attempt to note ability to adapt to climate and different soils encountered in farming at lower elevation. “Adapted to Seed Production” represents phenological attributes which render successful seed production more or less likely.
Table 3. Assessing potential for success in field seed production.

<table>
<thead>
<tr>
<th>Species</th>
<th>Survival &amp; Vigor</th>
<th>Climate</th>
<th>Soils</th>
<th>Adapted to Seed Production</th>
<th>Susceptibility to Predation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em></td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
</tr>
<tr>
<td><em>Agoseris glauca</em></td>
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<td>E</td>
<td>E</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td><em>Anaphalis margaritacea</em></td>
<td>M</td>
<td>P</td>
<td>E</td>
<td>P</td>
<td>M</td>
</tr>
<tr>
<td><em>Aster foliacius</em></td>
<td>M</td>
<td>M</td>
<td>E</td>
<td>M</td>
<td>M</td>
</tr>
<tr>
<td><em>Carex nigricans</em></td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Carex paysonis</em></td>
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<td>E</td>
<td>E</td>
<td>P</td>
<td>E</td>
</tr>
<tr>
<td><em>Danthonia intermedia</em></td>
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<td>P</td>
<td>M</td>
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<td><em>Deschampsia cespitosa</em></td>
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<td>M</td>
<td>E</td>
<td>M</td>
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<tr>
<td><em>Elymus glaucus</em></td>
<td>M</td>
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<tr>
<td><em>Elymus scribneri</em></td>
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<tr>
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<td><em>Penstemon procerus</em></td>
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<td>E</td>
<td>E</td>
<td>E</td>
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<tr>
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<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td><em>Phleum alpinum</em></td>
<td>M</td>
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<tr>
<td><em>Poa alpina</em></td>
<td>M</td>
<td>P</td>
<td>M</td>
<td>M</td>
<td>P</td>
</tr>
<tr>
<td><em>Poa nevadensis</em></td>
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<td>E</td>
<td>E</td>
<td>E</td>
<td>E</td>
</tr>
<tr>
<td><em>Polemonium viscosum</em></td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>P</td>
<td>NA</td>
</tr>
<tr>
<td><em>Potentilla diversifolia</em></td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>P</td>
<td>E</td>
</tr>
<tr>
<td><em>Stipa nelsonii</em></td>
<td>E</td>
<td>E</td>
<td>E</td>
<td>M</td>
<td>E</td>
</tr>
</tbody>
</table>

The success or failure of any seedlings in this test should not be interpreted as valid for generalizations about that species. Attributes can vary from one population of a species to another. Attributes such as stature, seed dormancy, pest resistance and cold tolerance can vary with elevation, soil type and aspect, (McArther, et al., 1987). For the specific species selections used in the test, some assignment of potential for success can be made. Those species producing one or more modest and poor ratings in the above table indicate the need for substantial research before seed can be commercially grown.

**Discussion**

Multiple year trials are important, for had climatic conditions varied even slightly, some of our poor performers might have exhibited improved success. Such small changes could be as simple as a moist, cool spring, which might have improved seed head production, panicle length and seed fill. Also, cooler and wetter fall weather might have improved winter survival. However, successive climatically favorable years could create a false sense of success, leading to premature production schemes and eventual failure.
Since most farmland is at low elevations, some issues noted here must be considered before growout programs are implemented. Of particular importance is overcoming the poorly synchronized growth patterns in low elevation seed production. We need to study the impact of long hot summers and very cold winters without protective snow cover so characteristic of western farmlands. We also need to determine the ability of species to adapt to the soil types of the alkaline basins, low on organic material; which contrasts with mildly acidic soils of high organic content found in mountain meadows.

Poor survival, unexpectedly short life spans and poor seed production of high elevation natives grown at lower elevations have been noted by other researchers, (Meyer and Monsen, 1989). The existence of improved cultivars of common native plants, such as Critana thickspike wheatgrass, *Elymus lanceolatus ssp. lanceolatus*, shows that within a species, some populations have distinctive traits which enhance their ability to survive in harsh climates or over a broad range of conditions. The challenge is to gather and trial selections over the range of a species to identify those with favorable attributes, learn how to produce seed from them, and make those selections available to farmers and revegetation personnel. This requires comprehensive testing and trials spanning a decade. We may find that some species have inherent limitations that rule out commercial production. On the other hand, we will likely find improved cultivars of many species which address the needs of revegetation better than do local, untested sources. Until recently, this was the model followed by federal and state agencies.

Lately a model requiring revegetation using only local seed sources, locally grown, has gained currency among state and federal agencies. Particularly strong in the U.S. Forest Service in Oregon and western Colorado, this movement ignores the fundamental lessons of fitness and seed production learned by the Natural Resources Conservation Service and Agricultural Research Service over many decades of research. The increasing tendency toward inexperienced personnel promoting local source seed production in the hands of local, inexperienced seed producers, planting untested seed, puts policy and implementation ahead of necessary research and science.

It is a policy which threatens to inflict serious costs and poor benefits on revegetation projects across the country. It is a policy based upon poor awareness of the specific needs of individual species and the many obstacles in producing seed from these species. Finally it is a policy that understands neither seed, nor farming nor the revegetation challenges we face.

Beyond policy challenges, this study suggests serious long term obstacles to field production of high elevation species. Three solutions are apparent: find or develop accessions that are broadly adapted to soils and climate; find high elevation seed production fields, or move seed production north. Early high temperatures and long hot summers are two obstacles to successful seed production. It is possible that some high elevation species, not sensitive to day length changes, would respond favorably to a shift in seed production north to areas where similar growing degree days and cooler springs exist at lower elevations where farmland is located. High elevation seed production fields are as scarce as entrepreneurs are to farm them and this represents an unlikely option. Developing broadly adapted cultivars remains the most likely solution for advancing inexpensive and reliable supplies of high elevation revegetation seed.
Literature Cited


Personal communications: Mark Majerus, Bridger Plant Materials Center; Steve Parr, Meeker Plant Materials Center.