Genetic Considerations in Propagating Native Shrubs, Forbs, and Grasses from Seed[1]

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Abstract.--Germination and emergence studies with native species important for wildland restoration have demonstrated major genetic variation in seed and seedling traits. Habitat correlated differences between ecotypes have been documented for many species. Large between-plant differences within populations also appear to be the norm based on recent studies. Nursery propagators need to consider this variation in both collection and propagation procedures, so that outplanted populations will represent adapted ecotypes with a full range of within-population variation.

INTRODUCTION

When native plant materials are collected from wild populations and propagated for subsequent outplantings, a whole spectrum of approaches is possible. At one extreme, the goal may be selection and 'improvement', where the explicit intent is to modify the genetic composition of the population to meet human-based performance criteria such as productivity, palatability, ornamental interest, or ease of establishment. This is the traditional approach of plant breeders. At the other extreme, the goal may be to restore a species to an area where it formerly existed using stock that genetically resembles the previously-existing population as closely as possible. The main difference between these two approaches is how they deal with genetic variation. In plant selection, the intent is to narrow the genetic base to increase the frequency of individuals with desirable traits. In propagation for ecological restoration, the goal is to try to prevent even inadvertent shifts in population genetic composition.

In this paper we will assume that the goal of the outplanting is ecological restoration. Long-term self perpetuation of the newly-established population is desired, not just a one-generation landscape planting. We compensate for our lack of understanding of the genetic basis for population persistence by

attempting to preserve in the outplanted population all the genetic options available to the original population. To achieve this goal through nursery propagation, or at least not to subvert the effort, we need to understand genetic variation in the regeneration strategies of native species, and how it might be subject to inadvertent selection during propagation. Variation at both the between-population and the between-individual levels is important.

Between-population Variation

We have known for quite a long time that many widely-distributed western shrub species are characterized by strong ecotypic differentiation (e.g., Tiedemann and Johnson 1983; McArthur 1984). Differences in habit, growth rate, flowering time, and many other traits persist when plants from different ecotypes are grown side by side in common gardens. Some of these traits affect the ability to survive and compete on different kinds of sites. For example, not all accessions of four wing saltbush (Atriplex canescens) are equally cold hardy (Monsen and Christensen 1975; Van Epps 1975). Using seed from a warm desert population for a northern outplanting could result in stand death in a severe winter. Upland Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) populations are more drought hardy than their floodplain basin big sagebrush (Artemisia tridentata ssp. tridentata) neighbors (Barker, McKell, and Van Epps 1983; Booth, Welch, and Jacobson 1990). Floodplain populations are more prolific seed producers, however, so that basin big sagebrush seed is more easily obtained in the marketplace. Planting this seed on upland sites is risky at best.

Another set of traits only recently shown to

vary ecotypically are those associated with seed germination and seedling emergence. Nursery propagators and analysts in seed laboratories often observe major lot-to-lot variation within a species in response to various dormancy-breaking treatments. Methods for obtaining germination of most of the viable seeds in most lots are developed for new species through trial and error (Stevens and Meyer 1990). Sometimes this is relatively easy; other times it is nearly impossible.

Research at the Shrub Sciences Laboratory over the last few years has shown that between-population variation in germination response can often be interpreted in an ecological context. In the regionally dominant shrub big sagebrush, for example, variation in dormancy level and germination rate at autumn and winter temperatures is related to time of ripening in the autumn and to winter severity and probable snowpack duration at the collection site (Meyer, Monsen, and McArthur 1990; Meyer and Monsen 1991, 1992). Populations from long-winter habitats mature seed early. It is strongly light-requiring and either dormant or very slow to germinate under autumn conditions. It begins to germinate under the snow only after many weeks, when spring snowmelt is likely to be imminent. Populations from warm desert fringe habitats produce their seed late. Seed is dispersed in early winter, is nondormant, and germinates in less than two weeks at both mild and near-freezing temperatures.

A similar habitat correlated pattern of germination response has been observed for the widely distributed early seral shrub rubber rabbitbrush (Chrysothamnus nauseosus; Meyer, McArthur, and Jorgensen 1989). Germination rate at near-freezing temperature is directly correlated with mean January temperature at the collection site, an index of winter severity. Collections from snowy winter sites germinate slowly under the snow, while warm desert populations germinate very quickly at such near-freezing temperatures. Mid and high-elevation rubber rabbitbrush collections may also show dormancy at autumn temperature (15°C), whereas incubation at high temperature (30°C) results in complete germination regardless of collection site climate. Because the seed is autumn-ripening and germinates completely in winter and spring, it never encounters high temperatures. Its ability to germinate at high temperature is ecologically irrelevant, though convenient for seed analysts.

Habitat-correlated variation in germination pattern has been found in several other woody plants of the Intermountain area, including curlleaf and true mountain mahogany (Cercocarpus ledifolius and C. montanus; Kitchen and Meyer 1990), spiny and smooth hopsage (Grayia spinosa and G. brandegei; Shaw and Haferkamp 1990; Meyer and Pendleton 1990), and winterfat (Ceratoides lanata; Meyer in press). In all these species, populations from warmer, drier sites had shorter chill requirements than those from colder, snowier sites. Antelope bitterbrush (Purshia

tridentata) and bluebunch wheatgrass (Pseudoroegneria spicata) also show strong between-population variation, though its ecological significance is less clear in these species (Meyer 1989; Meyer and Monsen 1989; Kitchen and Monsen in press).

In the woody species discussed so far, it is possible to trigger germination in virtually all viable seeds in any lot by applying a sufficiently long chill. The chill period expected at the site of seed origin is generally sufficient to elicit germination of all viable seeds. Regulatory mechanisms in these species function only to time germination optimally iii the year following seed production, rather than providing for between-year carryover of seeds. The chill requirement prevents germination in fall or too early in winter, but permits complete germination after the risks of winter are reduced. Species that form such transient seed banks are usually relatively easy to propagate from seed without inadvertent selection on germination traits.

Many native perennial forb species, as well as some shrubs and grasses, have mechanisms that permit between-year carryover of a fraction of the seed as well as timing germination optimally for the fraction that germinates within any year. In firecracker penstemon (Penstemon eatonii), for example, habitat-correlated variation in germination response results in patterns that are custom-adapted to different kinds of sites (Meyer 1992). Populations from long-winter subalpine habitats produce seeds that are dormant and have very long chill requirements. Populations from mid-elevation habitats, where winters are quite variable from year to year, produce two kinds of dormant seeds, those that germinate after a chill of intermediate length, and those that do not respond to chilling the first year. Populations from warm desert fringe habitats, where winter is the best time for establishment, have seeds that are mostly nondormant at dispersal. When these are subjected to chilling, they diverge into two fractions, those that germinate quickly during and after chilling and those rendered secondarily dormant by a short chill. The high elevation populations carry over seed that has a longer first-year chill requirement than can be met even at a long-winter site. The middle elevation populations carry over seed that is chill-nonresponsive regardless of snowpack duration. The low elevation populations carry over seed that is induced into secondary dormancy by the short chill periods encountered at such sites. Different ecotypes of the same species can thus have varied and even contrasting responses to traditional dormancy-breaking treatments. These differences persisted in seed collected from plants grown in common gardens and are therefore genetically based to at least some degree (Meyer and Kitchen in review a).

Collections of the perennial forb blue flax (Linum perenne) also show strongly habitat correlated variation in germination response

(Meyer and Kitchen in review b). High elevation populations produce seeds that are dormant or slow to germinate in autumn but that germinate in response to long chill periods. Mid-elevation populations may be nondormant and potentially autumn-germinable with a fraction induced into dormancy by chilling, or they may be largely dormant in autumn with a fraction that is chill-nonresponsive the first year. Low elevation populations are largely nondormant and indifferent to chilling, as is the cultivar 'Appar'; these germinate opportunistically when moisture is available, as long as temperatures are not too high. Imbibition at high temperature often induces secondary dormancy as well as suppressing germination. In field retrieval studies, a mid-elevation collection from near Provo, Utah was able to carry a fraction of seed over through two winters at low, middle, and high elevation sites, while 'Appar' had germinated completely at all three sites by the end of the first spring. The inability to form persistent seed banks may limit the long term population persistence of cultivars selected for ease of initial establishment, especially in forb species that are early seral and short-lived as individuals. Unlike seed of most penstemons, blue flax seed afterripens quickly in storage, so that the regulatory mechanisms that limit germination largely disappear in year-old seed.

Blue flax populations differ not only in their germination patterns but in seed size and ,seedling growth rate (Kitchen and Monsen unpublished data). For seventeen native collections, mean seed weight varied over a twofold range and was positively correlated with shoot growth rate, which ranged from 0.2 to 1.2 mm/day. The ecological significance of these differences is not known, but may involve trade-offs between seed weight and number. Presumably small seeds and slow growth rates have been selected for in some populations, though they may appear 'undesirable' from a plant breeder's point of view. The cultivar 'Appar' did not follow the trend of native collections. It had the smallest seed size but the second-fastest growth rate, showing that the traits are not always coupled.

Similar variation in parameters associated with seedling vigor has been documented for 50 native bluebunch wheatgrass accessions from eight states (Kitchen and Monsen in press). Seed (floret) weight varied over almost a threefold range and was positively correlated with both ability to emerge from deep planting and seedling growth rate. Again, those traits traditionally associated with 'low seedling vigor' in grass breeding programs must be associated directly or indirectly with selective advantage in the wild populations where they are characteristic.

Within-population Variation

The existence of genetically-based between-population variation in seed germination and seedling traits means that between-individual

variation in these traits is very likely to exist as well. Presumably the genetic divergence of one population into two contrasting populations could take place through the differential survival of contrasting individuals because of the fitness consequences of their traits. In other words, the difference between two populations could be due largely to a shift in proportions of different kinds of individuals. By the same logic, a population that is subject to changing selection regimes through time could respond with a change in proportions of individuals favored in different kinds of years. In an environment where weather varies widely and unpredictably from year to year, a population with a mix of different kinds of individuals would have a high probability of survival. In this case an individual would be a seed-producing plant and the survival traits would be those associated with successful regeneration from seed. The population as a whole might be more likely to persist if it were made up of contrasting individuals that produced seeds specialized for successful establishment in particular kinds of weather years. The alternative scenario, with each plant producing a mix of seeds with different specializations but with all plants similar to each other, is also possible.

Looking at between-individual variation in seed germination traits can help answer these questions. We have this kind of information for only a few species so far, but the pattern to date is quite consistent. There are major between-individual differences in seed germination traits, but these differences are not absolute. The differences usually take the form of changes in the proportions of different response types. For example, eight individuals of a Provo Canyon population of firecracker penstemon all produced seeds that were dormant at harvest (Meyer 1992). Each plant produced some seeds that were germinable after chill and some that were not chill-responsive. But the chill-responsive seed fraction varied from 22 to 89%. Propagation of this bulk lot using chilling as a means of breaking dormancy would bias the resulting population in favor of individuals producing a higher chill-responsive fraction, because a chill-responsive seed is more likely to have come from a plant producing a high proportion of this type.

This shift apparently happened in our efforts to propagate flax-leaf penstemon (Penstemon linarioides; Meyer and Kitchen in review a). All our wild-collected bulk lots of this species had a very small chill-responsive fraction, less than 15%. Twelve plants grown from the few seeds that germinated produced seeds that averaged a chill-responsive fraction of 69%. We provided a selective regime where readily germinable seeds had very high survival probabilities, but selection in the field apparently favors a higher chill-nonresponsive proportion. An extended experiment would be necessary to determine whether we really deleted a significant portion of the adaptive range of the population in one

generation of selection. It is probable, but by no means certain, that sufficient genetic variation was retained to allow natural selection to reverse the process in an outplanted population.

Evidence of inadvertent selection during propagation was also obtained in the course of a common garden study with blue flax (Meyer and Kitchen in review b). Means based on eight common-garden grown individuals of each of several relatively conservative wild collections showed that changes were consistently in the direction of less conservative. All the native accessions showed highly significant between-plant differences even after this inadvertent selection; the cultivar 'Appar' showed no significant between-plant differences.

Another feature of variation between plants that we have detected at least twice is the apparent effect of environment during ripening. In a middle elevation wild population of rubber rabbitbrush, we looked at germination rate under conditions simulating snowpack for individuals that ripen seed early, midseason, and late in the fall, with six individuals in each group (Walker and Meyer 1992). On each individual, we collected seeds from open branches and from branches that had been covered with net bags soon after pollination. Early-ripening seeds from open branches germinated more slowly in the cold than midseason seeds, which in turn germinated more slowly than late-season seeds. These differences held even though there were significant between-individual differences within each group. Presumably early-ripening seeds would be favored in long-winter years while late-ripening seeds would be favored in short-winter years (Meyer, McArthur and Jorgensen 1989). When branch microclimate was modified by net bags, the different flowering time groups had different responses. Seeds from bagged branches on early-ripening bushes germinated much more quickly in the cold than unbagged seeds from the same plants, as if they were developing later in the fall. Seeds from bagged branches on late-ripening bushes were slower than those from unbagged branches, as if they were developing earlier. Bagging had no effect on seeds produced midseason. Within each group, relative differences between plants were maintained whether branches were bagged or not. Our interpretation of these results is that there are genetic differences between individuals within a flowering time group, but that expression can be modified by shifts in ripening environment. We cannot tell from our data the extent to which differences between flowering time groups are due to differences in ripening environment, but it must certainly be a factor.

Investigators often report between-year differences in seed germination patterns for bulk lots collected from the same population (e.g., Young and Evans 1977). But it is difficult to know whether such differences are due to differences in ripening environment or to the effects of sampling a different set of

individuals when making up the bulk lot. In a study with Palmer penstemon (Penstemon palmeri), we collected seeds from the same ten individuals growing in a common garden in two successive years (Meyer and Kitchen in review a). Seeds in this species are largely nondormant at harvest and maintain a persistent seed bank through chill-induced secondary dormancy (Kitchen and Meyer 1992; Meyer and Kitchen 1992). The trait we wished to examine was the proportion of seeds that remained germinable after a 4-week dormancy-inducing chill treatment. In the first year of collection (1990), post-chill germination varied from 9 to 69%, with a mean of 36%. The next year, mean post-chill germination was much higher, 78%, with a range from 44 to 99%. Post-chill germination percentages were significantly correlated between years. Again we concluded that between-plant genetic differences were important, but that expression could be modified through shifts in ripening environment. The environmental difference that mediated this shift was not obviously discernable.

We have no information on between-plant differences in seedling growth rate for any of these species. The blue flax common garden experiment revealed significant between-plant differences in seed size for most wild accessions but not for the cultivar 'Appar' (Meyer unpublished data). It seems quite likely that genetically based between-plant differences in seed size and seedling traits exist for many native species.

Practical Implications

The goal in nursery propagation is to produce healthy, relatively uniform plants using methods that maximize efficiency and minimize waste. Propagation of natives for ecological restoration is cost-effective and worth the trouble for a commercial operation only if it can be integrated into established routines. But many routine procedures can effect changes in the population genetic composition of the resulting group of plants. By being aware of possible variation in seed characters, germination requirements and growth patterns within a species, it may be possible to take relatively simple measures to avoid inadvertent selection. These measures might be taken at any stage, from initial seed collection in the wild to final culling before delivery.

Seed Collection

The first choice to be made in any ecological restoration project using nursery-grown stock is selection of the source population. This may not be up to the nursery; many clients supply already-harvested seed or specify clearly the source population where the collection is to be made. In cases where the nursery is responsible, every effort should be made to match collection site as closely as possible to outplanting site in such features as geographic location, climate,

soil, and matrix vegetation. Many western species occur over an astonishing range of habitats. Sometimes the client will specify that the collection must be made within a certain distance of the outplanting site. This in itself does not guarantee that a collection will belong to an appropriate ecotype. Probably the single most important clue is the composition of the surrounding vegetation. Plant communities provide an integration of climate, microclimate, and soils variables that are difficult to observe or measure directly. When working with clients who are not primarily concerned with genetic 'purity' issues, a match using such ecological criteria is at least as likely to result in a successful outplanting as one based on distance criteria alone.

When making the seed collection, it is important to try to obtain a representative sample of the population as a whole. This means collecting from as many individuals as possible, rather than taking the whole collection from a few prolific plants. Try to avoid biasing the collection in favor of large, heavy seed producers, as this would result in a shift in the proportions of different genotypes relative to the wild population. Seedlots for nursery propagation do not have to be large, so you can afford to collect systematically from a large number of plants, collecting approximately the same amount of seed from each. Both purists and detractors will tell you that your sample will be biased no matter how you make the collection. The point is to reduce bias by consciously using methods that sample as objectively as possible. Sometimes, depending on the species, it may be worth the trouble to keep the collection separated by individual mother plants.

Seed collection for ecological restoration should be made from the original wild population if at all possible, rather than from field-grown plants derived from the original population. Every generation away from the selective regime of the original site can result in genetic shifts. The luxury of collecting from the wild is available to nursery propagators, while those attempting restoration from seed may have to live with genetic changes that take place in seed increase fields.

Seed Cleaning and Processing

The main risk to genetic composition during seed processing is the possibility that some selection on seed size will take place. The agronomic assumption that bigger is better does not necessarily hold in this case. It is true that for many species bigger seeds or fruits are more likely to be filled and viable. But you should resist the urge to throw out a significant fraction of good seed in the interests of obtaining a cleaned lot with higher viability. Of course, well-cleaned seed is easier to handle at all stages of the propagation process, and some concessions must be made. But the seed should not be over-cleaned; look at the

screenings or the blow-over to make sure that you are not overdoing it. Smaller seeds could sometimes have an adaptive advantage in the field, or could be linked to some advantage such as increased seed number.

Viability Evaluation

A knowledge of seed lot viability is essential to wise interpretation of germination response patterns. For example, if viability is known to be low, then emergence can be improved by overseeding without imposing much selection. But if emergence is poor even though viability is high, the problem is dormancy that has not been overcome. Overseeding in this case may yield filled cells, but the resulting population of seedlings may be genetically biased toward lower dormancy.

There are legal testing requirements for seed sold in the marketplace, but wild-collected seed for nursery propagation often does not pass through this testing process. This makes in-house testing of some sort a necessity. For freshly-collected seed of many native shrubs and most forbs, a simple cut test gives a good idea of viability, as filled seeds in these species are usually viable. Many grasses can be checked for fill using a light table. For older lots that may have lost viability and for species where fill is not a good indicator, tetrazolium stain viability tests are often performed (Grabe 1972).

The usual procedure in testing wildland seed is to obtain germination of most of the viable seed and then to determine the viability of remaining ungerminated seed using tetrazolium stain testing. The standard procedures used are outlined in Rules for Testing Seeds (Association of Official Seed Analysts 1988). Many wildland species are included in the rules (Stevens and Meyer 1990). The post-test determination of viability of ungerminated seed is an essential step for many native species because of the lot-to-lot variation in response discussed above.

Pre-sowing Treatments

For many species, dormancy-breaking treatments are a necessary prerequisite for successful propagation. This is where the greatest amount of inadvertent selection can take place, at least as far as germination traits are concerned. The best insurance against unwanted selection is to use treatments that break dormancy completely, i.e., in every viable seed.

Seed dormancy is not a simple phenomenon, and dormancy levels can be affected by many factors. For species that are dormant at harvest but afterripen (lose dormancy) in dry storage, the best approach may be to store the seed warm (25-30°C) for a few weeks; year-old lots usually germinate fully with no problem. This group includes many grasses (e.g., squirreltail, Elymus

elymoides; Allen, Debaene, and Meyer in press) as well as some forbs (e.g., blue flax; Meyer and Kitchen in review b).

A majority of temperate region species require moist chilling to break dormancy and do not afterripen appreciably in dry storage. The chilling period should be long enough to break dormancy in all or most of the seeds in the lot. It is possible to use shorter chill periods and more seeds to get a given number of seeds to germinate, but this practice could result in selection for genotypes with shorter chill requirements. The seeds may be chilled prior to planting or in flats or containers in a cold room, an unheated building, or outdoors. For bare root operations, fall planting is a good option as long as winters at the nursery are guaranteed to be long and snowy enough to meet the chill requirements of the most dormant seeds in the lot. Timing of spring emergence can be controlled through the use of insulating mulch.

Using a chilling period that is long enough is an effective way to avoid selection in lots that do not contain a chill-nonresponsive fraction. Getting chill-nonresponsive seeds to germinate requires more devious techniques. For penstemons, warm pretreatment (i.e., holding the seeds imbibed at 15'C for four weeks) prior to chilling tends to increase the fraction of chill-responsive seeds, sometimes dramatically (Meyer 1992, Meyer and Kitchen in review b). Combining gibberellic acid with chilling shortens the chill requirement and reduces the size of the chill-nonresponsive fraction for some penstemons, but may affect seedling quality (Kitchen and Meyer 1991). The use of dormancy-breaking chemicals holds promise for some difficult-to-germinate species, but one should be aware that germination response to chemicals also varies among and within populations and is probably also under genetic control. Again, the ideal chemical treatment is one which induces germination of all viable seeds.

As a last resort, propagation of seed from individual plants can be used to ensure that each mother plant is represented in the outplanted population, even those whose chill-responsive fraction was very low. This tactic could be used to assure population representativeness in any situation where individual plant responses are thought to be widely differing.

Another rule of thumb is not to use chilling as a treatment unless it is known to be effective. We tend to think that chilling at the very least will have the positive effect of speeding post-chill germination, but the result might be surprisingly negative. As discussed above, some native forbs can be induced into secondary dormancy by chilling, and between-plant differences are large.

When hardseeded species such as legumes are propagated, it is probably best to scarify artificially rather than to overseed to compensate for hardseededness in the lot.

Otherwise, selection for a smaller hardseeded fraction could result. Selection has been applied artificially in crop legumes to reduce hardseededness, so it is known to be under genetic control.

If possible, you should be aware of the dormancy status of seeds as a consequence of treatment before the seeds are removed from treatment and/or planted. Petri dish germination tests are easy and can be performed on subsamples of seedlots as they afterripen in dry storage or undergo chilling. These can then be interpreted using pretreatment germination or viability percentages as a point of reference. This takes some of the guesswork out of the effort to get full or at least maximal germination in minimal treatment time.

Post-sowing Considerations .

The agronomic perspective teaches that rapid germination, emergence, and growth are desirable traits. Propagation practices that favor these traits are considered to be harmless at worst and usually beneficial. This has resulted through time in selection for these traits in cultivated plants. The blue flax cultivar 'Appar' may be an example of how selection during propagation can yield a population whose germination responses are more like those of a crop plant than a wildland plant, whether or not the selection was deliberate. When propagating plants for ecological restoration projects, it is necessary to strike a balance between the necessity for producing high quality, uniform stock and the danger of culling variants that may represent an important part of the gene pool. Thinning out the larger of two plants in a cell at least some of the time may result in uneven stock size, but it helps prevent deletion of genotypes whose delayed emergence or slow growth may have a value in the wild. The client may be willing to accept much more motley-looking stock if it comes with assurance that artificial selection has been avoided deliberately in the interests of maintaining genetic diversity.

CONCLUSIONS

We have reached a point in time when the skills of plant propagators will be used for more than the crafting of plant populations to meet human needs and expectations. The art and science of ecological restoration, the re-creation of plant communities that have been lost, presents challenges that are very different from the challenges of growing plants for human ends. These challenges will be met through an integration of the practical knowledge embodied by the nursery industry with the scientific knowledge generated through ecological research. Research on seeds and regeneration ecology must play a central role in, this integration. Hopefully this paper marks a beginning in providing the kind of ecological information that growers need to meet the challenge of what is

bound to be an ever-increasing market, as we as a species accept our responsibility to mend as best we can what we have broken.

ACKNOWLEDGMENTS

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