

Promoting Genetic Diversity in the Production of Large Quantities of Native Plant Seed

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Adaptive genotype
strategy promoted
and tested in nursery
field plots studies
and plantings in
British Columbia.

In most parts of North America efforts to revegetate land degraded by human activities currently depend on domesticated grass and legume species of European origin. In most managed forests, newly built roads and log decking areas are routinely seeded with such forage mixtures. These seeding activities are conducted with good intentions, primarily for erosion control, aesthetic improvement, and soil rehabilitation. But there are several reasons why revegetation with native plants is preferable to the use of domesticated exotic species, even when full ecosystem restoration is not the goal:

- agronomic species and varieties have been selected for centuries to have high productivity and resilience (given sufficient light, moisture and nutrients), typically becoming a permanent feature wherever they are introduced;
- as a result, they often out-compete native plants and prevent, rather than facilitate, the recovery of native vegetation, especially on rich sites;
- even though most grasses will eventually be shaded out as shrubs and trees re-establish themselves on forest land, there will always be gaps and patches in which the exotics tend to persist;
- from those footholds, exotic plants can spread into nearby areas by seeds or rhizomes;
- some exotic species may hybridize with related species of native plants, resulting in a contaminated gene pool and

unknown environmental impacts by new hybrids;

- other native wildlife (such as bears) may encounter richer than normal sources of food in exotic vegetation, such as clovers and cool-season grasses, resulting in altered behavior and detrimental interactions with humans, especially on roads and roadsides;
- the microflora of bacteria and mycorrhizae in the soil can be altered by the development of exotic vegetation;
- some sites are so disturbed or at such high elevations that stock varieties of agronomic plants can't adequately establish; and
- the continued spread of already ubiquitous plants further serves to homogenize and domesticate our few remaining wildlands, a trend to which many recreationists and conservationists object because it reduces the local sense of place.

Consequently, reintroducing native plants to degraded lands is an integral component of ecosystem restoration (Harker and others 1993, Lippitt and others 1994, Linhart 1995). Yet the widespread desire to maintain, repair, or rebuild natural vegetation is usually constrained by the high cost and poor availability of native plant material. Agricultural grasses and legumes continue to be used for roadside seeding and industrial reclamation, even in the face of the above arguments, because large quantities of seed are reliably produced at low prices. This seed is

regularly sold for pasture and hay field use around the world, not just for the limited market to be found in revegetation and reclamation uses. Even when native species are grown under cultivation, they represent a specialty product for growers, one that presents propagation and management challenges, and one that typically serves only a relatively small regional market. As a result, few seed growers are willing to get into the native plant seed production business, so availability of desired species often remains low or nonexistent, and seed prices remain high. Equipment has been developed to facilitate the harvesting of seed from wild stands of native plants (e.g., Morgan and Collicutt 1994), but quantities of wild-collected seed are often insufficient or too expensive when the desired plant species is sparsely distributed or the disturbed area to be revegetated is vast.

Plant breeders and seed growers have recognized the potential to bring native grass species into cultivation for several decades, especially in western North America where the rehabilitation of overgrazed native rangeland has long been a priority (Pahl and Smreciu 1999, Booth and Jones 2001). First grown and sold as "common" seed (with no guaranteed set of traits), many native grasses are now grown as specific "cultivars" (cultivated varieties) in an attempt to improve the performance and marketability of these species. Cultivated seed is available for dozens of native grass species, but at the expense of the genetic diversity and adaptability found in wild populations of most plants. This is because cultivar licensing and registration is geared to traditional plant breeding with its process of directional selection and a purposeful narrowing of genetic variability. Selection for crop uniformity is done not just for varietal identification, but also to facilitate mechanized production and harvesting techniques. Though the plant material is identifiably a native species, its breadth of morphological and physiological attributes represents a narrow sample of the species' potential and the species' range. Even when grown and sold as common seed rather than a registered variety, many years of growing seed in cultivation at a

single location often results in local adaptation through inadvertent selection and a narrowing of the genome (Williams 1964, Linhart 1995, Munda and Smith 1995), though presumably not to the same degree as under artificial selection.

Throughout British Columbia, Canada, large, sparsely populated areas of land are routinely disturbed by logging road construction, surface mining and other industrial activities. Though the climax natural vegetation for much of the province consists of closed forests of conifers, it is considered essential to quickly

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sow grass and legume mixtures to control erosion of any exposed soil (Carr 1980). In addition, open meadows, grasslands, and savannas have been lost to suburban sprawl or have been degraded by overgrazing, off-road vehicle use, and exotic plant invasion. Efforts to revegetate or restore these disturbed lands currently depend almost exclusively on Eurasian agronomic species, or a few native cultivars derived from populations outside the province. Collection of wild seed is largely limited to small-scale volunteer efforts.

To address the lack of commercial quantities of native plant seed, we

embarked on a 5-year research program to collect, propagate and screen common native grasses, sedges, legumes, and other forbs for use in the northern interior of British Columbia. Starting out with very little knowledge about the ecology, range, or breeding systems of candidate plant species, the challenge was to produce large quantities of seed at prices below that of wild-collected seed, while maintaining a high level of genetic diversity in this plant material. How could we benefit from concentrated production of single, identified native plant species in cultivated fields, without fully "domesticating" these species?

The Debate

The development of alternative strategies for the management of population genetics is an evolving and controversial issue in restoration ecology (Millar and Libby 1989, Knapp and Rice 1994, Linhart 1995, Shaw and Roundy 1997, Havens 1998, Lesica and Allendorf 1999, Smith and Winslow 2001). While scientists and practitioners agree that only suitably adapted plant material should be introduced to a restoration site, disagreement seems to center on the geographic scale or ecological specificity of that adaptation (e.g., regional climate versus microclimate, the importance of soil or elevational differences). There is also the question of whether local adaptation (genetic specialization) or broader adaptability (genetic diversity) is preferable when undertaking a program of native plant cultivation or site restoration.

Several decades of ecological research have demonstrated the existence of genetic adaptation and ecotypic differentiation in local populations of many plant species, often over short distances and historical time periods (as reviewed by Linhart and Grant 1996). Consequently, it has been argued that these local adaptations need to be recognized and preserved when propagating plants for use in ecological restoration (Knapp and Rice 1994, Lippitt and others 1994, Linhart 1995). For example, it has been suggested that herbaceous plant material should be collected 328-3,280 feet (100-1,000 meters) from the intended restoration planting site

069	656	304	656	158	069	056	147	
085	268	151	328	333	779	115	014	398
398	582	158	115	056	398	050	779	
123	164	740	014	164	345	357	164	656
069	050	040	050	231	333	231	210	
(unplanted alley for access)								
158	058	289	304	123	573	050	357	
304	740	123	231	834	085	345	085	115
398	040	085	333	050	398	056	231	
333	014	164	014	268	289	123	834	740
123	115	573	158	740	231	268	136	

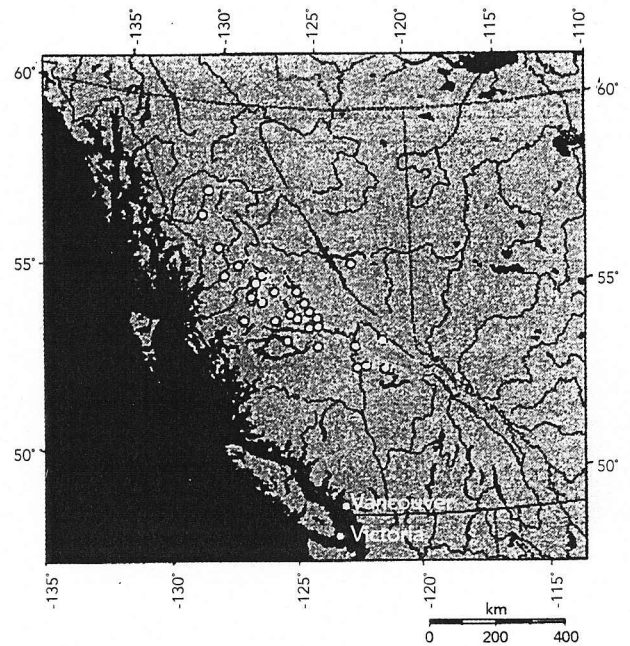


Figure 1. Sample planting layout (left) for a portion of two rows in a seed increase plot designed for blue wild rye using 30 accessions (each identified by a number). The seed was collected from different locations in the northern interior of British Columbia (right). Over a period of three years, the Burtons and their colleagues collected 1,002 seed accessions of 41 species from low- and mid-elevations across the northern interior of British Columbia.

(Linhart 1995). Indeed, advocacy for the use of “local only” plant materials can take on near-religious proportions even where scientific imperatives are lacking, perhaps as an extension of an equilibrational view of nature (and the corollary that organisms are perfectly adapted to their environment), or because of a preference for local, small-scale, volunteer enterprises.

A contrasting approach to genetic management suggests that it may be more prudent to simply facilitate the development of locally adapted ecotypes by making sure an appropriate diversity of genetic raw material is available for natural selection. A history of glaciation, dramatic biome shifts, climate change, and altered disturbance regimes has “mixed and stirred” a large variety of plant genotypes and plant species in many parts of North America (Burton and others 1988), with current populations including both recently developed genetic combinations and relics of past conditions. Every plant population has a unique combination of genotypes, and no propagation program can adequately sample the genetic diversity of hundreds of millions of genotypes found in a widespread plant species

(Allard 1970, Marshall and Brown 1975). So unless there are recognizable reasons for doing so, such as rare species, disjunct populations, or unusual habitats, a strategy of “facilitating” adaptive genotypes seems more appropriate than “preserving” any arbitrary set of genotypes of native plants for use in ecological restoration. Fenster and Dudash (1994, p. 47) point out that “Artificial mixing of distant gene pools may parallel the dynamics of gene flow during the evolutionary history of a species; ...preservation of the genetic integrity of a species may be an ideal with no natural basis; therefore, it should not be used, *a priori*, as an obstacle to the mixing of gene pools.” Bennett (1970, p. 124) also concludes that “success or failure depends upon adaptability in the crop, that is, upon the provision of recombinational variability.”

We believe, as do a number of other researchers, that inclusion of genetic material beyond local populations ensures that the genetic diversity and vigor required for native species to respond to climate change and other stresses will remain in place. For predominantly inbreeding or apomictic species, a high-

diversity source of plant seed would consist of multiple lines (derived from many source populations) of selfed genotypes; for outcrossing species, high-diversity seed would consist of deliberate or random hybrids of plants originating from many source populations. Project policies of the Society for Ecological Restoration (1994) advocate the planting of “regional ecotypes,” not necessarily local populations only, at restoration project sites. This strategy avoids both the danger of inbreeding depression and the spread of genes (“genetic swamping”) from vigorous cultivar lines. Just as importantly, working with high-diversity, regionally adapted plant material allows seed growers to produce seed suitable for a larger area and a larger potential market than site-specific local populations. Genetic breadth and population robustness have thus become the goal of several native plant seed production programs throughout North America (Booth and Jones 2001).

If and where local genetic adaptation is functionally important, local environmental filters will select appropriate strains from the broader mix, so long as there is genetic variability on which to

draw. Williams (1964), Jensen (1988), and Jones and Johnson (1998) support this idea that nature will “fine tune the population for maximum fitness to the site.” Of course, the strategy of maximizing genetic variation is not generally applicable to the restoration of rare plant species or those exhibiting localized differentiation of varieties or potential new species (Falk and others 1996). In general, we agree with the recommendations of Lesica and Allendorf (1999) to use hybrid populations or mixtures of genotypes for the restoration of severe disturbances that occupy medium to large areas of land.

At the other extreme, the structure of the seed trade industry and the training of most professional agronomists results in the promotion of registered varieties in the sale and purchase of plant seed. Most registered cultivars of native plant species (Helm 1995) are the products of selective breeding programs and, by definition, represent a fraction of the natural genetic diversity found in a given species. As a result, this plant material may do extremely well under certain conditions and poorly under other conditions, but with little genetic capacity to adapt to local differences in climate, soils, or biotic conditions. Most restoration projects are therefore faced with the choice of using: 1) local seed; 2) regional multi-lineal or polycross seed; or 3) selected cultivar seed (Lesica and Allendorf 1999). The choice of seed and the development of their respective genetic management strategies clearly depend on the breeding system of the plants involved (Fenster and Dudash 1994, Knapp and Rice 1996), the size and intensity of disturbance being restored (Lesica and Allendorf 1999), and the objectives of a given restoration project. For example, it is generally acknowledged that there is more room for the use of multiple populations and their hybrids in the restoration of outcrossing species than in species with high selfing rates (Fenster and Dudash 1994, Havens 1998). Also, the conservation of a rare species would always take priority over issues of “genetic integrity” within the species (Havens 1998).

We consider the “multi-lineal,” “bulk hybrid” or “polycross” approaches to be a realistic compromise between the use of



Figure 2. Symbios employee, Adam Hossack, shows off a plot of newly established alpine bluegrass (*Poa alpina*). Seed-increase plots such as this one were as large as 952 m² in size. The labeled, white pot markers identify designated accession locations. Photos by Phil Burton

locally collected native seeds and selected strains of either native or exotic origin. Other approaches with similar aims include the “convergent-divergent improvement” technique outlined by Munda and Smith (1995), and the development of “ecovars” selected with equal emphasis on genetic breadth and agronomic characteristics (Lyseng 1993, Booth and Jones 2001). Related approaches include the use of “mass reservoirs” or “panmictic populations” (Frankel 1970), and the “composite methods” or “hybrid populations” advocated by plant breeders, such as N.F. Jensen (1988), to generate variability for use in crop improvement programs. These methods have been used for several decades as an adjunct to selective breeding programs for cereal grains. They offer a commercially feasible and ecologically responsible alternative for both seed growers and restoration practitioners. Most land managers (or, at least, those who do not have a mandate of ecological restoration) simply default to using the easily-obtained, low-priced cultivated Eurasian species in their revegetation programs if native seed is not available for sale in large quantities and at reasonable prices. Regionally-adapted native seed can

be grown in large quantities on speculation, not just on a site-specific or project-by-project basis, thus encouraging the wider production and use of native seed for revegetation purposes. In addition, a large pool of genetic variability is retained and can be successfully recombined, filtered, and grown out at many planting sites and ecologically distinct microsites throughout the original range of plant collections.

Borrowing from Tree Seed Orchard Design

Over a period of three years, we collected 1,002 seed accessions of 41 plant species from low- and mid-elevations across the northern interior of British Columbia (52° N to 60° N latitude, between the Coast Mountains and the Rocky Mountains, Figure 1). Though covering a wide geographic area, this region is characterized by a continental sub-boreal or sub-alpine climate found in broad mountain valleys and lower slopes and on interior plateaus, with long snowy winters and short cool summers. We did not collect seed from alpine areas. Each accession consisted of mixed seeds from a large

number of plants of the same species, growing within walking distance of each other. The plants chosen for study are all widespread and common herbaceous species, collected from disturbed or open habitats. Seeds were tested in several years of laboratory germination assays, propagated in a greenhouse, and 31 species suitable for continued evaluation were established in seed-increase plots.

Rather than just growing haphazard mixtures or single lines of the sampled populations in seed-increase plots, we wanted to maximize the potential for outcrossing and we wanted to retain the ability to track the survival and productivity of individual accessions. To meet these objectives, we borrowed from the well-established field of tree “seed orchard” design. Open-pollinated seed orchards are widely used for genetic tree improvement in forestry, because most coniferous species are strongly outcrossing (Namkoong and others 1988, El-Kassaby and Askew 1998). Selected trees are established from seed or cuttings representing many different populations (“provenances”) originating from across the range of the species or the range into which progeny are intended to be planted. Established at a location favoring seed production and isolated from off-site pollen contamination, these orchards are carefully laid out in such a manner as to promote cross-pollination among tree populations that would not usually encounter each other in the wild. Consequently (and often contrary to public perception), the offspring produced by conifer seed orchards contain a great deal of hybrid vigor and greater genetic variability than a comparable sample of individuals from any wild population of the same species (El-Kassaby and Askew 1998). Further refinements to an orchard may include removing trees whose offspring perform poorly in progeny trials.

We applied a computerized tree seed orchard design program named COOL (Bell and Fletcher 1978) to lay out single species seed-increase plots (Figure 1). For each species, the program assigned accession numbers to available planting positions at random, although options exist in the COOL program to restrict duplication



Figure 3. Seed is harvested from seed-increase plots with hand sickles or a motorized seed stripper, as Carla Burton is doing in this plot of blue wildrye (*Elymus glaucus*). Complete harvesting of multi-line plots of plants that ripen at different times requires taking multiple passes over the course of several days or weeks to glean all the seed.



Figure 4. High-diversity seed produced in increase plots can be used directly for small revegetation and restoration projects, or it can be grown out for one generation in larger production fields. Here, contract grower, Leroy Taylor, vacuums out a Brillion seed drill before sowing a second small field for native plant seed production.

among vertical, horizontal and diagonal neighbors (Bell and Fletcher 1978). We prepared "seed orchards" made according to this design for each of 31 promising species (Table 1), and established plots in cultivated fields near the town of Smithers in northwestern British Columbia (Figure 2).

We designed the planting layouts for origin-identified transplant stock (grown from seed in a greenhouse) to facilitate maximum cross-fertilization among source populations. Due to the extensive nature of our initial wild seed collection, even those species exhibiting little out-crossing behavior still produce seed from a wide diversity of sources, and all are climatically adapted to the region. The seed produced in these "orchards" should thus contain many lines of inbred seed (for those species that are predominantly selfing), or a very large number of possible population hybrids (for those species that are predominantly outcrossing). Much of the work in this enterprise involved detailed plot layout and planting, followed by manual weeding and monitoring. By carefully tending all accessions of plants and by repeatedly harvesting seed from the stand (since some accessions mature at different times, Figure 3), we hope to retain the broadest possible range of genetic variability in the seed so produced. Though active selection was purposely avoided, it is inevitable that our seed excludes some genotypes that didn't germinate in the greenhouse due to complex dormancy mechanisms, but this can be considered acceptable when the intended use of the crop is for sowing revegetated areas. In addition, by establishing these hybridizing seed-increase plots at only one location, there is likely to be a gradual loss of genetic diversity through the differential survival and reproduction of genotypes. This genetic deterioration is partially offset by the annual infusion of seedlings from new wild-collected plant material to replace any mortality in the layout.

Evaluation in Progress

Seed produced in our cultivated plots is now being used to establish larger seed

Table 1. Plant species native to the northern interior of British Columbia, brought into cultivation for production of high-diversity seed.

Plant Family	Scientific Name	Common Name	Accessions	
Asteraceae	<i>Achillea millefolium</i>	common yarrow	75	
	<i>Anaphalis margaritacea</i>	pearly everlasting	68	
	* <i>Arnica chamissonis</i>	meadow arnica	*1	
	<i>Arnica cordifolia</i>	heart-leaved arnica	24	
	<i>Aster conspicuus</i>	showy aster	22	
Cyperaceae	<i>Aster foliaceus</i>	leafy aster	5	
	<i>Carex aenea</i>	bronze sedge	29	
	<i>Carex macloviana</i>	Falkland Island sedge	34	
Fabaceae	<i>Carex mertensii</i>	Merten's sedge	47	
	<i>Lathyrus ochroleucus</i>	creamy peavine	35	
	<i>Lupinus arcticus</i>	arctic lupine	41	
Juncaceae	<i>Lupinus polyphyllus</i>	large-leaved lupine	21	
	<i>Vicia americana</i>	American vetch	32	
	<i>Luzula parviflora</i>	small-flowered wood-rush	24	
Liliaceae	* <i>Allium cernuum</i>	nodding onion	*3	
Onagraceae	<i>Epilobium latifolium</i>	broad-leaved willow-herb	17	
Poaceae	<i>Agrostis exarata</i>	spike bentgrass	19	
	<i>Bromus ciliatus</i>	fringed brome	39	
	<i>Calamagrostis canadensis</i>	bluejoint reedgrass	42	
	<i>Calamagrostis rubescens</i>	pinegrass	14	
	<i>Elymus glaucus</i>	blue wildrye	89	
	<i>Elymus trachycaulus</i>	slender wheatgrass	22	
	<i>Festuca occidentalis</i>	western fescue	56	
	<i>Festuca saximontana</i>	Rocky Mountain fescue	14	
	<i>Leymus innovatus</i>	hairy wildrye	9	
	<i>Poa alpina</i>	alpine bluegrass	13	
	<i>Trisetum spicatum</i>	spike trisetum	28	
	Polemoniaceae	<i>Polemonium pulcherrimum</i>	showy Jacob's-ladder	6
	Rosaceae	<i>Dryas drummondii</i>	yellow mountain-avens	22
<i>Geum macrophyllum</i>		large-leaved avens	28	
Scrophulariaceae	* <i>Collinsia parviflora</i>	small-flowered blue-eyed Mary	*2	

Note: Some species (*) represented by very few populations were added late in the program (after most seed collection expeditions), or are being grown for specific local restoration projects.

production fields (Figure 4), and for some operational revegetation projects. We established field trials at 22 sites across northern British Columbia to compare different seed densities, species combinations, seasons of sowing, the use of mulches, fertilizer and other treatments. We concluded that some native species can be just as successful as the agronomic species currently used for roadside seeding. We noted a possible hybrid vigor in the performance of plot-produced seed compared to wild-collected seed (although our cultural methods also improved over the same time period), and observed no evidence of outbreeding depression or maladaptation from using multi-lineal polycross seed. A component of these field trials (Burton and Burton 2001) further identified optimal densities of seed

and fertilizer to achieve plant cover goals at minimal cost.

Having demonstrated the short-term feasibility of our approach to increasing the availability of genetically diverse native plant seed, determination of the long-term risks and benefits awaits further research and monitoring. This seed, now becoming available in commercial quantities, is being used to revegetate the sides of newly built logging roads and ski trails, old campgrounds, decommissioned roads and log landings, and to restore the degraded vegetation of newly acquired nature reserves.

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