

SEED TRANSFER OF WOODY SHRUBS IN ALBERTA – ARE CURRENT SEED ZONES APPLICABLE?



May 2013

Prepared By:

Dr. Shauna-Lee Chai

Dr. Brian Eaton

Jay Woosaree

Alberta Innovates – Technology Futures

Bag 4000, Hwy 16A & 75 Street

Vegreville, AB T9C 1T4

Dr. Deogratias Rweyongeza

Dr. Erin Fraser

Alberta Environment & Sustainable
Resource Development

9920-108 St, Edmonton, AB T5K 2M4

This report may be cited as:

Chai, S-L., B. Eaton, J. Woosaree, D. Rweyongeza and E. Fraser. 2013. Seed Transfer of Woody Shrubs in Alberta – Are Current Seed Zones Applicable? Prepared by Alberta Innovates - Technology Futures, Vegreville, Alberta and Alberta Environment and Sustainable Resource Development, Edmonton, Alberta. 41 pp.

Cover image:

Blueberry shrub planted at experimental site by the Boreal Research Institute at NAIT for Shell Canada Energy at Peace River, Alberta. Photo by: S-L. Chai.

ISBN 978-1-4601-1107-6 Seed Transfer of Woody Shrubs in Alberta – Are Current Seed Zones Applicable – May 2013 – online version

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EXECUTIVE SUMMARY

The present system of seed zones was developed primarily to guide seed transfer for commercial tree species, while conserving the local flora for all commercial and non-commercial vegetation in Alberta. Owing to this broad objective, current Alberta seed zones are not species-specific, even though plant species differ greatly in their reproductive biology and life history. The Alberta energy sector is increasingly using shrubs in reclamation, which calls for regulating collection and use of shrub seed and vegetative propagules to preserve local adaptation on artificially reclaimed sites. At the outset, it is assumed that due to differences between tree and shrub species in mating system, pollen, seed dispersal and propagation, seed zones adopted from forestry may not be appropriate for regulating seed transfer for shrubs. Therefore, there is a need for research, and mapping of population genetic variability in major shrub species used for reclamation in Alberta, and if necessary, development of a seed zone system specifically adapted to shrubs.

This report investigates the need for a seed zone map specifically adapted to shrub species. The objectives were to: (1) review literature on life history characteristics of commonly used shrubs and compare these characteristics to white spruce (*Picea glauca*), one of the primary tree species for which seed zones in Alberta were developed; (2) provide an estimate of the current use of shrubs for re-vegetation in Alberta's boreal region; and (3) summarise the business case and methodology for developing a seed zone map for shrubs in Alberta.

Our main findings were that seed transfer and zoning are partially dependent on the life history characteristics of a species, especially the breeding system. Life history characteristics of conifer trees are different from those of shrubs; conifers are long-lived, largely diploid, and have a primarily outcrossing, open breeding system with a near-continuous distribution within their range. In contrast, shrub species used in re-vegetation activities in Alberta have varied life histories, ranging from obligate outcrossing to self-fertilising to clonal species, are diploid to highly polyploid, and although wide-ranging, exhibit a less continuous distribution than conifer tree species.

Based on a review of available literature on life history characteristics of 13 shrub species commonly used in re-vegetation projects in Alberta, and the conifer tree species white spruce, we found that a number of breeding guilds could be identified. Ordination of breeding system characteristics revealed six guilds of species with similar breeding system characteristics:

1. *Salix interior* (sandbar willow)-*Elaeagnus commutate* (wolf-willow)
2. *Salix bebbiana* (Bebb willow)
3. *Arctostaphylos uva-ursi* (bearberry)-*Amalanchier alnifolia* (Saskatoon)
4. *Picea glauca* (white spruce)-*Alnus viridis* (green alder)-*Alnus incana* (river alder)
5. *Vaccinium myrtilloides* (blueberry)-*Viburnum edule* (low bush cranberry)-*Cornus sericea* (red-osier dogwood)-*Shepherdia Canadensis* (buffaloberry)
6. *Prunus pensylvanica* (pincherry)-*Prunus virginiana* (chokecherry)

We found that the breeding system of shrub species such as *Alnus* sp. is similar to that of white spruce. Thus the current seed zones designed for conifers are appropriate for *Alnus* sp. and other shrubs with similar life histories. In contrast, species such as *Arctostaphylos uva-ursi* and *Amalanchier alnifolia* have a breeding system that differs from that of white spruce. For these

species, the current Alberta seed zones may not be appropriately applied, as breeding system characteristics imply that these species require even smaller seed zones to maintain local adaptation. Climate change may, however, upset traditional rules for maintaining local adaptation, and may even necessitate translocation of some species over large distances to avoid local extirpation.

A survey of shrub seed use in the province showed that in 2012, approximately 350,000 shrub seedlings were planted out by the energy industry for re-vegetation in Alberta's boreal region; shrub use is expected to rise in the future as reclamation practitioners endeavour to emulate species composition in undisturbed areas. Given the high volume of shrub use across the province, uncertainty in using tree seed zones to guide the collection and use of shrub material, concerns about the future availability of appropriate provenances, and the potential impact of climate change, long-term provenance trials specifically targeted at shrubs species are required. The characteristics to be assessed when developing a seed zone scheme for shrubs include germination, reproduction, survival under climate change scenarios and rapid multi-stemmed growth (vegetative biomass), rather than rapid growth of a single stem as used to assess tree provenances in the past.

Provenance testing can reduce risk in re-vegetation activities by providing reliable information on how a particular species is expected to perform in a given location, and provide some assurance that provenances chosen for re-vegetation are appropriate, and are likely to grow successfully in the new location. Using the approach of identifying breeding guilds, not all 43 shrub species currently used for re-vegetation in Alberta would have to undergo provenance trials. Instead, one representative species could be chosen for provenance trials, to represent a number of other species that possess similar life history characteristics. Until shrub provenance research is conducted however, it is prudent for collectors and users of shrub seed to adopt the existing Alberta seed zones to self-police their movement of reproductive material for the purposes of re-vegetation.

Alberta Innovates-Technology Futures (AITF) has significant expertise and laboratory facilities that could contribute to provenance testing research. It is anticipated that that the Northern Alberta Institute of Technology (NAIT), Alberta Environment and Sustainable Resource Development (ESRD) and industry will have key roles to play in supporting such an initiative.

1.0 INTRODUCTION

The movement of tree seed for reforestation in Alberta is regulated by 90 geographically distinct seed zones, designed to emulate locally adapted wild tree populations (ASRD 2009a, Figure 1). Seed zones are geographic subdivisions of Natural Regions and Subregions and reflect climate, ecology and early results of coniferous tree species provenance trials. Free movement of tree seed for replanting is permitted within a seed zone but not among zones, in an attempt to prevent maladapted seed from being planted, and to preserve locally adapted seed stock. If sufficient quantities of seed for reclamation cannot be sourced within a seed zone, a variance application may be made to Alberta Environment and Sustainable Resource Development to use seeds from a different seed zone.

The present seed zone map for Alberta is limited to tree species planted for commercial use, with timber yield being the main criterion used in experimental testing of seed zones (for example, Rweyongeza 2011). However, with increasing interest from the energy industry in using shrub species (for example, Saskatoon, blueberry, choke cherry, dogwood, bearberry and buffalo berry) in reclamation (Alberta Environment 2010), rather than tree species alone, a map delineating appropriate seed sources or provenances for shrub species in Alberta is required. Appropriately-sized seed zones are a tool to minimise risk associated with planting seed maladapted for the geographic location of any particular re-vegetation project. Although smaller than necessary seed zones ensure that local adaptation is preserved, they complicate seed procurement and increase the cost of reclamation. On the other hand, larger than appropriate seed zones simplify seed collection and reduce the cost of reclamation, but risk using maladapted stock during re-vegetation projects.

Currently, the largest users of shrub seed in Alberta operate in the Lower Athabasca oil sands region. The largest single group of shrub seed users in the province is a cooperative of five oil sands companies – Suncor Energy, Imperial Oil, Canadian Natural Resource Limited, Shell Canada Energy and Syncrude Canada Limited. Other potential users include the *in situ* oil and gas industries, local, provincial and federal government agencies, and non-governmental organisations. The movement of shrub seed in Alberta is currently unregulated, but reclamation practitioners are encouraged to follow the seed zones developed for tree species as outlined in the *Alberta Forest Genetic Resource Management and Conservation Standards* (ASRD 2009a).

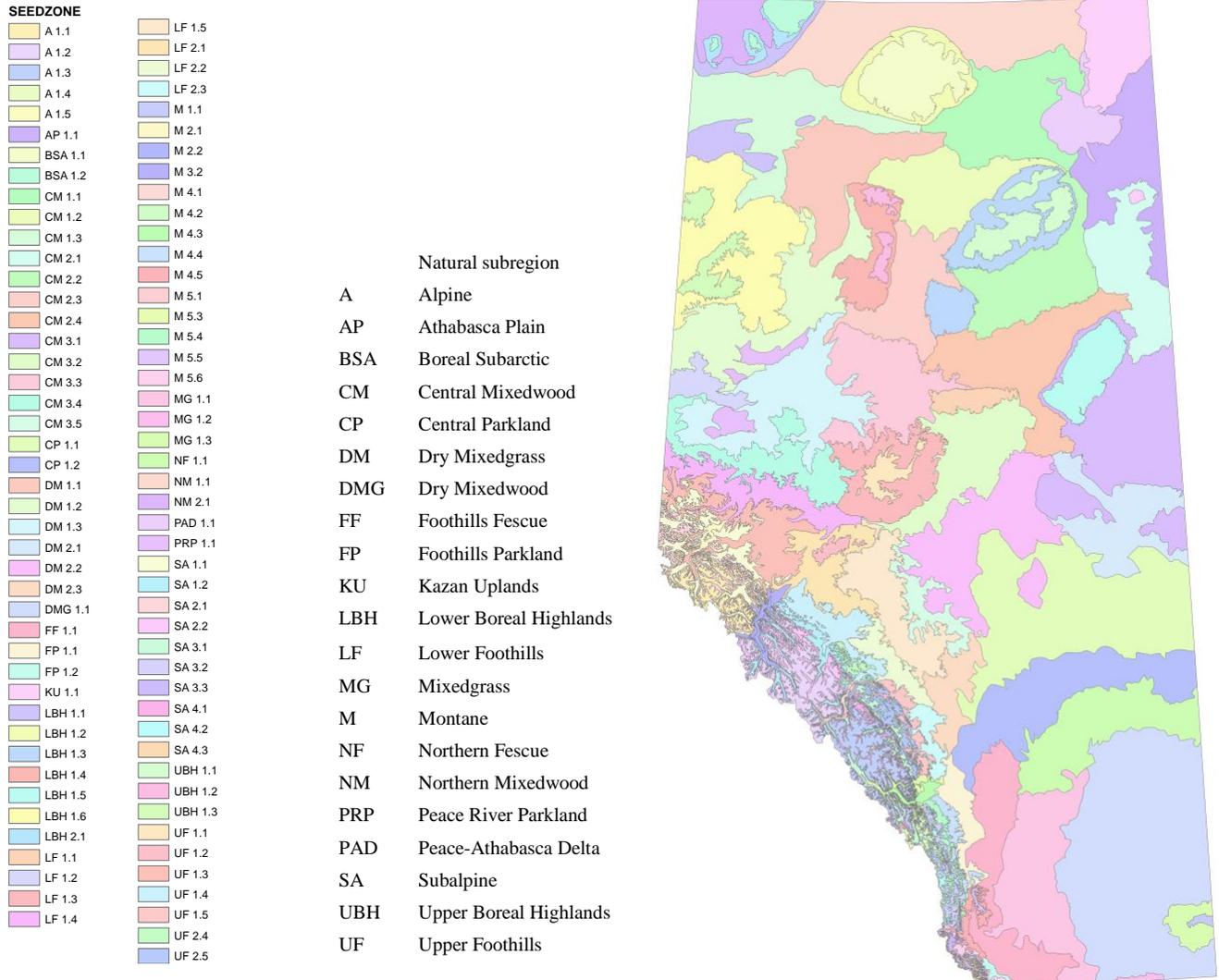


Figure 1. Seed zone map of Alberta. Each colour represents a seed zone intended to define an area of locally adapted tree populations (ASRD 2009a). The map is based on Alberta's natural regions, climate data and provenance trials for white spruce. For example, DM 1.1 – DM 2.3 represent seed zones in the Dry Mixedwood along a climatic gradient.

2.0 THE EFFECT OF LIFE HISTORY TRAITS ON GENE FLOW AND SEED TRANSFER ZONES FOR RE-VEGETATION

Seed transfer zones have their origins in the establishment of commercially important conifer plantations, and the recognition that there are strong regional differences in expressed phenotypic traits (Kitzmilller 1990). Hybridisation between individuals of different populations can lead to outbreeding depression due to the replacement of local alleles with those suited for a different location (Smith & Halbrook 2004). Seed transfer zones are designed to mitigate the threat of outbreeding depression in native plant re-vegetation projects (Smith & Halbrook 2004). The development of seed transfer zones for the wide variety of wild species potentially used in re-vegetation is difficult, because little is known about the genetic basis for local adaptation, especially at human-altered sites (Smith & Halbrook 2004).

Generally, species with limited pollen dispersal, limited seed dispersal, or breeding systems dominated by vegetative reproduction or self-fertilisation (autogamy) favour limited gene flow among individuals or populations. Species with limited gene flow are more likely to respond to natural selection or suffer genetic drift at local scales because the homogenising effect of gene flow is largely absent. Such species will acquire localised adaptations and require relatively small seed transfer zones for re-vegetation purposes (Linhart 1995, Hufford & Mazer 2003). By contrast, in highly outcrossing species, relatively large seed zones are applicable, since ecotypic (discontinuous) differentiation is unlikely, due to the homogenising effect of gene flow.

2.1 Characteristics of breeding systems that influence gene flow

Gene flow is the primary homogenising force on a species' genome that prevents local adaptation or genetic drift (Futuyma 1979). Gene flow is facilitated by the movement of pollen, seed, bulbils or other propagules, and is significantly affected by the plant's breeding system. The breeding system of a plant species refers to factors that determine how plants mate, and with whom. This includes pollination systems (whether a species is outcrossing or self-pollinating), dispersal methods, whether it hybridises with other species or subspecies and whether asexual or sexual reproduction is most important to its spread and persistence. Breeding systems are highly variable across species, and are not necessarily standardised within individuals of a species, or across the species' range (Richards 1997, Smith & Halbrook 2004).

2.1.1 Pollination and dispersal

Reproduction in a species can range from complete self-pollination (where pollen from the anthers of a plant fertilizes the stigma of the same plant), to complete cross-pollination (where each plant only bears flowers of one sex – male or female, or mechanisms ensure self-incompatibility between the ovule and pollen of the same plant even if flowers of both sex are borne on the same individual). More precisely, plant reproduction can be described as being on a continuum ranging from vegetative, to self-pollination, to cross-pollination. The mode of reproduction expressed by a species can vary according to environmental conditions and the genetic makeup of individuals (Smith & Halbrook 2004). Pollination is generally regarded as the most important source of gene flow amongst plants, as it is the means by which hybridisation

occurs (Levin & Kerster 1974, Hamilton & Miller 2002, O'Connell et al. 2007). The importance of gene flow by pollen increases as population sizes decrease (Ellestrand 1992). Pollination may occur via wind, water, insects or vertebrates.

Generally, pollen and seed are dispersed only a few meters from the source plant, which minimises variability in mating partners; however, a small proportion of pollen can travel over kilometers (Levin 1981). Current knowledge of the importance and magnitude of long distance dispersal is severely constrained by data limitations (Nathan 2006). Distances travelled can be represented by leptokurtic distributions, meaning that most pollen or seed travels an intermediate distance from the parent plant, with relatively fewer short or long-distance dispersal events (Handel 1983). Pollen that travels by wind can usually travel further than animal dispersed pollen (Richards 1997). Thus, wind-pollinated species are expected to have higher levels of gene flow compared with insect-pollinated plants (Young et al. 1996, Weidema et al. 2000, Schuster and Mitton 2000), implying that larger seed transfer zones can be ascribed to wind-pollinated species than animal-pollinated species. Pollination by larger animal species that are strong fliers such as bumble bees, hawk moths, bats and birds can also result in long distance dispersal of pollen. Moving water may also facilitate long distance dispersal of pollen. The application of molecular markers in pollen dispersal studies to track paternity suggests that long distance pollen dispersal is more common than previous studies have documented (Kramer et al. 2007).

Seed dispersal distance is another important determinant of gene flow. Because most plant colonisations occur through seed (Nathan 2006), the effect of gene flow through pollen is greatly enhanced by subsequent seed production and dispersal. The longer the seed dispersal distance, the greater the gene flow. The relative importance to gene flow of pollen dispersal distance compared with seed dispersal distance is debatable. The common generalisation is that pollen dispersal occurs over larger spatial scales than seed dispersal (Nathan 2006), but some studies report the opposite (Bacles et al. 2006). Seeds also carry twice the genetic complement compared to pollen, which suggests that seeds can play a greater role in gene flow (Hamilton & Miller 2002, Kramer 2008).

2.1.3 Polyploidy (ploidy)

Some shrub species such as Saskatoon, bearberry, pin cherry and choke cherry demonstrate polyploidy, which means they have more than two copies of each chromosome, unlike the diploid condition observed in conifer tree species (Smith & Halbrook 2004). Polyploidy in plants represents a major mechanism of adaptation and speciation as polyploids often possess novel physiological and life-history traits that may allow them to occupy different ecological niches than their diploid counterparts (Levin 1983). Polyploids are thought to be better adapted to extreme ecological environments than their diploid relatives as demonstrated by the ability of some western North American shrub complexes to tolerate drought (Mahalovich & McArthur 2004). The downside to ploidy however, lies in reduced reproductive efficiency compared with the diploid condition; ploidy levels may differ among individuals of a species, preventing the production of viable offspring when such individuals mate (Smith & Halbrook 2004). Nonetheless, ploidy may be a factor worth considering when selecting provenances for re-vegetation in sites in Alberta, as climate models predict that parts of the province will experience increasing incidents of drought in the future (Barrow and Yu 2005).

2.1.4 Pattern of genetic variability

The pattern of genetic variability within a species is important in establishing seed transfer protocols. Species with discrete genetic variation over shorter distances will require smaller seed transfer distances to maintain local adaptation. Self-pollinated species and species with limited seed and pollen dispersal fit in this category. Seed transfer for such species would be managed through smaller seed zones. In contrast, species with a continuous (clinal) pattern of genetic variation where genes are continuously exchanged among populations over a large region can permit longer distance seed transfers. Cross-pollinated species with wind dispersed seed and pollen, and species with long-distance pollen dispersal via insects, fit in this category. Seed transfer for such species can be managed through large seed zones without risking maladaptation.

Molecular markers such as microsatellites and allozymes cannot be used to reliably obtain information on genetic variability for determining seed zones, because these molecular markers are generally deemed selectively neutral and therefore do not respond to selection, as do adaptive traits (Henrick 2001, Johnson et al. 2004, Smith & Halbrook 2004). Provenance trials are the only way to reliably assess variation in adaptive traits, and seed zones established based on molecular markers should be considered tentative until investigated using provenance trials (Johnson et al. 2004).

2.1.5 Comparison between conifer trees and shrubs

Conifer trees are long-lived and have a primarily outcrossing, open breeding system with a near-continuous distribution within their range. As expected (given the aforementioned traits), provenance trials have shown that variation in cold hardiness, phenology and tree growth in many conifers is clinal or continuous (Johnson et al. 2004). In general, species with large ranges can be expected to be more genetically variable than species with smaller ranges, and woody, long-lived species can be expected to be more genetically variable than short-lived species (Linhart 1995). Unlike some shrub species, few conifers exhibit variation in levels of ploidy, with most conifer species being diploid.

In contrast to conifer tree species, shrub species commonly used for re-vegetation in Alberta have varied life histories. These shrub species vary from obligately outcrossing to self-fertilising to clonal species, and range from species that are diploid to highly polyploid. Although wide-ranging, the distribution of shrubs in Alberta is less continuous than that of conifer tree species (Figure 2). Most studies have demonstrated ecotypic rather than clinal variation in shrubs, but this could be an artifact of sampling too few populations to detect clinal variation (Johnson et al. 2004).

2.2 Climate change

The geographic distribution of plants is controlled primarily by climate. Climate change may upset traditional rules for maintaining local adaptation, and may even necessitate translocation of some species to avoid local extirpation. With climate change, it is anticipated that drought will surpass low winter temperatures as the primary limiting factor for the establishment and distribution of plant species in Alberta (Barrow and Yu 2005). This phenomenon increases the

importance of having a seed zone map to ensure that suitable provenances are used to guide the movement of seed across the landscape.

If the climate or other environmental conditions at a site have changed more rapidly than adaptive traits have evolved through natural selection, the possibility exists that non-local provenances may be better adapted to a site. Because local populations are adapted to past conditions at a site, they may be poorly adapted to future climates when conditions are changing rapidly and in one direction (for example, increasingly warm and dry). Non-local provenances have been used in forestry to improve productivity in other jurisdictions (for example, improvements of loblolly pine in the southeastern US using more southern provenances, Johnson et al. 2004); a similar approach may be useful in reclamation in Alberta, especially in the northern portion of the province.

A key finding in long-term provenance studies conducted in the United States is that seemingly poorly adapted seed sources were not maladapted to the average conditions of a site, but rather were unable to survive the rare climatic events that occurred at intervals of 10 years or more. This highlights the need for long-term provenance trials rather than short-term common garden studies (Johnson et al. 2004).

2.3 Seed zoning and transfer in other jurisdictions

In the USA, shrubs are also grouped with conifers in terms of seed zones, while grasses and herbs are managed differently. For species with no information available on genetic variation, proxies such as USDA plant hardiness zones, forest tree seed zones, elevation band/watershed, climate matching or ecoregions can be used (Johnson et al. 2004, Miller et al. 2011). Ecoregions are useful for estimating seed zones, especially in regions with relatively low topographic or climatic variation (Miller et al. 2011).

In Britain, the *Forest Reproductive Material Regulations* control the movement of seed used for forestry. Tree and shrub species are treated similarly, with 46 *controlled* species as well as a voluntary system for certification of other native trees and shrubs (Forestry Commission 2007).

3.0 RELEVANT LIFE HISTORY TRAITS OF COMMONLY USED SHRUBS AND TREES IN ALBERTA

This section provides information on life history traits relevant to seed zone considerations for shrubs in Alberta that are commonly used in re-vegetation programs. The information can be used to group shrubs with similar characteristics, and to compare these species with conifer trees, as current seed zones are constructed based on data collected from commercial conifer tree species (Table 1).

***Alnus viridis* (Ait.) Pursh (green alder)**

This species is also known as *Alnus viridis* subsp. *crispa* (Matthews 1992a); common names include mountain alder, American green alder and green alder.

Green alder is a perennial shrub that occurs in a variety of habitats, including the banks of streams, lakeshores, and bogs, the understory of black spruce, white spruce, and jack pine stands, in open and closed deciduous forests (as long as the canopy is not too dense), in shrub communities, and on open, moist tundra. Individual plants can reach 3 m in height, and may occasionally reach 6-9 m. The species often forms dense thickets, but may occur singly as well (Matthews 1992a). Green alder is able to fix nitrogen due to its association with nitrogen-fixing bacteria *Frankia* spp. (Normand & LaLonde 1982); thus, this species may facilitate the establishment of later-successional species. The species is widely distributed, occurring from Alaska across all of Canada, Greenland, and south to New England, the Great Lake States and the Pacific Northwest of the USA.

A. viridis is a diploid species ($2n=28$) (Moss 1992). It is a monoecious species, but alders with this characteristic rarely self-pollinate (Harrington et al. 2008). Allozyme studies suggest that there are high rates of gene flow and weak genetic differentiation between populations of the green alder, with only 5% of total genetic diversity among populations studied in Quebec (Bousquet et al. 1987a). Studies across four Canadian provinces also revealed very low genetic differentiation between green alder populations (Bousquet et al. 1987b).

Green alder flowers are wind pollinated; the seeds are winged nutlets that rely on wind and water for dispersal. These seeds do best on bare mineral soil, such as that found in avalanche tracks, sediment deposited by flowing water, and talus slopes. Germination of seeds in disturbed habitats such as these is the main form of propagation for this species (Haeussler & Coates 1986). Green alder will sprout from root crowns if the plant is damaged or cut, but it does not spread through asexual propagules.

***Alnus rugosa* (DuRoi) Spreng (river alder)**

This species is also called *Alnus tenuifolia* and *Alnus incana* ssp. *tenuifolia* (Johnson et al. 1995). Common names include gray alder, thinleaf alder, mountain alder and river alder. This western subspecies of the gray alder is found throughout the western half of North America from Alaska, the Yukon, and the Northwest Territories, down through British Columbia and Alberta, and into Mexico (Fryer 2011).

River alder prefers wet to moist sites, and is frequently found along streams in the mountains of western North America. It is moderately shade tolerant; while it will grow in forest understories, it is more commonly found on open sites. It is adapted to nearly all types of disturbance, including those of a severe nature (Fryer 2011). This species is able to fix nitrogen due to its association with nitrogen-fixing bacteria *Frankia* spp. (Normand & LaLonde 1982), and may therefore facilitate the establishment of later-successional species.

River alder is a diploid species ($2n=28$) (Moss 1992). It is a monoecious species, but alders with this characteristic rarely self-pollinate (Harrington et al. 2008). It exhibits high rates of interpopulational gene flow, based on allozyme variation, and most genetic diversity is found within populations (Bousquet et al. 1988). Pollination is by wind, while dispersal is by wind and water (Fryer 2011). Asexual reproduction likely contributes little to increased cover of the species where it occurs. River alder may sprout from root crowns after fire, but lateral expansion of individual plants via asexual means is ineffective (Huenneke 1985).

***Amelanchier alnifolia* (Nutt.) (Saskatoon)**

Saskatoon is a species of open areas and forest edges (Moss 1992). Berries of the species were harvested in large quantities by First Nations people of North America (Turner et al. 1990). Today it is planted as an ornamental and to produce a commercial fruit crop (Harris 1970). Several cultivars have been developed (St. Pierre et al. 2005). The species is hardy and grows mostly by vegetative reproduction where it can spread by stolons forming dense thickets (Hermesh & Cole 1983, Moss 1992, Johnson et al. 1995); it rarely spreads by seed (Brinkman 1974). Regeneration by seeds is limited by moisture, low spring temperature and/or disease (Brinkman 1974). Pollination is by insects and a limited amount of self-fertilisation (Olson 1984). Frequent blossom visitors include representatives of the families Sphecidae (wasps) and Andrenidae (bees). The species is dispersed by birds and small and large mammals including black bear, deer, upland game birds and songbirds (Brinkman 1974).

Varieties in Alberta overlap in distribution and include (Fryer 1997):

A. a. var. *alnifolia* (Nutt.) Nutt. ex M. Roemer Saskatoon serviceberry

A. a. var. *cusickii* (Fern.) C.L. Hitch. Cusick's serviceberry (Hitchcock & Cronquist 1973)

A. a. var. *humptulipensis* (G.N. Jones) C.L. Hitch.

***Arctostaphylos uva-ursi* (L.) (bearberry)**

A. uva-ursi is circumboreal in distribution. It is a taxonomically controversial species that has been separated into subspecies on the basis of variation in pubescence characteristics. More recent analysis suggests that variation in the species is nearly continuous; the taxa are not morphologically distinct and retention of formal names for subspecies is not recommended (Rosatti 1987). Two ploidy levels are common – diploids and tetraploids, and populations sometimes have both levels (FNA 1993). Intraspecific taxa may be recognised once variation in morphology and ploidy is further assessed (FNA 1993).

Reproduction is primarily asexual (Stallard 1929); the species flowers early in spring before insects are out (Haslerud 1974). Some pollination is by thrips (*Ceratothrips ericae* and *Haplothrips setiger*) and bumble bees throughout the species range. The species is self-compatible (García-Fayos & Goldarazena 2008).

***Cornus sericea* Michx. (red-osier dogwood)**

Common names for this species include red-osier dogwood, American dogwood, creek dogwood, and red dogwood. Gucker (2012) provides a recent summary of information on this species.

Red-osier dogwood is a native deciduous shrub that may grow 1-6 m tall; it often forms clumps or dense thickets by stolons, rooting stems and adventitious lower branches. Although it is most commonly found in moist to wet sites such as shorelines, meadows, floodplains, marshes, swamps, bogs and fens, red-osier dogwood may also be found in forests, shrub thickets, and sand dunes. It is more common in floodplains and valley bottoms than on uplands. The species is

tolerant of scouring and flooding (Gucker 2012). It is found throughout Canada and much of the United States, but is more common in northern latitudes.

C. sericea is a diploid species ($2n=22$) (Moss 1992) and an obligate outcrosser (Hummel et al. 1982). Lovell (1898) observed that bumblebees were important pollinators of this species in Maine, USA, though other insect groups, including other types of bees, flies and butterflies, also visited red-osier dogwood flowers. In contrast, Thompson et al. (1985), working in New Brunswick, found that bumblebees never visited *C. sericea*, while approximately 50% of visitors to dogwood flowers were other bee species; the remainder were dipterans and coleopterans.

Based on differences in seed germination rates in 55 populations of red-osier dogwood in Alberta, Acharya et al. (1992) suggested that populations isolated by greater than 50 km may exhibit genotypically different abilities to germinate. Seed dispersal is by birds and mammals, and there is the potential for long-distance dispersal via these agents; dispersal distances of at least 215 m have been documented (Robinson & Handel 1993). Passage through an animal gut, or deposition in fecal matter, seems to increase the germination success of red-osier dogwood (Krefting & Roe 1949, Rogers & Applegate 1983). Secondary dispersal may occur when rodents remove and cache red-osier dogwood seeds from bird feces (Vander Wall et al. 2005).

Vegetative spread and regeneration are important for red-osier dogwood; asexual propagation can occur via aboveground stems, stolons and/or root crowns following damage, or from rooting of prostrate stems. Stolons can extend as far as 3 m from the parent plant (Gucker 2012).

***Elaeagnus commutata* Bernh. (wolf-willow)**

Common names for this species are silverberry, wolf-willow and American silverberry. Esser (1994) provides a summary of basic information for this species.

This native species is a deciduous, long-lived perennial shrub which sometimes forms thickets or loose colonies; individual stems may live up to 19 years (Whysong & Bailey 1957). Silverberry can be found in a range of habitats, including open, sunny grasslands and cooler open forests and woodland thickets; in Alberta, it is usually associated with disturbed habitats (Moore 1964). The species is shade intolerant. In Alberta, it may form dominant communities in aspen parkland habitat, where it enhances cover of other species through its nitrogen-fixing ability (Whysong & Bailey 1975). It is also found as a member of the western snowberry (*Symphoricarpos occidentalis*) community of central Alberta, and as an understory species in white spruce-aspen and jack pine forests in uplands and black spruce-tamarack bogs in northeast Alberta (Visser & Danielson 1988). It can be found in Alaska and the Yukon, as far east as the Great Slave Lake and south from British Columbia to Quebec in Canada, and to Minnesota, South Dakota, Colorado, and Utah in the United States.

Wolf-willow is a diploid species ($2n=28$) (Moss 1992). In a study using random amplified polymorphic DNA (RAPD) techniques on eight silverberry populations in Saskatchewan, Chowdhury et al. (2000) estimated that approximately 72% of the observed genetic diversity was within populations.

Wolf-willow reproduces both sexually (flowers) and asexually (rhizomes). The main pollinators of this species are insects. In Poland, honey bees are the main pollinators of silverberry (Chwil & Weryszko-Chmielewska 2011). Seed dispersal is by birds. Seeds will remain viable for 1-2 years in cold, dry areas. Wolf-willow is considered to have excellent vegetative propagation potential (Baig 1992). It spreads rapidly from underground rhizomes,

from which single aerial stems originate. This is the main form of reproduction for the species (Esser 1994).

***Picea glauca* (Moench) Voss (white spruce)**

P. glauca is a common forest tree reaching 40 m in height. $2n=24$ (Moss 1992).

The *Gene Conservation Plan for Native Trees of Alberta* (ASRD 2009b) describes *P. glauca* as follows:

At mid altitudes in the Rocky Mountains, the species hybridises with *P. engelmannii* and is believed to produce *Picea glauca* var. *albertiana* (S. Brown) Sarg. in southern Alberta due to this hybridisation. *P. glauca* reproduces only by seed which are wind dispersed. High (clinal) genetic variation has been reported in the species. Large genetic differences among individuals and differences among populations within ecological zones have been observed. However, individuals grown from seed collected in parts of Manitoba and eastern Canada have shown good survival and vigor in Alberta.

Pollination and seed dispersal are by wind (Chambers & MacMahon 1994). The distance seed can travel varies with wind speed and is affected by topography since seed trees are often found in lower topographic positions (Bridge & Johnson 2000). Dispersal distance is also affected by forest structure (Horn et al. 2001). Updrafts allow long distance seed dispersal (Horn et al. 2001). Most filled seed is found within 100 m of the seed source (Dobbs 1976). Over 90% of seeds disperse within 50 m of the seed source and fewer than 4% disperse farther than 100 m (Nienstaedt & Zasada 1990). Low levels of self-pollination exist and leads to reduced seed set (Husband & Schemske 1996). Reproductive success in wind-pollinated trees is not expected to be highly impacted by habitat fragmentation in large stands (≥ 180 reproductive trees) (O'Connell et al. 2006).

High levels of genetic diversity are reported for *P. glauca* in natural populations, with most of the genetic variation residing in individuals within subpopulations. For example, Rajora et al (2005) found that, of the total genetic variation in the studied region, only 2% was attributable to variation among populations.

***Prunus pensylvanica* (L.f.) (pincherry)**

Two varieties of pincherry are recognised, both of which occur in Alberta: *P. pensylvanica* var. *pensylvanica* and *P. pensylvanica* var. *saximontana* Rehd. The species inhabits open areas and has a lifespan of 20 to 40 years (Anderson 2004). It reproduces both by seed and vegetatively. Flowers are bisexual (monoecious) (Grisez et al. 2003). The species is self-incompatible (Hall et al. 1981, Shiell et al. 2002). Vegetative reproduction can lead to the formation of thickets (Gill & Healy 1974). Pollination is by insects (honey bees). Dispersal is by birds, small mammals (Marks 1974) and gravity (Gill & Healy 1974).

***Prunus virginiana* L. (chokecherry)**

This species inhabits forest edges and woodlands. It is a slender shrub or small tree up to 10 m high. The species has both diploid and tetraploid forms; $2n=16, 32$ (Moss 1992). A recognised variety in Alberta is:

Prunus virginiana var. *melanocarpa* (A. Nels.) Sarg. - black chokecherry (Kartesz 1994).

Reproduction is by rhizomes or seed produced from obligate cross-pollination. *P. virginiana* is fire adapted and re-sprouts rapidly from rhizomes (Wasser 1982). Pollination is by flies, butterflies, early-flying bees of *Andrena*, *Bombus*, *Anthophora* and *Osmia*, and occasionally by hummingbirds (Vicens & Bosch 2000, Miliczky 2008). The species is partially self-compatible (Shiell et al. 2002). *P. virginiana* showed an increase in biparental inbreeding after habitat fragmentation in experiments conducted in forests of southeast Manitoba (Suarez-Gonzales 2011). Dispersal is by birds, large and small mammals (Webb & Wilson 1985); birds important in dispersal include *Bombycilla cedrorum* (cedar waxing) and *Turdus migratorius* (American robin) (Parciak 2002).

***Salix bebbiana* Sarg. (Bebb willow)**

Common names for this species include Bebb willow, beak willow, beaked willow, long-beaked willow, diamond willow, *chaton*, *Petit Minou*, and smooth Bebb willow. Tesky (1992) provides a summary of basic information for this species. It hybridises with *S. candida* (Argus 2012).

This species may be found as a large shrub up to 3 m tall, or a small tree with multiple stems and a bushy top standing 4.6 – 7.6 m tall. The roots of the species are shallow and dense. It is often found in early seral stage willow communities along river and stream banks and seeps. It usually grows as stands of widely scattered shrubs. It is considered a habitat generalist, and exhibits some tolerance to drought (Savage et al. 2009, Savage & Cavender-Bares 2011). It is commonly found across much of North America, extending especially far southward in the western half of the continent. In Canada, the species is found in all provinces and most of the territories.

Bebb willow is a diploid species ($2n=38$) (Dorn 1976) and can reproduce both sexually and asexually. Individual plants are dioecious. Large volumes of lightweight seed are produced in the spring, and are wind-dispersed. Seeds are only viable for a few days, and require moist, exposed mineral substrate in full sunlight for establishment. The seeds do not require a period of dormancy before germination, and are able to germinate at a wide range of temperatures (5-25 C) (Densmore & Zasada 1983). This species exhibits poor shade tolerance at the seedling stage (Atchely & Marlow 1989).

The main pollinator of *S. bebbiana* is bees (the type of bee was not specified; Rawson 1974). Asexually, Bebb willow can establish from root shoots and basal stem sprouts, from buried stem and root fragments, and from buried branches. However, Densmore & Zasada (1978) found that cuttings of Bebb willow were entirely unable to produce roots. The species is, however, able to sprout rapidly from damaged root crowns (Tesky 1992).

***Salix interior* Rowlee (sandbar willow)**

Some authors list the sandbar willow occurring in Alberta as *S. exigua* var. *exigua*. *Salix interior* hybridises with *S. exigua* var. *exigua* (FNA 1993). See Anderson (2006) for a recent summary of available information for this species. *S. interior* is commonly found in plains and lower montane habitats throughout most of the western United States, and into southern Alberta and British Columbia.

Common names for this species are sandbar willow, narrow-leaved willow and coyote willow. It is a native, winter-deciduous shrub that typically reaches heights of 2 to 8 m, but may grow up to 10 m tall. This species often forms large colonies from spreading roots, and may resprout from root crowns. Dominance of a site by one or a few clones is common, and individual clones may cover areas of 325 m² (Douhovnikoff et al. 2005). The species is considered a riparian pioneer, often colonizing river flood plains after disturbances such as flooding. Shade intolerant, *S. interior* usually forms narrow bands along aquatic or wet features such as streams, gravel bars, lakeshores, ditches, and bottomlands. Sandbar willow is both drought resistant and tolerant of flooding. Willows as a group are very frost tolerant as well.

Sandbar willow is a diploid species (2n=38) (Dorn 1975) able to propagate both sexually - through seed production, and asexually - through root sprouts. Plants are typically dioecious, though monoecious individuals have been found bearing staminate, pistillate and mixed catkins (Smith 1940). In a three-year study in California, seed release peaked on May 31 (average; range was May 8 - June 30), apparently to coincide with spring flood recession on the rivers in the study area (Stella et al. 2006). Sandbar willow seeds are numerous and small, and are dispersed typically by wind and water. They are non-dormant and quickly desiccate if not on a moist substrate. Seed viability drops quickly, with no survival beyond 3 weeks. The seeds usually germinate within 24 hours of landing on a suitable substrate, which usually entails bare, wet alluvial deposits in full sunlight. Seedling mortality is high, often reaching 100% in some sites and years (Douhovnikoff et al. 2005). When able to establish, individuals can grow as much as 30 cm in height per year (Nellessen 2004).

The species is primarily pollinated by a range of insects, including flies (Diptera), wasps, honeybees and bumblebees (Hymenoptera), and beetles (Coleoptera) (Mosseler & Papadopol 1989, Pendleton et al. 2011). Asexually, *S. interior* can develop dense thickets of clones from root sprouts, with stems developing from shoot buds on lateral roots. Individuals are usually shrub-like, but may resemble small trees as they age. Asexual clones seem to drive much of this species' success in areas where it is able to establish. Because seedling mortality is so high, establishment of sandbar willow may be limited even on favourable sites, unless there is already a resident population.

***Shepherdia canadensis* (L.) Nutt. (buffaloberry)**

S. canadensis is a spreading shrub 1-3 m in height (Moss 1992). Subspecies *S. canadensis* forma *xanthocarpa* Rehd. exists in Alberta (Vines 1960). Dispersal is by black bear, deer, bighorn sheep and gravity (Walkup 1991). Reproduction is sexual and vegetatively by roots (Walkup 1991). The species is dioecious (distinct male and female individuals; Hitchcock & Cronquist 1973), a condition that occurs in only about 6% of flowering plants (Renner & Ricklefs 1995). Pollination in dioecious species is commonly by small generalist insects (Thomson & Brunet 1990). Pollination in *S. canadensis* is mainly by Diptera (97 %) (Syrphidae and Empididae;

Borkent & Harder 2007). *S. canadensis* is the least aggressive colonizer of 20 shrubs and trees that have been tested in Canada (Guy 1989). $2n=22$ (Cooper 1932).

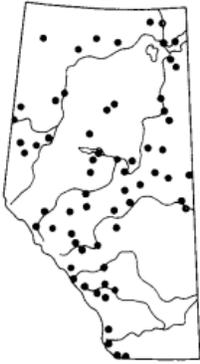
***Vaccinium myrtilloides* (Michx.) (blueberry)**

V. myrtilloides hybridises with several species (Aalders & Hall 1961) including low sweet blueberry (*V. angustifolium*). Reproduction is by seed or vegetatively from rhizomes (Hall 1955). Pollination is by *Bombus* spp. (bumble bee) and *Apis mellifera* (honey bee) (Reader 1977). *V. myrtilloides* is generally regarded as an obligate entomophilous outcrossing species (Vander Kloet & Hall 1981), but self-pollination was observed in natural bogs of southern Ontario (Reader 1977). Population genetic analyses of allozyme data showed high levels of variation within populations of *V. myrtilloides* in eastern North America, although total genetic diversity was lower than expected for outcrossing species (Bruederle et al. 1991). Dispersal occurs by birds, large and small mammals (Mohr & Kevan 1987) and long distance dispersal occurs especially by the American robin as it migrates (Vander & Hall 1981). *V. myrtilloides* is an indicator species in northern ecosites of Alberta (Beckingham & Archibald 1996).

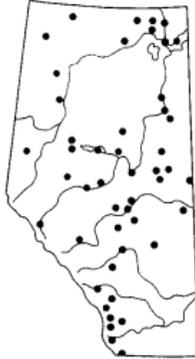
***Viburnum edule* (Michx.) (low bush cranberry)**

V. edule occurs as a dominant or co-dominant understory species in coniferous and deciduous forests in both open and closed situations (Matthews 1992b). The berries are edible and were an important food source for First Nations people in the Bella Coola region of British Columbia (Lepofsky et al. 1985). The species can be propagated from seed (Gill & Healy 1974) or vegetatively from both root and stem cuttings (Holloway & Zasada 1979). The plant is monoecious and sexual reproduction can occur by self-pollination or cross-pollination. Syrphidae (syrphid flies), and Halictidae and Andrenidae (bees) are common pollinators of *V. opulus* in Ontario (Krannitz & Maun 1991). Seeds are dispersed by song birds and large and small mammals including black bear and deer (Haeussler & Coates 1986). *V. edule* re-sprouts from stumps and roots. The species is rhizomatous, but does not appear to spread from the parent by the rhizomes (Haeussler & Coates 1986). It has high tolerance to frost and can grow in low temperatures. In dry climates, it is restricted to wetter areas (Haeussler & Coates 1986).

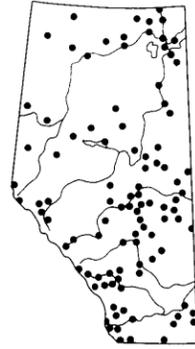
Alnus viridis



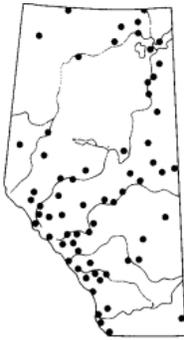
Alnus incana



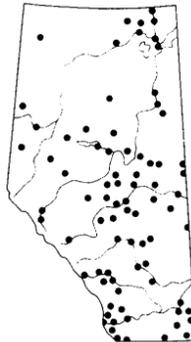
Amelanchier alnifolia



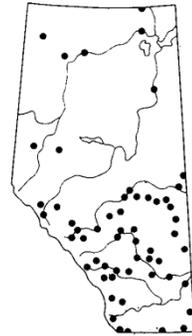
Arctostaphylos uva-ursi



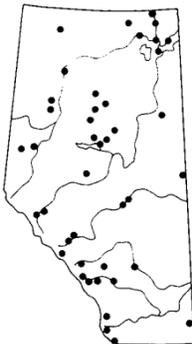
Cornus sericea



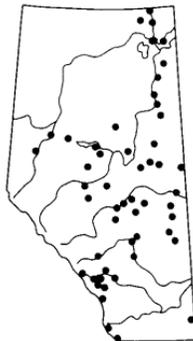
Eleagnus commutata



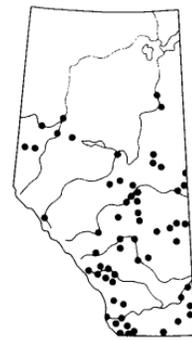
Picea glauca



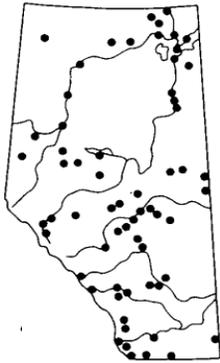
Prunus pennsylvanica



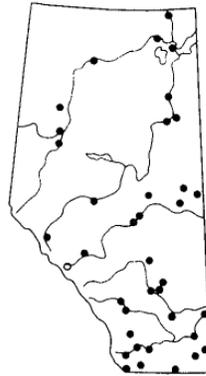
Prunus virginianus



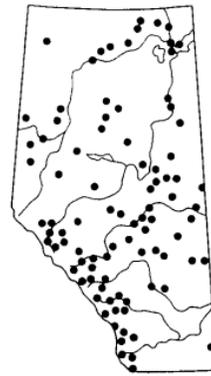
Salix bebbiana



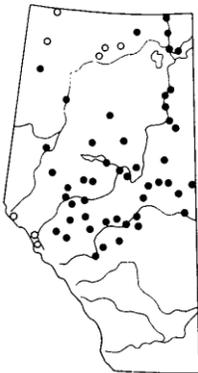
Salix interior



Shepherdia canadensis



Vaccinium myrtilloides



Viburnum edule

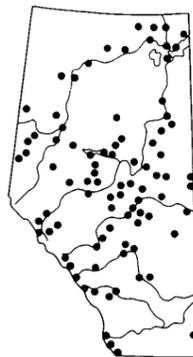


Figure 2. Distribution of 13 shrub species used in re-vegetation and *Picea glauca* – a commercial tree species for which current seed zones in Alberta were established (maps taken from Moss 1992).

Table 1. Comparison of life history characteristics in *Picea glauca* and 13 shrub species commonly used in re-vegetation activities in Alberta.

Family	Species	Mode of Reproduction	Pollination	Chromosome number	Dispersal	Genetic variation
Betulaceae	<i>Alnus viridis</i> (green alder)	Seed (monoecious plant, self-fertilizes rarely), root crowns	Wind	2n=28 diploid	Wind and water	Genetic variation resides within population
Betulaceae	<i>Alnus incana</i> (river alder)	Seed (monoecious plant, self-fertilizes rarely), root crowns	Wind	2n=28 diploid	Wind and water	Genetic variation resides within population
Roseaceae	<i>Amelanchier alnifolia</i> (Saskatoon)	Seed (rarely, mostly outcrossing, limited self-fertilisation) stem, root (primarily)	Sphecidae (wasps) and Andrenidae (bees)	2n=34, 68 diploid, tetraploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	
Ericaceae	<i>Arctostaphylos uva-ursi</i> (bearberry)	Primarily asexual by roots and stem, also by seeds (sexual)-self-compatible	Thrips, Bombus spp	2n=26,52 diploid, tetraploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	Clinal variation
Cornaceae	<i>Cornus sericea</i> (red-osier dogwood)	Seed (obligate outcross), stems, stolons, root crowns, prostrate stems	Insects – dipterans, hymenopterans, coleopterans	2n=22 diploid	Birds and mammals; can be relatively long distance (at least 215 m); secondary dispersal by rodents	May be genetic variation between populations >50 km apart, based on genotypically different germination abilities

Family	Species	Mode of Reproduction	Pollination	Chromosome number	Dispersal	Genetic variation
Elaeagnaceae	<i>Elaeagnus commutata</i> (wolf-willow)	Seed (obligate outcrossing), rhizomes	Insects	2n=28 diploid	Birds	Genetic variation resides within population
Pinaceae	<i>Picea glauca</i> (white spruce)	Seed	Wind	2n=24 diploid	Wind	Genetic variation resides within population
Roseaceae	<i>Prunus pensylvanica</i> (pincherry)	Stem, root, seed (obligate out-cross)	<i>Apis</i> spp. (honey bees)	2n=16, 32 diploid, tetraploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	
Roseaceae	<i>Prunus virginiana</i> (chokecherry)	Seed (generally outcrossing, partially self-compatible), Rhizome	Flies, butterflies, early-flying bees of <i>Andrena</i> , <i>Bombus</i> , <i>Anthophora</i> and <i>Osmi</i> , occasionally hummingbirds	2n=16, 32 diploid, tetraploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	
Salicaceae	<i>Salix bebbiana</i> (Bebb willow)	Seed (obligate outcross), root crowns	Bees	2n=38 diploid	Wind	
Salicaceae	<i>Salix interior</i> (sandbar willow)	Seed (predominately obligate outcrossing), root sprouts, lateral roots	Insects - dipterans, hymenopterans, coleopterans	2n=38 diploid	Wind and water	

Family	Species	Mode of Reproduction	Pollination	Chromosome number	Dispersal	Genetic variation
Elaeagnaceae	<i>Shepherdia canadensis</i> (buffaloberry)	Seed (obligate outcross, dioecious), rhizome	Diptera-small generalist insects	2n=22 diploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	
Ericaceae	<i>Vaccinium myrtilloides</i> (blueberry)	Seed (obligate outcross), stem root	Andrenids, Bombus spp, <i>Apis mellifera</i>	2n=24 diploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	Genetic variation resides within population
Caprifoliaceae	<i>Viburnum edule</i> (low bush cranberry)	Seed (predominantly out-crossing), stem, root		2n=18 diploid	Excellent dispersal capability over long distances by birds and large mammals (>10 km)	

3.1 Breeding guilds in shrubs

Based on a review of available literature on breeding system characteristics of the 13 shrub species compiled in this report, and including information on the conifer tree species *Picea glauca* for comparative purposes, a number of breeding guilds can be identified. A non-metric multi-dimensional scaling (NMDS) ordination of breeding system characteristics was performed, and revealed six guilds of species with closely related breeding system characteristics (Figure 3):

1. *Salix interior* (sandbar willow)-*Elaeagnus commutata* (wolf-willow)
2. *Salix bebbiana* (Bebb willow)
3. *Arctostaphylos uva-ursi* (bearberry)-*Amelanchier alnifolia* (Saskatoon)
4. *Picea glauca* (white spruce)-*Alnus viridis* (green alder)-*Alnus incana* (river alder)
5. *Vaccinium myrtilloides* (blueberry)-*Viburnum edule* (low bush cranberry)-*Cornus sericea* (red-osier dogwood)-*Shepherdia Canadensis* (buffaloberry)
6. *Prunus pensylvanica* (pincherry)-*Prunus virginiana* (chokecherry)

Species such as *Alnus* sp. which are in close proximity to *Picea glauca* on the ordination diagram can be surmised to possess similar breeding system characteristics. Therefore, the current seed zone map designed for conifer tree species is also potentially an appropriate guide for seed transfer in *Alnus* sp. For species such as *Arctostaphylos uva-ursi* and *Amelanchier alnifolia* however, which have dissimilar breeding system characteristics to *Picea glauca*, Alberta's current seed zone map is potentially not applicable as breeding system characteristics imply that these species require even smaller seed zones to maintain local adaptation.

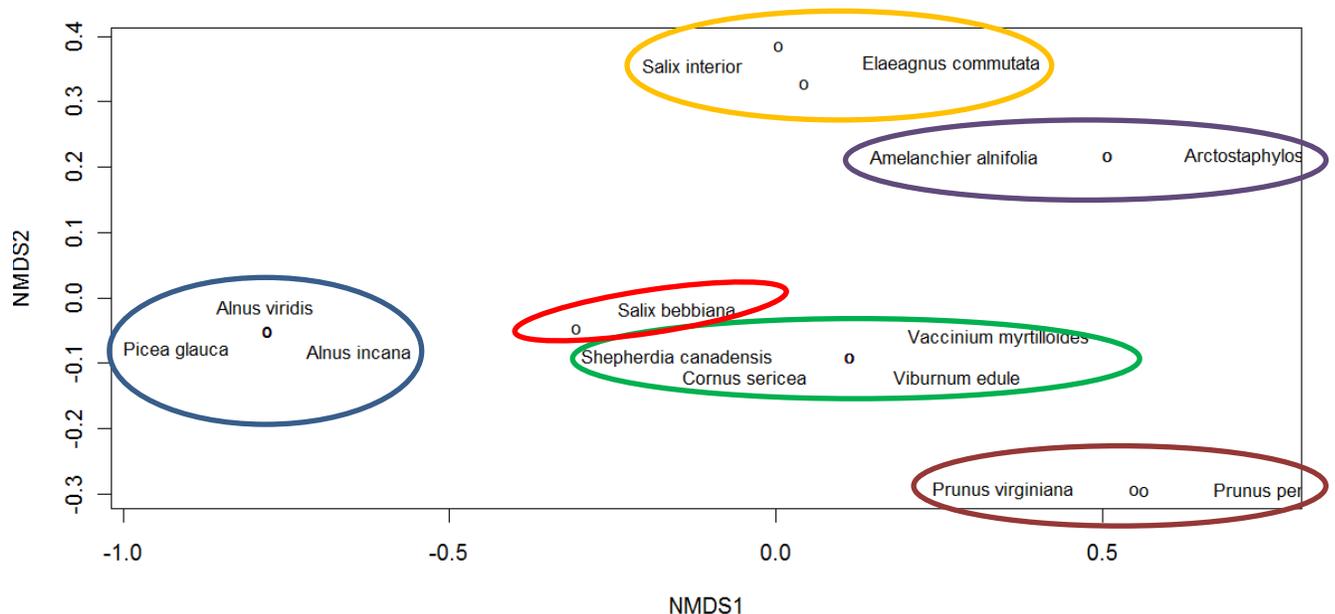


Figure 3. Ordination of species according to the characteristics of their breeding system (pollination/clonal, pollen and seed dispersal and ploidy variation). Coloured circles indicate clusters of species with similar breeding systems.

4.0 INTERIM APPLICATION TO THE COLLECTION AND USE OF SHRUB SEEDS AND VEGETATIVE PROPAGULES

This literature review on the life history of shrubs commonly used for re-vegetation in Alberta was conducted to identify reproductive characteristics of shrubs that could influence the transferability of their seed and vegetative propagules across the province. Inferences derived from this review can inform practitioners who collect and use reproductive materials, and policy makers who regulate the transfer of these materials about the applicability of the tree-based Alberta seed zone system to shrubs. Major revelations from the literature review are as follows:

1. Although few species such as *Alnus* sp. have a breeding system that is similar to that found in conifers such as spruces, most shrubs exhibit a mixture of sexual and asexual propagation and outcrossing and self-fertilisation mechanisms.
2. Few shrub species (except for *Alnus* sp.) are wind-pollinated; otherwise shrubs are predominantly pollinated by insects, birds and mammals.
3. Except for *Alnus* sp., seeds for most commonly used shrubs are dispersed by birds, mammals and water.
4. Most of the shrubs commonly used in re-vegetation have a shorter lifespan than that of conifers and deciduous tree species.

In light of these characteristics of shrubs that differentiate them from commonly used forest tree species such as pines, spruces and larch, shrubs can be expected to be genetically differentiated at shorter distances and in more discrete geographic units than conifers. Although provenance testing for shrubs will be needed to confirm the extent and pattern of population differentiation across the province, it is expected that the area that could be considered a seed zone for shrubs is smaller than the current Alberta seed zones that regulate transfer of reproductive materials in conifers and poplars.

The major lesson learned from this review is that from a practical seed procurement perspective, with the need to safeguard adaptation in artificially regenerated sites, and conserve local flora, the current seed zones provide the best available guidance for the regulation of transfer of shrub reproductive material in the absence of data from shrub research. Until shrub provenance research is conducted, it is prudent for collectors and users of shrub seed to adopt the existing Alberta seed zones to self-police their re-vegetation need for reproductive material.

5.0 BUSINESS CASE AND METHODOLOGY FOR PROVENANCE TRIALS IN SHRUBS

We conducted interviews with the major shrub users in Alberta, as well as relevant staff from ESRD involved with shrub use and researchers who experiment with shrub propagation, to examine how shrubs are used in re-vegetation activities and estimate the number of shrubs used on a yearly basis. In 2012, approximately 350,000 shrub seedlings were planted out by the energy industry for re-vegetation in Alberta's boreal region. Shrubs seedlings sometimes comprised a significant percentage of total woody seedlings used in re-vegetation activities (Table 2), and shrub use is expected to rise as reclamation practitioners endeavour to emulate

species composition in undisturbed areas when reclamation is conducted (Alberta Environment 2010). The majority of seed transfer in the province occurs in the mineable oil sands region, through a cooperative of five oil sands companies: Suncor Energy, Imperial Oil, Canadian Natural Resource Limited, Shell Canada Energy and Syncrude Canada Limited. The cooperative has expressed concern about the future availability of shrub seed provenances, especially near mined areas. Some seed banking is carried out at the provincial seed bank at the Alberta Tree Improvement & Seed Centre in Smoky Lake to address this concern. Members of the cooperative have also expressed uncertainty in using the current designation of tree seed zones, which has never been tested for its applicability to shrub species.

Other large-scale shrub seed use in the province occurs through the *Faster Forests* programme following *in situ* oil extraction. The *Faster Forests* programme has four participants: Meg Energy, Nexen, Statoil and ConocoPhillips Canada (Appendix 1).

Approximately 43 shrub species are now used in re-vegetation activities in the oil sands region of Alberta (Appendix 2). Currently, the movement of shrub seed is unregulated, but re-vegetation practitioners are advised by ESRD to follow the existing seed zone map originally designed for conifer tree species. Monitoring of shrub growth and mortality according to provenance is not conducted, due partly to the difficulty in tracking numerous small seed lots. The success of re-vegetation activities using particular seed provenances is therefore untested, and can pose significant risk to reclamation.

Given the magnitude of shrub use across the province, uncertainty in using tree seed zones and concerns about the future availability of appropriate provenances, especially under climate change scenarios, long-term provenance trials specifically targeted to shrubs species are required. The characteristics to be assessed in a seed zone scheme for shrubs include germination, reproduction, survival in a changing climate and rapid multi-stemmed growth (vegetative biomass), rather than rapid growth of a single stem, which has been the main characteristic used to assess tree provenances. Provenance testing can reduce risk in re-vegetation activities by providing reliable information on how a particular species is expected to perform in a given location, and provide some assurance that provenances chosen for re-vegetation are appropriate and are likely to grow successfully. Based on the approach outlined in Section 3.1 of identifying breeding guilds, not all 43 shrub species would have to undergo provenance trials. Instead, a representative species could be chosen from each breeding guild for provenance trials to represent a number of other species that possess similar breeding characteristics.

The general methodology for developing seed transfer guidelines are (adapted from Johnson et al. 2004):

1. Determine sample range based on administrative or 'seed-need' criteria
2. Collect seeds from numerous evenly distributed sources including common and extreme environments
3. Plant seeds in a common environment using a statistically appropriate design (for example, randomized complete block)
4. Measure a variety of adaptive traits over at least 2-3 years. Traits typically include germination rate, total growth and growth rate, phenology (bud burst and bud set dates), cold hardiness, and plant form (shoot-to-root ratio, height-to-diameter ratio). In non-conifer species, additional significant traits might include ploidy level, key

- morphological traits (floral, leaf, phyllotaxy), and relevant ecophysiological traits (such as stomatal conductance or micronutrient concentrations)
5. Analyse data to determine which traits have significant differences among seed source locations
 6. For traits that differ by seed source, use regression to test correlations with climatic or physiographic gradients
 7. Variation within a seed source is estimated to determine overlap among different populations along a gradient

Table 2. Number of shrub seedlings planted out in 2012 for re-vegetation in Alberta’s boreal region.

Company/Program	No. of shrub seedlings planted out	Percentage of woody seedlings planted that were shrubs
Suncor Energy	43,528	6%
Imperial Oil	12,750	-
Canadian Natural Resource Limited	3,000	-
Shell Canada Energy	16,000	30%
Syncrude Canada Limited	200,000	20%
<i>Faster Forests</i> Program (in situ)	71,352	12%
Total	346,630	

There are opportunities to conduct meaningful research on shrub provenances and develop seed zones appropriate for shrub species in Alberta. The Boreal Research Institute at NAIT has expressed interest in conducting such research. They are currently experimenting with propagation methods for five shrub species in Peace River. Alberta Tree Improvement and Seed Centre at ESRD has been the leader in long-term provenance trials for commercial tree species in the province, and their leadership and support will be integral to any provenance testing initiative for shrub species. Alberta Innovates –Technology Futures (AITF) has significant expertise and laboratory facilities, including climate chambers, green houses and a molecular genetics laboratory that could contribute to provenance testing research.

ACKNOWLEDGEMENTS

We thank Leonard Barnhardt and Donna Palamarek from ESRD and the Alberta Tree Improvement and Seed Centre for their advice and provision of information. Thanks are due to Ann Smreciu (Wild Rose Consulting Inc.), Amanda Schoonmaker (NAIT), Tim Vinge (ESRD) and Dave Polster (Vancouver Island University) for sharing their experience and research in shrub use for re-vegetation purposes. We appreciate the input received from industry representatives Lelaynia Cox, Eric Girard, Dustin Theberge, Andrew Carpenter, Steve Tuttle and Lori Neufeld on their experience in using shrubs for re-vegetation. Thanks to Melanie Thibault for sourcing literature. For reviewing the report, we thank Dr. Ludovic Capo-chichi (AITF).

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GLOSSARY

- Adventitious - a stem arising from an organ other than a root.
- Allozyme - different structural forms of the same enzyme coded for by different alleles.
- Biparental inbreeding - inbreeding that occurs in plants through the mating between close relatives, as opposed to self-fertilisation in an individual plant.
- Breeding system - the factors that determine how plants mate, and with whom; e.g. pollination, phenology.
- Bulbils - a small bulb or bulb-like body produced on above ground parts of a plant.
- Catkin - a spike of flowers having scaly, usually deciduous bracts; e.g. found on willows or birches.
- Clinial variation - the continuous pattern of genetic variation where genes are continuously exchanged among populations over a large region.
- Complete cross-pollination - cases in which each plant only bears flowers of one sex – male or female, or mechanisms ensure self-incompatibility between the ovule and pollen of the same plant, even if flowers of both sexes are borne on the same individual.
- Complete self-pollination - where pollen from the anthers of a plant fertilises the stigma of the same plant.
- Dioecious - plant species in which distinct male and female individuals are present.
- Diploid - individuals of a species carry two copies of each chromosome (e.g. 2N).
- Ecophysiological traits - physiological processes of organisms developed in response to their environment.
- Ecotypic variation - a discontinuous pattern of genetic variation within a species where most genetic variation is found between populations.
- Entomophilous - plants species which are pollinated by insects.
- Genetic drift - random changes in the frequency of alleles in a gene pool; more common in small populations.
- Leptokurtic distribution - this distribution has higher peaks around the mean compared to the normal distribution, which leads to thick tails on both sides.
- Microsatellites - sections of DNA consisting of very short nucleotide sequences repeated many times. Microsatellites are often used as a marker in determining genetic diversity in population studies.
- Monoecious - a plant bearing both male and female flowers.
- Outbreeding depression - offspring from hybridisation between individuals of different populations can have lower fitness than progeny from crosses between individuals from the same population; this may result from the replacement of local alleles with those suited for a different location.
- Phyllotaxy - the arrangement of leaves on the stem of a plant.
- Pistil - the ovule-bearing or seed-bearing female organ of a flower.
- Pistillate - having a pistil or pistils.
- Ploidy - the number of chromosome sets present in an organism.
- Polyloid - condition where a species has more than two copies of each chromosome.
- Propagule - a plant part capable of being propagated or acting as an agent of reproduction; e.g. seed.
- Provenance - refers to the geographic place of origin of plant material (e.g. seeds).

Pubescence - covered with fine short hair.

Rhizomatous - having, resembling, or being a rhizome.

Rhizome - a root like subterranean stem that commonly produces roots below and sends up shoots progressively from the upper surface.

Seed zone - geographic subdivision based on climate where plant species are locally adapted.

Self-fertilisation (autogamy) - fertilisation by the union of male and female gametes from the same individual.

Stamen - the pollen-bearing organ of a flower.

Staminate - a plant or flower bearing a stamen or stamens.

Stolon - a prostrate plant stem found at or just below the surface of the ground that produces new stems from buds at its tips or nodes.

Stomata - small apertures in the epidermis of leaves, stems, and other structures of a plant through which gases are exchanged.

Stomatal conductance - the rate at which carbon dioxide enters, or water vapor exits, through the stomata of a leaf.

Tetraploid - a condition where a species bears four copies of each chromosome.

Appendix 1. Shrub species planted in 2012 under the *Faster Forests* programme

Species	ConocoPhillips Canada	Meg Energy	Nexen	Statoil
Green alder	5480	1730	11,140	3855
Red Osier Dogwood	1840	600	4960	4105
Saskatoon	6200	80	1000	0
Willow	550	100	1450	4005
Choke Cherry	300	480	480	4380
Bog birch	3270	540	10,410	4097
Buffalo berry	0	0	0	300
Total no. of shrubs	17,640	3,530	29,440	20,742
No. of re-vegetation sites	71	23	192	220

Appendix 2. Inventory of registered shrub seed at ESRD as of February 25, 2013

Species Name	Inventory Amount (kg)	No. of Seedlots
<i>Acorus calamus</i> - Sweet Flag (Rat Root)	0.2414	2
<i>Alisma plantagoaquatica</i> - American Waterplantain	0.3763	1
<i>Alnus incana</i> - River Alder	0.7233	12
<i>Alnus viridis</i> - Green Alder	7.5517	37
<i>Amelanchier alnifolia</i> - Saskatoon	1.8673	21
<i>Arctostaphylos uva-ursi</i> - Bearberry	10.6189	14
<i>Beckmannia syziganche</i> - Slough Grass	0.1580	1
<i>Betula pumila</i> - Bog Birch	2.3112	11
<i>Calla palustris</i> - Water Arum	0.0224	1
<i>Carex aquatilis</i> - Water Sedge	0.1815	2
<i>Carex pseudocyperus</i> - Cypress Sedge	0.1380	2
<i>Carex utriculata</i> - Beaked Sedge	0.2016	3
<i>Chamerion angustifolium</i> - Fireweed	0.0208	5
<i>Cornus canadensis</i> - Bunchberry	0.6852	10
<i>Cornus sericea</i> - Red Osier Dogwood	11.0993	29
<i>Dasiphora floribunda</i> - Shrubby Cinquefoil	0.1411	7
<i>Galium trifidum</i> - Bed Straw	0.0148	1
<i>Ledum groenlandicum</i> - Labrador Tea	0.0918	7
<i>Linnaea borealis</i> - Twinflower	0.1484	7
<i>Lonicera involucrata</i> - Honeysuckle	0.1230	2
<i>Potentilla norvegica</i> - Norwegian Cinquefoil	0.0400	1
<i>Potentilla palustris</i> - Marsh Cinquefoil	0.0321	2
<i>Prunus pensylvanica</i> - Pincherry	15.7411	33
<i>Prunus virginiana</i> - Chokecherry	29.0461	21
<i>Ribes lacustre</i> - Black Currant	0.0029	2
<i>Ribes oxycanthiodes</i> - Gooseberry	0.0126	3
<i>Ribes triste</i> - Wild Red Currant	0.0535	5
<i>Rosa acicularis</i> - Prickly Wildrose	12.4480	14
<i>Rosa woodsii</i> - Woods' Rose	0.1330	2

Species Name	Inventory Amount (kg)	No. of Seedlots
<i>Rubus idaeus</i> - Raspberry	2.0045	9
<i>Rumex occidentalis</i> - Western Dock	0.0466	1
<i>Schoenoplectus lacustris</i> - Lakeshore Bulrush	0.0339	1
<i>Schoenoplectus tabernaemontani</i> - Great Bulrush	0.0660	2
<i>Scirpus microcarpus</i> - Small Fruit Bulrush	0.0052	1
<i>Sheperdia canadensis</i> - Buffaloberry	2.0314	25
<i>Sorbus scopulina</i> - Mountain Ash	0.2390	2
<i>Sparganium angustifolium</i> - Narrowleaf Bur-reed	0.0575	1
<i>Symphoricarpos albus</i> - Snowberry	0.1311	10
<i>Typha latifolia</i> - Cattail	0.0630	2
<i>Vaccinium myrtilloides</i> - Blueberry	2.4207	29
<i>Vaccinium oxycoccos</i> - Small Bog Cranberry	0.0027	1
<i>Vaccinium vitis-idaea</i> - Lingonberry	0.1838	12
<i>Viburnum edule</i> - Low Bush Cranberry	4.5972	27
Total	106.1	381