Population Genetic Issues Associated with Revegetation Using National Park-Collected Plant Materials

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Introduction

Revegetation is increasingly used by restoration ecologists in an attempt to return areas to a pre-disturbance state. The ecologists involved in these activities are becoming more aware of the fact that population genetic issues play an important role in the revegetation process. The source of the material to be seeded or planted as well as the method of collection is critical to a successful outcome. This report is designed to inform restoration ecologists in the National Park Service and other agencies of the population genetic implications of releasing park-collected genetic materials for use in revegetation as well as providing information regarding the population genetic structure of 39 plant species of interest to the NPS and the Natural Resources Conservation Service (NRCS) as candidates for germplasm release.

This report fulfills obligations to Rocky Mountains Cooperative Ecosystem Studies Unit (RM-CESU), Cooperative Agreement Number: H2380040001, to Colorado State University. This report provides the most up to date scientific information to address:

1. Does genetic theory or specific literature on the proposed releases suggest that NRCS's proposal presents a substantial threat to the genetic integrity of the corresponding native plant populations in the National Park system? Potential threats that should be investigated include, but are not limited to
    a. Reduced fitness caused by "outbreeding depression ",
    b. "dilution" of local populations with poorly adapted genotypes, and,
    c. manipulation of NPS germplasm in a manner that might meet the needs of the commercial agricultural and horticultural sector, but be contrary to the NPS policy of preserving genetic integrity.
2. Are there particular categories of species which, based on breeding system, propagule dispersal mechanism, population distribution, etc., are more likely to be at risk or to cause problems? Can this risk be mitigated?
3. What degree of genetic manipulation should be allowed?
4. How can NPS prevent an undesirable degree of genetic manipulation? Consider both accidental and intentional manipulation.

Population Genetics

One aspect of population genetics that is relevant to the revegetation of disturbed areas is the concept to genetic diversity. Plant species differ in amount and distribution of genetic variation. At the level of species, diversity is often measured as the percentage of polymorphic loci (P), the mean number of alleles per locus (A), and heterozygosity or the genetic diversity index (H). These same measures can be used to quantify the level of genetic variation found within individual populations. The manner in which genetic diversity is partitioned, i.e., within versus among populations of a species is also known as population genetic structure.

Of greatest interest when considering introductions of genetic material between or among populations is the degree to which populations are genetically differentiated. This differentiation can be measured using one of a number of metrics that quantify the proportion of total variation found among populations. G_{ST} is identical to Wright's (1951) classic measure F_{ST} when loci have two alleles (Nei 1973), as is the case for dominant DNA marker data such as that generated by RAPD, AFLP, and ISSR analyses. When more than two alleles are present per locus, G_{ST} is equivalent to the weighted average of F_{ST} for all alleles (Nei 1973). Values of F_{ST} (or G_{ST}) should be interpreted as follows: 0-0.05 = little genetic differentiation; 0.05-0.15 = moderate genetic differentiation; 0.15-0.25 = great genetic differentiation; >0.25 = very great genetic differentiation (Wright 1978). On average, for allozyme loci plant species maintain 22% of their total genetic variation among populations (i.e., $G_{ST} = 0.22$; Hamrick and Godt 1989). Other measures of population differentiation are Φ_{ST}, which is derived from dominant DNA data using an analysis of molecular variance (AMOVA; Excoffier et al. 1992), R_{ST}, which is used with codominant microsatellite (or SSR) data assuming a stepwise mutation model (Slatkin 1995), and Θ for SSR data when an infinite alleles model is assumed (Weir and Cockerham 1984). The two measures used for dominant DNA data, Nei's G_{ST} and Φ_{ST}, are usually very similar for the same dataset (Nybom 2004). In contrast, the two diversity measures used for codominant data often differ considerably for the same dataset (Nybom 2004).

Why is genetic differentiation important to the question of revegetation? – briefly, see in more detail below.

Life History Traits Correlated With Population Genetic Structure - Allozymes

One of the most widely cited papers in the field of plant population genetics is that of Hamrick and Godt (1989) in which the authors surveyed the allozyme literature and looked for correlations between plant traits and the distribution of genetic variation within species. Several important and interesting trends were found, which are summarized in Table 1. Population genetic structure is influenced to the largest extent by the plant breeding system (Hamrick and Godt 1989). In selfing species, 51% of the total genetic variation within species is distributed among populations, while only 10 – 20% is distributed among populations in outcrossing species. The categories of taxonomic status, life form, regional distribution, mode of seed dispersal, and successional status also exhibited significantly different values of G_{ST} among plant traits, with life form being the second most important trait correlated with genetic structure.

Mating system is an important determinant of population genetic structure because it often has the largest effect on gene flow distances. Gene flow is affected by a combination of pollen and seed movement, but in most plant species, pollen moves greater distances than do seeds. As a result, the genetic homogenizing effect of gene flow is due in large part to the mating system of the plant species. In predominantly selfing species, pollen usually does not move beyond the individual plant, allowing the effects of mutations and genetic drift to build up within populations. This causes population differentiation to occur. When pollen moves over larger distances, as is possible in outcrossing species, populations are less likely to diverge from one another as alleles move back and forth among populations. As can be seen by the G_{ST} values in Table 1, wind pollination is more effective at homogenizing populations than is animal pollination.

The effect of the mode of seed dispersal on genetic structure is similar to that of mating system. Methods of seed dispersal that lead to greater gene flow have a more homogenizing effect on the genetic variation among populations, while those that lead to very short distance seed dispersal cause an increase in the genetic structuring of populations. While this prediction holds, the exact pattern of mean G_{ST} values shown in Table 1 is difficult to interpret.

Asexual or clonal reproduction is another plant trait that may affect population genetic structuring, although the effect was not significant in the Hamrick and Godt (1989) study. In theory, asexual reproduction would affect population genetic structure in a similar way to self-pollination. Any effects of mutation or drift would be maintained within populations, causing differentiation among populations. However, few plant species reproduce only via asexual means, so there would likely be at least low levels of gene flow that might homogenize populations. Clonal growth via rhizomes, stolons, or other forms of branching growth will clearly lead to a genetic patchiness of genotypes within populations, unless genets (i.e., clones) grow quite intermingled with one another.

Table 1. Summary of distribution of allozyme variation among populations of species classified according to their life history traits (extracted from Table 4 in Hamrick and Godt 1989).

Category[a]	**Plant Trait**	**G_{ST} (Std Error)**[b]
Taxonomic Status:	Gymnosperms	0.068 (0.013) b
***	Monocots	0.231 (0.023) a
	Dicots	0.273 (0.017) a
Life Form:	Annual	0.357 (0.024) a
***	Short-lived perennial, herbaceous	0.233 (0.019) b
	Short-lived perennial, woody	0.088 (0.024) -[c]
	Long-lived perennial, herbaceous	0.213 (0.144) -
	Long-lived perennial, woody	0.076 (0.010) c
Geographic Range:	Endemic	0.248 (0.037) a
NS	Narrow	0.242 (0.024) a
	Regional	0.216 (0.019) a
	Widespread	0.210 (0.025) a
Regional Distribution:	Boreal-temperate	0.036 (0.007) b

***	Temperate	0.246 (0.015) a
	Temperate-tropical	0.233 (0.049) a
	Tropical	0.173 (0.021) a
Breeding System:	Selfing	0.510 (0.035) a
***	Mixed-animal	0.216 (0.024) b
	Mixed-wind	0.100 (0.022) c
	Outcrossing-animal	0.197 (0.017) b
	Outcrossing-wind	0.099 (0.012) c
Seed Dispersal:	Gravity	0.277 (0.021) a
***	Gravity-attached	0.124 (0.031) b
	Attached	0.257 (0.032) ab
	Explosive	0.243 (0.048) ab
	Ingested	0.223 (0.033) ab
	Wind	0.143 (0.020) ab
Mode of Reproduction:	Sexual	0.225 (0.013) a
NS	Sexual and asexual	0.213 (0.027) a
Successional Status	Early	0.289 (0.021) a
***	Mid	0.259 (0.022) a
	Late	0.101 (0.013) b

[a] Levels of significance: ***, $p < 0.001$; NS, not significant.

[b] Mean values of G_{ST} followed by the same letter within categories do not differ significantly at the 5% probability level.

[c] A "-" indicates that these data were excluded from statistical tests because of small sample sizes.

Life form was second only to mating system in its correlation with G_{ST} values across allozyme studies ($r = 0.53$ versus $r = 0.46$; Hamrick and Godt 1989). The two categories together accounted for 84% of the variation explained by the model. Annuals and short-lived herbaceous species had G_{ST} values 3 to 4 times higher than those of long-lived woody perennials.

Early and mid-successional species displayed high values of G_{ST} while late successional species had low levels of population differentiation (Hamrick and Godt 1989).

Another factor likely to affect genetic differentiation among populations, but one that was not discussed by Hamrick and Godt (1989), is polyploidy. Many plant species exhibit more than one chromosome number across their range, and populations with different chromosome numbers are obviously genetically different from one another. In other cases, populations of mixed ploidy levels exist. Since plants of the same species that differ in chromosome number often are reproductively isolated from one another in that they frequently produce sterile or at least less fertile offspring when they mate, this is a factor that must be considered during revegetation efforts.

One final factor that causes population differentiation is natural selection. Because species' ranges generally encompass a diversity of habitats and microhabitats, natural selection will likely favor different genotypes in different parts of the range or in different ecosystems. Thus, plant species may be differentiated into ecotypes, or distinct genotypes resulting from adaptation to local conditions (Hufford and Mazer 2003). As will be discussed further below, there are likely to be greater negative consequences of introducing novel genotypes to an area during revegetation when those genotypes differ due to selection as opposed to when they are a result of neutral genetic variation (e.g., the product of genetic drift).

Molecular Data

An important question is whether the correlations between the distribution of variation in allozyme data and plant traits holds for molecular (i.e., DNA marker) data. Nybom (2004) recently addressed this question in a review of the patterns and distribution of genetic diversity observed using several types of DNA markers. These include RAPD (Randomly Amplified Polymorphic DNA), AFLP (Amplified Fragment Length Polymorphism), ISSR (Inter-simple Sequence Repeat), and SSR (Simple Sequence Repeat, also known as STMS – Sequence Tagged Microsatellite Sites - or microsatellite) markers. The first three marker types yield dominant DNA data, meaning that bands are scored as present or absent, and heterozygotes are generally impossible to distinguish from dominant homozygotes. SSRs are codominant in that bands produced during a PCR reaction represent a single locus, and each homozygote can be distinguished from heterozygotes. Despite these differences, codominant and dominant DNA markers yield similar estimates of among-population diversity (Nybom 2004). Likewise, RAPD markers and allozyme markers provide similar estimates of average among-population diversity in plants (0.29 and 0.22, respectively). Plant traits were used as variables in an analysis of variance in RAPD-derived and SSR-derived estimates of G_{ST} and F_{ST} to determine if molecular data correlate with these traits in a similar way to allozyme data. Using RAPD data, life form and mating system contributed significantly to variation in population genetic structuring. The same trends were seen as in the allozyme data, with annual and short-lived perennial plants exhibiting higher G_{ST} values than long-lived perennials and selfing species having higher G_{ST} values than mixed mating or outcrossing species. For SSR data, life form, mating system, mode of seed dispersal, and successional status were significant contributors to variation in F_{ST}. F_{ST} values estimated from SSRs for life form and mating system followed the same pattern as G_{ST} estimated from RAPDs. Values of F_{ST} were higher for species with gravity-dispersed or attached seeds compared to wind or water and ingested seeds. Early successional species had higher values of F_{ST} than mid- or late successional species. In short, the results from DNA data were similar in magnitude and follow the same pattern as those obtained from allozymes.

Information on NRCS Candidate Species from Review of the Primary Literature

Literature Search

Biological Abstracts was used to search the primary literature using both common and scientific names for references on each of the 39 target species. This proved to provide a more complete listing of life history and ecology-related citations than other online databases available via the Colorado State University library. Complete reference lists were then compiled for each species. After reading through the titles and, where available and relevant, the abstracts for each citation, papers that appeared to provide useful information were obtained from the Colorado State University library, from online sources, or from interlibrary loan. These papers were then read for information relevant to population genetic structure (see categories below), and information on each species was compiled. There was a large amount of variation in the amount of information available on the species. Some, such as *Elymus glaucus*, were well-studied and papers provided information in most or all of the categories. Others, such as *Eriogonum subalpinum* and *Achnatherum robustum* yielded few citations and none that provided any information of relevance. Species for which mating system information was still lacking were searched again in the online database Web of Science. There is some overlap of citations between Biological Abstracts and the Web of Science, but the latter did provide some additional references not found in the initial search.

Summary Categories

After the available data on each species were compiled, the species were separated into categories based on their traits that affect or are correlated with population genetic structure. Mating system and life form were given the most attention, since these were categories that proved to be correlated with G_{ST} or F_{ST} regardless of the type of genetic marker used. The categories are 1) Woody, long-lived perennials, 2) Composites, 3) Outcrossing grasses, and 4) Selfing grasses. There were several species that did not fit into any of these four categories or for which sufficient data were lacking to confidently determine their placement. These were placed into a fifth category of unknowns. Most of the species in this Unknown category are likely animal-pollinated, but it is not possible to determine the degree of outcrossing for each without further information. Table 2 shows the placement of the 39 plant species into the five categories.

Table 2. Categories used to provide generalizations about the likely population genetic structure of the 39 candidate species for release by the NRCS. A “?” in the category column signifies that this is likely the correct category for the species, but that it is pending further information on the mating system of the species.

Category	Scientific Name	Plant Family	Degree of Population Genetic Structure
Woody, long-lived:	*Ilex verticillata*	Aquifoliaceae	Lowest
	Sambucus canadensis	Caprifoliaceae	
	Viburnum cassinoides	Caprifoliaceae	
	Myrica pennsylvanica	Myricaceae	
	Physocarpus opulifolius	Rosaceae	
	Rosa woodsii	Rosaceae	
Composite:	*Achillea lanulosa*	Asteraceae	Low
	Aster integrifolius	Asteraceae	
	Aster macrophyllus	Asteraceae	
	Aster novi-belgii	Asteraceae	
	Aster umbellatus	Asteraceae	

	Pityopsis graminifolia	Asteraceae	
	Solidago canadensis	Asteraceae	
	Solidago puberula	Asteraceae	
	Solidago rugosa	Asteraceae	
Outcrossing Grass: ?	*Achnatherum robustum*	Poaceae	Low
?	*Agrostis scabra*	Poaceae	
	Bouteloua gracilis	Poaceae	
?	*Bromus anomalus*	Poaceae	
	Festuca rubra	Poaceae	
	Leymus salinus	Poaceae	
?	*Poa ampla*	Poaceae	
	Poa fendleriana	Poaceae	
?	*Pseudoroegneria spicata*	Poaceae	
?	*Sorghastrum nutans*	Poaceae	
?	*Stipa comata*	Poaceae	
Selfing Grass:	*Elymus glaucus*	Poaceae	High
?	*Elymus hystrix*	Poaceae	
?	*Elymus trachycaulus*	Poaceae	
?	*Muhlenbergia montana*	Poaceae	
	Sporobolus airoides	Poaceae	
Unknown:	*Phacelia sericea*	Hydrophyllaceae	Unknown
	Menodora longiflora	Oleaceae	
	Eriogonum subalpinum	Polygonaceae	
	Eriogonum umbellatum	Polygonaceae	
	Potentilla glandulosa	Rosaceae	
	Potentilla gracilis	Rosaceae	
	Penstemon procerus	Scrophulariaceae	
	Penstemon rydbergii	Scrophulariaceae	

While it is possible to divide the candidate species into categories that make logical sense based on the traits of the species and the correlation with or effect of those traits on population genetic structure, it is important to realize that these categories are merely generalizations. There is a lot of variation among species, which is evident in the fact that the model of Hamrick and Godt (1989; Table 1) explained only 30-50% of the variation in G_{ST} values.

Suggested Future Areas of Research

As a result of the strong effect of mating system on population genetic structure, the highest priority was placed on obtaining mating system information for each of the candidate species. However, published information on mating system does not appear to be available for many of the species. In some cases, a reasonable guess could be made based on the mating system of congeners or on characteristics of the plant family. In other cases, research is needed to determine the level of outcrossing. Other plant traits were lacking for many plant species as well. Finding published information on seed dispersal mechanism was also rare, as were mode of pollination, successional status, and studies of genetic structure.

Data For Each Species

Information on Family, Duration, & Growth Form from:
USDA, NRCS. 2004. The PLANTS Database, Version 3.5 (http://plants.usda.gov).
National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
Accessed 10-15-04
All of the candidate species are perennials. Thus duration was not included as a category.

Achillea lanulosa

Family: Asteraceae
Growth Form: Herb
Pollination: Flesh-fly pollinated (Pagano & Lanza 1994; Rathman et al. 1990)
Mating System: Probably outcrossing, (*A. millefolium*, a closely related congener, is SI) (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Tetraploids (2n = 36) (Clausen et al. 1940; Gervais 1977)
Successional Status:
Genetic Structure: High level of morphological variation (Clausen et al. 1940)
- Two subspecies, each with more than one ecotype (Clausen et al. 1940)
- Altitudinal differentiation for traits that are likely to be adaptive (Clausen et al. 1940; Gurevitch 1992, 1992b)

Additional information: Hybridize with tetraploid *A. nigrescens* in Quebec; Also hybridize in Quebec with hexaploid (2n = 64) *A. millefolium* s.str. escaped from cultivation to form mostly sterile pentaploids (2n = 45) (Gervais 1977)

Achnatherum robustum

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:

Agrostis scabra

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System:
Clonal Reproduction: Non-rhizomatous bunchgrass (Vergara & Bughrara 2003)
Seed Dispersal:
Chromosome Number(s): Hexaploid (2n = 42) (Vergara & Bughrara 2003)
Successional Status: Mid – late (Tillman 1986)
Genetic Structure: Variation among populations in Ontario in metal tolerance, apparently due to natural selection (Archambault & Winterhalder 1995)
Additional information:

Aster integrifolius

Family: Asteraceae
Growth Form: Forb, subshrub
Pollination:
Mating System: Probably outcrossing (11 other *Aster* spp. are SI) (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal: Probably wind
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:

Aster macrophyllus

Family: Asteraceae
Growth Form: Forb
Pollination:
Mating System: Obligate outcrossers (Jones 1978 cited in Chmielewski 1999)
Clonal Reproduction: Rhizomatous (Lamboy et al. 1991)
Seed Dispersal: Probably wind
Chromosome Number(s): octoploid (2n = 72) (Chmielewski 1987; Lamboy et al. 1991; Van Faasen & Sterk 1973)
Successional Status: Early successional (Bell et al. 2000; Crow et al. 1991; Shropshire et al. 2001)
Genetic Structure: Polymorphic at all 7 isozyme loci studied; mean of 3.1 alleles per locus; mean heterozygosity per locus 0.353 (N = 44) (Lamboy et al. 1991)
- High genetic identity with other species in *Aster* section *Biotia* (Lamboy et al. 1991)

Additional information:

Aster novi-belgii

Family: Asteraceae
Growth Form: Herb
Pollination:
Mating System: Obligate outcrossers (SI) (Briggs et al. 1989; Jones 1978 cited in Chmielewski 1999)
Clonal Reproduction: Rhizomatous (Briggs et al. 1989)
Seed Dispersal: Probably wind
Chromosome Number(s): var. novi-belgii and var. crenifolius: 2n = 6x = 48 (Labrecque & Brouillet 1996)
Successional Status:
Genetic Structure:
Additional information:

Aster umbellatus

Family: Asteraceae
Growth Form: Forb
Pollination: Insect pollinated (Chmielewski 1999)
Mating System: Obligate outcrossers (Jones 1978 cited in Chmielewski 1999)
Clonal Reproduction: Rhizomatous (Semple et al. 1991)
Seed Dispersal: Wind dispersal using pappus attached to achene (Chmielewski 1999; Chmielewski & Ruit 2002)
Chromosome Number(s): diploid (2n = 18) (Semple et al. 1991; Van Faasen & Sterk 1973)
Successional Status:
Genetic Structure: two varieties exist; range maps included (Semple et al. 1991)
Additional information: A facultative wetland species (Chmielewski 1999)

Bouteloua gracilis

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Highly cross fertilized (Fu et al. 2004; Snyder & Harlan 1953 cited in Aguado-Santacruz et al. 2004)
- Facultative Apomixis (Gustafsson 1946 cited in Aguado-Santacruz et al. 2004)

Clonal Reproduction: Rhizomatous; mean plant size at Central Plains Experimental Range, LTER, near Ft Collins, CO = 394 cm^2 (Aguilera & Lauenroth 1993)

- Under certain circumstances may also spread by stolons (Stubbendieck et al. cited in Aguado-Santacruz et al. 2004)
- Spread by tillers, remain physiologically linked (bunchgrass) (Fair et al. 2001)
- Plants can be long-lived (38 – 400 yrs; Coffin & Lauenroth 1990, Fair et al. 1999) but will not spread clonally beyond certain spatial limits (Aguado-Santacruz et al. 2004); and avg genet lifespan is 3.7 yrs (Fair et al. 1999)
- Number of individuals (ramets?) per genet ranges from 1 – 5 (mean 1.33) (Fair et al. 1999)
- Facultative Apomixis (Gustafsson 1946 cited in Aguado-Santacruz et al. 2004)

Seed Dispersal: Wind and inside herbivores (Fralegih et al. 1996)

- Inside cattle (Wicklow & Zak 1983), then buried by dung-burying beetles, which causes higher germination due to decreased drying (Wicklow et al. 1984)
- ~ 1 seedling recruited per year in 5 m^2 plot (Fair et al. 1999)

Chromosome Number(s): Tetraploid (Fu et al. 2004); Variable (2n = 20, 40, 42, 60, 61, 77, 84) with 20 = diploid, 40 = tetraploid, and 60 = hexaploid (Gould 1979)

Successional Status: Late successional dominant (Allen & Allen 1984; Reichhardt 1982)

Genetic Structure: Inhabits wide ecological range (Fu et al. 2004)

- Demonstrates high degree of morphological variation, even within fields (McGinnies et al. 1988)
- High levels of genetic variation detected with RAPD markers, but intrapopulation variation (88.53% of total variation; 97.8% of total variation) was higher than interpopulation variation (11.47%; 2.2%) (Aguado-Santacruz et al. 2004; Phan et al. 2003, respectively); however, increasing the number of sites used to contribute to seed batches significantly increases genetic variation present (Fu et al. 2004)
- Genetic variation was not associated with geographic distance between populations (Phan et al. 2003)
- Pairwise Φ_{ST} values (proportion of variation residing between two populations) for 4 populations in Mexico(?) range from 0.0649 to 0.2153 (Aguado-Santacruz et al. 2004)
- Levels of genetic variation comparable to other outcrossing grasses (Aguado-Santacruz et al. 2004)
- All individuals were genetically unique, but no population-specific RAPD alleles were detected (Aguado-Santacruz et al. 2004; Phan et al. 2003)
- Although plants reproduce asexually and recruitment is low (Karl et al. 1999), it might be predicted that clonal spread will prevail over sexual spread. However, much variation was seen when plants sampled from at least 7 m apart, highlighting the importance of sexual reproduction in population structure of this species. (Aguado-Santacruz et al. 2004)

Additional information: Heavily mycorrhizal (Allen & Allen 1984)

- C4 grass (Fair et al. 1999)
- No genetic shift was seen across two seed multiplications of wild-collected and cultivar seed (Fu et al. 2004), and only small shifts were seen in another study (0.6% and 1.9%) (Phan et al. 2003)

Bromus anomalus

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Diploid (2n = 14) (Ainouche & Bayer 1997)
Successional Status:
Genetic Structure:
Additional information:

Elymus glaucus

Family: Poaceae
Growth Form: Grass
Pollination: Low levels of gene flow estimated (*Nm* = 0.205) (Knapp & Rice 1996)
Mating System: Selfing (Asay & Jensen 1996; Knapp & Rice 1996)
Clonal Reproduction: Individual clones relatively short-lived (Asay & Jensen 1996); Non-rhizomatous (Knapp & Rice 1996)
Seed Dispersal: Stands persist thru reseeding since clones short-lived (Asay & Jensen 1996)
Chromosome Number(s): Allotetraploid (from *Hordeum* and *Pseudoroegneria*) (2n = 28) (Asay & Jensen 1996; Jensen 1993; Salomon et al. 1991)
Successional Status: Often a community dominant (Wilson et al. 2001)
Genetic Structure: High level of population differentiation based on allozymens (F_{ST} = 0.549), with surprisingly high differentiation among subpopulations (F_{ST} = 0.124). Attributed to selfing and patchy natural distribution. (Knapp & Rice 1996)
- % of variation found among populations = 54.9% (Knapp & Rice 1996) or 42% (Wilson et al. 2001)
- Low variation within populations, high homozygosity (98.5% or 9.9%) of individuals (Wilson et al. 2001; Knapp & Rice 1996, respectively); 77% of loci polymorphic, mean of 2.96 alleles per locus (Wilson et al. 2001)
- Higher genetic variation than usually seen in selfing species (Wilson et al. 2001)
- Very few populations had unique alleles (Wilson et al. 2001)
- No correlation between genetic and geographic distance (Knapp & Rice 1996)
- Sterility barriers exist between some ecotypes (Asay & Jensen 1996; Snyder 1950, 1951 cited in Wilson et al. 2001)
- Species consists of several ecotypes (Asay & Jensen 1996) and subspecies (Barkworth 1993; Hitchcock et al. 1969 cited in Wilson et al. 2001)

- Appear to be two genetic groups based on elevation; high elevation plants differ physiologically from low elevation plants (Wilson et al. 2001)

***"In order to minimize the chances of planting poorly adapted germplasm, seed of *E. glaucus* may need to be collected in close proximity to the proposed restoration site." (Knapp & Rice 1996)

***Using local seed may not provide seed that is similar to pre-disturbance populations at a site, but pops within 5 km are often (but not always) more genetically similar to one another than more distant populations. There was no correlation between physical and genetic distance in this species. Instead, it might be more beneficial to use seed from several sources and/or choose source of seed based on similar selection pressures/habitats to find seed that might be locally adapted. (Wilson et al. 2001)

***Self-pollination eliminates some concerns of seed transfer:

1) Non-local seed will not break up locally adapted gene complexes in nearby plants because plants will be primarily selfing.

2) The entire genome of homozygous, selfing plant functions as a linkage group, so local plants may not have optimally adapted gene complexes anyway. These are only formed through recombination, which is irrelevant in homozygous, selfing species. Introducing non-local genes will not likely have a negative effect.

Additional information: Coastal strains considered best adapted for general use with interior strains more promising for self-seeding cover crops (Hafenrichter et al. 1949, 1968 cited in Asay & Jensen 1996)

- High degree of phenotypic variation, still present in common gardens (Wilson et al. 2001)

- Natural hybridization (even intergeneric) involving this species is common (Stebbins et al. 1946 cited in Wilson et al. 2001)

Elymus hystrix

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Allotetraploid (from *Hordeum* and *Pseudoroegneria*) (2n = 28) (Salomon et al. 1991; Salomon & Lu 1994)
Successional Status:
Genetic Structure:
Additional information:

Elymus trachycalus

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Self-fertile (Aung & Walton 1987, 1989)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): allotetraploid (from *Hordeum* and *Pseudoroegneria*) (2n = 28) (Aung & Walton 1987, 1989; Jensen 1993; Salomon & Lu 1994)
Successional Status:
Genetic Structure: subspecies exist
-There is variation across wild accessions from the Canadian Rockies (Acharya et al. 1992) and across breeding lines in salt tolerance (Pearen et al. 1996)
- The most morphologically and geographically diverse of the species of Elymus in N. Amer.(Dewey 1982 cited in MacRitchie & Sun 2004)
Additional information: Salt tolerant (Acharya et al. 1992; Pearen et al. 1996)
-Used to genetically improve wheat and barley varieties

Eriogonum subalpinum

Family: Polygonaceae
Growth Form: Shrub, subshrub, forb
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:

Eriogonum umbellatum

Family: Polygonaceae
Growth Form: Subshrub, Shrub, Forb
Pollination: Butterfly (Auckland et al. 2004)
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status: Early-successional? (Day and Wright 1989)
Genetic Structure: has over 25 varieties (Reveal 1968; Welsh et. al 1975)
Additional information:

Festuca rubra

Family: Poaceae
Growth Form: Grass
Pollination: Wind (Dmytrakh 1989; Kevan & Tikhmenev 1996)
-Pollen movement distances varied greatly across days depending on factors like wind direction and velocity and humidity (Rhebergen et al. 1991)
- After about 3 m, pollen flow dropped off by 50%, but some grains were captured 32 m from the source population (Rhebergen et al. 1991)

Mating System: Thought to be primarily outcrossing, but genetic variation in frequency of selfing seen; up to 60% selfing in some genotypes (Jenkins 1931b, Auquier 1977 cited in Humphreys 1982) while in some studies it has behaved as an obligate outcrosser (Kevan & Tikhmenev 1996)
- Seed set from selfing is on avg approximately 50% of that obtained from outcrossing (Humphreys 1982)
- Selfing estimates were 0.43, 0.59, 0.68, and 0.18 for 4 different genotypes (Humphreys 1982)
- Features of flowering (time of receptivity and opening, etc) suggest autogamy and geitonogamy (Kevan & Tikhmenev 1996)

Clonal Reproduction: rhizomatous (Dubé & Morisset 1995); stolons (Aiken & Fedak 1992); *F. rubra* ssp. *fallax* is non-creeping and lacks rhizomes (Huff & Palazzo 1998)
- Ramets have high capacity for lateral spread, with frequent fragmentation (Hensen 1998)
- Genets vary in ability to form rhizomes (Herben et al. 2001)
- 2 types of shoots produced – intravaginal shoots lead to dense tussocks, while extravaginal shoots are produced at a greater distance from the main portion of the plant and lead to vegetative spread (Herben et al. 1994)

Seed Dispersal: Anemochory (wind dispersal) with winged diaspores (- at least in ssp. *litoralis*) (Hensen 1998; Valbuena & Trabaud 2001) and inside animals (endozoochory) (Hensen 1998)
- both long and short range dispersal seen (Hensen 1998)
- Avg of 3-7 genets/ m^2 established per year (Suzuki et al. 1999)

Chromosome Number(s): in Canada, hexaploids (n = 21), octoploids (n = 28), and intercytotype hybrids are found; also one aneuploid (2n = ca. 28) found (Dubé, Morisset, & Murdock 1985; Dubé & Morisset 1995); in California, *F. r.* ssp. *densiuscula* chromosomes were hexaploid (2n = 42) (Aiken & Fedak 1992); Rutgers U lines were octoploid (*F. r.* ssp. *rubra*) and hexaploid (*F. r.* var. *littoralis* and *F. r.* ssp. *fallax*) (Huff & Palazzo 1998)
- Chromosome numbers of 2n = 49, 50, 63, and 70 (along with other evidence) suggest that some individuals may be of intra- or interspecific hybrid origin (Aiken et al. 1988)
- Genetic variation in plasticity is seen (Herben et al. 2001)

Successional Status: Late (Verschoor et al. 2002); mid-successional in salt marsh systems (van Wijnen & Bakker 2000)
Genetic Structure: subspecies and varieties exist
-Variation within and among populations in tolerance to Fe and Mn in The Netherlands (Dueck et al. 1984)
- Biotypes differ in their environmental requirements for floral production (Murray et al. 1973)
-Large number of genets found within populations based on RAPD data (Suzuki et al. 1999; Harberd & Owen 1969 cited therein)
Additional information:

Ilex verticillata

Family: Aquifoliaceae
Growth Form: Tree / shrub
Pollination:
Mating System: Dioecious, so obligately outcrossing (Brizicky 1964; Hill 1987)
Clonal Reproduction: Stoloniferous (Hill 1987)
Seed Dispersal: Bird-dispersed (Gargiullo & Stiles 1991, 1993)
Chromosome Number(s):
Successional Status: Early-mid (Sakai & Sulak 1985)
Genetic Structure:
Additional information: Deciduous
- Wetland species in Eastern US (Jones 1985)

Leymus salinus

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Outcrossing (Atkins et al. 1984)
Clonal Reproduction: May form short rhizomes (Atkins et al. 1984)
Seed Dispersal:
Chromosome Number(s): Ssp. *salinus* has tetraploid (2n = 28) and octoploid (2n = 56) populations, with one population having tetraploid and hexaploid (2n = 42) individuals; ssp. *salmonis* is tetraploid (2n = 28) (Atkins et al. 1984)
Successional Status:
Genetic Structure: 3 subspecies (range map) (Atkins et al. 1984; Barkworth & Atkins 1984)
Additional information:

Menodora longiflora

Family: Oleaceae
Growth Form: Subshrub, shrub, forb
Pollination:
Mating System:
Clonal Reproduction: Unlikely via roots – have deep taproot (http://www.systbot.gu.se/staff/evawal/oleaceae/menodora.html)
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:
Citations at http://www.systbot.gu.se/staff/evawal/oleaceae/menodora.html

Muhlenbergia montana

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Probably selfing (cleistogamous panicles may be present) (Flora of North America, Vol. 25, p. 145)
Clonal Reproduction: Most spp in genus caespitose (= without rhizomes?) (Herrera-ARrieta & Grant 1994)
Seed Dispersal:
Chromosome Number(s): Tetraploid (2n = 40) (Herrera-Arrieta 1995)
Successional Status:
Genetic Structure:
Additional information:

Myrica pensylvanica

Family: Myricaceae (Ericaceae?)
Growth Form: Shrub / tree
Pollination: Wind, inflorescences = catkins (Hall 1975)
Mating System: Dioecious, so obligately outcrossing; slightly higher number of male than female plants in natural populations (Hall 1975)
Clonal Reproduction: Rhizomatous (Hall 1975)
Seed Dispersal: Nutlets persistent on shrubs, dispersed by birds and rodents (Hall 1975)
- Nutlets made buoyant by inflated bracteoles (Wilbur 1994)
Chromosome Number(s): 2n = 16 (Hall 1975)

Successional Status: Early (Collins & Quinn 1982; Morris et al. 1974); One of the first woody shrubs to invade coastal areas in Canada, but shaded out by *Picea glauca* (white spruce) within 15 yrs (Hall 1975)
Genetic Structure: Different morphological forms (Wells 1968)
Additional information: No evidence of hybridization (Hall 1975)

- Resprouts from rhizomes or stem bases following fire (Hall 1975)
- Nitrogen-fixing (bacterial endophyte in root nodules) (Collins & Quinn 1982; Morris et al. 1974)
- Possibly alleleopathic (Collins & Quinn 1982)

Penstemon procerus

Family: Scrophulariaceae
Growth Form: Subshrub, shrub, forb
Pollination: Bumblebee spp (Bauer 1983; Biernaskie & Carter 2004); Flies (Schmid 1976); wide range of insect pollinators (Macior 1971)
Mating System: 16% fruit set in pollinator exclusion cages; 96% when open pollinated (Bauer 1983)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Most diploid (2n = 16) but plant examined from Rocky Mtns was tetraploid (2n = 32) (Clausen et al. 1940)
Successional Status:
Genetic Structure: Ecotypes exist based on altitude (Clausen et al. 1940)
Additional information:

Penstemon rydbergii

Family: Scrophulariaceae
Growth Form: Subshrub, shrub, forb
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:

Phacelia sericea

Family: Hydrophyllaceae
Growth Form: Shrub, subshrub, forb
Pollination:
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure: local varieties and subspp exist (http://www.nargs.org/potm/potm_dec03.html)
Additional information:

Physocarpus opulifolius

Family: Rosaceae
Growth Form: Shrub
Pollination: female syrphid flies (Waldbauer 1984); Unspecialized – carried out by numerous insects that visit flowers for pollen or nectar, including Hemiptera/Heteroptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera (Wheeler & Hoebeke 1985)
Mating System:
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information:

Pityopsis graminifolia

Family: Asteraceae
Growth Form: Forb
Pollination: Bumblebees and lepidopterans (Brewer & Platt 1994a)
Mating System: Geitonogamy possible? (Brewer & Platt 1994a)
Clonal Reproduction: rhizomatous (Brewer & Platt 1994b; Hartnett 1985, 1990; Semple et al. 1980)
- Fire increases both sexual and asexual reproduction (Hartnett 1985), but effect on asexual reproductive pattern depends on timing of fire (Brewer & Platt 1994b)
Seed Dispersal: wind (using pappus) (Brewer & Platt 1994a)

Chromosome Number(s): Diploids (2n = 18)and tetraploids (2n = 36) (includes distribution map); var. *tracyi* is hexaploid (2n = 54) (Semple et al. 1980a, b)
Successional Status:
Genetic Structure: Populations at burned sites exhibit higher phenotypic variation (caused by plasticity or genetic variation?) (Hartnett 1985)
Multiple varieties exist (Semple et al. 1980a, b)
Additional information: Flowering induced by fire, then undergoes mass sexual reproduction (Brewer & Platt 1994a)

Poa ampla

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Agamospermous – a facultative apomict (Larson et al. 2001)
- May produce either sexual or asexual seed (Williamson 1981)

Clonal Reproduction: Agamospermous seed (Larson et al. 2001)
Seed Dispersal:
Chromosome Number(s): 2n = 63 (Heisey and Nobs 1982 cited in Larson et al. 2001)
Successional Status:
Genetic Structure: cultivar Sherman (of *Poa secunda* = *P. ampla*) did not show any polymorphisms using AFLPs, i.e., it was a single fixed genotype (Larson et al. 2001)
Additional information: Called *Poa secunda* in Larson et al. 2001

Poa fendleriana

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Dioecy in *P. f.* var. *fendleriana* and *P. f.* var. *longiligula*; also autonomous agamospermy (apomixis) (Soreng 1984).
- Incompletely dioecious (Hitchcock 1950 cited in Larson et al. 2001)
- Dioecy; sexual and asexual reproduction, both by seed ; range maps of sexual and asexual reproduction for the subspecies (Soreng & Van Devender 1989)

Clonal Reproduction: autonomous agamospermy (apomixis) (Soreng 1984)
Seed Dispersal:
Chromosome Number(s): 2n = 28 + 1, and 2n = 56 (Soreng 1990 cited in Larson et al. 2001)
Successional Status:
Genetic Structure: Three subspecies exist
- High levels of genetic diversity based on AFLPs (Larson et al. 2001)

- Avg Jaccard's similarity coefficient among pairwise comparisons of individual plants within *P. fendleriana* using AFLPs = 0.68 (Larson et al. 2001)

Additional information:

Potentilla glandulosa

Family: Rosaceae
Growth Form: Subshrub, shrub, forb
Pollination:
Mating System: Some ecotypes are selfing with small, inconspicuous flowers, others are self-incompatible with large, showy flowers (Clausen et al. 1940)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Diploid (2n = 14) (Clausen et al. 1940)
Successional Status:
Genetic Structure: Several subspecies and ecotypes, all interfertile; map of ecotypes (Clausen et al. 1940)

- Hereditary morphological variation exists at the level of individuals within populations, populations within ecotypes, and hybrids among ecotypes, and among ecotypes (Clausen et al. 1940)
- Coastal and inland populations differ significantly in ability to withstand drought due to temperature-induced changes in leaf morphology (Teeri 1978)

Additional information:

Potentilla gracilis

Family: Rosaceae
Growth Form: Forb / subshrub
Pollination: Bumblebees move between nearest neighbors (Zimmerman 1982)

- Pollinated largely by small solitary bees (Waddington 1979)

Mating System: occasionally sexual and primarily apomictic reproduction suggested (Clausen et al. 1940)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Highly variable, even within populations; octoploid to 16-ploid (2n = ca. 56 to ca. 109) (Clausen et al. 1940)
Successional Status:
Genetic Structure: two subspecies (range map) and ecotypes exist (Clausen et al. 1940)
Additional information:

Pseudoroegneria spicata

Family: Poaceae
Growth Form: Grass
Pollination: Wind (Johnson et al. 2002)
Mating System: Outcrossing; highly self sterile (Larson et al. 2000)
Clonal Reproduction: tillering (Mueller & Richards 1985); usually caespitose, but can be rhizomatous (Larson et al. 2000)
Seed Dispersal: Seed production is poor but variable across plants and years (Quinton et al. 1982)
Chromosome Number(s): generally diploid (2n = 14) (Aung & Walton 1987; Jensen 1993) but autotetraploid populations may be seen in nature (Larson et al. 2000)
Successional Status:
Genetic Structure: Subspecies exist
- Ecotypic variation occurs (Daubenmire 1939, 1960; Passey & Hughie 1963; Main 1974; Harris & Goebel 1976; and Dobrowolski 1979 all cited in Dibble & Spomer 1987)
- Ability to withstand wide range of moistures NOT due to ecotypic variation (Dibble & Spomer 1987)

Additional information:

Rosa woodsii

Family: Rosaceae
Growth Form: Shrub
Pollination:
Mating System: Probably outcrossing (4 of 5 other species listed were SI) (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): Diploid (2n = 14) (El-Lakany 1972)
Successional Status: Present after 30 years (Wali 1999)
Genetic Structure:
Additional information:

Sambucus canadensis

Family: Caprifoliaceae
Growth Form: Tree / shrub / subshrub
Pollination:
Mating System:
Clonal Reproduction:

Seed Dispersal: Bird-dispersed (Gorchov 1987; Malmborg & Willson 1988; Patton & Judd 1988)
Chromosome Number(s): 2n = 38 (Mehra & Bawa 1968)
Successional Status:
Genetic Structure: variation in production of cyanogenic glycosides across and within natural populations (Buhrmester et al. 2000)
Additional information:

Solidago canadensis

Family: Asteraceae
Growth Form: Herb
Pollination: Insect pollinated: honeybees, bumblebees, soldier beetles, and surphid flies (Werner et al. 1980 cited in Melville & Morton 1982); a wide variety of Hymenoptera (bees & wasps), Diptera (flies), Lepidoptera (butterflies & moths), together with several species of Hemiptera (True bugs) and Coleoptera (beetles) (Melville & Morton 1982); wasp and locust-borer (coleopteran) (Blackwell & Powell 1981); Primarily honeybees (Gross & Werner 1983); Bumble bees (Morse 1977)
Mating System: Obligate outcrossers (SI) (Melville & Morton 1982)
Clonal Reproduction: rhizomatous production of new shoots (ramets) (Bradbury 1981; Hartnett 1990)

- Clones are often large and it is difficult to distinguish among genets (Bradbury 1981)
- Ramets remain connected up to 4 yrs (Bazzaz 1984)
- Genets composed of 1 to several units of 10 – 20 interconnected ramets (Bazzaz 1984)

Seed Dispersal:
Chromosome Number(s): diploid (2n = 18) (Kapoor 1978; Melville & Morton 1982)
Successional Status: Early – Mid; invades in first year and becomes dominant by third (Hopkins & Wilson 1974)

- Persists until outcompeted by trees and other late successional plants (Bazzaz 1984)

Genetic Structure: Subspecies exist (Famous 1980)

- Two varieties present in Ontario intergrade and are interfertile (Melville & Morton 1982)
- Recruitment occurs for a short time after disturbance, despite high quantity of seed rain later from established plants; so genetic structure of populations is determined by the initial seed genotypes available (Bazzaz 1984; Hartnett & Bazzaz 1985)
- However, number of genets remained constant despite genet mortality after ~ 15 yrs, so there must be some recruitment that maintains the diversity of genets (Hartnett & Bazzaz 1985)

Additional information: While vegetative growth is a means of competition with surrounding plants, all dispersal is via seeds in this species (Melville & Morton 1982)

Solidago puberula

Family: Asteraceae
Growth Form: Forb
Pollination:
Mating System: Probably outcrossing (all other congeners listed [=6] were SI) (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): diploid (2n = 18) (Kapoor 1977, 1978)
Successional Status:
Genetic Structure:
Additional information:

Solidago rugosa

Family: Asteraceae
Growth Form: Forb
Pollination: Insect pollinated (Rutter 1994)
Mating System: Outcrossing (SI) (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal:
Chromosome Number(s): forma villosa 2n = 18 (Kapoor 1978); (S. rugosa var sphagnophila = S. aestivalis): hexaploid with 2n = 54 (Kapoor 1977)
Successional Status:
Genetic Structure:
Additional information:

Sorghastrum nutans

Family: Poaceae
Growth Form: Grass
Pollination: Outcrossing (SI) (Gustafson et al. 2004)
Mating System:
Clonal Reproduction: Rhizomatous (McKendrick et al. 1975; Sangster 1983)
Seed Dispersal:
Chromosome Number(s): Allotetraploid (2n = 40) (Read & Maika 1987)
Successional Status: Late (Tillman 1986)
Genetic Structure: Genetic variation exists among populations in economically important traits (atrazine tolerance) (Kube et al. 1989)

- 87.8% of variation within populations of Illinois, 12.2% among; $F_{ST} = 0.121$ (Gustafson et al. 2004)

- The data suggest that there are ecotypic differences in this species (Gustafson et al. 2004)

Additional information: Growth and success increased by mycorrhizae (Wali 1999)

Sporobolus airoides

Family: Poaceae
Growth Form: grass
Pollination:
Mating System: Selfing (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal: Seeds remain viable after passing thru cows (Barrow & Havstad 1992)
Chromosome Number(s):
Successional Status:
Genetic Structure: Different ecotypes exist in Mexico that differ in physiological and life history traits (Cox et al. 1990)
Additional information:

Stipa comata

Family: Poaceae
Growth Form: Grass
Pollination:
Mating System: Either selfing or mixed mating (Fryxell 1957)
Clonal Reproduction:
Seed Dispersal: Seeds found 1 m into an agricultural field, dispersed from adjacent pasture in which the species made up ~15% of the plant cover (Hume & Archibold 1986)

- Bison may disperse seeds, but passage thru their gut decreases germination rates (Gokbulak 2002)

Chromosome Number(s): 2n = 44, (also a finding of 2n = 38, but this differs from all other reports for the species) (Reeder 1977)
Successional Status: Present after 17 years (Wali 1999); Mid-successional (Frederick & Klein 1994)
Genetic Structure: 2 varieties in Canada and USA (includes distribution map) (Barkworth 1978)
Additional information:

Viburnum cassinoides

Family: Caprifoliaceae
Growth Form: Tree / shrub
Pollination: Pollinated primarily by native bees, syrphid flies (esp. females), and cerambycid beetles (Hansen & Osgood 1984; Miliczky & Osgood 1979; Waldbauer 1984)
Mating System: May be outcrossing (congener was SI) (Fryxell 1957)
Clonal Reproduction: Rhizomes (Flinn & Wein 1977)
Seed Dispersal:
Chromosome Number(s):
Successional Status:
Genetic Structure:
Additional information: Capable of resprouting from rhizomes after fire (Flinn & Wein 1977)

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