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# Genetic Aspects of the Biodiversity of Rangeland Plants

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## **Abstract**

*Biodiversity is the variety of life and its processes. Diversity cannot be described unless the differences between organisms can be detected and measured. The concept of genetic diversity is usually confined to individual organisms, populations, and species and may be considered as heritable differences among taxa capable of gene exchange. New macromolecular methods together with traditional morphological, cytogenetic, hybridization, and breeding-system analytical methods are providing greater detail that allows a finer resolution of genetic diversity. Rangeland plant biodiversity studies of shrub, forb, grass, and tree taxa are demonstrating genetic diversity at several levels. Case studies of several taxa illustrate that there is an unevenness of genetic diversity data available from rangelands and, in general, rangeland plant genetic diversity studies are in the beginning stages. The influences of past climatic changes on plant genetic diversity are also only just beginning to be understood. Both conservation and use of rangeland plant resources have genetic bases. Genetic diversity studies are important for discovering and documenting the sources and patterns of variation. That information is vital if genetic diversity is to be protected and preserved so that rangeland plant resources can be effectively used and sustained to maintain future options.*

## **INTRODUCTION**

West (1993) defined biological diversity (biodiversity) as the variety of life and its processes, including the variety of living organisms, the genetic differences among them, the communities, ecosystems, and the landscapes in which they occur, plus the interactions of these components.

Chambers and Bayless (1983) made a telling point that we believe needs emphasis: The diversity of any group, whether it is a local population or a multispecies community, cannot be described unless the differences between individuals or species can be detected and measured.

Our treatment addresses plant genetic diversity on rangelands. Stubbendieck et al. (1986) list 200 important North American range plants. The Range Plant Handbook (USDA Forest Service 1937) treats 339 species (mostly) or genera of rangeland plants with some reference to an additional 500 species and states that western rangelands are naturally inhabited by over 1,200 genera and 10,000 species of flowering plants. However, this represents only a small portion of plant biodiversity and an even smaller portion of overall biodiversity. To illustrate these points, the number of described species (a measure of biodiversity) of organisms (Wilson 1988, Cook 1991) found over the world has been estimated as follows:

Virus	1,000
Monera	5,000
Protista	50,000
Fungi	45,000
Plantae	280,000
Animalia	1,100,000
Total	1,481,000

Wilson (1988) believed the absolute number, including undescribed species, might exceed 5,000,000; Pimentel et al. (1992) placed that number at 10,000,000. Considering only plants, the levels of taxonomic biodiversity, in a hierarchical descending order, are as follows:

Kingdom
Division
Class*
Order
Family*
Tribe**
Genus*
Section**
Species*
Variety**
Form**
Population

\*Many of these categories (taxa) have subordinate subdivisions, e.g., subclass, subfamily, subgenus, and subspecies, when the lineage is complex.

\*\*In simpler lineages, not all categories are used, e.g., tribe, section, variety, and form may or may not be included.

## GENETIC DIVERSITY AND WORKING GENETIC DEFINITIONS

Genetic diversity has been recognized as meaning (Schonewald-Cox et al. 1983) (1) species diversity, (2) allele diversity, (3) allele frequency differences (between individuals within populations and between populations), or (4) the combination of species diversity with allelic variations. An allele (allelomorph) is one of a pair, or series, of alternative forms of a gene that can occur at a given locus in homologous chromosomes. A shorter definition of genetic diversity is the heritable differences among individuals of species or other taxa capable of gene exchange (McArthur 1984). Genetic diversity is at the base levels of biodiversity, as viewed above, but is manifest with decreasing impact from population to species to genus because gene exchange becomes rarer as the scale of taxonomic units broadens.

Measuring genetic diversity began with the science of genetics when Gregor Mendel discovered the principles of gene segregation and independent assortment in garden pea (*Pisum sativum*) hybrids by examining the nature of inheritance of such traits as plant height and seed color and shape (Gardner 1968, Monaghan and Corcos 1985, Corcos and Monaghan 1993) in the mid-nineteenth century. Measures of genetic diversity are becoming more and more sophisticated as new techniques are developed (Table 1).

Morphological traits continue to be important in assaying genetic diversity, but these traits are not always simply

inherited. As it turns out, Mendel was fortunate to select simply inherited traits because many genetic traits are quantitatively inherited through many genes and are consequently more difficult to analyze. Elegant numerical and statistical procedures are currently available as analytical tools, often in the form of software packages, e.g., parsimony analysis, principal components analysis, canonical analysis, discriminant analysis, cluster analysis, etc. These techniques are especially useful in understanding more complex inheritance patterns such as quantitative inheritance and continuous variation (Falconer 1960).

Traditional genetic traits, including the more analytically difficult quantitative ones, are coded for by deoxyribonucleic acid (DNA) for most organisms, including higher plants. DNA is the replicating hereditary material that is organized into the genes of the nuclear chromosomes of Mendelian inheritance (genes that segregate and independently assort). It should be noted, however, that chromosomes also have noncoding or genetically inert regions and some areas of highly redundant or surplus DNA for which function is poorly understood. There are also genes in cell organelles such as chloroplasts and mitochondria that are non-nuclear, i.e., cytoplasmic. A complete set of nuclear chromosomes is known as a genome ( $x$ ). A diploid ( $2n$ ) individual has two sets of chromosomes, one set from the maternal parent and one from the paternal parent. The reproductive cells of the plant undergo reduction division (meiosis) and are consequently  $n$  or haploid. Production of a new plant through sexual reproduction restores the  $2n$  chromosome number.

Many plant groups have a high frequency of polyploidy. Polyploidy is the condition of multiple genomes being present in an organism. For example, a plant that has four sets of chromosomes is tetraploid ( $4x$ ). However, most polyploids behave genetically as sexual diploids, so that if, for example, the base chromosome number (genome) is 9 then the genetic formula would be  $2n = 4x = 36$ . The terms *haploid* and *diploid* have two meanings:  $x$  and  $2x$  as the first two entries in a polyploid series (haploid, diploid, triploid, tetraploid, etc.—referring to multiples of the base chromosome number), but also  $n$  and  $2n$  at any level of  $x$  to signify the gametes (gametophytes or sex cells) and parental plants (sporophytes). Polyploids may be autopolyploids where the constituent genomes are identical or allopolyploids where constituent genomes are different though similar enough to function together in the same organism. In reality most polyploids are something in between these extremes. Aneuploidy is the loss or gain of one or a few (less than a genome) chromosomes. Other genetic materials are cytoplasmically inherited, i.e., hereditary transmission is dependent on the cytoplasm or structures in the cytoplasm rather than on nuclear genes. Some genetic material is maternally effected, i.e., inheritance from the mother to offspring is unaffected by inheritance from the father as, for example, the cytoplasmic genes mentioned above. Paternal inheritance (such as chloroplast DNA in pinyon pine) also occurs, but is rarer.

In addition to morphological and chromosomal traits, molecular, including macromolecular, traits can serve as genetic markers (Table 1). Some of these are direct proteinaceous products of chromosomal DNA, e.g., isozymes are

TABLE 1. MEASURES OF GENETIC DIVERSITY<sup>1</sup>

Morphometrics	Serology (Immunology)
Alpha Taxonomy	Chemotaxonomy
Numerical Taxonomy	Nucleic Acids
Chromosomes	DNA
Genomes	DNA/DNA Hybridization
Ploidy	nuclear DNA
Mapping	cpDNA
Protein Sequencing	mDNA
Protein Electrophoresis	rDNA
Seed Storage Proteins	RFLP
Rubisco	RAPD
Isozymes	Physiological Ecology
Allozymes	Breeding Studies

<sup>1</sup>For definitions see the texts, Vickery and Wullstein (1987), Crawford (1990), and Cook (1991).

functional enzymes that can be identified by electrophoresis and used to analyze genetic variation within and among plant populations and taxa. Current use of the term *isozyme* is restricted to enzymes encoded by different loci, thus separating isozymes from a special class of functional enzymes that are encoded at a particular locus, in which case they are referred to as allozymes or enzyme alleles (Gottlieb 1982). Protein- and nucleic-acid sequencing techniques are powerful tools that are useful in quantifying genetic variation at all levels from individuals in a population to all forms of life. Genetic and evolutionary distances can be mapped using these techniques (Crawford 1990). Currently in the forefront are the DNA analyses, RFLPs and RAPDs. Both techniques involve the generation of multiple identical copies of DNA strands produced by the polymerase chain reaction (PCR) that uses the DNA polymerase ("production machinery") of a thermal alga to amplify template DNA in vitro (Mullis 1990). RFLPs (restriction fragment length polymorphisms) are the products of enzymatic "scissors" that excise portions of DNA from specific starting and ending points from nuclear chromosomes or from organelle genomes. RFLPs are used to map fragment positions to make comparisons in the DNA strands of the organisms being studied. RAPDs (random amplified polymorphic DNA) analysis is the comparison of many short DNA strands of similar length that can allow quick, powerful analyses. Other molecular techniques and appropriate references are listed in Table 1. The PCR technique is useful for looking at genetic diversity in the past as well as in currently living organisms. For example, DNA from fossil material as old as Miocene (ca. 20,000,000 years BP) can be multiplied and analyzed (Golenberg et al. 1990).

Whole syndromes, e.g., breeding systems, photosynthetic pathways, germination characteristics, and a whole array of macromolecules are useful in establishing patterns of genetic diversity and phylogenetic relationships (Ford 1964, Harborne 1973, Brussard 1978, Gates 1980, Willson 1983, Richards 1986, Nei 1987, Lovett Doust and Lovett Doust 1988, Crawford 1990).

In general, the techniques of measuring genetic diversity are complementary. Vickery and Wullstein (1987) compared six approaches to the classification of the six species includ-

ing nine experimental populations of *Mimulus*, section *Erythranthe*. This species complex is a closely related group occupying riparian areas of western North America. Vickery and Wullstein used alpha taxonomy (phenetic classification of herbarium, field, and greenhouse specimens), numerical taxonomy (100 morphological or sensory traits of greenhouse-grown plants), experimental hybridization (in all combinations), chemotaxonomy (floral flavonoid pigments), allozyme-isozyme (11 enzymes), and DNA/DNA hybridization (between the experimental populations). They concluded that the six methods are only partially congruent, but definitely complementary. The numerical taxonomic and experimental hybridization methods produced the clearest distinctions and groupings, but all methods added clarity and detail. This set of experiments did not include DNA or protein sequencing, which may have been even more definitive. More, rather than fewer, measures of genetic diversity contribute to establishing relationships and quantifying variation.

#### INDIVIDUAL AND POPULATION GENETIC DIVERSITY

Natural evolutionary processes and human-directed selection work at the individual (intrapopulation) and population (interpopulation) levels. It is at these levels that gradual, adaptive changes occur (Charlesworth 1990). This viewpoint is the consensus for how evolution occurs (Mayr 1991). Other views suggesting more relative importance of larger-scale mutation and random genetic drift also would operate at these levels more effectively than at levels above the population, although such views are not as generally acceptable to modern population biologists as the gradual, adaptive model originally suggested by Charles Darwin (Charlesworth 1990, Mayr 1991). Unfortunately, most of the studies on rangeland plant species are at higher levels, e.g., subspecies, species, and genera (see next section).

Some examples of intrapopulation and interpopulation variation that is of prime importance on rangelands whether the focus of attention is evolutionary processes or human-directed selection and management deal with grazing resistance or tolerance, drought resistance, and pest (insects and

disease) resistance. It is well known that some forage plants are better adapted to grazing than others at various levels of consideration, e.g., perennials versus annuals, species versus species, population versus population, individual versus individual (Hanks et al. 1973, Rickard et al. 1975, Caldwell et al. 1981, Hodgkinson and Williams 1983, Delucia and Schlesinger 1991, Halls et al. 1994, Jaindl et al. 1994). This differential adaptation is essentially genetic and has important management implications. Likewise, drought (Wilson and Sarles 1978, Ehleringer and Cooper 1988, Hardegree and Emmerich 1990, Johnson et al. 1990) and pest (Asay et al. 1983, Nelson et al. 1989, Haws et al. 1993) resistance have genetic components. When genetic gain through selection is an objective, other characteristics such as nutritive quality and biomass production become important. Gain in quality traits like these is accomplished by identifying individuals (or clones) with those traits and increasing by selective means the frequency of those traits or individuals in the next generation (Carlson and McArthur 1985, McArthur 1988, Karn and Tober 1990, Vogel et al. 1993). Sometimes it is desirable to merge traits from different populations rather than individuals within the same population. Besides the traditional breeding techniques just described, a small amount of pioneering work has been accomplished incorporating the area of biotechnological or genetic engineering into plant improvement research on rangeland plants (McArthur 1988). Genetically engineered plants and microbes show promise for increasing productivity and shortening selection time, but they also pose potential risks for altering the environment in unknown ways (Olson 1986).

Observable characteristics are not always heritable. Traits may be variably expressed in genetically identical individuals. This phenomenon is known as phenotypic plasticity (Wayne and Bazzaz 1991). The relationship between genotype and phenotype is not one to one but one to many. This relationship must be discovered to select for traits in a breeding program or to understand and manage population dynamics. Discovering the relationship between genotype and phenotype may be difficult. The use of clonal materials in multiple environments (reciprocal transplant gardens) and temporal observation of trait expression are some of the methods used to elucidate this relationship (Pendleton et al. 1988, McArthur et al. 1992a).

#### CASE STUDIES OF GENETIC DIVERSITY

As in many other aspects of science, research on rangelands lags behind other areas in respect to genetic diversity. Genetic diversity of commercial tree species, agronomic crops, and other areas has received much more attention than rangeland plant species (Miksche 1976, Simmonds 1976, Hamrick et al. 1979, Hamrick 1982). Studies of genetic diversity, implementing principally the measures of Table 1, are found in many recent books, e.g., Harper 1977, Futuyma 1979, Nei and Koehn 1983, Scandalios 1984, Hartl and Clark 1989, Falk and Holsinger 1991, Adams and Adams 1992, and current research periodicals, e.g., *Agronomy Journal*, *American Journal of Botany*, *American Naturalist*, *Crop Science*,

*Ecology*, *Evolution*, *Forest Science*, *Genetics*, *Genome*, *Heredity*, *Journal of Ecology*, *Journal of Evolutionary Biology*, *Journal of Heredity*, *Nature*, *Science*, *Oecologia*, *Silvae Genetica*, *Systematic Botany*, *Theoretical and Applied Genetics*.

A particularly elegant case study of genetic diversity is that of the Hawaiian silversword alliance (Asteraceae-Madiinae). These descendants of long-range dispersed North American tarweeds have been characterized by hybridization, chromosome pairing, and cpDNA studies among the three extant Hawaiian genera (28 species) and their mainland relatives (Carr and Kyhos 1986, Kyhos et al. 1990, Baldwin et al. 1991). For the balance of this section, we discuss some examples of genetic diversity for rangeland species of shrubs, forbs, grasses, and trees.

#### SHRUBS

Shrub dominance often defines rangelands, i.e., lands not intensively managed by agronomic or forestry principles, so it is appropriate that we begin our case studies of genetic diversity with shrubs. Shrubs, however, do not constitute any cohesive phylogenetic unit (McArthur 1989). Shrubs are widely distributed in plant communities dominated by other life forms (Küchler 1964), but are dominants, usually, only in habitats that place plants under considerable stress such as drought or aridity, nutrient-poor soils, fire, shade, poor soil aeration, winter cold, short growing seasons, and wind (McArthur 1984, 1988, West 1992). Most of these conditions are best met in arid or semiarid continental climates that also characterize most of the world's rangelands (Walter 1973). Küchler's (1964) data base provides some additional insight on shrub diversity and speciation (Table 2). Fifteen plant families were identified as having dominant shrubs on Küchler's (1964) map, Potential Natural Vegetation of the Conterminous United States. Shrub values include extending the grazing season and increasing community diversity and ecosystem stability (McArthur 1988).

Hall and Clements (1923) produced a classical work some 70 years ago, entitled *The Phylogenetic Method in Taxonomy, The North American Species of Artemisia, Chrysothamnus, and Atriplex*. They chose the three genera for their pioneering monograph because they were set up to study in western North America and because these shrub genera had "taxonomic and ecologic interest. They have been objects of the most active evolution, with which has gone the widest distribution, both as to climate and soil. Ecologically, they are unsurpassed in the number of dominants and subdominants they furnish to the vegetation."

Hall and Clements (1923) used morphological and distributional information in their treatment and made substantive contributions in regard to plant relationships. We here review some more current genetic diversity work on these genera.

The genus *Artemisia*, with up to 400 species worldwide, includes the plant that most nearly epitomizes the American West, sagebrush. McArthur et al. (1981) limited the term sagebrush to the endemic American subgenus *Tridentatae*, which includes some 25 taxa (species, subspecies, varieties,

forms) centered around big sagebrush (*A. tridentata*), with its five subspecies: basin big sagebrush (*A. t. ssp. tridentata*), mountain big sagebrush (*A. t. ssp. vaseyana*), Wyoming big sagebrush (*A. t. ssp. wyomingensis*), subalpine big sagebrush (*A. t. ssp. spiciformis*), and xeric big sagebrush (*A. t. ssp. xericensis*). Sagebrush forms a polyploid complex,  $x = 9$ , to  $8x$  (McArthur et al. 1981, McArthur and Sanderson, unpublished) of mostly autopolyploid, interfertile taxa and populations. Genetic diversity and gene exchange have been documented in continuing studies through artificial hybrid seed set data and morphological, seed germination ecology, browsing preference, coumarin, flavonoid, monoterpene, and RAPDs DNA profiles, of parental populations and artificial and natural hybrids (Hanks et al. 1973, McArthur et al. 1979a, 1981, 1988, 1992b, McArthur and Welch 1981, Welch and McArthur 1981, 1986, Welch et al. 1987, 1991, Meyer et al. 1990, Stevenson et al. 1990, Bray et al. 1991, Meyer and Monsen 1991, Wilt et al. 1992, Weber et al. 1994). With genic modifications of a single autopolyploid genome, sagebrushes (*Tridentatae*) vary widely in many characteristics, including size. Pygmy sagebrush (*A. pygmaea*) is prostrate; basin big sagebrush may be up to 4.5 m tall. Natural hybrid zones among big sagebrush subspecies are providing insights into the nature and stability of hybrid zones (McArthur et al. 1988, Freeman et al. 1991). Hybridization has apparently been important in the origin of several sagebrush taxa (Ward 1953, Beetle 1960, Goodrich et al. 1985, McArthur and Goodrich 1986, Winward et al. 1986, McArthur et al. 1988, Rosentreter and Kelsey 1991, Winward and McArthur 1995).

The genus *Chrysothamnus* (rabbitbrush) consists of 16 species and some 50 recognized taxa, including subspecies. The genus is wholly shrubby and is endemic to western North

America (Anderson 1986a, McArthur and Meyer 1987). Its five sections are distinguished by characteristic floral, stem, and achene differences. Three species complexes, each with several subspecies, dominate the genus: rubber rabbitbrush (*C. nauseosus*), Parry rabbitbrush (*C. parryi*), low rabbitbrush (*C. viscidiflorus*). The genus is essentially diploid,  $2x = 18$  with a limited amount of tetraploidy known only from the low rabbitbrush complex (Anderson 1986b). Some taxa are good colonizers of disturbed sites; some are broadly adapted and others are more specific. Gang and Weber (1995) have recently shown gene diversity by RAPDs DNA markers in a single population and a tight geographic cluster of ten populations of rubber rabbitbrush (*C. nauseosus* ssp. *hololeucus*). Earlier work on rubber, resin, phenolic compounds, volatile compounds, nutritive quality, seed germination syndromes, and host specificity of gall-forming tephritid flies has documented genetic diversity in rabbitbrush (Hanks et al. 1975, McArthur et al. 1978, 1979b, Dodson and George 1986, Hegerhorst et al. 1987a, 1987b, Meyer et al. 1989, Bhat et al. 1990, Halls et al. 1994, Floate et al. in review).

The genus *Atriplex* (shrubby forms = saltbush) is a large genus consisting of some 250 species worldwide (Osmond et al. 1980, McArthur and Sanderson 1984). Western North American forms include both herbs and shrubs. The approximately 20 North American shrubby saltbushes include several large genetically diverse species (Blauer et al. 1976, Stutz 1978, McArthur and Sanderson 1984), e.g., fourwing saltbush (*A. canescens*), shadscale saltbush (*A. confertifolia*), Gardner saltbush and allies (*A. gardneri* complex). Shrubby saltbushes rampantly naturally hybridize; many species have high polyploid forms,  $x = 9$  (Stutz et al. 1979). We discuss here only fourwing and shadscale saltbushes.

TABLE 2. NUMBERS OF GENERA AND SPECIES AND GROWTH FORMS OF SELECTED FAMILIES.<sup>1</sup>

Family	Shrub genera Number	Species western U.S., all growth forms	World total, all growth forms	Growth habits <sup>2</sup>
Anacardiaceae	1	9	150	S, T
Asteraceae	17	126	2546	H, S
Caprifoliaceae	5	28	317	S
Chenopodiaceae	8	29	441	H, S
Ericaceae	1	82	1211	S, T
Ephedraceae	1	10	40	S
Fabaceae	19	70	3276	H, S, T
Fagaceae	3	20	700	S, T
Fouquieriaceae	1	1	9	S, T
Lamiaceae	5	24	1175	H, S
Polygonaceae	1	20	250	H, S
Rhamnaceae	6	68	295	S
Rosaceae	23	81	760	H, S, T
Scrophulariaceae	4	22	454	H, S
Zygophyllaceae	2	2	22	S

<sup>1</sup>Adapted from McArthur (1984).

<sup>2</sup>Growth habits of congeneric relatives: H = herbs, S = shrubs, T = trees.

Fourwing saltbush includes a remarkable polyploid series extending from  $2x$  to  $20x$  (Stutz and Sanderson 1979; Sanderson and Stutz 1994). The  $20x$  populations are among the highest chromosome numbers known in flowering plants. Fourwing saltbush also has a remarkable breeding system. Polyploid forms, especially the widely studied tetraploids, are known to be trioecious with genetic males, genetic females, and a labile monoecious or hermaphroditic gender (McArthur 1977, McArthur and Freeman 1982, Barrow 1987, Pendleton et al. 1992) thought to be a gender fitness adaptation to environmentally heterogeneous, patchy environments (McArthur et al. 1992a, Freeman et al. 1993). Fourwing saltbush populations are also known to be variable in adaptation to soil salinity (Welch 1978, Richardson and McKell 1980) and winter hardiness (Van Epps 1975) and to vary in nutritive content (Welch 1978, Welch and Monsen 1981), stem rooting (Richardson et al. 1979), seed production, fill and germination (Springfield 1970), growth rate and form and site adaptation (Stutz et al. 1975, McArthur et al. 1983a, Stevenson et al. 1990, Watson 1990), and in genetic marker isozymes (McArthur et al. 1986), flavonoids (Sanderson and Stutz 1994), and RAPDs DNA (Stutz et al. unpublished).

Shadscale saltbush, like fourwing saltbush, has a remarkable polyploid series, going from  $2x$  to  $10x$  (Stutz and Sanderson 1983). Like several other western rangeland shrub species, the higher polyploids of shadscale tend to be smaller and adapted to more xeric environments than diploids (Sanderson et al. 1989). Shadscale populations are differentiated by ploidy level, morphology, and flavonoid chemistry into two major and ten smaller geographic races (Sanderson et al. 1990).

The shrub examples above come from just two of the families listed in Table 2 (sagebrush and rabbitbrush from Asteraceae and saltbush from Chenopodiaceae). These families, along with Ericaceae and Rosaceae, are perhaps the most important contributors to the shrub flora of western rangelands in terms of numbers of species, populations, and individuals. Some other examples of rangeland shrub genetic diversity are listed below, but we make the point that our knowledge base is not well developed, nor are the examples exhaustive. The number of shrub species of Table 2 are only those that belong to a genus that is listed by K uchler (1964) as having species that are important in the vegetation (McArthur 1984, 1993).

The genetic diversity of *Gutierrezia* (matchbrush and relatives) and *Parthenium* (guayule and relatives) (Asteraceae) and their respective congeners has been studied by chromosome number ( $x = 4$  for *Gutierrezia*,  $x = 18$  for *Parthenium*), with diploid ( $2x$ ) and polyploid ( $> 2x$ ) species and races and structure, plant morphology, and cpDNA (Solbrig 1971, Estilai et al. 1985, Lane 1985, Hashemi et al. 1986, 1987, 1988, Lane and Jansen 1990, Suh and Simpson 1990). *Grayia brandegei* (spineless hopsage) (Chenopodiaceae) populations differ in phenotype, geographic distribution, and chromosome number ( $x = 9, 2x, 4x$  populations) and exhibit an unusual heterodichogamous breeding system (Stutz et al. 1987, Pendleton et al. 1988). The *Purshia/Cowania* (bitterbrush/cliffrose) complex (Rosaceae) has been characterized by plant morphology, chromosome number ( $x = 9, 2x$ ),

hybridization and breeding system, seed germination syndromes, and DNA patterns (Stutz and Thomas 1964, Nord 1965, Koehler and Smith 1981, McArthur et al. 1983b, Baker et al. 1984, Meyer 1989, McArthur and Pendleton 1990, Pendleton and McArthur 1994, Jabbes and Brunsfeld unpublished). *Ceanothus* (Rhamnaceae) is a North American endemic with 51 of its 55 species found in western North America and most of them limited to that region. This group of plants is homoploid ( $x = 12, 2x$ ) and divided into two large sections, each of which has considerable amounts of intrasectional gene exchange, but little intersectional gene exchange as determined by natural and artificial hybridizations and genomic analyses (Nobs 1963, Franklin et al. 1985). Taxonomic difficulties regarding the large genus *Salix* (Salicaceae) ( $x = 19, 2x-8x$ ) are being resolved using isozyme and DNA patterns (Brunsfeld et al. 1991, unpublished).

We conclude these brief examples of rangeland shrub biodiversity with reference to three studies that compare ecogenetic patterns among suites of shrubs in communities. Slauson and Ward (1986) reported that antelope bitterbrush (*Purshia tridentata*), true mountain mahogany (*Cercocarpus montanus*), mountain snowberry (*Symphoricarpos oreophilus*), and Utah serviceberry (*Amelanchier utahensis*) had different patterns of intraspecific genetic variability in experimental garden plots. Chamise (*Adenostoma fasciculatum*), wedgeleaf ceanothus (*Ceanothus cuneatus*), and whiteleaf manzanita (*Arctostaphylos viscida*) exhibit intraspecific and interspecific genetic variability across natural environmental gradients (Baker et al. 1982). Criddle et al. (1994) report that big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and antelope bitterbrush (*Purshia tridentata*) populations grown in uniform gardens maintain genetically based metabolic heat (temperature coefficient of metabolism) relationships based upon their collection sites.

#### FORBS

Forbs are important components of rangeland plant communities. They provide much of the ecological and botanical diversity on rangeland sites, increase seasonal forage quality and site nutrient capital (especially legumes), and generally enhance aesthetics and buffer wildfire effects (Shaw and Monsen 1983, Rumbaugh and Townsend 1985, McArthur et al. 1987, McArthur 1988). Legumes (Fabaceae) are probably the most important rangeland forbs (some legumes are shrubs and trees as well—see Table 2). Legumes are valuable forage plants that have been consciously used as forage plants by pastoralists for over 11,000 years (Mathison 1983), but legumes also include some poisonous plants, notably some species of the large genus *Astragalus* (Williams and Barneby 1977). Adaptive and nutritive quality variation has been documented for a number of rangeland legumes, both native (*Hedysarum* spp. [sweetvetch], *Lupinus* spp. [lupine]) and more intensively for introduced (*Astragalus* spp. [milkvetch], *Hedysarum* spp. [sweetvetch], *Medicago falcata* and *M. sativa* [alfalfa]) materials (Rumbaugh and Townsend 1985, McArthur 1988).

There are many rangeland forbs in the large Asteraceae family (USDA Forest Service 1937). Some examples of genetic diversity in this family on rangelands include that of Pacific aster (*Aster ascendens*), pussytoes (*Antennaria* spp.), gumweeds (*Grindelia* spp.), balsamorhiza (*Balsamorhiza* spp.) and mulesears (*Wyethia* spp.), and the golden asters (*Chrysopsis* spp., *Heterotheca* spp., *Pityopsis* spp.). Pacific aster is one of some 500 aster species, many of them North American. It is  $x = 13$  and occurs as  $2x$  and  $4x$  races. Genomic and morphological analyses demonstrate that Pacific aster is of hybrid origin from *A. falcatus* ( $x = 5$ ) and *A. occidentalis* ( $x = 8$ ), and that local populations include a rich array of genetic diversity (Allen 1985, 1986). The North American pussytoes ( $x = 14, 2x-10x$ ) includes 20 sexually reproducing dioecious species and five morphologically variable, polyploid agamic complexes that harbor abundant genetic diversity, as documented by isozyme, morphological, hybridization analyses, and genomic studies (Bayer and Stebbins 1987, Bayer 1988). Genomic and hybridization analyses demonstrate population differences and genetic diversity in several species of gumweeds ( $x = 6, 2x-4x$ ) (Dunford 1986). Populations of the related balsamorhizas (*Balsamorhiza* spp.) and mulesears (*Wyethia* spp. [ $x = 19, 2x-5x$ , some aneuploidy]) demonstrate within and between population differences in morphological and chromosomal characteristics (Helton et al. 1972, Robson et al. 1988). Morphological, anatomical, habit, habitat, and chromosome studies of the golden asters ( $x = 5, 9, 2x-4x$ , some aneuploidy) reveal genetic diversity at several taxonomic levels (Semple et al. 1980).

Other examples of rangeland forb genetic diversity include those of low larkspur (*Delphinium nelsonii*), flax (*Linum* spp.), Rocky Mountain beeplant (*Cleome serrulata*), Utah sweetvetch (*Hedysarum boreale*), and penstemon (*Penstemon* spp.). Populations of low larkspur have been shown to differ in isozyme patterns and fitness over a distance of 50 m (Waser and Price 1985, Waser 1987). Flax species, including the Eurasian (*L. perenne*) and North American (*L. lewisii*) perennial blue flax species ( $x = 9, 2x$ ), have been characterized by cpDNA patterns, morphology, hybridization, and breeding systems (Ockendon 1968, Coates and Cullis 1987, Pendleton et al. 1993). The physiological and morphological characteristics of Rocky Mountain beeplant affect fitness components over moisture gradients within populations (Farris 1987, 1988). Seedling establishment characteristics, nitrogen fixation capability, and nutritive value among populations of Utah sweetvetch revealed sufficient genetic diversity to assure adaptation to a wide array of sites in a garden and greenhouse study (Johnson et al. 1989). Populations of several species of *Penstemon* have distinctive seed germination syndromes that are correlated in various degrees with habitat (Kitchen and Meyer 1991, Meyer and Kitchen 1992). The scope of this report precludes presentation of other examples of rangeland forb genetic diversity. Genetic studies of rangeland forbs are, however, woefully incomplete.

#### GRASSES

Grasses include not only the staff-of-life grains, but also the most important and extensive forages for livestock and

wild ungulates in virtually all habitats (Heath and Kaiser 1985). The grass family, Poaceae, is enormous, with about 10,000 species worldwide. About 40 species receive significant use as sown pasture plants (Knight 1983). These plants are not important on rangelands, except for particular genotypes of orchard grass (*Dactylis glomerata*), smooth brome (*Bromus inermis*), and fescue (*Festuca* spp.) that are adapted to drier climatic regimes than are ordinary for their respective taxa (Knight 1983, McArthur 1988). Those species are not native to North America nor are many other grass species that are used in rangeland improvement projects (McArthur 1988). However, there are many excellent native grasses as well. The importance of grasses on North American rangelands is illustrated by the inclusion of 94 grasses among the total of 200 important range plants by Stubbendieck et al. (1986).

For case study illustrations, we have chosen to review some rangeland grasses of the tribe Triticeae, Indian rice grass (*Oryzopsis hymenoides*) of the tribe Stipeae, and orchard grass (*Dactylis glomerata*) and cheatgrass (*Bromus tectorum*) of the tribe Poeae.

The tribe Triticeae is large, 325 species, and includes many forage grasses, as well as the familiar cereal crops wheat, barley, and rye (Dewey 1984). Forty-eight species (three annuals, 45 perennials) are native to North America, including wheatgrasses (*Pascopyrum smithii*, *Pseudoroegneria* spp.), ryegrasses (*Elymus canadensis*, *Leymus cinerius*) and bottlebrush squirreltail (*Elymus elmoides*) (Dewey 1982, McArthur 1988). The base chromosome number for Triticeae is  $x = 7$ , with a polyploid range of  $2x-12x$  (Dewey 1984). Dewey and colleagues determined genomic formulas for many Triticeae taxa on a worldwide basis by chromosome pairing studies in synthetic hybrids, e.g., Dewey 1982, 1983, Asay et al. 1987, Wang 1988, Jensen and Bickford 1992, Jensen et al. 1992). These researchers have found that the genomes are sorted out in a wide array of combinations in various polyploid taxa with similar (identical?) genomic combinations sometimes being present in Eurasian and North American taxa. Genetic diversity within and among populations has allowed widespread natural and managed distribution and selection for a large array of plant materials for particular purposes in respect to growth rates, nutritive quality, site adaptation, insect resistance, etc. (Dewey 1980, Asay et al. 1983, 1985, McArthur 1988). Currently, efforts are under way to develop native bluebunch (*Pseudoroegneria spicata*) and Snake River (*Elymus wawawai*) wheatgrasses for seedling vigor and grazing tolerance from the abundant genetic diversity present in natural populations of these taxa (Jones et al. 1991, Kitchen and Monsen 1994). Additional noteworthy aspects of genetic diversity in ecotypic adaptation (phenological development and growth rate) for bottlebrush squirreltail (Clary 1975), and in isoenzymes in weedy rye (Sun and Corke 1992) have been documented. An entire issue of *Plant Systematics and Evolution* (vol. 160, no. 1-2, 1988) was devoted to molecular aspects of genetic diversity within the Triticeae, e.g., RNA, DNA, and isozymes (McIntyre 1988, McIntyre et al. 1988, West et al. 1988).



Indian ricegrass is  $2x$  ( $x = 24$ , with some aneuploidy). Populations are widely distributed in the North American West on both clay and sandy soils. Use of Indian ricegrass as a reclamation plant is limited because of problems of seed dormancy and shattering before harvest. Population variability in physiological and ecological traits and hybridization with other Stipeae are evidences of genetic diversity (Jones 1990).

Orchardgrass occurs in mixed ploidy ( $x = 7$ ,  $2x-4x$ ) populations on the Iberian Peninsula where  $2x$  and  $4x$  plants partition the habitat based on physiological, metabolic, and phenological differentiation (Lumaret et al. 1987, 1989). Results from cpDNA studies suggest that  $4x$  plants are autopolyploid.

Cheatgrass has expanded from its Eurasian and North African homeland to North America and become a serious westwide rangeland weed (Mack 1981). It is a cleistogamous annual ( $x = 7$ ,  $2x$ ) that through multiple introductions and a hundred annual cycles has differentiated into locally adaptive populations as measured by isozymes, plant biomass, and seed production, weight, and germination characteristics (Novak et al. 1991, 1993, Rice and Mack 1991a, Meyer unpublished). Populations are locally adapted, with some being more heterogeneous than others (Rice and Mack 1991a, 1991b, 1991c).

## TREES

Trees are generally not characteristic of rangelands, except for upland sites, e.g., quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*); pygmy forests, e.g., pinyon-juniper woodland (*Pinus* spp.-*Juniperus* spp.); and riparian corridors, e.g., willows (*Salix* spp.), cottonwoods (*Populus* spp.) (USDA Forest Service 1937, Stubbendieck et al. 1986). Some of these taxa may be considered as trees or shrubs depending upon local habitat and growth conditions, e.g., oaks and willows. Morphological, breeding-system, and macromolecular studies are revealing interesting patterns of genetic diversity within and between populations of these rangeland tree species, e.g., juniper (Ernst 1989, Van Haverbeke and King 1990, Tausch, unpublished data), pinyon (Lanner 1974, Bailey and Hawksworth 1988, Keim, unpublished data), cottonwoods (Keim et al. 1989, Paige et al. 1991), willows (Brunsfield et al. 1991, unpublished).

## GENETIC DIVERSITY-ENVIRONMENT INTERACTION

Many rangeland plants, as a group, are highly variable genetically and show various levels of hybrid introgression within and between taxa. Most rangelands represent the kinds of xeric and ecologically heterogeneous environments where genetic diversity generally increases (Nevo and Beiles 1989). These are also areas with a high susceptibility to the high level of climatic variation of the Quaternary (Tausch et al. 1993). The Quaternary, approximately the last 2 million years of the Pleistocene + Holocene, has had considerable and continuous climatic variation (Smiley et al. 1991) with up to

24 glacial events of 50,000 to 100,000 years in length (Van Donk 1976). The many genetically variable plant species present on rangelands and elsewhere (Kerr 1992) appear to be a product of adaptation to the past cycles of climatic variability (Tausch et al. 1993). Measuring that diversity can be a difficult task (Roberts 1992), but its incorporation into conservation policies can increase the options for decisions on the preservation of biological diversity (Brooks et al. 1992).

Vegetation response to climatic change can be described with three models of response: migration, orthoselective, and relic. Migration involves shifts in geographic position in response to climatic change. Orthoselective species are those that manage to remain in place over wide oscillation in climate. Relic species are found in areas where climatic change has been minimal. Many of the rangeland species described above best fit the orthoselective model of vegetation response to climate change (Nowak et al. 1994), indicating adaptation to changing, heterogeneous environments over long periods of time. Other species, particularly those from more mesic environments, generally fit the migration model (Bradshaw and McNeilly 1991). Relic taxa are rare on rangelands, e.g., the interpretations of Stutz et al. (1975) for gigas diploid *Atriplex canescens* and of Bowns and West (1976) for *Coleogyne ramosissima*.

Ogden (1989) has proposed the term *coenospecies* for persistent taxa that have varied in ecologic isolation and taxonomic distinction and more or less frequently hybridized in the past. Such genetic variability represents an adaptation to repeated cycles of changing climate in heterogeneous environments (Pease et al. 1989, Holt 1990). Such taxa are globally represented (Ogden 1989, Schoonmaker and Foster 1991). Most rangelands have sufficiently heterogeneous (patchy) environments and contain genetically variable species. The presence of interfertile species (coenospecies), such as the many found on rangelands that have been described above, increases the genetic diversity of those areas (Wayne and Bazzaz 1991). Their presence can substantially affect competitive dynamics and can potentially increase the rapidity with which a plant community can respond to environmental changes (Tausch et al. 1993). An understanding of the phylogenetic diversity within species or taxonomic groups can also substantially affect species conservation priorities (Faith 1992).

## DIVERSITY AND DEVELOPMENT

The science of genetics is a discipline structured to measure, quantify, and track variation. Its principles form the basis of manipulation of plant materials toward a desired end through controlled breeding, selection, and aspects of biotechnology. So, on the one hand, the discipline lies at the heart of understanding and quantifying biodiversity and, on the other, its principles can be used to limit biodiversity by serving to provide plant materials that are not natural and that replace natural plant materials. Both of these aspects of genetics are valuable and important, depending on perspective (Namkoong 1991, McArthur 1993).

We have shown through case studies and literature citations that rangeland genetic diversity is an important, albeit largely underdeveloped, field of study. Only by knowing what the resource is and by understanding its dynamics can we know what resources we have to manage and subsequently manage those resources for the desired objectives; recognizing that an objective may be nonmanagement or wilderness. Humankind with a unique cognizance and control of living things and environments has a responsibility, we think, to share the planet with our fellow-traveling sister species. Furthermore, humankind has an ethical responsibility to future generations to keep the sister species and their genetic diversity around both for the joy of life of future generations and for keeping their options open. Humankind has had an impact on biodiversity since prehistory (Ledig 1992). That influence has greatly increased of late.

Another responsibility of humankind, we think, is to take care of itself. That is done, in part, by understanding the plant genetic resources and making them more productive in feeding ourselves and domestic and wild animals, and in culturing, and managing, to various intensities, parts of our landscape. Naturally occurring, genetically selected, and even biotechnologically produced plant materials can be used for these purposes. Application of the principles of the science of genetics allows us to do these seemingly disparate things. The choice is ours, options are open, discussions and actions will continue. These can come to a better end result as the understanding of the genetic diversity foundation is solidified.

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