

MANAGING EXOTIC VERSUS NATIVE FLORA AND FAUNA

WHAT IS NATIVE?

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Abstract: Recent interest in the use of native species for rangeland restoration has emphasized how little we know about intraspecific variation in most range species. I discuss the different types of variation that occur within a species and, more importantly, why we should care that this variation exists. Although for most range species we have no information on the degree to which populations are locally adapted, it is often assumed that this type of "home team" advantage exists. I discuss the potential consequences of this assumption and how a plant's breeding system can affect the likelihood that adaptation occurs. I also examine the possibility that it often may be better to use a noninvasive exotic species in a restoration effort than inappropriate germplasm of a native species.

Key words: breeding system, gene flow, genetic drift, genetic pollution, intraspecific variation, local adaptation, phenotypic and genetic variation, selection.

There has been a recent surge of interest in the patterns, causes, and consequences of intraspecific variation for restoration projects in western rangelands. Although a fair amount of information is available on differences among species, much less information is available on variation within a species. Even for important range forage species, much of our information on intraspecific variation remains relatively anecdotal. As a result, current judgements as to what is native or what is "native enough" to use in the restoration of a particular site are often strongly influenced by preconceived notions rather than "hard" data.

PHENOTYPIC AND GENETIC VARIATION

In describing intraspecific variation, it is important to distinguish between phenotypic and genetic variation. Phenotypic variation is variation that can be quantified by physical measurements of the organism (phenotype). These measurements can range from parameters of plant phenology, such as flowering time, to allocation patterns, such as seed production or root:shoot ratios. Physiological traits such as photosynthetic rates or water-use efficiency are also phenotypic traits that often are of interest, although these data often are more difficult (and expensive) to obtain. As described in more detail below, the phenotype represents the interaction of a particular genotype and a particular environment. In a very real sense, the phenotype "emerges" from this interaction.

Although describing genetic variation as simply differences among genotypes or the frequency distribution of genotypes in a population is correct, it is not very informative or helpful to the resource manager. In general, the type of genetic variation that is of most interest to ecologists and restorationists is represented by variation in "quantitative" or "polygenic" traits. These quantitative traits often represent traits of ecological or adaptive significance such as growth rate, flowering time, etc. The phenotypic variation generated by genetic variation in polygenic traits represents the interactive and additive effects of many genes acting in concert. Phenotypic expression of polygenic variation usually takes the form of a fairly continuous frequency distribution of phenotypes. In contrast, variation in "major genes" often results in fairly discrete phenotypic classes. The classic example of this type of variation is Mendel's crossing experiments with garden peas. This type of variation is also quite common in flower color polymorphisms where there are discrete color classes (e.g., blue vs. white lupine flowers). For both polygenic and major gene traits it is often possible to ascribe adaptive significance to variation in genetic composition.

In contrast, "hidden" genetic variation, represented by variation in electrophoretic markers (e.g., allozymes) or DNA sequences, is usually considered "neutral" to selection. In other words, because variation in allozymes or DNA sequences usually have an undetectable effect on phenotypic expression, this type of variation is "invisible" to selection. The selective neutrality of this type of genetic variation makes it very useful for describing mating systems or evolutionary

processes such as genetic drift or gene flow. However, these types of genetic markers are usually (but not always) unhelpful in providing information on plant adaptation.

SELECTION AND LOCAL ADAPTATION

When considering issues of plant adaptation and evolution, an important concept that often is not appreciated is that the phenotype, and not the genotype, is the focus of natural (or artificial) selection. For example, in the development of a new crop variety, a plant breeder cannot select directly for a particular genotype. Rather, the breeder selects for a particular phenotypic value of a trait that she or he hopes represents a particular genotype and will "breed true" for that trait. The strength of this correspondence between trait phenotype and genotype is the heritability for that trait (Falconer 1989:163-166). The degree to which a trait is heritable is completely dependent on the interaction of genotypic variation and environmental variation. Certain traits that are highly heritable under one set of environmental conditions may exhibit low or zero heritability in another environment. This results from differences in the way the genotype and environment interact to "build" the phenotype (Lewontin 1974).

Whether they know it or not, managers interested in using germplasm that is locally adapted are interested in a particular type of genotype-by-environment interaction. In its local adaptation, the phenotypic trait of interest is some measure of plant "fitness" such as survival, growth, or reproduction. The particular genotype-by-environment interaction of interest is the situation where the local germplasm performs best (i.e., a "home team advantage"). Because it emerges from this interaction, local adaptation is a potentially changeable (even volatile) property. Local adaptation can disappear with changes in the environment, or in the genetic composition of a population, or both.

BREEDING SYSTEM, ADAPTATION, AND GENETIC DRIFT

The probability that selection can create a locally adapted population depends largely on the breeding system of the plant species in question. All else being equal, the probability for the development of locally adapted ecotypes is higher for inbreeding plants. Inbreeding decreases gene flow within and among populations. This reduction in gene flow lowers the probability that locally evolving "gene complexes" will be swamped by genes from nonadapted plants outside the local selective regime. Theoretical and empirical studies have found that even low rates of gene flow can effectively prevent selection from creating locally adapted populations. Management decisions as to allowable seed collection areas need to use the best available estimates of the degree of outcrossing in the species (or population) under management. For example, in outcrossing conifers, seed collection zones are fairly large (i.e., regional) whereas in a highly selfing

grass the proper collection area may be within a single hectare. This would be especially true if the grass population exists in some sort of specialized habitat (e.g., serpentine soils).

Although inbreeding can promote local adaptation, it also can facilitate population differentiation that results, not from selection, but from random processes (i.e., genetic drift). The clearest case of this type of nonadaptive differentiation occurs during genetic "bottlenecks" that may accompany the colonization of a new site. In this scenario, a particular genotype disperses into and colonizes, by chance, an open habitat. Because the colonist can self-pollinate and reproduce, a local patch of closely related (full sibs) plants develops that may be quite different genetically from the main population. An external observer, lacking knowledge about the past history of chance colonization, may erroneously conclude that this patch of plants is adapted to some local selective regime. The main point here is that very distinct genetic differences within and between populations do not always indicate the operation of selection (especially with inbreeders).

UNCONSCIOUS SELECTION DURING SEED COLLECTION AND INCREASE

Although more detailed information and guidelines on seed collection protocols can be found in Knapp and Rice (1994), the primary goal of field collections from a population should be to sample the whole population. Although this may sound simple, achieving this goal can be very difficult. Often collections are made only once from a population and thus may miss genotypes setting seed either before or after the collection date. For ease of collection, often only a small area of the population is intensively sampled. There is also a tendency to collect from larger, more obvious plants and to collect from easily accessible areas (e.g., flat terrain). Taken together, these sampling biases may significantly shift the genetic composition of the collection population relative to the field population. Shifts in both the mean and the variance (i.e., diversity) in the genotypic distribution of the population often can result. These genetic shifts are exacerbated by similar instances of unconscious selection that may occur within the agronomic environment of seed increase operations. Because of the economic pressure to mechanize and increase harvest efficiency, there is often the possibility for selective harvesting of only a subset of the planted population. Harvesting on a single day and at a single height, although more agronomically efficient, may result in a seed collection with low variation in both flowering time and plant stature. In other words, late-flowering, short-stature genotypes may not be harvested even though the genetic resources that they represent may be crucial to the long-term survival of the population when planted back into the "wild". The economics of seed production, where maximization of seed production per unit area is often the primary goal, may also result in major genetic shifts in the population. Under

benign agronomic conditions (e.g., plenty of water and nutrients), genotypes that grow rapidly when resources are abundant may produce a disproportionately large number of seeds. The resulting seed mixture will then be dominated by these "agronomic" genotypes that may perform poorly when planted back into the "wild" where resources may be in short supply. In this case, unconscious selection has acted to reduce the frequency of stress-tolerant genotypes that may be important for population persistence during "lean" years.

GENETIC CONTAMINATION OR "GENETIC POLLUTION"

As might be expected, the term genetic pollution often elicits a strong negative response, even when the precise meaning of the term is unclear. Genetic pollution can be thought of as a maladaptive shift in the genetic composition of a population. This shift is brought about by misguided management activities where inappropriate (in an adaptive sense) genotypes are introduced in sufficient numbers to "swamp" the resident population. The resident population is thought to represent a kind of genetic memory of past selective events; events that may occur very infrequently. In the scenario usually presented, the introduced genotypes grow rapidly for a few generations under relatively benign conditions and effectively reduce or eliminate the resident genotypes by competition or hybridization. An infrequent but severe selective event characteristic of the site then occurs (e.g., 17-year locusts or 50-year droughts) that completely eliminates the nonadapted introduced genotypes. As a result, both the resident and the introduced population are now gone. Although direct evidence for this type of genetic pollution scenario is scarce, data from provenance testing in conifers are suggestive. Millar and Libby (1989) cite an example from common garden studies of Douglas-fir (*Pseudotsuga menziesii*) where fast-growing coastal ecotypes were killed during infrequent bouts of low temperatures. The potential detrimental effects of genetic pollution when coupled with the irreversible nature of the process (it's very difficult to "weed out" genes) might argue for the use of noninvasive exotic species at a particular site until more in-

formation on the resident population is available. In any case, the fact that we cannot, at this point, cite many direct studies of genetic pollution does not mean that the phenomenon is unimportant. As this summary may indicate, many of the genetic questions relevant to restoration projects are not going to have easy answers. In fact, many of the most important questions revolve around genetic processes that are the most difficult to measure or study, such as gene flow rates or the importance of genetic pollution in long-term adaptation. Although precise measurements of such phenomena may not be forthcoming in the near future (if ever), we can use more easily obtained indices of genetic structure and process to make informed management decisions. For example, as noted above, even rough estimates of the breeding system of a plant can be of enormous help in deciding probable spatial scales of adaptation. In sum, deciding "what is native" will require (1) an appreciation for the importance of intraspecific variation, (2) the proper use of the best available (although imperfect) estimates of genetic parameters, (3) an understanding of the many trade-offs between genetic diversity and local adaptation, and (4) a willingness to use imprecise indices to make decisions that may have long-term and irreversible consequences. In other words, "business as usual" for a natural resource manager.

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