Keynote

Common Ground and Controversy in Native Plant Restoration: the SOMS Debate, Source Distance, Plant Selections, and a Restoration-Oriented Definition of Native

Thomas N. Kaye

541-753-3099
kayet@peak.org
Institute for Applied Ecology
4550 SW Nash
Corvallis, Oregon 97333 USA

Abstract

Propagation and planting of native plants for habitat restoration is a multi-faceted process. There are many issues over which there is general agreement among restorationists, but there are a number of subjects that cause disagreement. For example, restorationists often agree that native plants should be emphasized, but disagree over where seeds or transplants should come from. In this paper, I examine four areas of controversy: the use single or multiple sources of a species at a given restoration site (the SOMS debate), source distance of plant materials, the use of native plant selections, and the importance of one's definition of "native plant." I conclude that some of these issues may be resolved through careful research, while others will remain a matter of personal opinion, and can only be resolved through a clear statement and scope of objectives of each restoration project.

Introduction

Native plant propagation, restoration, and conservation are complex activities that require many steps and decisions, and face many challenges. On one hand, there is broad agreement, at least among restorationists, over the importance of native plants and the benefits of habitat restoration. But on the other, there is widespread uncertainty and dissent about how to achieve these restoration goals. What should be planted and where? How should plant-materials for restoration be obtained? Where should they come from? What is the overall goal? The objective of this paper is to identify areas of agreement and disagreement to help frame debates in

Proceedings of the Conference: Native Plant Propagation and Restoration Strategies. Haase, D.L. and R. Rose, editors. Nursery Technology Cooperative and Western Forestry and Conservation Association. December 12-13, 2001. Eugene, OR.

native plant restoration, and thus improve our ability to discuss and conduct this work from a position of mutual understanding and productive dialog.

Areas of Agreement

There is little dispute that native plants are an appropriate choice for habitat restoration projects. Native vegetation provides habitat for the native plants themselves and a vast diversity of other organisms, from wildlife to below-ground soil bacteria, and from common to endangered species. Native plants perform valuable ecosystem functions, such as soil erosion control, nutrient capture, and shade in riparian areas, all of which improve water quality. Healthy plant communities also provide storm water retention and browse for large wildlife. Spring wildflowers in forests retain nutrients released into the soil by tree leaf decay, thus holding these nutrients on-site, making the forest more productive (Risser 1998). Native plants often have unique associations with native insects, providing insect adults with food from nectar and pollen, as well as to larvae from their leaves and other tissues.

There are also several aspects of the restoration process on which most conservationists agree. For example, it is important to set clear, achievable restoration goals. Also, restorationists will be most effective if we document and share all steps of the restoration process and follow-up with monitoring so that we can learn from our successes and failures. We tend to agree that noxious weeds are an impediment to establishing native plants and conserving endangered species. Many of us also recognize that a restoration project is not over once the initial work is completed — restored habitat may need to be monitored and maintained indefinitely by appropriate management. Finally, the economics of using natives are incentives that many restorationists advocate: native species may require fewer resources to maintain (e.g., less water, fertilizer, and mowing) than non-natives, and the commercial propagation of native plants offers a new market for seed growers and nurseries.

But there are important disagreements in the field of native plant restoration. Many of these can be resolved through experimentation and communication. However, some are based on a difference of perspective or goals, and it will be important for the development of our field to articulate these issues and distinguish between technical and the philosophical concerns.

Controversies

Among the many controversial topics faced by restorationists are issues such as target habitat-type (what plant community should be established?); invasive weed control (what techniques should we use: herbicides, biocontrol agents, soil-scraping, fire, solarization, mowing?); planting material type and technique (direct seeding vs. out-planting of greenhouse starts); the importance of mycorrhizae, *Rhizobium*, and soil food webs; target population size (how big must a restored population be to minimize potentially hazardous stochastic processes?); endangered species (avoiding "take," habitat conservation vs. reintroduction); and cultivation of plant materials (how can different sources be grown at the same nursery and still be considered separate?).

Below I address a few controversies surrounding sources of native plant materials for restoration, such as should single or multiple sources of a given species be planted at a given restoration site? How far should plant materials be moved? Are native plant selections appropriate? And finally, what is a native species?

Single or multiple source: the SOMS debate

A contentious issue in conservation biology today is whether or not seed sources should be mixed at a restoration site. The SOMS debate, for Single Or Multiple Source, is an argument between those who advocate using plant materials from a single source population and those who favor (or tolerate) mixing materials from more than one source population.

This controversy is as important today as the 1970's controversy over whether to have single large or several small nature reserves (the so called SLOSS debate, see Diamond 1975, Terborgh 1976, and Simberloff and Abele 1976). Genetic principles behind both sides of the SOMS debate are the concepts of inbreeding and outbreeding depression (see Box 1 for a review of these subjects).

Keeping every seed source strictly separate and never allowing mixing or gene flow mimics habitat fragmentation and population isolation, factors that lead to genetic problems including inbreeding depression, drift, reduced diversity, and reduced effective population size. Put another way, it may be possible to be too strict about keeping gene pools separate. On the other hand, mixing sources of plant materials may involve the combination of plants from widely different geographic regions and habitats, and could lead to outbreeding depression (Box 1) and the loss of unique genetic qualities of individual populations. An advantage of using multiple sources is an increased likelihood that at least some of the plant materials will be successful at a given site, and mixing may be recommended when seed sources are derived from small, fragmented population.

Source distance

A related controversy is over the distance plant materials may be moved from source to restoration site. One side of this debate contends that plant materials should be brought only from the closest, most ecologically and/or genetically similar site, while the other argues for the free movement of plant materials from distant sources, as long as the species is native.

Allowing seeds to be moved from distant locations may make more plant materials available at a lower cost than local materials. Acquiring seeds may be much easier, and restoration may therefore be possible at more sites and larger scales.

Keeping sources local may make costs higher, but it improves the chance that the plants will be locally adapted with a "home-site advantage" (Montalvo and Ellstrand 2000b; see Box 2 for a discussion of local adaptation), and therefore may increase restoration success. In addition, local sources reduce the risk of outbreeding depression from crosses between the restored population and neighboring wild populations. Such crosses can also result in hybridization and/or introgression between ecotypes, subspecies, or species, with subsequent risks of local population decline or extinction (Rhymer and Simberloff 1996, Allendorf et al. 2001), and direct threats to endangered species (Levin et al. 1996).

Plant selections

Selections of native plants are often used for large-scale restoration projects. Plant selections are usually made from a large group of wild collections that are screened for desirable size, survival, and fecundity, then released to growers for commercial production.

For example, researchers at the Agricultural Research Service recently developed hardy natives for rangeland restoration (Dedrick 2000). Their selection and release procedure illustrates the process well. For example, they grew collections of squirreltail (*Elymus elymoides*) from seven western states in common gardens for three years to compare plant growth and seed production (Wood 2000). They selected one strain of this perennial grass for its consistent high-yield of seeds and large size, and released it to growers under the name "Sand Hollow" squirreltail.

This selection has several beneficial qualities. Its superior ability to produce large amounts of seed makes it a good choice for growers, who can generate large amounts of economical seed for restoration projects. Sand Hollow's ability to grow well in many arid environments, tolerate fire, and successfully compete with western weeds, such as cheatgrass (*Bromus tectorum*), make it a good choice in areas where wildfires have damaged sagebrush communities and favored invasive plants, and it may improve habitat for small rodents on which large birds of prey depend (Wood 2000). Since cost savings and high rates of establishment and growth are important to the success of any restoration, vigorous selections are an attractive choice of plant materials.

The arguments against this approach are numerous, however. Since the use of selections often represents a long-distance translocation, selections may not always do well in a given restoration site, especially if that site differs from the selection's original habitat (another example the home-site advantage hypothesis). Further, they may interbreed with local populations of the same species, with the potential for outbreeding depression in their progeny both on the restoration site and in adjacent wild populations.

Selections may also have lower genetic variability than most wild-collected material, potentially making them less able to adapt to a changing environment. And finally, native plant selections may be only a step behind horticultural varieties in their human-induced divergence from wild strains, in some cases making them "quasi-native species," at best. Put another way, they are the product of human selection rather than natural selection, which raises the question, can they still be considered native?

What is native?

These controversies each have aspects that may be resolved through study of a given species (as in Boxes 1 and 2), but they also point to the importance of one's philosophical perspective, not the least of which is one's definition of native. A broad definition of native is "indigenous, originating in a certain place." But the goals of restorationists may need a more specific definition when deciding which species will be appropriate for planting in any given area. Wilson et al. (1991) suggested that an ecological definition of native should include consideration for a species' presence in an area prior to Euro-American settlement, its geographical patterns of genetic variation, and its preferred habitat. For example, a population of a native species might be considered non-native for restoration purposes if it represented a genotype not found in that area and/or occurred in a different habitat from the restoration site (i.e., one would not plant a wetland species on an upland site, even if the species was native to the region).

A restoration-oriented definition of native could take this form:

> *A species occurring in an area since pre-settlement times that is adapted to the local ecosystem and is sufficiently like adjacent conspecific populations that, if crossed with them, would produce healthy progeny similar to them in genetic composition.*

The phrase "genetic composition" is intended to mean that the progeny resemble the local parental allelic content and diversity.

Although a narrow definition of native goes to the core of the debates outlined above, it is also not universally accepted. Even so, the identification of genetic and ecological boundaries within a given species, subspecies, or variety has been widely discussed, and even implemented by government agencies. In forestry, "seed collection zones" that recognize these issues have been used to guide tree-seed transfer policies in the U.S. since 1939 (McCall 1939), and there is substantial interest in expanding such policies to all plants (Montalvo and Ellstrand 2000).

Alternative approaches to identifying suitable plant materials include keeping seeds within an ecoregion or subecoregion (e.g., Omernik 1996, McMahon et al. 2001), watershed, county, or some set distance from a restoration site. Such a simplistic approach could be efficient, but will ignore the fact that each species is different and may need a unique zone. Genetic units of conservation, such as Evolutionarily Significant Units (proposed by Ryder [1986]), could be developed for individual plants, but the current cost of this type of analysis will limit its application to a few high-priority species.

Conclusion: the Importance of Project Objectives

In the mean time, one's position on debates such as those discussed here will depend on the results of careful research projects, opinion, and (hopefully), a large dose of common sense. The goals and funding of an individual project will also influence decisions about issues such as whether or not to use a native plant selection, and how far to transport plant materials. For example, if funding is extremely limited and the goal of restoration is simply to hold soil in place, a manager may choose to ignore source location or genotype when obtaining plant materials, or even use a non-native plant on a restoration site. But if the intention is to successfully recreate a historic landscape, with functioning plant communities and populations that closely resemble wild ones and continue to evolve as they would, a narrow definition of native, careful interpretation of recent research, and practical attention to the ecology and genetics of source materials will be required.

Box 1. Inbreeding and outbreeding depression

Inbreeding depression

Inbreeding depression can occur when close relatives mate (or plants self-fertilize) and their offspring display reduced vigor or fitness. Inbreeding depression is a well-known and studied phenomenon, and often occurs in small, fragmented, or isolated populations, or when mating is frequent between close neighbors (Figure 1). It results when deleterious recessive alleles are paired (creating homozygotes) so that their negative effects are expressed in the progeny. When these genes are not paired (as after outcrossing), they may be masked by a more favorable allele (as a heterozygote), so the progeny function normally. In plants, inbreeding depression can be expressed at any stage in the life cycle, including seed germination, seedling establishment, plant growth rate and survival, flowering, and seed production.

Populations suffering from inbreeding depression can often benefit from outcrossing with individuals in other populations, which may result in higher heterozygosity, improved health of individuals, and greater population viability. This is one factor used to support the use of multiple sources of plant materials in restoration (one side of the SOMS debate).

One recent example of inbreeding depression (Richards 2000) in a weedy perennial plant, white campion (*Silene alba*), showed that isolated populations had high inbreeding depression (in the form of low seed germination success), crosses between related individuals resulted in reduced germination success, and gene-flow was higher between unrelated individuals. This study is important because it demonstrates the potential for a "rescue-effect" for populations experiencing inbreeding depression by intentionally mixing unrelated individuals into such a population.

Outbreeding depression

Outbreeding depression, which is a reduction in fitness of progeny from distant parents (Figure 1), has a much shorter history of study and is less documented and understood than inbreeding depression. In a recent (27 November 2001) search of a scientific literature database (Agricola) spanning 1986 through the present, I found 468 papers on inbreeding depression but only 25 references to outbreeding depression. Even so, this hot topic in genetic and conservation research has been demonstrated in various organisms, including salmon (Gharrett 1999), fruit flies (Aspi 2000), and chimpanzees (Morin et al. 1992). Some animal studies have found a positive effect of outbreeding, however, such as in bats (Rossiter et al. 2001). Among plants it may occur in larkspur (Waser and Price 1991, 1994), skyrocket (Waser et al. 2000), a carnivorous pitcher plant (Sheridan and Karowe 2000), Hawaiian silversword (Friar et al. 2001), a Mediterranean borage (Quilichini et al. 2001), a subshrub (Montalvo and Ellstrand 2001), and an exotic roadside weed (Keller et al. 2000).

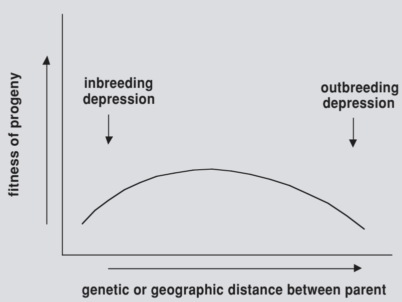

Figure 1. Inbreeding and outbreeding depression are a function of the distance between parents. Mating between close relatives (or near neighbors) may result in inbreeding depression, while the progeny of genetically distant parents (or organisms from different populations) may cause outbreeding depression.

In many cases, crossing between unrelated individuals results in progeny with *increased* fitness, followed by the expression of outbreeding depression in later generations. Most researchers (e.g., Lynch 1991, Waser 1993) believe that there is hybrid vigor in the first generation followed by reduced fitness in later generations from loss of ecological adaptation (at least one of the original parents was poorly adapted to the site) and/or disruption of coadapted gene complexes.

One interesting study of outbreeding depression in plants comes from a paper on partridge pea (*Chamaecrista fasciculata*, an annual legume) by Fenster and Galloway (2000). The authors collected plants from various populations ranging from 100 m to 1000 km apart, performed controlled crosses, and grew the parents and progeny in common gardens. They found that first-generation hybrids between plants from different populations outperformed their parents, regardless of the geographic distance between sources. By the third generation, however, this increase in fitness declined. The level of decline varied with distance between parent populations, with crosses between plants from <1000 km apart yielding third-generation plants at least as vigorous as their original parents. Thus, crosses of up to 1000 km had a short-term beneficial effect, and little long-term risk (at least through the third generation).

There have been too few studies of outbreeding depression to make generalizations about the level of risk, however. Other studies have documented negative effects of outbreeding across short distances (tens of meters to 100 m) (Price and Waser 1979, Waser and Price 1989, 1991, 1994) or between different habitats (Montalvo and Ellstrand 2001), while others have found great variability in the effects of outbreeding, even in the same species (e.g., Waser et al. 2000).

The threat of outbreeding depression is one argument against mixing seed sources during plant restoration (another side of the SOMS debate). It is also one of the dangers of moving plants a great distance to a restoration area where they could interbreed with a local population.

Box 2. The home-site advantage hypothesis

Plants used in restoration are often widespread species, with considerable variation over their geographic range. In many cases, they show ecotypic variation, in which populations differ genetically and individuals from a given environment or region grow better in their home zone than in another region. This has been recognized for tree growth and forest production for many years, even centuries (Langlet 1971), but has not been demonstrated well for shrubs and herbaceous plants. The notion that local plant materials can improve restoration success has been termed the home-site or home-team advantage hypothesis (Figure 2) (e.g., Montalvo and Ellstrand 2000a).

A recent study by Montalvo and Ellstrand (2000b) examined this issue in depth for a native subshrub, California broom (*Lotus scoparius*), in southern California. The authors collected seeds from 11 populations of two taxonomic varieties from three distinct plant associations. They analyzed plants from each population genetically and grew them all together at two of the original collection locations, measuring overall plant fitness (survival x growth) after one year.

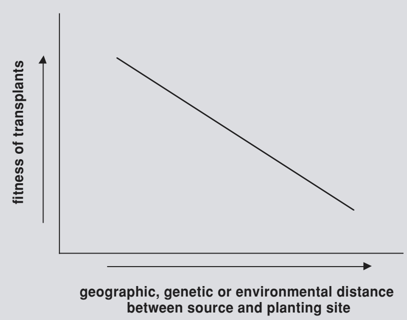

*Figure 2. The home-site advantage hypothesis predicts that individuals from a local site will have higher fitness in their home area than individuals from more distant sources. Montalvo and Ellstrand (2000b) found evidence to support this hypothesis in their study of California broom (*Lotus scoparius*), in which plant performance decreased as the source and home-site diverged environmentally and genetically. Geographic distance of the source was a poor predictor of how well plants performed at the test sites.*

The results indicated strong support for the home-site advantage hypothesis. Geographic distance of the seed source from the out-planting site was a poor predictor of plant performance, but both genetic distance and environmental similarity of the source to the planting site were strongly correlated with plant success. The authors concluded that genetic and environmental similarities of source populations should be considered when source materials are selected for restoration projects.

This study was badly needed and very informative in the debate over how far plant materials should be moved for restoration, but further research is required in this area. In stark contrast to these results is the success of exotic species that can occupy and invade new habitat far from their region of origin, and outcompete the local native species. In addition, some plant selections do well in many habitats over a wide region.

Acknowledgments

I am grateful to Jen Cramer for help with literature searches. Dick Brainerd, Keli Kuykendall, Bruce Newhouse, Barb Wilson, and Peter Zika engaged in helpful discussions.

Literature Cited

Allendorf, F.W., R.F. Leary, P. Spruell, and J.K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 16:613-622.

Aspi, J. 2000. Inbreeding and outbreeding depression in male courtship song characters in *Drosophila montana*. Heredity 84:273-282.

Dedrick, A.R. 2000. Enhancing plants of western rangelands. Agricultural Research 48:2.

Diamond, J.M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7:129-146.

Fenster, C.B. and L.F. Galloway. 2000. Inbreeding and outbreeding depression in natural populations of *Chamaecrista fasciculata* (Fabaceae). Conservation Biology 14:1406-1412.

Friar, E.A., D.L. Boose, T. Ladoux, E.H. Roalson, and R.H. Robichaux. 2001. Population structure in the endangered Mauna Loa silversword, *Argyroxiphium kauensis* (Asteraceae), and its bearing on reintroduction. Molecular Ecology 10:1153-1164.

Gharrett, A.J. 1999. Outbreeding depression between odd-and even-broodyear pink salmon. Aquaculture 173:117-129.

Keller, M., J. Kollmann and P.J. Edwards. 2000. Genetic introgression from distant provenance reduces fitness in local weed populations. Journal of Applied Ecology 37(4): 647-659.

Langlet, O. 1971. Two hundred years of genecology. Taxon 20:653-721.

Levin, D.A., J. Francisco-Ortega, R.K. Jansen. 1996. Hybridization and the extinction of rare plant species. Conservation Biology 10:10-16.

Lynch, M. 1991. The genetic interpretation of inbreeding and outbreeding depression. Evolution 45:622-629.

McCall, M.A. 1939. Forest tree seed policy of the U.S. Department of Agriculture. Journal of Forestry 37:820-821.

McMahon, G., S.M. Gregonis, S.W. Waltman, J.M. Omernik, T.D. Thorston, J.A. Freeouf, A.H. rorick, and J.E. Keys. 2001. Environmental Management 28:293-316.

Meffe, G.K. 1996. Genetic and ecological guidelines for species reintroduction programs. Journal of Great Lakes Research 21:3-9.

Montalvo, A.M. and N.C. Ellstrand. 2000a. Fitness consequences of non-local transplantation: preliminary tests of the home team advantage and outbreeding depression hypotheses. In J.E. Keeley, M.B. Keeley, and C.J Fotheringham (eds.). Proceedings of the 2nd interface between ecology and land development in California. U.S. Geological Survey, Technical Report, Washington D.C.

———. 2000b. Transplantation of the subshrub *Lotus scoparius*: testing the home-site advantage hypothesis. Conservation Biology 14:1034-1035.

———. 2001. Nonlocal transplantation and outbreeding depression in the subshrub Lotus scoparius (Fabaceae). American Journal of Botany 88:258-269.

Omernik, J. 1996. Level III and IV Ecoregions of Oregon and Washington. National Health and Environmental Effects Research Laboratory, U.S. Environmental Protection Agency, Corvallis, Oregon. (1 page map).

Quilichini, A., M. Debussche, and J.D. Thompson. 2001. Evidence for local outbreeding depression in the Mediterranean island endemic, *Anchusa crispa* Viv. (Boraginaceae). Heredity 87:190-197.

Risser, P. 1998. Native plants: what have you done for us lately? Pp. 5-6 in R. Rose and D. Haase (eds.). Native Plants Propagating and Planting. Nursery Technology Cooperative, Department of Forest Science, Oregon State University, Corvallis, Oregon.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27: 83-109.

Rossiter, S.J., G. Jones, R.D. Ransome, and E.M. Barratt. 2001. Outbreeding increases survival in wild greater horseshoe bats (*Rhinolophus ferrumequinum*). Proceedings of the Royal Society of London Biological Society 22:1055-1061.

Ryder, O.A. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution 1:9-10.

Sheridan, P.M. and D.N. Karowe. 2000. Inbreeding, outbreeding, and heterosis in the yellow pitcher plant, *Sarracenia flava* (Sarraceniaceae), in Virginia. American Journal of Botany 87:1628-1633.

Simberloff, D.S., and L.G. Abele. 1976. Island biogeographic theory and conservation practice. Science 191:285-286.

Terborgh, J. 1976. Island biogeography and conservation: strategy and limitations. Science 193:1029-1030.

Waples, R.S. 1991. Pacific Salmon, *Oncorhynchus* ssp., and the definition of "species" under the Endangered Species Act. Marine Fisheries Review 53:11-22.

Waser, N.M. 1993. Population structure, optimal outbreeding, and assortative mating in angiosperms. Pages 173-199 in N.W. Thornhill, ed., The Natural History of Inbreeding and Outbreeding: Theoretical and Empirical Perspectives. University of Chicago Press, Chicago.

Waser, N.M. and M. Price. 1989. Optimal outcrossing in *Ipomopsis* *aggregata*: seed set and offspring fitness. Evolution 43:1097-1109.

——. 1991. Outcrossing distance effects in *Delphinium nelsonii*: pollen loads, pollen tubes, and seed set. Ecology 72:171-179.

——. 1994. Crossing distance effects in *Delphinium nelsonii*: outbreeding and inbreeding depression in progeny fitness. Evolution 48:842-852.

Waser, N.M., M. Price, and R.G. Shaw. 2000. Outbreeding depression varies among cohorts of *Ipomopsis aggregata* planted in nature. Evolution 54:485-491.

Wilson, M.V., D.E. Hibbs, and E.R. Alverson. 1991. Native plants, native ecosystems, and native landscapes: An ecological definition of "native" will promote effective conservation and restoration. Kalmiopsis 1:13-17.

Wood, M. 2000. Hardy natives at home on the US range. Agricultural Research 48:4-7.