DRAFT – DRAFT - DRAFT
DO NOT CITE OR DISSEMINATE WITHOUT AUTHORS' PERMISSION

Decision-making protocols for propagation and introduction of native planting stock

Bart Johnson and Bitty Roy
for the
Friends of Buford Park - Mt. Pisgah Stewardship Technical Advisory Committee

We gratefully acknowledge the contributions of the Plant Introduction Subcommittee of the Friends of Buford Park - Mt. Pisgah Stewardship and Technical Advisory Committee (STAC), including Jason Blazar, Aryana Ferguson, Bruce Newhouse and Trevor Taylor, as well as the comments and insights of all concerned parties who participated in our discussions

Introduction

In recent decades, the introduction of native plant species in ecological restoration projects has become an increasingly important and also controversial practice. Concerns range from the effectiveness of monitoring and evaluating project success to whether genetically appropriate stock was used. The latter issue relates both to long-term project success as well as to intentional or unintentional modifications to the genetic composition of local plant populations.

In the Pacific Northwest, there are emerging regional efforts to collaborate in the procurement and propagation of native seed supplies and plant stock. We of the Friends of Buford Park Stewardship Technical Advisory Committee (FBP STAC) feel it is necessary to develop protocols regarding FBP participation in such efforts. These protocols should address a number of key issues including, but not limited to: a) developing seed lots from Howard Buford Recreation Area (HBRA) populations to be used within, or shared outside the park, b) determining which seed or plant lots are acceptable to be introduced into the HBRA from populations located elsewhere in the Willamette Valley, and c) governing nursery practices for propagating seed lots for "bulk out" purposes under contract with others from seed lots located outside the park or for collecting and propagating seeds collected within HBRA

The criteria for determining what native planting stock is appropriate to use or decline for different projects, locations and ecological contexts revolve around a complex set of issues. It is a "wicked" problem in that it is unlikely that we will ever have sufficient knowledge to make decisions with the levels of confidence we desire. Rather, we must weigh a variety of uncertainties and risks of using a plant stock against the potential benefits. In particular, it can be challenging to weigh the potential effects of plant introduction on the genetic structure and diversity of extant populations (risks and potential benefits) against the costs of developing site-specific seed sources, and in some cases the values of using or not using native plants for revegetation and restoration, especially if the alternative is no action.

One major genetic concern is local adaptation. Plants adapt to their physical and biotic environments. If plants are locally adapted, then bringing in genetic material from off-site may decrease the 'fit' of an existing plant population to its environment, for example, through the breakdown of co-adapted gene complexes. There are literally thousands of studies that show that plants are often adapted to their abiotic and (Linhart and Grant. 1996) and biotic environments (Sork et. al. 1993).

Other genetic issues include concerns about both inbreeding depression and outbreeding depression. Inbreeding results when relatives mate or when organisms self-fertilize. Inbreeding leads to an increase in homozygosity because individuals that have similar (or the same) sets of alleles are mating with one another. Inbreeding is mostly a problem only for plants which normally outcross and which thus are more likely to suffer from inbreeding depression. Inbreeding depression is defined as a reduction in fitness as a result of inbreeding. Inbreeding depression results because many mutations cause a loss of biological function. If loss of function occurs in a recessive allele, an organism's fitness may not be affected if it is a heterozygote at that locus because enough protein can still be made. However, inbreeding can increase the number of such recessive deleterious alleles that will occur in a homozygous state, and thus expose them to selection, leading to mortality or loss of reproduction (Futuyma 1998). In small populations of a principially outcrossing species, inbreeding is likely because most individuals will be related to some degree. Inbreeding depression is particularly likely when formerly large populations of species with an outcrossing mating system become reduced in size and isolated from potential sources of immigrants (citation***). Inbreeding is less of a problem for primarily selfing species (estimated at about 30% of all plant species; Richards 1997) because they have purged their genome of deleterious alleles over time.

Inbreeding can also contribute to an increase in the probability of genetic drift. In theory, when populations of outcrossing species become sufficiently small, random changes in genetic diversity (that is, genetic drift) can become a key factor leading to the kind of loss of diversity described above. Genetic drift is defined as a change in gene frequencies due to the random selection of alleles during mating. It is expected to be a factor only when populations are small. Genetic drift is a form "evolution", because evolution only implies a change in gene frequencies. It is not adaptive, however, because it leads to a random reduction in genetic diversity, rather than the honing of a species to its environment through natural selection. Genetic theory suggests that the periodic immigration of a few individuals can be enough to counterbalance genetic drift (Hartl 1997). Populations with inbreeding depression may benefit from the introduction of individuals from off-site stock that can enhance genetic diversity. On the other hand, such introductions can potentially lead to outbreeding depression, defined as a depression in fitness resulting from the crossing of unrelated individuals, usually from different populations (Waser and Price 1989, Waser 1993). Outbreeding depression can result from the introduction of non-adaptive genes to a population, and can also occur if coadapted gene complexes are broken down through the introduction of plants that do not contain these coadapted complexes (Templeton 1986).

The goal of counteracting reductions in genetic diversity due to decreased population size, habitat loss or degradation, or reduction of gene flow from historic levels is another rationale for using a non-local seed source or multiple sources. Like inbreeding, however, low genetic diversity per se is not necessarily a problem (citation). Rapid reductions in genetic diversity can, however, be an issue, especially for outcrossing species as noted above. Furthermore, low genetic diversity may restrict a species' or population's ability to react to changes in their environment, including altered soil conditions, hydrology and disturbance regimes, or climate change (citation). The key point is that simply because a population seems likely to have, or even demonstrably does have low genetic diversity, it is not necessarily a problem. We would argue that there should be evidence for such a problem before assuming there is one. Should an introduction intended to supplement genetic diversity merely change local gene frequencies, it might not be a major concern: if selective pressures really are acting on the genetic diversity of a population, one would expect gene frequencies to adjust accordingly over time. However, the potential swamping of a local population with novel, non-adaptive genes, or effects of outbreeding depression should be given equal consideration.

The joint evaluation of these issues and more requires a framework for evaluating the risks and benefits of different possible outcomes in the context of the species in question and the ecological context in which the restoration would occur. These factors can lead to very different conclusions about the suitability of a particular propagule source for a specific restoration project. One key pragmatic desire of many project managers, especially those working for large agencies with multiple projects and those working out propagation protocols with growers, is to set a "maximum distance" from the seed or plant source to the restoration site. We believe that such a simplification dramatically increases the likelihood of setting too high or even too low a threshold for distance and discuss below other, but still tractable, approaches for making better evaluations of potential risks and benefits.

Selecting Propagule Sources

Conventional wisdom and applied experiments (Keller and Kollman 1999, Keller et al. 1999, 2000 and other references) suggest that seeds or plants from nearby sources are preferable to those from further distances because they are more likely to be adapted to local conditions and to come from a population with historic gene flow to the project area. Both local adaptation and historic gene flow are likely to increase the likelihood of success for the introduction and bolster the logic for the selection of a particular propagule source. Historic gene flow, or the lack thereof, also affects the potential for causing outbreeding depression in nearby populations. A second factor is whether the donor germplasm is derived from a similar ecotype (local ecological units associated with specific habitat types, and having evolved in the recent past in similar biophysical conditions of climate, soil, plant community, etc.) as the historic or extant population of the project area. One rule of thumb to minimize the risk of introducing non-adapted stock or of causing outbreeding depression in existing local populations is to be as conservative as possible in minimizing distance and matching ecotype. But how conservative does it need to be? The answer may be very different depending on species life history, and on the population and landscape characteristics of the donor population in relation to the project area and nearby populations of the same species. Furthermore, there may be times when it would be beneficial to introduce stock that contains different genetic material to enhance the genetic diversity of a small, isolated remnant population. This may be particularly true when habitat loss and fragmentation have reduced historic levels of gene flow among populations, and when there is evidence of inbreeding

Most plant introduction or restoration projects are either aimed at introducing one or more species (and sometimes entire plant communities) that have been extirpated from a site, or at increasing the number of individuals of a species that currently inhabits the site. In projects that involve multiple species, both situations may occur simultaneously. On a species-by-species basis, the difference between these types of situations can make a substantial difference in how one evaluates the selection of a suitable propagule source. For all projects, however, one can tease out two key issues that should be considered in selecting a source of plant propagules: (a) the likelihood of a successful plant introduction in which plants will become established, grow, reproduce and persist over time and over multiple generations, and (b) the effects of the introduction on the genetic diversity and local adaptation of extant or nearby plant populations. In this light, one can consider three key project types as set out in the following questions:

(1) Is the project an introduction of a new population in an area where no extant populations occur within a distance at which substantial gene flow might be expected?

(2) Is the project an introduction of a new population within a distance from an existing population at which substantial gene flow might be expected?

(3) Is the project an enhancement of an existing plant population?

For each of these three cases, successful reintroduction is a key issue. However, the relative concerns for genetic effects of the introduction vary dramatically, being negligible for (1), and increasing in importance as one moves through (2) and (3). The third situation offers the most options and the most potential problems. Using propagules derived from the existing population is the most conservative genetic approach and sidesteps the issues of poor adaptation to site conditions and the possibility of outbreeding depression. If there is evidence of inbreeding depression, however, this may suggest that the use of at least some off-site stock could be beneficial. On the other hand there may be substantial cost factors involved in propagating on-site plant materials for each individual site, which could inhibit or prevent projects from occurring. In terms of the following discussion, the third situation can be considered as a special and extreme case of the second, where the “distance” to the extant population is zero, and introduced plants may be intermingled with existing ones.

The risks entailed in using distant plant stock for (1) are primarily those of wasting time and resources if the introduction fails. For (2) and (3) however, successful introduction increases the chances of both intended and unanticipated genetic effects. To fully predict the outcomes of a plant introduction is beyond the scope of current knowledge. We have listed below the factors that should be considered in making such a decision. However, for most species and situations there are significant and often overwhelming gaps in our knowledge. To this end, we have developed initial ideas for three decision making tools described below: a framework for organizing information relevant to evaluating a potential reintroduction, a checklist for evaluating life history traits that affect the movement and recombination of genes, and a genetic effects rapid assessment matrix based on a four key factors that generally can be assessed and which can serve as a “first cut” for evaluating the risks of introducing off-site stock.

As part of the planning process for reintroductions at Mt. Pisgah by the Friends of Buford Park (FBP) the FBP Stewardship Technical Advisory Committee (STAC) has endorsed the following overall guidelines to guide decision-making:

Protocols for plant introductions on Mt. Pisgah must weigh, balance and address:

- Issues of potential beneficial or deleterious genetic affects of using non-local[1] stock
- The likelihood of a successful plant introduction in which plants will become established, grow, reproduce and persist over time and over multiple generations
- Benefits of using native plants versus the reality of incomplete knowledge (costs of inaction due to incomplete knowledge - analysis paralysis)
- Use of non-native species (e.g., sterile nurse crops)
- Introduction of non-target pest species

Protocols for nursery operations at Mt. Pisgah must weigh, balance and address:

- Unintended introduction of off-site pollen, seed or plants of target species
- Introduction of non-target pest species
- Possible practical goals for the nursery: a) propagation for on-site use, b) grow-out of species for trade or sale, and c) use as a demonstration nursery
- Location of on-site nursery relative to populations of native/sensitive species
- Growing out plants, but not to flowering v. allowing plants to flower and set seed

Impetus to use non-local stock:

- To restore genetic diversity in small, isolated, normally outbreeding populations if inbreeding depression or reduced genetic diversity is a concern
- To reintroduce extirpated species; to restore native plant community composition and structure as habitat
- Because no local stock is available in needed quantities that is likely to meet project timelines or budget (we note that convenience should never trump conservation)

Impetus not to use non-local stock:

- Concern for outbreeding depression due to introduction of non-adaptive alleles or break-up of adaptive gene complexes
- Uncertainty and risk regarding both short and long-term effects on fitness
- Reduction or loss of an existing local gene pool by swamping with non-local genetic material

Keywords and issues: precautionary principle; long-term genetic consequences; ecotype replication; adapting to change; genetic swamping; “relaxed” adaptive genes; coadapted gene complexes; residence time of outbreeding depression (how long an effect); genetic contamination/genetic load/swamping/outbreeding depression; inbreeding depression/genetic drift/fragmentation/population isolation; effective population size; genetic diversity/homozygosity/heterozygosity; interspecific and intraspecific hybridization; restoration failure/weed invasion/native vegetation and habitat; implications of disturbed habitat; F1 & F2 hybrids/backcrossing/hybrid breakdown

---

[1] *the term *non-local stock* is used here to indicate any situation in which seed or plants are collected from one location or plant population and then introduced anywhere other than being mixed back into the same area or plant population from which they were collected. We use both the terms location and population for two reasons. The first is that it can be difficult to accurately assess the boundaries of a plant population since this depends on gene flow. The second is that sometimes plants are being introduced to an area where there is no existing population of that species.

Factors to be considered in selection of propagule source

The following is a list of factors to be considered in deciding when it may be appropriate to use a particular source of native plants or seeds for introductions. Together they help build a picture of the ecological context of the proposed introduction and provide useful information for evaluating potential genetic consequences and other project results. For any given species and situation, many of the following factors will not be known. The list serves both as a framework for identifying and organizing information relevant for an evaluation and as a checklist of what is known and what is unknown. Greater gaps in knowledge should lead to greater caution in action.

One potential strategy to link the list of factors to operational criteria for decision-making would be to have a set of adopted protocols that provide a first cut on the likely acceptability of an introduction. When a proposed introduction fits within the guidelines, or "prescription", the analysis of factors would be used to establish whether there are any strong mitigating factors against the introduction. When a proposed introduction falls outside the prescription, the weight of evidence would shift toward finding strong supportive evidence or rationale to mitigate against potential risks. Toward this end, we have begun to develop two additional tools to assist decision-making in the light of incomplete knowledge. They are a checklist for evaluating life history traits that affect the movement and recombination of genes (Figure 1) and a genetic effects rapid assessment matrix (Appendix 1). When either of these tools indicates a high risk of undesirable outcomes, it may trigger and direct a deeper investigation and evaluation of the factors below.

The factors are grouped under nine broad categories: life history traits; population characteristics; habitat conditions; landscape ecological relation of donor and recipient sites; collection and propagation protocols; genetic status of donor and recipient populations; population or species knowledge, goals and implications of restoration project; and project parameters.

1. Life history traits (affect movement and recombination of genes, likelihood of localized adaptation and what "local" implies)

- Reproduction
    - Breeding system: Degree of selfing and outcrossing, apomictic, clonal growth
    - Potential for intraspecific or interspecific hybridization, including ploidy levels
    - Life span: Annual, biennial or perennial
    - Time to reproductive maturity and fecundity with age or size
- Pollen movement
    - Vector(s): wind, insect, etc.
    - Distance distribution and potential for directionality
- Seed dispersal
    - Vector(s): wind, water, gravity, mammal, bird, ant, etc.
    - Distance distribution and potential for directionality
- Vegetative (clonal) dispersal
    - Types: Bulblets, runners, rhizome or stem fragments
    - Distance distribution and potential for directionality

2. *Population characteristics (affect the likelihood, magnitude, rate, and desirability of gene flow from introduced to extant populations)*
    - Proximity of nearest extant populations
    - Size of extant populations in terms of numbers of individuals (ramets or genets) as well as the effective population size in terms of population genetics
    - Expected size and location of proposed introduced population over time in relation to size and location of extant populations and as affected by magnitude, rate, distance and direction of gene flow (e.g. movement of pollen, seed or plants due to prevailing winds, water movement, etc.)
    - Significance of extant population and/or species status (e.g., federal or state listings)
    - Potential for hybridization with other species, subspecies, races or varieties on site or nearby

3. *Habitat conditions (affect success of introduction, and potentially whether local gene pool may or may not be most suitable for altered site conditions)*
    - Presence of altered, disturbed or introduced soils
    - Presence of altered disturbance regimes (hydrology, fire, disease, etc.)
    - Current community structure and composition, including status of weedy competitors
    - Availability of suitable regeneration niches
    - Changes from historic gene flow due to habitat alteration, fragmentation or population reductions
    - Projected future changes to site and habitat (e.g., from adjacent development or fragmentation, novel disturbances, climate change, etc.)

4. *Landscape ecological relation of donor and recipient sites (affects expected genetic suitability of introduced stock)*
    - Distance between sites
    - Ecotype: Latitude, elevation, temperature and moisture regime, soils, slope and aspect, community type
    - Ecoregion: Expected levels and direction of gene flow (pollen movement/immigration of individuals) in historic landscape

5. *Collection and propagation protocols (potential genetic modifications to donor gene pool)*
    - Adequate parental diversity in collection protocols
    - Potential for inadvertent selection on donor gene pool in propagation, breeding or grow due to cultural practices or site conditions
    - Risk of inadvertent introductions of pests or pathogens

6. *Genetic status of donor and recipient populations (influences genetic consequences for extant populations)*
    - Relative genetic diversity of populations
    - Evidence of inbreeding depression
    - Relative number and proportions of shared/different genes (good donor population to combat inbreeding depression may contain recipient population's diversity as a subset)
    - Within- and among-population distribution of genetic diversity in species
    - Knowledge of coadapted gene complexes

7. *Population or species knowledge (evidence available for assessing potential benefits or risks based on factors listed above)*
    - Evidence for inbreeding depression
    - Evidence for heterosis or outbreeding depression in intraspecific F1 hydrids and further generations
    - Evidence for local adaptation and/or potential for increased genetic load due to introduction
    - Evidence for potential hybridization, including interspecific hybridization with congeners as well as intraspecific hybridization with subspecies, varieties or races, including races with different ploidy levels

8. *Goals and implications of restoration project (affects relative weighting of propagule selection issues and uncertainties), which may include*
    - Revegetation with native species
    - Establishment of native vegetation as wildlife habitat
    - Conservation of genetic diversity and evolutionary potential
    - Genetic/population supplementation of extant population or metapopulation
    - Consequences of not doing the introduction, as well as potential alternatives strategies

9. *Project parameters (affect ability to consider and evaluate alternatives)*
    - Amount of seed or plants required
    - Potential for local seed source development, as well as current seed availability
    - Project timelines and budget
    - Potential for research, test plots or other investigations to help resolve issues

Likelihood and/or rate of movement and recombination of genes

Lower **Higher**

Breeding System

__ Selfing __ Mixed __ Outcrossing
__ Apomictic
__ Clonal growth

Potential for hybridization

__ Low __ Medium __ High

Life span

__ Perennial __ Biennial __ Annual

Time to reproductive maturity

__ Long __ Medium __ Short
Estimated years ____________

Fecundity

__ Low __ Medium __ High

Pollen dispersal

__ Low __ Medium __ High
Dispersal mechanisms:____

Seed dispersal

__ Low __ Medium __ High
Dispersal mechanisms:____

Vegetative (clonal) dispersal

__ None __Rhizome fragments
__ Resprouting __ Stem fragments
__ Bulblets __ Runners

Overall ranking for how life history traits affect magnitude, distance and rate of gene flow

1 **2** **3** **4** **5**
Very low Very high

Figure 1. A partial checklist for evaluating life history traits that affect the movement and recombination of genes. In particular, these factors affect both the expected likelihood and rate of introgression of genes from introduced plants into a nearby extant populations. Whether gene flow and introgression are considered desirable or not depends on the rationale for introduction.

Appendix 1. Genetic Effects Rapid Assessment Matrix

The genetic matrix is a simplified tool for rapid assessment of the relative likelihood of successful establishment and persistence of off-site planting stock, and of potential undesirable genetic outcomes through the introduction. It is not meant to replace data, nor does it take into account all the potentially important factors, many of which are described in the body of this paper. Rather it is built on what we feel are three key factors: plant breeding system, size of the extant population relative to the proposed introduction, and taxon status (sensitive or potentially hybridizing), all in relation to a fourth factor, distance of the potential propagule source from the introduction site.

The matrix distinguishes two types reintroduction effects from a genetics standpoint: a) the likelihood of successful plant/population establishment, growth and reproduction, which primarily depends on whether the stock will be sufficiently well-adapted to site conditions to persist over time. The second is the effects of the introduction on extant populations of the same species located on the introduction site or otherwise close enough for substantial gene flow. The primary concerns for deleterious genetic effects are for swamping of local genetic diversity, hybridization, increased genetic load or outbreeding depression.

The principal value of the matrix is that it can give first-order guidance to decisions in the absence of other evidence. It is based on the idea that distance of the propagule source from the introduction site is a potentially key factor affecting reintroduction outcomes and utilizes three interacting factors that generally can be reasonably assessed. Whenever there is more information available, it should be used to improve decision-making. Whenever the matrix indicates a potential problem, greater caution or further evidence is recommended.

We do not recommend an optimal or maximum "distance" for propagule source because such an estimate will vary strongly based on the three factors listed above. We note that the first choice of a 'distance' is whether or not the propagule should come from the extant population, should one exist. When it is an option, the safest choice is to collect propagules from the extant population unless there is strong evidence that adding extra-population genetic diversity may be beneficial, for instance to counteract inbreeding depression or otherwise provide greater genetic diversity in the face of a changed or changing environment. In nearly all cases, the potential risks and benefits of using off-site plant stock cannot be sufficiently evaluated, and this uncertainty must be weighed against economic factors that involve the costs of collecting, propagating and sourcing propagules on a site-by-site basis versus broader-scale collection, propagation and use. This means that one is constantly attempting to balance economic and evolutionary factors. We believe that a precautionary approach to long-term genetic effects should trump convenience. At the same time, there may be cases in which the risk of deleterious genetic effects may be outweighed by other ecological effects of no action.

To the extent possible, considerations of distance should distinguish between physical distance, environmental distance and effective dispersal distance. Physical distance is simply the spatial separation of the donor and recipient sites. Environmental distance relates to the relative match of donor and recipient population environmental conditions ("thinking ecotypically"). In many cases, similarity of environmental conditions is likely to have more impact on the genetic suitability of planting stock than physical proximity. Effective dispersal distance can be considered as the integration of the expected distance, directionality, rates and extent of historic gene flow. All these factors depend on the modes and vectors of pollen and propagule dispersal, for instance wind, insects, water, and birds. The rates and extent of historic gene flow are particularly important to consider. Most pollen and seed dispersal follows a leptokurtic distribution, falling off sharply with distance. Even when the physical distance of donor and recipient populations is within the range of expected pollen or seed dispersal, local exchange of genes is likely to be much higher than dispersal at a distance. To mimic historic rates of gene flow might require periodically moving small amounts of pollen or individuals. Most restoration project involve faster rates and much greater overall gene flow than would have been expected historically and thus could have significantly different qualitative and quantitative effects. In the absence of other knowledge, physical distance may be the best available surrogate for effective dispersal distance, since it is to some extent correlated to the probability of gene flow. Exceptions such as the directional movement of propagules along rivers and pollen by prevailing winds may be common, however.

The logic of the matrix is that, all else being equal, the effects of increasing distance of the propagule source from the introduction site are such that:

a) Distance is less likely to be a problem for success on site for outcrossers than for selfers
b) Distance is less likely to lead to undesirable genetic effects on site or nearby for selfers than for outcrossers
c) The consequences of undesirable genetic effects on site or nearby are greater for sensitive species and those which are more likely to hybridize
d) Species with small populations relative to the introduction are more vulnerable to genetic swamping and genetic load.
e) When the species is not extant on site or nearby, the issue of undesired genetic effects is minimal for the initial introduction

The rationale for these premises is as follows:

a) In terms of successful establishment and persistence on the site, the potential for reduced fitness is greater for predominantly selfing species (selfers) than for predominantly outcrossing species (outcrossers)[2] due to the greater likelihood that selfers are strongly adapted to local conditions. This is a consequence in part of reduced gene flow and inbreeding, which tends to strengthen the effects of selective pressures. On the other hand, while selfing may lead to localized genetic structuring this is not necessarily adaptive and, for instance, could be an expression of genetic drift.

b) The potential for causing negative effects on an extant population is smaller for selfers than for outcrossers because of the reduced probability of introgression of genes. For outcrossers, the introduction of off-site propagules from a population with different genetic composition can, at a minimum, be expected to change gene frequencies and has the potential to result in increased genetic load or outbreeding depression through dilution or break down of coadapted gene complexes. For selfers, the likelihood of negative effects is extremely low unless the off-site plants are mixed directly among the plants of an established population. In this case, although there is little danger of introgression, there is the possibility that the established genotypes could be outcompeted by outside population plants that may have higher fitness in the short run but be poorly adapted in the long run, for instance, to infrequent but periodic extreme environmental events. At the same time, there are potential benefits for both selfers and outcrossers through increased genetic diversity on site, which could give some buffering for novel extreme events or climate change and could also counteract genetic drift or, for outcrossers, inbreeding depression.

---

[2] Most species are neither exclusively self-fertilizing nor exclusively outcrossing but fall somewhere between these extremes. We use the terms “selfers” to indicate species that are predominantly self-fertilizing and “outcrossers” to indicate species that are predominantly outcrossing. Species that fall somewhere in between will likely exhibit responses to introduction intermediate to these two main categories.

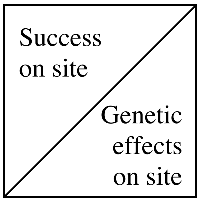
c) The stakes for undesirable genetic effects on an extant population are greater when applied to a sensitive species, by which we include both federal and state-listed species and those of special concern due to actual or predicted downward trends. At the same time, when there is strong evidence for inbreeding depression or genetic drift in an outcrossing species, the impetus to mitigate the problem are higher as well. In terms of hybridization, we include interspecific hybridization with congeners as well as intraspecific hybridization with subspecies, varieties or races, including races with different ploidy levels. Hybridization in and of itself is not necessarily a problem. On the one hand, however, hybridization may lead to decreased fitness in F1 and further generations, which could be a problem in some situations. On the other hand, hybridization due to introductions could lead to the unintentional breakdown of long-term genetic structuring expressed in subspecies, varieties or races, including races with different ploidy levels.

d) The potential for negative genetic effects due to introduction of propagules from a distance primarily depends on the size of the extant population relative to the introduction. If the extant population is large relative to the introduction, then there is little threat to the on-site gene pool. If it is small there is an increased chance of swamping the gene pool of the extant population due to a simple numeric advantage or, as noted above, because the non-local genotypes could have higher fitness in the short run but be poorly adapted in the long run. Selfers have less vulnerability to swamping than outcrossing species since introgression is small or non-existent, but still may be swamped due to numeric advantages of the introduced plants. The risks when the extant population is small relative to the introduction are highest for sensitive or potentially hybridizing species that are predominantly outcrossing.

e) Genetic effects on the initial introduction site are a non-issue when there is no extant population close enough for substantial gene flow. What is "close enough" depends on such factors as the modes and vectors of pollen and propagule dispersal, and directional dispersal due to such factors as prevailing winds or water movement, as described above. However, once an introduction has occurred, there is no guarantee that the plants and their progeny will not be used for future introductions by people with less knowledge of, or concern for, their origins.

Genetic Effects Rapid Assessment Matrix
To identify potential undesirable outcomes through the introduction of off-site plant stock

Note: Divided boxes under breeding system headings depict relative concerns for success on site and genetic effects on site as shown below. See preceding text for rationale for each category.



Codes:
DP = Distance problematic
DLP = Distance less problematic
NP = Distance not problematic
-- or ++ → lesser or greater likelihood for problems

Sensitive: a listed or otherwise uncommon species, subspecies or variety of special concern
Hybridization issues: high potential for hybridization among species, subspecies, varieties or races
Small or large population: a measure of existing on-site or nearby population size relative to the size of the introduction
Predominant breeding system: mixed mating systems will engender concern intermediate to the two extremes

Species Status and On-site/Nearby Extant Population Size	**Predom. Breeding System**	
	Selfing	**Outcrossing**
Sensitive species or hybridization issues Small population	DP DP	DLP DP++
Sensitive species or hybridization issues Large population	DP DLP--	DLP DP
Non-sensitive species, no hybridization issues Small population	DP DLP	DLP DP
Non-sensitive species, no hybridization issues Large population	DP DLP--	DLP DLP
Reintroduction species not extant on site or nearby	DP NP	DLP NP

Literature Cited

Futuyma, D. J. 1998. Evolutionary Biology. Sinauer, Sunderland, Massachusetts.

Hartl, D. L., and A. G. Clark. 1997. Principles of population genetics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Linhart, Y. B., and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics **27**:237-277.

Keller, M., and J. Kollman. 1999. Effects of seed provenance on germination of eight weeds and grassland species. Agriculture, Ecosystems and Environment **72**:87-99.

Keller, M., J. Kollman, and P. J. Edwards. 1999. Palatability of weeds from different Eurpopean origins to the slugs Deroceras reticulatum Müller and Arion lusitanicus Mabille. Acta Oecologica **20**:109-118.

Keller, M., J. Kollman, and P. J. Edwards. 2000. Genetic introgression from distant provenances reduces fitness in local weed populations. Journal of Applied Ecology **37**:647-659.

Richards, A. J. 1997. Plant Breeding Systems, 2nd edition. Chapman & Hall, London.

Sork, V. L., K. A. Stowe, and C. Hochwender. 1993. Evidence for local adaptation in closely adjacent subpopulations of northern red oak (Quercus rubra L.) expressed as resistance to leaf herbivores. American Naturalist **142**:928-936.

Templeton, A. R. 1986. Coadaptation and outbreeding depression. *in* M. E. Soulé, editor. Conservation Biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA.

Waser, N. M. 1993. Population structure, optimal outbreeding, and assortative mating in angiosperms. *in* N. W. Thornhill, editor. The Natural History of Inbreeding and Outbreeding. University of Chicago Press, Chicago.

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

Some Key Local Adaptation References

Linhart YB, Grant MC
Evolutionary significance of local genetic differentiation in plants
ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS 27: 237-277 1996

Smith, BM; Diaz, A; Winder, L; et al.
The effect of provenance on the establishment and performance of Lotus corniculatus L. in a re-creation environment
BIOLOGICAL CONSERVATION, 125 (1): 37-46 SEP 2005

Cole, CT
Genetic variation in rare and common plants
ANNUAL REVIEW OF ECOLOGY EVOLUTION AND SYSTEMATICS, 34: 213-237 2003

Hufford, KM; Mazer, SJ
Plant ecotypes: genetic differentiation in the age of ecological restoration
TRENDS IN ECOLOGY & EVOLUTION, 18 (3): 147-155 MAR 2003

A Few Outcrossing Distance and Outbreeding Depression References

Fischer M, Matthies D
Mating structure and inbreeding and outbreeding depression in the rare plant Gentianella germanica (Gentianaceae)
AMERICAN JOURNAL OF BOTANY 84 (12): 1685-1692 DEC 1997

Galloway, LF; Etterson, JR
Population differentiation and hybrid success in Campanula americana: geography and genome size
JOURNAL OF EVOLUTIONARY BIOLOGY, 18 (1): 81-89 JAN 2005

Gravuer, K; von Wettberg, E; Schmitt, J
Population differentiation and genetic variation inform translocation decisions for Liatris scariosa var. novae-angliae, a rare New England grassland perennial
BIOLOGICAL CONSERVATION, 124 (2): 155-167 JUL 2005

Schaal, BA; Leverich, WJ
Conservation genetics: Theory and practice
ANNALS OF THE MISSOURI BOTANICAL GARDEN, 92 (1): 1-11 2005

Segarra-Moragues, JG; Palop-Esteban, M; Gonzalez-Candelas, F; et al.
On the verge of extinction: genetics of the critically endangered Iberian plant species, Borderea chouardii (Dioscoreaceae) and implications for conservation management
MOLECULAR ECOLOGY, 14 (4): 969-982 APR 2005

WASER NM, PRICE MV
Crossing-distance effects in Delphinium-nelsonii - outbreeding and inbreeding depression in progeny fitness
EVOLUTION 48 (3): 842-852 JUN 1994