A Restoration Practitioner's Guide to the Restoration Gene Pool Concept

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ABSTRACT

Choosing plant materials for each desired species is often one of the most difficult steps in developing a restoration plan. The Restoration Gene Pool concept was developed to clarify the options available to the ecological restoration practitioner in terms of plant materials. We present a decision-making flowchart incorporating the issues delineated in the Restoration Gene Pool concept. We intend to provide practitioners with a framework to make objective and defensible plant materials choices in keeping with the objectives and philosophy of the restoration project. The flowchart consists of a series of boxes with single or multiple statements to be judged as true or false. The statements deal with issues such as genetic identity, plant metapopulation, functional guild, ecoregion, invasive weed presence, site soil and climate, endangered species presence, commercial seed availability, seed contracting potential, and availability of material bred for improved stress tolerance. Implementing the flowchart is a straightforward way to apply the Restoration Gene Pool concept to a particular project, but we encourage each practitioner to personalize the flowchart to make it as practical as possible for the situations that she or he most often encounters.

Keywords: plant materials, genetic identity, metapopulation, ecoregion, Restoration Gene Pool concept, ecological restoration

One of the first steps in formulating an ecological restoration plan is the development of a plant species list. While this is typically straightforward, the next step, making choices among plant materials for a given species, may be more complex. In some cases the desired species may not be commercially available, while in other cases there may be multiple plant materials to choose from. In still other cases, the only commercially available material of the desired species may be deemed ecologically or genetically inappropriate for meeting project objectives.

Ecological restoration practitioners have long been faced with a choice between native and introduced plant material—a choice confounded by a general lack of consensus concerning what constitutes "being native" (Millar and Libby 1989, Roundy and oth-

ers 1997, Brown and Amacher 1999). The Restoration Gene Pool (RGP) concept (Jones 2003) assigns plant materials to one of four restoration gene pools (primary to quaternary) in order of declining genetic correspondence to the target population for the restoration project. In this approach to plant material selection, adaptation is decoupled from genetic identity because they often do not correspond, particularly when the ecosystem function of the disturbed site has been irreversibly or significantly altered. In such situations, plant material with highest genetic identity (the primary restoration gene pool) may not be successful, in which case material from a higher-order pool may be substituted. This decision can be made individually for each plant species in the restored plant community within the scientific context that ecosystem management demands. The RGP concept provides a place for cultivars of native species and noninvasive introduced plant material when use of native material is not feasible.

Brown (2004) makes the case for using the functional guild concept to condense the species list to a reasonable number of species that 1) satisfy requirements for ecosystem structure and function and 2) deter establishment of undesirable species. Functional guilds are used to condense species lists into groups consisting of individual species that possess similar ecological structure and function (Walker 1992, Naeem and Wright 2003, Brown 2004)—an approach that may be more pragmatic than inclusive of every species on the species list (Walker 1992). Inclusion of a functional guild may also reduce site vulnerability to invasion by undesirable species of the same functional guild (Fargione and others 2003), while inclusion of multiple desirable species of a particular functional guild may increase stability (Chapin and others 1997). Others argue that this may be an unrealistic expectation at large scales (D'Antonio and Meyerson 2002).

Walker (1992) suggests that guilds should be subdivided according to

non-trivial functional attributes until the remaining species are mostly redundant. This may largely resolve the presence of residual functional variation among species within functional guilds as described by Brown (2004). For example, cool-season grasses could be subdivided according to growth habit, phenology, or life history. While the functional guild approach may appear to conflict with the view that each species is innately important to ecosystem function (Ehrlich and Ehrlich 1981), Chapin and colleagues (1997) point out that this conflict is resolved when each species is interpreted as a member of a functional guild. In other words, duplication within a functional guild is less critical to ecosystem structure and function than having a single representative of each functional guild present.

The RGP concept (Jones 2003) provides a framework for clarifying the issues involved in choosing plant materials for each species itemized in a condensed species list developed using functional guilds. The purpose of the RGP descriptor (1°, 2°, 3°, 4°) is to succinctly describe the relationship between the target plant population and the restoration plant material. Each pool is briefly described below, but we refer the reader to an earlier publication (Jones 2003) for a more thorough discussion.

We recognize that the four pools are unlikely to have equal merit in the eyes of the ecological restoration practitioner. Nevertheless, we include all of them here for the sake of completeness. Many practitioners will prefer strict use of the primary RGP (indigenous material), while others will tolerate the use of the quaternary RGP (vicarious, non-native species). Besides personal preference, this is also a function of project objectives. When genetic identity issues are paramount, primary RGP material will be considered essential to project success. This is the case not only because of the possibility of maladaptation of non-

indigenous material, but also because of the potential for irreversible contamination of the local gene pool for cross-pollinated species in particular (Millar and Libby 1989, Knapp and Rice 1994).

However, in situations where immediate repair of ecosystem function is deemed more critical than possible long-term consequences of compromising species composition, the quaternary RGP will be an acceptable alternative (Ewel and Putz 2004). While acknowledging the risks of non-native species, these authors argue that greater risk-taking is warranted when environmental conditions have been severely modified by human activity. They believe that introduced species that provide essential ecological or socio-economic services may be used to good advantage. They acknowledge that, in some cases, these needs are better met by introduced species than native species.

If an introduced species is to be used, it should be well established that it has no invasive properties. Ewel and Putz (2004) note that some non-native species are relatively innocuous, whereas others have dramatic negative effects on ecosystem structure and function. They addressed the risks of species introduction by making several suggestions for assessing a species' potential invasiveness. The subject of predicting potential for invasiveness has been addressed by numerous invasive species biologists (Mack 1996, Goodwin and others 1999, Kolar and Lodge 2001, Hegen and Trepl 2003, Sutherland 2004). Nevertheless, many restoration ecologists and practitioners will find the use of introduced species under the moniker of restoration inappropriate, preferring to refer to projects that include them as rehabilitation or reclamation instead.

Restoration Gene Pools
Primary Restoration Gene Pool

- 1° RGP material may be 1) collected from the restoration site or from a site or bulked across multiple sites (metapopulations) that have been determined either by presumption or, preferably, by genetic study to be genetically connected to it by gene flow (seed and/or pollen transfer) (Option A); or 2) collected from a site or bulked across multiple sites of the same plant community type as the target site elsewhere in the same Level III ecoregion (U.S. Environmental Protection Agency 2006) (Figure 1), but without genetic connectivity (Option B).
- Material is "natural" rather than "genetically manipulated" (subjected to selection and/or hybridization) and may be certified as "source-identified" pre-variety germplasm (PVG) (Figure 2; Jones and Young 2005).

While the practitioner's typical preferred alternative is to use material indigenous to the site (Option A), contract seed production is not always feasible because of expense or the project's scheduled time frame. Seed costs may be high because demand for such material may be limited beyond the restoration project. Costs might be more reasonable if there were sufficient commercial demand for the product such that it could become part of the business' product line.

When Option A is not feasible, the practitioner should investigate Option B, material of the same metapopulation as determined by a genetic study. Material from the same plant community type, for example, Shiflet's (1994) rangeland cover types, elsewhere in the Level III ecoregion (U.S. Environmental Protection Agency 2006) (Figure 1) may be used as a surrogate.

Levins (1966) originally described metapopulations for animal populations as a group of subpopulations connected by immigration or emigration. A plant metapopulation is analogous to an animal metapopulation, but the

Figure 1. Level III ecoregions of the coterminous United States (U.S. Environmental Protection Agency 2006).

The figure legend lists:

1 Coast Range
2 Puget Lowland
3 Willamette Valley
4 Cascades
5 Sierra Nevada
6 Southern and Central California Chaparral and Oak Woodlands
7 Central California Valley
8 Southern California Mountains
9 Eastern Cascades Slopes and Foothills
10 Columbia Plateau
11 Blue Mountains
12 Snake River Plain
13 Central Basin and Range
14 Mojave Basin and Range
15 Northern Rockies
16 Idaho Batholith
17 Middle Rockies
18 Wyoming Basin
19 Wasatch and Uinta Mountains
20 Colorado Plateaus
21 Southern Rockies
22 Arizona/New Mexico Plateau
23 Arizona/New Mexico Mountains
24 Chihuahuan Deserts
25 Western High Plains
26 Southwestern Tablelands
27 Central Great Plains
28 Flint Hills
29 Central Oklahoma/Texas Plains
30 Edwards Plateau
31 Southern Texas Plains
32 Texas Blackland Prairies
33 East Central Texas Plains
34 Western Gulf Coastal Plain
35 South Central Plains
36 Ouachita Mountains
37 Arkansas Valley
38 Boston Mountains
39 Ozark Highlands
40 Central Irregular Plains
41 Canadian Rockies
42 Northwestern Glaciated Plains
43 Northwestern Great Plains
44 Nebraska Sand Hills
45 Piedmont
46 Northern Glaciated Plains
47 Western Corn Belt Plains
48 Lake Agassiz Plain
49 Northern Minnesota Wetlands
50 Northern Lakes and Forests
51 North Central Hardwood Forests
52 Driftless Area
53 Southeastern Wisconsin Till Plains
54 Central Corn Belt Plains
55 Eastern Corn Belt Plains
56 Southern Michigan/Northern Indiana Drift Plains
57 Huron/Erie Lake Plains
58 Northeastern Highlands
59 Northeastern Coastal Zone
60 Northern Appalachian Plateau and Uplands
61 Erie Drift Plain
62 North Central Appalachians
63 Middle Atlantic Coastal Plain
64 Northern Piedmont
65 Southeastern Plains
66 Blue Ridge
67 Ridge and Valley
68 Southwestern Appalachians
69 Central Appalachians
70 Western Allegheny Plateau
71 Interior Plateau
72 Interior River Valleys and Hills
73 Mississippi Alluvial Plain
74 Mississippi Valley Loess Plains
75 Southern Coastal Plain
76 Southern Florida Coastal Plain
77 North Cascades
78 Klamath Mountains
79 Madrean Archipelago
80 Northern Basin and Range
81 Sonoran Basin and Range
82 Laurentian Plains and Hills
83 Eastern Great Lakes and Hudson Lowlands
84 Atlantic Coastal Pine Barrens

mechanisms of gene flow connecting subpopulations are pollen movement and seed dispersal. Metapopulations are important because they are much less likely to go extinct than an individual subpopulation. Additionally, metapopulations are the units upon which evolutionary forces operate (Ehrlich and Raven 1969).

Genetic studies, particularly those employing DNA markers, can be used to define geographic boundaries of plant metapopulations (Larson and others 2004, Jones 2005). For instance, by using amplified fragment length polymorphism (a selectively neutral DNA marker system), Larson and colleagues (2004) identified 21 statistically supported groups of bluebunch wheatgrass (*Pseudoroegneria spicata*) populations. Many of these 21 metapopulations had a geographical correspondence to boundaries delineated on Level III (Figure 1) or Level IV ecoregion maps. The geographical boundaries of the metapopulation also serve as the boundaries of the primary RGP. Thus, material from a single site or multiple sites within these boundaries may serve as primary RGP material for any target site within these boundaries. However, in the absence of prior genetic research, we suggest that the boundaries of the same plant community type within the same Level III ecoregion be used as a surrogate for empirically determined metapopulation boundaries.

Secondary Restoration Gene Pool

- The 2° RGP is considered when 1° RGP material is 1) unavailable or 2) insufficiently stress tolerant or competitive to succeed, as determined by the practitioner's best judgment derived from past experience.
- Material originates from a different metapopulation, a different plant community type within the same Level III ecoregion, or a different Level III ecoregion. Such material is presumed to be genetically disconnected from the restoration site material because of the absence of gene flow between them, though not biologically isolated, meaning that no significant sterility is found in their hybrid.
- Material may originate from a single source (natural) (Option A) or from hybridization or bulking of multiple sources from ecologically similar sites (natural) (Option B). Option A is preferred when genetic specificity is desired, and Option B is preferred when genetic diversity is considered more important.
- Material may or may not have been subjected to artificial selection using plant-breeding methodology, but if genetic manipulation occurs, this defaults the material to Option C.
- Option A could be certified as either a cultivar or any class of PVG. Options B and C could be certified as a cultivar or PVG "selected" or "tested" classes, but not source-identified class (Jones and Young 2005).

Single-source material (natural track) with a specific local origin (Option A) may be preferred when genetic identity is paramount and increased fitness is unnecessary. Otherwise, a multiple-origin and/or bred material (genetically manipulated track) may be preferred (Option B). In cross-pollinated species in particular, hybridization is used to increase

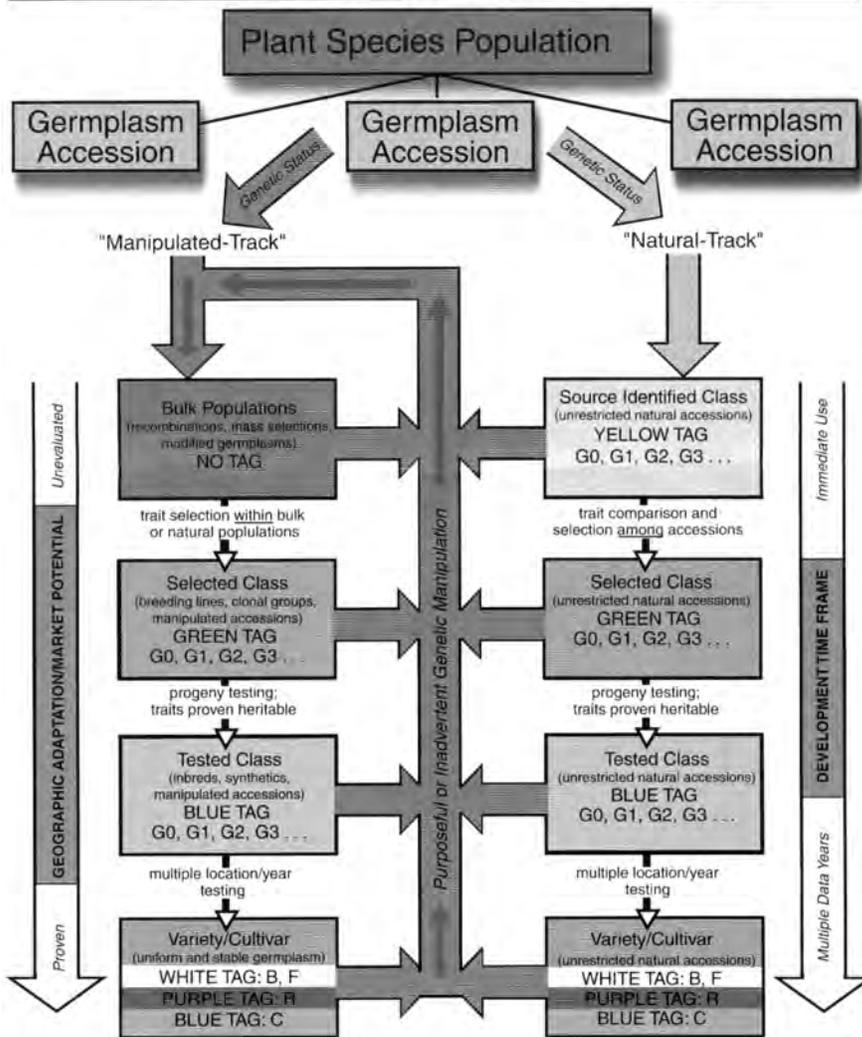## SEED CERTIFICATION NOMENCLATURE AND LABELING FOR PLANT GERMPLASM TYPES

Figure 2. Pre-variety germplasm according to AOSCA (Young and others 2005).

When certifying seed, the Association of Official Seed Certifying Agencies (AOSCA) identifies particular plant material as natural or "genetically manipulated" (Young and others 2005, Figure 2). When material has been increased from a single-site collection (2°A RGP) or bulked across ecologically similar sites (2°B RGP), it qualifies as "natural" track (Figure 2, right-hand column) (S.A. Young, pers. comm.). However, when either 1) hybridization or bulking of material from disparate sites or 2) artificial selection, as described above takes place, the resultant material (2°C RGP) is on the genetically manipulated track (Figure 2, left-hand column). The use of the two tracks to describe native plant materials is further discussed in Jones and Young (2005).

Tertiary Restoration Gene Pool

- The 3° RGP is considered when 2° RGP material is insufficiently stress tolerant or competitive to succeed.
- Material is developed by hybridization of the desired taxon with a closely related taxon in order to introduce traits of interest into the plant material of choice. The closely related taxon is presumed to be partially biologically isolated from the desired taxon, that is, significant, but not complete, and sterility is found in their hybrid. For purposes of this discussion, taxa could refer to different ploidy levels, genetically supported subspecies, or closely related, yet distinct, species.
- Seed is always genetically manipulated but could be certified as either a cultivar or PVG-selected or tested classes, but not source-identified (Jones and Young 2005).

The tertiary RGP is actually a special case. It may exist for the most widely used restoration species, but because it requires a major research effort, it is typically not available for species that are less commonly sold in the seed trade.

genetic diversity of plant material. While there is potential for outbreeding depression (Hufford and Mazer 2003, Jones 2005), the introduction of "not-too-distant" genetic variation should have a positive influence (Templeton 1986). Advantages include increased genetic diversity upon which natural selection may operate and enhanced fitness due to hybrid vigor, both of which are especially critical when populations are subjected to modified environments (Moritz 1999). Knapp and Rice (1994) suggested a strategy of combining or inter-mating seed from several locales that are representative of the target site. Such an approach was applied in the development of P-7 bluebunch wheatgrass germplasm, a multiple-origin polycross (Jones and others 2002, Jones 2003).

Restoration settings are often particularly challenging because of biotic or abiotic modifications to ecosystem processes or functions (Vitousek 1990). Therefore, artificial selection of plant materials (Fehr 1987) may be appropriate to enhance stress tolerance or competitive ability (Option C). In addition, selection may be required to develop material that successfully produces seed in cultivation. This may require attention to such traits as seed yield, seed retention, and seed germinability.

Quaternary Restoration Gene Pool

- The 4° RGP is considered when the other RGPs are insufficiently stress tolerant or competitive to succeed or when their seed is unavailable.
- Material is of a species other than the desired taxon, although it has similar ecological structure and function, that is, it is a member of the same functional guild. It may be an unrelated native species (Option A) or a noninvasive, introduced species (Option B).
- Seed for either option may be natural or genetically manipulated and could be certified as either a cultivar or any class of PVG (Jones and Young 2005).

The quaternary RGP may be employed when the desired species is not available or when it is no longer able to function properly within a damaged ecosystem (D'Antonio and Meyerson 2002). While implementation of the quaternary RGP may restore ecological processes, it obviously does not place evolutionary processes on a natural trajectory, as the other RGPs do to varying degrees. For this reason, many practitioners do not consider the quaternary RGP acceptable for legitimate ecological restoration, preferring instead the use of the terms "rehabilitation" or "reclamation" for such situations (Aronson and others 1993, Society for Ecological Restoration International 2004). However, in the RGP concept, if a species native to the continent, though not indigenous to the project site, is preferred to an exotic from another continent, Option A may be implemented instead of Option B. In practice, the use of exotics is more acceptable the further the current biotic and abiotic conditions are from the desired target (D'Antonio and Meyerson 2002, Ewel and Putz 2004).

Considerable interest is present in using the quaternary RGP as a means to an end by what has been termed "assisted succession." To the best of our knowledge, this term was first used by Hironaka (1994) to describe the use of a plant species, either native

or introduced, to secure a site in the face of invasive weeds in order to facilitate the establishment of desirable natives. Using chemical and mechanical methods, Cox and Anderson (2004) successfully seeded native species into sown crested wheatgrass (*Agropyron cristatum*) stands established after wildfire to suppress cheatgrass (*Bromus tectorum*). In contrast, little success was achieved by establishing directly into cheatgrass.

Decision-making Flowchart

In Figure 3, we present a decision-making tool in the form of a flowchart for use in applying the RGP concept. This tool presents pertinent issues to the practitioner in a stepwise fashion. The flowchart delineates an objective approach to answer a rather subjective question: Which plant materials should be used in an ecological restoration project? Its purpose is to force the practitioner to analyze options, given the limitations and realities of a particular situation, rather than to simply apply a rote technique. The flowchart is not intended to be immutable. Rather, the practitioner should tailor it to fit his or her specific applications, and to reflect personal philosophies or institutional policies. We believe the flowchart will clarify plant material selection issues for the practitioner and permit better communication and justification of plant material decisions made for the project.

In the flowchart, an all-statements-true/any-statement-false selection is made at each decision point, ultimately leading to one of the four restoration gene pools or two specialized options in bold-outlined text boxes as explained below. Multiple options are also given for primary (A/B), secondary (A/B/C), and quaternary (A/B) RGPs. The natural and manipulated tracks used by seed certification officials (Young and others 2005, Jones and Young 2005) are indicated by dashed-line and solid-line text boxes, respectively.

It should be noted that the flowchart offers two options that have not been previously discussed, but may be of great significance (see bold-outlined text boxes, Figure 3). If primary RGP material is not available and the indigenous seedbank can be expected to eventually recover on its own following disturbance, use of fast-growing, non-persistent plant material may be used as a cover crop to stabilize the soil rather than introducing non-indigenous plant material of the secondary RGP. This includes the common practice of seeding sterile cereal hybrids to preclude soil erosion by closing the gaps created by disturbance, until the seedbank regenerates the indigenous flora (Robichaud and others 2000).

Secondly, material not representative of the functional guild and, therefore, not qualifying for any RGP, may be necessary in extreme circumstances. For example, reclamation-grade material may be used to stabilize the site, protecting it from recurring wildfire, invasive weed species, or soil degradation. While this action could never be considered an ecological restoration activity, it may be a necessary step to effect restoration in the future through assisted succession (Jones 1997).

Application of the Flowchart

Box 1 (Figure 3) lists two statements (1 and 2) to judge whether the project objectives are consistent with the goal of restoration with indigenous genetic material only and two statements (3 and 4) to verify that site condition is good enough to accomplish this goal. If all four statements are true, and the site is expected to recover on its own without seeding (box 3), the recommendation is made to employ an annual or short-lived perennial cover crop to stabilize the site until the ecosystem repairs itself. However, if the site cannot be expected to recover without seeding, then seed must be obtained for the project. If indigenous
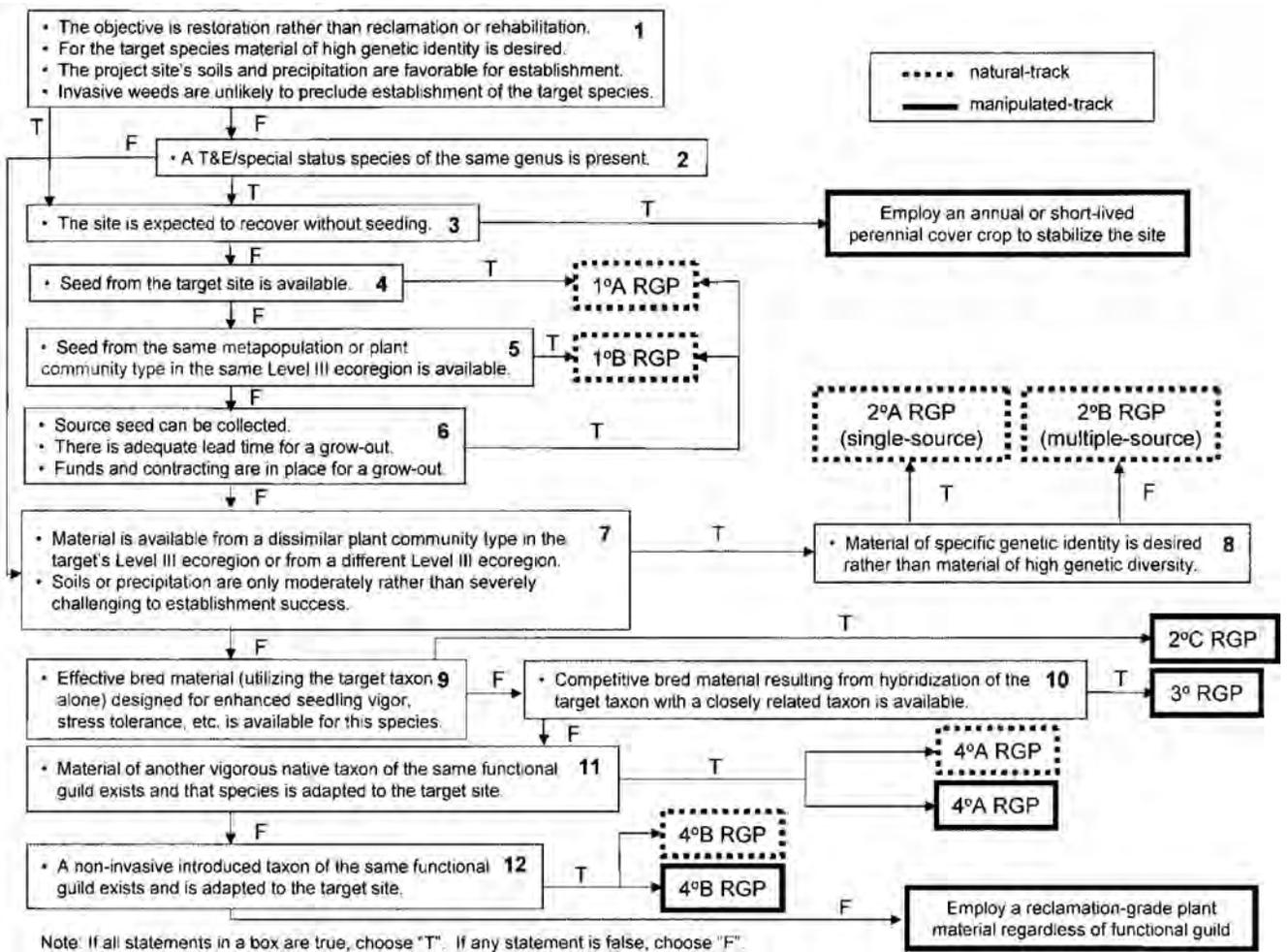
Figure 3. Restoration Gene Pool decision-making flowchart.

(natural track) seed is available (box 4; 1°A RGP) or, secondarily, seed from the same metapopulation or plant community type in the same Level III ecoregion (box 5; 1°B RGP), such natural-track seed may be applied to the site. Alternatively, either may be produced under contract (box 6).

If, instead, any of the statements in box 1 are false, one may proceed directly from box 1 to box 7, skipping the primary RGP. However, a provision is made for situations when threatened or endangered /special status species are present (box 2). In such cases, special attention is given to the primary RGP even if any box 1 statements are false. It may be desirable to maintain as genetically pristine a state as possible on sites that must be managed with respect to legal limitations.

If the options in boxes 4-6 are unavailable, the alternative is to downgrade to the secondary RGP or greater (box 7). Note that when soils or precipitation are deemed severely challenging to establishment success, the false response to the second statement in box 7 steers the user toward the tertiary RGP. If the response to box 7 is "true," secondary RGP material is chosen ("true" for box 7), and one may have the option of choosing between material of specific genetic identity—single-source natural track (2°A RGP)—and material of high genetic diversity—multiple-source natural track (2°B RGP) (box 8). If artificial selection is necessary for restoration success, a third option is provided—genetically manipulated track (2°C RGP).

From this point (box 7), if the primary RGP material is unavailable or soils or precipitation are severely challenging, bred material should be considered next (box 9). Bred material may be developed from germplasm of the desired taxon alone ("true" for box 9), in which case the flowchart leads to the 2°C RGP option. Alternatively, bred material may be developed through hybridization between the desired taxon and a closely related taxon, typically another species, subspecies, or ploidy level (box 10). By definition, this is the tertiary RGP.

If none of these options are available ("false" for box 10), then the quaternary RGP, those taxa within the desired taxon's functional guild, should be considered (box 11). Quaternary RGP materials may be North American natives (4°A RGP) or, if unavailable or ineffective ("false" for box 11), non-invasive introduced taxa (4°B RGP). In both cases, the material may be either natural or genetically manipulated. Finally, if these last

options have been exhausted ("false" for box 12), a reclamation-grade plant material may be used regardless of functional guild.

Acknowledgments

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