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Ecologically Appropriate Plant Materials for Restoration Applications

THOMAS A. JONES

The areas targeted for restoration are often the modified ecosystems that are rapidly becoming the planetary norm, and when ecosystem modification has been extensive, local genotypes may not be the most effective for repair. Here, local has value is presented as a paradigm for the restoration of such systems as a corollary to local is best for systems that have sustained less modification. In many cases, adaptation may be enhanced through genetic variation or applying artificial selection, particularly for generalist species. Ecologically appropriate plant materials are those that exhibit ecological fitness for their intended site, display compatibility with other members of the plant community, and demonstrate no invasive tendencies. They may address specific environmental challenges, rejuvenate ecosystem function, and improve the delivery of ecosystem services. Furthermore, they may be improved over time, thereby serving to ameliorate the increasingly challenging environments that typify many restoration sites.

Keywords: ecological restoration, local adaptation, native plant materials, novel ecosystems, restoration genetics

Ecological restoration is most often applied to assist the recovery of an ecosystem that has been degraded, damaged, or destroyed (SERI 2004). Because areas targeted for restoration often display impaired ecosystem function and ecosystem services (for the definitions of key terms, see box 1), a primary aim of restoration is reinitiating natural processes that reestablish desired ecosystem form and function (Jones et al. 2010). Consequently, the development of plant materials for restoration should be conducted with these principles in mind.

In the present article, I discuss three issues, sometimes overlooked or misunderstood, that restoration practitioners should ponder for effective restoration practice given such challenges: (1) emphasizing the whole for the achievement of restoration objectives, (2) using genetic variation to counter environmental challenges, and (3) appreciating the practical considerations that distinguish restoration applied to pristine ecosystems from that applied to novel ecosystems. This discussion is followed by a presentation of three biological principles (the individualistic concept, ecological fitting, and general adaptation) and their application to the questions of when and how ecological restoration can be accomplished through the development and use of more effective plant materials. I conclude with a definition of ecologically appropriate plant material and a justification for its development and use in ecological restoration.

Three issues integral to effective restoration practice

Let us consider three issues that affect the effectiveness of restoration practice.

Emphasizing the whole for the achievement of restoration objectives.

When the primary emphasis of a restoration effort is on local plant genotypes per se, the emphasis on ecosystem repair may become secondary, and it may be presumed that only local genotypes may effect repair. In such cases, local genotypes may be chosen not because they are effective but because they are local. Such an approach is lacking if it does not recognize that the genotypes needed to restore the desired ecosystem function and services may differ from those that were present in the past (Stockwell et al. 2003). The neglect of the ecosystem as a whole in order to emphasize the integrity of one of its parts—for example, a plant population—may inadvertently lead to an undesired consequence—that is, the failure to correct the ecological damage that prompted the restoration effort in the first place. In short, when it comes to restoring the land, the land itself should receive primary consideration.

For the development of restoration plant materials, the use of local genotypes may be a place to start, but when evolutionary potential is limited, it may not be the best place to finish (Broadhurst et al. 2008, Hoffman and Sgrò 2011,

Box 1. Glossary of terms.

Term	Definition
Artificial selection	The modification of a population's genotype by culling undesired individuals
At-risk community phase	A subdivision of an ecological state based on plant community, soils, and ecological properties that is vulnerable to a transition across an ecological threshold to a less desirable ecological state (Bestelmeyer et al. 2010)
Contemporary evolution	An adaptive genetic change within a short time frame due to selection pressure, especially as induced by anthropogenic disturbance (Stockwell et al. 2003)
Ecological fitness	The ability of a plant or population to persist and propagate itself on a site
Ecological state	One of multiple possible soil–plant–community combinations for an ecological site (lands with similar soils, landform, or climate), separated from others by threshold boundaries and irreversible without significant management input
Ecologically appropriate plant materials	Those that exhibit ecological fitness on their intended site, that demonstrate compatibility with other desirable species in the ecological community, and that do not display a tendency to invade adjacent sites; may encompass hybridization (to augment genetic variation to fuel natural selection) or artificial selection (to improve general adaptation and stress tolerance) if necessary to attain restoration objectives, particularly for widespread, cross-pollinating generalist species
Ecosystem services	Products and processes rendered by ecosystems that benefit humanity (e.g., pollination, watershed protection, wildlife habitat, food, carbon sequestration, recreation)
General adaptation	The tendency of a population to display ecological fitness across a variety of environments (Jones 2013)
Generalist species	Those whose populations display a high degree of general adaptation (tolerant of translocation; Rehfeldt 1994)
Genetic structure	The pattern of a species' genetic diversity distributed across geographic space
Genetically appropriate plant materials	Those that are locally adapted, regionally appropriate, and genetically diverse, being developed without artificial selection for specific traits or hybridization among genetically disparate populations (Johnson et al. 2010)
Local adaptation	The adaptation of a population to its particular locality as a result of natural selection (Kawecki and Ebert 2004)
Novel ecosystem	An ecosystem characterized by novel species assemblages or ecosystem function that has resulted from intentional or inadvertent human action, though not requiring human activity for its continued existence (Hobbs et al. 2009)
Plant material	Seeds or other propagules of a cultivar, germplasm, population, or genotype
Release	<i>Verb</i> : administrative action making a new plant material available to seed growers, nurseries, and restoration practitioners; <i>noun</i> : released plant material
Specialist species	Those whose populations display a high degree of local adaptation (intolerant of translocation; Rehfeldt 1994)

Sgrò et al. 2011, Weeks et al. 2011). Maintaining stasis in vulnerable natural populations through preservation may have the effect of limiting genetic variation and short-circuiting the natural selection that confers adaptation and continued persistence (Lankau et al. 2011). A failure to recognize the importance of augmented genetic variation in restoration plant materials demonstrates a lack of confidence in the reality and utility of natural selection (Lankau et al. 2011). In addition, the probability of implementing the most adapted plant material is limited by a local-only constraint. Instead, Lankau and colleagues (2011) suggested choosing seeds that are preadapted to the novel environments that

are likely to prevail in the future. Consequently, a genuine need may exist for genetically manipulated plant materials expressly designed to restore ecosystem structure, function, and services under real-world conditions that are more problematic than those previously present.

A primary objection to such plant materials is the potential for genetic mismatch (Rogers and Montalvo 2004). *Genetic mismatch* occurs when plant materials are planted on a site to which they are unadapted. In restoration practice, a genetic seed source is matched to a site on the basis of its presumed adaptation to the climate and soil of the site. It is the responsibility of the restoration practitioner to

make a concerted effort to choose the best-adapted material available. Although documented cases of genetic mismatch are acknowledged as being scarce, this infrequency has been attributed to an insufficient length of time for a problem to arise, to bureaucratic or recordkeeping failures, or to sampling issues (Rogers and Montalvo 2004). However, another possibility is that mismatches are relatively infrequent when biological principles are properly applied to the choice of plant materials for restoration. Furthermore, evolutionary biologists are increasingly recognizing that the problem of genetic mismatch tends to be corrected by natural selection against poorly adapted genotypes (Carney et al. 2000, Rice and Emery 2003, Erickson and Fenster 2006, Broadhurst et al. 2008, Lankau et al. 2011, Sgrò et al. 2011, Weeks et al. 2011).

Using genetic variation to counter environmental challenges. Although restoration using exclusively local genotypes is innately appealing, the question should be asked as to whether this option is truly the most desirable or feasible. Practitioners sometimes assume that autogenic processes will be triggered once desired species composition and structure have been implemented, but this is unlikely to be a valid assumption when a human-induced legacy of intervention is present (Herrick et al. 2006, Jackson and Hobbs 2009). As conditions of the restoration site drift away from historic conditions and ecological modification continues over time, a historic target moves further out of reach. Natural systems are dynamic; therefore, the outcome of restoration cannot be controlled (Clewell 2000), and its results may be unintended (Hobbs et al. 2010). And if natural states are mutable and elusive, the premise of restoring to a historical standard becomes anachronistic (Jackson and Hobbs 2009).

Being honest about an approach to restoration plant materials means being honest about the difficulties faced in ecological restoration. In general, restoration is difficult and can be expected to become more so. In restoration efforts, problematic environments (e.g., at-risk community phases and alternative ecological states) are commonly targeted (Bestelmeyer et al. 2010). Furthermore, restoration pathways may be complex and unpredictable, and some ecological damage is irreversible, which suggests the need for alternative restoration objectives.

Although the challenges of the restoration environment as they are detailed above should be obvious, a greater appreciation is needed for how this reality affects plant materials employed in ecological restoration. The “natural” approach to plant materials has been driven by the common assumption that nature can be preserved by protection, but the reality is that intervention is increasingly required to alter undesirable ecosystem trajectories, even in protected settings (Hobbs et al. 2010, Lankau et al. 2011). For the extraordinary task of restoring modified ecosystems, we need to bring all of our scientific resources to bear. Plant materials with superior adaptation to challenging environments are key to this effort.

In order to support the case for local plant materials, an example of genetic mismatch is sometimes highlighted to demonstrate the negative impact of a rare climatic event on nonlocal plant materials. Alternatively, however, such incidents may be regarded as natural selection in action (Hoffmann and Sgrò 2011), therefore justifying the need for greater genetic variation in restoration plant materials, because environments are labile and are likely to continue to change (Rice and Emery 2003). Therefore, evolutionary biologists have encouraged plant material developers to augment genetic variation in their plant materials by incorporating material that is generally adapted to the site but not necessarily local (Broadhurst et al. 2008, Hoffmann and Sgrò 2011, Sgrò et al. 2011, Weeks et al. 2011). Increased genetic variation can enhance genetic flexibility and can provide additional raw material to drive natural selection, potentially conferring adaptation to a modified environment. Although a population with an optimal genotype and low variance is ideal for a static environment, the optimum genotype becomes a moving target when an environment is labile (Rice and Emery 2003). Under such circumstances, low genetic variation may become detrimental. However, others have emphasized the potential negative impact of increased genetic variation, calling it a “double-edged sword” (Rogers and Montalvo 2004) and citing as concerns the inclusion of unadapted germplasm and the potential for outbreeding depression.

Genetic variation is generally greatest near the center of a species’ range, where gene flow is intercepted from a broader diversity of locally adapted populations (Davis and Shaw 2001). When such a center of genetic diversity is identified, its genetic material may be useful for developing plant materials for distant yet environmentally similar sites. In contrast, genetic material conferring adaptation to environmental extremes is more likely to be found at the edge of a species’ range, although the magnitude of genetic variation there may be relatively low because of small population sizes and founder events (Rice and Emery 2003). This kind of genetic variation is less useful for enhancing general adaptation in nonlocal situations, but it may be useful to confer adaptation to the extreme conditions found at the species’ distributional edge if the species is expected to migrate in that direction—for example, because of climate change.

Appreciating the differences that distinguish pristine from novel ecosystems. The use of local plant materials is justified when environments are nearly pristine and restoration is relatively straightforward. Some scientists have considered the valid use of nonlocal plant materials to be limited to extreme cases of environmental alteration (Johnson et al. 2010). However, such conditions are rapidly becoming the norm in restoration practice. *Novel ecosystems* display modified species composition, ecosystem structure, or ecosystem function (Hobbs et al. 2009). Under such circumstances, strict application of the local-is-best strategy may no longer apply. As Wilkinson (2004) stated, “It is an approach for which I have

considerable sympathy as I have a traditional background for a British ecologist, strongly rooted in natural history and, as such, [greatly] value biodiversity. However, I am reluctantly coming to the conclusion that the scale of human-caused changes to the Earth may mean that this *entity approach* will have to be at least partly abandoned” (p. 2041; in favor of an approach based on ecological and evolutionary processes).

This thought may be disturbing to preservationists, who may view anything less than entirely local plant material as an unwise exchange of restoration orthodoxy for a “slippery slope.” Nevertheless, one cannot continue to rely solely on local genotypes simply because they are local and theoretically best adapted if experience demonstrates otherwise. Preservation is not always feasible, and when it is not, alternatives must be considered. This is not to say that local plant materials are generally inferior or genetically manipulated plant materials are generally superior. Instead, the deliberate choice that best addresses the conditions at hand may better serve both nature and humanity as the current epoch of environmental change unfolds. In contrast to the local-only viewpoint, Gould (1998) called for “caring, tasteful, and intelligent modification of nature for respectful human utility” (p. 9). This call was echoed by Palmer and colleagues (2004), who recommended designed ecological solutions through conservation, restoration, and intervention. Likewise, Kareiva and colleagues (2007) pointed out that the domestication of nature is inevitable but that humans may choose paths of domestication that are desirable for both humanity and nature.

Ecological restoration from natural and human perspectives

The tactics of ecological restoration should be based on ecological considerations for the amelioration of past environmental damage and tolerance of present environmental stresses. This stands in contrast to a model whose central emphasis is on the reintroduction of taxonomic entities that were once present before damage modified the ecosystem. Furthermore, although ecology is the *lingua franca* of land restoration and repair, it is important to remember that a plant’s ecology is made up of its genetic, evolutionary, and physiological responses to its environment. Therefore, to be most effective, all four of the relevant disciplines (ecology, genetics, evolutionary biology, and physiology) should be integrated into one’s approach to restoration plant material development.

Restoration efforts are simply the beneficial activities of man intended to correct the consequences of previous deleterious events. Consequently, the questions then become whether human effort can actually reverse these modifications, genuinely restoring the landform and geological processes, biological components, ecological structure and function, and evolutionary processes that prevailed prior to the disturbance and which approach to restoration plant materials is likely to be successful in a new world of novel ecosystems.

Three biological principles pertinent to the development of restoration plant materials

Below, I consider three well-supported biological principles and then apply them to these questions: Gleason’s (1926, 1939) individualistic concept of the plant association, Janzen’s (1985) concept of ecological fitting, and the underappreciated role of general adaptation.

The individualistic concept of the plant association. The first principle is the coincidental—as opposed to predetermined—nature of vegetation, as expressed in Gleason’s (1926) individualistic concept of the plant association. Gleason (1926) developed his ideas about ecological succession as an alternative to those of Clements, which were far more prominent in the early twentieth century. Clements proposed a concept in which a plant association was viewed as something akin to a living organism. His model of succession was deterministic, meaning that a site’s vegetation tends to move in a single direction, self-corrects when outside forces alter that course, and ultimately reaches a predetermined and fixed outcome.

Gleason’s (1926) model, in contrast, was based on his observation that the vegetation on every piece of land was unique. Contrary to Clements, Gleason (1926) described the plant association at a site as a *coincidence*—a consequence of two interacting random forces: fluctuating botanical immigration and fluctuating environment. Furthermore, Gleason (1926) attributed any similarity between the vegetation on two sites to the chance similarity of these two forces between the two sites. Gleason (1926) employed quantitative methods, and he believed that his 13 years (1911–1923) of field data supported the idea that distributions of species obeyed the simple laws of probability rather than a preordained course. He deduced that a local environment might be optimal for some species but marginal or exclusive for others.

In a later paper, Gleason (1939) defined a plant association to be “a temporary and fluctuating phenomenon dependent... on the selective action of the environment and on the nature of the surrounding vegetation” (p. 93). Although Gleason’s (1939) theory was initially rejected by plant ecologists, his ideas came to be widely accepted in the latter half of the twentieth century. For example, White and Walker (1997) argued that a species may be absent at a site either because it cannot compete or because it never arrived there, and a species may be present either because it is a good competitor or because it is continually dispersed there. In addition, White and Walker (1997) acknowledged that highly adapted material may be absent from a site if it was not previously present in the general vicinity, which is in keeping with Mack’s (2003) observation that a community can be composed only of species that happen to reach its location. All these contentions are rooted in Gleasonian thinking.

Ecological fitting. A second principle is that local adaptation is not a prerequisite for desirable ecological function. Janzen

(1985) reported that Santa Rosa National Park in Costa Rica was “crawling with complex biotic interactions” (p. 308). He reasoned that, because 98% of the species present at Santa Rosa were widespread over tens of degrees of latitude, these species could be regarded as *evolutionarily quiescent* at Santa Rosa, meaning that their evolution occurred primarily elsewhere. He postulated that when a species first arrived at Santa Rosa, it would have displayed a patchy distribution, reflecting its ability to ecologically fit into various local habitats on the basis of its preadapted state, without invoking on-site natural selection. As Janzen (1985) stated, “a species does not have to evolve in a habitat in order to participate in the interactions in that habitat. Widespread species are not adapted to their habitats; they just are” (p. 310). What Janzen (1985) meant by this remark is that local adaptation is often lacking in widespread species, but the species may still be widely adapted because of *ecological fitting*, the chance preadaptation to a new habitat.

Ecological fitting in the context of restoration, then, can result when existing nonlocal genotypes are purposefully translocated into novel environments. Wilkinson (2004) described how plant introductions since 1843 have transformed the barren landscape of Ascension Island in the South Atlantic into a luxuriant tropical ecosystem, complete with a cloud forest. Presumably, all of this adaptation was accomplished with only a minimal contribution from natural selection. This is because plant materials flourished or disappeared on the basis of their preadaptation—or lack thereof—to local conditions rather than because of on-site evolution or coevolution with sympatric species.

The importance of general adaptation. The third principle is that local adaptation is much less important than has been commonly believed. When comparing two populations in each of their two respective local environments (i.e., a reciprocal planting design), *general adaptation* is evidenced by the superiority of one population in both environments, whereas *local adaptation* is evidenced by the superiority of each population in its own local environment and inferiority in the alternate environment. The preeminence of local adaptation has long been assumed (Sgrò et al. 2011, Weeks et al. 2011), and many researchers have concurred with this assumption on the basis of a conceptually flawed methodology (Kawecki and Ebert 2004) or through an analysis of relatively small individual data sets, such as those enumerated by Johnson and colleagues (2010).

Recently, however, two *meta-analyses* (collective analyses of large numbers of individually published data sets) have appeared in the research literature (Leimu and Fischer 2008, Hereford 2009), and they tell a different story. Encompassing nearly 2000 local and nonlocal comparisons, and using Kawecki and Ebert’s (2004) improved methodology, these two meta-analyses document that general adaptation, rather than being rare, is similar in frequency to local adaptation. In addition, Hereford (2009) found that adaptive trade-offs among environments were weak and explained only 2% of

the observed variation. Consequently, he concluded that any costs of adaptation to one environment were generally too small to preclude simultaneous adaptation to another. This suggests that selection for general adaptation may be a viable approach for developing more effective plant materials.

It should also be emphasized that even these meta-analysis estimates are biased in favor of local adaptation. First of all, only two populations at a time were compared in these analyses, which inflates the frequency that local will be best relative to comparisons involving a greater number of populations. Second, the data sets included in the meta-analysis often included dramatically different environments, which increases the likelihood of positive results (Hereford 2009). Third, in plant material development efforts, considerable effort is expended in identifying populations with superior performance through testing, so the chances that a random local population would perform better than a plant material released on the basis of a performance evaluation would be expected to be even lower. Therefore, the significance of local adaptation is likely to be considerably less than has been previously believed. Consequently, additional research related to general adaptation is merited.

Application of the three biological principles to restoration plant materials

Consideration of these three biological principles suggests that local plant materials are unlikely to be the panacea that they are sometimes expected to be. Although they possess adaptive value as a consequence of past evolutionary forces, they are not necessarily intrinsically superior for most restoration applications from an ecological or evolutionary standpoint. First, the absolute credence of local plant materials is based on their role as a single ecosystem component rather than on their contribution to the function of the whole ecosystem. Second, they may not possess the genetic potential to respond to the new physiological and ecological challenges to which they are exposed in restoration environments. Third, they have not evolved under the conditions of the novel ecosystems that are now assembling.

Some argue that human effort as applied to restoration plant materials is futile and deleterious, because nature is more complex than man can ever understand, much less emulate. In other words, anything less than natural is deemed unworthy of restoration practice. This sort of criticism of nonlocal or genetically manipulated plant materials may reflect a general suspicion of human motives toward nature. However, it also ignores two important issues. First, insistence on solely natural material is counterintuitive, because the impetus for restoration in the first place is a human-modified environment. Second, not only have the players of the ecological game changed, even the rules of the game have changed. Therefore, is it reasonable to expect natural mechanisms to correct themselves within the single human lifespan in which the restoration practitioner hopes to see success? Such an expectation anticipates

a specific set of end results but may fail to appreciate the mechanics of how to get there and whether it is even possible to do so (Hobbs et al. 2009).

Artificial selection in generalist species. Evolutionary biologists have recognized the utility of artificial selection for developing more effective restoration plant materials (Lankau et al. 2011, Sgrò et al. 2011). Both hybridization and selection are essential elements of evolutionary change—the former because it introduces new genetic variation and the latter because it sorts and reassembles that variation to confer adaptation. For some species, adaptation is determined primarily by genotype–environment interactions, meaning that there is a close match between genotype and the environment. Rehfeldt (1994) referred to such species, which display a high degree of local adaptation, as *specialists*. Other species, termed *generalists*, are more broadly adapted and more tolerant of translocation (Rehfeldt 1994). For generalists, then, genetic mismatch is less of an issue than for specialists.

For generalists, artificial selection has considerable potential to increase general adaptation to challenging environments. Consequently, it may be sensible to evaluate and artificially select plant materials of widely distributed generalist species for enhanced *ecological fitness* (i.e., the ability to survive and reproduce in challenging environments). The intent is to improve adaptation of a plant material to an array of environments that possess similar environmental limitations. Such plant materials may be matched to environments on the basis of general climatic and edaphic conditions rather than through very specific (and numerous) matches based on local conditions. The former, in fact, is what has been done in practice in the case of the rangelands of the western United States for some time: the meta-analyses of Leimu and Fischer (2008) and Hereford (2009) confirm the utility of this longstanding practice for generalist species.

Ecologically appropriate plant materials as an alternative to the local-only approach. Johnson and colleagues (2010) emphasized the use of genetically appropriate plant materials, equating them with local, nongenetically manipulated plant materials. Although this notion is a traditional biological viewpoint, it is rapidly being modified in light of an increased emphasis on contemporary evolution by evolutionary biologists (Stockwell et al. 2003) and a new appreciation of the importance of novel ecosystems by ecosystem-level ecologists (Hobbs et al. 2009). For novel ecosystems, genetic appropriateness loses a portion of its relevance, but the importance of the ecology of adaptation and ecological fitness increases. Therefore, the use of genetically appropriate plant material on a site that has been substantially modified may not necessarily be ecologically appropriate.

Here, I propose an emphasis on ecologically appropriate plant materials for restoration. As they are considered here, ecologically appropriate plant materials embody three

characteristics: ecological fitness on the site, compatibility with other members of the ecological community, and a lack of invasive spread to adjacent sites. Note that this definition of *ecologically appropriate* has no implication regarding a local or nonlocal origin. For sites with minimal disturbance, ecologically appropriate plant materials, as they are described here, may be local in origin and require no trait enhancement through plant breeding. Also falling in this category are rare plant species, species with limited geographical distributions, and plant materials of more common or widespread species intended for sites characterized by relatively unique or extreme environments. Therefore, for such applications, *ecologically appropriate plant materials* is synonymous with *genetically appropriate plant materials sensu* Johnson and colleagues (2010), to which I have previously referred as the primary restoration gene pool (Jones 2003). However, for novel ecosystems, ecologically appropriate plant materials offer the additional option of employing plant breeding methodology to augment genetic diversity and enhance performance (Jones 2009), as defined by the three characteristics noted in the *ecologically appropriate* definition above. A statement of the appropriate use of plant breeding methodology in developing restoration plant materials for modified environments, and a response to the objections to such an approach, have been presented elsewhere (Jones and Robins 2011).

Ecologically appropriate plant material practices, based on specific strategies, may be implemented to address specific environmental challenges, to ameliorate dysfunctional ecosystems, and to improve the delivery of ecosystem services (table 1). In many cases, local plant materials may be able to genetically respond to changing environmental conditions through contemporary evolution (in figure 1, see the lightweight dashed arrow; Stockwell et al. 2003). However, human effort may genetically enhance the performance of ecologically appropriate plant materials incrementally over time (in figure 1, see the medium-weight solid lines). This may help to narrow the steadily increasing gap between the advancing modern-day environmental challenges and local plant material performance. This gap may be further narrowed if the ecologically appropriate plant materials exhibit augmented levels of genetic variation that fuel contemporary evolution (in figure 1, see the three heavyweight dashed arrows for seedings of incrementally improved ecologically appropriate plant materials released and seeded at times A, B, and C).

Keeping ecological appropriateness in mind, the local-has-value approach can be considered as a plant materials paradigm for novel ecosystems. Therefore, it may serve as a counterpart to the local-is-best approach (Johnson et al. 2010), a more appropriate paradigm for systems in which ecosystem function is relatively unaltered. Here, I summarize the salient features of these two paradigms (table 2). Johnson and colleagues (2010) agreed that, in cases of extreme modification of the natural environment, local populations may be less than optimal. This does not mean, however, that

Table 1. Six examples of ecologically appropriate plant material practices and their associated strategies.

Ecologically appropriate practice	Strategy
Augment local genetic variation with novel genetic variation from selected locales	Provide raw genetic material to fuel contemporary evolution (Jones and Monaco 2009)
Identify seed transfer ecoregions using global environmental variables	Match existing seed sources to defined seed transfer ecoregions given a specific climate-change scenario (Potter and Hargrove 2012)
Apply artificial selection for enhanced stress tolerance	Increase establishment and growth of plants on sites characterized by specific abiotic or biotic stresses (Jones 2009)
Select populations with desired functional traits	Repair ecological processes damaged by invasive plants (Herrick et al. 2006, Jones et al. 2010)
Include plant materials of specific functional groups in the seed mix	Preempt invasive species by occupying their ecological niches with seeded material (Funk et al. 2008)
Introduce an ecosystem engineer	Overcome inertia of an undesirable ecological state, thereby promoting a transition to the desired state (Byers et al. 2006)

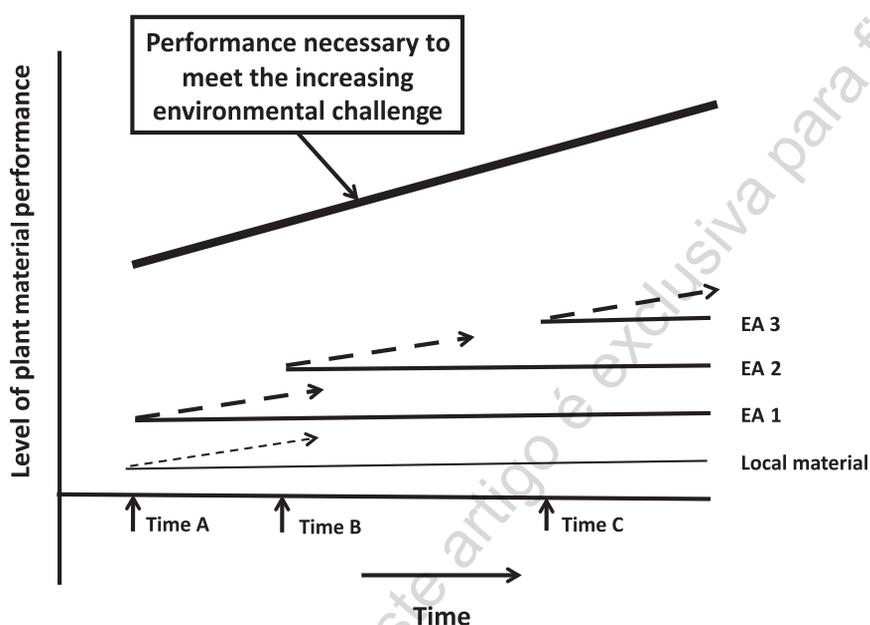


Figure 1. As novel ecosystems become entrenched over time and concomitant environmental challenges increase, the gap between the performance necessary to meet these challenges and the performance of local material increases unless the difference is made up by contemporary evolution (signified by dashed arrows). Three ecologically appropriate (EA) plant materials, sequentially improved over time for enhanced adaptation to the modified conditions and released and seeded at time A (EA 1), time B (EA 2), and time C (EA 3) may potentially narrow this gap, particularly when they display contemporary evolution of their own. Source: Adapted from Jones (2013).

local populations in such circumstances do not have value. They continue to serve as reservoirs of relevant genes as long as residual properties (Briske et al. 2008) of the intact ecosystem persist. The local-has-value paradigm encourages the indirect use of local plant material in developing preadapted genotypes. Leopold (1953) concurred when

he said, “Who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering” (p. 147). In addition, using a local-has-value approach to develop populations with augmented genetic variation may prime a favorable trajectory of plant response to the environment through contemporary evolution.

Currently, a great diversity in attitudes toward plant materials is present within the restoration sector (Rogers and Montalvo 2004, Smith et al. 2007). Adherents of local plant material commonly cite the significance of local adaptation and outbreeding depression (Smith et al. 2007). Others, including many in the seed industry, cite the economic concerns of maintaining an inventory of numerous local plant materials (Smith et al. 2007), particularly given the large volumes of seed often needed on short notice for unpredictable restoration projects. In some cases, local plant materials are either commercially unavailable or prohibitively expensive (Smith et al. 2007), and in other cases, the same issues constrain the use of nonlocal plant materials. However, although the choice of plant material for ecological restoration may be driven by performance, availability, and cost, the first preference of many restoration practitioners is for local plant material unless its use is restricted by one of these three factors (Jones 2003).

In the future, ecologically appropriate plant materials may offer attributes such as enhanced stress tolerance, competitiveness with invasive weeds, ecological fitness, ecosystem repair, and the delivery of a wider array of ecosystem services. As environmental challenges mount, novel ecosystems increasingly predominate, and classical restoration becomes less achievable (Hobbs et al. 2009), it is likely that human-influenced systems will

be increasingly managed for ecosystem services in a future sustainable world (Palmer et al. 2004). Consequently, ecologically appropriate plant materials will become increasingly valued by restoration practitioners, especially by those who have experienced multiple restoration failures in the past. Genetically appropriate plant materials are valued for

Table 2. A comparison of the local-is-best and the local-has-value paradigms for 19 features.

Feature	Local-is-best paradigm	Local-has-value paradigm
Ecosystem status	Pristine	Novel (Hobbs et al. 2009)
Conservation ethic	Preservationist	Interventionist (Hobbs et al. 2011)
Disciplinary orientation	Population biology, botany	Ecosystem-level ecology
Primary restoration objective	Preservation of the plant community	Repair of the whole ecosystem
Successional model	Clementsian succession	Gleason's (1926, 1939) individualistic concept
Evolutionary model	Local adaptation conferred by natural selection	Janzen's (1985) ecological fitting with preadapted genotypes (Lankau et al. 2011)
Species geographic distribution	Either rare or featuring a limited distribution	Widespread
Species generation time	Long (e.g., woody species)	Short (e.g., grasses)
Seed production locale	<i>In situ</i>	<i>Ex situ</i> (i.e., in cultivation)
Environmental variation	Landscapes characterized by steep environmental gradients (Hereford 2009)	Relatively homogeneous landscapes
Species mating system	Generally self-pollinating or apomictic	Generally cross-pollinating
Rehfeldt (1994) species categorization	For specialist species and unique or extreme environments of generalist species	For most environments of generalist species
Plant material type	Genetically appropriate (Johnson et al. 2010; equivalent to ecologically appropriate for pristine ecosystems)	Ecologically appropriate
Plant material genetics	Preservation of preexisting genetic structure as a legacy of evolution	Harnessing of assisted evolution, including genetic augmentation and artificial selection (Jones and Monaco 2009)
Plant material adaptation	Adaptation to climatic variables (Johnson et al. 2010)	Adaptation to novel biotic and abiotic stresses, expression of ecological fitness in modified environments
Artificial selection	Selection is inappropriate (Johnson et al. 2010)	Encompasses selection for critical functional traits (Jones et al. 2010)
Number of target environments	Many; presumes adaptive trade-offs among environments	Fewer; seeks general adaptation across environments, because adaptive trade-offs among environments are weak (Hereford 2009)
Number of plant materials per species	More numerous	Fewer
Expense of seed	More expensive	Less expensive

their adherence to naturally occurring patterns of genetic structure (Johnson et al. 2010), but because of the decline in frequency of restoration sites for which genetically appropriate and ecologically appropriate plant materials are synonymous—namely, pristine ecosystems—the restoration practitioner will increasingly be forced to choose between plant materials that are either genetically or ecologically appropriate.

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