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REVIEW ARTICLE

Bridging theory and practice to inform seed selection for restoration

Laura C. Shriver[1], Samuel E. Jordan[1], Rob Massatti[2], Seth M. Munson[1,3]

Abstract

Introduction: Land managers often face the critical decision of what plant materials to select for ecological restoration. Selection depends on factors that span ecological conditions and human interventions in the restoration process, which can strongly influence the recovery of a degraded ecosystem.

Objectives: To improve the seed selection process, we compared scientific literature and guidance from five federal agencies to bridge seed selection "theory" and "practice" in the interior western and central United States.

Methods: We extracted recurring themes and keywords associated with abiotic, biotic, land management, and producer practices that influence seed selection and analyzed their proportional use between agency guidance and scientific literature.

Results: We identified significant overlap between key concepts in guidance and literature, highlighting the interconnectedness between science and management. However, nuanced patterns emerged across seed selection themes, including more focus in the literature on local adaptation and genetic structure, ramifications of introducing gene flow and artificial selection during plant production, and provenancing strategies to address changing climatic conditions. In contrast, agency guidance focused on genetically appropriate and environmentally suitable seed selection and practical concerns, including seed cost, availability, and diversity. Seed selection studies in the literature were concentrated in the Great Basin and Colorado Plateau, scattered in the Great Plains, and were largely experimental.

Conclusions: Our review suggests new opportunities for co-production of science and decision-making frameworks among researchers, land managers, and seed producers to inform seed selection guidance for restoration.

Implications for Practice: Key differences between the agency guidance and scientific literature indicate opportunities to integrate theory and practice to improve seed selection. Research and guidance to mitigate the genetic risks associated with seed sourcing, production, and use, and to develop climate change adaptation strategies could improve seed selection and restoration outcomes. Incorporating observational and experimental studies into restoration and seed production could inform adaptive management and accelerate the development of seed selection guidance. Modifying seed provenancing strategies could meet emerging needs for restoration sites and strengthen outcomes. Our synthesis of science-based, management-ready decision-support tools can help reduce barriers to implementing seed selection guidance in practice.

Key words: land management, local adaptation, plant functional traits, restoration genetics, seed provenancing, seed transfer zones

Introduction

Selecting plant materials (seeds, propagules, or whole plants from species or intraspecific sources; hereafter "seed") that promote plant community and ecosystem recovery is a primary goal of land managers who conduct restoration (Gann et al. 2019). The demand for native seed has grown with increasing ecosystem degradation caused by land use intensification, invasive species, enhanced wildfire activity, and climate change (PCA 2015; St. Clair et al. 2022; NASEM 2023). Improving ecosystem condition in response to these stressors is an immense task for federal agencies who manage 260 million hectares, or 28% of land in the United States (Vincent et al. 2017). For instance, the Bureau of Land Management (BLM), the largest federal land management agency, uses 1.4 million kg of seed per year to perform restoration across widespread tracts of degraded land (Oldfield & Olwell 2015). As this need grows, information to ensure appropriate seed is selected will increase in importance to meet agency goals to conserve and maintain natural resources for future generations.

In the past few decades, there have been extensive efforts to develop and provision federal land managers with much-needed seed (PCA 2015). Using native instead of non-native seed for restoration on federal lands has become increasingly favored

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[1]U.S. Geological Survey, Southwest Biological Science Center, 2255 N Gemini Drive, Flagstaff, AZ 86001, U.S.A.
[2]Landscape Stewardship Collective, Flagstaff, AZ 86004, U.S.A.
[3]Address correspondence to S. M. Munson, email smunson@usgs.gov

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and mandated in the last 20 years to support ecosystem integrity (Richards et al. 1998; NASEM 2023). The release of interagency guidance, the National Seed Strategy for Rehabilitation and Restoration (hereafter, "Seed Strategy"), in 2015 laid a framework for expanding the native seed industry in the United States to ensure a reliable seed supply for restoration (PCA 2015). The native plant industry has continued to grow since then, resulting in an increasingly rich supply of native seed (NASEM 2023). However, the ideal species and sources for restoration, referred to by the Seed Strategy as "the right seed, in the right place, at the right time (PCA 2015)," are not available or known for every restoration project.

We conceptualized seed selection factors along two axes: ecological conditions, which include abiotic and biotic factors, and human interventions, which include producer and land manager practices (Fig. 1). Abiotic factors encompass climate, soil type, and other site physical conditions (Gann et al. 2019; Erickson & Halford 2020) and biotic factors include species' traits, genetics, and community interactions (Bucharova et al. 2022; Wadgymar et al. 2022). Seed selection also considers land manager practices that include using seed transfer zones to guide sourcing decisions, project goals, and socioeconomic elements like policy and budget (Richards et al. 1998; Erickson & Halford 2020). Finally, producer practices cover choices about what species and seed sources to agriculturally increase and how to harvest, store, and certify their products (Erickson & Halford 2020; Pedrini & Dixon 2020).

The degree to which each of these factors is prioritized and overlaps with others in seed selection often varies widely depending on the scientist or manager who is providing guidance and making decisions (NASEM 2023). Regardless, scientific studies contribute ecological theory and principles, robust methods, and quantitative results that can create new insight to optimize seed selection (e.g. Bucharova et al. 2019; Leger et al. 2021; Winkler et al. 2024). As such, the scientific literature examines emerging and novel seed selection approaches that may improve restoration outcomes. In contrast, the practice of ecological restoration often prioritizes established practices and must contend with limited resources and other real-world barriers to implementation (NASEM 2023). Agency guidance is typically developed in the context of the goals of ecological restoration but may not always consider the current state of research knowledge. As such, comparing the information provided between agency guidance and the scientific literature can identify important knowledge gaps, which, if closed, may help increase efficiencies, enhance coordination, and support successful restoration outcomes (e.g. PCA 2015; Gann et al. 2019).

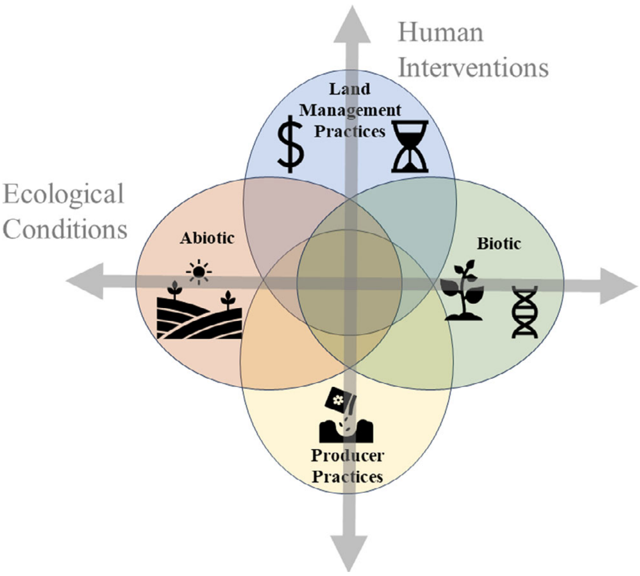

Figure 1. Conceptual diagram of the primary factors that contribute to seed selection decision-making along two axes: ecological conditions that include abiotic (e.g. climate, soil type, and physical site conditions) and biotic factors (e.g. species' traits, genetics, and community interactions), and human interventions that include producer (e.g. seed development, seed certification, and cultivars) and land management practices (e.g. actions related to goals, budgets, and policies) in the restoration process.

Here, we review scientific literature that informs seed selection and compare this to guidance for federal agencies on selecting seed in practice. Our objective was to evaluate the degree to which federal agency guidance considers ecological and human intervention factors in the selection process and aligns with current research (Fig. 1). We leverage insights from this assessment to synthesize the state of knowledge relevant to seed selection practices. Specifically, we compare how biotic and abiotic factors, management practices, and producer practices are incorporated into seed selection between the literature ("theory") and agency guidance ("practice") to identify knowledge-action gaps and opportunities to improve the seed selection process. Our review focused on unforested, water-limited ecosystems where seed-based restoration is widely used but is constrained by low and variable precipitation and high temperatures compared to forests or wetlands (Havrilla et al. 2020; Shackelford et al. 2021). We limited the review to the interior western and central United States, where these ecosystems are common and federal agencies manage and provide management guidance across large tracts of land.

Methods

Scientific Literature Review

We searched for relevant literature using Google Scholar by combining a static search term string and variable search terms. The static search term string included "native plant material" OR "seed source" OR "seed provenance" AND "United States" to ensure the search output would include content on seed selection and be relevant to the United States. Variable search terms were individually combined with the static search term string with the Boolean function "AND." Variable search terms included "disturbance," "dryland," "grassland," or "restoration" to clarify site conditions, and "climate," "soil," "ecoregion," "genetic," "genomic," "local adaptation," "seed transfer zone," "trait," "functional trait," "cultivation," "production," "agronomic," "cultivar," or "land management" to ensure articles addressed how abiotic factors, biotic factors, land manager practices, and (or) producer practices related to seed selection. Although terms are shown here in quotes to differentiate them, we did not include quotes in Google Scholar searches to include plurals and derivatives.

We reviewed literature that met the following criteria: (1) published in peer-reviewed academic journals that addressed grasses, forbs, or shrubs (excluded trees and non-vascular plants) in unforested, water-limited ecosystems, (2) were conducted in, or relevant to, the interior western and central United States (Fig. 2), (3) had applicable information for seed sourcing (e.g. species or seed source selection). We stopped looking for additional articles in searches when we encountered 20 consecutive articles that did not meet search criteria or that we already reviewed. Our searches returned 593 potential articles, of which 183 from the time period 1994–2024 met the above three criteria for review (Shriver & Munson 2025).

We determined study locations and created a map of the ecoregions (Level III, EPA 2024) in which the studies occurred or were relevant. We classified articles by study type based on the primary approach employed to generate guidance for selecting seed: experimental (manipulated variables in a lab, field, or model simulation), methodological (developed new techniques or analyzed existing techniques), observational (examined study subject without manipulation), perspective (provided viewpoint based on opinion, idea, or insight), review/synthesis (summary of published research). We extracted study objectives, key concepts, findings, and conclusions in relation to seed sourcing in the literature review (Shriver & Munson 2025). Similarly, we identified recurring recommendations and directions about seed sourcing from agency guidance.

Federal Agency Guidance Review

We reviewed federal agency guidance on seed sourcing for restoration and rehabilitation projects (Table 1). We included five federal agencies that manage land and (or) provide guidance on seed sourcing within the U.S. Department of the Interior: BLM, National Park Service (NPS), and the U.S. Fish and Wildlife Service (USFWS); and the U.S. Department of Agriculture: U.S. Forest Service (USFS) and the Natural Resources Conservation Service (NRCS). To find agency guidance, we searched on Google for "plant materials policy OR guidance" and the name of each agency above. We only included documents with national-level guidance (excluded regional or project-specific plans) and confirmed their relevance with members of the Plant Conservation Alliance, a federal interagency committee who coordinate the Seed Strategy (PCA 2015)—which we also reviewed. We only included sections of each document with information relevant to seed sourcing for analyses, as several documents included policies unrelated to seed selection (Table S1).

Keyword Analysis

We conducted a keyword analysis with words used in the literature and federal agency guidance in relation to seed selection

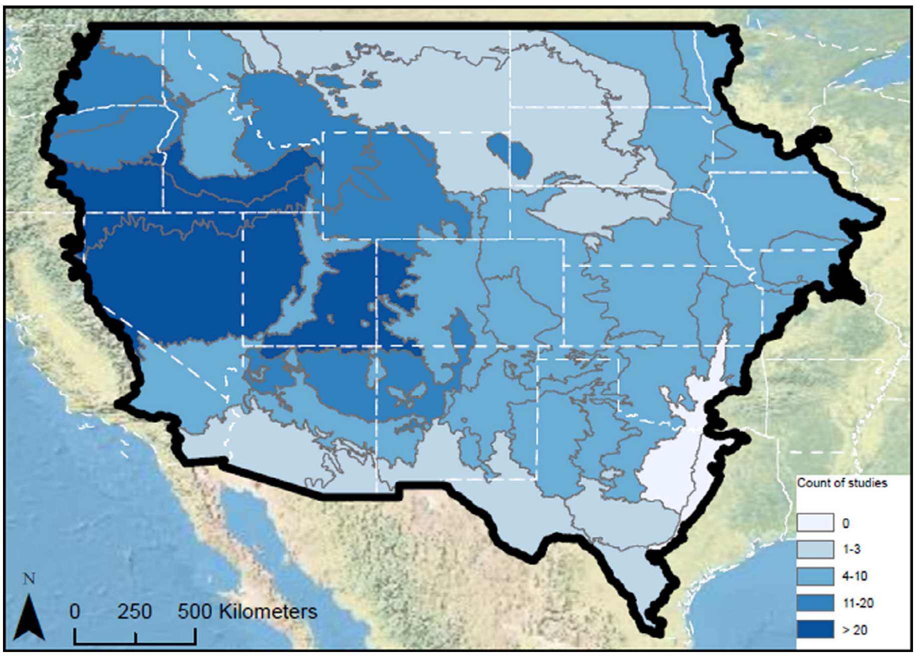

Figure 2. Number of studies addressing seed selection by ecoregions of the interior western and central United States. Of the 183 studies included in our literature review, 97 specified location(s) were included in the map, while 59 did not specify a location and 27 covered a very large geographic area and were not included. Our review focused on unforested water-limited ecosystems of the interior western and central United States. We delineated this study area (outlined in black) with the Sierra Nevada and Cascades ecoregions in the west and the eastern edge of the Great Plains in the east . This area is where unforested water-limited ecosystems are more concentrated. The basemap is the USA Topo Maps (Copyright: 2014 National Geographic Society, i-cubed) and Level III ecoregion boundaries were derived from shapefiles provided by the Environmental Protection Agency (EPA 2024).

Table 1. Federal agency and the guidance document(s) reviewed that informs plant material selection.

Agency	Guidance documents
Bureau of Land Management	BLM (2008), BLM (2007), BLM (1992)
National Park Service	NPS (2006)
U.S. Fish and Wildlife Service	USFWS (2006), USFWS (2002), USFWS (2003)
National Resource Conservation Service	NRCS (2016), NRCS (2017b), NRCS (2019), NRCS (2020), NRCS (2021), NRCS (2022b), NRCS (2022a), NRCS (2022c), NRCS (2023), NRCS (2024a)), NRCS (2024b)
U.S. Forest Service	USFS (2008), USFS (2012))
Interagency (Plant Conservation Alliance)	PCA (2015)

(Table 1) to identify similarities and differences between the bodies of work. We chose keywords by compiling a list of common relevant words from articles found in our reviews and combining words that were synonymous (e.g. ecological region and ecoregion) or used in the same context (e.g. genetic contamination, pollution, and swamping) (Table S2). This resulted in 39 keywords, which we categorized into abiotic factors, biotic factors, producer practices, land management practices, or a combination of these based on how they were primarily used (Tables 1 & S2). We employed the "kwic" function in the quanteda R package (Benoit et al. 2018) to determine the number of times each keyword was used in each of the literature and agency guidance and divided these values by the total keywords used in each body of work to determine the relative frequency of each keyword. We used a Pearson's chi-square test with continuity correction to determine if either individual keywords or categories of keywords were used equally between agency guidance and the literature and applied Monte Carlo simulations to compute *p* values from the asymptotic chi-squared distributions of the test statistic using the "chisq" function in the corpora R package (Evert 2023). All analyses were conducted in R version 4.4.1 (R Core Team 2024). We used emergent themes from the reviews of both scientific literature and agency guidance to expand on the keyword analysis.

Comparison of Theory and Practice

Most studies in our literature review were experimental or perspective, followed by review/synthesis and methodological, with the fewest number of observational studies (Fig. 3). The large number of experimental studies reflects the need to understand how species and seed sources perform in controlled environments to infer mechanisms promoting success. Abundant perspective pieces provide a conceptual understanding of how to select seed, but tests of these concepts as hypotheses with empirical data are lacking. Fewer observational studies indicate an opportunity to examine trait and genetic characteristics of plants in their natural biophysical settings and combine these observations with new methods to improve restoration, as this has been done to increase crop production (Leger et al. 2024).

In the literature, studies were concentrated in the ecoregions that form the Great Basin and Colorado Plateau cold deserts, with the adjoining Columbia Plateau, Blue Mountains, Middle Rockies, and Wyoming Basin also receiving considerable attention (Fig. 2; Shriver & Munson 2025). In contrast, the warm desert ecoregions of the Southwest had fewer studies, and coverage in ecoregions of the Great Plains was patchy. These patterns may reflect concentrated efforts of BLM native plant materials development programs in the Great Basin, Colorado Plateau, and Mojave Desert ecoregions that support seed development and research (PCA 2015). In addition, seed-based NRCS conservation programs in the Great Plains have historically produced a significant amount of research (NRCS 2025).

Across literature and agency guidance, seed selection depended heavily upon biotic factors, with 15 of the 39 keywords assigned to this category. Biotic keywords were used most frequently (46.7% of all keyword uses for literature and guidance combined), followed by abiotic (19.9%), biotic + land management (15.0%), producer practices (7.9%), abiotic + biotic (6.1%), producer practices + land management (3.7%), and land management (0.7%) (Table S3; Fig. 4).

Abiotic Factors

Because climate and soils primarily influence the distribution of plant species, both the literature and guidance connected seed selection to abiotic factors and concepts that combined abiotic and biotic factors. Keywords associated with abiotic factors were used 7.2% more in the literature than agency guidance, but the combination of abiotic + biotic factors was used 7.7% more in agency guidance compared to the literature

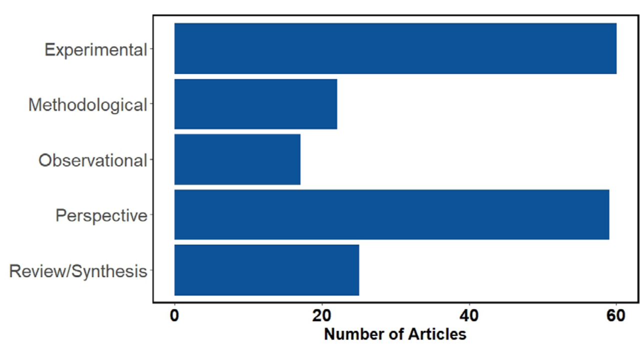

Figure 3. Number of reviewed articles on seed selection in the scientific literature by study type.

(Table S3). Agency guidance often recommended selecting species and sourcing seed by matching the climate, soil, topography, and other abiotic conditions of the restoration site to species habitat requirements or to the source population site (BLM 2007, 2008; USFS 2008; NRCS 2020, 2021, 2023, 2024a). The BLM and NRCS guidance specifically recommended using the Ecological Site classification system, which designates distinctive land units with similar ecological potential based on biophysical conditions that are expected to respond similarly to management actions and disturbance (NRCS 2017a). Guidance from the BLM and USFS recommended using seed sources from the same ecoregion as the project site (BLM 2008; USFS 2012). Ecoregions are larger areas than ecological sites where the ecosystems and associated environmental characteristics are similar (PCA 2015). For species selection, the NRCS recommended using reference sites to determine appropriate target conditions and restoration goals (NRCS 2017b, 2019, 2023), and USFWS recommended using an ecological frame of reference to contrast current site conditions to historic conditions (USFWS 2006).

The literature regularly considered abiotic factors because they influence where species are found, how their morphological traits vary, and their patterns of genetic diversity (Baughman et al. 2019; Wadgymar et al. 2022). The most common abiotic keyword "climate" (5.6% of agency and 14.2% of literature) frequently informed seed transfer guidance (Johnson et al. 2012; Bower et al. 2014; Doherty et al. 2017), though some research indicated that soil information should also be incorporated into seed zones (Gibson et al. 2019). Climate is fundamental to several decision-support tools available in the literature and in agency guidance to help managers select seed (Table 2). Climate change was considered at a similar frequency in the literature and in agency guidance (Fig. 4). In agency guidance, climate change was discussed as a challenge to maintaining and restoring healthy ecosystems and as a consideration in selecting appropriate seed sources and restoration techniques (USFS 2012; PCA 2015). The literature discussed the potential impacts of climate change on seed selection decisions, particularly how climate change may make local sourcing less relevant in places where the climatic conditions plants are locally adapted to no longer exist (Aitken & Whitlock 2013; Prober et al. 2015; Ramalho et al. 2017).

Biotic Factors

Most keywords belonged in biotic categories: biotic, abiotic + biotic, and biotic + land management. Biotic keywords factored heavily into seed selection recommendations in agency guidance (24.6%), and even more so in the literature (47.1%) (Table S3). Both bodies of work included genetics in sourcing recommendations, and agency guidance frequently referred to "genetically appropriate" seed (7.8% agency, 0.4% literature, Fig. 4), which means seed is environmentally adapted to the restoration site, genetically diverse, and unlikely to cause genetic contamination or undermine local adaptations (USFS 2012; PCA 2015). Determining genetic appropriateness is often achieved through local seed sourcing or selecting sources that are geographically close to the restoration site and (or) from an ecologically similar area (McKay et al. 2005; Bucharova et al. 2019; Erickson & Halford 2020).

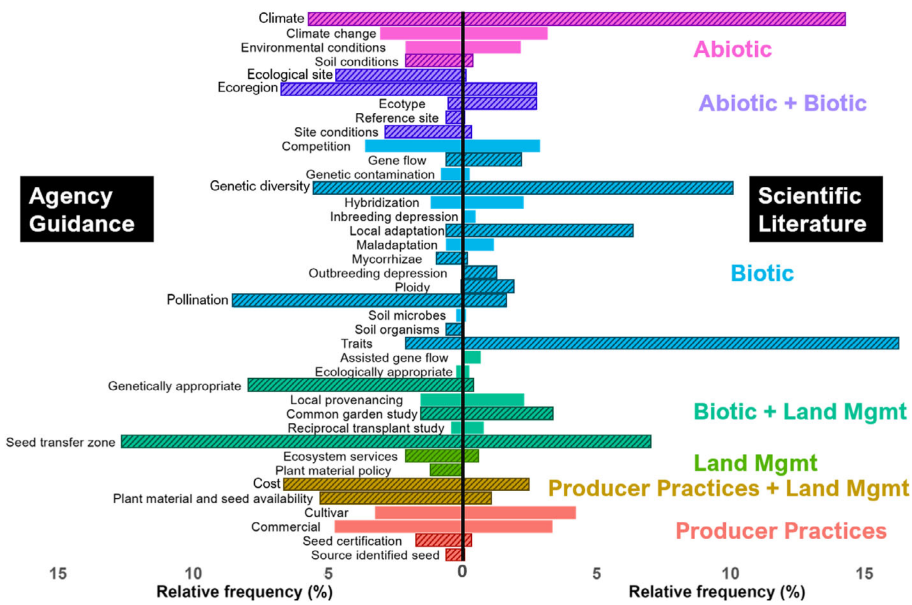

Figure 4. Relative frequency of keyword use in agency guidance and scientific literature. Frequencies are the number of times a keyword is used relative to the total keyword count within each body of work. Dark hashing within bars denotes a statistically significant difference in the relative frequency of an individual keyword used between the agency guidance and scientific literature, as calculated by Pearson's chi-squared test with continuity correction ($p \leq 0.05$). Note that when all keywords are grouped within a single category, there were significant differences in the relative frequencies for abiotic + biotic, land management (Mgmt), and producer practices + land management categories between the agency guidance and scientific literature (Table S3).

Table 2. Decision-support tools and frameworks to inform plant material selection.

Tool name	*Description and intended use*	*Source*
Abiotic—climate		
Climate Distance Mapper	Ranks the suitability of seed sources for current or future climates in the Desert Southwest	Climate Distance Mapper Tool (USGS) (Shryock et al. 2018)
Climate Matching Framework	Method to create species-specific provisional seed transfer maps with climate-matching	Doherty et al. (2017)
Climate-Smart Restoration Tool/ Seedlot Selection Tool	Tools to help find where seed can be planted or where seed should come from in current and future climates	Climate Smart Restoration Tool, Seedlot Selection Tool (St. Clair et al. 2022)
Biotic—seed provenance		
Provenance Figure	Visualizes provenance strategy trade-offs between increasing local adaptation versus providing genetic variability	Bucharova et al. (2019): figure 1
Provenance Decision Tree 1	Guides provenance decisions based on climate change distribution model and the degree of genetic and (or) environmental difference between populations	Breed et al. (2013): table 1
Provenance Decision Tree 2	Guides provenance decisions based on species range and climate	Ramalho et al. (2017): figure 1
Provenance Table	Describes provenance strategies and their benefits, risks, and most appropriate uses	Havens et al. (2015): table 1
Assisted Gene Flow Guidance	Seven recommendations for assisted gene flow to facilitate local adaptation to climate change	Aitken and Whitlock (2013): recommendations begin on page 380, summarized on page 383
Biotic—minimize genetic risks		
Genetic Risk Decision Tree	Decision tree for evaluation of risk in native populations of adverse genetic change from revegetation	Byrne et al. (2011): figure 1
Restoration Genetics Guidelines	Five recommendations from ecological genetics that may be useful for restoration genetics	McKay et al. (2005): recommendations begin on page 436
Sourcing Guidelines	Five guidelines for choosing genetically appropriate plant material sources	Lesica and Allendorf (1999): guidelines are on page 47
Biotic—plant traits		
Traits in Restoration	Five examples of how traits can be integrated into restoration planning	Merchant et al. (2023): box 1
Trait Screening	Methods to screen for adaptive seed and seedling traits	Leger et al. (2021)
Production—cultivar use and selection		
Sourcing Decision Support Tool	Assess benefits and risks of planting wild or cultivar sources in different contexts	Kramer et al. (2019): Figure 1
Restoration Gene Pool Concept	Guides sourcing decisions and provides information about cultivars and introduced plants when using local native sources are not feasible	Jones (2003)
Production—genetic diversity		
Agriculture and Restoration Traits	Summarizes trait differences and implications for genetic conflicts between conventional agriculture and native species restoration	Leger et al. (2024): tables 1 (genetic conflicts), 2 (trait divergence)
Seed Development Guidance	Guidance for maintaining diversity while collecting, producing, and processing seed	Pedrini et al. (2020)
Seed Use Guidance	Guidelines for propagation and restoration to maintain genetic variation	Espeland et al. (2017): Guidelines begin on page 109
Seed Cleaning Guidance	Guidelines for seed cleaning to optimize quality and achieve representative genetic diversity	Frischie et al. (2020)
Seed Collection and Use Guidance	Recommendations for seed collection and use to maintain genetic diversity	Vander Mijnsbrugge et al. (2010): Table 1
Seed Production Guidance	Ten rules to collect and maintain genetic diversity in producing native plant materials for restoration	Basey et al. (2015)

Table 2. Continued

Tool name	*Description and intended use*	*Source*
Land management—seed transfer zones and prioritization		
Disturbance-based Planning 1	Method to optimize the planning of new plant materials based on disturbance patterns	Winkler et al. (2024)
Disturbance-based Planning 2	Method to prioritize management regions and plant material needs based on historic disturbance	Barga et al. (2023)
Seed Transfer Zone map	Online interactive map including climate-based provisional seed zones, Great Basin provisional seed zones, ecoregions, and empirical seed zones	Western Wildlands Environmental Threat Assessment Center Seed Zones Map

Local sourcing is widely recommended in both agency guidance and the literature and assumes that local populations are adapted to local ecological conditions and therefore likely to establish at a restoration site (Broadhurst et al. 2008; Breed et al. 2013; Vitt et al. 2022). Although the keyword "local adaptation" was used relatively more in the literature (6.4%) than agency guidance (0.5%, Fig. 4), some agency documents recommended using local seed with (BLM 2008; USFS 2012) or without (USFWS 2003; NPS 2006; NRCS 2017b, 2019) explicitly mentioning local adaptation. Local adaptation is widespread in plant populations, but it may not always manifest according to expectations (Hereford 2009; Baughman et al. 2019). For instance, populations may not be locally adapted to current weather patterns if they are adapted to climate conditions that no longer exist (Havens et al. 2015; Bucharova et al. 2019; Meek et al. 2023). Further, some local populations are small, fragmented, and have low genetic diversity that may limit their ability to adapt to future environmental change (Broadhurst et al. 2008; Jones 2017; Bucharova et al. 2019).

In the literature, provenancing strategies, or methods to select seed sources to meet goals at the restoration site, are increasingly diverging from the "local is best" paradigm (Aitken & Whitlock 2013; Havens et al. 2015; Bucharova et al. 2019). Climate-focused approaches include predictive provenancing, which uses non-local genotypes from areas with similar climatic conditions to those projected at the restoration site, and climate-adjusted provenancing, which mixes local and non-local genotypes sourced along a climatic gradient (Havens et al. 2015; Prober et al. 2015; Bucharova et al. 2019). Other strategies include composite provenancing, or mixing a large proportion of seed from local populations with progressively smaller amounts of seed from increasingly distant sites to mimic patterns of natural gene flow; admixture provenancing, or mixing local provenances with collections across the species' range to maximize adaptive potential; and regional admixture provenancing, which is similar to admixture provenancing but confined to a defined "region" around the target site with similar ecological conditions and a common biogeographic history (Havens et al. 2015; Prober et al. 2015; Bucharova et al. 2019). Studies testing and comparing provenancing strategies have thus far shown mixed empirical success and more studies are needed to test strategies across taxa, space, and time (Breed et al. 2018; Bucharova et al. 2019; Vitt et al. 2022).

Creating seed mixes of multiple species is suggested by agency guidance (NRCS 2016; St. Clair et al. 2022, 2024a, 2024b), but agencies do not discuss mixing separate populations of the same species that would facilitate different provenancing strategies. Mixing populations is associated with genetic risks (Knapp & Rice 1994; Lesica & Allendorf 1999; Byrne et al. 2011), which the literature discusses in depth (Fig. 4). Genetic risks include genetic contamination of resident populations and the creation of reduced fertility or infertility, or outbreeding depression, that can decrease restoration success (Lesica & Allendorf 1999; McKay et al. 2005; Byrne et al. 2011). The risk of outbreeding depression can be minimized by assessing the likelihood and possible consequences of gene flow (Lesica & Allendorf 1999; McKay et al. 2005;

Byrne et al. 2011). For instance, agency guidance suggests avoiding the use of seed that can interbreed with rare plant species (BLM 2007, 2008) and (or) using materials that are unlikely to undermine local adaptation (USFS 2008). Another, often overlooked, risk of mixing populations is genetic incompatibility due to polyploidy (i.e. populations with different chromosomal numbers) (Aitken & Whitlock 2013; Gibson et al. 2017). Combining plants with different ploidy levels, either in production fields or at restoration sites, leads to increased risk of outbreeding depression and the potential to reduce seed yield or produce infertile offspring (Gibson et al. 2017; Kramer et al. 2018; Richardson et al. 2023).

While agency guidance has yet to address broader provenancing strategies that may support landscape management under changing climate scenarios, it does mention the importance of genetic diversity, even though this keyword is used relatively less (5.4%) than the literature (10.1%, Fig. 4). Agency guidance suggests maximizing and maintaining the genetic diversity of restoration materials or populations under conservation (NPS 2006; USFWS 2006; BLM 2008) and explains that genetic diversity is needed for populations to respond and adapt to changing climates and ecological conditions (USFS 2008). Decision-support tools and frameworks described within the literature illustrate opportunities for agency guidance to incorporate genetic diversity and preadaptation to confront future management challenges (Table 2).

Considering biotic site conditions using reference, undisturbed communities, or pre-disturbance records was also acknowledged as important for species and source selection during landscape management (Gann et al. 2019; Erickson & Halford 2020). Distinct plant populations or genotypes within a species that are locally adapted to specific ecological conditions are often called "ecotypes" (Hufford & Mazer 2003), and the BLM guidance specifies that if plants exhibit ecotypic variation, then local sources should be used (BLM 2008). More generally, plant traits, or morphological, physiological, and other characteristics, are a useful way to select species that may respond to ecological conditions or affect ecosystem function in a desirable way (Larson et al. 2023). Further, some taxa have strong trait-environment associations, such as low specific leaf area in arid conditions (Butterfield et al. 2017), which may be useful in delineating seed transfer guidance (Yoko et al. 2020). Despite their utility and frequent use in the literature, there is debate on whether functional traits are used by restoration practitioners in selecting seed (Gornish et al. 2023; Merchant et al. 2023). The keyword "trait" was used relatively more in the literature (16.2%) than agency guidance (2.0%, Fig. 4), but some agencies, particularly NRCS, mention selecting for desirable plant characteristics in relation to ecosystem services without using the keyword "trait." For instance, NRCS guidance describes selecting species with deep roots to increase soil organic matter (NRCS 2021) or for erosion protection (NRCS 2024b). Guidance is rapidly increasing on how incorporating traits into restoration practice can expand the selection of existing species that can establish and recover desired ecosystem conditions at a restoration site (Table 2).

Seed selection may also consider biotic interactions, including between the target plant and its pollinators (Bucharova et al. 2022), mycorrhizal fungi and other soil organisms (Larson et al. 2022), and among multiple plant species (Espeland & Richardson 2015). Agency guidance refers to the keyword "pollination" at a higher frequency (8.4%) than the literature (1.6%, Fig. 4), including how to select species to support pollinators (NRCS 2016; St. Clair et al. 2022, 2023, 2024b), and in the context of gene flow and interactions with seed sources (BLM 2008; USFS 2012). Agency guidance also mentions the potential impacts of seed selection on beneficial soil microbes (BLM 2008) and soil organisms (NRCS 2024b). Plant competition may influence restoration outcomes, and some agency guidance cautions against using species with strong competitive abilities, especially non-native species (BLM 1992; USFS 2012) and those that may displace rare plants with special status (BLM 2007, 2008). However, other guidance suggests land managers choose species that suppress weeds or undesirable plants (NRCS 2023, 2024b). This conflicting guidance suggests that selecting "competitive" or "non-competitive" plants may depend on environmental context and project goals. The literature assesses the competitive ability of native with invasive plant species (Herget et al. 2015; Baughman et al. 2016) or between desirable species seeded together (Espeland & Richardson 2015).

Producer Practices

Producer practices were the only keyword category that did not have statistically significant different use between agency guidance and literature (Table S3). However, individual keywords associated with producer practices or producer + land management practices were used relatively more in agency guidance and reflect efforts to guide managers to choose appropriate species and seed sources for project goals and budget. For instance, BLM guidance outlines options within the commercial market, including whether seeds are germplasm releases or certified (BLM 2008). Germplasm releases, which include cultivars, are agriculturally produced seeds that can be developed on a natural track where any potential selection or testing is focused on desirable traits present in wild populations, or on a manipulated track where individuals from wild populations are genetically manipulated through hybridization, combining seed sources, and (or) artificial selection (Jones & Young 2005; BLM 2008). Agency guidance recommends using certified seed (BLM 2008; St. Clair et al. 2022, 2024a) or seed that would meet certification standards (USFS 2012), so its origin and level of genetic manipulation are known. This guidance is rooted in the literature, which discussed the effects of artificial selection on plant traits and genetics (Jones 2009; Kettenring et al. 2014; Leger et al. 2021). Historically, the seed industry focused on improving seed for agricultural productivity and natural resource conservation through plant breeding and artificial selection of traits that enhance performance and are amenable for commercial agronomic propagation (Jones 2009; Kettenring et al. 2014). However, researchers have raised concerns about cultivars, and the keyword "cultivar" was used relatively more in the literature (4.2%) than agency guidance (3.1%; Fig. 4). Concerns include increased genetic contamination and competition with locally adapted plants, reduction in genetic diversity, and selection for agronomically suitable traits that may not be suitable in restoration settings (Kettenring et al. 2014; Leger et al. 2021; 2024).

Empirical studies comparing wild sources to cultivars have yielded mixed results, with some finding no performance differences (Wilsey 2010); better performance in cultivars (Gustafson et al. 2004); better performance in wild sources (Uselman et al. 2018); and context-dependencies, including whether invasive species are present (Herget et al. 2015; Baughman et al. 2016). Contemporary restoration guidelines (PCA 2015; Pedrini & Dixon 2020) generally eschew cultivar use for ecological restoration, and BLM guidance recommends using local sources over cultivars when possible (BLM 1992, 2007, 2008). However, some researchers argue that there is a role for cultivars and artificial selection in restoration, especially in harsh, altered ecosystems (Jones & Monaco 2009; Chivers et al. 2016).

On both sides of the artificial selection debate, scientific literature indicates that maintaining or increasing genetic diversity is essential to producing restoration materials (Knapp & Rice 1994; Chivers et al. 2016; Espeland et al. 2017). Recommendations for maintaining genetic diversity of seed involve avoiding unintentional selection that may lead to genetic and trait shifts (Basey et al. 2015; Pedrini et al. 2020; Pizza et al. 2021). Differentiation of a suite of traits away from natural populations, referred to as "domestication syndrome," includes reduced seed dormancy, higher seed retention, rapid germination and growth, and synchronized phenology (Basey et al. 2015; Chivers et al. 2016)—these traits may not be desirable in natural systems and restoration settings (Leger et al. 2021, 2024). Methods to maintain genetic diversity include matching restoration and production site conditions, avoiding unintended hybridization, harvesting seed throughout the growing season, and collecting wild seed randomly and evenly across an entire population (Table 2). Many of these strategies are outlined in the BLM agency guidance (BLM 2008).

Agency guidance also discussed practical concerns, including the cost (6.5%) and availability (5.2%) of seed relatively more than the literature (cost: 2.4%, availability: 1.1%, Fig. 4). Federal agencies have worked to increase the supply of native seed (Oldfield & Olwell 2015; PCA 2015; Jones 2019), but critically, current ecological restoration efforts require more seed than is currently available (NASEM 2023). The literature acknowledges the lack of commercially available native seed and offers suggestions to increase availability across the United States, including stabilizing variability in supply and demand and increasing knowledge for growing native species in agricultural settings (White et al. 2018; Camhi et al. 2019; Jones 2019). Inconsistent demand stems from unpredictable wildfires that spike demand and prices (Richards et al. 1998; White et al. 2018; Jones 2019) and variation in the type of seed purchased as budgets, goals, and interpretations of policies that may differ by land manager and change through time (Peppin et al. 2010; Jones 2019; Harrison et al. 2020). Additionally, many native species have not been grown in agricultural settings before and may have traits that are not amenable to agricultural production (White et al. 2018; Jones 2019). The National Academies of Sciences, Engineering, and Medicine (2023) suggested that federal agencies assist seed suppliers by taking steps to reduce uncertainty, share risk, and increase the predictability of purchases while also creating and sustaining an outreach program to provide seed suppliers with critical tools and information.

Land Management

Keywords associated with land management or a combination biotic + land management practices were used 2.6 and 9.1% more frequently in the agency guidance than the literature, respectively (Table S3). Federal policy increasingly relies on native plants, and agency guidance encourages use of local native seed but allows use of non-native species when using native plants is not suitable or possible (BLM 1992; USFWS 2002; NPS 2006; USFS 2008, 2012; NRCS 2019, 2020, 2021, 2022a). Use of local native seed is influenced by cost and availability (BLM 1992, 2007, 2008; USFS 2008), management goals (BLM 1992; NPS 2006), and timing (USFS 2008). Cost may be a particularly important factor in selecting seed. For instance, BLM guidance suggests using commercial sources or cultivars to decrease costs over collecting and growing out local seed (BLM 2007, 2008). Local seed is often more expensive and less consistently available than cultivars and non-natives (Camhi et al. 2019; McCormick et al. 2021). Project goals also influence seed sourcing, including the use of native or non-native species, as suitability may depend on whether goals aim to restore historical native plant communities, recover ecosystem services, or achieve rapid stabilization (Gann et al. 2019).

Seed transfer zones, which are fixed areas in which seeds can be transferred with minimal risk of maladaptation (PCA 2015), were frequently discussed in the literature (7.0%), and relatively more so in the agency guidance (12.5%, Fig. 4). Agency guidance suggests managers use seed transfer zones when they are available (BLM 2008; USFS 2012; St. Clair et al. 2022, 2023). Seed transfer zones include empirical zones, which are species-specific and developed with empirical data, and provisional zones, which can be used when empirical guidance is not available (Bower et al. 2014). The most widely used provisional seed transfer zones in the U.S. are based on winter minimum temperature and aridity, which are adaptively important across taxa (Bower et al. 2014). These climate-based provisional seed transfer zones can be further refined with guidance from molecular genetic and climatic variability data (Massatti et al. 2020) or by combining them with ecoregions (Bower et al. 2014; Kramer et al. 2015). Empirical seed zones are often developed through common garden or reciprocal transplant studies, which grow different genotypes or populations in one environment (common garden study) or exchange them across multiple environments (reciprocal transplant study). By minimizing environmental effects on trait expression, inherited genetic variation can be correlated with environmental variables (e.g. Johnson et al. 2012; Johnson et al. 2023). Empirical seed zones are also created by correlating adaptive genetic variation inferred from DNA to environmental drivers important to species performance (Shryock et al. 2017; Crow et al. 2021), which may be further refined by incorporating patterns of genetic diversity and structure resulting from historical processes (Massatti et al. 2018; Massatti & Winkler 2022). Empirical seed zones are lacking for most native species, but tools are available to help managers use available seed transfer zones and prioritize management areas (Table 2).

Future Directions

There is a wealth of scientific knowledge related to seed selection that informs federal agency guidance for ecological restoration. Our reviews and quantification of key terminology within literature and agency guidance highlight both successful communication between scientists and managers to meet common goals (i.e. where terms are used by both groups) and opportunities for each group to better understand needs or important knowledge (i.e. where terms are disproportionately used by one group or the other). We view this latter contrast as an indicator of where new knowledge can be created and guidance can incorporate recent findings. Our synthesis of scientific literature and agency guidance highlights the following synergisms as potentially valuable to future management and research collaborations. First, increasing the use and application of observational and trait-based studies may inform adaptive management to improve restoration outcomes. Second, testing provenancing strategies and developing climate-resilient seed transfer guidance that incorporates abiotic and biotic conditions across taxa, time, and space may provide management options as weather patterns and variability change. Third, developing evidence-based guidance to minimize genetic risks in mixing seed may address uncertainty and improve seed sourcing outcomes. Fourth, stabilizing demand and fostering knowledge sharing may increase the supply of native seed by strengthening connections between land managers and producers. Fifth, developing management-ready decision-support tools may decrease barriers to implementation of practices based on new research (see Table 2 for examples of existing tools). These opportunities for collaboration can strengthen the native seed supply to help ensure land managers and practitioners have the seed they need for future restoration efforts.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Sections of agency guidance included in keyword data analysis.
Table S2. Keywords and their associated search term(s).
Table S3. Keyword use by category.

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