Four paths toward realizing the full potential of using native plants during ecosystem restoration in the Intermountain West

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On the Ground

- Using native species in seed-based restoration efforts is critical for recreating or maintaining healthy, resistant, and resilient ecosystems and communities in the Intermountain Western United States.
- The use of seed from native species has increased dramatically in the last few decades, and so have research and the development of new guidance for best practices.
- Despite all the valuable effort to date, we have yet to see the full potential of native plant species restoration in this region.
- Several important paths to improved success of native plant restoration are clear: recognize and leverage intraspecific variation and local adaptation in plants, increase the development and use of seed transfer guidance, build seed production partnerships to benefit restoration and local communities, and be ready and willing to adopt changes to the way things are done when the evidence is clear that change will help.
- The challenge of returning native plants to degraded dryland ecosystems will always be prone to failures, but improved success is possible if researchers, policy makers, restorationists, seed growers, and others work to bring new science, guidance, and recommendations to scale.

Keywords: native species, ecological restoration, seed selection, seed zone, seed cooperative, seed partnership.

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Introduction

Ecosystems are always changing. Throughout the world, many factors are increasingly pressuring ecosystems altering their trajectories.[1] Global climate change, variable localized weather patterns, catastrophic wildfires, exotic plant invasions, and natural and/or human-induced disturbances all affect plant communities.[2,3] Negative changes in plant communities have serious trophic level impacts for nature and people.[4] Land managers work to foster positive trajectories in plant communities to create or maintain sustainable and healthy ecosystems. Plant communities resistant and resilient to current and future pressures are essential to conserving natural resources and functional environments for use by future generations.[4–6] Today, many arid dryland systems throughout the world are degraded and invaded by exotic species to the point that restoration of more desirable vegetation is needed.[7–9] However, restoration in these harsh environments is complicated, expensive, and prone to failures.[8]

Our objective is to discuss and promote the use of native plants in restoration programs, specifically those of the sagebrush steppe ecosystems of the Intermountain West of the United States. Other papers in this issue discuss the value of native species (particularly perennial bunchgrasses) in the resilience, restoration, and conservation of these ecosystems.[10,11] We review the history and current trends of using native plants in seed-based restoration at large scales, and then suggest and discuss several promising paths forward for improving the success of native plant restoration. We are confident substantial improvements are ahead, and many useful concepts and approaches have yet to show their true merit. Although we are focused on the current situation in the Intermountain West, our overall suggestions are applicable to other regions and ecosystems struggling with native plant species restoration.

Why focus on native plant restoration?

Native plants and the multispecies communities they form are complex. The native plants of the Intermountain West number nearly 4,000 species.[12] Each species has evolved a complicated suite of traits allowing them to acquire resources despite a fluctuating environment. Plants continuously vie for these resources across the landscape and over time as weather and disturbance regimes change. To be successful, plants must survive in connected populations, and acquire enough resources to complete their life cycle. Within a community, some species thrive in conditions in which others do not. Additionally, some plant species are coadapted to fostering and relying on community success in addition to their own success.[13,14] Therefore, a diverse community of native plants has the best chance of being resistant and resilient to change.

Native plants have been the cornerstone of human livelihoods in sagebrush (*Artemisia* spp.) steppe for generations. For some, this relationship extends to time immemorial and is inseparable from their own origin and identity.[15] For others, the bounty of these ecosystems sustained more recent ancestors via livestock grazing on publicly owned lands.[16] Until the last few centuries, native plants were the only plants in the Intermountain West, covering all possible surfaces, and adapting to every one of the myriad combinations of soil, terrain, climate, disturbance, and interactions with other species.[17] However, native plants are no longer the only plants, and livelihoods tightly linked to native plant communities are no longer the only livelihoods.

Native plant communities across many million hectares in sagebrush steppe currently struggle to thrive and maintain themselves and are being lost or degraded at such a rate that the sagebrush steppe is one of the most imperiled major ecosystems in North America.[16,18,19] Large-scale deployment of seeds into remote and untended lands using intentionally chosen species via mostly publicly funded efforts has been occurring and increasing for decades. For example, the U.S. Bureau of Land Management alone has spent nearly a quarter billion dollars on seeding and related activities across nearly 1.5 million hectares (over 3.5 million acres) of public lands in the last 10 years.[20] Despite these efforts, rates of loss and degradation of native plant communities are on the rise.[21] Success rates of seed-based restoration have been low in the sagebrush steppe[22–26] as well as in other arid and semiarid lands around the globe.[7] Challenges to successful restoration are numerous and complex, from increasing pressure of invasive species, dramatic changes to wildfire cycles, variable weather and shifting climate patterns, native seed supply chain limitations, and the interactions of these factors with the ever-changing politics of managing lands and ecosystems for a growing number of public and private uses.

With the large scale and low success of native plant restoration in the sagebrush steppe despite decades of effort, one could assume every possible option has been tried, and still nothing works. However, despite valiant efforts and innovation to restore with native plants, this assumption is faulty.

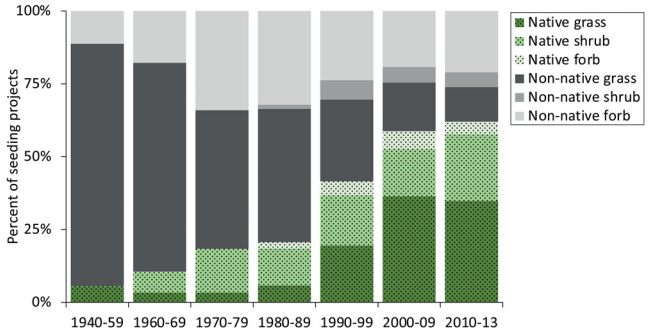


Figure 1. Trends in the use of native (green, speckled) vs. non-native (gray) seed in the Great Basin 1940-2013, by functional group, as a percent of the total seeding projects completed each decade that includes each type of seed. An important pattern not shown is that a great majority of recent seeding projects include both native and non-native species, meaning many projects tallied as using native species may also include non-native. The number of seeding projects per year during this time (also not shown) steadily increased from dozens per year in the 1940s to several hundred per year by the year 2000. Data are from the Land Treatment Digital Library, adapted from supplemental material presented by Pilliod et al.[78]

There is a relatively short history of using native species in reseeding and restoration in this region, and an even shorter history of a comprehensive understanding of which seeds should be planted where and how. After unsuccessful trials in the Intermountain West using midwestern forage grasses at the beginning of the 20th century, managers invested little effort into reseeding drylands of this area until the introduced species crested wheatgrass (*Agropyron cristatum*; originally from Russia, Turkey, and Kazakhstan) showed promise in the 1930s and 1940s and became the subject of substantial breeding and research.[25,27] Machinery capable of operating on wildlands was also being developed at this time, culminating in the initial versions of the rangeland drill in the 1950s,[28] which facilitated a major increase in the scale of wildland seeding. Since then, around a dozen introduced species of grasses, forbs, and shrubs have dominated seeding efforts on arid and semiarid lands. In the Great Basin specifically, introduced species were the only species planted in most seedings until after the year 2000 (Fig. 1). Native plant species were included in less than a quarter of seeding efforts before 1990, and only a small percentage of those were seedings containing exclusively native plant species. Before the early 2000s, the most common native seed used in the Great Basin was limited to <20 varieties of species, nearly all of them with a history of selection or breeding for traits not tightly linked with success from seed in realistic restoration scenarios, and few originating from the specific regions where they were seeded for restoration.[29,30]

There has been an increase over the last 20 years in the use of native plant species in restoration, which are now seeded more frequently than introduced species. Jones and Larson[31] reported an impressive 4-fold increase in seed production fields dedicated to native plant species from 1996 to 2000. However, this increase has occurred simultaneously with a great deal of research and learning to improve their success. As a result, the standard approach to seeding is not yet re-

flective of the best approach, because the best approach is changing with new knowledge and innovations, and adopting change on the ground is complicated and takes time. For example, recent work concludes multiple native plant species interact to improve one another's success using coadapted traits.[13] However, practitioners in our region cannot yet implement seedings at scale with multiple, coadapted populations of different native species due to limited seed source availability. In the last 10 years, practitioners and researchers have increasingly worked together to understand the efficacy of historic and contemporary practices and begun to incorporate evidence-based, new approaches to native plant restoration, and progress has been made.[32] Compare this to many decades of selection, breeding, and testing efforts toward producing 18 largely successful varieties of crested wheatgrass,[27] and it is clear there is untapped potential ahead for many native species.

Given the dire need for successful restoration in the Intermountain West, and the history of native plant use, we focus on four important avenues to improve native plant restoration success, and thereby, improve ecosystem function and resilience. These and other recommendations for achieving improved native plant success are detailed in the Plant Conservation Alliance's 2015 National Seed Strategy.[32,33]

1. Recognize and leverage intraspecific variation and local adaptation
2. Create, test, and increase the use of seed transfer guidance
3. Build native seed partnerships to benefit restoration outcomes and local communities
4. Be ready and willing to adopt changes when the evidence is clear

Why work so hard to be successful with native plant species in the sagebrush steppe when there is already a suite of desirable nonnative species that establish reasonably well? This long-standing, regional debate will continue, and it is not our aim to end it or pick sides (see Johnson et al. this issue, for a related discussion).[10] Rather, our goal is to enrich the collective understanding of how far native plant restoration has come, and how much farther it can go before its full potential can be seen. Also, awareness of the importance of native plant diversity to the value and function of our wildland ecosystems is growing. Many new guidelines and policies are calling for increased use of native plant species in restoration, from the U.S. White House and Congress,[34,35] to other federal agencies,[36–38] to state governments and regional working groups,[39,40] to hundreds of private and nonprofit organizations.[33] These demonstrate that the desire for improved use and abundance of native plant species is not a fad, and is instead a growing priority from many national, state, regional, and local directions. Together, they signal successful native plant restoration is the best path to keeping wild ecosystems supporting the biodiversity and species interactions that make them work for people and wildlife, now and into the future. We demonstrate we have not yet seen the best possible restoration outcomes with native plants, and there is more potential ahead. Getting there will take time and coordination, but we are confident there are clear paths toward improved success.

On the subject of innovation, the famed inventor Thomas Edison noted "When you have exhausted all possibilities, remember this: you haven't" and "My so-called inventions already existed in the environment…I've created nothing. Nobody does."[41]

Four paths to improved native plant restoration success

Recognize and leverage intraspecific variation and local adaptation

Plants are unable to move to avoid challenging conditions, except through reproduction and seed dispersal. They are adapted to succeed where they grow by developing, over many generations, useful traits and strategies. These traits and strategies may differ between individuals or populations of the same species across their habitat.[42] These differences may be small or large and lead to intraspecific genetic variation, in which physically separate populations of the same species differ in how and when they grow and reproduce and pass on these differences to their offspring (Fig. 2). When this intraspecific variation results in each population being most successful in its home habitat, and less successful than other populations in a new habitat, this is known as local adaptation. Although local adaptation is not a guaranteed result of intraspecific variation, research on many species worldwide indicates it occurs more often than not.[42–50] Why wouldn't it be common for immobile lifeforms to be adapted to the conditions they live in, and come to be different from those living in other conditions?

The Intermountain West hosts many endemic and rare plant species, but is also characterized by several important and dominant species which are widespread across varying terrain, climates, and soils.[51] With the same species living in many different conditions, it is not surprising that intraspecific variation and local adaptation were found to be widespread in a recent review and meta-analysis covering 3,234 individual populations of 104 species of Great Basin native plants.[48] Over the past 75 years, variation among populations of the same species in traits such as survival, seed production, plant size and vigor, and timing of life stages were frequently observed.[48] These traits are central to initial or long-term restoration outcomes and could be the difference between success and failure of a restoration project.

On one hand, the presence of local adaptation and between-population variation of traits complicates the restoration of these species. The need to appropriately match seeds of each species for each site and learning what is appropriate and making it available via agricultural increase, is undoubtedly a challenge[52,53] that could seem overwhelming. On the other hand, such variation and adaptation among populations is an opportunity for improving restoration success. That is, recognizing and using these traits and patterns of adap-



Figure 2. Intraspecific variation in leaf structure and growth form in 12 different populations (in columns from left to right) of a single species, hoary tansyaster (*Machaeranthera canescens*), being grown together in a single greenhouse before transplantation to multiple common gardens where their adaptation to different climates is studied and used for producing seed transfer guidance. These different populations from across the central and northern Great Basin clearly have different traits likely related to how they secure resources from their habitats of origin. Photo courtesy of USDA Rocky Mountain Research Station staff.

tation makes them assets, not nuisances. Each trait variation circulating within each population is currency to be invested in improved success, if correctly harnessed. Richness, diversity, and abundance of native plant species are indicators of healthy ecosystems.[54] By maximizing richness and diversity, native plant communities can better resist invasion because the variation in structure, function, and phenology maximizes resource uptake by native plants, and preempts their use by invasive species.[10,11] Ensuring ecosystems contain diversity (i.e., species diversity, functional diversity, phenotypic diversity, evolutionary diversity, phylogenetic diversity, and genetic diversity) allows species to continue adapting to changing environmental conditions.[55] Additionally, some traits in wild populations of the sagebrush steppe, especially those populations that have withstood repeated disturbances or prolonged presence of invasive species,[56–58] may be successful in more than just their local habitats.[59] Screening a selection of regional plant populations for these widely successful traits or strategies can further improve seed sourcing for restoration.[60]

Using complex natural variation to our greatest advantage requires that it be understood. For example, Blumenthal et al.[50] examined 99 different collections of bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) and found smaller seeds and smaller, more efficient leaves were common among populations from drier habitats. Identifying and seeding populations with these drought-adapted traits is likely to improve restoration success in drier habitats over approaches that sought traits related to rapid and large early growth.[30] In addition to a better understanding, a pragmatic approach must be taken to partition the complexities of this variation into a manageable number of pieces. Fortunately, progress is underway with the creation of seed transfer guidance (i.e., provisional, and empirical seed zones) for many native plant species important to restoration of the sagebrush steppe. This guidance seeks to address the complex variation in native plants with a strategic approach.

Create, test, and increase the use of seed transfer guidance

Most gardeners and growers are familiar with the 2012 USDA Plant Hardiness Zone map on display in many plant nurseries or on the back of home garden seed packages sold in the U.S. This is the standard for determining which plants are likely to thrive in gardens or farms based on average minimum winter temperature. However, most gardeners also know the correct hardiness zone alone does not guarantee success; plants also need appropriate soils and adequate water and sunlight. Similarly, seed transfer guidance is being developed for native plant restoration. This guidance includes mapped seed zones,[61] which details how far populations of native plants can be moved from their points of origin and still be in habitats and climates to which they are adapted. The development of these seed zones considers measured genetic adaptation, diversity, gene flow, relatedness among populations, and changes in environmental conditions across the landscape.[62–67] This seed transfer guidance, whether generalized for all species (i.e., provisional seed zones) or cus-

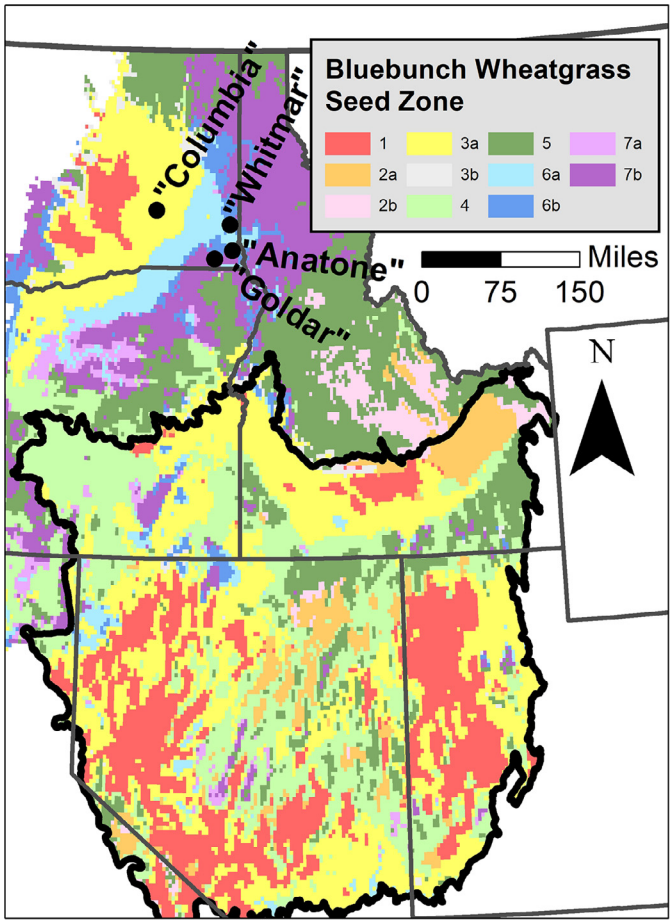


Figure 3. Empirical seed zones for bluebunch wheatgrass (*Pseudoroegneria spicata*)[62] marked by 11 colors, along with the locations (stars) of the four cultivars and named varieties[79-82] of this species most often used across the Great Basin (outlined in black). Modern seed sourcing guidelines recommend collecting and producing large quantities of seed for at least one seed source per seed zone with significant restoration need, or more than one for zones with very disjunct locations, such as zones 1 and 3a.

tom made for individual species (i.e., empirical seed zones), is more complex than the Hardiness Zone guidance, because it describes where plants are adapted to thrive without any additional inputs or protections beyond sowing the seed. The Western Wildland Environmental Threat Assessment Center's Threat and Resource Mapping online portal hosts easily accessible maps, GIS data, and supporting information for regionally specific provisional seed zones as well as climate-matched and empirical seed zones for almost two dozen native plant species,[61] with more species on the way.

Using seed transfer guidance to inform wildland seeding or planting decisions is not new. The forestry industry in the Pacific Northwest has successfully used a system of seed zones for conifer trees to improve replanting success and timber yield since the 1960s.[68] However, because seed guidance for most native grasses, forbs, and shrubs is rather recent, most are still seeded without local adaptation or seed transfer guidance considerations. For example, bluebunch wheatgrass (*Pseudoroegneria spicata*) is a native grass species with empirical seed transfer guidance, derived from common garden experiments,[62] yet the most used cultivars or named varieties of bluebunch wheatgrass throughout the entire Intermountain West[31] are sourced from a narrow region of the Pacific Northwest (Fig. 3).[30] This disconnect between modern seed transfer guidance and currently available seeds is not unique to bluebunch wheatgrass. However, the operationalization of seed transfer guidance is helping collectors, growers, and managers reduce this disconnect for many species.

Seed transfer guidance can be overwhelming at first glance because seed zone maps resemble a box of crayons melted across a map, complete with confusing codes and numbers associated with each color. However, coordination of projected seed needs can help prioritize species and seed zones for native seed source development and make this complex guidance actionable. For example, Jensen and Stettler[69] reported 90% of fire rehabilitation projects on federal lands in the Great Basin over the last 30 years occurred in only three of the 20 provisional seed zones found in the region. Thus, initial efforts to improve native plant seed source availability should focus first on finding and producing sources that succeed in those seed zones most in need of restoration.

Seed transfer guidance and seed zones are the best management tools available to balance the need to recognize complex patterns of local adaptation and inherent genetic diversity of our native plants with the need to manage market complexity and develop economies of scale to lower native seed costs and improve native seed success. Collaboration between researchers and land managers can guide the creation, testing,

and revision (as needed) of seed transfer guidance. Planning for and using the right seed in the right place can create native plant communities that are resilient and resistant to future disturbances.[33] However, the large supplies of seed needed to achieve these goals must be agriculturally grown, rather than wild-collected, and farmers and growers would ideally be coordinated into collaboratives that strategize and prioritize the needs of their regions. Fortunately, skilled farmers and growers abound, and headway is being made.

Build native seed partnerships to benefit restoration outcomes and local communities

Millions of pounds of seed are used every year across the Intermountain West to revegetate or enhance lands across patchworks of jurisdictional boundaries that have experienced disturbance, yet many areas are left unseeded due to lack of supply. How native plant seed sources are identified, collected, and propagated has historically been only loosely coordinated. Increasing the use of the most appropriate seeds for specific sites is a major goal of most agencies, tribes, and landowners. However, to be successful, all involved need to shift from a reactive decision-making process to a proactive prediction-based process that allows for more successful longer-term planning.[70]

To supply locally adapted native seeds for large-scale restoration production systems requires the development of partnerships between seed collectors, researchers, farmers, nurseries, seed storage facilities, seed purchasers, and restoration ecologists.[32,33] These partnerships will foster communication to ensure land managers have the right native seed to use in public and private restoration efforts. This may be one of the most logistically challenging steps to move toward realizing the widespread and consistent use of appropriate native seeds for restoration.[70] The time between seed collection to having enough seeds ready to plant in large projects is 3 to 5 years at best, and longer if plants are challenging to grow, or if populations undergo screening for traits shown to be successful.[60] Therefore, land managers need to project the priority seed zones and quantities of seed they are likely to need several years in advance. Fortunately, regional native seed partnerships can provide collective resources, guidance, and confidence in planning to its member farmers and managers to meet these logistical challenges, which aids seed collection and production systems in meeting the need.

Native seed cooperatives are sprouting up across the West and globally. A recent example of the teamwork needed to achieve these collaboratives is a new program in the northern Great Basin called EcoSource Native Seeds and Restoration.[71] This nonprofit organization is building partnerships with restorationists and growers to provide the most appropriate, locally sourced native seeds across the region. EcoSource provides a hub for partners to connect and plan restoration programs using locally sourced and locally grown native seeds, as well as a forum in which restoration practitioners work with all entities in the native seed supply chain to plan every aspect of getting the most appropriate seed needed to restore healthy and functioning native plant communities. These partnerships generate the organization, prioritization, and coordination needed to get locally appropriate native seed on the ground in large-scale restoration projects.

Through the formation of seed partnerships, bottlenecks within the native seed and plant material development process can be clarified and coordinated.[40] Working together, stakeholders can increase species availability and diversity, while incorporating best available science like local adaptation and seed transfer guidance. Coordination of native seed needs will reduce volatility in demand, thereby stabilizing market price, and reducing risk to native seed producers.[32,40] Regionally coordinating seed source development and production can also bring more growers into the market, which can support local economies and connect them with efforts to restore land.[40]

Be ready and willing to adopt changes when the evidence is clear

Our final recommendation is perhaps the simplest, but the most important. Progress can only be made if the best tools and practices are used, and the least effective ones retired. We have more to learn about using native plants to successfully restore resilient native ecosystems but have already learned more than we have currently adopted. This is a particularly salient point for large scale, native plant restoration in the sagebrush steppe, which is often criticized for being unsuccessful and can be slow to change and reflect the rapid explosion of new science and guidance from the last 10 to 20 years. Adopting new guidance and evolving our practices in this region will take many hands over many years, but it will also take a common belief that improved success can be achieved by embracing evidence-backed changes.

An example illustrating a solution yet to be adopted pertains to the cleaning and storage of sagebrush seed. Sagebrush seed is predominantly wildland collected each fall, and seed production in wild stands varies annually.[72] It has long been noted that sagebrush seed is highly viable when first collected, but can swiftly lose viability (over weeks or months) in storage.[73] Together, these facts nearly guarantee that the yearly supply of sagebrush seed rarely meets demand, and a lot of seed is currently wasted either by deterioration in storage or by hasty use arising from very real "use whatever we have" emergencies. However, sagebrush seed experts have known for decades that maintaining high viability of sagebrush seed after years in storage can be achieved by a combination of seed cleaning, humidity maintenance, and controlled storage immediately after seed collection.[72–74] Researchers learned in the 1980s and 90s that low moisture content of seeds and low humidity storage were crucial for maintaining sagebrush seed germinability in storage, and concluded the then-current industry standard of 6% to 12% purity[75] for sagebrush seed lots was too low.[76] More recently, Karrfalt and Shaw[74] and Walters[73] concluded that immediately drying and cleaning sagebrush seed to 66% to 80%+ purity soon after collection, then storing at low ambient humidity and near-freezing temperatures, results in storage without major viability losses for 5 or

more years. These cleaning, drying, and storage protocols have already been made available[77] and require standard equipment common to most seed processing and storage facilities. This demonstrates an implementable solution to a longstanding and common problem. The ability to bank sagebrush seed for many years without major loss of viability would allow managers to maintain more diverse and strategic seed stocks and make it easier to get viable seed to appropriate sites when needed. However, there has yet to be either bottom-up (via seed producers voluntarily drying and cleaning to these standards to produce a higher quality product) or top-down (via legal or buyer-specified changes to seed moisture and purity standards for marketable sagebrush seed) implementation of this useful guidance. This case illustrates that lack of adoption can be a barrier to solving problems, rather than lack of solutions.

Our final recommendation is intended to be a friendly reminder, not a criticism. There is no fault in struggling to reintroduce complex organisms to changing and unpredictable ecosystems at an immense scale or struggling to adopt new information. This is and will remain challenging to achieve. However, there is fault in giving up when new and unused tools and approaches are available or on the way.

Bottom line: We are on the right path, but we are not there yet

Native plants are one of our most powerful tools for protecting and conserving healthy and resilient ecosystems. Successful native plant restoration facilitates conservation of innumerable species interactions, such as between plants, their consumers, and their pollinators, that provide the foundation of ecosystem services upon which humans and wildlife depend. Despite decades of dedicated and respectable work to improve the use of native plants and the success of restoration efforts, the full potential of native plant restoration in the sagebrush steppe of the Intermountain West has yet to be seen. We have discussed important concepts and paths to improve restoration success that are available, and additional progress is being made. However, implementation of new science, guidance, and recommendations is neither quick nor simple. Improved native plant restoration success is within our reach as a dispersed, skilled, and passionate network of land managers, landowners, producers, and researchers. Agreement on key imperatives is an important step. While these times may feel desperate, because the pace of landscape degradation is increasing faster than our ability to prevent further harm or restore damaged lands, it is reassuring to know there are effective new approaches to restoration yet to be brought to scale, and new discoveries occurring regularly. Dedicating coordinated and collaborative resources, time, and energy to achieve better restoration outcomes is unquestionably a good idea for native plant communities, which can, in turn, continue to sustain both the natural world and our livelihoods.

Declaration of Competing Interest

The content of sponsored issues of *Rangelands* is handled with the same editorial independence and single-blind peer review as that of regular issues.

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