Maximizing Seed Resources for Restoration in an Uncertain Future

LINDA M. BROADHURST, THOMAS A. JONES, FORREST S. SMITH, TOM NORTH, AND LYDIA GUJA

Seed is fundamental to broadscale plant restoration when the goal is to re-establish species and ecosystems. But climate change is expected to significantly influence plant reproduction, affecting seed availability and viability as well as planting opportunities. Meeting growing restoration targets within these constraints in new and unfamiliar climates will be challenging. Consequently, we need to develop a range of flexible strategies to ensure that sufficient volumes of viable seed are available to take advantage of planting opportunities under novel environmental scenarios. This requires coordinated leadership to align funding and planting timelines, using seed production areas to improve seed supply, building and maintaining infrastructure to stockpile seed, encouraging research to overcome storage and germination constraints, and developing and implementing new technologies in all of these areas. Increased tolerance to risk and failure will also be required as the application of current restoration practices may not be appropriate as the climate changes.

Keywords: land degradation, restoration, climate change, seed production

Globally, some 10%–20% of drylands are degraded; forests have disappeared in 25 countries, with more than 90% of forest cover lost in a further 29; one quarter of Earth's terrestrial surface is occupied by cultivated systems; and inland wetlands are in worse condition overall than any other major ecosystem (Hassan et al. 2005). This broadscale degradation is now affecting ecosystem services, food and energy security, human health and well-being, and water availability (Reed et al. 2011), necessitating significant political and social action to moderate these negative effects. Climate change now places additional pressures on global biodiversity (IPCC 2013), presenting many new challenges for the conservation of dwindling natural resources (Harris et al. 2006, Dawson et al. 2011, Maclean and Wilson 2011). Although preserving natural habitats is generally more preferable than restoration (Young 2000), in highly degraded regions, plant restoration is a major objective for land-management agencies (Hoegh-Guldberg et al. 2008). The importance of plant restoration is globally recognized through the Convention on Biological Diversity, which aims to restore 15% of degraded ecosystems within the next 5 years (i.e., by 2020; see target 15, *www.cbd.int/sp/targets*). To help meet this target, seed-based plant restoration is being undertaken at various spatial scales ranging from small local initiatives to large broadscale government and privately funded programs. The scale of some of these larger restoration projects is immense (table 1). Fundamental to these projects, regardless of size, is the need for seed, but for larger projects, the volumes of seed required are considerable. For example, 2000 kilograms (kg), or 4400 pounds (lb), of seed was used to restore approximately 28 square kilometers (km^2) in southeastern Australian over 8 years, more than 500,000 kg (1,100,000 lb) of seed was harvested over 12 years to restore 90 km^2 of northern tallgrass prairies in Minnesota (Gerla et al. 2012), and the US Bureau of Land Management's Idaho seed warehouse purchased more than 1,600,000 kg (3,600,000 lb) of native and nonnative seed in 2005 alone (Lambert 2006). Consequently, climate-induced changes to seed availability and viability will significantly influence the scale and timing of future restoration projects in some regions.

Recent and prolonged droughts experienced in Australia (the Millennium Drought, 1995–2007), the southern United States (2010–2013), and across Europe (2000–2009; European Environment Agency 2010) raise significant concerns for the sustainability of broadscale seed-based restoration projects in the future. Some of the major climatic changes expected over coming decades include increased annual precipitation over high northern latitudes, decreased precipitation in Mediterranean-climate regions (i.e., those located in the Mediterranean basin, South America, Africa, and Australia), and a compounding change in the occurrence, severity, and spatial distribution of extreme weather events (Diffenbaugh and Field 2013). In addition, even if carbon dioxide (CO_2) emissions significantly decline in the near future, warming trends will continue for several more decades (Diffenbaugh and Field 2013). Despite the growing demand for seed to meet increasing restoration targets (Merritt and Dixon 2011)

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Table 1. Examples of large restoration projects around the globe.

Country	Scale	Reference
Kenya (Green Belt Movement)	1977–1997: 6000 centers for seedling production, 30 million trees planted on private land	(Gritzner et al. 2011)
	2014: more than 250,000 trees planted	(GBM 2014)
Macedonia	6 million trees	(Gritzner et al. 2011)
Dubai Desert Conservation Reserve	6200 trees and shrubs over 25.9 km^2	(Gritzner et al. 2011)
China	4 forest belts over 1500 kilometers	(Gritzner et al. 2011)
United States	Utah Dixie National Forest: 162 km^2 of reseeding	(Gritzner et al. 2011)
	Minnesota: 90 km^2 northern tallgrass prairie	(Gerla et al. 2012)
Australia	8000–12,000 hectares (19,768–29,652 acres) aerial seeding	(Gritzner et al. 2011)
	20 Million Trees program	(AGDE 2014)
North Africa	Reforestation of 350,000 hectares (864,500 acres)	(Gritzner et al. 2011)

and the significant investment of resources into broadscale restoration initiatives, such as those underway in the United States and China (Doyle and Drew 2008, Lu et al. 2012), relatively little consideration is being given to how climate change will affect seed supply or the success of future restoration projects.

It is imperative that we recognize the possible impacts that climate change will have on restoration if we are to successfully navigate our way through this time of significant global change. But while the future will present many challenges, it will also provide opportunities to develop innovative, research-driven approaches to restoration. Here, we focus on two interrelated key issues crucial to the future success of seed-based restoration efforts: (1) seed availability and (2) the more effective use of seed resources. We focus on broadscale restoration (i.e., 10s to 1000s km^2) in temperate regions where very large volumes of seed from numerous species are required. We also provide some potential strategies to overcome future seed constraints and indicate where investment and leadership are required to ensure that restoration opportunities are maximized in the coming decades.

Seed availability

Many native plant species, including those used for restoration, are characterized by having easily dispersed seed, narrow collection windows, small seed crops of mixed maturity, atypical development patterns (Hay and Probert 2013), and high interannual variability in seed production (e.g., seed masting; Kelly 1994). Other barriers to obtaining wild-collected seed include limited numbers of individuals and populations, weed contamination in natural stands, and populations being located on dangerous or rough terrain. These factors not only constrain seed availability but can also significantly increase the cost of wild collection. For example, we know that seed sourced from wild populations in Texas can be two to three times more expensive than that acquired through horticultural production and can produce a poorer restoration outcome. Limited and unpredictable seed availability is also a significant issue in Australia, where more than 90% of restoration seed is sourced from natural vegetation (Broadhurst et al. 2015). The unpredictability, unreliability, and high cost of wild seed can be further exacerbated in highly fragmented landscapes if seed quality and quantity are compromised by inbreeding (Aguilar et al. 2006, Broadhurst et al. 2008). Consequently, changes to the timing and volume of precipitation and rising temperatures predicted for some regions are likely to further affect the availability of seed for restoration projects (table 2). For example, shifts in phenology, floral abundance, and duration may occur in regions with rising temperatures (Hegland et al. 2009), whereas drought stress is likely to reduce seed number and size and increase seed abortion (Morgan 1984). Climate change may also weaken important plant mutualisms such as pollination and floral fidelity, exacerbating existing constraints on seed production in regions where vegetation fragmentation is high through changes in pollinator behavior, abundance, and pollen transfer (Aguilar et al. 2006, Chacoff and Aizen 2006, Cheptou and Avendaño V 2006, Chacoff et al. 2008, Tylianakis et al. 2008, Farre-Armengol et al. 2014). For plant species capable of dispersing to more suitable areas as climates change, seed quality and quantity may be initially limited by time lags between plant and pollinator colonization (Parmesan 2006). The contamination of wild-collected seed may also increase if the prediction of more invasive species in agricultural systems (Peters et al. 2014) also extends to natural ecosystems. The ethics of collecting seed under these circumstances must also be considered, because this resource still needs to support natural population regeneration, as well as mutualistic species that rely on seed for food or to complete their life cycles.

Species bias. Many restoration programs are biased toward a few core species that can be reliably and readily sourced, stored at ambient conditions, and easily germinated. Although these "workhorse" species do deliver environmental outcomes in a cost-effective manner, they represent just a fraction of the species required to reconstruct diverse and

Table 2. Summary of potential changes to seed availability and viability associated with climate change and options or recommendations for managing seed resources.

Climate influence	Likely effects	Outcome	Options or recommendations
Rising temperatures	Phenological shifts	Smaller seed crops	Stockpile seed
	Reduced flowering and/or length of flowering	Smaller seed crops	Create SPAs; stockpile seed
	Changes to pollinator behavior and abundance	Inbreeding produces poor quality seed or small seed crops	Create SPAs; stockpile seed
	Alteration of dormancy depth	Germination delay or failure	Seed pretreatment; create SPAs; research
	Increased wild seed abortion	Smaller seed crops; low vigor	Create SPAs; stockpile seed; research
	Altered germination cues	Poor germination	Seed pretreatment; research
	Increased weeds	Contamination of stocks and/or restoration sites	Seed cleaning; stockpile seed
	Altered seed longevity	Rapid decline in viability and/or vigor (except alpine species)	Stockpile seed under optimal conditions
Reduced water availability	Reduced flowering and/or length of flowering	Smaller seed crops	Create SPAs, stockpile seed
	Changes to pollinator behavior and abundance	Inbreeding produces poor quality seed or small seed crops	Create SPAs; stockpile seed
	Reduced wild seed production	Smaller seed crops	Create SPAs; stockpile seed; research
	Increased wild seed abortion	Smaller seed crops; low vigor	Create SPAs; stockpile seed; research
	Smaller seed	Poor germination or low vigor	Create SPAs; stockpile seed; research
	Alteration of dormancy depth	Germination delay or failure	Seed pretreatment; create SPAs; research
	Altered germination cues	Poor germination	Seed pretreatments; research
Increased frequency of severe events	Damage to or loss of plants	Smaller seed crops	Stockpile seed, create SPAs
	Impacts on pollinators	Inbreeding produces poor quality seed or small seed crops	Stockpile seed, create SPAs
Poor seasonal outlook	High risk of planting failure	Poor restoration outcome	Stockpile seed for good planting years
Higher soil temperatures	Altered germination cues	Poor germination	Seed pretreatments; research
	Reduced seed persistence	Rapid decline	Requires research
	Symbioses and mutualisms	Poor germination; failure to thrive	Requires research

resilient ecosystems. *Underutilized species* are those that fail in restoration (both in direct seeding and native seed production) or are perceived to have little functional value in initial regeneration, despite these species being key elements of the plant community being restored.

Seed dormancy and germination. Seed dormancy is ubiquitous among most vegetation types apart from tropical evergreen rainforests and semi-evergreen forests (Baskin and Baskin 1998). But our poor understanding of dormancy alleviation and germination requirements for most species is limiting the number of species available for restoration. The temperature and moisture experienced by seed during maturation can influence dormancy depth, rates of dormancy decline, and germination response (Donohue 2009, Walck et al. 2011). Future shifts in temperature and moisture regimes are therefore likely to influence germination behavior (Walck et al. 2011) and restoration success. Alleviating dormancy using pretreatments such as physical scarification (Turner et al. 2013) and smoke (Roche et al. 1997) can be scaled up for field application, but in practice, the success of these approaches is unpredictable (Daws et al. 2014, Tormo et al. 2014). Given that we have little experimental evidence to explain this variability in field-based results, it is extremely difficult to predict whether climate change will influence this component of restoration in the future. In addition, the role of symbiotic and beneficial microorganisms in restoration remains largely untested despite evidence suggesting that the addition of symbiotic nitrogen-fixing bacteria can be highly beneficial for some species (Thrall et al. 2005). What is clear, however, is that our limited knowledge of dormancy and germination requirements already constrains our ability to successfully restore complex plant communities and that this will be exacerbated in the future. Improving our understanding of seed biology is crucial if we are to restore a broader and more representative range of species, but this will require direct research investment.

Using seed more effectively

Climate-related changes to seed availability will require the judicious use of seed resources. Although restoration targets and opportunities fluctuate annually, in our experience, some restoration is generally undertaken in most years. It is unclear whether this is an effective approach, because restoration success is generally subjectively evaluated and poorly articulated (Zedler 2007). As far as we are aware, few standardized evaluation methods—or any mechanism to aggregate data at regional or national levels to allow comparative analyses and improve restoration practices—exist. Data sharing, including standardized data collection protocols and transparency across the range of restoration agencies from government to individual landholders, would significantly improve our understanding of restoration success. Data-aggregation initiatives such as the Atlas of Living Australia (*www.ala.org.au*) and iDigBio (*www.idigbio.org*) may provide suitable platforms for capturing and sharing these data.

New approaches. As climate changes, planning restoration activities using a more agricultural-based approach to evaluate the risk of planting based on variables such as soil moisture and using long-range weather predictions (e.g., Southern Oscillation Index predictions for El Niño) might be a more effective strategy. This may be especially relevant in regions where reductions in the amount and frequency of precipitation and increasing temperatures will shift and/or narrow planting windows. Precipitation-sensitive species or those whose success is influenced by timing and planting techniques (e.g., tallgrass prairie grasslands; Bakker et al. 2003, Larson et al. 2011, Frischie and Rowe 2012) are examples of plant groups that may require a more strategic planning approach in the future. Climate-related changes to soil temperature and moisture may also influence germination cues and possibly even the persistence of soil-stored seed (Walck et al. 2011), necessitating changes to current restoration practices. Shortening or realigning restoration programs to better match favorable environmental conditions does, however, require a basic understanding of germination biology. For example, if seed are no longer exposed to germination cues in the soil (e.g. chilling) and pretreatment is required, a basic understanding of the timing and length of appropriate pretreatments will be necessary.

Implications for restoration funding. The changes we predict for seed availability and use require an acceptance by policymakers, funding agencies, and practitioners that restoration must become more responsive to new, often unpredictable, environmental cycles and that some failure is inevitable. In reality, failure is already an often-unreported part of restoration (Zedler 2007), limiting our ability to learn and improve restoration practice. Flexibility in funding and workforce planning is also needed to support the little to no activity and probable funding shortfalls in poor planting years, as well as the rapid mobilization of resources in years and in regions where conditions indicate a higher likelihood of restoration success. Constraints associated with short-term and inflexible funding cycles are already a well-recognized problem in the seed industry (e.g., Broadhurst et al. 2015), but without strategic long-term investment, such as seed warehousing in the western United States for postfire recovery, many land managers and agencies will be unable to develop restoration practices that are responsive to change.

Improving the seed supply chain. Seed production areas (SPAs) are one mechanism to overcome seed-supply issues and/or requirements to use local seed. Initiatives such as the Great Basin Native Plant Selection and Increase Project, the South Texas Native Plant Restoration Project, and the Colorado Plateau Native Plant Program in the United States and the UK Seed Hub in the United Kingdom already recognize the importance of securing seed supply. The benefits of SPAs include being able to reliably produce more seed than that available from wild populations, reducing the impact of collecting from wild and often stressed populations and generating seed of known genetic quality or to fulfill a specific landscape purpose (e.g., toxic soils). To our knowledge, SPAs mostly involve short-lived species such as grasses, herbs, and forbs that can be readily cultivated and/or commercialized. This bias needs to be corrected and strategies developed to supply seed for other key plant groups, such as longer-lived shrubs and trees. Although these latter species are often considered to be relatively easy to collect, in reality, seed is often unpredictable and unreliable, and at the time of writing, we are aware of a significant shortfall of seed for several key eucalypt species in southeastern Australia.

Although SPAs can help to secure seed supply, they are fixed in time and space, as are wild populations, and will not be immune to climate change. For example, production costs will be higher if inputs such as water, nutrients, and energy need to be increased to maintain production. Altered pollinator availability and abundance could also occur, as has been predicted for wild populations. Some of these responses can be moderated by adapting cultivation practices, but changes such as phenological shifts cannot and may be especially important for photoperiod- or chilling-sensitive species (Pittillo and Collins 2010, Zohner and Renner 2014). Long-term seed production in one region may also standardize germination traits that are moderated by the maternal environment (Cedan et al. 2013, Postma and Ågren 2015). Maintaining parental lines in production environments similar to their original habitat can alleviate this pressure in the short term, but these plants may not be immune to longer-term climate change. Future environmental change also introduces new considerations for seed production, making it even more important to better define parameters such as the length and area of production and the method of establishment.

Producing seed for the future. Although there is increasing interest in SPAs, little information exists to guide producers on how to do this under current climatic conditions, let alone to meet future predictions. New approaches to seed production to increase genetic diversity through strategic intraspecific hybridization (polycrossing) followed by *in situ* natural adaptation (Jones 2003) may help develop seed better suited to future conditions. A possible approach for some species may be to create admixed populations using material from a wide genetic spectrum irrespective of point of origin (Breed et al. 2013), which is then planted in several ecologically similar sites. Although this could result in some maladaptation (genetic load), these plants are likely to be removed during establishment and ongoing management, producing a more genetically diverse but ultimately high-performing population (Breed et al. 2013). Following several generations of *in situ* natural selection, the novel materials produced could then be combined to create a new population with higher general adaptation across the range of environmental diversity. Translocating this population to restoration sites would allow contemporary evolution to continue and natural selection to generate the most suitable plant genotypes *in situ*. This "prime-the-pump" strategy has the advantage of being simple and inexpensive to apply; however, it is sufficiently flexible to accommodate plant material needs for new restoration projects at any time.

Seed stockpiling. The impacts of increasing climatic variability on seed supply suggest that stockpiling seed to meet future requirements will be required. Stockpiling under the appropriate storage conditions is a viable option, because the inherent longevity of orthodox (desiccation-tolerant) seed acts as a buffer against viability decline (Probert et al. 2009). Globally, significant investment is being made in conservation seed banks to secure species against extinction (e.g., the Millennium Seed Bank of the United Kingdom; the Australian PlantBank; and the Svalbard Global Seed Vault of Norway). But similar strategic and scientifically supported investment for restoration is lacking, with the exception of the Bureau of Land Management (BLM) National Native Plant Material Development Program (NPMDP). The storage facilities required to support future restoration projects are potentially large, because these will need to accommodate both the range of species and the volumes of seed required for broadscale restoration (Merritt and Dixon 2011). Some agencies, such as the BLM, have already invested significant resources in restoration seed storage facilities, such as those at Ely (363,000 kg, or 800,000 lb, at a cost of US$4.8 million; BLM 2013) and Boise (450,000 kg, or 1,000,000 lb; Lambert 2006). The leadership shown by these initiatives, including the significant financial investment, must be replicated in susceptible regions to provide land managers with the capacity to (a) store seed until planting conditions are suitable, (b) take advantage of years when seed is plentiful, and (c) rapidly respond following natural disasters. Although this approach may be suitable for government-managed land, it may not necessarily suit commercial producers. Nevertheless, a compromise could be possible whereby seed producers are subsidized to incentivize them to produce and store large quantities of seed—although this may disrupt the seed market, affecting both seed and species availability. Irrespective of how storage facilities are funded, this investment must be made soon to allow restoration seed to be stockpiled while environmental conditions are still relatively favorable for production and collection.

Managing seed resources under climate change

Meeting the seed-related restoration challenges that we predict will require strong international and national leadership to coordinate and drive strategic investment in science and infrastructure. This early recognition of future challenges allows us to develop adaptive mechanisms to maximize the biodiversity gains that restoration can achieve in an increasingly uncertain future. The role of private, government, and nonprofit sectors in seed production and restoration will require repositioning and closer collaboration in the future. For example, profitable projects may be better placed within the private sector, which has the expertise to successfully manage commercial enterprises, whereas more "problematic" species requiring significant expertise and/or research may be better funded through public-sector mechanisms. The ideal model, however, would be a private–public partnership with a collective vision to improve environmental outcomes rather than to achieve market dominance. The need for small-scale and niche producers and collectors is likely to continue to maintain the supply of seed for key species, such as those that are more difficult and time consuming to collect or process. But this niche market sector will require subsidization, because seed availability is already low for many of these species and is likely to reduce further as climates change. New types of markets for native species, such as the Native Seed Network (*http://nativeseednetwork.org*), an Internet-based seed market for buyers and vendors, are already expanding and evolving to meet the needs of conservation-minded urban and suburban consumers. Although the environmental outcomes of these are generally localized and urban, these consumers can provide valuable cash flow for producers to help them expand their native seed production to the levels required to restore habitats on ecologically impactful scales.

Changing attitudes and expectations. More concerted efforts to overcome restoration failure and a tolerance for higher levels of risk will be required as restoration is undertaken in new and unfamiliar climates. Long-term monitoring programs, such as those in the Lake Champlain Basin (*http://sol.lcbp.org/DataSourcesReferences.html*) and the Chesapeake Bay (*www.chesapeakebay.net/trackprogress*) restoration programs, will be key to facilitate and improve adaptive learning during a time of rapid change. We also encourage native seed industries to strive to supply a greater diversity of species for restoration, each underpinned by the broadest genetic base possible. Clearly, the full diversity of native species and their genetic diversity or adaptive potential cannot be established in cultivation, and land managers will need a portfolio of approaches to meet future challenges. Seed-collection guidelines must also be reviewed and continually updated to incorporate empirical evidence into new best practices for sustainable seed collection and use. This is especially important because relatively few seed-collection guidelines exist worldwide (Broadhurst et al. 2008), with fewer providing guidance on how to respond to impending climate change. With carefully considered strategic investment in the next 5–10 years, the seed-related constraints we predict need not necessarily negatively affect future restoration. Indeed, our hope is that the potential seed supply constraints we have outlined will act as a catalyst to drive highly creative and innovative thinking to improve restoration efficiencies and cost effectiveness.

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Linda M. Broadhurst (linda.broadhurst@csiro.au), Tom North, and Lydia Guja are affiliated with the CSIRO National Research Collections Australia and the Centre for Australian National Biodiversity Research, in Canberra, Australia; TN and LG are also affiliated with the Department of the Environment at the Australian National Botanic Gardens, in Canberra. Thomas A. Jones is affiliated with the USDA Agricultural Research Service, Forage and Range Research Laboratory, in Logan, Utah. Forrest S. Smith is with the South Texas Natives and Texas Native Seeds Projects at the Caesar Kleberg Wildlife Research Institute at Texas A&M University–Kingsville, in Texas.