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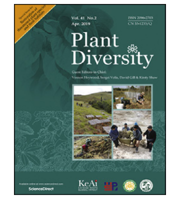

Capturing, protecting and restoring plant diversity in the UK: RBG Kew and the Millennium Seed Bank

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ABSTRACT

Ex situ seed banking is a practical and cost-effective means of preserving wild plant diversity and a crucial complement to the *in situ* conservation and restoration of species and habitats. As pressures on the natural environment have grown, so has the call for seed banks to provide scientifically-robust, practical solutions to seed-related problems in nature conservation, from single-species recovery and reintroduction to the restoration of complex, dynamic communities at the largest scales. In this paper, we discuss how the Royal Botanic Gardens, Kew and its Millennium Seed Bank have responded to this call in the United Kingdom. We demonstrate that banked seed collections can provide a range of otherwise-unavailable, high quality, known-origin, genetically-diverse biological materials. The data, expertise and specialist facilities that accompany these collections are also valuable, helping overcome constraints to the collection, production and effective use of native seed. Challenges remain - to ensure *ex situ* collections protect the species and genetic diversity that will enable plants to adapt to a changing environment, and to find new ways for seed banks to mobilise their resources at a landscape scale.

1. Introduction

With one in five of the world's vascular plants currently threatened with extinction (RBG Kew, 2016), the conservation and restoration of plant diversity is an urgent issue. Whilst the conservation of intact wild populations is vital, habitat degradation and destruction, invasive pests and diseases, climate change and other human-induced impacts on the environment mean the survival of many species is likely to depend on assisted recovery or reintroduction projects (*sensu* McDonald et al., 2016) and *ex situ* conservation in botanic gardens and elsewhere (Smith, 2016). A framework for action is provided by the Global Strategy for Plant Conservation (CBD, 2012), which outlines 16 targets including commitments to secure the *in situ* conservation of least 75% of known threatened species (Target 7) and the *ex situ* conservation of at least 75% of threatened species, with at least 20% available for recovery or restoration use (Target 8).

Botanic gardens contribute a unique set of skills and resources to delivering the GSPC, including plant identification, collection, plant production, direct management of wild species and habitats, research and public engagement activities (Smith, 2016; Hardwick et al., 2011). The leading role of botanic gardens in *ex situ* conservation is particularly marked, with at least 30% of plant species diversity held in the living collections or associated seed banks of botanic gardens around the world (Mounce et al., 2017). This represents an exceptional resource for conservation, although the need to assess the size and quality of these collections and fill significant biogeographical and phylogenetic gaps is recognised. It will also be important to build capacity in under-represented tropical areas and provide more effective coordination at an international level, learning from progress made in developing a Global System for the conservation of crop diversity (Mounce et al., 2017; Smith, 2016).

Seed banking has become an increasingly important form of *ex situ* conservation in botanic gardens, with almost 57,000 taxa conserved in more than 350 institutions around the world, including 37,000 taxa at the Royal Botanic Gardens (RBG) Kew's Millennium Seed Bank (MSB) at Wakehurst Place (O'Donnell and Sharrock, 2017). Seed banking is a practical, cost-effective means of conserving wild plant diversity (Li and Prichard, 2009). Methodologies for the long-term storage of desiccation-tolerant orthodox species are well established, with cryopreservation, micropropagation and other techniques increasingly permitting

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the storage and subsequent use of desiccation-intolerant and short-lived species (Hay and Probert, 2013; Walters et al., 2013; Li and Prichard, 2009; Walters et al., 2008).

As the science and practice of nature conservation and ecological restoration have grown, so has the call to expand the capacity of seed banks to provide scientifically-robust, practical solutions to seed-related problems, from single-species conservation and small protected sites to complex, dynamic communities at the largest scales (Smith, 2016; Merritt and Dixon, 2011; Miller et al., 2016). In this paper, we discuss the MSB's response to this call in the UK, outlining our programme and providing examples of how our seed collections and associated expertise have contributed to *in situ* species reintroduction and habitat restoration projects. Significant progress has been made, but the need remains to adapt and respond to changing environmental conditions and approaches to nature conservation, to increase our impact and find new ways to contribute at a landscape scale.

2. The MSB's UK programme

The MSB's UK programme is currently structured around three projects: the UK Flora project, which continues to make collections across the entire UK flora for conservation at the MSB; the UK National Tree Seed Project (UKNTSP), which is building genetically representative collections of native woody species from across their range in the UK; and the UK Native Seed Hub (UKNSH), which uses the seed collections and associated expertise to increase the quantity, quality and diversity of native plant material available to practitioners in the UK.

2.1. Building diverse, high quality, representative collections

A primary focus of the UK Flora Project has been to secure at least one collection from the broadest possible range of native and archeophyte species (*sensu* BSBI, 2007), with priority given to threatened and endemic taxa. The MSB currently conserves 7435 wild-origin and regenerated (cultivated) collections from the UK, comprising 2077 native and archeophyte taxa (Table 1). This represents 75% of the UK's total native and archeophyte flora and 78% of threatened taxa, a high proportion reflecting both the relatively small size of the UK flora and the intensity of collecting effort in recent decades. Work to collect outstanding taxa continues, including very rare or highly specialised species, taxonomically-complex microspecies and those that do not reliably produce seed in the UK.

In recent years, an increasing emphasis has been placed on intraspecific sampling depth – making large, multiple-origin collections that capture and conserve genetic diversity within and between populations of a single species across its range in the UK (Willis et al., 2018). This approach has been facilitated by collaboration with conservation geneticists at Kew and elsewhere and is typified by the UKNTSP, which applies a rigorous sampling strategy to capture genetic diversity at national, eco-geographical and individual mother plant scales (Kallow and Trivedi, 2017; Trivedi and Kallow, 2017). Whilst completing this work for the UK's woody flora is a priority (RBG Kew, 2015), in-depth sampling strategies are also being developed for threatened non-woody species and those likely to provide the greatest ecosystem benefits and adaptability to environmental change (Willis et al., 2018).

The quality and quantity of seed held in the UK collections is also critical – the collections must be legally acquired, accurately identified, of high viability and large enough to permit routine curation in the seed bank and meaningful conservation or research use (Way, 2003). The MSBP's Seed Conservation Standards (MSBP, 2015) provide a framework for high quality seed collecting and conservation, and partners are provided with training and detailed guidance on sampling techniques, data collection, the preparation of herbarium specimens, drying and packaging, tissue sampling etc. (for example, RBG Kew, 2001; Kallow, 2014). Taxonomic, locality, altitude, habitat, sampling, germination and viability data are available for most UK collections (Fig. 1) and, although many collections are small (Fig. 2), efforts are being focussed on making larger collections where this can be done without compromising the natural regeneration of the donor population. Viability data is available for 55% of UK collections (Fig. 1), with a majority of collections tested displaying high viability of 80% or greater (Fig. 3).

2.2. Enhancing access and use

Whilst the diversity and quality of seed is critical, the conservation value of a seed collection is also a function of how accessible the material is for research, reintroduction, habitat restoration and other uses (Liu et al., 2018). Small samples of MSB seed - typically of 60 seed or less – are available free of charge for non-commercial purposes via the MSB Seed List. Between 2012 and 2017, 1290 samples from the UK collections were dispatched via this list, 930 (72%) for research purposes, 206 (16%) to produce plants for the living collections at RBG Kew and other botanic gardens and 154 (12%) for environmental purposes including regeneration, reintroduction and habitat restoration projects (data extracted from the MSB's Seed Information Database, 31st January 2018). In the UK, the UKNSH has made larger quantities of seed available at cost-recovery prices via the UKNSH Seed List and through a range of partnership, project and consultancy work. Between 2011 and 2018, the UKNSH provided plant materials and technical assistance to 57 projects, working with 31 partner or client organisations including the Wildlife Trusts, the National Trust, the South Downs National Park, Natural England, local authorities, ecological

Table 1
Overview of UK native and archeophyte seed collections held in the MSB.

	Collections in MSB[a]	Taxa in the MSB[b]	Taxa in UK flora[b]	% of UK flora in MSB
Wild-origin	6131	1904	2759	69%
Regenerated	1304	542	2759	20%
Total	7435	2077	2759	75%
Threatened[c], wild	925	303	430	70%
Threatened[c], regenerated	415	143	430	33%
Total	1340	336	430	78%

[a] Data for MSB collections were extracted from the MSB's Seed Bank Database on 5th February 2018, comprising angiosperm native and archeophyte taxa collected in the UK, including sub-specific taxa and microspecies.
[b] MSB data were cross-reference with the UK's angiosperm native and archeophyte flora using data from the Botanical Society of Britain and Ireland (BSBI, 2007) incorporating changes identified in Stace (2010) and additional data from McCosh and Rich (2011).
[c] Threatened taxa identified using IUCN Red List categories EX-VU (JNNC, 2018).

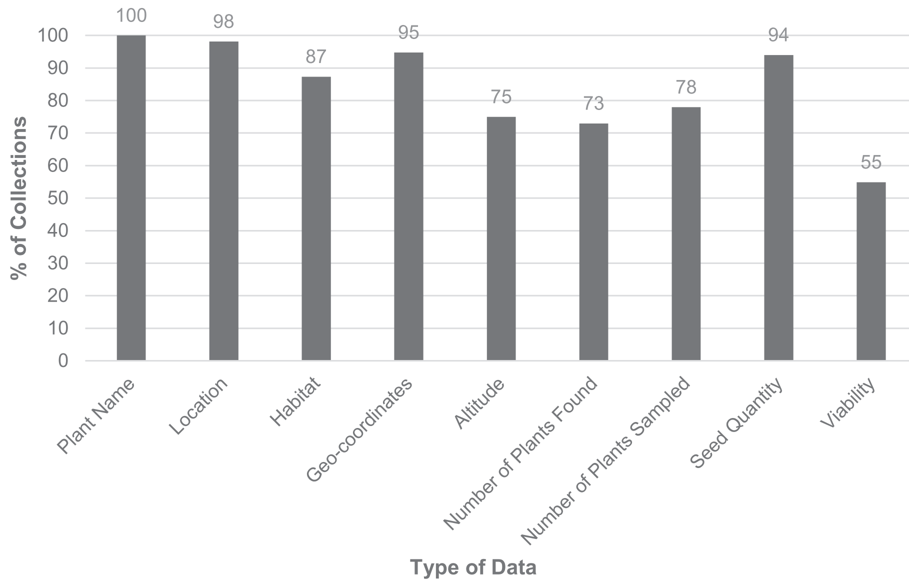

Fig. 1. Availability of key data for UK native and archeophyte collections held in the MSB. Includes collections currently in processing, where data may not be complete. Data extracted from the MSB's Seed Bank Database on 5th February 2018.

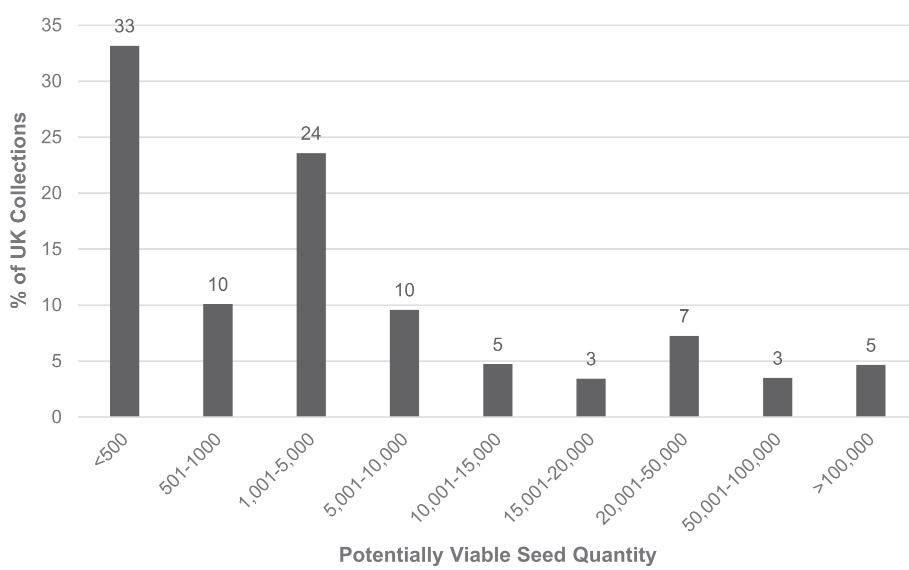

Fig. 2. Potentially viable seed quantity. Percentage of native and archeophyte UK collections in different classes of estimated potentially viable seed quantity, excluding non-viable seed detected by X-ray or cut-testing of dry samples. Collections lacking quantity data - principally those currently being processed - are excluded. Data extracted from the MSB's Seed Bank Database on 5th February 2018.

consultancy firms, Toyota Motor Manufacturing (UK) Limited and Toyota GB (PLC). Examples of this work are presented in Section 3 and Section 4 of this paper.

Efforts are also underway to enhance access to the data recorded during the collection, processing and ongoing curation of the seed collections. Basic biological data – seed weight, morphology, storage behaviour, germination protocols etc. – are made available via RBG Kew's Seed Information Database (RBG Kew, 2018). We believe this represents a valuable and under-utilised resource for plant conservation and hope to do more to expand and interpret these data for application under nursery and field conditions. Seed collecting data forms that accompany each wild collection are valuable biological records, contributing to distribution data mapped and made available by the Botanical Society of Britain and Ireland (BSBI). A new BSBI mapping tool to overlay MSB collections with species-distribution data is in development, enabling the MSB and collecting partners to assess where new wild collections are required and practitioners to see where seed collections may be available for use. Data-sharing agreements allow more bespoke, detailed use of MSB data for conservation use. Data relating to UKNTSP collections, for example, has been supplied to the Future Trees Trust and Woodland Trust to identify new registered seed sources for *Tilia cordata* Mill. and *Carpinus betulus* L.

3. Making seed available

The availability of high quality, genetically-diverse seed and plants of known native-origin can impose a significant constraint on ecological restoration (Broadhurst et al., 2016; Oldfield and Olwell, 2015; Miller et al., 2016; Nevill et al., 2016), particularly

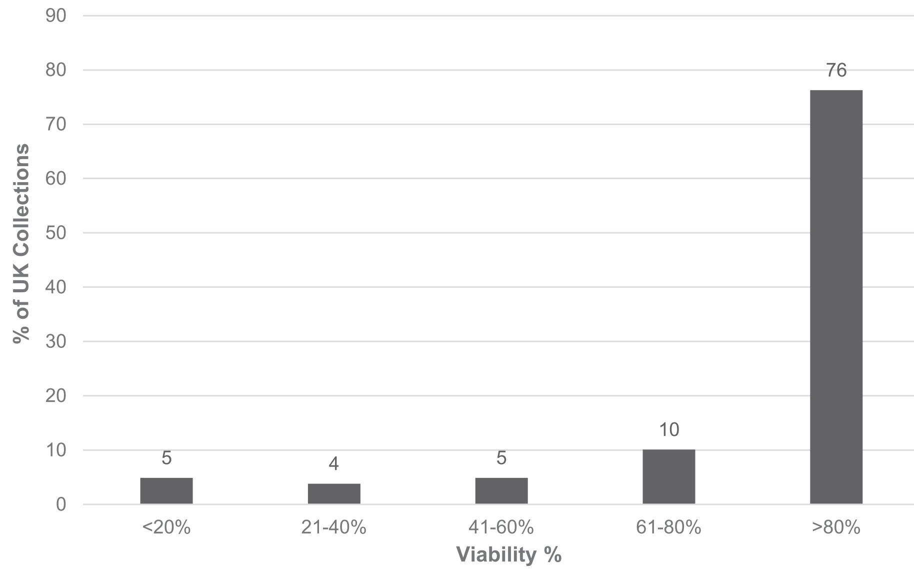

Fig. 3. Seed Viability. Percentage of native and archeophyte UK collections in different viability classes, based on the most recent MSB viability test. Collections without viability data are excluded. Data extracted from the MSB's Seed Bank Database on 5th February 2018.

when projects seek to move beyond a relatively narrow range of high demand, easily-cultivated 'workhorse' species (Broadhurst et al., 2016; Ladouceur et al., 2017). Seed banks can provide the seed and associated expertise in seed processing, storage and use to expand this limited restoration species pool (Ladouceur et al., 2017) and make a broader range of biological material available to practitioners.

3.1. Species recovery and reintroduction

The breadth and increasing diversity of collections held in the MSB represent an exceptional resource for species recovery and reintroduction projects, particularly of rare, highly threatened and protected species where appropriate material from other wild or cultivated sources is unlikely to be available. In some cases – *Ranunculus ophioglossifolius* Vill. and *Chenopodium urbicum* L., for example - collections held in long-term storage have been used to augment dwindling wild populations or reintroduce otherwise extinct populations to their original growing site. In at least one case, *Bromus interruptus* (Hack.) Druce, MSB collections have facilitated the reintroduction of an endemic species that has become extinct in the wild.

In some cases, wild collections held in the bank may be large enough to be used directly in small-scale projects. In others, the ability to regenerate small wild collections - growing plants to harvest a greater number of seed - has proved essential. *R. ophioglossifolius*, for example, is restricted to populations at two sites (Holland et al., 1986), one of which, at Inglestone Common, Gloucestershire, has declined to the brink of extinction. In 2007, a small wild collection was made at the site. In 2015, this collection was regenerated by the UKNSH under carefully controlled conditions mimicking the muddy, seasonally-inundated habitat provided by grazed pool edges. A successful protocol was developed and 124,926 seed were harvested, providing material to propagate 200 plants for planting at Inglestone in 2016. To promote the long-term persistence of this annual species, plants were introduced to the site at the flowering stage to maximise seed production and dispersal. Counts of buds, flowers and fruiting heads in summer 2016 provide an estimate that approximately 60,000 seed entered the system in the first year, with large numbers of seedlings observed in autumn 2016 (Lansdown, 2016). Although most of these plants died during exceptionally dry weather in early 2017, a small number persisted to produce an estimated 600 further seed (Lansdown, 2018), suggesting the introduced population is capable of self-regeneration under both optimal and severely sub-optimal conditions.

Since 2011, the UKNSH has regenerated 49 collections of 44 species, focussing on material that would not be available from any other source, typically rare or difficult species or specific, known-origin material for a specialist project or use. UKNSH protocols have been designed to minimise losses in wild genetic diversity during regeneration and thereby maximise the adaptive potential and long-term sustainability of reintroduced populations (Schröder and Prasse, 2013; Basey et al., 2015). Where possible, original collecting data is used to inform the selection of the wild seed collection for regeneration. Large systematically-sampled populations from sites providing a good ecological match to the reintroduction site are prioritised. A range of laboratory and nursery-based techniques are employed to promote high germination and establishment rates, with grow-outs that fall below a threshold 50% conversion rate discarded. In seed production, congeners are separated to avoid unintentional hybridisation, harvesting is carried out sequentially throughout the season to retain the varied phenology of the wild population and cultivation is limited to a single generation to avoid losses in genetic variability and minimise adaptation to cultivation conditions.

3.2. Habitat restoration and creation

Wild and regenerated single-species collections held at the MSB, although small by commercial standards, have proved large enough to create bespoke mixtures for small-scale habitat restoration and creation projects or to supplement bulk-harvested materials to create species-rich mixtures for use at larger scales.

In the UK, landscape partnership projects provide a valuable opportunity to link *ex situ* seed collections and associated expertise to practical conservation at landscape scales. The South Downs Way Ahead Nature Improvement Area (NIA) brought 29 organisations together to deliver improved management of 42,000 ha of chalk ecosystem between 2012 and 2015 (SDNPA, 2015). Responding to partner concerns about the limited availability of local-origin seed for many calcareous species, the UKNSH regenerated South Downs origin collections of 25 species, making crops of hundreds of thousands or millions of seed available to practitioners. These collections have been used to produce plug plants to enhance existing grassland, for direct sowing to restore grassland following scrub clearance, to reinstate grassland damaged by road construction in protected areas and to provide a bespoke mixture of larval and nectar food plants to create butterfly habitat. Importantly, the NIA also provided a forum for discussion, training and advice on seed sourcing, collecting, processing and use, amplifying the resources of RBG Kew by building awareness and capacity in local authorities, conservation organisations and land managers.

Capturing and using seed to reassemble complex plant communities can benefit from the mixed approach suitably-equipped seed banks are able to provide, including capacity for wild collecting, regeneration, mechanised seed harvest, seed testing and long-term storage. In 2014, for example, the UKNSH worked with ecological consultants RSK-Environment to capture and restore priority habitats damaged by excavations for the construction of underground cabling for the Rampion off-shore wind farm (Gilbey and Chapman, 2016). The objective was to harvest seed from the broadest possible range of species at three priority habitats on the excavation route - two calcareous grassland sites in the South Downs and one species-rich mesotrophic grassland site in the Sussex Weald. Seed was then processed and placed in long-term storage at the MSB, ensuring high quality material was available for post-construction restoration three to five years later. Botanical surveys of each site enabled the identification of target species and collecting strategies, considering how species abundance, phenology and morphology influence collection timing and technique. A bulk matrix of grasses and some forbs was collected by repeated brush harvests using a Logic MSH420 brush harvester, supplemented by hand harvests of species that could not be captured mechanically. Brush harvests were analysed to determine species composition and collections were cleaned, viability tested and stored in the MSB. This technique maximised the species and phenological diversity of the final restoration mixes - at the calcareous grassland site at Tottington Mount, for example, 23 species were captured in over 9 kg of seed material (Tables 2 and 3).

Table 2
Analysis of brush harvests carried out at Tottington Mount, West Sussex, for RSK-Environment.

Taxon	% of total by weight[a]	% viability$_2$
Achillea millefolium L.	0.07%	not tested
Agrostis sp.	0.27%	89
Bromus erectus Huds.	36.37%	100
Cerastium fontanum Baumg.	0.04%	not tested
Holcus lanatus L.	0.41%	100
Linum catharticum L.	0.02%	not tested
Lotus corniculatus L.	0.35%	not tested
Medicago lupulina L.	3.24%	100
Phleum pratense L.	0.13%	100
Pimpinella saxifraga L.	4.08%	76
Plantago lanceolata L.	1.33%	71
Trifolium pratense L.	8.61%	95
Trifolium repens L.	0.02%	not tested
Other species	0.90%	not tested
Debris	28.35%	not tested
Total Seed Weight, excl. debris (g)	9315	

[a] Three one-gram samples were taken using a riffle divider, separated into taxa and non-seed debris and weighed. The weight of each species is expressed as a percentage of the weight of the samples as a whole. Viability tests were carried out on species recorded as 'frequent' at the site using standard MSB methodologies (Davies et al., 2015a). Viability % = (G+F+A)/X x 100, where G = number of germinated seed, F = number of fresh ungerminated seed, A = number of abnormal seedlings, X = number of seed sown (excluding empty and infested seed).

In total, 28 kg of brush harvested seed and 42 single-species collections were made available for restoration at the three sites, with the first seed dispatched and sown in autumn 2016.

4. Overcoming constraints to the use of native seed

Where seed can be made available, the failure of seeds to germinate and establish sustainable restored populations places a significant – perhaps the greatest (Miller et al., 2016) – additional constraint on successful ecological restoration. This failure may be due to climate, herbivory or other external factors, but may also be related to the seed itself, including low seed quality (Ryan et al., 2008; Marin et al., 2017); complex and poorly understood dormancy mechanisms (Miller et al., 2016); genetic fitness (Broadhurst et al., 2008); and site preparation, reintroduction and management practices that do not provide appropriate germination and establishment niches (Wagner et al., 2011). The restoration of more challenging species or complex plant communities is consequently inhibited (Broadhurst et al., 2016), large quantities of seed are wasted (Merritt and Dixon, 2011) and the ability of native seed producers to bring a wider range of species into large-scale production is reduced (Tishew et al., 2011; Ladouceur et al., 2017).

Seed banks, particularly those located within botanic gardens, are in a strong position to help overcome these constraints, combining *ex situ* collections of wild plant material and a range of supporting scientific and technical skills, including germination ecology and propagation, horticulture and conservation genetics (Hardwick et al., 2011).

4.1. Dormancy, germination and plant establishment

Most collections in the MSB are subject to an initial germination test to provide viability data and enable the future propagation and use of the seed (Davies et al., 2015a), employing a range of environmental conditions and dormancy-breaking treatments (Davies et al., 2015b). Very small collections are not routinely tested, although non-destructive X-ray data does provide a guide to seed quality (Terry et al., 2003). Germination data exists for 57% of UK collections (data extracted from the MSB's Seed Bank Database, 9th February 2018), covering 77% of UK species held in the MSB. Globally, germination data exists for 70% of collections held in the MSB (Liu et al., 2018), much of which is made publicly available online via the Seed Information Database (RBG Kew, 2018). These data do not represent proven propagation protocols, but can provide useful clues about germination ecology, including variation within and between collections of the same species.

In some cases, a more focussed research effort is required to understand complex germination requirements, produce practicable germination protocols and permit the production and effective use of seed in conservation projects (Wagner et al., 2011). Attempts to reinforce and reintroduce populations of Critically Endangered (JNNC, 2018) *Galeopsis angustifolia* Ehrh. ex Hoffm., for example, have been frustrated by very low availability of wild seed and complex dormancy mechanisms. The UKNSH has worked for several years to develop a propagation protocol for this species and, in 2016, successfully applied an embryo-excision technique to propagate 276 seedlings and produce a regenerated collection of 32,000 seed. A long-term 'move along' experiment (*sensu* Baskin and Baskin, 2003) is also underway, mimicking natural environmental conditions to better understand the germination ecology of *G. angustifolia* and assist the conservation management of the species. Regenerated collections will be used to reinforce the existing population at Cleeve Common, Gloucestershire, and be sown at new sites by Colour in the Margins, an arable restoration project forming part of the Back from the Brink endangered species

Table 3
Hand harvests carried out at Tottington Mount, West Sussex, for RSK-Environment.

Date Collected	Taxon	Number of seed[a]	% viability$_2$
07/07/2014	*Ranunculus bulbosus* L.	15,261	98
07/07/2014	*Briza media* L.	31,294	98
24/07/2014	*Koeleria macrantha* (Ledeb.) Schult.	1624	89
24/07/2014	*Linum catharticum* L.	13,304	68
24/07/2014	*Anacamptis pyramidalis* (L.) Rich.	306,531	not tested
22/08/2014	*Lotus corniculatus* L.	15,853	100
22/08/2014	*Centaurea scabiosa* L.	2662	96
22/08/2014	*Blackstonia perfoliata* (L.) Huds.	23,942	94
22/08/2014	*Cirsium acaule* Scop.	626	78
22/08/2014	*Phyteuma orbiculare* L.	847	100
11/09/2014	*Galium verum* L.	7181	94
11/09/2014	*Centaurea nigra* L.	7937	94

[a] Number of seed is the estimated potentially viable seed, excluding non-viable seed detected by X-ray or cut-testing of dry samples. Viability tests were carried out using standard MSB methodologies (Davies et al., 2015a). Viability % = (G+F+A)/X x 100, where G = number of germinated seed, F = number of fresh ungerminated seed, A = number of abnormal seedlings, X = number of seed sown (excluding empty and infested seed).

programme. The UKNSH is providing regenerated seed of five arable species for Colour in the Margins – *G. angustifolia, Adonis annua* L., *Ranunculus arvensis* L., *Silene gallica* L. and *Torilis arvensis* (Huds.) Link – and will synthesise MSB and nursery data to develop detailed propagation protocols for a total of ten species.

4.2. Multi-disciplinary approaches

Much of the MSB's work in the UK emphasises the value of applying multiple skill-sets and resources to the conservation or restoration of a species or habitat.

An exemplar of this multi-disciplinary approach is provided by RBG Kew's contribution to the development of a Species Recovery Plan for *Nuphar pumila* (Timm) DC. a perennial aquatic plant which is Critically Endangered in England (Stroh, 2014) and survives as a single population at Cole Mere, Shropshire. Viability and germination studies at the MSB found that seed produced at Cole Mere displays high viability, but that germination is significantly influenced by seed maturity at the point of collection and the duration of post-harvest ripening (Peach et al., 2017). Propagation protocols from seed and root fragments were developed and, although the seed is recalcitrant and cannot be banked in conventional dry-cold storage, *ex situ* living collections have been established at Wakehurst Place and Kew (Peach et al., 2017). A study was also carried out by RBG Kew's Conservation Genetics team to assess the genetics of the Cole Mere population in comparison with surviving populations in Scotland and putative samples of the hybrid *Nuphar* × *spenneriana* Gaudin. (Gargiulo et al., 2017). Although the sample size was limited, this work found no evidence of hybridisation, suggested populations in England and Scotland are not strongly differentiated and made recommendations for the controlled use of Scottish material in reintroduction attempts in England. This work was carried out in collaboration with Richard Lansdown, Chair of the IUCN SSC Freshwater Plant Specialist Group, who also conducted a comprehensive ecological study of the species and conditions at Cole Mere (Lansdown, 2017). Together, this work provides a robust evidence base and practical guidance for the conservation of *N. pumila* in England.

5. Responding to future challenges – amplifying impact and working at the biggest scales

As challenges facing the natural environment intensify and evolve, so does the policy, science and practice of nature conservation. In the UK, as elsewhere, the need to understand, restore and reconnect ecosystems on landscape-scales has been well documented (Lawton et al., 2010) and consistently reflected in government policy (Defra, 2011; Defra, 2018). Natural capital approaches, emphasising the value and sustainable management of ecosystems and the services they provide to people, have also become important (Defra, 2018), requiring new insights into ecosystem function, resilience and adaptability (RBG Kew, 2018).

Responding to these challenges provides new and exciting opportunities for the MSB and other seed banks to mobilise their collections, data and expertise. A focus on multiple-origin collections and genetic diversity, for example, will build collections that protect locally-adapted ecotypes (Vander Mijnsbrugge et al., 2010), maximise variation and adaptive potential in restored populations (Broadhurst et al., 2008) and enable adaptive sourcing strategies to cope with changing environmental conditions (Weeks et al., 2011; Breed et al., 2013; Jones, 2013). Ready access to these materials and data can help researchers identify genetic boundaries, assess diversity within and between plant populations and facilitate the identification of adaptive traits, supported by rapid advances in sequencing technology (Nevill et al., 2016). Understanding these traits will, in turn, help model plant responses to environmental change and identify useful characteristics including adaptability to climate change and resistance to invasive pests and diseases (Willis et al., 2018).

New approaches also require significant and sometimes difficult shifts in the focus of seed bank activity. Resources for intensive, comprehensive sampling must be found alongside the continuing need to collect and protect endangered species, often from a single population; collecting towards long-term conservation targets must be balanced against responses to immediate project or partner demand; large collections that maximise genetic variation must sit alongside targeted sampling aimed at capturing specific traits; safeguarding long-term collections in the bank must be balanced against maximising the availability and use of seed. Perhaps the greatest challenge relates to scale. Involvement in larger projects like the South Downs NIA has enabled the MSB to mobilise its seed resources beyond the conservation of a single-species or small, highly protected sites, but stretched the capacity of infrastructure and procedures designed for small wild seed collections. UKNSH regenerated harvests are typically in the range of 1–2 kg of seed, large by MSB standards but well short of delivering the many kilograms or tons of restoration-ready material required at the largest scales (Merritt and Dixon, 2011).

To have the greatest impact, seed banks must apply their resources and expertise to help large-scale producers overcome constraints to the production of a broader, more diverse and higher quality range of native material (Merritt and Dixon, 2011; Tishew et al., 2011; Menz et al., 2013; Nevill et al., 2016). Seed banks are in a strong position to assist (Table 4) particularly those with access to the multi-disciplinary resources of a botanic garden (Hardwick et al., 2011), but must consult and collaborate closely with those who specify, produce and use native seed (Abbandonato et al., 2017; De Vitis et al., 2017). In the UK, the MSB has made

Table 4
Examples of constraints to the production of a broader, more diverse and higher quality range of native seed, with potential solutions seed banking botanic gardens can provide.

Constraint	Solution
The availability of genetically-diverse, known-origin founder stock is limited.[a]	• Make seed available from appropriate wild or regenerated collections. • Develop seed production areas or seed orchards. • Provide training and resources in wild seed collecting techniques.
Dormancy mechanisms or lack of propagation experience inhibit successful germination.[a,c,d,e]	• Provide germination data and propagation protocols. • Research and develop methodologies for seed pre-treatment and priming. • Provide training and resources for propagation and establishment.
The growing requirements of some species or ecotypes are not fully understood.[a, d, e]	• Laboratory and field-based studies to develop cultivation protocols for native species. • Comparative studies to detect intraspecific variation in germination and cultivation requirements.
Intraspecific diversity and genetic boundaries are not fully understood for many species, limiting the ability of collectors and producers to identify and fill gaps in provision.[a,b]	• Studies of intraspecific diversity and population structure for priority species.
Production processes reduce the genetic diversity of regenerated seed.[b,c,h,i]	• Genetic studies to identify where diversity is lost in the production process and how this can be mitigated.
Production processes reduce the viability of regenerated seed, which may be untested.[c,f,g]	• Training and technical support in seed processing and storage. • Seed testing services. • Developing and promoting standards for native seed testing (for example, ISTA, 2017). • Developing and promoting quality assurance schemes.
Market and regulatory conditions do not provide sufficient demand or lead-in time for the production of less commonly-used species or ecotypes.[b,d,e,j]	• Provide evidence in support of the use of a broader range of native plant material. • Develop and promote best-practice guidance for those who specify and use seed. • Provide evidence and technical assistance in the development of quality assurance, accreditation

[a] MacIntyre (2017).
[b] Nevill et al. (2016).
[c] Miller et al. (2016).
[d] Ladouceur et al. (2017).
[e] Tishew et al. (2011).
[f] Ryan et al. (2008).
[g] Marin et al. (2017).
[h] Basey et al. (2015).
[i] Schröder and Prasse (2013).
[j] Abbandonato et al. (2017).

insufficient progress in this regard and will need to build new bridges with industry in the years ahead. Initiatives like the Native Seed Science, Technology and Conservation Initial Training Network (www.nasstec.eu), which concluded in 2017, provide a good model, demonstrating the value of bringing researchers, seed banks, seed producers and practitioners together to find and share science-based solutions to practical problems in the production and use of native seed.

6. Conclusion

Ex situ plant conservation through seed banking is a crucial complement to the *in situ* conservation and restoration of species and habitats. Banked seed collections can provide the biological materials for reintroduction and restoration programmes, either directly as seed or plants, or indirectly via regenerated collections. The data, expertise and specialist facilities that accompany collections are valuable too, helping overcome constraints to the collecting, production and use of seed in the landscape. Adaptability is key - to ensure *ex situ* collections protect the species and genetic diversity that will enable plants to adapt to a changing environment, and to ensure seed banks themselves find new ways to apply their resources to the requirements of 21st century conservation. Advances in *ex situ* conservation mean there is now no technological reason why any plant species should become extinct (Smith et al., 2011) – a strong imperative to make the best possible use of the opportunity this represents.

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