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Ensuring the genetic diversity of potatoes

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1 Introduction

1.1 Overview

In this chapter, we aim to provide a brief assessment of the contribution of genebanks to potato science and industry.

Significant improvements in the cropping system can, of course, be accomplished through better production and management practices, machinery, agrichemicals and marketing. In this chapter, we focus only on better genetics – although genetic components do also potentially interact with most of these other means of advancing crop production. For example, while we might improve irrigation management, the inherent water use efficiency of the cultivar will most likely also influence the final formula for optimal production.

Current potato varieties already provide a crop that stands out for productivity, affordability, palatability and versatility with a widespread positive effect on society (DeJong, 2016). However, production constraints and consumer and farmer needs do change over time. Thus, there is value to society in continually finding ways to use genetics to make potato crop better in every way possible – if not, then public funding of a genebank has little justification. Thus, a primary and overarching concept is that genebank staff need to have a corresponding attitude of innovation in all they do in order to maximize the genebank's support of innovation in the crop.

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Primitive cropping provided a genetic buffer in which diversity, by planting of different landraces, was broad over space but relatively narrow over time. Thus, at least some individuals in the diverse mix of landraces grown across the landscape every year were likely to be productive in any one season, while others would be productive in different seasons, making total crop failures unlikely. In modern agriculture, in contrast, breeders seek to fine-tune a very limited number of clones to specific environments and optimize cropping systems for maximum production. Thus, diversity is now narrow over space. But because of disease/stress/pest challenges and with production technology and consumer demands varying over time, germplasm must be preserved in a condition that is ready to be quickly deployed – so genetic diversity can be broad over time, as needed.

The sports model is a good parallel. We should not condemn the strategy of depending almost wholly on a few star players, since this often results in winning the game. But then one also needs to hedge by having backups ready to take the field very quickly if the stars are injured. Thus, 'monocultures' of crops are not bad as long as we have genebanks, and breeding programmes using them, which can quickly deploy alternatives.

1.2 Basic genebank mission

We have established that genebanks serve the basic function of holding useful genetic variation in reserve. The method of accomplishing this is usually presented under the five general headings of acquire, classify, preserve, evaluate and distribute. Many concepts about these objectives are basic and do not change over time. Here, we provide general concepts, relying on the reader interested in more details to refer to references contained therein. For example, the 2014 Potato Crop Germplasm Committee Vulnerability Report (http://www.ars-grin.gov/npgs/cgc_reports/potatovuln2014.pdf) and a previous review (Bamberg and del Rio, 2005) provide good overviews. Other issues are evolving rapidly, so we provide suggested key words with which the reader can access the latest information on the internet. The basic challenges and opportunities under each of the five objectives will be reviewed, particularly noting more recent developments and their impact.

Here again, a parallel from common experience – a tool store – provides a useful illustration of the basic concepts surrounding the genebank mission:

Acquisition is stocking the store with a diversity of tools to maximize the breadth of tasks the customer is able to do. These should include familiar tools to address well-known problems, but also unfamiliar tools that address the unknown or unexpected. Thus, the genebank should acquire stocks with, for example, known superior resistance to a common disease, but also stocks with uncharacterized general sequence diversity and breadth of phenotypic resistance mechanisms which might provide a source of resistance to a disease or pest or environmental condition yet unknown. **Classification** of germplasm is needed, for the same reason that a store must organize and clearly label related tools so that staff can easily manage the inventory and customers can do the most efficient shopping. **Preservation** is needed for the same reasons that the tool store maintains the functionality and sufficient inventory of the product. This includes monitoring viability with germination testing and having plenty of propagules available. Having a genebank with germplasm that is dead, diseased or with too few propagules to distribute is like a store with only a display model of a tool that is actually non-functional. **Evaluation** has its importance in the principle that, to maximize service to the customer, the tool store should maximize available information about the tools' functions. Thus, staff should provide instruction manuals and, ideally, do additional tests on the tools themselves as

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time and resources permit. Genebank staff should be involved in the kind of evaluation that examines – and thereby improves – the quality of genebank service. Examples include studies that evaluate which accessions deserve particular emphasis because they are exceptionally rich in genetic diversity and which genebank techniques minimize the risk of losing diversity. **Distribution** applies primarily to *working* genebanks described in this chapter. In contrast, a 'doomsday' vault like the Svalbard Global Seed Vault in Norway, or the United States base collection at the National Laboratory for Germplasm Resources Preservation (Keyword 'NLGRP') at Ft. Collins, Colorado emphasizes long-term backup preservation, not ongoing rapid distribution for research and breeding. Finally, distribution of useful germplasm has unintended negative consequences without a programme to exclude systemic plant pathogens. In the tool store analogy, this is like making sure tools meet all global safety standards and are free of dangerous defects.

The five categories above provide a good working framework, but it is easy to imagine cases in which they overlap and interact with each other. For example, evaluation informs classification and both have implications for preservation and distribution. If a DNA-based evaluation reveals unexpected close similarity of two accessions, it implies they ought to be classified into the same taxon, and it also implies some degree of genetic redundancy that makes preserving and distributing both of them a lower priority.

A sixth consideration is often avoided because it seems negative: Even if we have the resources needed to expand the store's capacity, it must be true that some tools have become obsolete and no longer merit a place on the store's shelves. In the case of germplasm, we know that broken genes that make the plant unthrifty are routinely purged in nature (Schoen et al., 1998). Since it takes extraordinary effort to maintain those traits or individuals that are, for whatever reason, very unsuited to genebank cultivation and reproduction, good management demands some attention to discarding and archiving obsolete germplasm.

1.3 Special considerations for potato

Overlaid on the general nature of genebanks discussed above are considerations particularly relevant to a potato genebank.

Many wild relatives. Potato currently has about 100 wild related species (Spooner et al., 2014, 2016), many of which are fairly easily accessible to the crop breeding pool.

Two forms of reproduction. The crop comprises highly heterozygous clonal cultivars, but wild species typically reproduce sexually. Botanical seed storage has obvious advantages in longevity, being less vulnerable to temperature and moisture extremes for shipping, and requiring less storage and shipping space. Thus, potato genebanks need technology for efficient clonal maintenance and distribution of disease-free plantlets, usually accomplished *in vitro* (Bamberg et al., 2016c), and botanical seed, usually dried, sealed and stored at −20˚C or colder. Botanical seed populations are typically multiplied by hand pollination in a greenhouse or screenhouse that excludes natural pollinators (bumblebees). The latest and best techniques are often best accessed through genebank websites or personal contact with genebank staff. Natural species of potato are diploid, tetraploid or hexaploid, with both inbreeding and outcrossing breeding systems.

Latin American origin. Except for two wild species in the United States, primitive cultivars and wild species originated from Latin America.

Systemic diseases. Viruses and other diseases require special care and quarantine testing for international germplasm import, routine within-country distributions from the genebank and during in-house germplasm handling in the genebank.

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Easy manipulation. Potato seeds are not 'recalcitrant', and often maintain good germination for decades in a simple household freezer. The majority of taxa grow and reproduce well in standard greenhouse conditions. With refinements of standard tissue culture techniques, organs like anthers can often be cultured to regenerate haploids; protoplasts can be made, fused and regenerated.

Multiple world genebanks. Other collections provide the opportunity for meshing data associated with sites of natural origin, evaluation data for accessions held in common, sharing technology and germplasm backups for each other.

1.4 New potato germplasm considerations

Some developments made, or will make, fundamental changes in how potato genebanks operate. Three fundamental problems of wild germplasm are crossing barriers to the cultivated forms, weedy traits and lack of efficient methods to evaluate a large amount of diversity. Hence, any advance in technology that mitigates these limitations increases the practical value of the genebank without adding any new stocks.

Information storage, access and management. Those involved professionally for less than 25 years may not be able to fully appreciate the tremendous advantage that computerization brought to germplasm management. In particular, staff gained the ability to quickly sort and search multiple information fields associated with any accession. The evolution of the Germplasm Resources Information Network over the past 30 years (keywords 'GRIN germplasm') was the culmination of these advances for germplasm in the United States, providing standardized online storage and access for virtually all genebank-related information, including germplasm ordering. An updated version, GRIN-Global, is now being adopted by genebanks worldwide which will further enhance interoperability, data sharing and facilitate users to precisely identify the best germplasm for their needs.

Electronic maps and GIS (geographic information systems). For collecting data, GPS devices based on GIS provided precise documentation of the natural origins of wild populations. Coupled with mapping programmes and aerial images overlaid with roads, other landmarks and climate data, it is possible to plot the relative natural origins of accessions. One can then plan the best route to visit sites targeted for collection (e.g. cited on herbarium specimens), and even predict likely habitats for exploration such as searching for commonly associated vegetation or slopes with the commonly favoured exposure (http://www.ars-grin.gov/nr6/coll_trips/SW2015.pdf). These resources are often available online for free.

DNA markers to assess general genetic diversity. Differences in random neutral markers provide a much more abundant and objective resource for stratifying genetic relationships and heterogeneity than by other assumed diversity-associated traits like variation in phenotypes, geographic origins or habitats. DNA markers became the standard for determining taxonomic relationships, whose acquisitions would be most valuable to the genebank, their accessions within a species encompassing the most diversity, and basic genebank 'housekeeping' functions like detecting mixes, mislabelling or other mistakes. Examples of the widespread application of DNA markers in the genebank are emphasized in other sections of this chapter.

Small modifications to elite clones. Although inbreeding is common in potato wild species, current cultivated potatoes are all heterozygotes fixed by clonal reproduction. Selecting elite potato cultivars takes much effort and time, so it would be highly desirable to make only small improvements to existing cultivars and not recombine the entire genome

in a breeding cross. The single-trait substitution into existing elite lines accomplished by backcrossing in inbreeding crops could only previously be attempted in potato by mutation breeding or selecting spontaneous clonal variants. However, the potential for small changes has expanded in the form of intentional regeneration of selected somaclones (Nassar et al., 2014) and transformations with foreign genes or targeted modifications of existing genes (Butler and Douches, 2016). While these new technologies hold great promise, the traditional method of mining germplasm by screening for desirable phenotypes and crossing is not obsolete (Miller, 2016). A related strategy that is getting increasing attention these days is reinventing potato cultivar breeding in the form of inbred diploids (Jansky et al., 2016).

Restriction of germplasm exchange. Raw germplasm is self-reproducing, and has no immediate commercial value, so was historically widely regarded as free. But the country of origin of germplasm resulting from potato collection and exchange is now recognized as having a sovereign right over the current access, as well as benefit sharing from commercial use of the germplasm. Thus access to germplasm is becoming highly regulated, in many cases germplasm has become virtually inaccessible. Expanded discussion of this topic is provided in Section 6.

1.5 Extended genebank services

The optimal tool store is more than a source of goods, and so it is with a genebank.

Administration and outreach. The successful tool store would ideally increase its commercial impact by advertising and extending its expertise to the public. Similarly, genebank staff often have specialized expertise that allows them to serve as reviewers or editors for manuscripts and grant applications, and on technical and policy committees both nationally and internationally, as well as *ad hoc* hosting of genebank visits, seasonal internships or graduate students. These contributions have the reciprocal benefit of keeping genebank staff in touch with the needs of the germplasm users, and crop producers and consumers. Staff can contribute to popular articles on genetic resources and otherwise help inform the public on the role of crop relatives in supporting the efficiency and safety of the food industry, while conserving natural resources and protecting the environment.

Custom service. We have already outlined genebank service in the form of optimized acquisition, classification, preservation, evaluation and distribution. However, both a store and a genebank can increase their impact through *custom* service. This happens when genebank staff are familiar with the research literature, build rapport with customers and direct some of their resources and expertise towards supplying custom information, propagules or samples to cooperative research projects with multiple germplasm users from an array of specialties.

On-site research. Staff research was introduced previously under the heading of *evaluation*. It not only increases information about the genebank's genetic tools, but makes staff able to give advice on the best tool and application from personal experience. Staff research can have particular impact if directed towards germplasm handling technology and exploration for new traits. For example, discovering more efficient techniques for making hybrids is a good topic for in-house genebank research, since it has broad payoffs both inside and outside the genebank, but is a problem that few specialists like breeders have time to intently pursue. Evaluation for novel traits is also a particularly apt research area, since genebank staff have the special opportunity to notice new phenotypes among the broad spectrum of exotic germplasm they routinely grow for other purposes.

1.6 Achieving a comprehensive genebank service

Putting all the objectives, services and research together, the optimal genebank would contribute to every step in the germplasm deployment process: it would assess the needs for acquisition both from the wild and elsewhere, organize expeditions, collect germplasm, research the nexus of *in situ* versus *ex situ* diversity, guide stocks through import quarantine, optimize organization of stocks by taxonomic and other classification, identify core subsets of accessions within species, develop and apply better technology, keep the maximum diversity in the raw germplasm alive through efficient seed increase and clonal *in vitro* maintenance and readily available to cooperators through germplasm orders, enhance raw germplasm, log data in GRIN or another publicly available database (such as Genesys), publish results in research journals and release hybrids or selections with value-added beyond that of the raw germplasm. This complete spectrum of germplasm support would be impractical for any researcher or breeder to provide for himself.

2 Acquisition of potato genetic material

There are three basic forms of acquisition: (1) direct collecting, (2) sharing, and (3) germplasm development.

2.1 Direct collecting

This is when novel germplasm is accessed from the wild environment (wild species) or farmers' fields or markets (cultivated species). Potato (*Solanum*) species occur from the southwest United States to southern Chile, mostly at higher elevations. There is a concentration of species diversity in Mexico and in Peru/Bolivia (Hijmans et al., 2002, p. 120). Genebanks may arrange and fund collecting expeditions to cover gaps in geography, taxonomy or particular needed traits. A parallel discipline to germplasm collecting exists with botanists who document the natural locations of plants in floras and herbaria, thereby becoming very familiar with particular geographic regions of interest. Collaboration with such professionals is of great use for planning germplasm collecting expeditions. A relatively recent development is the ability to use DNA markers to assess factors that influence the efficiency of collecting germplasm. Since such collecting research has been of particular emphasis at the US Potato Genebank (USPG), we highlight some relevant findings here.

Comparing ex situ *and* in situ *diversity.* Is genetic diversity in the wild changing through time? If so, how representative are the *ex situ* preserved samples when compared to the original *in situ* samples? del Rio et al. (1997a) and Cadima-Fuentes et al. (2016) provided DNA marker evidence that re-collections of natural populations from the same sites but at different years of collection are significantly genetically different. The unfortunate implication is that *ex situ* sites cannot be relied upon as backups of populations in the genebank, but the fortunate implication is that they are worth re-collecting for novel diversity.

Determining associations between eco-geographic and genetic patterns. Traditionally, collecting samples from diverse geographical origins was recommended to increase diversity (Frankel and Soule, 1981; Perry and McIntosh, 1991). However, it would be even more effective if areas of high or distinctive genetic diversity were predicted by specific

eco-geographical parameters. A series of studies in geographically diverse populations of potato species *S. jamesii*, *S. fendleri*, *S. sucrense* and *S. verrucosum* tested whether genetic diversity was correlated with different ecological, geographical and reproductive variables (del Rio et al., 2001; del Rio and Bamberg, 2002; del Rio and Bamberg, 2004). In all cases, genetic associations among populations were efficiently detected with DNA markers. However, associations with eco-geographical variables were rarely detected. Hamrick (1987) warned that habitats may be quite heterogeneous, even within small areas, which can explain why genetic differentiation among populations was generally independent of spatial separation. Only for the inbred species *S. verrucosum* was spatial separation predictive of genetic distance, perhaps because inbreeding exposes all the population's genetics to adaptation to the characteristic environment at locations.

Easy versus remote. It has been shown that collecting is biased towards sites with easy access (i.e. places close to roads and villages). Hijmans et al. (2000; 2002) reported this as 'infrastructure bias', noting that about 60% of the wild potato collections in Bolivia were made within 2 km of a road. Bamberg et al. (2010) tested whether the extra time and effort needed to get to 'remote' sites pays off in the capture of more diversity than at easy sites. In paired sites at three mountain ranges in southeast Arizona, more diversity in *S. fendleri* was sometimes captured at the more remote site, but sometimes at the easy site. Thus, both types of locations need to be sampled and assessed in the lab.

Predicting and assessing genetic diversity hot spots and mega-populations. One 'easy' site, the Santa Catalina Mountains, northeast of Tucson, was identified as having particular genetic richness, despite relatively few samples. Hence, a more intensive collecting strategy was deployed at this site in September 2009. AFLP markers confirmed that this was a rich site (Bamberg et al., 2011) having 24 marker alleles unique to the entire region. This demonstrated that preliminary DNA evidence of genetic richness can identify sites that deserve a higher priority for more thorough collecting.

The ultimate in efficiency for collecting and other *in situ* work would be to identify 'mega-populations': easily accessible, very large and robust, very localized single populations that possess the maximum possible share of known diversity for that species. Such populations would be the wild equivalent of top-ranked members of core collections in the genebank. Bamberg et al. (2016) reported such a single natural population at Mesa Verde, Colorado, that captured >80% of the known genetic diversity for *S. jamesii*. In addition to its value for collecting, this area could be considered a site for habitat protection and an *in situ* reserve, as continuity of the evolutionary response of a species is also an important objective in conservation. Areas with such high genetic diversity could have evolutionary potential critical for adapting to climate change.

Impact of agrichemicals on reproductive traits and genetic diversity. Agricultural practices might be narrowing the genetic diversity at natural habitats, even if those activities are not extinguishing the populations. For example, indirect pesticide contamination may occur in natural populations growing near agricultural fields. If so, then populations growing distant from agriculture would be predicted to be richer in genetic diversity. Two research projects evaluated 15 different species known to grow within or very close to fields in the Andes, and assessed two aspects: the impact of pesticides on traits related to plant's reproductive capacity (del Rio et al., 2012a) and the effect on genetic diversity (del Rio et al., 2012b). The results revealed that the pesticide affected reproductive traits, in particular reducing the production of viable pollen and the duration of flowering. However, DNA markers used to measure changes in allele frequencies at different loci did not detect genetic drift caused by the hypothesized pesticide-mediated selection.

How many populations are enough? Many of the approximately 100 potato species are represented by only a few populations, but we have hundreds of some species. An obvious question is whether there is a standard pattern for the general accumulation of diversity. We used DNA marker data on three model species to examine the actual rate of accumulation of polymorphic loci as populations were added over time, or if they had been randomly added on the basis of the empirical frequencies of polymorphic loci (Bamberg and del Rio, 2016). Addition of new polymorphic loci greatly slows after one has about 100 populations. Of course, it is impossible to know if valuable new alleles and traits exist in a population in the wild but not yet in the genebank, or if these species are representative of all potato species. But this model suggests that if the current total number of populations in USPG could be doubled (all species had 100 populations), one could consider it 'enough' since additional populations would net greatly diminishing returns in allelic diversity.

2.2 Sharing

This is the exchange of germplasm already sequestered in a formal genebank or in a public or private collection. Potato is a crop grown from tuber 'seed' pieces, so there is an extensive industry to produce vigorous propagules with low pathogen levels. This necessitates multiple localized *de facto* clonal genebanks for numerous cultivars in the form of state 'seed certification' organizations. There are also private organizations of citizens who preserve and share germplasm, motivated by a common enthusiasm for expanding the palette of available food vegetables. With varying degrees of formality, they collect, grow, evaluate for culinary quality and exchange exotic germplasm. If the national genebank builds a rapport with state seed certification and NGO collections such as Seed Savers Exchange, an efficient network can result, whereby the genebank staff know where particular germplasm items are available. If the genebank does not maintain those items itself, it can refer germplasm requesters to those alternative sources.

Unless labelling mistakes have occurred, clonally propagated stocks with the same name should be genetically equal among genebanks. In contrast, botanical seed populations with the same origin data might vary due to sampling differences. Often samples from a single seedlot are split and then separately regenerated in different genebanks for many years. Differences in propagation and seed multiplication techniques could theoretically introduce selection or drift that altered one or both of the samples. We tested this by comparing pairs of populations of different potato species which were reputed duplicates between USPG and the Vavilov Institute Potato Genebank (VIR) in Russia (Bamberg et al., 2001) and the International Potato Center Genebank (CIP) in Peru (del Rio et al., 2006). Very few genetic differences were detected between these reputed duplicates from different genebanks. One important implication is that all evaluation data from one genebank can be applied with confidence to the corresponding germplasm sample in an alternative genebank.

2.3 Germplasm development

Germplasm may be 'acquired' in the sense that novel subsets are developed from existing raw accessions. This is not an unnecessary burden on genebank capacity, but, on the contrary, is very encouraging since it demonstrates that value is present and being mined

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in the raw germplasm. For example, a rare useful mutant in a population may become a new acquisition as a clonal isolate, or fixed in a true-breeding seedlot. Populations of different interspecific hybrids or stocks with different ploidies that promote crossability may become distinct genebank holdings. Such items are usually indexed separately as 'genetic stocks' or 'breeding stocks'. Useful traits that are enhanced can cover the entire continuum from basic anatomical and physiological mutants, those aimed at benefitting farmers (e.g. disease and pest resistances), or those aimed at benefitting consumers (e.g. nutritional improvements). A relatively recent challenge to genebanks is the increasing opportunity to be a central source for large *families* characterized for both genetic markers and an array of useful traits. Clonal maintenance and distribution of hundreds of lines for a single germplasm accession requires a great deal of genebank resources. One possible solution on the horizon: fixing segregated genetic variants in the form of inbred botanical seedlots – that is, recombinant inbred lines. More details on germplasm development are presented in Section 5.

2.4 Impediments

A discussion of acquisition reasonably includes impediments. Collecting in the wild has inherent limitations since wild potatoes grow across vast areas, often accessible only by primitive roads or trails. Unfortunately, the habitats where potatoes are found, and the associated flora, are not consistent or obvious, making it difficult to predict exactly where to look. Plants in the wild are often not showy and in some cases only available for collecting at certain times in some seasons (e.g. not collectable at all in a dry year). Even when previous reports are available, as in herbarium records, the locations given may not be sufficiently precise or accurate to allow the germplasm collector to find the exact small area where potatoes are growing. In some cases plants may be found, but viable propagules for the genebank are not available for collection.

Two other factors impeding acquisition are restricted exchange or collecting due to germplasm ownership, or due to quarantine regulations aimed at preventing import of pathogens. These topics are discussed in detail in Section 6.

3 Classification of potato genetic material

Classification may be divided into three somewhat overlapping types of germplasm categorization.

3.1 Taxonomic classification

Species is one of the primary identifiers used to categorize and document accessions in potato genebanks. But potato has a particularly large number of recognizable distinct forms, often including intermediates, so there has been much difference in opinion as to how to best set species' limits. Since potato is a major commercial food crop, its genebanks have often had the advantage of a professional taxonomist devoted to the classification of their stocks. Since 1987, Dr D. M. Spooner has served as the taxonomist for USPG. The reader interested in additional details is directed to his publications (Keywords 'Spooner publications') which offer a wealth of information on his own novel research

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on potato systematics, extensive reviews of the works of others, the details of the latest taxonomic treatment (Spooner et al., 2014, 2016) and, particularly, his personal 30-year retrospective as a potato taxonomist (Spooner, 2016).

Splitting. If two distinct forms exist with different traits for agriculture, one might be motivated to taxonomically 'split', differentiating those by species name for the sake of utility, even if intermediate forms exist. Potato sub-taxa or even species have been concluded to lack predictivity (Khiutti et al., 2015; Jansky et al., 2015), but if genetics is the basis of both taxonomy and traits, the challenge is finding the connection that must exist (Bamberg et al., 2016). With splitting, intermediate accessions will have the awkward denomination of 'hybrid', potentially obscuring how they fit into the overall pattern of species relationships. Or, if ambiguous accessions are more aggressively assigned a species name, they may flip in subsequent determinations, creating instability and confusion in genebank documentation. Splitting creates a need for higher-level names to show which species are related. This has often been accomplished in potato by assigning species to 'Series', 'Groups' or 'Clades'.

Lumping. Alternatively, in a 'lumping' scheme, distinct forms may be combined with their intermediates into a single species. Unless the two original species were not suspected of being relatives, lumping inexorably reduces information, making the species name less significant in the utilitarian sense. For example, a single species name for a collie, bloodhound and poodle *does* provide the useful information that they are the same at a general level, *but only for those who did not already know that*. Such lumping in dog types automatically shifts emphasis to the lower-order names for use by those working on a less general level, where all dog breeds are definitely not interchangeable. The same is true for the genebank – if species is the primary identifier, lumping increases the need to designate and more routinely use sub-specific names or other differentiating descriptors like ploidy. This is true whenever these lower rank names are not simply arbitrary, but really do represent objective significant genetic or phenotypic differences – which is sometimes the case with potato (Hardigan et al., 2015).

Is an objective baseline for species boundaries in potato possible? One cannot appeal to the empirically determined biological species concept, since no potato treatment proposes combining all of the many taxa known or assumed to be able to produce fertile F2 progeny, except as per utility as described in Bradeen and Haynes (2011, p. 7). A less extreme objective baseline would be to set a single minimum quantity of general genetic difference between species. Or, even better, to require that lumping creates species in which all accessions are more closely related to each other than to any accession in a different species. Accessions usually, but not always, group together by species (Hardigan et al., 2015; Jacobs et al., 2011). Even the latest treatment (Spooner et al., 2014) can have separate species for which all descriptor metrics overlap, suggesting that a hypothetical individual or accession could exist that would properly key to two species names. Spooner (2016) opines that a simple 'formula' for species limits will 'forever be an elusive goal'. But there is hope in noting that the advance of technological and analytical tools has often clarified what previously seemed unresolvable.

In practice, taxonomic authority is often codified by centralized computerization. Genebank and database administrators decide on a certain recognized taxonomy and organize the database to reflect it, as occurs with the USA GRIN system. Thus an 'official' taxonomy may be reinforced by virtue of being the *only* option presented to users who access the database for germplasm and information.

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3.2 Core collections

As already mentioned, there is an increased need to 'classify' below the species level when lumping broadens the diversity within a species or when, for any reason, a species has so many variable accessions that the typical germplasm user needs a smaller representative set to make evaluation practical. One approach is designating core collections, where the goal is a minimum number of accessions (e.g. 10%) that capture the maximum diversity (e.g. 90%) within species (Bamberg and del Rio, 2014 and references therein). The simplest decision in core selection is when exact duplicates are identified and one is eliminated. Core collection members can be designated and ranked by their density of diversity, so that the germplasm user is able to balance genetic coverage against the cost of testing more samples (see Bamberg et al., 2016a and references therein).

Although core collections can be composed to capture diversity for various parameters (e.g. country of origin), the modern trend has been to avoid stratifying by such traits that are not necessarily linked to general genetic diversity. Instead, DNA markers based on sequence differences are used. These are presumed to be mostly neutral – have little or no phenotype impact that could result in a genotype by environment (GxE) skew. If a DNA marker technique generates many independent polymorphic loci and is consistent and free of bias, it can provide a very objective approach for comparing germplasm. Practicality of such markers has also improved with greatly reduced cost per data point over time. However, we still lack the optimal marker system that can do everything needed: (1) detect more than two alleles per locus; (2) test a bulk of many seedlings, thereby characterizing the net diversity of a heterogeneous population in a single sample; and (3) use mapped markers so that results of various experiments at different times and places can be readily combined and compared.

The core collection concept may also be applied to the whole genebank, where one designates a reduced array of representative species intended particularly for initial screening surveys when there is no *a priori* information on the trait. The USPG has created and validated such a 'mini-core' of 25 potato species (Bamberg et al., 2016a).

3.3 Cogs

One might set 100 populations per species as a reasonable maximum, since gain in diversity was observed to slow markedly after acquiring that many (Bamberg and del Rio, 2016). These populations may be heterogeneous, indicating there is much potential diversity to classify within. With such a large amount of potential variation to classify, a quick, simple and low-cost approach is attractive. We recently successfully tested whether the remarkable power of human visual subjective categorization could be systematically merged with the scientific method to classify within species. The term 'cog' (short for cognate = born together) was coined for a group within species composed by rapid visual impression and then validated as distinctive by replication and empirical genetic and phenotypic tests (Bamberg et al., 2016b).

4 Preservation of potato genetic material

Managing the technical aspects of seed and clonal multiplication, storage and viability takes a major share of genebank's time and resources, but a detailed discussion on this

topic is beyond the scope of this chapter. The reader interested in specifics of the latest recommended techniques may access genebank websites or contact genebank staff, since advice on how to propagate the germplasm is part of genebank service. A recent treatment of *in vitro* methods at the genebank is available (Bamberg et al., 2016c).

In the following section, we highlight a few results of studies we have done using DNA markers to examine the impact of various techniques on the preservation of the genetics of genebank populations. This is important, because if weaknesses are found, the genebank would need to direct limited resources to stop attrition of diversity.

4.1 DNA markers for assessing diversity

Effects of seed increase. Most wild potato species are propagated as botanical seed resulting from growing and intermating multiple parents of a seedlot that has a low number of seeds or low germination. Seeds are light, small and long-lived, thus convenient for shipping and storage. However, in contrast to clonal propagation, sampling seedlots introduces the possibility of genetic drift among generations. When del Rio et al. (1997b) examined the impact of genebank seed increase on different generations of *S. fendleri* and *S. jamesii* accessions as models, significant differences were not found, suggesting that seed increase does not result in large genetic shifts.

Seedling selection. One specific way that genetic shifts could take place within populations during seed multiplication is inadvertent exclusion of some genotypes at transplanting. One plants extra seeds to ensure that there are enough plants (typically >20) to intermate and produce a new generation of seeds. Consequently, some extra seedlings are always discarded at transplanting. Bamberg and del Rio (2006) examined the risk of losing diversity at the seedling transplant stage if small seedlings are discarded. In most cases, seedlings within populations actually looked identical. But when smaller seedlings were present in a population, no genetic differences were observed between them and their normal sibs. The occasional difference seen in seedling size is due to either random environmental effects or genetic differences that are too small to be detected by the marker system used.

Use of balanced bulks for seed multiplication. Similar to the threat of mis-sampling the population at transplanting, loss of alleles could occur if some seed increase parents make an unbalanced contribution of offspring to the next generation (Breese, 1989). When bulk intermating, one does not know if some plants contributed more or less as fathers, but bulking an equal number of seeds from each plant logically ought to balance maternal representation in the next generation. This, therefore, is a widely recommended alternative to a general bulk of seeds (Rao et al., 2006). However, balanced bulks require a significant investment, essentially doubling the number of samples that need to be prepared, stored and documented – is it worthwhile? When we investigated (Bamberg and del Rio, 2009), for the great majority of populations, plants naturally produced similar numbers of berries, making an intentional balanced bulk moot. However, we also examined two populations identified as having the most variable seed production among parents. Even in this extreme case, over 12 replicate seed increase generations, only about 4% of RAPD loci had alleles practically vulnerable to loss. Thus, we conclude that balanced maternal bulks have small genetic benefits in the next seed increase generation.

Heterogeneity within populations. Since drift cannot affect loci with fixed alleles, heterogeneity dictates the appropriate strategy for germplasm protection, preservation and evaluation. Potato species would be expected to differ, since some are clearly natural

selfers and others are self-incompatible. We used RAPDs (Bamberg and del Rio, 2004) and SNPs (Bamberg et al., 2015), with four species representing different ploidies and breeding systems as models to estimate population heterogeneity. Diploid and tetraploid outcrossers had the most marker heterogeneity. A single plant of these species does not represent the population very well, but bulk samples of about 20 plants have a high probability of uniformly capturing almost all the variation.

General status of vulnerability of alleles in the genebank. As described above, sampling opportunities like seedling selection and non-balanced seed bulking do not appear to be major threats to maintaining alleles in the genebank across generations of sexual reproduction. Random neutral DNA markers suggest that the reason for this is threefold: (1) low-frequency alleles are not very common in populations, in part because some species are inbreeders, (2) to confidently maintain low-frequency alleles in a population, one needs population sizes that are practically impossible to attain in the genebank, so it is a rather hopeless cause to try to keep truly vulnerable alleles unless they are isolated and maintained clonally, and, most importantly, (3) low-frequency alleles vulnerable in any given population are almost always *fixed* in another population, making them invulnerable to loss in the context of the whole genebank (Bamberg and del Rio, 2003). The most vulnerable situation is when an allele is found only in one population of its species, and it also has a low frequency within its population. But the evidence suggests that alleles that are rare within a population are usually common or fixed in another population (Bamberg and del Rio, 2009) and alleles that occur in only one population are usually present in a relatively high frequency there (Bamberg and del Rio, 2009).

5 Evaluation and enhancement of potato genetic material

5.1 Evaluation

A daunting challenge. Evaluation to detect phenotypes useful for improving the crop is as very broad a topic as the many disciplines of potato study – genetics, pathology, physiology, entomology, horticulture, nutrition, biochemistry, production and management, and more – and cannot be addressed in detail in this chapter. As previously mentioned, the time and resources needed to evaluate a large number of germplasm in several different ways is a major limitation to its use, and any advances in technology for phenotyping will increase the practical value of exotic germplasm.

Basic evaluation that identifies the germplasm. DNA markers have great advantages since they provide many data points and are stable in any environment and from any of the plant's tissues at any stage of development. But the link between DNA markers and useful traits will be weak without accurate and relevant phenotype data. For example, we know that strong GxE exists such that some germplasm only exhibit desirable high performance for certain traits when evaluated as field tubers, not tubers grown in greenhouse pots (Hale et al., 2008). Similarly, we also need accurate descriptive and natural origin information, because provenance and taxonomic identity may also be associated with practical phenotypic traits. For example, certain species originating from certain locations are associated with greater frost tolerance (Hijmans et al., 2003). The greatest inefficiency and potential blurring of such patterns occurs when erroneous descriptive data make

two identical germplasm items appear to be different. In del Rio and Bamberg (2000) we investigated a population of *S. sucrense* with implausible origin data. We could not, of course, determine its precise origin with DNA markers, but *could* show it was not an exact duplicate of another population in the genebank and thus was worthy of separate maintenance and evaluation. On the other hand, we also showed that AFLP and SNP markers could solve the mystery of why a certain population of *S. okadae* reputedly from Bolivia had characteristics found only in populations from Argentina – it quite clearly was a mislabelled identical duplicate sample of another *okadae* population from Argentina already in the genebank (Bamberg et al., 2016b).

5.2 Enhancement

Interest in using exotics for enhancement is what motivated establishing centralized genebanks as an alternative to an inefficient *ad hoc* approach by multiple unorganized separate research and breeding programmes. The use of exotic germplasm for potato improvement dates back to the mid-nineteenth century, when South American land races were imported to Europe and North America after the late blight epidemics. The common belief was that centuries of asexual reproduction had made potato crop weak and susceptible to diseases (Goodrich, 1863). The introduction of both 'new blood' and sexual propagation was expected to restore the vigour of the crop. Of course, sexual propagation eliminated many of the pathogens that had led to the decline in vigour over time. The addition of new germplasm probably also benefitted the crop, although most of the new seedlings were inferior to existing cultivars, as modern breeders would predict. Notable successes were Garnet Chile and the Chilean cultivar Daber, which figured prominently in the pedigrees of many North American and European cultivars (Glendinning, 1983; Bradshaw et al., 2006).

The next major effort to introgress wild germplasm was nearly a century later, when breeders in both North America and Europe began using the hexaploid wild species *S. demissum* as a source of late blight resistance genes (Stevenson and Clark, 1937; Ross, 1986). However, breeders found this germplasm challenging to work with and, when resistant cultivars were developed, strains of the pathogen were able to overcome the *S. demissum R* genes. Heterosis was noted, though, when adapted hybrids between cultivated and wild potatoes were generated (Ross, 1986).

The *S. demissum R* gene breeding efforts ushered in a new era of germplasm enhancement in potato. *Solanum chacoense* was used as a source of late blight and common scab resistance in the development of the cultivar Lenape (Akeley et al., 1968). As an unexpected bonus, the wild germplasm appears to also have contributed exceptional processing quality. Lenape is in the pedigrees of many major potato cultivars developed for chip production (Love et al., 1998). However, an unexpected negative contribution of *S. chacoense* was high tuber glycoalkaloid content (Zitnak and Johnston, 1970).

In 1963, Sherret Chase suggested that an analytic breeding scheme might be appropriate for potato. In this scheme, cultivated potato would be reduced to the diploid level, where crossing and selections would be carried out. Then, the germplasm would be returned to the tetraploid level for the production of cultivars (Chase, 1963a,b). This scheme was adopted by several programmes worldwide and has been described by many (Mendiburu and Peloquin, 1977; Peloquin et al., 1989; Jansky et al., 1990; Carputo and Barone, 2005; Thieme et al., 2008; Ortiz et al., 2009). Basically, parthenogenesis is used to create potato dihaploids, which are crossed to diploid wild relatives. The resulting hybrids are selected

for agronomic traits and the new traits introduced by the wild relatives. Then, sexual polyploidization is employed to return the germplasm to the tetraploid level.

The analytic breeding scheme has contributed to the development of several successful cultivars. Yukon Gold is the product of a cross between a tetraploid cultivar and a 2*n* pollen-producing Phureja x dihaploid hybrid (Johnston and Rowberry, 1981). Dakota Russet resulted from crossing a tetraploid cultivar to a diploid hybrid containing *S. raphanifolium*. Other cultivars are more indirect products of analytic breeding. For example, the selections S438 and S440 are products of sexual polyploidization between a tetraploid *S. tuberosum* clone and a dihaploid x *S. tarijense* hybrid. S438 and S440 are parents of the chip processing cultivars Accumulator, Kalkaska, Lelah, Nicolet, Tundra and White Pearl, while S440 is the grandparent of the chip processing cultivar Pinnacle.

Even in the absence of a systematic breeding effort such as the analytic breeding scheme, wild relatives have been incorporated into the pedigrees of many cultivars. Some of these introgressions date back to the early efforts to bring in late blight resistance genes from *S. demissum*. Other breeding endeavours have focused on pest and pathogen resistance from a handful of wild species, especially *S. acaule*, *S. chacoense, S. fendleri, S. maglia, S. microdontum, S. spegazzinii, S. stoloniferum, S. toralapanum* and *S. vernei* (reviewed by Plaisted and Hoopes, 1989; Bradshaw et al., 2006). Typically, after a cross is made to a wild species, several generations of backcrossing to cultivated potato are necessary to recover commercially acceptable phenotypes (Black, 1949; Rudorf, 1958; Lauer, 1959; Bradshaw et al., 2006).

For all of these efforts, genebanks provided support, making stocks more secure, accessible, healthy and better documented with catalogues, and eventually online access, providing enhancers with information they would otherwise have to glean from the literature.

Genebanks also facilitated enhancement by providing a platform for evaluation and through genebank-sponsored and in-house evaluation. They have provided, preserved and distributed model stocks for technical research. Staff and associated programmes developed technology and related information. Examples are discovering how to induce haploids by simple crossing, making interploidy hybrids through use of gametes with the sporophytic chromosome number (2*n* gametes), establishing crossability groups (Endosperm Balance Number, EBN), creating monoploids that isolate a single allele per locus to facilitate sequencing and employing protoplast fusion to combine species that do not naturally hybridize. Details of these methods have been reviewed elsewhere (Hanneman, 1999; Bradeen and Haynes, 2011).

6 Legal custody and access to potato genetic material

Undisputedly the largest single event effecting the collection, acquisition, conservation, exchange, distribution and ownership of plant genetic resources in the past twenty-five years is the Convention of Biological Diversity (CBD; https://www.cbd.int/doc/legal/cbd-en.pdf). First opened for signatures at the United Nations Conference on Environment and Development (known as the Rio 'Earth Summit'; https://www.un.org/geninfo/bp/enviro.html), CBD came into force in December 1993, with 168 countries ratifying it. The foundation of CBD was built on three principles: *the conservation of biological diversity*, *the sustainable use of its components* and *the fair and equitable sharing of the benefits arising out of the utilization of genetic resources* (Article 1 CBD). The definition

of genetic material, *any material of plant, animal, microbial or other origin containing functional units of heredity*, is sufficiently broad to allow interpretations for inclusion of virtually all forms of materials distributed from genebanks, including DNA. Finally, CBD reaffirms that countries have sovereign rights over their genetic resources, which includes the right to equitable sharing of benefits arising from their use. This also gives countries the *de facto* right to control and regulate access.

Although CBD was conceived as an instrument to enhance the conservation and use of genetic resources, two factors, sovereign rights and the economic value, that such rights might entail, halted much of the sharing of germplasm at the national level in the developing world. The rationale is complicated and multifaceted, yet a lack of infrastructure, policy and legislative and economic mechanisms to finance and carry out conservation in many countries resulted in a general lack of conservation measures and very limited access (Chandra and Idrisova, 2011). If a country does not have the capacity to regulate and set a value on its genetic resources, and most countries do not, the result is not to allow access until such time as a value can be determined. Since this is challenging, access to genetic resources in the developing world is limited. In addition, the much-needed conservation efforts expounded by CBD are unfortunately slow to become a reality as plant species continue to be threatened with extinction. As an example, outside of efforts by the USDA in the United States, there are virtually no publicly available collections of wild potato species in the past 17 years.

In response to the difficulty in the implementation of CBD at the national level, as well as the lack of benefit sharing from the use of plant genetic resources, a second instrument, the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA; http://www.fao.org/plant-treaty), came into force in June 2004. The ITPGRFA covers only 64 crops (Annex 1 crops); however, the Annex 1 list includes all cultivated and wild potato species section tuberosa *except S. phureja*. *S. phureja* is not the only crop notably missing from Annex 1 (sugar cane, wild *Manihot* spp., peanut and soya bean are also excluded from Annex 1), yet it does uniquely pose a fascinating dilemma. The recent taxonomic revision of cultivated potato (Spooner et al., 2014) eliminates the species designation *S. phureja* and lumps *S. phureja* with four other Annex 1 species into *S. tuberosum*. How this will be dealt with in the future by the South American countries which negotiated the exclusion of *S. phureja* in the Annex 1 listing will be interesting.

While both CBD (and its Nagoya Protocol) and ITPGRFA defined conservation, access and benefit sharing as key components, as mentioned earlier, for potato they have fallen short of actually implementing new programmes for conservation or access. Although the key principles for implementing access have been outlined for prior informed consent (PIC) and mutually agreed terms (MAT), uniform standards defining what is needed for compliance of PIC and MAT do not exist. Progress has been made, however, with the ITPGRFA defining the terms for transfer of Annex 1 germplasm with the standard material transfer agreement (SMTA). Unfortunately, far too few countries, and even most party nations, have yet to implement the regulations and infrastructure for the transfer of germplasm with the SMTA. In fact, the vast majority of germplasm transferred with an SMTA is from non-national collections (IT/GB-6/15/20; *Report from Institutions that have signed Article 15 Agreements*, Sixth session of the Governing Body of the ITPGRFA). Few, if any, national plant germplasm collections from developing countries have been made broadly available with easily assessable and searchable websites as a result of the ITPGRFA.

Despite significant issues such as use restricted to breeding, training and research, no time limit to the terms of the SMTA and set payment of benefits (sales) with no adjustment

for crop or % incorporation of covered material, it is supported by a multilateral system with defined terms. This greatly facilitates the transfer of germplasm as terms for transfer and use are already defined and do not need to be negotiated on a one-to-one basis as is the case with CBD. The potato genetic resources community is, therefore, fortunate that potato is included in Annex 1 of the ITPGRFA, but more needs to be done by the national programmes to allow access under the terms of the ITPGRFA to potato germplasm under national control. The ratification of the ITPGRFA by the United States (ratification consented by Senate vote, 28 August 2016; https://www.congress.gov/treaty-document/110th-congress/19/resolution-text) should contribute to building confidence on the ITPGRFA and hopefully enable needed capacity building for greater collaboration with national programmes for the collection, sharing and conservation of potato genetic resources.

A final note supporting the need to enhance capacity for the access to potato germplasm from national programmes is that approximately 94% of all material transferred through the multilateral system with an SMTA was distributed by the eleven genebanks in the Consultative Group on International Agricultural Research (CGIAR; http://www.fao.org/3/a-mo439e.pdf). This clearly illustrates the points made above that access to germplasm from party countries to the ITPGRFA is not happening and one overreaching reason for this is the lack of capacity and infrastructure to do so. In the case of potato, however, there are many positive changes in the Andean countries. Most notable is the announcement that Bolivia became a contracting party to the ITPGRFA on 4 December 2016 (http://www.fao.org/plant-treaty/news/detail-events/en/c/448725/). Additionally, the Instituto Nacional de Innovacion Agraria (INIA, the Peruvian National Program for Agriculture) hopes to initiate collections of wild potato in 2017 (Ellis, pers. comm.).

7 Conclusion and future trends

Legal custody of germplasm is one prerequisite for access and another is the distribution across international boundaries and the assurance that such distribution does not spread diseases or pests. The widespread distribution of clonal plant material poses the risk of simultaneous distribution of plant diseases and pests (Brasier, 2008). National agricultural pest and disease agencies are charged with keeping unwanted pests and pathogens out of their country and hence there are strict certification requirements for all countries that imported plant material is free of harmful pests and pathogens. Although this prevents their spread, it also prevents the exchange, access and use of genetic resources such as potato. If the exporting country does not have the infrastructure, expertise, technology or ability to perform the tests needed for phytosanitary certification, the genetic resources cannot be moved outside the country of origin. This is too often the case in developing countries and thus constitutes a major limitation to global access and the use of genetic resources for crops such as potato.

Potato crop wild relatives and cultivars/varieties from some potato genebanks (James Hutton Institute, UK and USDA, USA) are distributed as seed which is generally easier to certify as phytosanitary clean and thus ship internationally. At the International Potato Center in Lima, Peru (CIP), the presence of the following viruses, shown to be seed transmitted, are tested for parental material pre-flowering: arracacha virus B -oca strain (ABV – O), alfalfa mosaic virus, Andean potato latent virus, potato yellowing virus, tobacco mosaic virus, potato virus T (PVT) and potato spindle tuber viroid (PSTVd). If any of the

viruses are present in the parental material, that plant is removed. Remaining plants are monitored throughout the growing season for symptoms and the screenhouses used for seed regeneration are maintained free of insects which transmit disease. Seeds regenerated under clean, insect-free conditions from disease-free parents can be certified as disease free and hence distributed internationally.

In the case of clonal material, not only does the genebank material have to be certified clean of phytopathogens, it also has to be shipped in a way that the material cannot become contaminated during shipping. As mentioned above, the shipping of disease-free *in vitro* material has become the standard for international shipment of clonal material from genebanks. The phytosanitary cleaning process of clonal potato accessions involves the introduction of the plants into *in vitro* culture, the treatment of the *in vitro* plantlets with thermotherapy (36–40°C for three weeks), followed by the aseptic isolation of a 0.3 mm meristem and the regeneration of *in vitro* plants from this meristem. Although the cleaning process is straightforward and highly effective with a success rate of 96% in potato at CIP (data unpublished), the diagnostic tests to confirm a disease-free status lag behind the physical phytosanitary cleaning of accessions and thus can delay the process for distribution of material for 1–2 years!

The time it takes to certify material as clean of diseases of import importance is a limiting factor for potato improvement programmes needing germplasm under a short or limited funding cycle. Next-generation DNA sequencing and other developments are targeting the limitation in the certification of disease-free status of potato germplasm. One such technology is small RNA sequencing and reassembly (sRSA: Kreuze et al., 2009), where the whole sequencing of small RNA from plants is proving to be a very sensitive method for detection of virus infection and could reduce the time for the confirmation of disease-free status of potato genebank accessions from a year or more to a month. Other developing technologies which could significantly facilitate the movement of non-*in vitro* clonal germplasm or advanced breeding lines/cultivars include the use of loop-mediated isothermal amplification assay-based systems (Liljander et al., 2015), which offer battery-operated portable cartridges able to detect the presence of viruses in less than an hour in the field or at point of entry of genetic resources. In the future, such portable assay systems could be powered by cell phones.

Another important factor in the access and benefit sharing equation is the role of genebanks in providing benefits to the communities whose ancestors 10 000 years ago began the process of the selection of potato landraces from which all existing cultivars originated. In the Andes, families traditionally planted twenty or more landraces of potatoes as an insurance policy. The bitter potatoes (*S. juzepczukii, S. ajanhuiri, S. curtilobum*) tend to be very hardy and, except for extreme years, always offer some production, and are hence critical for the sustenance of farming communities. The landraces of the non-bitter potatoes (collectively classified as *S. tuberosum* by Spooner et al. (2014)) tend to be more environmentally, and thus annually, unpredictable. This centuries-old insurance of planting large numbers of varieties ensures that, when one desired cultivar does not produce well one year, chances are another will. Unfortunately, this insurance in planting large numbers of cultivars is breaking down in some Andean communities. A recent report from the communities of Santa Cruz de Pichiu in Peru notes:

> *In the last 20 years the number of native varieties have dramatically declined from 60 to 80 varieties to 6 or 8 varieties of potatoes.* (translation by D. Ellis; p. 2. Aguilar, A.M. 2016)

In an effort to help restore the natural balance in sustenance potato farming communities in the Peruvian Andes, the CIP genebank has been involved in a programme since the late 1998 focusing on the repatriation of native potato landraces back to the communities whose forefathers preserved them. Starting with returning native potato landraces collected and conserved by CIP over the past 45 years to a few select communities, the CIP genebank repatriation programme has now benefitted over 90 indigenous communities in Peru. The repatriation programme returns disease-free seeds of landrace potatoes to communities which were collected near or were known to grow in the localities in which these communities reside. To date, CIP has given back (repatriated) to native Peruvian farmers over one-third of its potato landrace collection.

Programmes such as the repatriation project provide a small effort towards the total need for support of the conservation of habitats, wild relatives and communities whose relatives were critical for the domestication of our crop and whose livelihoods still depend on farming landraces by traditional means. These very communities and environments are key to sustaining the diversity we need for continued improvements to maintain potato yields. A changing climate is having a major impact in the Andes and thus the diversity of potato and its wild relatives. The *ex situ* conservation of this genetic diversity in genebanks is the only guarantee that future generations will have the same opportunity we have today to use this diversity for sustained potato productivity.

8 Where to look for further information

In addition to the references cited below, the authors invite readers to consult CIP and USPG websites for the most current information on genebank issues.

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