

Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

Swarup Kumar Chakrabarti
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The Potato Genome

Compendium of Plant Genomes

Series editor

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Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant *Arabidopsis thaliana* in 2000, whole genomes of about 70 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

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The Potato Genome

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*This book series is dedicated to
my wife Phullara, and our children Sourav,
and Devleena*

Chittaranjan Kole

Preface to the Series

Genome sequencing has emerged as the leading discipline in the plant sciences coinciding with the start of the new century. For much of the twentieth century, plant geneticists were only successful in delineating putative chromosomal location, function, and changes in genes indirectly through the use of a number of “markers” physically linked to them. These included visible or morphological, cytological, protein, and molecular or DNA markers. Among them, the first DNA marker, the RFLPs, introduced a revolutionary change in plant genetics and breeding in the mid-1980s, mainly because of their infinite number and thus potential to cover maximum chromosomal regions, phenotypic neutrality, absence of epistasis, and codominant nature. An array of other hybridization-based markers PCR-based markers, and markers based on both facilitated construction of genetic linkage maps, mapping of genes controlling simply inherited traits and even gene clusters (QTLs) controlling polygenic traits in a large number of model and crop plants. During this period a number of new mapping populations beyond F_2 were utilized and a number of computer programs were developed for map construction, mapping of genes, and for mapping of polygenic clusters or QTLs. Molecular markers were also used in studies of evolution and phylogenetic relationship, genetic diversity, DNA-fingerprinting, and map-based cloning. Markers tightly linked to the genes were used in crop improvement employing the so-called marker-assisted selection. These strategies of molecular genetic mapping and molecular breeding made a spectacular impact during the last one and a half decades of the twentieth century. But still they remained “indirect” approaches for elucidation and utilization of plant genomes since much of the chromosomes remained unknown and the complete chemical depiction of them was yet to be unraveled.

Physical mapping of genomes was the obvious consequence that facilitated development of the “genomic resources” including BAC and YAC libraries to develop physical maps in some plant genomes. Subsequently, integrated genetic-physical maps were also developed in many plants. This led to the concept of structural genomics. Later on, emphasis was laid on EST and transcriptome analysis to decipher the function of the active gene sequences leading to another concept defined as functional genomics. The advent of techniques of bacteriophage gene and DNA sequencing in the 1970s was extended to facilitate sequencing of these genomic resources in the last decade of the twentieth century.

As expected, sequencing of chromosomal regions would have led to too much data to store, characterize, and utilize with the-then available computer software could handle. But development of information technology made the life of biologists easier by leading to a swift and sweet marriage of biology and informatics and a new subject was born—bioinformatics.

Thus, evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has traveled much beyond biology and involves biophysics, biochemistry, and bioinformatics!

Thanks to the efforts of both public and private agencies, genome sequencing strategies are evolving very fast, leading to cheaper, quicker and automated techniques right from clone-by-clone and whole-genome shotgun approaches to a succession of second-generation sequencing methods. Development of software of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

It became a reality to chemically—and so directly—define plant genomes, popularly called whole-genome sequencing or simply genome sequencing.

The history of plant genome sequencing will always cite the sequencing of the genome of the model plant *Arabidopsis thaliana* in 2000 that was followed by sequencing the genome of the crop and model plant rice in 2002. Since then, the number of sequenced genomes of higher plants has been increasing exponentially, mainly due to the development of cheaper and quicker genomic techniques and, most importantly, development of collaborative platforms such as national and international consortia involving partners from public and/or private agencies.

As I write this preface for the first volume of the new series “Compendium of Plant Genomes”, a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, eight crop and model plants, eight model plants, 15 crop progenitors and relatives, and three basal plants are accomplished, the majority of which are in the public domain. This means that we nowadays know many of our model and crop plants chemically, i.e., directly, and we may depict them and utilize them precisely better than ever. Genome sequencing has covered all groups of crop plants. Hence, information on the precise depiction of plant genomes and the scope of their utilization is growing rapidly every day. However, the information is scattered in research articles and review papers in journals and dedicated web pages of the consortia and databases. There is no compilation of plant genomes and the opportunity of using the information in sequence-assisted breeding or further genomic studies. This is the underlying rationale for starting this book series, with each volume dedicated to a particular plant.

Plant genome science has emerged as an important subject in academia, and the present compendium of plant genomes will be highly useful both to students and teaching faculties. Most importantly, research scientists involved in genomics research will have access to systematic deliberations on the plant genomes of their interest. Elucidation of plant genomes is not only of interest for the geneticists and breeders, but also for practitioners of an array of plant science disciplines, such as taxonomy, evolution, cytology, physiology, pathology, entomology, nematology, crop production,

biochemistry, and obviously bioinformatics. It must be mentioned that information regarding each plant genome is ever-growing. The contents of the volumes of this compendium are therefore focusing on the basic aspects of the genomes and their utility. They include information on the academic and/ or economic importance of the plants, description of their genomes from a molecular genetic and cytogenetic point of view, and the genomic resources developed. Detailed deliberations focus on the background history of the national and international genome initiatives, public and private partners involved, strategies and genomic resources and tools utilized, enumeration on the sequences and their assembly, repetitive sequences, gene annotation, and genome duplication. In addition, synteny with other sequences, comparison of gene families, and, most importantly, potential of the genome sequence information for gene pool characterization through genotyping by sequencing (GBS) and genetic improvement of crop plants have been described. As expected, there is a lot of variation of these topics in the volumes based on the information available on the crop, model, or reference plants.

I must confess that as the series editor it has been a daunting task for me to work on such a huge and broad knowledge base that spans so many diverse plant species. However, pioneering scientists with life-time experience and expertise on the particular crops did excellent jobs editing the respective volumes. I myself have been a small science worker on plant genomes since the mid-1980s and that provided me the opportunity to personally know several stalwarts of plant genomics from all over the globe. Most, if not all, of the volume editors are my longtime friends and colleagues. It has been highly comfortable and enriching for me to work with them on this book series. To be honest, while working on this series I have been and will remain a student first, a science worker second, and a series editor last. And I must express my gratitude to the volume editors and the chapter authors for providing me the opportunity to work with them on this compendium.

I also wish to mention here my thanks and gratitude to the Springer staff, Dr. Christina Eckey and Dr. Jutta Lindenberg in particular, for all their constant and cordial support right from the inception of the idea.

I always had to set aside additional hours to edit books besides my professional and personal commitments—hours I could and should have given to my wife, Phullara, and our kids, Sourav, and Devleena. I must mention that they not only allowed me the freedom to take away those hours from them but also offered their support in the editing job itself. I am really not sure whether my dedication of this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

Kalyani, India

Chittaranjan Kole

Preface

Potato (*Solanum tuberosum* L.; $2n = 4x = 48$) is the fourth most important food crop of the world after rice, wheat and maize, with a worldwide production of 381.68 million tons in the year 2014 (FAO). This highly productive non-cereal food crop, domesticated in the highland tropics of the Andes mountains in South America, has been declared the 'Food for the Future' by the United Nation's Food and Agriculture Organization, who celebrated the year 2008 as the 'International Year of the Potato'. By 2020, it is estimated that more than two billion people worldwide will depend on the potato for food, feed, or income. Potato is a member of the asterid clade of eudicot that represents 25% of the flowering plant species and it belongs to the Solanaceae, a family of about 90 genera and 2800 species. The family Solanaceae contains several well-known cultivated crops such as tomato (*Lycopersicon esculentum*), eggplant (*Solanum melogena*), tobacco (*Nicotiana tabacum*), pepper (*Capsicum annum*), petunia, and potato (*Solanum tuberosum*). The International Code of Nomenclature of Cultivated Plants (ICNCP 2009) recognized four species of cultivated potato, i.e. *Solanum tuberosum*, with two cultivar groups, *Andigenum* containing diploids, triploids and tetraploids, and the *Chilotanum*, from which our modern tetraploid cultivars arise; *Solanum ajanhuiri* (diploid); *Solanum juzepczukii* (triploid); and *Solanum curtilobum* (pentaploid).

Despite the importance of potato as a world food crop, the genetics and inheritance of many important qualitative and quantitative agronomic traits of this crop were poorly understood. The reasons for the scanty knowledge on genetics of this crop are attributed to tetraploidy, the high degree of heterozygosity and the absence of homozygous inbred lines or any collection of genetically well-defined marker stocks. In addition, the long generation time and the frequently observed distorted segregation ratios discouraged geneticists from choosing the potato as a model species for genetic research. However, for a critical investigation of complex biological processes like tuberization, yield, disease resistance, etc. and to enable rapid, genome-based breeding strategies, a comprehensive genetic analysis of the crop was a prerequisite. To resolve this problem the international community of potato researchers took on the task of deciphering the entire genetic code of potato by sequencing. Thus, the Potato Genome Sequencing Consortium (PGSC) was initiated in January 2006, consisting of 29 laboratories spread over 15 countries, i.e. Argentina, Brazil, China, Chile, Denmark, India, Ireland, Italy,

The Netherlands, New Zealand, Peru, Poland, Russia, the United Kingdom and the United States of America. The consortium deciphered 727 MB of 844 MB potato genome using a unique homozygous doubled-monoploid potato clone (DM) and a hybrid sequencing approach consisting of Illumina sequencing-by-synthesis, Roche/454 Pyrosequencing, and the classical Sanger sequencing platforms. The PGSC sequenced the potato genome as a public effort and made it freely available to all the researchers. Free access to the potato genome data triggered extensive post-genomic work on gene discovery, marker development, evolutionary and plant diversity studies, improved breeding, and engineering of new phenotypes in potato, etc. Other scientific communities also utilized the sequence data to understand basic plant biology, biochemistry, and comparative genomics. This is evident from >880 citations of the *Nature* article on the potato genome sequencing by May 2017.

The present compilation is an attempt to assess the post-genomic research on structural and functional genomics, transcriptomics, repetitive sequences and their application, resistance genes and their application, nutrient use efficiency, and abiotic stress management in potato, etc. We hope the information compiled in this book will be useful for students, researchers, teachers, industry personnel and all other people interested in potato improvement, production and protection. The primary users of this book will be universities, public sector institutes as well as government and industrial potato biologists/breeders who are involved in research to understand biological and agronomic processes in potato. It will be our privilege to receive any suggestion for future improvement. We are grateful to Series Editor Prof. Chittaranjan Kole for giving us opportunity to prepare this book. We are highly thankful to Springer team for their valuable inputs.

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The Historical, Social, and Economic Importance of the Potato Crop

1

Oscar Ortiz and Victor Mares

Abstract

The potato has a fascinating history, from its origin and domestication in the Andean Region, where it was essential for feeding a growing population, for example, the Inca Empire, to its introduction into farming and food systems in Europe and elsewhere in the world. This crop has been the key factor in terms of food security, nutrition, population growth and urbanization in many regions. In recent decades, the potato has become a dominant crop in countries such as China and India, and its cropping area and production have increased more than those of any other food crop in Africa. Besides the social and economic importance of potato, extensively discussed in several published articles and briefly mentioned in this chapter, we discuss two relevant issues that are intimately related to potato genomics and breeding and which make potato a crop that has a lot to offer for the future. Those issues are the potato's contribution to food and nutrition security, and the cultural and genetic importance of biodiversity conservation in the Andes; these issues are strongly related to gender, since women in traditional societies have contributed—and still contribute—to an enormous wealth of knowledge in relation to biodiversity conservation and utilization. The adaptability shown by the potato crop over thousands of years indicates the potential role of the potato as a climate-smart crop, particularly based on its short vegetative period, water utilization efficiency, and productive capacity per unit of input.

1.1 The Unique Saga of the Potato

The history of the potato is, arguably, the most fascinating of all crops. The route it has followed from its origin and domestication in the Andean region, where its cultivation started about

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8000 years ago, and where it became an essential crop for food security in pre-Columbian times (Fiedel 1987; Moseley 1992; Hastorf 1993), to becoming the third most important food crop in the world has been extensively documented in books, reviews and essays (Salaman 1949; Brown 1993; McNeill 1999; Reader 2008). These studies describe very well, both in scientific and anecdotal terms, the amazing saga of the potato on its way from South America to Europe over several centuries and its adaptation to farming and food systems in all the European countries and elsewhere in the world. This globalization process of the potato, which started in the sixteenth century, is still going on today. In addition to its history, the enormous and unparalleled social and economic importance of the potato in different societies in both the New World and the Old World has been narrated and described in great detail in several articles and books (Salaman 1949; De Jong 2016). The potato is credited with the distinction of being the most crucial agricultural factor in the course of human events in the last eight centuries, including its effect on food security, its prowess in nourishment of people on a great scale, aiding explosive population growth in Europe, and urbanization (Nunn and Qian 2011; De Jong 2016). Before that, in its land of origin and domestication, pre-Hispanic societies reached high levels of political organization and cultural and technological development, based on the potato as one of their main staple crops and source of food security and nutrition. Its domestication and continuous process of adaptation to highly diverse agroecosystems in the Andes of South America generated a broad genetic diversity, resulting in a crop that is very well adapted to climatic variability, and able to substantially increase and sustain food production. This remarkable versatility of the crop drove the development and consolidation of highly organized societies, which reached their pinnacle with the Inca Empire. The conquest of this empire by the Spaniards in the sixteenth century gave rise to the subsequent expansion of the potato in the Old World, a process that proved to be a major event in the history of

humanity. At the peak of the development of Andean societies, just before the clash with the Western world, it has been estimated that the potato fed and nourished a population of around ten million people in South America (Reader 1990), with no historical trace of a famine in those societies. Potato domestication and cultivation are examples of the skills of Andean societies who developed agricultural knowledge and its associated technology, such as terrace cropping, irrigation management, and post-harvest processing. Also, since wild potatoes contain solanine and tomatine, toxic compounds that protect the plants against herbivores and pathogens and which are not eliminated by cooking, ancient Andean farmers solved the problem by breeding non-poisonous varieties that started the potato revolution, as those new plants were converted into a crop suitable for human consumption (see <http://www.smithsonianmag.com/history/how-the-potato-changed-the-world>). We should add that one of the first processed potato products known worldwide, the freeze-dried potato, originated in the Andes also thousands of years ago as a storage technique and a way of making bitter potatoes edible. Ortiz (2006) argued that the information, knowledge, and technology associated with potato cultivation, breeding and post-harvest management were disseminated throughout the Andes with the potato itself, transported by migrant populations to the new territories progressively occupied by ancient Andean settlers, and that this process that began with the domestication of the crop still continues to this day.

Although the importance of the potato in the development of pre-Columbian Andean societies is highly relevant, and its impact is greater than that of any other contemporary crop (it could be argued that maize was also extremely important), it is the history of the impact of the potato on a global scale, following its introduction into Europe, that makes a most singular story. In this section, we merely mention some highlights since many excellent reviews have already described this process. The first remarkable effect of the introduction of the potato into Europe was

its contribution to the significant increase in the European population during the period from the second half of the eighteenth century to the middle of the nineteenth. This population growth responded to the very significant increase in food production brought about by the expansion of potato cultivation in European countries. It has been estimated that the introduction of the potato resulted, over the years, in the doubling of the food supply in Europe (Mann 2011). The potato is said to have brought a solution to the historical periodic food scarcity in Europe, where food shortages were a recurrent problem (Vandenbroeke 1971). It has also been argued that the potato, by providing plentiful food to increasing populations, was one of the factors that allowed European countries to dominate the world during the colonial centuries (McNeil 1999), facilitated the Industrial Revolution to some extent, and contributed to the recovery after the major European wars in the twentieth century.

However, an infamous and tragic episode of the arrival of the potato into European farming and the dependence it created on a single crop is provided by the history of the potato in Ireland. Several publications describe how the potato became so entrenched in Irish farming and livelihoods that it became the main and almost exclusive staple food for the Irish peasantry, and this was conducive to a very large increase in the population in the country, which soared from three million to eight million in five generations in the period ending in 1840. At that point in time, the potato crop failed in several successive years as a result of a massive outbreak of late blight disease. The tragic consequence was the Irish potato famine, which caused the deaths of more than one million poor farmers from starvation and the emigration of a similar number of people, mostly to the United States and other English-speaking countries, such as Canada and Australia (see Trueman 2016).

In recent decades, the potato has become a dominant crop in emerging countries such as China and India, which are now the largest world producers and consumers of the tuber. China's official policy is to turn the potato into

its main source of food security in the near future (Baroke 2015; Frederick and Lei 2015; Qu and Xie 2008). Similar efforts are being carried out in India (Singh and Rana 2013) and elsewhere (Azimuddin et al. 2009; Devaux 2014; Devaux et al. 2014). In addition, the arable potato area has increased more than that of any other food crop in Sub-Saharan Africa in the last three decades. For example, in East Africa, potato production has nearly quadrupled since the 1990s (Gildemacher 2012), and the potential for growth is still significant because consumption per capita is relatively low (Havenkort et al. 2009). Worldwide, potato production has increased at an annual rate of 4.5% over the past 10 years, exceeding the growth in production of any other major food commodity in developing countries, where there is a pressing need to satisfy the growing demand for food and nutrition.

Besides the social and economic importance of the potato, briefly mentioned above, in the following sections we discuss two relevant issues intimately related to potato genomics and breeding. These issues are the potato's contribution to food and nutrition security, and the cultural and genetic importance of potato biodiversity in the Andes, which is intrinsically related to gender aspects. Those attributes of the potato are in addition to its potential role as a climate-smart crop, a condition related to its short vegetative period, its water utilization efficiency, and adaptation to a diversity of agro-ecosystems: all characteristics that make the potato a crop with much to offer for the future.

1.2 Potato's Contribution to Food and Nutrition Security

The potato has traditionally been considered a food security crop, usually implying the sheer volume of a reliable foodstuff, which was critical in the pre-Columbian eras in South America. Even nowadays, the potato is regarded as a crop that provides food for the poor, particularly in developing regions (Lutaladio and Castaldi

2009). A clear example is provided by the increasing reliance of North Korea on the potato as a key crop to solve the chronic food shortages that led to a famine some two decades ago. Following that event, the potato cropping area in the country and correlated per capita consumption increased fourfold, from 11.5 to 49.0 kg per year (FAOSTAT 2013). In rich countries, some misconceptions about the potato's nutritional value are still prevalent, and it is erroneously believed to be a fattening, high carbohydrate foodstuff (Fitzgerald 2014). However, the truth is that the potato is not only a key crop for providing food security to developing regions but also is a highly nutritious food that provides more calories, vitamins, and nutrients per area of cropped land than any other staple crop. Contrary to the above-mentioned erroneous beliefs, potato is a rich source of vitamin C (U.S. Department of Agriculture 2007; Love and Pavek 2008), potassium, and dietary fiber (Nunn and Qian 2011). It is also an excellent source of vitamin B6 and a provider of relatively high amounts of other B complex vitamins, such as thiamin, riboflavin, folate, and niacin, as well as minerals such as magnesium, phosphorus, iron, and zinc, all making the potato ideal for a healthy diet when a few other food components such as dairy and legumes are added to supplement it with calcium, vitamin A and vitamin D (the few nutrients of which the potato is not a good source). Thus, the potato adds a new dimension to food security, widening it to nutrition security in a world in which malnutrition is still prevalent, not only because of the lack of access to food, but also due to the low quality of accessible food from local crops. The potato crop, due to its short duration, is able to produce food during the hunger months (when other crops such as maize are no longer available) in several countries in Sub-Saharan Africa (Demo et al. 2015). The nutritional quality of potato, the wide range of agro-ecosystems where it is able to grow, and its high dry matter and nutrient outputs per unit of land area make this crop the best option for food and nutrition security for large sectors of the human population, both in the developing and the developed regions of the world (DeFauw

et al. 2012; Devaux 2014; Devaux et al. 2014; FAO 2008; De Jong 2016); this is particularly applicable to highland agriculture, where not many productive and nutrition options exist. Due to the growing trends of consumption, particularly in developing regions, and the increasing importance of potato as a staple food worldwide, its nutritive value has enormous potential as a vehicle to improve people's health in both the developed and the developing countries (Love and Pavek 2008). It has been shown that the addition of zinc (Zn) through soil and foliar fertilization of potato plants can increase tuber Zn concentrations with some positive effects on crop yield (Kromann et al. 2016; White et al. 2016). High rates of foliar and soil Zn application produced a 2.51-fold and a 1.91-fold tuber Zn increase, respectively. No difference between cultivars was observed. The same experiments showed that tuber iron (Fe) concentrations were not increased with Fe fertilization. However, as the genetic variation for Fe in potato is large, the Fe content in the tuber content can be improved through breeding (Haynes et al. 2012). Current biofortification breeding work undertaken at the International Potato Center (CIP) has increased mineral concentrations by recurrent selection at the diploid level, resulting in new generations of biofortified potatoes with about 27% increased concentrations up to 35 ppm of Fe and 32 ppm of Zn concentrations on a dry weight basis (Amoros et al. 2017). At present, a strategic interploidy crossing with top tetraploid parental lines is being carried out, leading to high-yielding, disease-resistant populations of biofortified potatoes. Moreover, recent evidence shows that the bio-availability of Fe from the potato is higher than that found in other crops. More than 50% of the potato Fe is released from the matrix during the in vitro digestion and is therefore available at the intestinal level. In vitro bio-accessibility of Fe from potatoes was shown to be 6.3 to 31.5% higher than that of pearl millet, fava bean, and rice (Andre et al. 2015).

However, increased potato productivity and production, fostered by new breeding and production technologies, have an impact that goes beyond food and nutrition security, positively

affecting farming families' livelihoods by increasing income or creating employment (Sullivan 2010; Thiele et al. 2010). It is important to realize that the potato is a crop with a wide range of ecological adaptability, able to grow in different latitudinal and altitudinal conditions where day length, temperatures, and rainfall are highly diverse (Hijmans 2001). In this respect, the ever-increasing pace of the development of genomics is promoting more focused breeding work oriented to producing new varieties that are more efficient in using water and soil nutrients, as well as more tolerant of biotic and abiotic stresses, thereby making the potato an outstanding climate-smart crop. This work is supported by more effective yield analysis based on crop growth modeling linked to proximal and remote sensing of plant reflectance (Quiroz et al. 2017) and also by new phenotyping techniques (Monneveux et al. 2014).

Taking into consideration the need to nearly double global food production by 2050, the potato still has a significant contribution to make to respond to this challenge, and it has already started to do so, because since 2012 more potatoes are being produced in the developing world than in developed countries.

1.3 The Cultural and Genetic Importance of Potato Biodiversity in the Andes

Being a clonal crop with a wide diversity of cultivated species and landraces, in addition to a clearly defined center of origin and domestication, the potato is unique in terms of the historic and modern relevance of in situ conservation of biodiversity. Although there is no full agreement about potato classification, a recently published comprehensive study of the systematics, diversity, genetics, and evolution of wild and cultivated potatoes (Spooner et al. 2014) supports a classification of the cultivated potatoes into four species: (1) *Solanum tuberosum*, with two cultivar groups (the Andigenum Group of upland

Andean genotypes containing diploids, triploids, and tetraploids; and the Chilotanum Group of lowland tetraploid Chilean landraces); (2) *Solanum ajanhuiri* (diploid); (3) *Solanum juzepczukii* (triploid); and (4) *Solanum curtilobum* (pentaploid). In addition, the same article mentions that there are some 3000 landraces (indigenous cultivated crops) still grown by indigenous farmers in South America, particularly in the high Andes, who tend to grow many landraces of all ploidy levels together in the same field. For instance, in Central Peru, the planting of large cultivar mixtures in small areas with large agro-ecological variability brought about by differences in altitude accounts for the conservation of at least 406 unique cultivars (de Haan 2009). This cropping system was a strategy developed by pre-Columbian farmers to cope with climate variability and extreme events prevalent in the High Andes. It is still common to find small potato plots in the Peruvian Andes where up to 20 landraces are grown together. Rather than regarding this system as technologically backward, apt to be replaced by a system based on single, modern varieties, it should be conserved based on two main attributes. First, it offers some important lessons as a highly successful adaptive system to cope with climate change and associated high climate variability (particularly extreme events such as drought or frosts). Second, this system is a very successful method of in situ biodiversity conservation. CIP has the largest ex situ (gene bank) potato collection in the world, which included 4787 cultivated and traditional Andean potatoes, up to February 2017. This is a way of securing the conservation of valuable genes for the future, particularly with threats of climate change, the evolution of production systems, and other agro-ecosystem changes. However, in situ conservation has the advantage of exposing the genetic material to the effect of the environment, which is currently important because native potatoes conserved for thousands of years are subject to new challenges and selection pressure that contribute to increased fitness in the face of climate change. Therefore,

this system, in addition to the cultural importance of potato as a food security and income-generating crop for the Andean populations, provides an invaluable wealth of genetic resources that need to be conserved for potential use in breeding varieties tolerant of or resistant to biotic and abiotic stresses. As FAO Success Stories on Climate-Smart Agriculture (<http://www.fao.org/3/a-i3817e.pdf>) point out, potato genetic resources will continue to represent key resources for building the resilience of agro-ecosystems around the world; and traditional Andean cropping systems provide suitable varieties and breeding stocks necessary to adapt production to changing climatic conditions. Thus, their conservation and sustainable use are a prerequisite for coping with climate change. The Global Environmental Fund (GEF)-funded, FAO-led Global Partnership Initiative on conservation and adaptive management of “Globally Important Agricultural Heritage Systems” (GIAHS), in coordination with the Peruvian Ministry of Environment, other local institutions and the participation of local communities, is helping to value these ingenious agricultural technologies to guarantee their conservation, while providing sustainable development conditions for present and future generations of Andean people (<http://www.fao.org/giahs/giahsaroundtheworld/designated-sites/latin-america-and-the-caribbean/andean-agriculture/en/>), and to date, 3500 smallholder farming families in 18 rural communities are conserving 177 native potato landraces. There is a very important relationship between in situ biodiversity conservation in traditional farming systems and genomic work, as evidenced by the Genomics and Biodiversity: Providing New Opportunities for Smallholder Potato Farmers project, funded by the German Federal Ministry for Economic Cooperation and Development (BMZ). The CIP in Peru and the Max Planck Institute for Plant Breeding Research (MPIZ) in Germany collaborated with several other partners in this project, which built on CIP’s attempts to use the biodiversity of potato genetic resources to improve late blight

resistance, while providing income to farmers and training national program scientists in using molecular tools that permit further exploitation of conserved germplasm (GILB 2003). The project contributes to genetic conservation, and it documents and systematizes the traditional participatory selection of new varieties in farmers’ fields. Another important CIP effort is its contribution to on-farm diversity by giving back, or repatriating, native Peruvian landraces to those farmers whose ancestors had conserved these varieties for millennia. As of 2016, CIP had repatriated over 7685 samples (>1250 unique accessions) to more than 90 different communities, including those in the “Potato Park,” which is a ~10,000 ha reservoir of potato genetic resources (see <http://cipotato.org/es/research/genebank/parque-de-la-papa/>). At present, the park holds more than 1200 varieties of Andean potato cultivated in the highlands, and it is a unique center of biological diversity of this crop, or of any other staple crop. However, lack of funding for this vital activity, which is sometimes erroneously regarded as an anthropological living museum rather than a modern scientific endeavor, is a stumbling block.

The current existence of potato biodiversity still being cultivated in the Andes has motivated public and private organizations to support the establishment of links between small farmers who cultivate a number of potato landraces and the market. CIP’s “Papa Andina” Project, implemented between 2001 and 2012, and including a wide range of public and private stakeholders, developed different approaches in order to make potato biodiversity available to the market and position the native potato as a valuable good. As a result, native potato varieties are now recognized as an essential ingredient of Peru’s world-class cuisine. You can now find native potatoes in the market and in restaurants, which were not there a decade ago. This integration of potato biodiversity into value chains is contributing to reevaluating the importance of conservation and use of native potatoes, and it positions Peru and other Andean countries as producers of potatoes that

cannot be found anywhere else in the world (IICA BID 2014; CIP 2014a, b).

In situ potato biodiversity conservation in the Andes is inextricably linked to traditional local culture and is heavily dependent on women's active decision-making and participation, which is based on a highly sophisticated traditional knowledge of plant diversity, breeding, and culinary properties that has been developed since the potato was first domesticated (Brush 2004; de Haan 2009). Although the potato is generally propagated by seed tubers, which produce clones from the parent plant, women in remote Andean communities were able to use true botanical seed to breed new varieties with novel characteristics, which were then propagated by seed tubers. This implies not only the need to conserve biological potato diversity (Pradel 2013) but also the importance of preserving, understanding, and disseminating women's deep knowledge of the value of this diversity and the techniques for maintaining it. One common problem when dealing with in situ biodiversity conservation and the women's role in it is that the approach is based on a cultural anthropological focus, which gives priority to the traditional way of life, particularly the customs, beliefs, and mythology of an ancient people, rather than the actual knowledge developed by that people (Sarapura et al. 2016). One unintended consequence of this point of view, which privileges the ceremonial and customary attributes of traditional societies over the wealth of poorly understood science and technology developed by those societies, is the fact that peasant communities in the Andes, particularly women, are excluded from national development programs (Diez Hurtado 2010). An interesting and rather different approach has been taken in the analysis conducted by Sarapura et al. (2016), which is based on a feminist standpoint that privileges the peasant women's knowledge and perspectives and the gender implications of the traditional management of native potatoes. Based on the realization of the highly relevant relationship between gender, culture, and potato biodiversity conservation, and the potential benefit for genomics work, due consideration to appropriate funding for potato work in the Andean Region is warranted.

1.4 The Future of the Potato as a Crop

As important as the history of the potato and its past and present economic and social importance are, it is absolutely essential to consider the future of the crop and the multiple aspects of its further development as a crop able to contribute to income generation of small farmers and to satisfy the increasing future nutritional needs of people all over the world. Consolidating the future of the potato calls for research work on several complementary research fronts, such as closing the current yield gaps still existing in several developing countries. This research includes improved agronomic management and the breeding of new varieties adapted and resistant to abiotic and biotic stresses in different and new agro-ecosystems, and dealing with the challenges brought about by the conditions imposed by climate change in current production areas. It also involves the further improvement of the nutritional content of the potato, particularly as a source of micronutrients.

Yield gap (Y_g) is the quantitative difference between a baseline yield (usually the average farmers' yield) and either the attainable (usually, experiment-based yield) or the potential yield (Y_p) over a specified spatial and temporal scale (FAO 2015). In developing regions, the potato yield gap is large, as shown for Sub-Saharan Africa (SSA) by a recent participatory yield gap analysis that included data from ten countries from West Africa, Eastern and Central Africa, and Southern Africa (Harahagazwe et al. submitted for publication). This analysis has shown that SSA (excluding South Africa) countries could easily increase by 140% the current annual production of 10.8 million metric tons if high quality seed of improved varieties resistant to and tolerant of abiotic and biotic stresses, along with improved agronomic management practices, were deployed in farmers' fields. However, productivity increases need to go hand in hand with the development of value chains that can bring opportunities to farmers to reduce the income gap.

The furthering of the importance of potato as a staple food for a high proportion of the human

population is largely determined by the significant increase in production and productivity in highly populated countries such as China and India. China produces more than 95 million tons of potatoes per year, which makes this country the world's largest potato producer (FAOSTAT 2015). However, domestic consumption is still low and a challenge to be surmounted by a policy to make potato a staple food comparable to rice. Two significant advantages of potato are that it requires 45% less water than rice or wheat and produces more kcal per unit of resources (Monneveux et al. 2013).

Climate change is one of the most important factors affecting agriculture on a global scale and its effects will increase as time, in decades, progresses. Climate change will affect current potato-producing regions by bringing about an increase in average temperature, the concomitant increase in the reproduction rate of vectors of pests and diseases, a variation in water availability caused by altered rainfall, and increased carbon levels in the atmosphere. Taking advantage of the large genetic diversity of potato species and the capacity of the crop to grow in many soil and climate conditions, scientists will be able to adapt/breed and grow potato cultivars more resilient to heat, water shortages, soil salinity, and diseases. This work is currently being conducted by CIP and its partners in different regions. It is complemented by the development of innovative water-saving irrigation techniques such as Partial Root Zone Drying (PRD), as reported by Yactayo et al. (2013).

In an interesting twist of history, it is highly likely that the potato will add another milestone to its saga by being the first crop to be grown on another planet. NASA and CIP are working together in a project conducted in Peru that is exploring the possibility of growing potatoes under Martian conditions (<http://potatoes.space/mars/>). They are using soil from Las Pampas de La Joya desert in Southern Peru, the world's driest and most nutrient-poor ecosystem, to test the performance of 65 varieties from the CIP's germplasm bank, selected for their capacity to grow under extreme conditions of variations in

day/night temperatures, water scarcity, and soil salinity. These varieties are already being planted in a closed environment that replicates the atmospheric conditions of Mars. The potato is a prime candidate to provide food security to human explorers traveling to Mars in a few decades due to the resilience of the crop and its large number of species, varieties, and landraces that provide a huge reservoir of genetic diversity, adapted to the most extreme conditions on Earth, such as high altitude, low oxygen pressure, water scarcity, soil salinity, extreme temperatures, and high UV radiation. In addition, the potato has a high density and high content of proteins, carbohydrates, soluble and insoluble fiber and micronutrients such as vitamin C, Zn and Fe (<http://cipotato.org/potato/potatonutrition/>). For CIP, however, this experience is helping to assess the adaptation of the potato to extreme environments that exist on Mars, but which in the future may become more common on Earth, and we need to be prepared for that scenario.

1.5 Conclusion

The potato has contributed to the development of different civilizations for thousands of years and still has a lot to offer to ensure that food and nutrition security for a growing population is achieved in the coming decades. Its genetic diversity has not yet been fully exploited to generate new varieties with sufficient adaptability for changing and diverse conditions, particularly the more frequent extreme conditions generated by climate change, which implies that there is still a wealth of potential enhancement of the potato's role in satisfying human need for secure, nutritious, and delicious food sources. The Andean region is still the repository of genes conserved in landraces that are an integral part of the culture of current farming communities, and there is the challenge of supporting those farmers to conserve the genetic diversity, and the knowledge and culture that have helped the world in the past, and will help it in the future.

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Abstract

A very narrow genetic base of cultivated potato has permitted the collection and conservation of its landraces and wild relatives as sources of resistant and agronomically desirable traits. Despite its importance for identifying genetic materials and understanding diversity, potato taxonomy is complex and problematic due to the crossability, polyploidy, and reproductive nature of the potato species. Currently, the collected germplasm is preserved in gene banks around the world and distributed to potato researchers with accompanying data. Many gene banks maintain potato collections in vitro, and technological innovations have been developed to assure the long-term preservation of potato genetic resources. Release of the first draft sequence of the potato genome reaffirms the importance of potato genetic resources. Collaboration between potato researchers and gene bank curators promotes the effective use of the genetic resources. Application of next generation sequencing (NGS) technologies would accelerate germplasm management, the evaluation of genetic diversity in situ and ex situ, and conservation planning of potato genetic resources.

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2.1 Introduction

The potato (*Solanum tuberosum* L.) is one of the most important staple crops in the world. It is a New World crop and was unknown to the rest of the world until the sixteenth century. Within the six following centuries, potato cultivation had spread from its center of origin, in the high Andes region in South America to the rest of the world. Potato is currently the fourth most important staple crop after rice, wheat, and maize

(de Haan and Rodriguez 2016) and provides a substantial part of the world's food supply, but it is susceptible to a wide range of pests and diseases. The genetic diversity is harbored in landraces and wild relatives considered to be valuable sources of variation for genetic enhancement and crop improvement, because the genetic base of the modern cultivated potato is very narrow (Hawkes 1979; Hanneman 1989; Jansky et al. 2013, 2015). Numerous expeditions have collected important potato genetic resources and conserved them in gene banks. Their effective collection, characterization, conservation and use will be an important key to future sustainable crop production and adaptation under climate change scenarios. At the same time, the evolution of genetic diversity is on-going in situ and in farmers' field in its center of origin (de Haan and Rodriguez 2016). In this chapter, potato taxonomy, history, current conservation status and future challenges in the genomic era are described in relation to recent biotechnological and genomic technologies.

2.2 Potato Taxonomy: Recent Updates

Species names are an important key to identifying genetic materials, understanding levels of diversity, linking studies across different publications, and identifying germplasm to be used for breeding programs. However, the taxonomy of wild and cultivated potatoes seem to be problematic, because of their interspecific crossability, auto- and allopolyploidy, mixture of sexual and asexual reproduction, possible recent species divergence, phenotypic plasticity, and the consequent high morphological similarity among species (Spooner and Berg 1992; Spooner 2009). Many potato species maintain their sexual compatibility, making it difficult to distinguish the boundary of a species.

Comprehensive taxonomic treatment by Hawkes (1990) reported that there are 235 potato species in total, 228 wild and 7 cultivated potato species. Since then, taxonomical studies have been carried out. Various studies, implementing

advanced molecular tools with a large number of samples covering a wide range of species, have suggested that a reconsideration of the taxonomic classification is needed (Jacobs et al. 2008, 2011; Spooner 2009). Lately, combinations of molecular and morphological studies have reduced the number of species to 107 wild and 4 cultivated (Spooner et al. 2014). A detailed historical overview and updates of the taxonomical descriptions of wild and cultivated potatoes were reviewed by Spooner et al. (2014).

2.3 Cultivated Potato Landraces

The distribution of cultivated potato landraces ranges over the upland Andes from western Venezuela to northern Argentina and in the lowlands of south-central Chile (Contreras et al. 1993), adapting to middle to high elevations (3000–4000 m above sea level, masl). Potato landraces are highly diverse in skin and flesh colors, and tuber shapes and it is assumed that perhaps 3000 landraces of potato are still grown by indigenous farmers in South America in semi-traditional and market-oriented production systems (de Haan and Rodriguez 2016; Spooner et al. 2014).

Cultivated potato species have a base chromosome number of $n = 12$ and include diploid ($2n = 2x = 24$), triploid ($2n = 3x = 36$), tetraploid ($2n = 4x = 48$), or pentaploid ($2n = 5x = 60$) types. Spooner et al. (2007) classified the cultivated potatoes into four species: (1) *Solanum tuberosum*, with two cultivar groups (the Andigenum Group of upland Andean genotypes containing diploids, triploids, and tetraploids and the Chilotanum Group of lowland tetraploid Chilean landraces); (2) *Solanum ajanhuiri* (diploid); (3) *Solanum juzepczukii* (triploid); and (4) *Solanum curtilobum* (pentaploid).

Solanum tuberosum is the original species from which modern cultivars were selected (Ames and Spooner 2008). The species comprises the Andigenum Group of upland Andean genotypes (containing diploids, triploids, and tetraploids) and the Chilotanum group of lowland tetraploid Chilean landraces. Andean genotypes are difficult to distinguish from each other due to

extensive gene flow. Furthermore, differentiation from the Chilean tetraploids is slight and incomplete (Gavrilenko et al. 2010). Current distribution of the *Chilotanum* group is restricted to the Chiloe Island of south-central Chile (Spooner et al. 2010). The *Chilotanum* group has contributed to the establishment of the current European and North American gene pool as well as global crop improvement (van den Berg and Groendijk-Wilders 2014).

A cultivated diploid species, *S. ajanhuiri*, was formed by hybridization between diploid cultivars of the *S. tuberosum* Andigenum Group ($2x = S. stenotomum$) and the diploid wild species *S. boliviense* (= *S. megistacrolobum*) (Rodríguez et al. 2010). Two major morphotypes, Ajawiri (bitter type) and Yari (non-bitter type), are present.

Solanum juzepczukii Bukasov is a triploid ($2n = 3x = 36$) cultivar, formed by hybridization between diploid cultivars of the *S. tuberosum* Andigenum Group ($2x = S. stenotomum$) and the tetraploid wild species *S. acaule* (Rodríguez et al. 2010). Its distribution range is from central Peru to southern Bolivia, and can be grown at an altitude of 4000 masl (Spooner et al. 2010) and in the frost-affected areas of the Altiplano (Hijmans 1999; Condori et al. 2014). Since this species contains high levels of glycoalkaloids, local people make “chuño” by freeze-drying potatoes, to prepare a detoxifying processed potato (Irikura 1989).

Pentaploid *S. curtilobum* ($2n = 5x = 60$) was likely formed by hybridization between tetraploid forms of *S. tuberosum* Andigenum Group ($4x = S. tuberosum$ subsp. *andigenum*) and *S. juzepczukii* (Hawkes 1990; Rodríguez et al. 2010). It also possesses frost hardiness as strong as that of *S. juzepczukii*. It is cultivated in the Andean Altiplano at an altitude range of approximately 4000 masl (Spooner et al. 2010). This species contains high glycoalkaloid and is used to prepare “chuño” as well (Irikura 1989).

2.4 Wild Potato

As aforementioned, potato species are highly complex in taxonomic classification. Currently, 107 wild species are recognized, including

diploids, tetraploids, and hexaploids ($2n = 6x = 72$), without including triploids and pentaploids (Hijmans et al. 2007; Spooner 2009; Spooner et al. 2014). Wild potatoes are distributed in a broad latitudinal range from the South-Western U.S. to Central Chile and Argentina (Hijmans et al. 2002; Spooner et al. 2014).

Two centers for diversity in wild potatoes have been recognized: one in North and Central America, with its center in Mexico, and the other in South America, with its center in the Andes, extending from Venezuela to Chile. This broad area of distribution, along with a broad range of altitudinal distribution, from sea level up to 4500 masl, indicates a wide range of adaptation (Hijmans and Spooner 2001; Hijmans et al. 2002, 2007). Their natural habitats are quite diverse, including cloud forests, cultivated fields, cliffs, as epiphytes, deserts, forests, and on the Pacific islands. This wide range of adaptation has also been reflected in a diversity of morphological traits (Hanneman 1989).

Adaptations to a wide range of habitats have made the wild species tolerant of different environmental stresses, and resistant to a broad range of pests and diseases, and other agricultural interests (Bamberg and Rio 2005; Barker 1996; D’hoop et al. 2008; Hawkes 1990, 1994; Hijmans et al. 2003; Jansky 2010; Ochoa 1999; Spooner and Bamberg 1994). These sources of breeding interests have been screened, identified, and listed by several authors. Genetic diversity, the availability of the germplasm, and usefulness have been the drive to incorporate wild genes into cultivated ones (Bamberg and Rio 2005).

2.5 The Potato Gene Pool and Crossability

The success of the use of wild relatives for genetic improvement relies a lot on their crossability with cultivated species. Although some barriers to cross-species compatibility in potato are known, such as differences in the endosperm balance number (EBN) and ploidy level, potato researchers have developed methods to overcome these hybridization barriers.

The gene pool is the most commonly used concept defining the degree of relatedness between species in Harlan and de Wet's (1971) study. It is based on the degree of crossability among species and it is classified as following; (1) primary; cultivated taxa and wild or weedy forms of the crop that cross easily with the crop and possess total fertility; (2) secondary; less closely related species from which gene transfer to the crop is possible with conventional breeding techniques; and (3) tertiary; species from which gene transfer to the crop is impossible, or if possible, requires sophisticated techniques. Although Harlan and de Wet's genepool concept has been widely accepted, it has not been applied to all crops, including the potato. The taxonomic classifications of the crop genus can be used as a proxy for relative crossability, as in the taxon group concept (Maxted et al. 2006).

Attempts to apply the genepool concept to the potato have been made (Bradeen and Haynes 2011; Veilleux and De Jong 2007). Spooner et al. (2014) proposed a concept especially for the potato, applying five crossability groups based on EBN and self-compatible/self-incompatible systems. The primary genepool of potato includes *S. tuberosum* ssp. *tuberosum* with all landraces and cultivars. All the cultivated potatoes are tetraploid ($2n = 4x = 48$) with 4EBN (Johnston et al. 1980). Potato has an extremely large secondary gene pool consisting of related wild species which provides a rich, unique, and diverse source of genetic variation.

The EBN is a model determining the success of interspecific crosses. It was first proposed by Johnston et al. (1980) to explain the success or failure of intraspecific crosses. It relates to a strong isolating mechanism present in the section *Petota* that affects the endosperm development, but the genetic basis is still under investigation (Ehlenfeldt and Hanneman 1988; Camadro and Masuelli 1995). The EBN classification reported in potato are 2x (1EBN), 2x (2EBN), 4x (2EBN), 4x (4EBN), and 6x (4EBN) (Spooner and Hijmans 2001). Hybridization within each group is expected to be successful rather than hybridization across groups, and thus the success of hybridization can be predicted.

Whereas the genepool concept and the EBN model offer guidance in the utilization of wild genetic resources, they also provide insight into phylogenetic relationship and taxonomy (Bradeen and Haynes 2011). Nevertheless, attempts to directly test species crossability are always important to provide concrete evidence (Jackson and Hanneman 1999).

Potato researchers have developed methods to overcome the hybridization barrier to transfer genes from wild species of the secondary and even tertiary genepool (Jansky 2006). Manipulation techniques to modify the ploidy level have already been reported (Hermundstad and Pelouquin 1985; McHale and Lauer 1981; Camadro and Espinillo 1990; Iwanaga et al. 1989). Even genes from the tertiary genepool can be introduced using bridge crosses (Hermsen and Ramanna 1973; Jansky and Hamernik 2009), mentor pollinations, and embryo rescue (Iwanaga et al. 1991; Watanabe et al. 1995), and somatic hybridization (Chen et al. 2013; Fock et al. 2001). The transgenic approach has been used for disease resistance (Missiou et al. 2004; van der Vossen et al. 2003; Wu et al. 1995; Zhu et al. 2012) and abiotic stresses in potato (reviewed by Kikuchi et al. 2015). Once commercial hybrids are obtained with valuable genes from wild species, they can be maintained clonally as tubers.

2.6 Domestication and Dissemination of the Potato

The center of origin of the cultivated potato is believed to be the Andes region of southern Peru and northern Bolivia, where they still grow wild relatives (Hawkes 1994). Archeological evidence and other data suggest that the potato was domesticated between 10,000 (Ovchinnikova et al. 2011) and 7000 years ago, in the southern Andes of Peru, north of Lake Titicaca (Hawkes 1990). Characters selected for domestication of wild potato involved producing larger tubers, with lower glycoalkaloid content, shorter stolons, and attractive colors of tuber skin and tuber flesh (Gavrilenko et al. 2013). Although the evolution

of the cultivated potato has not reached a conclusive result, phylogenetic and biogeographic patterns have been studied for each cultivated species (de Haan and Rodriguez 2016). The DNA sequence data of orthologous nuclear genes have elucidated the allopolyploid origin of *S. tuberosum* (Spooner et al. 2008, 2010; Rodriguez and Spooner 2009; Rodriguez et al. 2009).

The tetraploid cultivar groups of *S. tuberosum* *Chilotanum*, which contributed to most modern cultivars cultivated in Europe and North America, are still controversial (Spooner et al. 2012). The group appears to have hybridized with a closely related species as well as the wild Chilean species *S. maglia* (Ugent et al. 1987) or hybrids of *S. tarjiense* (Hosaka 2003; Spooner et al. 2014). However, there still remains a possibility of an Andean origin with the early introduction into Chile (Hawkes 1990, 1999).

The domestication process of the *S. tuberosum* Andigenum Group is believed to have started from wild progenitors of the *Solanum brevicaulis* complex (*S. bukasovii*, *S. canasense* and *S. multisectum*) in southern Peru (Spooner et al. 2005a). These species would have an ancestral relationship to the diploid *S. tuberosum* Andigenum Group (= *S. stenotomum*), which is believed to be the most primitive form of cultivated potato (Hawkes 1990). Multiple origins (Grun 1990; Hawkes 1994; Huamán and Spooner 2002) and hybrid origins (Rodríguez et al. 2010) of cultivated potatoes have also been suggested. The progenitor species have developed into the current cultivated potato through repeated sexual polyploidization processes in different cultivation zones.

Since its first appearance in Europe, the potato has rapidly spread worldwide. A detailed history of the potato introduction from its origin to the rest of the world is described by de Haan and Rodriguez (2016). Molecular studies have revealed that the origin of the European potato was dominated by the Andean potato in the 1700s, and later the Chilean potato was introduced into Europe and became predominant long before the late blight epidemics (Ames and Spooner 2008; Ríos et al. 2007; Spooner et al.

2005a, 2005b). The successful introduction of South American materials into higher latitudes involved an adaptation to long-day circumstances (Hawkes 1994). Cultivated potatoes were introduced to North America in 1691 from Bermuda, where they had been grown from an earlier introduction from England since 1613. The potato was taken to India and China in the seventeenth century by British missionaries and at about the same time, potatoes were introduced to different parts of Africa, and New Zealand in 1769 (Hawkes 1994).

2.7 Potato Genetic Resources

Genetic resources are a strategic resource for sustainable crop production. Their efficient conservation and use are critical to keep feeding increasing world populations. Gene banks play a key role in the conservation and distribution of germplasm for crop improvement and research for sustainable food production. An intensive and systematic potato germplasm collection was initiated in Central and South America in the 1920s by Russian scientists and formed the basis of the potato germplasm collection of the N.I. Vavilov Institute of Plant Industry in St. Petersburg (Ovchinnikova et al. 2011). Since then, much effort has been invested in collecting, maintaining, exchanging, and evaluating these collections. As a result, currently potato genetic resources are preserved in gene banks around the world and are available for potato breeders and researchers.

2.7.1 Germplasm Conserved in Gene Banks

The Food and Agriculture Organization of the United Nations (FAO) (2010) reported there were approximately 98,000 accessions currently conserved *ex situ* and 80% of them are maintained in 30 key collections. Within these, 25,727 potato accessions are registered in GENESYS (<https://www.genesys-pgr.org/> accessed March 17, 2017). A list of major genebank collections

of the Solanaceae species (nightshade, including tomato, eggplant and potato) is available (Machida-Hirano 2015).

Cultivated potatoes are conserved mainly as clonal collections, such as tuber, in vitro and cryopreservation; on the other hand, wild potato species are primarily collected and conserved in the form of botanical seeds (Salas et al. 2008). Preservation by botanical seed reduces the maintenance cost, increases the conservation period (20 + years) and eliminates systemic viruses such as the Potato Spindle Tuber Viroid (Bamberg and Rio 2005), therefore, preservation of botanical seeds should be considered an option for potato conservation.

Potato germplasm, including wild and cultivated potatoes, is conserved in gene banks throughout the world. The Global Crop Diversity Trust (GCDT) (2006) reported that at least 23 gene banks have a total of nearly 59,000 accessions of potato germplasm with a considerable number of duplications. The report classified the collection into four categories; (1) wild relatives; (2) native cultivars; (3) modern cultivars of the common potato (*Solanum tuberosum* susp. *tuberosum*); and (4) other germplasm (e.g. inter-specific hybrids, breeding clones, etc.). Wild species are the largest group present in the collections, followed by native cultivars collected from centers of diversity in Latin America. The most important collections are in Latin America, Europe, and in North America and a few countries in Asia. Recently, ex situ conservation status was assessed to identify potato crop wild relatives (CWR) in need of conservation. A total of 49,164 records for 73 species of CWR was found, with 76% of them possessing geographical coordinates, which corresponds to 11,100 germplasm accessions.

Most of the gene banks have web-searchable databases of their gene bank holdings. Passport information, taxonomy, phenotypic and evaluation data of agronomical traits are available to help gene bank users search and identify accessions to be ordered, for example:

- the Centre for Genetic Resources, the Netherlands, <http://cgngenis.wur.nl/>;
- the Leibniz Institute of Plant Genetics and Crop Plant Research, https://gbis.ipk-gatersleben.de/GBIS_I/detail.jsf;
- the U.S. National Plant Germplasm System, <https://npgsweb.ars-grin.gov/gringlobal/search.aspx>;
- the Genebank Project, National Agriculture and Food Research Organization https://www.gene.affrc.go.jp/databases_en.php?section=plant).

The GENESYS database (<https://www.genesys-pgr.org/>) is a comprehensive database of plant genetic resources for food and agriculture supported by the GCDT. This database can cross-search accessions conserved in different gene banks. An inter-gene bank network has also been developed to coordinate activities on potato genetic resources conserved in different gene banks. The Association of Potato Intergenebank Collaborators (APIC) has produced a global inventory of wild potato genetic resources collaboration with gene banks in Europe, the United States, Peru, and Argentina. The database was first developed with about 12,000 entries and contained more than 5300 accessions identified with a collector number (Huamán et al. 2000a). Now the database is hosted by the International Potato Center (CIP) and can be found online (<http://germplasmdb.cip.cgiar.org/index.jsp>), containing passport, taxonomical, and evaluation data. The Working Group on Potato of the European Cooperative Programme for Crop Genetic Resources Networks (ECP/GR) is working to coordinate and extend the potato genetic resources conservation in the European Union. The network has developed a central database of both cultivated and wild potatoes. The databases can be found on <http://ecpgr.cgn.wur.nl/eupotato/> and the European Cultivated Potato Database <https://www.europotato.org/menu.php>.

As a precaution, duplication is recommended to safeguard the collection from partial or total loss caused by natural or human-made catastrophes (Engels and Visser 2003; FAO 2014). Some sister gene banks have already made a back-up of their holdings. Germplasms of *Solanaceae* seeds

have been deposited in the Svalbard Global Seed Vault (<https://www.croptrust.org/our-work/svalbard-global-seed-vault/>). The vault was donated by Norway to the international community and is being supported by the GCDT.

2.7.2 In Vitro Collections of Potatoes

Many gene banks around the world are maintaining potato genetic resources including wild types. The current accession number of potato in these gene banks is as follows:

- International Potato Center (CIP), Peru, 6768;
- Leibniz Institute of Plant Genetics and Crop Plant Research (IPK)/The Groß Lüsewitz Potato Collection (GLKS), Germany, 6124;
- Northern Region 6 (NR6), USA, 5808 (Niino and Arizaga 2015);
- Vavilov Institute of Plant Industry, Russia, 9000;
- Central Potato Research Institute (CPRI), India, 3500;
- Potato Research Institute, Czechoslovakia, 2225 (Kaczmarczyk et al. 2011).

The preservation of potato genetic resources (GRs) in gene banks is mostly in field collections, by vegetative propagation due their allogamous nature. Vegetatively maintained potato GRs are vulnerable to loss from natural disasters and damage caused by pests and diseases. Also, this way of preserving potato GRs requires a sufficient area of land, funding and continuous maintenance.

2.7.2.1 Short-Term and Mid-Term Storage

In vitro gene banks are a means to overcome the disadvantage of field gene banks. In vitro cultures can easily be propagated and regenerated in plantlets with the latest progress achieved in plant tissue culture techniques. The advantages of tissue cultures are their maintenance in a sterile and pathogen-free environment and growth in a controlled environment. For the establishment of in vitro gene banks, tissue

culture systems and subculture systems for species are needed without contamination of materials. Some rare and endangered plants with no previous information on tissue culture establishment have required the development of new tissue culture protocols (Niino et al. 2014). Several slow growth (minimal growth) methods have been established for short-term (3 months) to mid-term (3 years) storage using low temperature, minimal nutrition, growth retardants, and so on, alone or in combination (Oka and Niino 1997). The main disadvantage of an in vitro gene bank is the induction of genetic variation or somatic mutations during subculturing. Maki et al. (2015) pointed out that DNA mutation occurs due to the long period of subcultures of the plants, while stored shoot tips in super-low temperature retained their original genetic structure. For this reason, a minimal growth method is desirable for preservation of in vitro materials in order to reduce the subculture numbers. The frequency of subculturing can be reduced by incubating them at low temperature, under low light intensity and varied photoperiods, and growing the micro plants on the Murashige and Skoog medium (MS medium, Murashige and Skoog 1962) supplemented with growth retardants or osmotic stress-inducing polyols (Gopal and Chauhan 2010).

The CIP maintains 4062 accessions in vitro under slow growth conditions. The MS medium used contains 40 g/l sorbitol, 20 g/l sucrose. Cultures are maintained at 6–8 °C under 22 $\mu\text{mol}/\text{m}^2\text{s}$ illumination and 16-h light. This allows in vitro plantlets to be stored for approximately two years without subculturing (Niino and Arizaga 2015). The IPK maintains 2855 potato accessions in vitro at 4 °C as microtubers. The cycle of slow growth maintenance consists of a warm phase with long-day at 20 °C for 2–3 months, a microtuber induction phase with short-day at 9 °C for 2–4 months and a microtuber storage at 4 °C for 12–15 months (Keller et al. 2006; Niino and Arizaga 2015). At the CPRI, more than 1500 parental lines and potato varieties are maintained in vitro on an MS medium supplemented with 40 g/l sucrose and 20 g/l mannitol at 6–8 °C and 16-h photoperiod