

John E. Bradshaw

# Potato Breeding: Theory and Practice



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Edinburgh, UK

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# Preface

The potato (*Solanum tuberosum*) is the world's fourth most important food crop after maize, rice and wheat with 377 million tonnes fresh-weight (FW) of tubers produced in 2016 from 19.2 million hectares of land, in 163 countries, giving a global average yield of 19.6 t ha<sup>-1</sup> (<http://faostat.fao.org>). About 62% of production (234 million tonnes) was in Asia (191), Africa (25) and Latin America (18) as a result of steady increases in recent years, particularly in China and India. Indeed, China (99 million tonnes) is now the number one potato producer in the world and India (44) is second, with the Russian Federation (31) third, Ukraine (22) fourth and the USA (20) fifth. As a major food crop, the potato has an important role to play in the United Nations "2030 Agenda for Sustainable Development" which started on 1 January 2016 (<http://faostat.fao.org>). The agenda includes 17 goals, the second of which is to end hunger, achieve food security and improved nutrition, and promote sustainable agriculture. By 2030, the aim of the agenda is to "ensure access by all people, in particular the poor and people in vulnerable situations, including infants, to safe, nutritious and sufficient food all year round". By then, the world population is expected to reach 8.5 billion and continue to increase to 9.7 billion in 2050. For potatoes, the need is to increase production and improve nutritional value to alleviate micronutrient deficiencies ('hidden hunger') during a period of climate change. A key aspect of this endeavour will be the breeding of new cultivars for a wide range of target environments and consumers.

Potato breeding during the twentieth century involved planned artificial hybridizations followed by multi-stage, multitrait selection over as many as eight clonal generations.

From the 1960s, programmes typically started each year with as many as 100,000 seedlings from 200 to 300 crosses (conventional breeding). The two main weaknesses of such breeding are the number of clonal generations required to select a new cultivar and the inability of intense early-generation selection to affect most economically important traits, which are quantitative in nature. Nevertheless, continued progress worldwide in adapting potatoes to new environments, farming prac-

tices and uses (markets) was made by cycles of such hybridization and selection, usually among the developing elite germplasm. Sometimes new traits were required, such as resistances to emerging pest and disease problems, and sometimes broader genetic bases were sought to deal with perceived plateaus in progress for traits such as yield. Thus, the twentieth century saw the use of potato landraces and wild relatives in introgression breeding and in base broadening. However, a striking feature of breeding in the twentieth century was the longevity of use of cultivars that became widely grown (e.g. Maris Piper in the UK). It can therefore be argued that new cultivars did not contribute as much as might have been expected to the improvement of potato crops worldwide.

Ways to make potato breeding faster, more efficient and more effective have become available since the 1990s (e.g. progeny testing, estimated breeding values from pedigree information, diagnostic molecular markers for marker-assisted introgression and selection, SNP arrays and genotyping by sequencing for genomic selection, *Agrobacterium*-mediated genetic transformation, and site-directed DNA sequence modifications including gene editing). They either have been, or are being, integrated into conventional breeding programmes of the kind described and discussed over 25 years ago by Bradshaw and Mackay (1994). However, it will be argued in this book, that we need to rethink the way that potato breeding is done in order to make the best use of advances in technology and genetic knowledge following the publication of the potato genome sequence in *Nature* on 14 July 2011 (Potato Genome Sequencing Consortium 2011). The challenge for a new generation of potato breeders and biotechnologists is to design breeding programmes that integrate marker-assisted selection of specific alleles, genomic selection of unspecified alleles and phenotypic selection, having decided when a gene editing or transgenic approach is more appropriate, given consumer acceptability of the latter. It therefore seems timely to re-examine options for breeding vegetatively propagated tetraploid cultivars of potato and to compare them with breeding potatoes for TPS (true potato seed) propagation, including diploid F<sub>1</sub> hybrid breeding. It will be important to consider long-term crop improvement (increasing the frequencies of desirable combinations of alleles over sexual generations) as well as short-term cultivar production (combining alleles in a single genotype). Indeed, the former is the driver of progress in the latter. It will also be important to consider the effective use of all of the germplasm available to potato breeders, namely modern cultivars, landraces and wild relatives; and the need to go beyond the barriers of sexual hybridization through genetic transformation.

The aim of the book is to provide more information and greater detail on the theory and practice of potato breeding than I have found possible in review articles (e.g. Bradshaw 2009; Bradshaw 2017) and book chapters (e.g. Bradshaw and Mackay 1994; Bradshaw 2007a, 2007b; Bradshaw and Bonierbale 2010). The book updates the information provided by Bradshaw and Bonierbale (2010), incorporates

the theory from Bradshaw and Mackay (1994) and my book on plant breeding (Bradshaw 2016), and extends the theory to cover genomic selection and diploid  $F_1$  hybrid breeding. It is divided into three parts and comprises nine chapters in what I regard as a logical order for considering scientific potato breeding. Part I deals with the history of potato improvement from domestication to present-day cultivars and potato genetics: in other words, the necessary background information and knowledge for designing a potato breeding programme in the twenty-first century. It includes an explanation of the major revision of the taxonomy of wild tuber-bearing *Solanum* species and the modifications to the classification of cultivated potatoes, both of which breeders need to appreciate. Part II deals with deciding breeding objectives and translating them into selection criteria in the order in which I think they need to be incorporated into the programme design: first, increasing potato yields as consideration of this determines the environments in which the breeding programme is conducted; second, improving potato quality as this needs to be done by assessing the limited number of tubers from the yield trials, at harvest, after storage and after cooking; and third, improving resistance to the most important of the many diseases and pests of potatoes, in laboratory, glasshouse and field tests with the limited number of seed tubers not required for the yield trials. Part III deals with the actual breeding methods and germplasm available for achieving the desired objectives: first, the use of landraces and wild relatives of potato in introgression breeding, base broadening and population improvement; second, breeding clonally propagated cultivars as the way to deliver potato improvement to farmers' fields; third, breeding potato cultivars that can be propagated through true potato seed (TPS) as an alternative way to deliver potato improvement to farmers' fields; and fourth, gene editing and genetic transformation as ways of making further improvements to already successful and widely grown cultivars.

In writing the book, I have drawn on my experiences over a 20-year period as a potato breeder and geneticist at the former Scottish Crop Research Institute in Dundee (now the James Hutton Institute). Throughout this time, I benefited from discussions with colleagues and the wider potato breeding community, particularly members of EAPR (The European Association for Potato Research) and EUCARPIA (The European Association for Research on Plant Breeding). I also benefited from participation in teaching, working groups and editorial work. In writing another book for Springer, I have once again received much help and encouragement from Kenneth Teng, and also appreciate the help from Rahul Sharma and Raja Dharmaraj of Springer during the production stage. The book was completed during our coronavirus lockdown from 24 March to 28 May 2020, during which time the support of my partner Shiona Mackie was much appreciated. I hope that the book will be of value to a new generation of potato breeders as they face the challenge of feeding a growing world population during a period of climate change. Globally, a large number of breeding programmes will be required to produce the necessary range of adapted

cultivars for the wide range of agro-ecological zones and regions within zones in which potatoes are grown, and the different potato characteristics needed for the various end uses of potato crops, namely staple food, vegetable for cash and crop for processing. For any given programme, the key to success will be to focus on the limited number of objectives that will have most impact on potato improvement, and to choose the right germplasm and breeding method to achieve those objectives. I wish the new generation of potato breeders every success in their endeavours.

Edinburgh, Scotland

John E. Bradshaw

20 July 2020

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**Part I**  
**Introduction**

# Chapter 1

## Domestication to Twenty-First-Century Potato Cultivars



### 1.1 Introduction

#### 1.1.1 *Global Importance of the Potato*

In 2016, the potato (*Solanum tuberosum*) was the world's fourth most important food crop after maize, wheat and rice (Table 1.1), with 377 million tonnes fresh-weight (FW) of tubers produced from 19.2 million hectares of land, in 163 countries (<http://faostat.fao.org>). Although the increases in production and yield of potatoes from 1966 to 2016 were not as great as those for the cereals, in 2016 the average yield of potatoes on a dry-weight basis compared favourably with the three cereals. Furthermore, 62% of potato production (234 million tonnes) was now in Asia (191), Africa (25) and Latin America (18) as a result of steady increases in recent years, particularly in China and India. Indeed, China (99 million tonnes) is now the number one potato producer in the world and India (44) is second, with the Russian Federation (31) third, Ukraine (22) fourth and the USA (20) fifth. Perhaps then it was not surprising that the United Nations named 2008 as the International Year of the Potato in recognition of its contribution as a major food staple to their Millennium Development Goals of providing food security and eradicating poverty. The potato also has an important role to play in the United Nations '2030 Agenda for Sustainable Development' which started on 1 January 2016 (<http://faostat.fao.org>). The agenda includes 17 goals, the second of which is to end hunger, achieve food security and improved nutrition, and promote sustainable agriculture. By 2030, the aim of the agenda is to 'ensure access by all people, in particular the poor and people in vulnerable situations, including infants, to safe, nutritious and sufficient food all year round'. By then, the world population is expected to reach 8.5 billion and continue to increase to 9.7 billion in 2050.

Where potatoes are a staple food, the need is to increase production and improve nutritional value to alleviate micronutrient deficiencies ('hidden hunger') during a period of climate change. In countries where food security has been achieved and

**Table 1.1** Crop production in 1966 and 2016 (<http://faostat.fao.org>), on a fresh-weight basis except for 2016 yields in parentheses which have been corrected for moisture content assuming cereals are 15% water and potatoes are 80% water

Crop	Production million tonnes		Area million hectares		Yield t/ha	
	1966	2016	1966	2016	1966	2016
Maize	245.6	1060.1	111.2	188.0	2.21	5.64 (4.79)
Wheat	303.8	749.5	215.8	220.1	1.41	3.41 (2.90)
Rice	261.2	741.0	125.7	159.8	2.08	4.64 (3.94)
Potato	282.0	376.8	21.5	19.2	13.1	19.6 (3.92)

the potato is grown as a vegetable, the need is to increase potato usage in an economically and environmentally sustainable way. The same is true for potatoes destined for processing. Finally, the potato is even being considered for human life support in space (Wheeler 2009). In all of these endeavours, a key aspect will be breeding new cultivars for a wide range of target environments and consumers.

### 1.1.2 Potato Breeding

The ultimate success of a new breeding programme depends on starting with the right objectives and germplasm. Choose the wrong objectives and nobody will want to grow your new cultivars which will have taken you much time, effort and resources over a period of some 12 years. Choose the wrong germplasm and you will fail to achieve your objectives despite all of your hard work. In this chapter, we are going to review the genetic improvement of potatoes from domestication to the present day. We will then be able to ask and answer the questions that will enable us to decide breeding objectives and starting germplasm. Only then can we get down to the details of available breeding methods.

## 1.2 Wild Relatives as Food

Wild tuber-bearing *Solanum* species grow in a wide range of habitats in 16 countries from the south-west of the USA (38°N), through Central America and the Andes, to Argentina and adjacent Chile (41°S) (Spooner and Hijmans 2001). The tuber is a subterranean swollen stem which evolved to survive from season to season as a dormant storage organ, and in which the form of energy storage is almost entirely starch. Today, we know that our cultivated potatoes also contain significant amounts of protein, minerals, vitamins, micronutrients and phytonutrients which include antioxidants (Singh and Kaur 2016). We also know that the journey from gathering wild tubers to cultivation and domestication started early in the human colonization of the Americas.

The earliest evidence of wild potato use comes from the extremes of their distribution in North America and Chile. Wild potato remains were found in a late Pleistocene settlement in south-central Chile dated to around 12,500 years before present (Ugent et al. 1987; Moseley 2001). Then, more recently, Louderback and Pavlik (2017) extracted well-preserved starch granules from ground stone tools found at North Creek Shelter, southern Utah and dated to between 10,900 and 10,100 years before present. The granules were identified as those of *S. jamesii*, which is known to be highly nutritious, having twice the protein, zinc and manganese content of cultivated *S. tuberosum* and three times the calcium and iron content. Thus, a summer-active and highly productive herbaceous perennial would have provided a reliable, year-round source of carbohydrate and minerals that significantly improved dietary quality.

### 1.3 Domestication and Glycoalkaloids

The taxonomy of the wild tuber-bearing *Solanum* species is complicated and has undergone major revisions as explained by Spooner (2016). Spooner et al. (2014) recognized 107 species, all classified as *Solanum* section *Petota* (tuber-bearing species) and partitioned into three nuclear clades. The three nuclear clades were similar to the four clades based on plastid DNA restriction site data but with plastid clades 1 and 2 merged, that is, nuclear clades are 1 + 2, 3 and 4. Li et al. (2018; figure 4) have provided the most recent and comprehensive taxonomy based on a phylogenetic analysis of 201 accessions of *Solanum* section *Petota* species, comprising 146 wild accessions and 21 diploid cultivated accessions from clade 4, 14 wild accessions from clade 1 + 2, 18 wild accessions from clade 3 and 2 non-tuber-bearing outgroup species (*S. etuberosum* and *S. palustre*). The phylogenetic trees were generated from 66,666 high-quality SNPs (single-nucleotide polymorphisms), identified from whole-genome sequencing, using singular value decomposition (SVD) quartets (two other methods gave similar results). All analytical methods strongly corroborated the partitioning of section *Petota* into outgroup, clade 1 + 2, clade 3 and clade 4 (by far the largest). They separated members of clade 4 into subclasses of cultivated, wild north (Peru) and wild south (Argentina, Bolivia and Chile). They corroborated the northern members of the *S. brevicaulle* complex as the progenitors of cultivated potato (Spooner et al. 2005a). They failed to separate cultivated *S. tuberosum* subspecies *phureja* and *stenotomum* into clades, supporting placing these names into synonymy based on prior microsatellite data (see below). They support much of the recent synonymy of the wild species in the *S. brevicaulle* complex and elsewhere in clade 4. Finally, they place *Solanum verrucosum*, the sole A-genome diploid species from Mexico, firmly in the southern South American subclade of clade 4. The reader is referred to the original paper for all of the detail (Li et al. 2018). However, some genebanks still use the classification of Hawkes (1990) which recognized 219 wild tuber-bearing species, arranged into 19 series of subsection *Potatoe* of section *Petota* of subgenus *Potatoe* of genus *Solanum*. Hence, breeders need to be aware of this older classification.

As just mentioned, it was Spooner et al. (2005a) who provided molecular taxonomic evidence for a single domestication in the highlands of southern Peru, from the northern group of members of the *S. brevicaula* complex of diploid species typified by *S. bukasovii* (now *S. candolleianum*: Spooner et al. 2014). However, it has proved difficult to date the earliest cultivation of potatoes. Hawkes (1990) concluded that the potato is an ancient domesticate based on preserved food plant remains found at various excavated sites on the coast of Peru and one site in the high Chilca canyon, south of Lima (Engel 1970). The Oxford Radiocarbon Accelerator dated the tuber remains found by Engel to about 7000 years before present. Rumold and Aldenderfer (2016) provided direct microbotanical evidence for the early use of potatoes at Jiskairumoko, an early village site in the western Titicaca Basin of the high south-central Andes (3890 m above sea level) dating to the Late Archaic to Early Formative periods (3400–1600 BCE, i.e. 5420–3620 years before present). Of 141 starch micro remains recovered from 14 ground stone tools, 50 were identified as consistent with cultivated or domesticated potatoes, based on reference to published materials and a study of wild and cultivated potato starch morphology. However, the authors could not say with certainty that the 50 micro remains were from cultivated/domesticated potatoes and not from wild potato species. Nevertheless, the authors were able to cite references to the evidence for small-scale farming being in place by 1600 BCE. In other words, domestication can probably be considered complete by this date. Moseley (2001) speculated on the process of domestication before the spread of potato cultivation throughout South America. Early Andean cultures were likely to have been ‘vertical’ ones, moving up and down the mountains with the changing seasons. It is likely that the herding of animals and the domestication of llama and alpaca preceded the settled cultivation of crops. Seasonal visits to favoured sites for food plants would mean that domestication would proceed gradually, with favoured types being re-planted to ensure harvests at subsequent re-visits.

Rumold and Aldenderfer (2016) also speculated that grinding could have removed toxic steroidal glycoalkaloids from potato tubers, thus making them safe to eat. However, it is usually assumed that lower levels of glycoalkaloids were achieved through selection for less bitter-tasting tubers during domestication (Simmonds 1995). Today tubers with concentrations of steroidal glycoalkaloids above 20 mg 100 g<sup>-1</sup> FW are considered unsafe for human consumption, resulting in symptoms typically associated with food poisoning (Friedman and Levin 2016). Interestingly, Johns and Alonso (1990) found that some genebank accessions of *S. bukasovii* (now *S. candolleianum*: Spooner et al. 2014), now considered the most likely progenitor of cultivated potatoes, had tuber glycoalkaloid levels (9–29 mg 100 g<sup>-1</sup> FW) which were consistently close to the levels found in many clones of cultivated diploid potatoes (*S. tuberosum* Stenotomum Group). They concluded that exploitation and domestication of this species would have required little or no selection for lower glycoalkaloid content, unlike their samples of other former candidates for domestication, namely *S. canasense*, *S. leptophyes* and *S. sparsipilum*, with levels of 42–164 mg 100 g<sup>-1</sup> FW. Johns and Alonso (1990) also found that *S. jamesii* had high levels of glycoalkaloids (115–128 mg 100 g<sup>-1</sup> FW), so perhaps

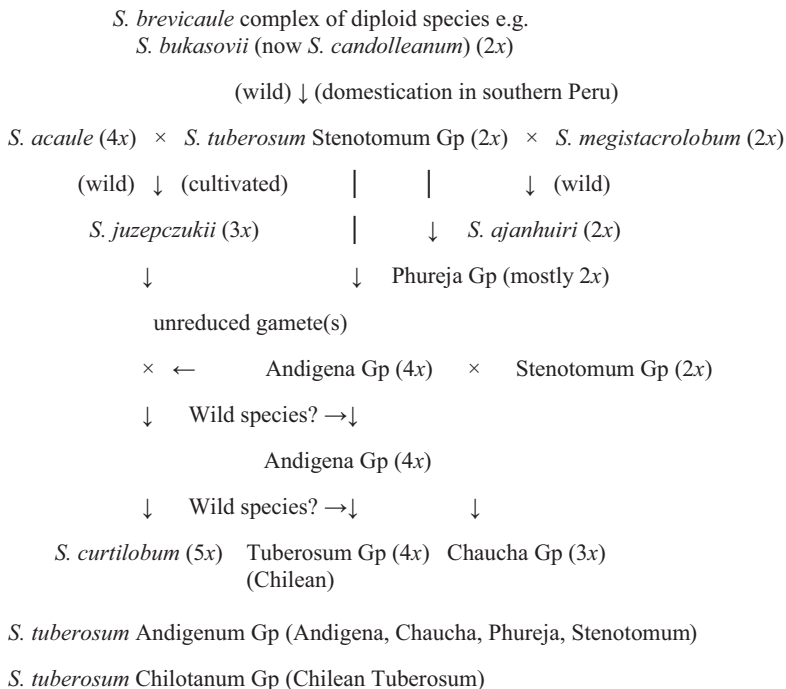
grinding was used for detoxification of potatoes at North Creek Shelter (see previous section). Whatever the method of detoxification, it seems fair to credit the early Andean farmers with making the potato an edible crop. In fact, Hardigan et al. (2017) have provided evidence from a *Solanum* section *Petota* diversity panel for farmer selection at two loci in the steroidal glycoalkaloids pathway, the squalene synthase locus (*SQS*) and the *GLYCOALKALOID METABOLISM 9* locus (*GAME9*).

Finally, Hawkes (1990) concluded that Andean farmers either baked their fresh potatoes in the embers of a fire or cooked them in an earth oven on hot stones, because after domestication the potato was grown for at least four millennia prior to the development of ceramics. We now know that the potato needs to be cooked because of the indigestibility of its ungelatinized starch (Burton 1989). Today such cooking is frequently by baking, boiling, steaming, roasting, deep-fat frying or microwave cooking, although in the Andes a broad diversity of additional preparation methods is still employed.

## 1.4 Cultivated Potatoes of South America

### 1.4.1 Classification of Cultivated Potatoes

The result of domestication was a diploid cultigen *S. tuberosum* Stenotomum Group ( $2n = 2x = 24$ ) from which all other cultivated potatoes were derived (Fig. 1.1). The widely accepted classification of cultivated potatoes is that of Dodds (1962) as modified by Spooner et al. (2007) using molecular data, although other schemes can be found in the literature. Dodds (1962) classified cultivated potatoes into five informal groups within one species (*S. tuberosum*) in which Andigena (tetraploid), Chaucha (triploid), Phureja (diploid) and Tuberosum (tetraploid) groups were derived from Stenotomum (diploid). Chaucha is the triploid hybrid of Stenotomum and Andigena and like Stenotomum is confined to the central Andes of Peru and Bolivia. Phureja was selected from Stenotomum by Andean farmers for lack of tuber dormancy and faster tuber development so that they could grow up to three crops a year in the lower, warmer, eastern valleys of the Andes. Phureja potatoes were therefore able to spread into northern Ecuador, Colombia and Venezuela and are the second most widely cultivated type in South America after Andigena (Hawkes 1990). Interestingly, Ghislain et al. (2006) found that 32 out of 102 accessions of Phureja in the CIP (International Potato Centre) collection of landraces were triploid or tetraploid, not diploid, in agreement with Hawkes (1990) that not all Phureja potatoes are diploid. This provides justification for not using ploidy as a species criterion. Goniocalyx (diploid) has been recognized as a northern subgroup of Stenotomum, noted for tubers with a bright yellow flesh (Hawkes 1990). Andigena potatoes are grown throughout the upland Andes of South America, presumably because farmers found the tetraploid superior to the diploids for yield and other traits. Tuberosum potatoes were selected from Andigena types for tuber production in long days in coastal Chile and are referred to as Chilean Tuberosum. They are a genetically



**Fig. 1.1** Origin of cultivated groups (Gp = Group) of *S. tuberosum* (Dodds 1962; Spooner et al. 2007) and cultivated species with bitter taste and frost tolerance (*S. ajanhuiri*, *S. juzepczukii* and *S. curtilobum*) (2, 3, 4 and 5x = diploid, triploid, tetraploid and pentaploid) (modified from Bradshaw 2019 with permission)

distinct group of potatoes with a different cytoplasm to Andigena potatoes (Raker and Spooner 2002; Hosaka 2004).

Spooner et al. (2007) also regarded Andigena, Chaucha, Phureja, Stenotomum and Tuberosum as a single species *S. tuberosum*, but now divided into just two cultivar groups. These are the Andigenum Group of upland Andean landraces containing diploids, triploids and tetraploids, and the Chilotanum Group of lowland tetraploid Chilean landraces. Spooner et al. (2007) also recognized the three frost-tolerant species cultivated in the Andes as separate hybrid species derived from crosses between domesticates and wild relatives (Fig. 1.1).

### 1.4.2 Frost-Tolerant Species and chuño Production

Three frost-tolerant species are cultivated in the Andes: *S. ajanhuiri* (diploid), *S. juzepczukii* (triploid) and *S. curtilobum* (pentaploid) (Fig. 1.1). These ‘bitter potatoes’ are grown at high altitudes (up to 4500 m for *S. juzepczukii*) in the central Andes of Peru and Bolivia (Hawkes 1990). *S. ajanhuiri* is the hybrid of *S. tuberosum* Group Stenotomum with the wild frost-resistant diploid species *S.*



*megistacrolobum*, *S. juzepczukii* is the hybrid of *S. tuberosum* Group Stenotomum with the wild frost-resistant tetraploid species *S. acaule* and *S. curtilobum* is the hybrid between an unreduced gamete of triploid *S. juzepczukii* and a normal gamete of *S. tuberosum* Group Andigena. In the high, cold mountains, an ancient method of potato preservation was chuño production where potatoes were in effect freeze-dried using the very low night temperatures and intense sunlight of the day (Hawkes 1990). The frozen potatoes were trampled by foot to eliminate any remaining water, and then washed and dried. The washing removed toxic glycoalkaloids. The outcome was a dehydrated product that could be stored over several years and used when fresh potatoes were scarce. Chuño production has continued in use to the present day, yielding a product highly prized by the peoples of the Andes.

### 1.4.3 Origin of Tetraploid Potatoes

First, we need to consider how *S. tuberosum* Group Andigena arose from Group Stenotomum. Sukhotu and Hosaka (2006) concluded from chloroplast and nuclear DNA markers that Group Andigena arose from Group Stenotomum through sexual polyploidization from unreduced gametes many times at many places in the fields of Group Stenotomum. This would explain the chromosome behaviour and tetrasomic inheritance of tetraploid *S. tuberosum*, the details of which have been revealed using a high-density linkage map in a biparental mapping population (Bourke et al. 2015). In other words, tetraploid *S. tuberosum* can be regarded as the autotetraploid of diploid Group Stenotomum. The tetraploids were subsequently modified through occasional selection by Andean farmers of natural hybrids with neighbouring wild species to give present-day Group Andigena. Scurrah et al. (2008) demonstrated that closely related species growing around farmers' fields can hybridize with Group Andigena and that some hybrid progeny would be selected by present-day Andean farmers. Furthermore, Hardigan et al. (2017) have provided data from a *Solanum* section *Petota* diversity panel that suggests that wild *Solanum* species assisted the spread of cultivated potatoes by transmitting alleles for tolerance of new ecological factors, enabling colonization of non-native habitats as the cultivated potatoes migrated south following domestication and polyploidization.

Second, we need to consider how *S. tuberosum* Group Tuberosum arose from Group Andigena. We need to appreciate that there are six distinct types of cytoplasm in potato, namely M, P, A, W, T and D as determined by Hosaka and Sanetomo (2012). For now, it is sufficient to say that P (Phureja) and A (Andigena) are sub-categories of M and T (Tuberosum) and D (wild species *S. demissum*) are sub-categories of W. Hosaka (2004) suggested that Chilean Tuberosum (T) cytoplasm is derived from the southern wild species *S. tarijense*. Hence, Group Tuberosum is not simply Group Andigena potatoes that were selected to tuber in long days. Furthermore, Spooner et al. (2007) showed that the T cytoplasm is found at low frequency in Andean landraces, including some diploids, indicating that the T cytoplasm moved northwards as well as becoming predominant in Chilean germplasm. Nevertheless, as mentioned earlier, it is clear that the long-day adapted landraces of

coastal Chile are genetically distinct from the short-day adapted ones of the Andes (Raker and Spooner 2002). Although uncertainty remains about the exact origin of Chilean *Tuberosum*, Hardigan et al. (2017) have provided a likely scenario based on Bolivian and Argentinian species alleles in Chilean-derived *Tuberosum*, namely that *Andigena* tetraploids interbred with wild species en route to their eventual destination in southern Chile where long-day adaptation was required for tuberization.

There is also uncertainty as to why tetraploid potatoes were superior to their diploid ancestors, and hence were selected in preference to them to become the major cultivated types in South America. One possible clue comes from the work of Stupar et al. (2007). They developed a synthetic autopolyploid series in potato (primarily Group Phureja) that included one monoploid ( $1x$ ) clone, two diploid ( $2x$ ) clones and one tetraploid ( $4x$ ) clone, in order to explore phenotypic and transcriptomic (about 9000 genes) changes associated with autopolyploidization. Interestingly, the diploid plants were the most vigorous and generated the greatest biomass with the monoploid inferior to both the diploids and the tetraploid. However, the diploid and tetraploid plants had similar gene expression patterns. Therefore, the eventual superiority of tetraploid potatoes may have come from their increased potential for heterozygosity rather than polyploidy per se, and this has implications for future breeding.

#### 1.4.4 Reproductive Biology of Potatoes

Potatoes, like their ancestral wild species, reproduce by sexual means through botanical seed and also by producing tubers. They flower and set true seed in berries after natural pollination by insects capable of buzz pollination (e.g. some bee species), which releases pollen from their poricidal anthers (Scurrah et al. 2008). Outcrossing is enforced in cultivated and most wild diploid species by a single *S*-locus, multiallelic, gametophytic self-incompatibility system (Dodds 1965). While self-incompatibility does not operate in tetraploid *S. tuberosum*, 40% (range 21–74%) natural cross-pollination was estimated to occur in Group *Andigena* in the Andes (Brown 1993) and 20% (range 14–30%) in an artificially constructed *Andigena* population (Glendinning 1976). This level of cross-pollination is sufficient to maintain genetic variation and heterozygosity in a population as shown by the early population geneticists. The stable equilibrium for the simple situation of just two alleles, *A* and *a*, at a locus in a tetraploid population which is partly self-pollinated was derived by Haldane (1930). The algebra is quite straightforward but very tedious and hence will not be repeated here. One starts with the five possible genotypes and their frequencies at equilibrium and then derives the five genotype frequencies in the next generation, based on a constant probability *s* that any plant will be self-fertilized and a probability  $1-s$  ( $= \lambda$  in Haldane's paper) that it will cross with some plant chosen at random from the population. Chromosomal segregation is assumed (i.e. no double reduction). As there is no change in frequency from one

generation to the next at equilibrium, the relevant equations can be solved to express the five genotype frequencies in terms of  $s$  ( $\lambda$  in Haldane’s paper) and the ratio of the frequency of  $A$  ( $p$ ) to  $a$  ( $q$ ) ( $p/q = u$  in Haldane’s paper). The results for  $s = 0.2, 0.4, 0.6$  and  $0.8$  are given in Table 1.2 for  $p = q = 1/2$ . It can be seen that with 40% ( $s = 0.6$ ) cross-pollination the  $AAaa$  genotype is most frequent whereas with 20% ( $s = 0.8$ ) cross-pollination  $AAAA$  and  $aaaa$  are the most frequent genotypes, followed by  $AAaa$ . If an equilibrium population is inbred further by self-pollination of all individuals each generation, inbreeding depression occurs for traits where non-additive genetic effects are in the same positive direction over loci; for example, for a single locus affecting yield: if  $AAAA = AAAa = AAaa = Aaaa = 20$  t/ha and  $aaaa = 10$  t/ha, the population yield will decline from 19.375 to 18.186 to 17.1755 to 15 t/ha as  $s$  increases from 0 to 0.6 to 0.8 to 1.

Sexual reproduction therefore creates an abundance of diversity by recombining the variants of genes that arose by mutation, and as we have just seen, potatoes are therefore highly heterozygous individuals that display inbreeding depression on selfing. The genetically unique seedlings that grow from true seeds produce tubers that can be replanted as seed tubers and hence distinct clones can be established and maintained by asexual (vegetative) reproduction. Thus, the reproductive biology of potatoes was ideal for creating and maintaining variation. As a consequence, farmers were able to select and vegetatively propagate what became the cultivated landraces of potatoes in South America. We can envisage a potentially complicated genetic structure for such landraces. Firstly, they could make up metapopulations of landraces which are grown by communities of farmers. Secondly, populations of clonal crops consist of two components, established clones and sexually produced volunteers. Farmers could spare volunteer plants when weeding and examine those that survive to harvest. They could then incorporate some of them into their stock of clonal propagules (seed tubers), possibly assigning them to the landraces they most resemble. Each landrace could therefore be a diverse assemblage of multiple clones sharing phenotypic characteristics rather than a single clone. Hence, landraces should be viewed as evolving entities, in contrast to modern cultivars which are expected to be maintained true to type (the definitive stock), and where seed

**Table 1.2** Genotype frequencies at equilibrium for a single locus with alleles  $A$  and  $a$  at frequencies  $p = q = 1/2$  under mixed selfing and random mating with tetrasomic inheritance, ignoring the phenomenon of double reduction, where  $s$  is the proportion of selfing (from Bradshaw 2016 with permission)

Genotype	$s = 0$	$s = 0.2$	$s = 0.4$	$s = 0.6$	$s = 0.8$	$s = 1$
$AAAA$	$p^4 = 0.0625$	0.0874	0.1239	0.1814	0.28245	$p = 0.5$
$AAAa$	$4p^3q = 0.25$	0.23865	0.21865	0.1836	0.1202	0
$AAaa$	$6p^2q^2 = 0.375$	0.3479	0.3149	0.2700	0.1947	0
$Aaaa$	$4pq^3 = 0.25$	0.23865	0.21865	0.1836	0.1202	0
$aaaa$	$q^4 = 0.0625$	0.0874	0.1239	0.1814	0.28245	$q = 0.5$

production systems to achieve this are a very important final stage in the breeding and multiplication of new cultivars.

### 1.4.5 Landraces of Potatoes

Following its creation in Lima, Peru in 1971, The International Potato Centre (CIP) assembled a collection of potato landraces native to Latin America (<https://cipotato.org/genebankcip/process/potato/potato-cultivated/>). It began with a donation from the Peruvian National Potato Programme of approximately 1800 potato accessions comprising traditional cultivars (landraces). The collection was placed in the CIP Huancayo Experimental Station of Santa Ana-INIA Huancayo. During its 45 years of existence, the number of cultivated potato accessions peaked at 17,326. However, after the staff at CIP had eliminated mixtures, atypical plants, and those with virus symptoms, and had also identified and eliminated duplicates, they were left with the current collection of 4727 accessions. These include 4421 traditional landrace cultivars from 17 countries (mainly from the Andean region) and improved cultivars. The landrace collection comprises 289 *Stenotomum* + 102 *Goniocalyx*, 206 Phureja, 14 *S. ajanhuiri*, 235 hybrids (diploid and tetraploid), 36 *S. juzepczukii*, 121 Chaucha, 3233 Andigena, 179 Chilean Tuberosum and 6 *S. curtilobum*. The improved cultivars comprise ones released mainly by Latin-American countries and genetic stocks used to identify resistance to diseases. The entire clonal collection is now conserved in vitro and distributed internationally as tissue-cultured materials. This global collection is maintained in trust and is distributed with the Standard Material Transfer Agreement (SMTA) under the terms of the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA). All accessions in the collection are maintained and available for use in research, breeding and training by humanity, now and into the future (<https://cipotato.org/genebankcip/process/potato/potato-cultivated/>).

The collection shows that South American farmers retained a much wider variety of tuber shapes and skin and flesh colours than is seen in wild species (Glendinning 1983; Simmonds 1995) and also greater than we see today in modern cultivars. Interestingly, potato tuber diversity was one of many examples given by Darwin, in *The Variation of Animals and Plants under Domestication* (Darwin 1868), of the principle that the valuable and selected parts of all cultivated plants show the greatest amount of modification. The wild relatives of cultivated potatoes have small tubers, round or oval in shape, with white flesh, and skins that are white or have a faint bluish-purple flush. In contrast, the tuber shapes of landraces were either regular, from compressed through elliptic to long ones, or unusual irregular ones such as coiled and concertina-shaped. Skin colour was pink, red, blue or purple, due to anthocyanins, or white, and the distribution of pigments could result in pigmented eyes or eyebrows, and splashed, scattered, spectacled, or stippled tubers. Flesh colour was yellow or orange, due to certain carotenoids, or white, and anthocyanin pigmentation could also occur (Ortiz and Huamán 1994). Interestingly, molecular

genetics research by De Jong et al. (2003) and Zhang et al. (2009) provided data that were consistent with the hypothesis of Dodds and Long (1955) that the allele for red skin was selected just once during the domestication of the potato.

South American farmers must have selected their potatoes for appropriate maturity and dormancy, higher yields and harvest index, and resistance to abiotic and biotic stresses. The results of Victorio et al. (1986) on harvest index are of particular interest. They grew 10 potato genotypes to maturity at two contrasting sites in Peru; one in La Molina at 230 m above sea level, in the warm (16.3 °C to 23.1 °C) coastal desert region where irrigated potatoes are grown in a season of length 120 days; the other in Huancayo in cooler (6.2 °C to 20.9 °C) conditions at 3273 m above sea level, which is typical of Andean potato farming with a season of 150 days and higher tuber production (yields) at a higher dry matter content (percentage). Good growth was obtained at both sites for the 9 cultivated genotypes whereas the wild species *S. acaule* grew slowly and only produced a small number of miniature (<0.5 cm diameter) tubers. The cultivated genotypes comprised six Tuberosum × Andigena hybrids, one Chaucha, one Stenotomum and one *S. curtilobum*. The latter grew well but differently to the other eight genotypes. The harvest index of the 9 cultivated genotypes ranged from 0.73 to 0.85 at Huancayo but dropped to 0.33 to 0.75 in La Molina. The only consistent differences between the two sites were shorter plants at Huancayo with an increased tuber dry matter percentage (20 to 28% compared with 14 to 21%). These results raise the question of whether or not worldwide there is still scope to select potatoes for a higher harvest index and better adaptation to the environments in which they are now being grown. Interestingly in a recent review, Haverkort and Struik (2015) quote 0.75 as the typical harvest index of potato compared with 0.4–0.6 for cereals.

It is perhaps fitting to end this section with an acknowledgement of the achievements of the Incas in the Andes during the fifteenth century (Moseley 2001). They developed a sophisticated agriculture appropriate for the high altitude, cold and dry climate around their Peruvian capital of Cuzco. They were able to grow crops of maize, potatoes and other food plants during summer on terraces built of dressed stone which trapped the heat of the sun and aided irrigation; then store the produce for use during winter. The Incas also had a suite of locally domesticated plants and animals. Perhaps there are still lessons for us today when thinking about what farming systems are appropriate for different parts of the world.

## 1.5 Introduction of Potatoes to Europe

The Spanish conquerors of the Incas were the first Europeans to see potatoes being cultivated in South America, with the first recorded sighting by the expedition of Jiménez de Quesada in what is now Colombia in 1537 (Hawkes 1990). Thirty years later (1567) we have the first record of cultivated potatoes outside of South America with their export from Gran Canaria in the Canary Islands to Antwerp in Belgium (Hawkes and Francisco-Ortega 1993). This was 6 years before they were first

recorded in Spain in 1573 in the market archives of the Hospital de La Sangre in Seville (Hawkes and Francisco-Ortega 1992). Hence, potatoes were probably first introduced from South America into the Canary Islands around 1562, and from there to mainland Europe (Hawkes and Francisco-Ortega 1993).

The early introductions of potatoes to Europe included the one shown in the first water-colour painting of a potato dated 1588 (late maturing, red-skinned tubers of irregular shape with deep eyes) and the one shown in the first printed illustration of 1597 (not as late maturing, white-skinned tubers of irregular shape with deep eyes) (Hawkes 1990). The painting was sent by Philippe de Sivry, Prefect of Mons in Belgium, to the herbalist Clusius in Vienna in 1589 and the illustration was by the Englishman, John Gerard, in his *Herball* of 1597 (Salaman 1926). The cooking methods mentioned by Gerard were baking in embers and boiling in water which subsequently became the main method because it is quicker, as little as 15 min in boiling water at 100 °C compared with 75 min baking at 180 °C. Nevertheless, hot baked potatoes became popular again on the streets of London in Victorian times, in the 1850s (Reader 2008), and are still popular today.

It was often assumed that these early introductions came as ships' stores from Colombia and were of Columbian, or possibly Peruvian, origin and hence were primarily tetraploid Group *Andigena* potatoes. Then as the growing of potatoes spread north-eastwards across Europe, selection took place for tubering in the long summer days of northern Europe. However, extant Canary Island potatoes comprise both Andean- and Chilean-type landraces so Rios et al. (2007) suggested that there were multiple early introductions of both types. Furthermore, they suggested that the early European potato was selected from the Chilean introductions because they were better adapted to European conditions. Potato introductions from South America were reviewed by Glendinning (1983), but one cannot say with certainty how many there were and what their contribution was to the subsequent spread of the potato in and from Europe, as reviewed by Hawkes (1990). It therefore seemed safest to assume that the early introductions of cultivated potatoes to Europe came from both the Andes and coastal Chile (Hosaka et al. 1994; Spooner et al. 2005b; Rios et al. 2007). However, Ames and Spooner (2008) then analysed DNA from 49 herbarium specimens and confirmed the presence in Europe of Andean potatoes from around 1700 and Chilean potatoes from 1811. Incidentally, Charles Darwin recorded in his journal of the voyage of HMS *Beagle* around the world, eating 'wild potato tubers' on 7 January 1835 near the northern end of the Chonos Archipelago (45°S) in Chile (Bettany 1889). Ames and Spooner (2008) concluded that the original introductions of potatoes did come from the Andes but that the Chilean potato became predominant in Europe long before the late blight epidemics of 1845 onwards. Hence, the late blight epidemics were not the stimulus for the introduction of Chilean potatoes. Using a *Solanum* section *Petota* diversity panel, Hardigan et al. (2017) found that significant allelic diversity (comparable to that in wild species) existed in the nineteenth century Chilean *Tuberosum* founders of North American breeding programmes, but their small number ensured a group of individually heterozygous but closely related descendants. Interestingly, molecular analyses of old Japanese cultivars were consistent with them being derived from Group *Andigena*