

# Potato in the age of biotechnology

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**Biotechnology-based tools are now widely used to enhance and expand the traditional remit of potato in food production. By modifying its functionality, the capacity of the potato to produce, for example, therapeutic or industrial compounds is now a reality, and its ability to resist disease can also be radically improved. Two developments have been crucial to expanding the role of potato: the recent advances in the fields of structural and functional potato genomics and the ability to integrate genes of interest into the potato genome. In this review we discuss how both developments have diversified the remit of this crop.**

## Potato production

In Europe in the 1700s it was believed that the consumption of potatoes led to leprosy, cholera, rickets and tuberculosis [1]. Today, potatoes are grown in ~125 countries and more than a billion people worldwide consume them on a daily basis. To support this demand, a multitude of varieties have been developed to resist pre- or post-harvest diseases, to target specific markets that require post-harvest processing (e.g. chipping) or to meet the nutritional requirements at the community level. As well as providing starch, potatoes are rich in vitamin C, have high levels of potassium and are an excellent source of fibre. Potato is an easy-to-grow plant and can provide more nutritious food faster and on less land than any other food crop, and in almost any habitat.

Since the 1960s, global potato production has remained relatively static (285.4 million tonnes  $\pm$  0.19 million tonnes) [2]. However, this does not reflect the dramatic rate of increase in production across India, China and the African continent, which have witnessed a nine-, five- and sixfold increase in potato production, respectively [2] (Figure 1). This is in contrast to a modest 1.6-fold increase across North America (USA and Canada) and a 54% decrease in production across the European Union (pre-2004 expansion of member states) over the same period [2]. A shift towards the use of potato in convenience foods (e.g. potato chips and fries) has been recorded in developed nations, but in developing economies the majority of the potato crop is still used for direct consumption [2]. Overall, potato is likely to maintain, if not increase, its relative economic importance in the decades ahead. As potato exerts a major socio-

economic influence on society today, countries that wish to remain competitive in the emerging global potato market must accelerate their development of yield-increasing technology (<http://www.cipotato.org/market/potatofacts/growprod.htm>) and find ways of creating novel markets.

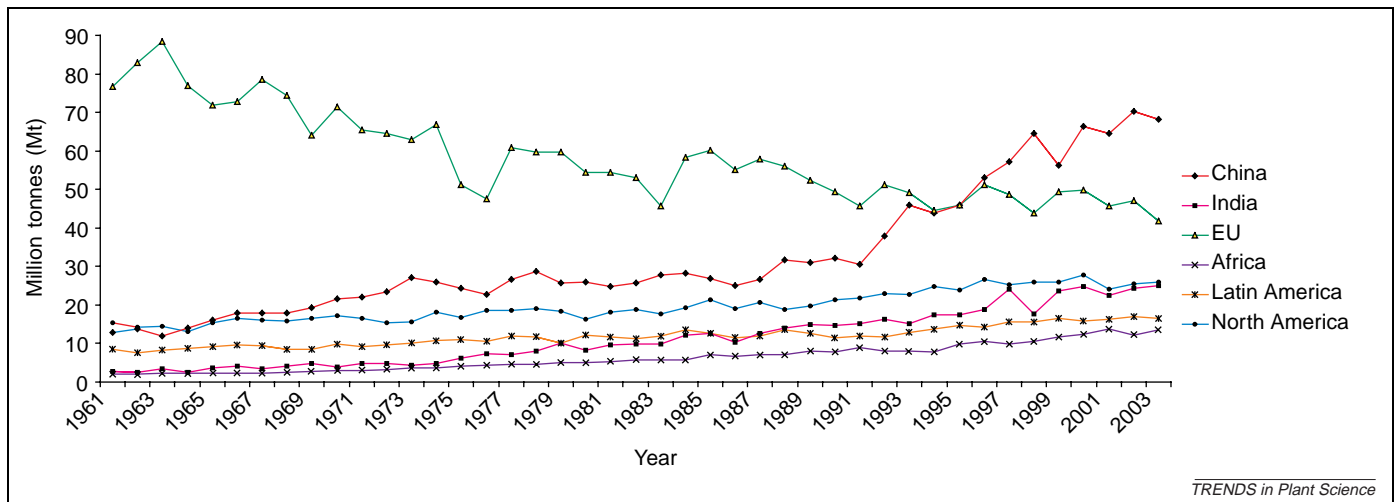
## Genomics-based research initiatives

The emergence of molecular marker-based genetic mapping in the mid-1980s represented an exciting step forward in the ability to characterize the genomes of higher animals and plants. To date, molecular marker-based maps of potato have facilitated the identification of genetic loci underlying many important agronomic traits in potato. These include at least 19 major disease resistance genes and numerous quantitative trait loci (QTLs) for disease resistance (reviewed in [3]), morphological, developmental and quality traits. These studies have served to confirm the long-standing hypothesis that many of the most important agronomic traits in potato (e.g. yield and dry matter content) are under the control of multiple genes, which exhibit a complex set of interactions with both each other and the environment.

Gaining a complete understanding of the genetics of such complex traits is central to our ability to use biotechnology for the improvement of potato. Fuelled by technological developments in the analysis of the human genome, several high-throughput genomics programmes have been established for potato (and many other plant species). The ultimate goal of these initiatives is to establish the identity and action of every gene in the potato genome. In the USA, the National Science Foundation (NSF) Potato Genome project (<http://www.potatogenome.org>) has enabled the sequencing of 130 000 expressed sequence tags (ESTs) from seven potato cDNA libraries (five core and two pathogen challenged), which has facilitated the production of a publicly available 10 000 cDNA micro-array ([http://www.tigr.org/tdb/potato/SGED\\_index2.shtml](http://www.tigr.org/tdb/potato/SGED_index2.shtml)). The Canadian Potato Genome Project (CPGP, <http://www.cpgp.ca>) has similar goals: (i) to produce high-quality cDNA libraries for at least 100 000 EST sequences from multiple libraries; (ii) to generate a micro-array consisting of at least 10 000 non-redundant genes; and (iii) to produce a large population of activation-tagged mutant plants for trait screening. Novel approaches, such as activation tagging [4,5] and virus-induced gene silencing (VIGS) [6], are essential tools for a heterozygous outbreeding autotetraploid such as potato for which the development of traditional knockout

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**Figure 1.** Timescale production (million tonnes, Mt) of potato across China, India, European Union (EU, pre-2004 expansion), Latin America, North America (Canada, USA) and the African continent between 1961 and 2003 (data collated from Food and Agricultural Organization of the United Nations Statistical Database [2]).

mutants using chemical and/or radioactive mutagenesis is not feasible.

Similar potato genomics programmes are underway in Europe, funded by both EU Framework Programmes and individual national bodies. Under the auspices of The Netherlands Genomics Initiative, the Centre for Biosystems Genomics (<http://www.cbsg.nl/>) has been tasked with unravelling the genetic networks associated with multi-factorial traits in potato (along with tomato and *Arabidopsis*). The programme comprises nine projects and covers various aspects of disease resistance, tuber quality and genetic variation. The GABI-CONQUEST programme in Germany is a similar initiative that has focused primarily on the candidate gene approach for the dissection of complex traits ([http://www.gabi.de/21seiten/a\\_00\\_e.php](http://www.gabi.de/21seiten/a_00_e.php)). More recently, an international Potato Genomics Sequencing Consortium (<http://www.potatogenome.net>) has been established with the primary objective of elucidating the complete sequence of the potato genome (840 Mb) by the end of 2008. This initiative, which is based on the construction of a BAC-based physical map, is grounded in a previously constructed ultra-high density (UHD) genetic linkage map of the parents of a diploid F<sub>1</sub> potato population, comprising 10 000 genetic markers [7] (<http://potatodbase.dpw.wau.nl/UHDdata.html>).

### Adopting biotechnology in potato breeding

It can take up to 15 years to develop a single potato cultivar through traditional breeding [8]. For the majority of the genetic mapping studies to date, the goal has been to provide a basis for marker assisted selection (MAS) strategies in breeding, where selection is practised on genetic markers linked to genes conferring beneficial phenotypes. This can permit early and efficient selection for the traits of interest, allowing 'stacking' of genetically distinct components of the same trait and potentially shortening the breeding process by several years. Despite its potential, few instances of MAS in potato breeding have been reported. This is largely because of the outbreeding, tetraploid genetics of cultivated potato and because many traits of interest to potato breeders are truly polygenic in

nature with a large environmental component. In this scenario, the efficacy of QTL mapping is much reduced, with the greatest difficulty being to develop markers that are diagnostic for (as opposed to just linked to) multiple small-effect QTLs. However, it is anticipated that this situation will be improved by the output of the aforementioned genomics-based studies, which will, in the longer term, allow the identification of many of the genes underlying the most important traits (e.g. carbohydrate metabolism). Instances where MAS is currently being used in potato breeding are largely confined to single dominant genes, or to large-effect QTL. An excellent illustration of this is the case of dominantly inherited disease resistance and large-effect QTLs for disease resistance, the majority of which have been found to be mediated by a single class of genes sharing conserved nucleotide-binding-site (NBS) and leucine-rich repeat (LRR) motifs (reviewed in [3]). On the basis of their map location, several NBS-LRR-type disease resistance genes have now been cloned and characterized to a level sufficient to offer real prospects for their MAS. Recently, Bernard Caromel *et al.* [9] showed the potential of MAS for the introgression of disease resistance genes in a potato-breeding scenario by demonstrating the effectiveness of this approach for 'stacking' two separate QTL for potato cyst nematode resistance into individual genotypes, which resulted in a more-robust resistance phenotype than would be obtained by the presence of a single QTL.

An alternative strategy for deploying resistance genes is through their direct introduction into potato breeding material using a transgenic approach. Since the first reports in 1986 [10,11], the successful nuclear integration of a heterologous gene(s) into the potato genome has been described for a range of starting tissues, including the *Agrobacterium tumefaciens*-mediated transformation of leaf tissue [12], tubers [13] and internodal segments [14], and direct gene transfer into leaf, tuber and internodes through particle bombardment [15]. The recent development of an efficient process of direct DNA uptake (in leaf explants) indicates that transgene expression levels equivalent to those mediated through the more commonly

used *Agrobacterium*-based systems can be obtained with particle bombardment [16]. This is of particular significance for the transfer of multiple transgenes, which in turn could facilitate in manipulating the metabolic pathways of potato [16]. The transformation of the plastid genome of potato has also been demonstrated [17,18], which can offer high returns in protein yield. Though a prerequisite for establishing plant manufactured vaccine systems, its applicability is limited to relatively simple, aglycosylated proteins.

Although large genotype-dependent variation can be expected for both the regeneration and transformation efficiency of potato varieties through *Agrobacterium*-based systems [19,20], new tools and approaches for the production of transgenic plants are now providing a fresh perspective into how gene transfer can be achieved. For example, Wim Broothaerts *et al.* [21] have successfully engineered transgenic rice, *Arabidopsis* and tobacco using *Rhizobium* spp., *Mesorhizobium loti* and *Sinorhizobium meliloti*; a significant development in light of the complex patent issues associated with *Agrobacterium*-based systems [22]. In addition, Tony Conner and colleagues have identified sequences within the potato genome that can be used to construct novel transformation vectors (T. Conner, personal communication) composed of plant-derived sequence, in contrast to using vectors of bacterial origin. This opens up the possibility of using an intragenic vector system to create non-transgenic GM lines.

For potato, the combination of map-based cloning with an *Agrobacterium*-based transgenic approach has permitted the characterization and introgression of genes from the wild species *Solanum bulbocastanum* (*RB* [23], *Rpi-blb1* [24], *Rpi-blb2* [25]) that confer strong resistance to *Phytophthora infestans* (Figure 2). Conversely, disease



**Figure 2.** Field trial demonstrating the performance of GM potato (cv. Kathadin) transformed with the *RB* gene next to border rows of the diseased control (cv. Norchip). Photograph taken 21 days post inoculation with *Phytophthora infestans* (US-8). Photograph courtesy of Dimitre S. Mollov and James M. Bradeen.

resistance in potato can be achieved via the introduction of heterologous genes into the potato genome, for example: resistance to the Colorado beetle (*Leptinotarsa decemlineata*) through the constitutive expression of the *Bt* gene (which expresses *Bacillus thuringiensis* toxins) [26,27]; resistance to *Verticillium dahliae* by over expressing a *Medicago sativa* cysteine-rich defensin [28]; and resistance to *Phytophthora erythroseptica* and *P. infestans* [29] through accumulation of the cationic peptide temporin A. Resistance to *P. infestans* (and *Alternaria solani*) has also been reported through gene silencing [30] and by elevating levels of hydrogen peroxide, which also conferred resistance to the bacterial soft-rot pathogen *Erwinia carotovora* [31]. Although potato virus Y (PVY) and potato virus X (PVX) resistance has been achieved through expression of the heterologous potato leaf roll virus ORF4 gene [32], RNA silencing has also been used to engineer strong resistance to PVY [33].

### Alternative production systems

Arguably, the most significant outcome arising from the technology-driven programmes of potato research has been the expansion of the use of potato into non-food applications. Modifying tuber starch content has been a goal for many years because of the commercial importance of processed starch as a food additive in, for example, high fructose syrup and various other technical processes [34]. Although the genetic complexity of tuber starch is evident by the identification of carbohydrate-metabolism-associated QTLs on the 12 chromosomes of potato (reviewed in [35]), significant milestones have been achieved through biotechnological approaches.

Such QTL mapping experiments, combined with the generation of a molecular-function map for carbohydrate metabolism [36], has offered researchers the potential to adopt an endogenous candidate gene approach to address such production issues as cold-sweetening in processed tubers [37], be that through a transgenic or a MAS approach (reviewed in [38]). For example, modification of the plastidic ATP and/or ADP transporter activity increased the amylose content of starch to 27% [39]. Additionally, further genetic manipulation has achieved a 60% increase in starch levels compared with wild-type plants [34]. A much-desired property for starch is freeze-thaw stability, which is typically achieved through chemical substitution. Through the antisense inhibition of three starch synthase genes, starch has been generated that maintains its stability through five freeze-thaw cycles [40]. Therefore, as the ability to modify potato starch via genetic modification is realized, it provides an opportunity to use native starch to achieve specific, valuable functionalities [41] – the commercial relevance of which is reflected in the number of notifications (25 to date) that have been made for field-testing GM potato with altered starch profiles (<http://gmo.info.jrc.it/>).

The ability to achieve high synthesis scales at low manufacturing costs has led to plants being used as bioreactors for the production of therapeutic molecules, and to plants emerging as a competitor to established industrial processes [42–44]. The suitability of potato for therapeutic molecule production has been demonstrated

with the crop being used in three of the six clinical trials completed to date [44], one of which was the first to demonstrate human immunogenicity to an *in planta*-produced vaccine candidate following the administration of tubers expressing a capsid protein of the Norwalk virus (causative organism of epidemic acute gastroenteritis) [45].

The potential of using an edible, plant-based vaccination system for protection against HIV-1 infection has been demonstrated using transgenic potato expressing the HIV-1 envelope glycoprotein gp120 [46]. In addition, the potential of using a potato-based vaccine in a global immunization programme against hepatitis B (global mortality rate of 1 million cases per year) has been illustrated, with 57% of individuals tested developing an immunogenic response following the ingestion of hepatitis B surface antigen (HBsAg)-expressing potato. Significantly this was recorded with a non-replicating vaccine that was delivered orally in the absence of an adjuvant [47].

Analysis of transgenic potato expressing the full-length spike protein of infectious bronchitis virus has highlighted its potential in a veterinary context as a vaccine delivery system in chickens [48]. An immunogenic response has been induced in mice fed with transgenic potato expressing the VP1 structural protein of the foot and mouth disease virus [49]. Furthermore, expression of the neutralizing epitope of swine porcine epidemic diarrhoea virus (PEDV) has led to the accumulation of the PEDV protein to levels of up to 0.1% of total soluble tuber protein [50].

The genetic modification of potato has also been used to improve the functional properties of tuber-derived flour through the over-expression of the wheat low-molecular-weight glutenin gene [51]. Eva Farre *et al.* have adopted a transgenic approach to reduce pre-sprouting dormancy by six to seven weeks [52] and transgenic potato plants have been modified to accumulate high levels (1.1% of dry weight) of a cyanophycin-like polymer, opening the way for the future production of biodegradable plastics using a plant-based production system [53].

### The GM issue

In 2005, 8.5 million farmers across 21 countries voluntarily cultivated >90 million hectares of GM crops (<http://www.isaaa.org/kc/bin/briefs34/pr/index.htm>). Yet, consumer apprehension towards GM technology still exists and centres on the public's desire for unbiased information on the perceived risks associated with the technology. So, focussing solely on GM potato, what are these perceived risks and have they or can they be addressed? Generic risks described for GM potato (and which typically are raised against all GM crops) relate to:

- The potential for transgene gene flow into adjacent non-GM populations.
- The potential allergenicity of the transgene post-consumption.
- The development of a super-pest that could render the transgenic phenotype obsolete.

The application of a novel, quantitative gene flow index to

potato calculates the propensity for transgene escape through pollen and/or seed-mediated gene flow as a score of 6 out of a maximum of 27 [54]. This low value was attained because of the high degree of male sterility in many varieties and a low transmission distance for pollen dispersal in the remaining male fertile material [55,56]. In addition, for crop-to-wild relative hybridization within Europe, potato is considered to be genetically contained owing to the lack of sexual compatibility between commercial potato varieties and the two related wild species *Solanum nigrum* and *Solanum dulcamara*. Combined with the clonal nature of the crop, this serves to minimize the potential for gene flow to emerging groundkeepers (volunteer potatoes arising from tubers left in the soil) post-harvest [57], which in turn can be negated through appropriate crop management.

In contrast to the issue of gene flow, which is dependent upon the biology of the potato plant (be it GM or non-GM), the allergenic potential of a GM potato crop is dependent upon the product of the transgene. As such, each GM potato line must be considered individually so that results that emanate from the risk assessment of one GM potato line are not used to brand all GM potato material generically. Such a scenario occurred in 1998, when studies conducted by Arpad Pustzai indicated that rats fed a diet of potato engineered to produce the snowdrop lectin GNA suffered from stunted growth and deficient immune systems. Although the research methodology was the focus of critical discussion within the scientific community (discussed in [1]), the general public were left with the impression that all GM potato lines had the potential to cause physical harm.

Genetic modifications in potato carbohydrate metabolism and/or capacity to resist disease are likely to result in changes to the profile of plant defence compounds in the tuber [58]. However, it is crucial to determine whether GM potato cultivated under field conditions will pose a risk to human and/or animal health. Recent work by Gareth Catchpole and colleagues [59] indicated that the metabolome of field-grown GM and conventional potatoes were substantially equivalent, apart from the targeted changes in the GM populations. The application of high-resolution metabolic and/or proteomic profiling [60–62] in this manner is an important step for determining substantial equivalence but, notably, is only one part of a multi-disciplinary risk assessment that is required before GM-derived material can enter the food chain. This exhaustive approach might seem superfluous given that potato tubers are considered to be mildly toxic [58], but adopting an overtly precautionary approach is both sensible and necessary in light of consumer sensitivities to the GM issue.

By contrast, the durability of GM crops must be considered in the context of what occurs in traditional cropping systems. As increasingly efficient conventional crop systems are commercialized, pests evolve to evade the novel control measures, thereby ensuring their survival (e.g. fungicide resistance in *Mycosphaerella graminicola* [63]). Significantly, pest evolution will occur irrespective of whether the novel plant phenotype is developed through conventional plant breeding or genetic modification.

**Box 1. NewLeaf™ potato**

Developed by the Monsanto subsidiary NatureMark (<http://www.naturemark.com>), NewLeaf™ was engineered to resist the Colorado beetle (*Leptinotarsa decemlineata*) and was made commercially available in 1995. Primarily grown in the American Pacific Northwest, NewLeaf™ was followed by NewLeaf Plus™ and NewLeaf Y™, which were resistant to potato leaf roll virus (PLRV) and potato virus Y (PVY), respectively [69]. Following decisions by the major food processors (e.g. McDonalds, Burger King, Frito-Lay and Proctor & Gamble) [69] to prohibit the inclusion of GM potatoes in their products because of activist pressure, NewLeaf™ growers had no choice but to revert to conventional germplasm and the subsequent reintroduction of large-scale applications of the primary insecticides (e.g. pyrethrin, organo-chlorines and carbamates) to which target insects have now developed high levels of resistance ([http://www.oznet.ksu.edu/dp\\_hfrr/extensn/problems/colpotat.htm](http://www.oznet.ksu.edu/dp_hfrr/extensn/problems/colpotat.htm)).

Consequently, strategies to maintain the durability of the novel crop (e.g. gene stacking and establishment of insect refuges) are applicable to both GM and non-GM crops.

For *Bt* potato (as it is for all *Bt* crops), the cultivation of non-*Bt* refuges adjacent to the *Bt* crop is essential to reduce the evolutionary pressure placed upon the target pest through the cultivation of the *Bt* crop. By growing susceptible plants to attract the target insect (e.g. Colorado beetle) the rate of increase in resistance within the beetle is delayed because the number of susceptible beetles within the population is maintained on the refuges (explained by [64]), thereby prolonging the efficacy of the crop. Gene stacking is equally important in maintaining the durability of a novel phenotype and has been adopted for the generation of a GM potato line (containing the *Rpi-blb1* and *Rpi-blb2* genes from *S. bulbocastanum* [24,25]) currently being tested for resistance to *P. infestans* (<http://gmoinfo.jrc.it/>). Because the commercialization of this material could have a significant impact on net grower income [65] (€417 million annually for Europe alone [66]), it is not surprising that field trials are being conducted.

Although there are valid economic and environmental reasons for commercializing such a crop [66], to ensure that the events linked to the cultivation of *Bt* potato in 2001 (Box 1) are not repeated, it is important that the regulatory agencies adopt a proactive approach to address consumer apprehension. Information sources such as GMO-Compass (<http://www.gmo-compass.org>) and the establishment of the European Food Safety Authority (EFSA) (<http://www.efsa.eu.int>), which was set up to re-establish consumer confidence in the European food network, will go some way to achieving this objective. Although an anticipated benefit from *P. infestans*-resistant GM potato could be a reduced commodity cost owing to increased yields, it is still a challenge to elucidate the direct benefits such a cultivar could offer consumers and/or stakeholders in those countries that do not experience food shortages or micronutrient deficiency. This contrasts with persons dependent upon agriculture for their survival, where specific GM potato lines tailored to address local abiotic and/or biotic stresses could present an alternative to existing systems [67].

**Looking ahead**

From the time of its introduction into Europe from South America approximately 400 years ago, potato has experienced continuous modification via man's unconscious and conscious action. This has resulted in its development from a poorly performing botanical curio into the fourth largest cultivated food crop in the world. Over the past 20 years, the application of biotechnology approaches has begun to unravel the intricacies of the potato genome and proteome. Consequently, researchers are capitalizing on the availability of novel data-sets to address fundamental biological questions. Allied with emerging high-throughput techniques and the excellent germplasm resources currently available (Box 2), the sum of large-scale genomics-based potato research should have a radical impact on our ability to link genes with traits in potato over the next decade.

Nonetheless, as scientists forge ahead in deciphering the workings of such major crops as potato, the general public remains apprehensive about what is being done. As a result, an emotive debate centred on the perceived risks of various tools of biotechnology (e.g. genetic modification) has prevailed. Unless the consumer can experience the direct benefits of the science, any perceived risk from a GM crop will outweigh the benefits [68], which is most relevant to the present European Union (EU) where objection to GM crops is the most vociferous. However, this could change in the near future with the modification of potato to produce industrial, pharmaceutical and veterinarian products. Indeed, the recent increase in the number of notifications submitted for Class B release of GM potato lines within the EU member states (<http://gmoinfo.jrc.it/>) is an early indicator to the public as to the expanding remit of potato, which we predict will further

**Box 2. Importance of maintaining genetic resources**

The preservation and study of wild potato germplasm is crucial to the development of potato, be that through a molecular genetics [23,24,70–73] or traditional breeding approach (reviewed in [35]). Indeed, the importance associated with maintaining biodiversity has been underpinned through the United Nation's Convention on Biological Diversity (<http://www.biodiv.org/convention/articles.asp>).

The genus *Solanum* comprises >1000 species, with the tuber-bearing section *Petota* comprising ~225 species, including the tetraploid *Solanum tuberosum* subsp. *tuberosum* and subsp. *andigena* (the andigena potato) [74]. Although worldwide potato production is dominated by the smooth tubers of *S. tuberosum*, local communities in the Andean region cultivate a range of species and primitive cultivars from the *Solanum brevicaulis* species complex that show a wide diversity of tuber types (<http://www.cipotato.org/>). Wild potato species inhabit a range of different mountain habitats and have therefore had to adapt to a wide range of biotic and abiotic stresses. This is in contrast to their cultivated relatives who, because of their relatively narrow eco-geographical origin, are adapted to relatively few environments and diseases [35]. Consequently, subsp. *andigena* and other semi-wild mountain taxa that show diverse disease and frost resistance qualities, among others, remain a major source of germplasm for commercial breeding. To maximize the utility of these resources, germplasm collections have been established (for a comprehensive list see <http://www.cgn.wagenin.gen-ur.nl/pgr/collections/crops/potato/genbanks.htm>). These gene banks represent a precious resource that continues to benefit current breeding programmes (<http://www.cipotato.org/>) and applied and strategic research agendas [23,25].

accelerate in the years ahead as the existing research base continues to expand.

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