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REVIEW

Improving breeding efficiency in potato using molecular and quantitative genetics

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Abstract

Key message **Potatoes are highly heterozygous and the conventional breeding of superior germplasm is challenging, but use of a combination of MAS and EBVs can accelerate genetic gain.**

Abstract Cultivated potatoes are highly heterozygous due to their outbreeding nature, and suffer acute inbreeding depression. Modern potato cultivars also exhibit tetrasomic inheritance. Due to this genetic heterogeneity, the large number of target traits and the specific requirements of commercial cultivars, potato breeding is challenging. A conventional breeding strategy applies phenotypic recurrent selection over a number of generations, a process which can take over 10 years. Recently, major advances in genetics and molecular biology have provided breeders with molecular tools to accelerate gains for some traits. Marker-assisted selection (MAS) can be effectively used for the identification of major genes and quantitative trait loci that exhibit large effects. There are also a number of complex traits of interest, such as yield, that are influenced by a large number of genes of individual small effect where MAS will be difficult to deploy. Progeny testing and the use of pedigree in the analysis can provide effective identification of the superior genetic factors that underpin these complex traits. Recently, it has been shown that estimated breeding values (EBVs) can be developed for complex potato traits. Using a combination of MAS and EBVs for simple and complex traits can lead to a significant reduction in the length of the breeding cycle for the identification of superior germplasm.

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Introduction

Potatoes (*Solanum tuberosum* L.) are the fourth most important human food crop, and the most important non-grain crop. Despite this, many current commercial cultivars suffer from a number of production and quality issues. In particular, disease susceptibility can be potentially catastrophic for a clonally propagated crop such as potato. New cultivars are therefore required, which are high yielding, disease resistant and produce tubers with satisfactory quality attributes. However, as conventional breeding takes a significant time (often more than 10 years) to produce improved germplasm, there is a pressing need to accelerate genetic improvement in potato. Recent advances that have the potential to improve breeding efficiency are therefore the focus of this review.

The cultivated potato has evolved significantly from the original landrace introductions into the Old World, through transformation of the relatively small and highly distorted tubers of primitive material to the comparatively large, uniform tubers of modern day cultivars. The primitive tuber offered significant advantage for a wild species, providing a secondary method of reproduction, enabling regeneration as clonal propagules in the absence of seed production.

This secondary strategy for propagation is complementary to the obligate outbreeding reproductive habit of the progenitor species, which could limit seed production in unfavourable seasons.

The inherent high level of heterozygosity that results from an outbreeding habit, linked with tetraploidy, has enabled potatoes to readily adapt to a wide range of environmental conditions through the development of locally adapted cultivars. High levels of genetic heterogeneity have also enabled the development of cultivars for multiple applications, such as fresh market use, French fry and crisp processing, and starch production. Although some selection and breeding may be achieved without detailed genetic knowledge, effective breeding programmes are now enhanced by both understanding and utilisation of the underlying genetics of the target breeding traits. Recent significant advances in molecular genetics and the analysis of highly complex quantitative traits, can be exploited by potato breeders to accelerate genetic gains, thus enabling more rapid improvements in potato cultivars.

Biological factors underpinning the highly heterozygous nature of potato

Potatoes have a highly heterozygous genotypic constitution due to the reproductive habit of the progenitor species and landraces, which also exhibit variation in their ploidy levels. The tuber-bearing *Solanum* species are grouped into section *Petota* Dumort., and recent taxonomic classifications recognised 110 wild species and four cultivated species (Spooner et al. 2007, 2009; Ovchinnikova et al. 2011), which range from diploid to hexaploid. Modern cultivars are the products of intensive breeding using *S. tuberosum* and 15 other members of section *Petota* (Ross 1986; Plaisted and Hoopes 1989; Ovchinnikova et al. 2011), and are therefore hybrid in nature.

Nearly all diploid *Solanum* species exhibit gametophytic self-incompatibility and are obligate outbreeders. In contrast, the polyploid potato taxa are capable of self-fertilisation (Jansky 2009). Despite this, substantial levels (c. 40 %) of cross-pollination were estimated between *S. tuberosum* ssp. *andigena* genotypes in a natural Andean population (Brown 1993). Such a level of outcrossing generates allelic heterozygosity within and between individuals, and mitigates levels of inbreeding depression that would otherwise result from self-pollination (Bradshaw et al. 2006).

The cultivated potato is also an autotetraploid ($2n = 4x = 48$) and displays tetrasomic inheritance. At any given locus, five distinct genotypes may be observed, further contributing to the high level of genetic heterogeneity (Howard 1970; Ross 1986; Hawkes 1990; Bradshaw 2007b; Jansky 2009). Cytological studies have revealed that homologous chromosomes in autopolyploids may exhibit segregation patterns based on a mixture of bivalent and multivalent pairing configurations at prophase of meiosis I (Swaminathan and Howard 1953; Wallace and Callow 1995; Stein et al. 2004). In addition, in multivalents 'double reduction' can result in alleles at target loci being delivered to the same gamete from sister chromatids (Bradshaw 2007a; Milbourne et al. 2008). The combination of an outbreeding habit, with an autotetraploid genetic constitution ensures that potato populations are highly genetically heterogeneous, which has enabled the potato to successfully adapt to a range of production environments and selected uses.

Genetic diversity of wild potatoes

The tuber-bearing *Solanum* wild species are highly diverse and are naturally distributed over a broad ecogeographical range, being indigenous to 16 countries (ranging from 38°N to 41°S) (Hawkes 1990; Spooner and Hijmans 2001). In addition, they range from medium-to-high to lowland altitudes, which exposes the plants to a range of climates that include freezing temperatures to semi-desert regions, and cool temperate to tropical rainforests (Hawkes 1994).

Many wild species possess genes for numerous traits not present in cultivated germplasm and represent a rich resource for improvements in disease resistance, abiotic stress resistance and tuber quality characters (Hanneman 1989; Spooner and Bamberg 1994; Jansky 2009). However, introgression of desirable genes from non-domesticated species often requires several generations of breeding to develop a commercial cultivar, partially due to linkage drag of genes for undesirable traits (e.g. presence of glycoalkaloids) along with genes for desirable characters. The deliberate introgression of genes from wild species began in 1909, and has been limited in success, although the successful introduction of dominant major genes and quantitative trait loci (QTLs) for resistance to late blight, viruses and cyst nematodes are significant exceptions (Bradshaw 2007b).

Breeding strategy

A conventional potato breeding strategy employs phenotypic recurrent selection over a number of generations (Bradshaw and Mackay 1994). Typically, large breeding populations are subjected to a progression of selection pressures to reduce the population size, while concurrently increasing the number of plants of each genotype under evaluation (Bradshaw and Mackay 1994; Jansky 2009). A breeder will typically select parents for potential pair-wise crossing on the basis of

complementary phenotypic characters (Bradshaw and Mackay 1994; Bradshaw 2007b). These parents will generally be high-performing cultivars which require additional improvement, or breeding lines that are proven elite parents and produce higher numbers of superior offspring.

Populations are screened over a number of clonal generations for a range of characters. It is often important to evaluate new cultivars over a number of years and in a number of appropriate environments, a process which can take over 10 years (Jansky 2009). Many traits contributing to the phenotype of a potato plant can be highly influenced by the growing environment, for example yield, tuber number, tuber size, specific gravity and processing quality (Jansky 2009).

Approximately 40 traits are considered during new cultivar development (Gebhardt 2013), broadly divided into yield-related and tuber quality characteristics, as well as tolerances to both biotic and abiotic stresses. This makes breeding potatoes more challenging in comparison to grains or forages, as a variety of market specific traits have to be considered as well as typical production traits due to its horticultural nature. Knowledge of the genetic and other environmental influences on the expression of the target traits is important (Table 1), and will influence methods for the identification of superior parents, screening of the derived populations and effective selection methods to identify superior phenotypes.

Genetics of desirable potato traits (simple to complex)

As the cultivated potato is an autotetraploid, breeding using genetic information requires a consideration of the effects of tetrasomic inheritance (Bradshaw 2007a; Jansky 2009). Despite the added complexity that autotetraploidy contributes, inheritance patterns still follow the principles of Mendelian genetics for traits under single gene control, albeit more complex, or quantitative genetics for traits under multiple gene control.

There are a number of qualitative traits in potato that are regulated by major genes. These include many disease resistance genes: *H1* for *Globodera rostochiensis* Ro1 and Ro4 (Toxopeus and Huijsman 1953; Simko et al. 2007), *Nx* or Rx_{adg} for *Potato virus X* (PVX) (Cockerham 1970; Simko et al. 2007), *Ny* or Ry_{sto} for *Potato virus Y* (PVY) (Cockerham 1970; Simko et al. 2007), and there are several major resistance genes for race specific *Phytophthora infestans* (late blight pathogen), notably *R1-R11* identified in the hexaploid *S. demissum* (Simko et al. 2007), and *RB/Rpi-blb1* from *S. bulbocastanum*, which provides resistance that is race non-specific (Naess et al. 2000). Major genes have also been mapped for the control of flesh, skin and flower colour, for tuber shape and for eye depth (Bradshaw 2007b).

Progeny tests can be used to determine the allele dosage for qualitative traits in prospective parents, as segregation ratios in the progenies will be in proportion to the allele dosage of the parent. Tetrasomic inheritance also has implications for which families need screening within a breeding programme. With simplex and duplex parents, the progeny requires screening for identification of gene presence, triplex parents will produce the vast majority of progeny with the gene, but screening will still be necessary due to double reduction, which can lead to low frequency loss of the target gene, and quadruplex parents require only confirmation of the genes' effectiveness prior to commercial release.

Although some traits are under the control of major genes, the majority of traits of interest are influenced by multiple genes with individually small effects. The genetic analysis of quantitative traits does not conform to the relatively simple segregating ratios of qualitative traits, but can still be analysed using family means and variances. When individuals within a family are scored for a quantitative trait, the mean phenotype of the family will be due to the joint action of the respective genes influencing the trait and any environmental interaction. Due to this interaction, the progeny will usually exhibit a normal distribution for the trait of interest. Different families will exhibit different means and variances due to their different genotypic content. Traits controlled by multiple genes may also exhibit additive and/or dominance effects exerted by allelic variants on trait expression. As the phenotypic variance exhibited within a population is the result of both genetic and environmental factors, if the environmental variation can be reduced by trial design to be close to zero, the genotypic variation will approximately equal the measured phenotypic variation (Falconer and Mackay 1996; Kearsey and Pooni 1998).

Robust progeny tests for phenotypic determination of superior progeny sets will determine the parental values for these traits, without identifying the location or number of genes that regulate trait expression. The analysis of quantitative traits is important for population improvement, method of selection and genetic gain (Moose and Mumm 2008). Livestock breeding programmes have greatly benefited from the estimation of the genetic merit of selection candidates based on phenotypic and pedigree information. For example, significant gains have been obtained for milk yield in Holstein cattle in the USA (Van Vleck et al. 1986). This analysis has recently been applied in a potato programme, leading to significant increase of predicted genetic gain for specific traits (Slater et al. 2014).

Development of genomic resources

Major advances in molecular genetics have helped plant breeders to accelerate genetic gain in crops. Genetic markers

Table 1 The main potato traits grouped in categories and listed by the complexity of their genetic control

Trait	Known or likely genetic control	References
Plant development and morphology		
Skin colour	Single genes. Brown skin dominant over pale. Individual loci control red pigment in the skin and eyes, and are closely linked	(Ortiz and Huaman 1994; van Eck 2007)
Flesh colour	Single genes. Yellow dominant over white, intensity due to modifier genes. Purple flesh dominant over white	(Ortiz and Huaman 1994; van Eck 2007)
Tuber shape	Possibly one to a few genes, round is dominant over long	(Ortiz and Huaman 1994; van Eck 2007)
Eye depth & eye brows	Contrary reports on dominance of shallow or deep eyes	(Ortiz and Huaman 1994)
Skin texture	Controlled by three genes, with heavy russeting caused by homozygosity at one or more location	(de Jong 1981)
Plant maturity	Polygenic with a major QTL	(Kloosterman et al. 2013)
Bruising	Unknown genetic control	(Dale and Mackay 1994; van Eck 2007)
Tuber size	Polygenic	(Celis-Gamboa et al. 2003)
Tuber uniformity	Polygenic	(Celis-Gamboa et al. 2003)
Dormancy	Polygenic	(Simmonds 1964)
Salt tolerance	Polygenic	(Donnelly et al. 2007)
Plant type	Polygenic, upright is dominant to prostrate	(Ortiz and Huaman 1994)
Visual preference	Polygenic due to multiple traits	(Maris 1988)
Drought tolerance	Likely to be highly polygenic	(Vos and Haverkort 2007)
Heat tolerance	Likely to be highly polygenic	
Yield	Likely to be highly polygenic	
Tuber postharvest quality		
Cold sweetening resistance	Heritable, polygenic	(Dale and Mackay 1994; van Eck 2007)
Dry matter/Specific gravity	Strongly heritable but affected by environment	(Dale and Mackay 1994; van Eck 2007)
Greening	Polygenic	(Dale and Mackay 1994; van Eck 2007)
Boil sloughing/texture	Polygenic	(Dale and Mackay 1994; van Eck 2007)
After cooking darkening	Polygenic	(Dale and Mackay 1994; van Eck 2007)
Crisp colour	Highly heritable, polygenic due to multiple traits	(Dale and Mackay 1994; van Eck 2007)
Tuber internals	Polygenic due to multiple traits	(Dale and Mackay 1994; van Eck 2007)
Disease resistance		
Potato virus S	Single gene	(Swiezynski 1994; Simko et al. 2007)
Potato virus X	Single genes	(Cockerham 1970; Simko et al. 2007)
Potato virus Y	Single genes	(Cockerham 1970; Simko et al. 2007)
Tomato spotted wilt virus	Single gene in tomato and capsicum, unknown in potato	(Bakker et al. 2011)
Potato cyst nematode	Single dominant genes, also polygenic	(Toxopeus and Huijsman 1953; Simko et al. 2007)
Potato leaf roll virus	Single genes with modifying genes and environmental interactions	(Swiezynski 1994; Simko et al. 2007)
Late blight	Multiple single genes and QTLs for various strains	(Umaerus and Umaerus 1994; Simko et al. 2007)
Early blight	Heritable, few genes	(Pavek and Corsini 1994; Simko et al. 2007)
Root-knot nematode	Highly heritable, 3 genes	(Phillips 1994)
Verticillium wilt	Heritable, polygenic	(Pavek and Corsini 1994; Simko et al. 2007)
Phomea dry rot	Heritable, polygenic	(Wastie et al. 1988)
Fusarium dry rot	Heritable, polygenic	(Pavek and Corsini 1994)
Root lesion nematode	Little is known on resistance, likely polygenic	(Phillips 1994)
Black dot	Little is known on resistance, likely polygenic	(Wastie 1994)
Silver scurf	Little is known on resistance, likely polygenic	(Wastie 1994)
Rhizoctonia black scurf	Polygenic	(Wastie 1994)
Rhizoctonia stem canker	Polygenic	(Wastie 1994)
Common scab	Polygenic	(Wastie 1994)
Powdery scab	Polygenic	(Wastie 1991)

based on DNA-level variation, provide the potential to assist in the identification of genes of interest to enable marker-assisted selection (MAS) for the development of new cultivars. Due to their relative abundance across the genome, single nucleotide polymorphisms (SNPs) are the most versatile molecular marker system to be developed to date. SNP frequency in potato has been estimated to be c. 1 per 24 base pairs (bp) within exons (Uitdewilligen et al. 2013), providing a striking illustration of the highly heterozygous nature of cultivated potato. Molecular markers developed from transcribed regions of the genome, often described as functional or 'perfect' markers (Andersen and Lübberstedt 2003), are expected to display superior performance to less closely linked genetic markers, due to the capacity to detect variation adjacent or coincident with the causal polymorphism.

Advances in molecular biology, particularly due to re-sequencing multiple genomes, have provided a wealth of knowledge and resources that can be used to assist genomics-based research on target traits. Varshney et al. (2005) described a number of bioinformatic tools and internet accessible databases, along with their respective applications, and Li et al. (2008b) also documented a collection of potato specific on-line resources, all of which have applications for potato breeding. Generating genomic resources for crops can now be performed easily, quickly and cheaply, making any list of resources rapidly outdated. However, to deliver maximal results in a genomics-assisted breeding programme, efforts must be made to continuously integrate new methods and information as they become available.

Potato genetic maps and genome sequence

Knowledge of the degree of association between target genes (presence and extent of genetic linkage), and the ability to trace inheritance of genes for key traits will provide valuable information to the breeder. Consequently, the development of genetic maps is usually a required intermediary step to the identification of DNA-based markers for implementation in potato breeding, and significant efforts have been applied to this activity (Bonierbale et al. 1988; Gebhardt et al. 1989, 1991; Tanksley et al. 1992; Milbourne et al. 1998; Dong et al. 2000; Van Os et al. 2006). Genetic maps have been constructed for traits of interest such as pathogen resistance (Leister et al. 1996; Grube et al. 2000; Gebhardt and Valkonen 2001), tuber quality traits (Chen et al. 2001; Bradshaw et al. 2008), and yield and agronomic traits (Bradshaw et al. 2008). Resources have also been deployed to statistical analysis for the construction of linkage maps for autotetraploids (Luo et al. 2004, 2006), and the development of computational software and algorithms for linkage map construction (Hackett and Luo 2003; Hackett et al. 2007, 2013).

The sequence of the potato genome has recently been determined for a *S. tuberosum* group Phureja 'doubled monoploid' homozygous genotype, leading to identification of over 39,000 protein-coding genes (Potato Genome Sequencing Consortium 2011). The sequencing programme also resulted in the identification of 755 genes that encode polypeptides that contain nucleotide binding (NB) and leucine rich repeat (LRR) domains (Bakker et al. 2011; Jupe et al. 2013), which account for the majority of currently identified plant resistance (R) proteins (Tameling and Takken 2008). The NB-LRR, or R genes have been characterised in up to 63 gene clusters within the potato genome (Bakker et al. 2011; Jupe et al. 2012, 2013), and using comparative genomics of functional R gene homologues, known in other Solanaceae species, candidate R genes effective against common pathogens can be identified (Peters et al. 2012; Quirin et al. 2012; Tomato Genome Consortium 2012; Andolfo et al. 2013). The identification of specific causal R genes will permit development of diagnostic genetic markers for rapid deployment.

The completion of the genome sequence has also led to the development of a highly multiplexed SNP chip (http://solcap.msu.edu/potato_infinium.shtml) as well as the ability to re-sequence selected portions of the genome for the delivery of large numbers of molecular markers in a rapid time-frame (Hamilton et al. 2011; Felcher et al. 2012). The delivery of comprehensive marker systems will undoubtedly increase the speed with which researchers can identify and deliver marker tools to breeders. With this expanding genetic and genomic resource available to potato research, it is likely that markers for genes controlling a larger collection of traits will be generated and will need to be implemented for the improvement of the crop, which will deliver further challenges.

What is required for the adoption of genomics-assisted breeding?

The use of molecular genetic markers provides the opportunity to significantly reduce both the duration and costs of a breeding cycle. Although a substantial number of genetic markers linked to genes for important agronomic traits have been identified over the past 20 years (Barone 2004; Gebhardt et al. 2005; De Koeyer et al. 2011; Gebhardt 2013), few reports have been made of their implementation into commercial potato breeding programmes (Dalla Rizza et al. 2006; Ottoman et al. 2009; Ortega and Lopez-Vizcon 2012; Schultz et al. 2012). The scale of available genomic resources will continue to increase as a consequence of improvements in next-generation DNA sequencing technology, high-throughput genotyping and bioinformatic analysis. Delivery of the potato genome sequence will

provide major opportunities to develop individual markers for target traits, as well as the use of whole genotype data for prediction of genetic merit (Potato Genome Sequencing Consortium 2011). The crucial question remains: what are the key requirements for genomics-assisted strategies to be adopted by potato breeding programmes?

A number of factors need to be considered for the effective use of DNA-based markers in MAS and its application in potato breeding. The relevant marker assays must be consistently reproducible in different laboratories and closely linked to, or preferably completely diagnostic for, the trait allele that is the target for selection (Collard et al. 2005; Collard and Mackill 2008). This will remove the requirement for additional phenotypic assessment to confirm the presence of the trait-specific gene. Markers positioned in flanking locations on each side of the gene will also improve the reliability of selection, as the presence of both marker alleles in genotypes will indicate an absence of intervening recombination events (Collard et al. 2005; Collard and Mackill 2008). The marker allele association should also be applicable across the wider crop genepool, rather than limited to single families or within pedigree lines.

The technical procedure for a marker assay needs to be simple and straight-forward, so that results can be obtained in a reliable and timely manner. High-throughput methods are therefore desirable in order to rapidly analyse the genotypic status of a large number of samples (Collard and Mackill 2008). The most widely used classes of markers in current plant molecular breeding practice are simple sequence repeats (SSRs) and SNPs. These markers are generally highly polymorphic, co-dominant, reliable, relatively simple and cheap to use, and they can also be multiplexed (Collard and Mackill 2008).

The use of markers must be cost-effective in comparison to conventional field and glasshouse-based screening procedures. Adoption of MAS into a breeding programme requires a benefit-cost analysis in order to verify the value to breeders. The cost of MAS for a given trait may be considered prohibitive due to the expense of DNA extraction, the number of assays required and the cost of equipment (Collard et al. 2005; Gebhardt et al. 2006; Collard and Mackill 2008; Moose and Mumm 2008; De Koeyer et al. 2011), although development of high-throughput equipment and assays can mitigate these factors. At the same time, the benefit-cost analysis will depend on the corresponding direct and indirect costs of a bioassay to obtain equivalent phenotypic data, including establishment and maintenance of field or glasshouse trials. Recently, MAS has been shown to be highly cost-effective in a number of crops (Yu et al. 2000; Van Sanford et al. 2001; Dreher et al. 2003; Kuchel et al. 2005; Collard and Mackill 2008), including potato (Slater et al. 2013). As the product of a single DNA extraction may be used for a series of molecular marker assays, multiplexed assays in particular were shown to make MAS highly cost-effective as part of a multi-trait selection strategy.

Above all, the adoption of molecular plant breeding strategies requires complementary training and expertise in both molecular biology and plant breeding (Moose and Mumm 2008). Breeders and breeding companies require training in the use of marker-derived data as an alternative to conventional screening methods, which will undoubtedly require the development of new customised databases, along with computational tools to integrate phenotypic data, pedigree data and marker data sets to enable optimal breeding decisions to be made.

Qualitative or quantitative traits can both be identified using MAS, but the effectiveness will be greater for qualitative traits, as only a single gene needs to be selected. A major advantage of MAS over phenotypic selection is the ability to implement screening with reliability much earlier than for conventional methods, particularly in terms of availability of plant material. Selection can be performed at, or soon after, the seedling stage. In potato, the most efficient point of application was shown to be at the second field generation, in order to continue conventional screening for traits that currently cannot be assessed by MAS (Slater et al. 2013). Phenotypic expression of a number of quantitative traits can be affected by the environment or development stage of the individual, a problem avoided by the use of MAS. Reliable data may also be collected from single plant samples, while the phenotypic data may require evaluation of many more replicates over multiple years or environments. MAS may also be used when biosecurity restrictions would not allow the phenotypic screening to be performed due to contamination risks, as for quarantine-restricted pathogens.

Marker analysis may also be applied to plants that are grown ‘off-season’ in a nursery. Target genotypes can be selected earlier, enabling relevant trait selection to be ‘fast-tracked’. Breeders can take advantage of these benefits using markers to greatly accelerate the breeding process (Ribaut and Hoisington 1998; Morris et al. 2003).

Genetic analysis for improvement in all traits (simple to complex)

Marker-assisted selection for qualitative traits

Marker-assisted breeding in potato has not yet been applied with the same vigour that has been observed in other crops, including cereals such as rice, maize, wheat and barley (Collard and Mackill 2008). This lack of adoption is presumably due to the complexities of autotetraploid genetics,

limited availability of detailed functionally associated maps, and the limited number of markers that are linked to genes for the numerous qualitative and quantitative traits of interest. The majority of studies to identify markers linked to traits have also been conducted on diploid populations, the results of which are not always transferable to tetraploid breeding populations (Moloney et al. 2010).

As previously stated, a number of traits are regulated by major genes, approximately 40 such qualitative genes have so far been mapped (Simko et al. 2007), together with a large number of markers that cover the majority of the potato genome (Van Os et al. 2006). Important genes for qualitative traits that have been the subject of marker studies include *H1* (Gebhardt et al. 1993; Pineda et al. 1993; Bakker et al. 2004; Gebhardt et al. 2006; Biryukova et al. 2008; De Koeyer et al. 2010; Schultz et al. 2010; Finkers-Tomczak et al. 2011; Schultz et al. 2012), *GroVI* (Jacobs et al. 1996) and *Gro1* for golden cyst nematode resistance (*Globodera rostochiensis*) (Barone et al. 1990; Ballvora et al. 1995; Paal et al. 2004), Ry_{adg} (Brigneti et al. 1997; Hämäläinen et al. 1997, 1998; Sorri et al. 1999; Kasai et al. 2000; Dalla Rizza et al. 2006; Ottoman et al. 2009; Whitworth et al. 2009), Ry_{sto} (Song et al. 2005; Heldák et al. 2007; Song and Schwarzfischer 2008; Valkonen et al. 2008) and $Ry\text{-}f_{sto}$ for PVY resistance (Flis et al. 2005; Witek et al. 2006), *Rx1* (Gebhardt et al. 2006) and Rx_{adg} for PVX resistance (Bendahmane et al. 1997), *Ns* for PVS resistance (Marczewski et al. 2002; Witek et al. 2006), *RB* for late blight resistance (Colton et al. 2006), R_{MCI} for root-knot nematode resistance (*Meloidogyne chitwoodi*) (Zhang et al. 2007), *Gm* and *Rm* for PVM resistance (Marczewski et al. 2006) and *Sen1* for potato wart resistance (Gebhardt et al. 2006).

Marker-assisted selection of QTLs of large magnitude in potato

One of the major disadvantages of molecular breeding for simple, monogenic (or vertical) disease resistance traits is the possibility that newly emerged pathogen races will prove to be virulent against individuals that contain these genes, and hence overcome the resistance. More complex (horizontal) resistance is governed by multiple genes, and is potentially more durable than monogenic resistance. This distinction is illustrated by the series of monogenic late blight resistance genes *R1-R11*, derived from *S. demissum*, of which several were rapidly overcome by the late blight pathogen following introgression into commercial potato cultivars (Umaerus and Umaerus 1994). Consequently, efforts have concentrated on the identification of multiple late blight resistance genes from various wild *Solanum* species for introgression into *S. tuberosum* backgrounds (Jacobs et al. 2010). The quantitative late blight resistance that was introgressed into the cultivar Stirling, among others, proved durable for over 20 years before being overcome in 2008 by the emergence of *P. infestans* 'genotype 13' (Bradshaw et al. 2009).

A significant number of studies have aimed to locate genes or QTLs for traits of interest. Van Eck (2007) provided a review of studies on morphological and tuber traits, while Simko et al. (2007) provided a review of studies on pest and disease resistance.

A large number of quantitative disease resistance genes have so far been mapped (Simko et al. 2007). These include QTLs for white cyst nematode resistance (*Globodera pallida*) (Sattarzadeh et al. 2006; Moloney et al. 2010); *Verticillium* wilt disease resistance (Simko et al. 2004); and *Potato leaf roll virus* (Marczewski et al. 2001, 2004). Marker-based studies have also been undertaken for tuber quality traits (Bradshaw et al. 2008; Kawchuk et al. 2008; Li et al. 2008a; Baldwin et al. 2011), skin colour (De Jong et al. 2003), tuber morphology (Li et al. 2005; Bradshaw et al. 2008), anthocyanin-pigmented potato tuber flesh (Zhang et al. 2009), agronomic traits (Bradshaw et al. 2008) and drought tolerance (Anithakumari et al. 2011). Other traits under complex polygenic control include dormancy, dry matter, starch content, fry colour, *Erwinia* resistance, tuberisation and yield (Bradshaw 2007b). In these instances, QTLs of sufficiently large effect may not be readily located.

Association mapping is a general approach to the detection of correlations between genotypic and phenotypic variation in a population based on the property of linkage disequilibrium. As compared to linkage mapping, which requires the use of highly related individuals such as full-sibs, association mapping can exploit the properties of more complex populations with various degrees of relatedness and are hence closer in nature to germplasm pools relevant to breeding practice. This approach can provide much higher levels of resolution for the genetic dissection of quantitative traits, and broadens the opportunity to sample relevant QTL alleles (Varshney et al. 2005). This method has been used to identify QTLs for late blight resistance (Gebhardt et al. 2004), maturity (Gebhardt et al. 2004; D'Hoop et al. 2008; Kloosterman et al. 2013; D'hoop et al. 2014) and quality traits (D'Hoop et al. 2008; D'hoop et al. 2014) using populations of commercial tetraploid potato cultivars. While Simko et al. (2004) used a candidate gene approach combined with association mapping to identify a QTL for Verticillium wilt resistance.

Quantitative genetic analysis of highly complex traits

There are a large number of potato traits that are regulated by multiple genes, or are quantitative in nature. Most important physiological and agronomic traits are under the

control of several to a very large number of genes, each of which may have relatively low individual effect. The desire to obtain genetic gain in such highly complex and low heritability traits has led some breeders to use progeny tests to identify superior parental combinations. Progeny tests will help to determine the breeding value of the parent for these traits, without needing to identify the location or number of genes that regulate the expression of the trait.

Phenotypic selection of individuals for highly complex traits has been shown to be less effective than the use of progeny tests for family selection. This was illustrated for the practice of selection using visual preference from the first field generation, in which the growing environment and seed tuber size was shown to have a larger effect than the individual genotype (Maris 1986). Progeny testing has been extended to a range of traits in potato breeding. For example, progeny tests for multiple traits (visual preference, quantitative late blight tuber and foliage resistances, white potato cyst nematode resistance and fry colour for processing families) have been routinely used by a Scottish breeding programme (Bradshaw et al. 2003; Bradshaw 2007b). This programme has recently been assessed after four cycles of breeding using progeny tests, and superior clones and parental types were identified with improved yield and disease resistance, although the yield increase was small (Bradshaw et al. 2009).

Analysis of progeny means will identify the broad sense heritability of the total parental genetic contribution to the family, while calculation of the narrow sense heritability will identify the additive genetic effect and would provide a real benefit to a breeding programme that aims to exploit continuous genetic gain.

Animal breeding programmes have adopted the estimation of breeding values using best linear unbiased prediction (BLUP) (Henderson 1984), to exploit the additive genetic variance. These programmes have benefited from the estimation of the genetic merit of selection candidates based on phenotypic values of all relatives using pedigree information in the analysis. Through the use of the phenotypic values from all relatives, including full-sibs, half-sibs and any other partial siblings, the amount of derived information is maximised and the most accurate genotypic value will be obtained, with a greater increase in accuracy for low heritability traits.

Recently, the use of BLUP estimated breeding values (EBVs) in potato breeding clearly demonstrated the advantage of using EBVs over progeny means in cross-generation prediction of performance, particularly for traits with low heritability (Slater et al. 2014). As the BLUP analysis uses information from all relatives in the analysis, more data is used to calculate the EBV. As pedigree is used as a covariate, EBVs represent the additive genetic effect transmitted from parents to progeny (Falconer and Mackay 1996). The BLUP analysis also provided EBVs for the families, all cultivars in the pedigree and for the individual genotypes themselves. BLUP can be applied to any desirable quantitative character, including those of low heritability.

The BLUP analysis and calculation of EBVs for a number of important traits also permitted a combined ranking of evaluated genotypes or the development of selection indices across multiple traits (Xu et al. 2012). This process should enable identification of genotypes based on properties of the population in addition to individual phenotypes, and provide a more accurate selection process for these traits, and potentially enabling breeding from the best progeny much earlier (Slater et al. 2014).

Combining conventional, genomics-assisted and EBV-based approaches for reduction of the breeding cycle

Conventional potato breeding is relatively slow, laborious and a difficult process in which to obtain genetic gain. Potatoes also exhibit severe inbreeding depression, requiring a breeding model that employs outbreeding, in contrast to crops that employ backcrossing to produce homozygous ‘pure’ lines. Outcrossing combined with autotetraploidy makes potato highly heterozygous and genetic improvement a complex task. In addition, the time required for all the conventional screening trials to be conducted, means that the identification of methods to speed up, and improve the selection of superior combinations of desirable traits will greatly benefit the process.

Current cultivars continue to be susceptible to a range of pest and disease problems, and so are capable of significant improvement for a range of complex characters. Modern breeding methods and technologies have been promoted as offering great benefit for the enhancement of breeding programmes, but still require validation and demonstration of their cost-effectiveness in order to be adopted by a practical breeding programme. In particular, MAS has the ability to select for traits several years earlier in a programme than would be practical using conventional screening methods. MAS will be more effective for qualitative traits, but will also be valuable for quantitative characters, especially if QTLs of large effect contribute to the measured character, or if a group of markers can be identified that are linked to a group of alleles of smaller effects influencing the trait. On the other hand, selection for quantitative traits can be conducted using biometric analysis for genetic gain, without the need to identify precisely which individual genes exert particular effects.

The applications and opportunities for plant biotechnology based on genetic modification were recently reviewed by Barrell et al. (2013). These approaches may

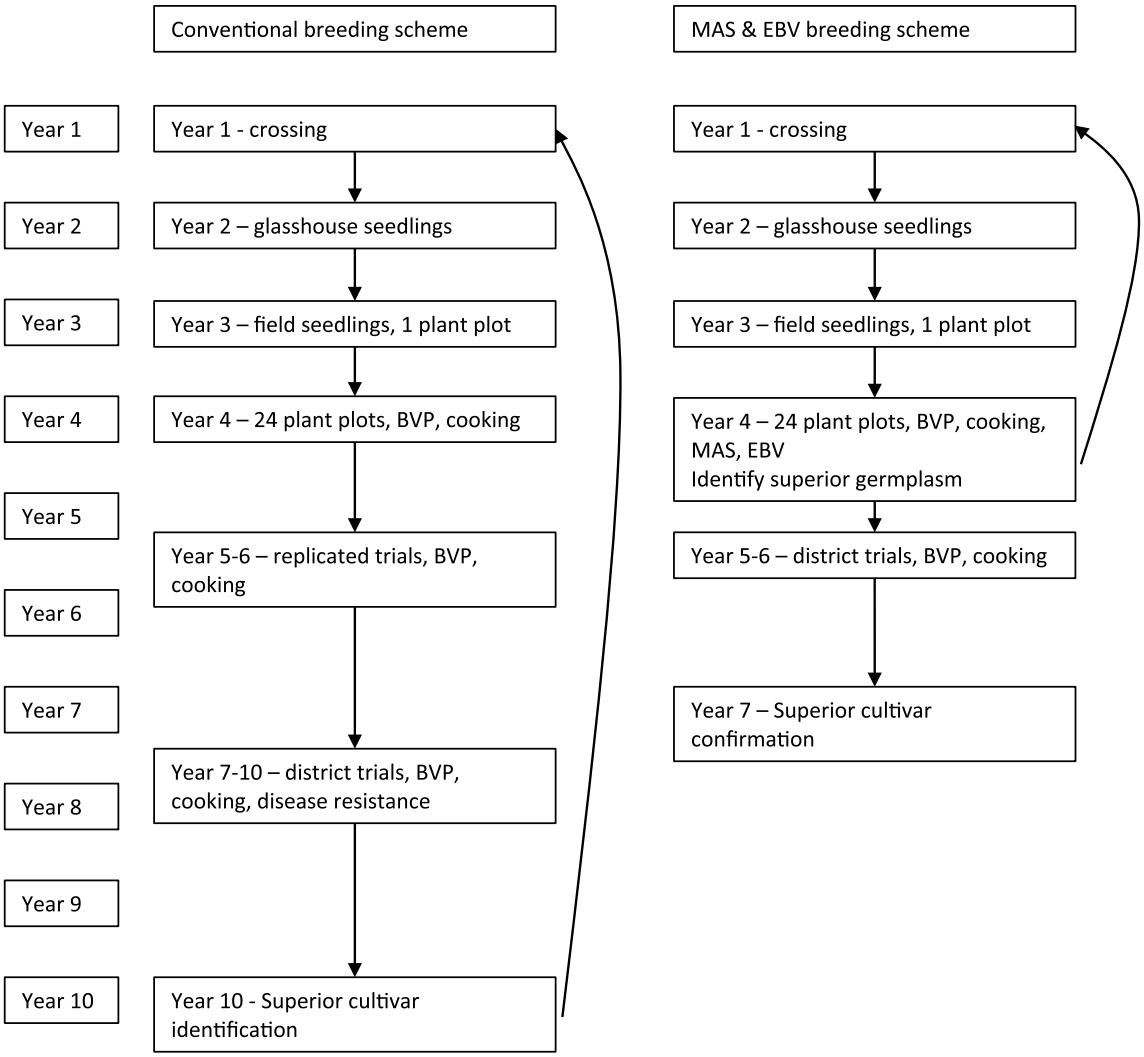

Fig. 1 Comparison of the breeding cycles in potato using conventional phenotypic selection of individuals, and MAS and EBVs to identify superior individuals after 3 years. *BVP* Breeder's visual preference

provide further opportunity for the stacking of major genes, although the use of these approaches within a breeding programme will still require the quantitative genetic analysis of the highly heterozygous breeding populations for improvement in those traits that are controlled by a large number of the 39,000 genes identified by the potato genome sequencing effort (Potato Genome Sequencing Consortium 2011). In addition, manipulation of the recipient genetic background based on molecular marker technology, particularly by genomic selection, could prove highly beneficial for optimisation of the transgene expression (Oud et al. 1995; Schmidt et al. 2004).

Genomic approaches will facilitate the rapid introduction of desirable genes into adapted backgrounds and the stacking of major genes to combine desirable traits. MAS can reduce the duration of the breeding cycle between crossing programmes in order to combine these genes with other desirable traits. A combination of MAS with EBVs for complex traits will result in a significant reduction in the breeding cycle for all measured traits. Consequently, the use of both of these breeding tools will ensure rapid progress in combining traits and improving genetic gain in potato breeding programmes. As these tools can be applied to any trait, no matter how complex, there is now an opportunity to see improvements in many traits, even those that have traditionally proven difficult to manipulate, such as yield (Jansky 2009). Therefore, adoption of MAS and EBVs will provide substantial benefits within a multi-trait breeding strategy, and allow the design of superior combinations and their analysis for maximum genetic gain.

Previous studies have shown that MAS can be cost-effectively applied at the second field generation (Slater et al. 2013), and EBVs can be calculated for more complex traits at the same stage (Slater et al. 2014). The

development of a selection index for all relevant traits will then enable gain for a combination of these traits. These advances will greatly accelerate the breeding cycle, as the combined use of MAS and EBVs can reduce the breeding cycle from over 10 to as few as 4 years (Fig. 1), and therefore, accelerate genetic gain relative to conventional breeding methods. At the same time, they will ensure that improvement is made in all measured traits, from those under simple genetic control to those under far more complex control.

MAS can be performed for a number of loci once they are validated against the phenotype of the desired trait. Studies of the potato genome sequence will allow the identification of gene sequences of known function, which should further help to identify candidate genes for related phenotypic traits. However, the identification of a large number of predicted genes within the sequence means that the majority are likely to have minor effects, whose function may not be easily detected and require quantitative genetic analysis, such as the calculation of EBVs.

As a number of agronomic traits are likely to be under highly complex genetic control, the analysis of these traits is likely to see the development of cultivars that are more productive for these traits under specific environmental and agronomic conditions. Use of MAS and EBVs, in conjunction with the diverse nature of the entire potato gene pool, will enable germplasm to be developed for specific targets or production areas. The reduction in the breeding cycle will allow rapid trait improvement and combination in superior germplasm, with progressive improvement of future cultivars.

The future development and implementation of even more powerful breeding technology in potato, such as genomic selection (Meuwissen et al. 2001; Heffner et al. 2009; Jannink et al. 2010; Hayes et al. 2013), is anticipated to reduce the breeding cycle still further. This reduction in the breeding cycle will allow rapid trait improvement and combination in superior germplasm, with progressive improvement of future cultivars. Use of genomic selection, in conjunction with the diverse nature of the entire potato gene pool, will enable germplasm to be rapidly developed for emerging issues, such as the threat of global climate change and associated changes in abiotic and biotic stresses.

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Ethical standard All experiments comply with the current laws of Australia and Scotland.

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