



Next Generation Breeding in Potato

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ABSTRACT

Potato is the world's number one non-grain commodity and ranks at fourth position after maize, rice and wheat. As a species, potato is very docile to cell culture, it also contains an extended history of applications in the field of biotechnology for the improvement of crops. The genomic insurgency from the recent past has significantly enhanced the overall knowhow of the genetic structure of all the crops. Crop genome sequences has totally reformed our view and understanding for genome association and genome development. Increased knowledge in markers along with the advanced phenotyping, genotyping by sequencing, genomewide association studies added a new way for determining marker-trait associations that can withstand genome based breeding programs. Accessibility of sequencing of genomic data has permitted editing of genome (localized mutagenesis), for obtaining sequences of gene that is anticipated by the breeders. To develop some genetic maps, markers application and genomics in the field of potato breeding these genetic characteristics have also assigned the tasks to the breeders. Many strategies are formulated to describe the potato loci, (contender) genes and alleles, and association of genotype with the phenotype are also stated. This review demonstrates how next generation phenotyping, genome-wide association studies and genome editing tools can be used to modify tools to genomics for the need of potato breeders to transform potato improvement.

Keywords: Next generation phenotyping, Genomewide association studies, genome editing, potato.

Introduction

Potato (*Solanum tuberosum* L.) is a vital crop and occupies 4th place in production among other food commodities behind maize (*Zea mays* L.), rice (*Oryza sativa* L.), and wheat (*Triticum aestivum* L.) worldwide (FAO, 2014). Potato is tetraploid and highly heterozygous crop which has the major importance for food, feed and the industrial use. It was cultivated on an area of 130.000 ha having the production of 4.175 million tons in Turkey (TÜİK 2015). Central Anatolia including Niğde portions almost 60% potato production in this regard. Potato has a wide range of production in the country, and has an important role in Turkish agricultural sector.

The cultivated European potato *Solanum tuberosum* ssp. *tuberosum* is autotetraploid ($2n=4x=48$), which means that they have four alleles

per locus. Homologous chromosomes pair at random during meiosis (Milbourne *et al.* 2007). Moreover, there are tuber-bearing varieties under cultivation that are non-tuberosum types ranging from diploid to hexaploidy Van den Berg and Jacobs (2007). Potatoes are outbreeding plants. Therefore, they obtain a high level of heterozygosity and are prone to inbreeding depression, making it difficult to obtain homozygous lines. The heterozygosity in commercial cultivars is preserved by the clonal propagation of tubers (Milbourne *et al.* 2007; The Potato Genome Sequencing Consortium 2011).

From start, potato has been nominated and reared in production areas for advanced echelons of locally adapted to several environmental conditions. This effect was gained in relatively short time because of the potato's highly diversified genetics, allowing the

selection and identification of the genotypes that are high performing in different type of environments. This type of genetic heterogeneity is a result of both out-breeding habit and the chromosomal changes that takes places in the chromosomes of the species (Slater *et al.* 2014a). Notwithstanding to all, hereditary advancement in multifaceted characters, like crop produce, is very sluggish to nearly absent (Jansky 2009), particularly at the time at which we associate it with different crops like as maize, wheat, and rice (Fischer and Edmeades 2010).

Presently, there are 7.25 billion people that exists on earth, and it is estimated that the population of world can get up to 70 million per annum for the next 40 years. It is expected that the population of the world will approximately be 9.2 billion by year 2050, Attentiveness of carbon dioxide (Co₂) and the ozone will reach upto 550 ppm and 60 ppm, correspondingly and the climate is going to be warm by 2°C as at present (Jaggard *et al.* 2010). It is anticipated by that time that about 90% of this world's population will be living in continents like Asia, Africa, and Latin America (FAO 2012, Silva 2014). To cope with this dramatically increasing population and hunger, plant breeders have been working very hard to increase the food production. Recently, plant breeding has switched from an entirely phenotypic-dependent procedure to have an improved dependence on genotype-based selection up to some level of extent (Varshney *et al.* 2014).

Considerable research is being carried out for the improvement of genomic possessions to increase the potato breeding as compared to the other crops, that concluded in an estimated potato genome (Potato Genome Sequencing Consortium 2011). All the work on genomic level has enabled the discovery of over 39,000 genes, together with many genes that regulates a biotic rinsing confrontation in potato (Bakker *et al.* 2011; Jupe *et al.* 2012; Jupe *et al.* 2013) and the quantitative trait loci (QTLs) for improving the traits for the quality of the plants (D'hoop *et al.* 2014; Uitdewilligen *et al.* 2013). Though, QTLs of huge result are improbable, however these characters show practical heights of heritability for some traits like yield (Slater *et al.* 2014b). The traits like yield and some others that are related to that are used to arise genome estimated breeding estimates for the traits that are being affected by genome selection (Meuwissen *et al.* 2001), applicable for the crop like potato, provided with huge number of SNPs that have been discovered with the help of sequencing of genomes (Uitdewilligen *et al.* 2013). Genome selection is being applied effectively for

several plants and animal expansion plans (Crossa *et al.* 2010; Daetwyler *et al.* 2010a; Grattapaglia *et al.* 2011; Lin *et al.* 2014; Resende *et al.* 2012; Riedelsheimer *et al.* 2012; VanRaden *et al.* 2009; Wiggans *et al.* 2011; Wolc *et al.* 2011, 2015). DNA sequencing have become increased visibility and extremely low pricing with the progress in recent developments for next generation sequencing (NGS) techniques. To sightsee the associations within genetic and phenotype range many possibilities are being opened with a tenacity that had never achieved earlier just because of these developments in the field of science. This review is about the discussion for the possible enforcement of next generation breeding techniques in potato, including the genotyping by sequencing (GBS), genomic selection (GS), genome wide association studies (GWAS), genome editing, next generation phenotyping, and their overview, advantages disadvantages and some future prospective of all the next generation approaches.

Genotyping by sequencing

Current progresses in the field of next generation sequences (NGS) helped reduced cost for the sequencing of DNA to the great extent. Therefore, sequencing by genotyping is used to produce a reliable high-throughput data for highly diversified and large number of genome species and samples (Elshire *et al.* 2011). GBS creates many SNPs for genetic examinations and genotyping (Beissinger *et al.* 2013). Main mechanism includes reduced price, limited handling of the samples, less PCR and decontamination procedures, no size fractionation, no reference limits, acceptance to scale-up as well as reliable barcoding (Davey *et al.* 2011).

GBS was basically designed for increased occurrence determination in association studies in crops like maize and, similarly restriction site associated DNA (RAD), has been stretched to the degree of species having an intricate genome. GBS has commonly been implemented in multiple crops to evaluate the breeding and mapping population ranging from 10-100s of 1000s of SNP markers being technically very simple, highly precise, GBS is suitable for the studies like population studies, germplasm characterization, plant genetics and breeding in highly diversified crops, (Poland *et al.* 2012 a).

Application of Genotyping by Sequencing

Genotyping by sequencing has become a supreme podium for the studies which range from single gene to the whole genome (Poland and Rife 2012). In the

field of plant breeding GBS has the most valuable applications. It offers a quick and cost-effective means for the genotyping among the breeding populations, letting plant breeders to contrivance genome wide association studies, genome diversity studies, analysis of genetic linkage, discovery of molecular markers and genomic selection (GS).

As genomewide association studies require hundreds of thousands to loads of markers to produce adequate data besides exposure, hence with the emergence of such NGS technologies, there is an obvious improvement in the marker resolutions as compared to the earlier resolutions and technologies (Edwards and Batley 2010). To evaluate and map the numerous interested characters in breeding running programs, recently genotyping by sequencing through the next generation sequencing approach was used to re-sequence assemblies of recombinant inbred lines (RILs) (Deschamps *et al.* 2012). Maize, wheat, barley, rice, potato and cassava and many other crops have been improved by genotyping by sequencing for the effective, reduced price and vast gauges of sequencing of genome (Poland and Rife 2012; van Poecke *et al.* 2013). The main purpose for the implementation of GBS is the expansion of molecular markers for the whole genome with increased absorption with reduced charge (Heffner *et al.* 2009, 2010; Jannink *et al.* 2010).

An inclusive 2,815 maize genotyping concurrences exposed 681,257 SNP markers that are banquet all over the whole genomic region, from that few SNPs are connected with recognized contender genes that are responsible for kernel color, sweetness, and flowering time (Romay *et al.* 2013). A set of 205,614 SNPs have been recognized so far subsequently re-sequencing 31 soybean genotypes (Lam *et al.*, 2010). Across 83 tetraploid potato cultivars, 12.4 gigabases of increased value sequence information were produced and plotted with the potato genome of reference that is 2.1 Mb. In addition, a mean different concentration of 1 SNP/24 bp in exon regions and 1 SNP/15 bp in intron regions was observed across 83 potato cultivars (Uitdewilligen *et al.* 2013).

Related to conventional Marker assisted selection, Genomic selection is an innovative method which cartels both phenotype and pedigree data with molecular markers to upsurge precision on genotypic morals in different breeding programs (Heffner *et al.* 2009). Conjectural as well as functional studies on GS disclosed great aspect to increased development of new cultivar. GS over the GBS method attitudes to be a vital element to the conventional crop development

and we can move genomic- assisted breeding to the commercial crops that have a large and complicated genome which is a vital property of this techniques (Poland and Rife, 2012).

Genotyping by Sequencing has become a convincing tool for the studies that are being held on genetic diversity in the crops (Fu and Peterson, 2011; Lu *et al.*, 2013; Fu *et al.*, 2014). For instance, Fu and Peterson (2011) operated with Roche 454 GS FLX Titanium expertise with lessened genomic illustration and increased bioinformatic tactics for examination of the collection of 16 various barley landraces, revealed 2,578 contigs, and 3,980 SNPs, and established a main topographical separation in the gene pool of sown barley. SNP detection etiquette to improve the analysis of diversity for 540 different plants of switchgrass tested from different 66 inhabitants and exposed edifying designs of genetic association with the deference to their ploidy level, geographic spread and ecotype was established a network-based by Lu *et al.* (2013). Gene diversity of 24 various accessions of mustard yellow, in which around 1.2 million reads with sequence (total about 392 million nucleotides) were produced, 512 contigs, and 828 SNPs were recognized by using genotyping by Sequencing etiquette (Fu *et al.*, 2014). 26.1% of total distinction exist in cultivar, breeding lines and landrace, and 24.7% among black-seeded and yellow-seeded germplasm was revealed by variety examination of these yellow mustard SNPs.

Genotyping by Sequencing is an outstanding stage for the implementation of plant breeding even if there are no reference genome sequences or without the earlier polymorphic DNA invention through integration of genotyping the huge populations and some molecular markers. Examination with the help of genetics and molecular marker expansion of rapeseed, lupin, lettuce, switchgrass, soybean, and maize has been shown to be suited to genotyping by sequencing approach (Bus *et al.*, 2012; Truong *et al.*, 2012; Yang *et al.*, 2012; Lu *et al.*, 2013; Sonah *et al.*, 2013).

Potato Breeding and Genomic Selection

Breeding of potato is a difficult task, as ~40 of the characters are inspected during the development of a fresh variety (Gebhardt 2013). These characters can be divided into different classes like indulgence to biotic stresses, abiotic stresses, yield-related traits and tuber quality features (Slater *et al.* 2014a). Information about genetics of each character and extent of ecological effect of the target traits is significant and will affect the preference of method

to be selected for selecting the advanced genotypes and the phenotypes. Some of the characters are dealt by only one gene nevertheless some are being controlled by numerous complex characters (Slater *et al.* 2014a). Potato breeding is much difficult and stimulating as compared to the other plants, not only because there are more market-specific traits that are also thought while dealing with breeding of potato but also because potato is extremely autotetraploid and heterozygous in nature. Target traits can be pretentious mainly with the environment in which they are grown, that can vary like meaningfully including yield, tuber number, tuber size, specific gravity, and processing quality (Jansky 2009). As a result, a conventional breeding plan involves selection of genotypes across several clonal peers in addition to many suitable sites for a variety of required characters, which can take the time over 10 years (Jansky 2009).

Recently, considerable developments have been done to understand the heredities of potato to expand breeding for brisker inherited gain. A conservative breeding scheme involves creation of a huge inhabitants, before employing phenotypic repeated selections over several peers, by the use of development for selection burdens for minimizing inhabitant extent although simultaneously swelling quantity under assessment for each genotype (Bradshaw and Mackay 1994; Jansky 2009).

Several improvements have been made in potato conventional breeding to enhance the yield and efficiency utilizing the minimum resources. The use of molecular markers offers the chance for the progress of breeding meaningfully with the reduction of both extent and prices in breeding cycle. Marker-assisted selection (MAS) can select the characters many years former in any breeding program than by using it practically in conventional breeding program. Marker assisted selection (MAS) can become useful technique for the characters like qualitative ones that are being administered by foremost genes but it may also be significant as well as for the characteristics like quantitative ones, if the QTLs with an increased significance donated to the known characteristic. There are very less reports for their profitable potato breeding programs used, though, a considerable quantity of markers that are related to the genetic factor for significant characters are recognized (Dalla Rizza *et al.* 2006; Ortega and Lopez-Vizcon 2012; Ottoman *et al.* 2009; Schultz *et al.* 2012). The breeders that are working with potato to accept marker assisted selection, compared to conventional screening the use of the markers must be low in cost,

as it is exposed to become the case for the control for the screening of pest and disease confrontation. (Slater *et al.* 2013).

Marker assisted selection can also be applied economically to the second generation (Slater *et al.* 2013) then at the same time the results can be premeditated for many compound (Slater *et al.* 2014b), the combination of both approaches could help to reduce the cycle for breeding purposes from more than 10 years until 4 years (Slater *et al.* 2014a). Such milestones can really speed up the breeding period and therefore upsurges genetic increase over conventional breeding methods in a very less time. MAS is also used mutually with the help of biased selection index, this is going to give guarantee for the expansion that is made within calculated characters. Additional decreases in the life span could only be probable with the help of selection through genomic strategy.

Genomic selection is different than marker assisted selection as it equally scrutinizes whole molecular marker data and can therefore restrain whole genetic alteration, while MAS only incarcerates a limited number QTLs variance. Moreover, GS do not practice specific complications that are related to GWAS as well as quantitative trait locus studies, like the embellish of marker results (Beavis 1998). As the achievements in the potato genome arrangements and the detection of many SNPs that are present in the whole genome (Uitdewilligen *et al.* 2013), appliance of GS for potato can be vigorously estimated in coming years, even with the heterozygous nature of potato genome (Slater *et al.* 2014a) will comprise few conscientious policies.

Genomic selection necessitates a significant quantity of markers that are vast all over the whole genome of potato. There are some studies that have discussed the same thing, with the following studies growing the sum of markers recognized throughout the genome in advancement for the genome-wide marker maps (Bonierbale *et al.* 1988; Dong *et al.* 2000; Gebhardt *et al.* 1991, 1989; Milbourne *et al.* 1998; Tanksley *et al.* 1992). The procedure dominated for the growth of a thick inherited linkage map populated with 10 thousand of amplified fragment length polymorphic markers (Van Os *et al.* 2006), which was used for the development of a map that assisted in the gathering the sequence potato genome.

GS in plants has received much attention and evaluations were performed recently in species such as maize (Guo *et al.* 2012; Zhao *et al.* 2012), wheat (Ladoet *et al.* 2013), sugar beet (Würschum *et al.* 2013) and trees (Resende *et al.* 2012abc). Heffner *et al.*

2011b performed some trials on genomic selection both in biparental populaces and transversely among several relatives in the program of breeding (Heffner *et al.* 2011a). Rutkoski *et al.* have performed some trials on GS for the development of stem rust confrontation in plants and provided a review (Rutkoski *et al.* 2010), approaches to trust the absent statistics deprived of arranged indications and work showing genomic selection for the resistance against fusarium head blight (Rutkoski *et al.* 2013). GS also provided some help for gene theory that the many variants that are affecting maize flowering time are clustered in a few common loci has been provided by the current widespread mapping exertions for time to flowering in maize (Buckler *et al.* 2009) (Table 1.)

The genome sequence achievement has permitted the knowing of several SNPs with somewhat sequenced genotypes which are associated to that (Uitdewilligen *et al.* 2013). We can use the specific SNPs as a compactly linked molecular markers set. The frequency of these SNP in potato has been predicted and its around 1 in 24 bp in the exons (Uitdewilligen *et al.* 2013), which illustrates degree for the arrangement range in potato. Arrangement of the potato sequenced genome provided a chance in the formation of an 8303-featured chip with SNPs (Felcher *et al.* 2012; Hamilton *et al.* 2011). Implementing genomic selection in plants is inadequate, possibly due to the restricted number assayed markers, as SNPs not segregating under examination population, or over problems of polyploid calling of SNP that's why SNPs chip in various other classes have measured a considerably huge percentage of impracticable statistics only because of missing data (Jan *et al.* 2016)

Hitches for SNPs bunch calling are the polyploids, primarily of the genotypic classes that are heterozygous, have been somewhat talked over the growth of custom packages of softwares (Voorrips *et al.* 2011) that software now allows the infinium calling (Illumina, San Diego, CA) for genotypic classes of five different classes data (Pembleton *et al.* 2013). GS also offers a suggestion for re-sequencing for the transfer for a huge amount of molecular genetic markers within no time.

Even though the SNP chips permits credentials of genes through GWAS with a large effect through, they may not detect the perfectly by the spectrum of frequency of alleles (i.e., ascertainment bias) and that's why might not be able to detect some of the related properties too. Genotyping-by-sequencing (GBS) methods can soon outdate single nucleotide polymorphism (SNP) chip systems potentially, that could deliver SNP profiles genome-wide by

relatively low price (Elshire *et al.* 2011; Xu *et al.* 2012). To attain this all, main problems confronted with methods of GBS presently are the quantity of properties examined, the size of absent information that must be remunerated, and amount of dominant types of marker that are involved in the information.

Main benefit of a huge quantity of SNPs, that these offer an experience to the entire genome, ensuring that available LD have all the QTLs present within at least one marker and thus having the mainstream of genetic change. The crops with slow LD decay, but many for the crops with rapid LD decay would involve thousands of markers. (Xu *et al.* 2012). Calus *et al.* (2008) anticipated that 0.25 of LD amongst the markers that are adjacent was enough for thriving imitation studies for the genomic selection. For potato, LD with large number has been revealed to be at distances of less than 1 cM and with so quick decay to less than 0.2 at inter-marker distances greater than 1 cM (D'hoop *et al.* 2010).

Meuwissen *et al.* (2001) anticipated genomic selection (GS), which was thought to resolve the glitches that are connected to marker assisted selection of composite traits. In different ways, this technique also applies to the molecular markers. Dissimilar with MAS, within markers for GS are not being used for the finding of a specific trait. In genomic selection, increased density marker management is needed with at least one marker to have all QTL in LD. Effects of markers and haplotypes throughout genome is used to estimate genomic estimated breeding value (GEBV) of breeding population for a single line using all the inclusive data on all probable loci.

GS of superior positions are easily accepted in any of the breeding population. For the empowerment of the successful genomic selection, a recognized population trial population should be preferred. Population must be the result from bi-parental cross as well as it should essentially be the characteristic of candidates to be selected in the breeding program in which genomic selection is going to be implemented (Heffner *et al.* 2009). Trial populace essentially be genotyped always with the huge markers number. Captivating the considerations of the minimum sequence price, finest is the execution of GBS that will yield increased value of polymorphisms. Sequence of the two collections of genotype and phenotype data, is random and can be performed side by side. One can start "training" molecular markers when both phenotypic and genotypic data are organized (Zhong S. *et al.* 2009).

Explanation of the reference genome of potato, including 39,000 protein coding genes, has created

lots of opportunities to identify candidate genes in regions associated with a trait of interest rapidly. For instance, detection of both StSP6A gene that helps in initiation of tubers in the crops (Navarro *et al.*, 2011) and the StCDF1 gene accountable in maturity of plants (Kloosterman *et al.*, 2013) was significantly assisted by sequencing of genome (Table 1)

Apparent rewards of genomic selection over outdated marker assisted selection have been effectively confirmed in breeding of animals (Hayes and Goddard 2010). The quick development in genotyping systems with increased yielding SNPs and sequencing technologies are allowing creation and confirmation of lots of markers, providing a “careful hopefulness” in the coming days for the successful application of GS in plant breeding.

Genome Wide Association Studies

Genome-wide association studies (GWAS) are extensively being applied in many crops as well as in potatoes to study complex traits in diversity and breeding populations. The association of phenotypic trait values with segregating alleles of molecular markers in a mapping population is referred to as QTL mapping. The intend of QTL mapping is to detect genomic regions that explain phenotypic variation in a trait of interest and the subsequent identification of potential causal genes in that region. QTL are regions on the chromosomes which are physically linked to a molecular marker allele. The QTL and the marker allele are inherited together to the next generation. Principal genes of a quantitative trait, which has a wide distribution of phenotypes, can be located on all chromosomes (Gebhardt *et al.* 2005). For linkage analysis, several types of mapping populations are suitable (Collard *et al.* 2005). After establishing the mapping population, it is genotyped with segregating molecular markers and phenotyped for the quantitative characteristic of our own interest. A linkage map is produced from the molecular marker data and QTL are detected by marker trait association.

QTL mapping in potato is mainly carried out on diploid level. This is due to the heterozygous nature of the potato plants. Many QTL studies deal with resistances to biotic stresses like *Phytophthora infestans* (Li *et al.* 1998), root cyst nematodes (Kreike *et al.*, 1994) and abiotic stresses (e.g. drought tolerance: Anithakumari *et al.* 2011). Furthermore, yield- and quality-related traits were studied with QTL mapping, such as specific gravity (Freyre and Douches, 1994), starch content and yield (Schafer-Pregl *et al.* 1998), cold-sweetening (Menendez *et*

al. 2002) and enzymatic discoloration (Werij *et al.*, 2007).

Although QTL mapping in tetraploid potato is not as straight-forward as in diploid potato, there are successful examples, such as the resistance studies for late blight (Bradshaw *et al.* 1998; Li *et al.* 1998; Meyer *et al.* 1998). Bradshaw *et al.* (2008) mapped 16 QTL for yield, agronomic and tuber quality traits in a tetraploid full-sub family mapping population. More examples were reviewed by Milbourne *et al.* (2007) and Van Eck (2007).

Alternatively, to the family-based linkage mapping approach, association mapping is a method to detect marker-trait relations in a given population of individuals that are related through ancestry. The method takes advantage of historical meiotic recombination and linkage disequilibrium (Flint-Garcia *et al.* 2003). It was first established in the study of complex inherited diseases in human populations, where it is not feasible to establish segregating mapping populations from crosses (Gebhardt *et al.* 2004). For AM, a populace consisting of a diverse germplasm including cultivars, breeding clones and landraces is assembled and phenotyped for the complex traits of interest. Molecular markers are then analyzed in the population and marker-trait associations between phenotypic and genetic variation are detected. In the case of candidate gene association mapping, the molecular markers are obtained from knowledge-based candidates, whereas markers for genome-wide association mapping randomly cover all chromosomes in high density.

Association mapping are based on linkage disequilibrium (LD). Non-random association of two alleles in any population is described as LD (Flint-Garcia *et al.* 2003). This is the case for loci that are near each other sharing the same chromosome (linkage). However, LD can also occur between alleles on different chromosomes (Flint-Garcia *et al.* 2003). There are different opinions regarding the extend of LD in tetraploid potato. D’hoop *et al.* (2010) reported 5 cM for genome-wide LD. Stich *et al.* (2013) suggest a linkage decay within 275 bp. Association mapping is an application of LD (Soto-Cerda and Cloutier, 2012), where the associated marker and the quantitative trait locus are in LD or physically linked in the ideal case (Gebhardt, 2013).

The genotypes of a potato population are a collection of individuals that are related by descent (Gebhardt *et al.* 2005). As a result, there is a possible bias towards relatedness in the statistical analysis, which means that a trait of interest can, for example, be linked to a gene pool or a geographic origin (Flint-

Garcia *et al.* 2003). The information about the degree of relatedness between genotypes in the mapping population plays a critical role in association mapping in order to avoid false positives. While a marker may not be linked to a QTL, there is a significant risk of finding a considerable association only based on the genetic relatedness between individuals (Pritchard *et al.* 2000).

There are several options to assess population structure in potato based on genetic markers. The two options arising from a factor analysis approach are principal coordinate (D'hoop *et al.* 2010; Pajeroska-Mukhtar *et al.* 2009; Urbany *et al.* 2011) and principal component analyses (D'hoop *et al.*, 2010), where genotyping information from molecular marker data is processed. In another approach, the marker data are analyzed by Bayesian clustering, implemented in the software Structure (Pritchard *et al.* 2000) and is being applied in the field of potato research in several studies (D'hoop *et al.* 2010; Li *et al.* 2008; Pajeroska-Mukhtar *et al.* 2009; Simko, 2004; Simko *et al.* 2006). Further options for population structure assessment are Analysis of Molecular Variance (AMOVA) and hierarchical clustering (D'hoop *et al.* 2010).

AM is useful for the detection of genetic difference that narrate variations in the complex traits in plants, as for example in corn (Wilson *et al.* 2004), wheat (Breseghello and Sorrells 2006), barley (Cockram *et al.* 2008) rice (Huang *et al.* 2012), perennial ryegrass (Skot *et al.* 2005), Arabidopsis (Aranzana *et al.* 2005), rapeseed and sugar beet (Stich and Melchinger 2009). There are many studies that have been conducted by using association mapping and considerable results have also been found. The genetic architectures of time to flower, leaf orientation, size of leaf, and resistance to disease traits in maize were separated by implementing linkage mapping and genomewide association mapping jointly in the nested association mapping panel, and numerous associated candidate genes were recognized (Buckler *et al.* 2009; Kump *et al.* 2011; Poland *et al.* 2011; Tian *et al.* 2011). GWAS now a day is being performed with many plant species including rice, foxtail millet, maize and sorghum (Huang *et al.* 2010, 2012; Kump *et al.* 2011; Jia *et al.* 2013; Li *et al.* 2013; Morris *et al.* 2012; Zhao *et al.* 2011). 1,083 sown *O. sativa* ssp. *indica* and *O. sativa* ssp. *japonica* varieties and 446 wild rice accessions (*Oryza rufipogon*) were gathered and with the help of low genome coverage was sequenced (Huang *et al.* 2012). Characterization of the alleles associated with 10 grain-related traits and flowering time was

conducted with the help of GWAS to use the inclusive information set of almost 1.3 million SNPs next to the high-concentration haplotype map of the rice genome was built using data accusation (Table 2). Gebhardt *et al.* (2004) first published the example of association mapping in tetraploid potato germplasm, who worked on an assembled collection of 600 potato cultivars for the detection of markers associated with the late blight resistance and maturity based on historic recombination events. Later on, studies on association mapping was carried out that were based on candidate genes responsible for resistance against *Verticillium dahliae* (Simko *et al.* 2004) and *Phytophthora infestans* (Malosetti *et al.* 2007; Pajeroska-Mukhtar *et al.* 2009). More examples on association based studies are yield and tuber quality related traits such as tuber starch content, tuber yield, starch yield and chip quality (Fischer *et al.* 2013; Li *et al.* 2008, 2005). Likewise, Urbany *et al.* 2011, studied tuber bruising susceptibility, tuber shape and plant maturity were studied by AM in potato (Tetraploid) (Table 2).

By GWAS, a broader way of looking at marker-trait associations (MTA) is possible. D'hoop *et al.* (2008) gave a first ever example of this achievement, although the number of markers used in the study was considerably low. Another example for genome-wide association mapping in a small genotype panel was illustrated by Uitdewilligen *et al.* (2013).

According to Flint-Garcia *et al.* (2003), there are three main benefits of AM over linkage mapping. Firstly, mapping tenacity of AM is better due to the higher number of meiotic events, whereas linkage mapping generally looks at the recombination in a single meiotic generation (Gebhardt, 2007). However, when working with potatoes, this is not such a considerable advantage, as Gebhardt *et al.* (2004) found that only relatively few meiotic generations separate individual genotypes. This is likely due to the clonal propagation of potato whereby the meiotic generation is conserved.

Secondly, a high number of alleles can be detected with association mapping. In a segregation population, the maximum number of different alleles possibly detected at one locus in the offspring of a diploid linkage mapping population are four and eight in a tetraploid linkage mapping population. In an assembled population of 200 tetraploid genotypes, the theoretical maximum number of different alleles at one locus is 800. Because of a reduced statistical power, marker-trait associations of very rare alleles are not likely to be detected. Therefore, association mapping is mainly suitable for the detection of

common variants (Flint-Garcia *et al.* 2003).

Thirdly, the markers can be applied right away in breeding programs. Detected markers are directly and broadly applicable when the mapping population consists of appropriate breeding material (Li *et al.* 2013; Stich and Melchinger 2010).

Results from AM are influenced by various reasons like population structure, relationship among parents (kinship), selection history etc., that can lead to the detection of false positives among markers and the QTLs.

Improving Potato Through Editing of Genome

Genome Editing Tools

Targeted gene alteration known as ‘genome editing’ results in the generation of new allelic variants in the genome of cultivated species (Barabaschi *et al.* 2016). Editing genome using SSNs (Sequence Specific Nucleases) offers a resourceful substitute to routined genetic engineering (i.e., extracellular DNA manipulation, transgenesis, cisgenesis, GMO). Major advancement in SSNs technology is rapidly becoming a next generation tool for robust genetic improvement and breeding of crop species. To date, three most widely used SSNs have been developed for genome editing, including ZFNs (Zinc Finger Nucleases), TALENs (Transcription Activator-Like Effector Nucleases) and CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR- associated proteins (Cas9) system. Among SSNs, CRISPR-Cas9 system is RNA-guided (gRNA or sgRNA) approach to target DNA sequence. The system depends upon the Cas-proteins endonuclease activity and high sequence specificity of crRNAs (CRISPR RNAs) to induce double-stranded breaks in DNA, adjacent to PAM (Protospacer Adjacent Motif) sequence. It received much attention and used widely, due to, its multiplexing capability, user-friendly, cost-effectiveness, and efficient way of producing target-specific constructs. (Xiong *et al.* 2015; Wang *et al.* 2015; Andersson *et al.* 2016; Butler and Douches 2016; Barabaschi *et al.* 2016; Khatodia *et al.*, 2016; Schiml and Puchta 2016). Site directed mutagenesis (SDM) and gene silencing evolved as potent concepts in plant research and breeding, to study the function of gene and to develop cultivars with improved traits (Quetier 2016). It depends on transient action of SSNs to induce double-strand breaks (DSBs) at specific genomic sites. The DSB causes targeted mutations and repaired endogenously, either through NHEJ (non-homologous end joining) or via HR (homologous recombination) (Butler *et al.*

2015; Araki and Ishii 2015). The NHEJ pathway is error-prone and efficiently yields small insertions and/or deletions (InDels) at specific locus, without use of exogenous DNA (Zhang *et al.* 2013). It is being widely accepted in plants to induce mutations and targeted gene knock-outs. A few studies have revealed that NHEJ-mediated indels can confer disease resistance in wheat (hexaploid specie) without the need to use a transgene (Li *et al.* 2012; Shan *et al.* 2013; Wang *et al.* 2014). In contrast, the homology-directed repair (HDR) way can familiarize a required DNA sequence or gene into a targeted site, subjected to the length of exogenous DNA, which is carried to the plant cells together with the nucleases (Butler and Douches 2016; Ding *et al.* 2016). HDR may results in gene stacking and allelic substitutions (Knoll *et al.* 2014).

Precise genome editing may face shortcomings in terms of off-target mutations. Multiple gene targeting ability of CRISPR/Cas9 may result in hybridization of gRNA to DNA sequence having mismatch bases, and can thus cause off-target mutations (Lee *et al.* 2016). The off-target effects can be minimized by careful selection of composition and structure of gRNA. Since, CRISPR/Cas9 system is based on nucleotide (RNA)-nucleotide (DNA) interaction, one can design the target sequence in more predictable way as compared to ZFNs and TALENs. Furthermore, the availability of accurate genome sequence information proves to be helpful in precise determination of target site (Barabaschi *et al.* 2016).

Genome Editing in Potato via Sequence Specific Nucleases (SSNS)

Recent reports on the genome editing of major crops of economic importance, including tomato (*Solanum lycopersicum*), soybean (*Glycine max*), wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*) and potato (*Solanum tuberosum*), have shown high efficiency of SSN platforms for site directed precise mutagenesis (indels) of desired gene for resolute modification (Table 4). Among the above-mentioned crops, the breeding of potato using genome editing tools is of great importance. Potato is autotetraploid, so the formation of new cultivar according to the routined breeding practices is very slow and intricate, due to tetrasomic inheritance and increased heterozygosity in nature (Muthoni *et al.* 2015). Genetic modification (GM), by stable integration of genetic material, has been used widely in research and breeding of potato, for a long time (Barrell *et al.* 2013). But there are some limitations

for commercialization of the developed GM plants in Europe or elsewhere. New breeding techniques such as gene knock-outs via site-directed mutagenesis (SDM) using SSNs, (where no recombinant DNA is introduced/maintained in plant chromosomes i.e., NHEJ resulting in small indels) has shown promising approach and not considered as GMOs (Araki and Ishii 2015). Moreover, efficient gene transformation and availability of genome sequence of potato made it an ultimate aspirant for genome editing system (The Potato Genome Sequencing Consortium, 2011). Here, we discuss the use of sequence specific nucleases i.e., mainly TALENs and CRISPR/Cas9 in potato breeding to target specific locus for SDM and gene silencing, without the introduction of exogenous DNA.

Cold storage of potatoes causes cold induced sweetening (CIS), which may leads to the accumulation of reducing sugars in tubers. When processed at high temperature, it accumulates acrylamide content in French-fries and chips, which are unacceptable to consumers due to its bitter taste and being carcinogenic (Dale and Bradshaw 2003). *VInv* (vacuolar invertase) gene plays a critical role in the production of reducing sugars in cold stored tubers (Kumar *et al.* 2004). RNAi mediated gene knock-down of *VInv*, significantly reduces CIS (Zhu *et al.* 2014), but being transgenic, subject to de-regulation before commercialization. Clasen *et al.* (2016) designed TALENs targeting *VInv* gene in tetraploid potato cultivar, Ranger Russet. Protoplast transformation was done to introduce TALEN encoding plasmids. TALEN-mediated mutagenesis of *VInv* without stable integration of plasmid DNA was investigated. The later point, is of great significance in clonally propagated plants such as potato in which homozygosity can neither be achieved through selfing, nor the genetic cross proves to be successful to eliminate integrated TALEN reagents. The results revealed that only 3% (18 out of 600 regenerated plants) contained targeted mutations. Moreover, only 5 plants out of 600 (0.83%), were detected with all four *VInv* alleles mutated. Interestingly, PCR with designed primers demonstrated, 7 events (0.33%) out of 18 mutant plants, having complete “knock-out” and were also “TALEN free”. Furthermore, *VInv* knock-out events having no integrated TALEN, were propagated in green-house trials and harvested tubers can be stored accordingly to probe the CIS effects. In addition to Ranger Russet, three other commercial varieties (Atlantic, Russet Burbank and Shepody) were also selected for targeted *VInv* gene knock-out in all alleles. Mutation frequency across

all four varieties ranged from 2% to 15.9%. So, TALENs can be sought as useful genome editing tool for SDM (Clasen *et al.* 2016) and targeted production of healthy and safe tubers without integrated SSN reagents (Sawai *et al.* 2014).

α -solanine and α -chaconine are naturally occurring steroidal glycoalkaloids (SGAs) in potato. A 20mg/100g fresh weight of tubers is the current safety limit of SGAs in edible tubers (Ginzberg *et al.* 2009). High concentration in green tubers and sprouts may cause toxicity, thus inadequate for human consumption. Studies revealed that *SSR2* enzyme plays a crucial role in cholesterol biosynthesis pathway (precursor), which induces the production of toxic SGAs in potato. *StSSR2* disrupted or *StSSR2* silenced potatoes by targeted gene knock down, achieved through TALENs curtailed the level of SGAs in tubers. Interestingly, the *StSSR2* TALEN-transformants obtained after targeted genome editing at all four loci in tetraploid potato, had no remaining intact alleles (Fig. 1). Thus, *StSSR2*-knockout potato deprived of transgene will be obtained by segregation after self-crossing the transformants (Sawai *et al.* 2014). TALEN platform can thus be employed in breeding potatoes for desired low SGAs content.

Similar SSN platform was employed for SDM in tetraploid potato (cv. Desiree) to knock out ALS (acetolactate synthase) gene through transient expression of TALENs in protoplasts. Although, targeted mutation in calli and regenerated shoots were 11-13% and 10%, respectively. However, gDNA sequencing of calli and plantlets confirmed no full knock out *ALS* mutants (Nicolia *et al.* 2015). Therefore, limited efficiency of targeted mutagenesis by TALENs and some off-target mutations, advocate the use of other potentially efficient SSNs (e.g., CRISPER/Cas9).

CRISPR/Cas9 is accounted for efficient site directed mutagenesis and gene silencing in potato (Butler *et al.* 2015; Wang *et al.* 2015; Andersson *et al.* 2016). In a study, CRISPR/Cas9 was designed with two sgRNAs to target *StALS1* gene (responsible for herbicide resistance) in *Solanum tuberosum* (Butler *et al.* 2015). Generation and inheritance of targeted mutation in calli and primary events of both diploid and tetraploid (cv. Desiree) potato genotypes were investigated, in combination with two T-DNA vectors (conventional 35S and modified geminivirus LSL). CRISPR/Cas reagents were delivered via, *Agrobacterium* to analyze transient expression in calli and generation of primary events. Modified enrichment PCR detected targeted mutations in calli of both diploid and tetraploid genotypes. Furthermore,

transformed calli were regenerated to determine the targeted mutations in primary events. On the basis of number of ALS alleles, 3-60% individual events have targeted mutations, whereas, 0-29% possesses targeted mutations above threshold level (Butler *et al.* 2015). No wonder, these percentages were higher as compared to the previous studies using TALENs for gene knock-out indicating its efficacy (Clasen *et al.* 2015; Nicolina *et al.* 2015). The results further indicate the transient expression of CRISPR/Cas reagents in primary events, without integration of geminivirus LSL T-DNA. Voytas and Gao (2014) were also of the view that transient delivery of sequence specific nucleases (SSNs) such as Cas9, using viral vectors, do not result in integration of vector into the plant genomes and effectively employed in targeted plant breeding. Similar outcomes were recorded in protoplast mediated transformation of TALENs to bring about mutations without integration. This is extremely important in polyploidy species in which crossing cannot remove SSN reagents. In order to determine the germline inheritance, one diploid and two tetraploid primary events were screened for Cas9 free progeny along with targeted mutations. Selfing was done in tetraploid mutant events, while diploid event was crossed with self compatible diploid line. Transmission of targeted mutations in three different populations ranged from 87% to 100% indicating high efficacy of targeted mutations in primary events using CRISPR/Cas9 genome editing tool. Cas9-free progeny along with desired mutagenesis suggest that these progenies could be used for further study or commercial development (Butler *et al.* 2015).

Likewise, CRISPR/Cas9 plasmid construct was transformed via-Agrobacterium in double haploid potato cultivar targeting *StIAA2* gene. Kloosterman *et al.* (2006) cloned and analyzed this gene and revealed that it encodes for Aux/IAA protein in potato. Monoallelic and biallelic homozygous mutants with targeted knock-out of *StIAA2* gene was obtained in T1 generation, confirmed through PCR results. Moreover, no off-target mutations were observed, which ascertains the efficiency of CRISPR/Cas9 over other SSN platforms (Wang *et al.* 2015). These findings were in line with those obtained by Butler *et al.* (2015).

CRISPR/Cas9 transient expression in protoplasts of tetraploid potato cultivar was examined to target Granule Bound Starch Synthase (*GBSS*) gene. Since, it is responsible for amylose synthesis, therefore, silencing of *GBSS* gene functionality will yield waxy potato (amylopectin rich potatoes). Three different regions of this gene were targeted by CRISPR/Cas9

construct and regenerated shoots showed a mutation frequency of 2% to 12% in at least one allele. While, frequency of multiple mutated alleles was found to be up to 67%. Non-homologous end joining (NHEJ) after double stranded break in DNA may result in small indels of 1bp to 10bp in most mutations. A PCR based HRFA (high resolution fragment analysis) was carried out to identify the multiple mutated lines upto a resolution of 1bp. Phenotypic studies of starch also confirmed full knock-out of *GBSS* in all four-allele mutated lines (Andersson *et al.* 2016). Conclusively, CRISPR/Cas9 transient expression would be desirable for novel potato germplasm development, with targeted gene knock-outs without any stable integration of DNA.

Genome Editing: A Paradigm in Potato Breeding

Genome editing has entered a new era. The ability to prompt specific mutations through SSNs would enable direct modification/introduction of related agronomic traits into elite lines for breeding. NHEJ repair pathway i.e., indels, forced the regulatory authorities to amend current regulations about GM crops. Although, traditional breeding of potato done at tetraploid level and vegetatively propagated, yet diploid breeding is getting popular in public and private sector. Recombinant inbred lines (RILs) developed after diploid breeding substantiate to be a potent tool for genome editing in potato. Genome editing reagents can be used to modify self-compatible and inbred lines and following modifications can be fixed by selfing. So, development of diploid, self-compatible germplasm is indeed the next generation approach for gene editing in potato (Butler *et al.* 2016; Barabaschi *et al.* 2016).

Next Generation Phenotyping of Potato Need of high-throughput/next generation phenotyping

Novelty in crop improvement techniques is incumbent for plant breeders, geneticists, biotechnologists and agronomists to fulfill world food production demands and counter the prodigious biotic and abiotic stress conditions (Godfray *et al.* 2010; Mittler and Blumwald 2010; Sankaran *et al.* 2015). Over the past 20 years, a significant improvement in genetic technologies (Marker-Assisted Selection (MAS), Next Generation Sequencing (NGS), Genomic Selection (GS)) and functional genomics has boost up the knowledge of plant genomes, but the capability to exploit available

genomic tools to their full potential are now limited by the ability to phenotype (Araus and Cairns 2014). Current approaches to phenotyping are slow, laborious, expensive and often destructive and allows the use of only a few sensors at a time (Furbank and Tester 2011; Cobb *et al.* 2013; Fiorani and Schurr 2013; Virlet *et al.* 2016). Since 2010, 'phenomics' and rapid high-throughput crop phenotyping methods evolved as next generation approach which significantly contributes to plant breeding (Furbank and Tester 2011; Walter *et al.* 2012; Dhondt *et al.* 2013; Fiorani and Schurr 2013; Cobb *et al.* 2013; Araus and Cairns 2014; Prashar and Jones 2014). The selection efficiency and plant performance over the years is greatly influenced by environmental factors. The environmental variations can be assessed efficiently by high-throughput phenotyping methods than current practices, thereby increasing selection efficiency (Sankaran *et al.* 2015; Virlet *et al.* 2016). Rapid and inexpensive genomic information is the outcome of advances in high-throughput genotyping. For phenotyping of thousands and millions of recombinant inbred lines (RILs), low cost, high-throughput genotyping has paved the way for the development of diversity panels and huge mapping populations (Araus and Cairns 2014). Developments in phenotyping are probably crucial to exploit the developments in conventional, transgenic and molecular breeding to ensure for the improvement in crop genetics for future food security.

High-Throughput Techniques and Platforms (HTPPS)

Automation and robotics; novel sensors; imaging (2D, 3D and high resolution) technologies (hardware and software) provide a range of applications for high-throughput phenotyping (HTP) of crops under controlled and field conditions (Kolukisaoglu and Thurow 2010; Fiorani and Schurr 2013; Li *et al.* 2014). The HTP techniques include the application of visible light imaging for estimation of germination rates, height size morphology and shoot biomass (Berger *et al.* 2010; Golzarian *et al.* 2011), fluorescence sensing for estimating photosynthesis (Baker 2008; Munns *et al.* 2010; Tuberosa 2012), thermal imaging for detecting canopy/leaf temperature and stomatal conductance (Pask and Pietragalla 2012; Li *et al.* 2014), near infrared spectroscopy and hyper-spectral imaging for measuring leaf area index (LAI), carbon isotope discrimination and various physiological changes induced by nutrient and water stress (Van Maarschalkerweerd *et al.* 2013; Monneveux *et al.* 2013), magnetic resonance imaging and X-ray

computed tomography for assessment of root system architecture (RSA) (Li *et al.* 2014; Yol *et al.* 2015). Cobb *et al.* (2013) reported the use of various image analysis software programs viz., PlaRoM (Yazdanbakhsh and Fisahn 2009), RootReader2D and 3D (Clark *et al.* 2011 & 2012), Gia-Roots (Galkovskiy *et al.* 2012), LeafAnalyzer (Weight *et al.* 2007), LAMINA (Bylesjo *et al.* 2008), LEAFPROCESSOR (Backhaus *et al.* 2010), TraitMill (Reuzeau *et al.* 2006) and LemnaTec 3D Scanalyzer (Golzarian *et al.* 2011) for high-throughput phenotyping. Various phenotyping platforms have been developed to augment the resolution, accuracy, throughput and precision of phenotyping, including aerial solutions, controlled environment based systems, and several ground/field based-platforms, each having its own pros and cons (Deery *et al.* 2014; Li *et al.* 2014).

HTPP's in Potato

High-throughput phenotyping techniques and platforms (HTPPs) have been employed in a number of crop species such as *Arabidopsis thaliana*, wheat, maize, rice, soybean, beans, legumes, sugar beet, tomato; and potato is no exception. Phenotyping of potato under drought stress conditions have been reported by Monneveux *et al.* (2013) and Wishart *et al.* (2014). Development of high yielding improved potato cultivars, tolerant to biotic and abiotic stress environments required phenotyping of different structural, morphological, physiological, biochemical, molecular and performance related traits. Recently, Phenofab and Keytrack System (KeyGene, The Netherlands) have been developed, that uses multiple imaging systems and thermal sensors including automated plant handling under controlled environment (Laboratory/Glass-house) conditions for quantification of plant growth and functions (Jalink and Van der Schoor 2015; Furbank and Tester 2011). Indeed, HTPP's under controlled conditions allow detailed non-invasive observation and phenotyping of individual plants in potted soil. However, there exists a bottleneck to correlate the phenotyping results obtained from glass-house/greenhouse with the field conditions. Particularly, in case of Potato which have large canopy size and depict restricted growth and development in pots, it becomes imperative to develop effective automated and non-invasive remote sensing, field high-throughput phenotyping platforms. This approach provides better insights into crop behavior as breeding and genetic analysis for most crop species including potato is usually carried out under natural conditions (Prashar *et al.* 2013). Thus, to address the bottleneck of field

high-throughput phenotyping of potato, field/ground-based HTPPs (often called ‘phenomobiles’) are often considered superior over controlled environment based platforms since they function directly in the field. Moreover they can be used across multiple sites and have a potential for high temporal and spatial resolution.

Recently, Rothamsted’s Field Scanalyzer have been developed which is fixed-site phenotyping platform, fully-automated and high-throughput, carrying multiple imaging sensors for non-invasive monitoring of plant growth, physiology and morphology (Virlet *et al.* 2016). The information obtained from Field Scanalyzer may be utilized, directly by potato breeders to produce new elite germplasm by estimating temporal, spatial and resource integrated traits. Some commonly used traits and non-invasive high-throughput approaches for phenotyping of potato is shown in Table 3. For instance, Prashar *et al.* (2013) estimated traits *viz.*, stomatal conductance and canopy temperature by infrared thermography (IRT) in potato (*Solanum tuberosum* L.). Thermal images were taken from a fork-lift (8 m height; covered 9 horizontal plots and 3-4 rows) fitted with ThermaCAM P25 infrared camera (FLIR systems, USA). Thermal images were processed via., ThermaCAM Researcher Pro 2.8 SR-1 software (FLIR systems). The study showed substantial differences in canopy temperature among various potato genotypes even with sufficient water supply. A negative correlation was found between tuber yield and canopy temperature. This information may be used further to associate with SNPs (Single Nucleotide Polymorphisms) for mapping regions that control stomatal conductance and canopy temperature. We can also combine IRT data with carbon isotope signatures ($\delta^{13}C$) to identify water stress tolerant potato genotypes (efficient transpirants). The combination of mapping approach and genotypic responses to water availability will be helpful in breeding genotypes that can conserve water (stomatal closure), but momentarily took advantage of available water. Dammer *et al.* (2016) illustrated the use of camera-sensor based phenotyping positioned on tractor, to monitor green canopy coverage of potato and correlate it with LAI values. It will be helpful in detecting diseases (Late blight of potato) and providing information for disease forecasting models or decision support systems.

Furthermore, there are some key caveats associated with ground-based HTPP’s such as soil compaction, high level of supervision, non-simultaneous measurements etc. These limitations can

be addressed by using low altitude, high resolution Unmanned Aerial Vehicles (UAVs) integrated with sensors (Thermal, Fluorescence, spectral 3D cameras and LIDAR). The traits mentioned in Table 3 can be estimated by mounted imaging tools and sensors on UAVs (Rotocopters and unmanned helicopters) in potato and several other row and field crops (Sankaran *et al.* 2015). One such example in potato is the use of UAV platform Piper Seneca fitted with NIR (near infrared cameras) and satellite multispectral imaging to study vegetation indices (*SAVI*; Soil Adjusted Vegetation Index and *NDVI*; Normalized Difference Vegetation Index). Since, potato is very sensitive to water stress especially during the late vegetative, tuber initiation and yield formation phase. These vegetation indices monitor vegetation growth and can predict tuber yield (Sivarajan 2011). Despite of the fact that UAV emerged as next generation phenotyping tool, which possess characteristics such as stability, reliability, high resolution, simultaneous field high-throughput phenotyping. Concerns on developing data processing algorithms/tools to convert sensory data into useful phenotyping data for genotypic selection, image blur and geometric distortion corrections, automated feature extraction ability, geo referencing needs to be improved to utilize the full potential of UAV’s in phenomics research (Zhang and Kovacs 2012; Sankaran *et al.* 2015). Therefore, with precise, accurate and optimal selection of robust phenotypic tool and platform, we can achieve goal of next generation phenotyping in potato. It also empowers genome-wide association studies (GWAS), high-resolution linkage mapping and for training genomic selection (GS) models in plant improvement.

Perspectives

Plant breeding is a major potential player keeping in view the global climate changes, diminishing land and water resources to address the world-wide food security issue. Whereas the molecular age has laid down the basis of molecular breeding for improving crop productivity, the start of genomic technologies and associated tools has been providing astounding abilities for the plant growth, development and fundamental characters for understanding of molecular basis. The purpose of this article is to unify latest high throughput advances in various fields of biology and conceptualize a technique that could markedly enhance the efficacy of plant breeding particularly in potato. Genotyping by sequencing, genomic selection (GS), genome wide association studies (GWAS), genome editing and next generation phenotyping techniques are new

and latest applications that are being used as next generation selection protocols for crop improvement (both in terms of quality and quantity). The low cost of genotyping by sequencing with a high density of SNP markers makes it a smart approach to inundate the mapping and breeding populations. High density of SNP markers from NGS will be widely applied to MAS, GS and GWAS. It could be foreseen that large crop genomes will be sequenced by the plant breeders/geneticists and high density of genetic linkage maps will be established from breeding populations. Future applications of GWAS, GBS, NGP, genome editing in crop improvement may allow plant breeders to conduct marker assisted selection or genomic selection on a novel germplasm

and/or species without prior having any molecular tools. Since, sequence based genotyping is available for the whole range of genomic studies, it will be a vital component in plant breeding and genetics in the upcoming years.

Through the applications of GWAS, GBS, NGP, genome editing or a combination of all the technologies aimed at potato breeding explained in this review, potato can provide an amplified quantity of the food intake that is required for the predicted increase in population over the forthcoming years. Approach to these biotechnological techniques are energetic for countering food security in developing countries.

Table 1. Crop species whom whole genome has been sequenced using different sequencing technologies.

Name	Ploidy level	Genome Size (Mb)	Sequencing technologies	References
<i>Vitis vinifera ssp.sativa</i> (Grapevine)	diploid	504	Sanger paired end /Illumina GA	Velasco <i>et al.</i> (2007)
<i>Gossypium raimondii</i> (cotton)	diploid	880	Roche 454 / Illumina GA	http://www.jgi.doe.gov/sequencing/why/gossypium.html
<i>Triticum aestivum</i> (‘Chinese Spring’ wheat)	Hexaploid	16000	Roche 454	http://www.wheatgenome.org
<i>Solanum tuberosum</i> (potato)	Tetraploid	856	Sanger/454/Illumina 79.2x coverage contig N50: 31,429bp scaffold N50: 1,318,511bp	Xu <i>et al.</i> (2011)
<i>Sorghum bicolor</i> genotype BTx623	Tetraploid	730	Contig N50:195.4kbp scaffold N50: 62.4Mbp Sanger, 8.5x coverage WGS	Paterson <i>et al.</i> (2009)
<i>Fragaria vesca</i> (Woodland Strawberry)	diploid	240	Rohe 454 /Illumina GA/ABI SOLiD	Shulaev <i>et al.</i> (2011)
<i>Zea Mays</i> Maize	diploid	2,300	contig N50 40kbp scaffold N50: 76kbp Sanger, 4-6x coverage per BAC	Schnable <i>et al.</i> (2009)

Table 2. Association studies that are carried out in different plants including potato.

Crop	Mating System	LD extent	Mapped Traits	References
Potato	Selfing	0.3-1, 3cM	Resistance to wilt disease, bacterial blight, Phytophthora, and potato quality (tubershape, flesh color, under water weight, maturity, tuber starch, tuber yield etc)	Gupta <i>et al.</i> 2004, 2005, 2014; Ravel <i>et al.</i> 2006, Simko <i>et al.</i> 2004 and malosetti <i>et al.</i> 2007.
Maize	Outcrossing	200-2000bp, 3-500kb, 4-41cM	Plant height, Flowering time, endosperm color, starch production, maysin and chlorogenic acid accumulation, cell wall digestability, forage quality and oleic acid level.	Stich <i>et al.</i> 2006; Remington <i>et al.</i> 2001; Tenaillon <i>et al.</i> 2001; Thornsberry <i>et al.</i> 2001, Thornsberry <i>et al.</i> 2007; Stich <i>et al.</i> 2005; Guillet-Claude <i>et al.</i> 2004; Palaisa <i>et al.</i> 2003; wilson <i>et al.</i> 2004; Andersen <i>et al.</i> 2005; Szalma <i>et al.</i> 2005; Lubberstedt <i>et al.</i> 2005; Belo <i>et al.</i> 2008.
Rice	Selfing	5-500kb, 50-225cM	Plant height, heading date, flag leaf length and width, tiller number, stem diameter, panicle length, grain length width, grain thickness, 1000-grain weight, width and length of milled rice grain.	Zhang <i>et al.</i> 2005; Agrama <i>et al.</i> 2007, Iwata <i>et al.</i> 2007; Mather <i>et al.</i> 2007; Rakshit <i>et al.</i> 2007; Agrama <i>et al.</i> 2008; Garris <i>et al.</i> 2003.
Soyabean	Selfing	10-50cM	Seed protein content	Zhu <i>et al.</i> 2003.
Hexaploid Wheat	Selfing	<1-10cM	Kernel size and milling, high molecular weight glutenin and blotch resistance	Tommasini <i>et al.</i> , 2007; Breseghello <i>et al.</i> 2006; Ravel <i>et al.</i> 2006; Chao <i>et al.</i> 2007.
Barley	Selfing	10-5-cM, 98-500kb, 300bp	Yield, yield stability, heading date, flowering time, plant height, rachilla length, resistance to mildew and leaf rust.	Chapman <i>et al.</i> , 2003; Kraakman <i>et al.</i> 2004; Kraakman <i>et al.</i> 2006; Caldwell <i>et al.</i> 2006; Malysheva-Otto <i>et al.</i> 2006; Morrell <i>et al.</i> 2005; Igartua <i>et al.</i> 1999; Ivandic <i>et al.</i> 2003.

Table 3: Some commonly used traits and non-invasive high-throughput approaches for phenotyping of potato (*Solanum tuberosum* L.)

Sr. No.	Traits	Devices/Sensors/Imaging techniques/Softwares	Advantages	Limitations	References
1.	Canopy Temperature	Thermal Imaging by Thermal Infrared thermometers	Reliable for high-throughput crop temperature phenotyping under water stress conditions in potato; Potential information about leaf and canopy transpiration and heat dissipation	Time of day (morning readings are usually lower due to lower incident of solar radiation and air temperature); Adjustment of proper measurement angle; Difficult to separate soil temperature from plant temperature in sparse canopies; Sound physics based result interpretation required.	Roth and Goyne (2004); Grant <i>et al.</i> (2007); Biskup <i>et al.</i> (2007); O'Shaughnessy <i>et al.</i> (2011); Li <i>et al.</i> (2014)
2.	Stomatal conductance	Infrared thermography (IRT)/Near infrared cameras *Plant Eye; Field scan (Semi-automated and Automated HTTPP)	Measured gas traffic and transpiration at cellular level; Easy, rapid and nondestructive method of screening for stomatal behavior; evaluate large population trials for genetic analysis.	Measurements influenced by humidity, time and other factors; Imaging sensor calibration and atmospheric correction are often required.	Munns <i>et al.</i> (2010); Pask and Pietragalla (2012); Fiorani and Schurr (2013); Prashar <i>et al.</i> (2013) *(https://phenospex.com/blog/field-phenotyping/)
3.	Chlorophyll fluorescence	Hyper spectral-radiometers/ Imaging sensors	Determined the influence of various genes and environmental conditions on photosynthetic efficiency (photosystem- II); Crucial to provide information about dissipation of excess light energy.	Several inaccurate measurements may occur due to changes of fluorescence during estimation of the PSII operating efficiency, Handling of large amount of data generated, expensive	(http://www.plantphenomics.org/); Furbank and Tester (2011); Monneveux <i>et al.</i> (2013) Yol <i>et al.</i> (2015)
4.	Chlorophyll content	Multi-spectral imaging/ Digital imaging/SPAD meter	Positive correlation between root dry mass, tuber yield and chlorosis.	Limitations in terms of solar angle, measurement time, leaf position, leaf surface status, calibration errors in chlorophyll meter.	Songsri <i>et al.</i> (2009); Vollmann <i>et al.</i> (2011); Moghaddam <i>et al.</i> (2011); Monneveux <i>et al.</i> (2013)

Continuing table 3

Sr. No.	Traits	Devices/Sensors/Imaging techniques/Softwares	Advantages	Limitations	References
5.	Leaf Area / Leaf area Index	Digital camera imaging using appropriate softwares/ Near Infrared cameras (*camera sensor consisted of a 3-chip MS2100 CCD camera) laser scanners or LIDAR LAMINA SOFTWARE (Automated and semi-automated image analysis)/ LEAF PROCESSOR (Novel tool leaf shape analysis)	Quick, efficient, easy manipulation of physiological data; High 2D and 3D accuracy; Shoot and canopy models enabled, Quantification of leaf size and shape	Synchronization with GPS and encoder position systems needed for geo-referencing, personal constraints in access, storage, analysis and management of imaging data.	Bylesjo" et al. (2008); Backhaus et al. (2010); Cobb et al. (2013); Fiorani and Schurr (2013); Yol et al. (2015); *Dammer et al. (2016)
6.	Carbon isotope discrimination	Near Infrared Reflectance Spectroscopy (NIRS)	Determined the amount of C ¹³ used by photosynthetic activity, positively correlated with stomatal conductance and drought tolerance in potato clones; development of genotypes with improved WUE.	Complicated, need of data transformation.	Ferrio et al. (2007); Monneveux et al. (2013); Yol et al. (2015)
7.	Root dynamics	PlaRoM- root extension profiling software (noninvasive video image technique)/3D digital imaging system and RootReader 3D/Gria Root (semi-automated 2D)/ X-ray CT (3D)	Allow non-destructive imaging, analysis and automatic phenotyping of RSA.	Controlled environment, understanding complex software packages, X-ray source effects for imaging time series to be evaluated	Tracy et al. (2010); Clark et al. (2011); Galkovskyi et al. (2012); Yazdanbakhsh and Fisahn(2012); Monneveux et al. (2013); Yol et al. (2015)

Acronyms; 2D (Two dimensional), 3D (Three Dimensional), GPS (Geo Positioning System),HTPP (High Throughput Phenotyping Platform), IRT (Infrared Thermography), LAMINA software (Leaf Shape Determination),LIDAR (Light detection and Ranging), PlaRoM (PLAntROot Monitoring platform), RSA (Root System Architecture), WUE (Water Use Efficiency), X-ray CT (X-ray Computed Tomography).

Table. 4.Examples of genome editing mediated gene modifications in major crops.

Crop species	Target Locus/gene	Genome-Editing Technique	Type of Modification	Frequency of mutation (%)	Off-Target Mutation	Purpose/Targeted Modification	References
Potato (<i>Solanum tuberosum</i>)	<i>St SSR2</i>	TALEN	MultiallelicIndels	-	Yes	Targeted breeding for low cholesterol and SGAs (steroidal glycoalkaloids) levels.	Sawai <i>et al.</i> (2014)
	<i>ALS</i>	TALEN	Indels	10%	N. D	SDM as tool in Plant Breeding	Nicolia <i>et al.</i> (2015)
	<i>St ALS1</i>	CRISPR-Cas 9	Indels	3%-60%	No	Herbicide resistance	Butler <i>et al.</i> (2015)
	<i>SI1A42</i>	CRISPR-Cas 9	Monoallelic and biallelic homozygous mutants Indels	83%	No	Functional studies of uncharacterized genes in potato (double haploid potato cultivar)	Kloosterman <i>et al.</i> (2006); Wang <i>et al.</i> (2015)
	<i>GBSS</i>	CRISPR-Cas 9	MultiallelicIndels	67% (multiple alleles); 2%-12% (one allele)	N. D	Amylopectin rich potato; Waxy Potato	Andersson <i>et al.</i> (2016)
Tomato (<i>Solanum lycopersicum</i>)	<i>VInv</i>	TALEN	MultiallelicIndels (1-4)	2% - 15.9%	Yes (3 or 4 bases mismatch)	Minimize accumulation of reducing sugars and also acrylamide levels; Targeted reduction of CIS	Clasen <i>et al.</i> (2016)
	<i>PROCERA</i>	TALEN	Biallelicindel	2.5%	N. D	Negative regulator of GA, mutants were tall, slender with light green vegetation	Lor <i>et al.</i> (2014)
	<i>RIN</i>	CRISPR-Cas 9	Indels (1 base insertion and deletion of upto 3 bases)	0%-100%	No	Regulate fruit ripening	Ito <i>et al.</i> (2015)

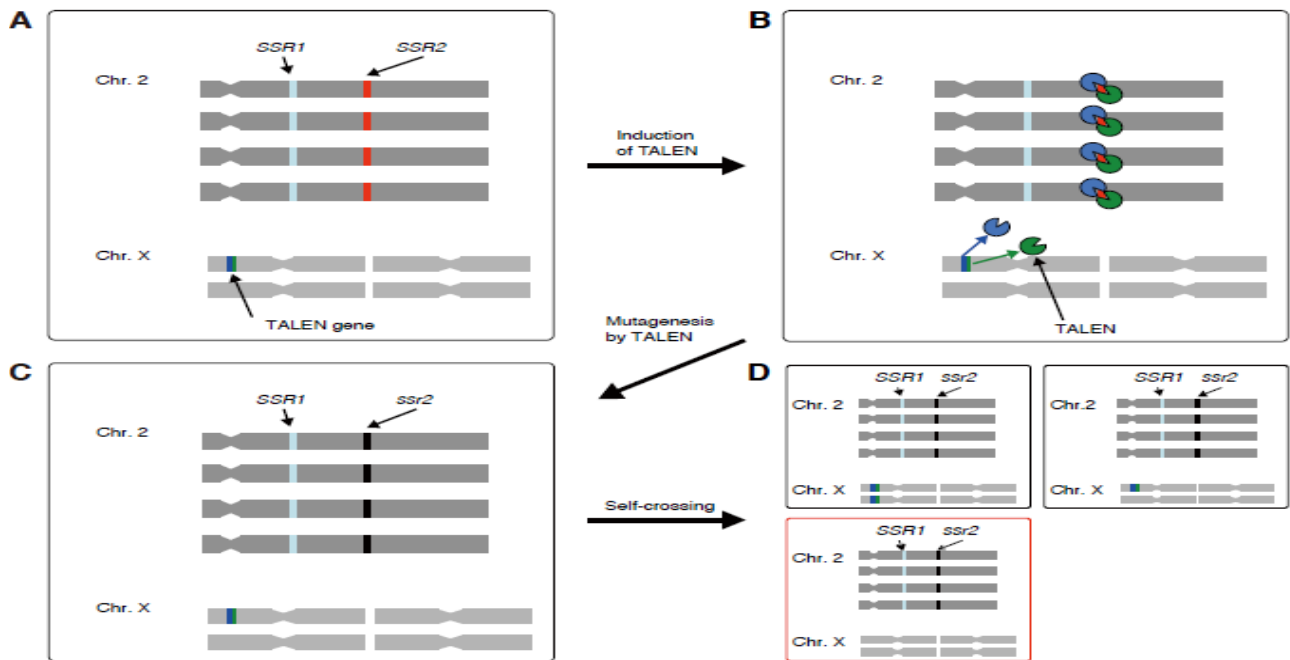
Continuing table 4

Crop species	Target Locus/gene	Genome-Editing Technique	Type of Modification	Frequency of mutation (%)	Off-Target Mutation	Purpose/Targeted Modification	References
Soybean (<i>Glycine max</i>)	<i>FAD2</i>	TALEN	Biallelicindel	33.3%	No	Improved soybean oil (poly-unsaturated fats) quality	Haun <i>et al.</i> (2014)
	<i>GFP</i>	CRISPR-Cas 9	Biallelicindel	78%-95%	Yes (2 loci out of 11)	Modification of soybean genes for improved agronomic and physiological traits.	Jacobs <i>et al.</i> (2015)
Wheat (<i>Triticum aestivum</i>)	<i>TaMLO</i>	CRISPR-Cas 9	Indel	28.5%	N. D	Adaptive Immune system against Powdery mildew	Shan <i>et al.</i> (2013)
Rice (<i>Oryza sativa</i>)	<i>OsBADH2</i> , <i>OsCKX2</i>	TALEN	Biallelicindel	12.5%, 3.4%	N. D	Selective removal of gene clusters, detect intergenic regions	Shan <i>et al.</i> (2013)
	<i>OsBEL</i>	CRISPR-Cas 9	Biallelicindel	2.2%	No	Herbicide resistant approach	Xu <i>et al.</i> (2014)
Maize (<i>Zea mays</i>)	<i>ZmIPK1</i>	ZFN	Inserting PAT gene	3.4% - 22.1%	No	Herbicide-tolerant plant	Kim <i>et al.</i> (2011)

N.D; Not Determined

Abbreviations: CIS (Cold-induced Sweetening); *GBSS* (Granule-Bound Starch Synthase), *SSR2* (Sterol Side chain Reductase 2); *ALSI* (Acetolactate Synthase 1); *1Inv* (Vacuolar Invertase Gene); *IAA* (Indole Acetic Acid); *SDM* (Site Directed Mutagenesis); *GA* (Gibberellic Acid); *RIN* (Ripening Inhibitor); *FAD2* (Fatty acid Desaturase 2); *GFP* (Green Fluorescent Protein); *BEL* (Bentazon Sensitive Lethal)

Figure 1. TALEN induced *SSR2* Knock-out in *Solanum tuberosum* L. (Picture courtesy: Sawai *et al.* 2014)



A) Insertion of TALEN expression cassette, unlinked to *St SSR2* target site (Red) (B) TALEN construct (Green&Blue) targeting *St SSR2* loci. (C) Mutations at all four *St SSR2* loci in tetraploid potato genome without modification of *St SSR1* (light blue) (D) *St SSR2* knockout potato without integration of transgene achieved by segregation after selfing the transformants.

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