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REVIEW ARTICLE

Molecular advances on agricultural crop improvement to meet current cultivating demands

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Abstract Sunflower, maize and potato are among the world's principal crops. In order to improve various traits, these crops have been genetically engineered to a great extent. Even though molecular markers for simple traits such as, fertility, herbicide tolerance or specific pathogen resistance have been successfully used in marker-assisted breeding programs for years, agronomical important complex quantitative traits like yield, biotic and abiotic stress resistance and seed quality content are challenging and require whole genome approaches. Collections of genetic resources for these crops are conserved worldwide and represent valuable resources to study complex traits. Nowadays technological advances and the availability of genome sequence have made novel approaches on the whole genome level possible. Molecular breeding, including both transgenic approach and marker-assisted breeding have facilitated the production of large amounts of markers for high density maps and allowed genome-wide association studies and genomic selection in sunflower, maize and potato. Marker-assisted selection related to hybrid performance has shown that genomic selection is a successful approach to address complex quantitative traits and to facilitate speeding up breeding programs in these crops in the future.

Additional keywords: Crop improvement, agricultural biotechnology, marker assisted selection, improved agronomic traits

Introduction

Agriculture is a human invention since more than 10,000 years and is estimated to have used more than 7,000 species to satisfy basic human needs (Esquinas-Alcázar, 2005). The primitive crop cultivars, known as landraces, were adapted to local growing conditions and practices, and therefore remained genetically diverse for traits such as product qualities, stress tolerance, disease resistance, and yield stability. Today's agricultural commodities and modern varieties derived from the genetic modification of wild plants through thousands of years of gradual selection, domestication and breeding, are more genetically uniform than their wild relatives (Fu, 2015). Given that plant genetic diversity increases options for innovative, plant-based solutions to major environmental challenges such as water scarcity, deforestation, energy and climate change, molecular plant breeding can be a valuable tool to meet these demands by rapid incorporation of important traits from wild relatives into established crops and by shortening new crop domestication time (da Silva Dias, 2015).

Nowadays affordable high throughput DNA sequencing, coupled with improved bioinformatics and statistical analyses, is bringing major advances in the field of molecular plant breeding. Multidisciplinary breeding programs on the world's major crop plants are able to investigate genome-wide variations in DNA sequences and link them to inherited highly complex traits which are controlled by several genes, such as hybrid vigor and flowering. Furthermore, there has been

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a step-change in speed and cost-effectiveness (Robinson *et al.,* 2014). The availability of dense genetic maps can facilitate researchers to perform flexible marker-trait associations, concerning the correlations between pathogen resistance and alternative genes, and develop high performance markers that will promote marker- assisted choice (MAS) selection for resistant populations in segregating breeding programs (Ben-Ari and Lavi, 2012).

Herein, the molecular advances on agricultural crop improvement to meet current cultivating demands are reviewed for three economically important crops worldwide, i.e. sunflower, maize, potato.

Sunflower (*Helianthus annuus* L., Asteraceae)

Sunflower is the foremost seed crop cultivated within the world (Fernández-Luqueño *et al.,* 2014). Sunflower oil contains less than 11% total saturated fat and does not contain any trans fat. Inexpensive production of biofuel from sunflower oil has been achieved (Boumesbah *et al.,* 2015). Furthermore, sunflower is an ideal plant for producing high quality rubber from its leaves and stems and some of the taller perennial species have high latex yield potential (Lu and Hoeft, 2009).

The multiple usages of sunflower products in food, feed, and industry are stimulating the discovery of new sources of biodiversity for sunflower molecular breeding programs in combination with the application of high throughput approaches and genetic manipulation. The primary objective for sunflower breeders it to increase the yield and agronomical performance of high oleic sunflower hybrids. To accomplish these goals, breeders need to address pathogens, pests, and environmental constraints that have the potential to drastically reduce yield where sunflowers are grown (Dimitrijevic and Horn, 2018).

Genomic resources

A rich and various germplasm assortment is the backbone of each crop improvement program. Assessing genetic diversity within a genetic pool of novel breeding germplasm could make crop improvement more efficient by the directed accumulation of desired alleles (Darvishzadeh *et al.,* 2010). Several bacterial artificial chromosome (BAC) libraries have been constructed for sunflower (Feng *et al.,* 2006; Gentzbittel *et al.,* 2002; Özdemir *et al.,* 2004). The libraries are equivalent to approximately 8 haploid genomes of sunflower and provide a greater than 99% probability of obtaining a clone of interest and they have been employed for isolating and physical mapping of loci such as the FAD2-1 locus (Schuppert *et al.,* 2006) or the fertility restorer Rf1 locus (Hamrit *et al.,* 2008). *In situ* hybridization techniques involving Fluorescent In Situ Hybridization (FISH) and BAC-FISH have being optimized for diversity and biological process studies between species of the genus Helianthus and development of a physical helianthus map allowing a cross reference to the genetic map (Giordani *et al.,* 2014).

Various EST sequencing programs have been carried out in sunflower, including the Compositae Genome Project, and other programs (Tamborindeguy *et al.,* 2004) and (Ben *et al.,* 2005). The Compositae Genome Program (http://compgenomics.ucdavis.edu/index.php) has developed and is utilizing a 2.6 million feature Affymetrix chip based on 87,000 unigenes from seven *Helianthus* spp. (Lai *et al.,* 2012). Interesting associations have been detected between Expressed Sequence Tags (ESTs) and Quantitative Trait Loci (QTLs) for salt tolerance and for domestication traits (Lai *et al.,* 2005). Until today, 94.33 % of HA412-HO ESTs are correctly mapped and 90,935 protein coding genes are predicted, excluding transposable elements (http://www.sunflowergenome.org). Extensive genotyping has been performed for vegetative and flower sunflower organs together with uncovering gene networks for oil metabolism and flowering time (Badouin *et al.,* 2017; Renaut 2017).

Efficient breeding strategy development

Biotechnology has the potential to help

evoke the full potential of this valuable crop (Fig. 1).

Resistance to pathogens

MAS technology has been used in sunflower breeding for various disease resistance traits (Brahm and Friedt 2000). With the development of an array of molecular markers and a dense genetic map of the sunflower genome, MAS for both single genes and QTLs is now possible (Babu *et al.,* 2004; Bowers *et al.,* 2012). For example, biotechnology offers a variety of methods for managing white rot caused by *Stromatinia cepivora* (also known as *Sclerotium cepivorum*) (Schnabl *et al.,* 2002), including defense activation, pathogen inhibition and detoxification (Lu, 2003). According to Hu *et al.* (2003), the enzyme oxalate oxidase can confer resistance against *Sclerotinia sclerotiorum,* (Lib.) de Bary which causes sclerotinia wilt (midstalk rot), in transgenic sunflower plants while according to Sawahel and Hagran (2006), overexpression of a human lysozyme gene in sunflower confers resistance to the pathogen. Recently, the quantitative nature of Sclerotinia resistance has been exploited and QTL analysis showed that different genomic regions may contribute to resistance in different tissues of the plant (Würschum *et al.,* 2014).

Alternative transgenic methods have been developed to reinforce sunflower resistance to diseases. A number of homologues resistance (R) gene have been isolated from sunflower, providing a valuable resource for engineering disease resistance in sunflower (Dimitrijevic and Horn 2018; Hewezi *et al.,* 2006; Qi *et al.,* 2016; Talukder *et al.,* 2016).

Quality traits. Sunflower with high oleic acid content is optimal for the biodiesel industry since the produced oil has up to 90% mono-unsaturated fatty acid concentration, which has high oxidative stability and uniformity. Therefore, producing high concentrations of industrially valuable fatty acids in plant seeds through biotechnological improvements along with modifications of the fatty acid composition can make vegetable oil more versatile for its use (Burton *et al.,* 2004).

One of the challenges for oil composition modification in sunflower is increasing the extent of the new fatty acids. Much work has been performed for the identification of genes involved in primary metabolic pathways and signal transduction at various growth and stress conditions (Liang *et al.,* 2017; Pan *et al.,* 2016; Velasco *et al.,* 2014) to gain insight into the mechanism of antioxidant defense. New genes have been identified and the metabolism of ROS and RNS have been analyzed under various biot-

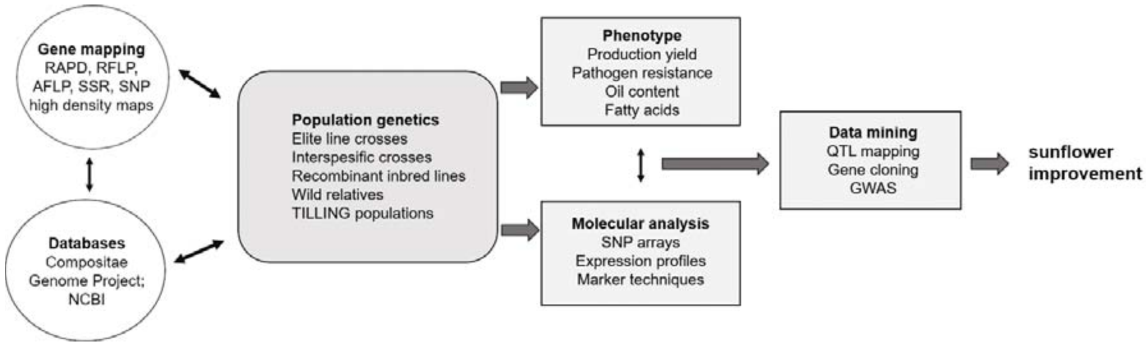

Fig. 1. Schematic depiction of the available resources in sunflower for marker-assisted selection and future genomic selection. Sunflower diverse genetic information is available for breeding and represents a large portion of genetic diversity that can be exploited for improving sunflower traits. Accessing sunflower genome sequences, large resources of SNP or high resolution maps and/or SNP arrays, along with huge amount of expression data can accelerate sunflower breeding by making the selection steps more efficient and precise. Marker-assisted breeding toward genomic selection can produce high quality breeding values.

ic and abiotic conditions (Chaki *et al.,* 2013; Chaki *et al.,* 2008; Chaki *et al.,* 2011).

Overall, transgenic sunflower has the potential to meet the demands for yield improvement, to increase the efficient use of renewable resources, such as land, water and soil nutrients, and to significantly benefit everyday life by providing additional nutritive and healthy foods and valuable industrial products.

Ease of use and robustness of molecular markers

Markers' validation assesses their linkage to and association with QTLs and their effectiveness in selection of the target phenotype in independent populations and different genetic backgrounds (Collard *et al.,* 2005). An overall QTL mapping has been performed using microsatellite and Single Nucleotide Polymorphisms (SNP) markers in sunflower giving the ability to assess the genetic diversity and population structure across different sunflower populations (Filippi *et al.,* 2015).

Validation of genomic Simple Sequence Repeats (SSRs) in four genotypes of sunflower (RHA266, PAC2, HA89 and RHA801) resulted in amplification of 74 sequences from a total of 127 analyzed. Out of them, 13% represented polymorphic loci, 45% monomorphic, 5% null alleles and the remaining 37% showed either no amplification product, nonspecific amplification or complex or difficult to resolve banding patterns (Talia *et al.,* 2010). The percentage of polymorphisms within sunflower that can be genetically mapped using SSR markers is shown to be less than 10% that comes in agreement with reports from other species (Varshney *et al.,* 2005).

Examples of markers/QTLs validation across various genetic backgrounds in sunflower include:

- A set of markers have been validated in a number of different genetic backgrounds for the Or5 gene conferring resistance to race E of the parasitic weed broomrape (*Orobancche cumana*), infecting the sunflower roots (Höniges *et al.,* 2008; Pérez-Vich *et al.,* 2004; Tang and Knapp, 2003).
- Markers have been validated for the dominant Pl genes determining resistance to different downy mildew races (Brahm and Friedt 2000; Hvarleva *et al.,* 2009; Ma *et al.,* 2017) and to the R1, Radv and Pu6 genes conferring resistance to rust (Bulos *et al.,* 2014).
- QTLs controlling three resistant (stem lesion, leaf lesion and speed of fungal control) and two morphological (leaf length and leaf length with petiole) traits have been validated for *S. sclerotiorum* across generations (Micic *et al.,* 2005) and across environments (Talukder *et al.,* 2016).
- QTLs have been validated for sunflower oil content, across generations, environments and mapping populations (Tang *et al.,* 2006b).
- Markers have been developed in sunflower for simple traits selection, based on gene mutations underlying the trait of interest. There has been identified a mutation in codon 205 in the acetohydroxyacid synthase gene AHAs-1 that confers resistance to imidazolinone (IMI) herbicides and developed a SNP genotyping assay diagnostic for it (Kolkman *et al.,* 2004).

Maize (*Zea mays* L., Poaceae)

Cultivation of maize is extensively widespread throughout the world and is surpassing any other grains (Council, 2019). With a fraction of total maize production being consumed by humans, its main products are ethanol, animal feed and processed corn starch and corn syrup (Klopfenstein *et al.,* 2013). Maize has high nutritional value but also is a fine source of various major phytochemicals such as carotenoids, phenolic compounds, and phytosterol, depicting its potential health benefits (Rouf Shah *et al.,* 2016).

Genome as the core base

B73 decoding. The 2.3-billion-base genome of an inbred line of maize called B73, an important commercial crop variety has been decoded (Schnable *et al*., 2009). It has been reported that the Palomero genome, a corn variety diverged from B73 about 9,000 years ago, is around 400 million nucleotides smaller and contains about 20% less repetitive DNA than B732 (Vielle-Calzada *et al.,* 2009). To map maize haplotypes a part of the gene-rich region of 27 maize varieties was sequenced. 'HapMap' revealed thousands of genes around the centres of the chromosomes, where they were unlikely to be shuffled around during recombination (Gore *et al.*, 2009). Schnable *et al.* (2011) demonstrated that the maize subgenomes are differentiated by genome dominance and both ancient and ongoing gene loss. Most of the economically important traits considered in maize breeding are inherited quantitatively. Multiple genes or quantitative trait loci (QTLs) affecting flowering traits, root characteristics, cell wall traits, and tolerance to biotic/abiotic stresses panicle morphology and grain development have been cloned, and gene expression research has provided new information about the nature of complex genetic networks involved in the expression of these traits (Buckler *et al.*, 2009; Chung *et al.*, 2011; Fernandez *et al.*, 2009; Messmer *et al.*, 2009; Poland *et al.*, 2011; Trachsel *et al.*, 2009). A meta-analysis of QTL associated with plant digestibility and cell wall composition in maize identified key chromosomal regions involved in silage quality and potentially associated genes for most of these regions (Truntzler *et al.*, 2010).

Association mapping (associating specific DNA polymorphisms with traits of interest based on linkage disequilibrium). McMullen *et al.* (2009) described the maize NAM population generated by crossing 25 diverse inbred lines to a common line, inbred B73. Sequenome-based SNP-typing assay was used to identify 1,359 SNPs in maize transcriptome and 75% of these SNPs were confirmed and applied in association analysis (Liu *et al.,* 2010). Currently, there are over 2 million maize ESTs in GenBank (Benson *et al.,* 2009). However, the assembly of these ESTs into gene models presents practical problems. Therefore, a full length cDNA library has been recently constructed for *Zea mays* (http:www.maizecdna.org/) (Soderlund *et al.,* 2009). A normalized cDNA library, covering most of the developmental stages of maize seeds, was also constructed and 57 putative transcription factors were identified (Wang *et al.,* 2010). The cDNA libraries can serve as primary resources for designing microarray probes and as clone resources for genetic engineering to improve crop efficiency.

Maize GDB (http://www.maizegdb.org/). Maize GDB is a database that provides documentation and data for the microarrays produced by the Maize Gene Discovery Project. An extensive expression atlas covering a wide array of tissues and developmental stages of maize using a NimbleGen microarray encompassing 80 301 probe sets was recently constructed (Sekhon *et al.,* 2011). Random-sheared, paired-end Illumina GAII reads have been generated from 103 maize, teosinte and maize landrace inbred lines at a depth ranging from 4-30x (Chia *et al.,* 2012; Hufford *et al.,* 2012). Microarray studies have also been performed to study cell wall metabolism in maize, with the aim of identifying tissue-specific or developmentally regulated gene expression of members of multigene families or to obtain a better understanding of regulatory networks that are exposed when cell wall-related genes are mutated (Guillaumie *et al.,* 2007a; Guillaumie *et al.,* 2007b). The MAIZEWALL sequence database and expression profiling resource has been developed (www.polebio.scsv.ups-tlse.fr/MAIZEWALL). Rajhi and co-workers performed transcriptome analysis in maize root cortical cells during lysigenous aerenchyma formation and discovered a number of genes whose expression changed in response to ethylene under waterlogged conditions (Rajhi *et al.,* 2011).

Maize small RNAs. Small RNAs in the wild type and in the isogenic Mediator Of Paramutation1 loss-of- function (mop1-1) mutant have been examined by deep sequencing to analyze the size distribution of maize small RNAs (Nobuta *et al.,* 2008). Small RNAs are playing roles as major components of epigenetic processes and gene networks involved in development and homeostasis. It has been recently demonstrated that a change in expression of a key component of the RNA silencing pathway is associated with both vegetative phase change and shifts in epigenetic regulation of a maize transposon (Li *et al.,* 2010).

RNA interference (RNAi) [RNA-mediated gene silencing by sequence-specific degradation of homologous mRNA triggered by double-stranded RNA (dsRNA)]. The RNAi system was used to improve resistance to maize dwarf mosaic virus on transgenic maize (Zhang *et al.,* 2011). Maize lines expressing RNAi to chromatin remodeling factors were shown to be similarly hypersensitive to UV-B radiation but exhibit distinct transcriptome responses (Casati and Walbot 2008). By using near infrared reflectance spectroscopy (NIRS), a set of 39 maize mutants with altered spectral phenotypes ('spectrotypes') have been identified (Vermerris *et al.,* 2007). A number of these mutants were shown to have altered lignin-to-carbohydrate ratios (Penning *et al.,* 2009). Sequence- specific DNA binding Transcription Factors (TFs) are key molecular switches that control or influence many biological processes, such as development or response to environmental changes. The Maize Transcription Factor Database provides a comprehensive collection of 764 predicted transcription factors from maize with available links to information on mutants, map positions or putative functions for these transcription factors (MaizeTFDB) (http://grassius.org/browsefamily.html?species=Maize). Information resources related to metabolomics can play major role not only in metabolomics research but also in synergistic integration with other omics data. MaizeCYc is a biochemical pathway database that provides manually curated or reviewed information about metabolic pathways in maize.

Molecular breeding for current needs

Molecular breeding, including both transgenic approach and marker-assisted breeding, is primary associated with the challenges for developing cultivars with combinations of adaptive traits (Brown *et al.,* 2011; Varshney *et al.,* 2011). For making molecular marker-assisted breeding successful, marker-trait associations are now known for almost all important economic traits, including thousands of mapped microsatellite or SSR markers, and additional recently, SNPs, and insertion-deletion (InDel) markers. For maize, there is an updated compilation of mapped QTL for abiotic stress resistance (http://www.plantstress.com; http://www.maizegdb.org; http://www.gramene.org). Additionally, a large number of genes controlling various aspects of plant development, biotic and abiotic stress resistance, quality characters, etc. have been cloned and characterized in maize, which are excellent assets for molecular marker- assisted breeding (Aslam and Ali 2018; Prasanna *et al.,* 2010).

Tolerance against drought. Since drought is considered to be the most important constraint across all areas where maize is cultivated, and global warming is predicted to further exacerbate drought's impact, a total management plan is necessary for increasing maize yield in stress-prone environments (Fig. 2). The high variability to drought stress and also the uncontrollable fact that drought response has great fluctuations across environments, have made it difficult to spot specific metabolic pathways which limits breeding efforts towards drought tolerance (Collins *et al.,* 2008). A Marker-Assisted BackCross (MABC) selection approach meant for improving grain yield under water limited conditions in tropical maize, was successfully conducted at CIMMYT (Ribaut and Ragot 2006) and more recently at sub-Saharan Africa (Beyene *et al.,* 2016). However, this approach delivers a restricted level of improvement in drought tolerance since it provides an improved version of an existing genotype (Ribaut *et al.,* 2009). Nevertheless, a molecular breeding approach-marker-assisted recurrent selection (MARS) can be used to overcome this problem. MARS studies exploit association mapping and can effectively double the rate of yield gain compared to conventional

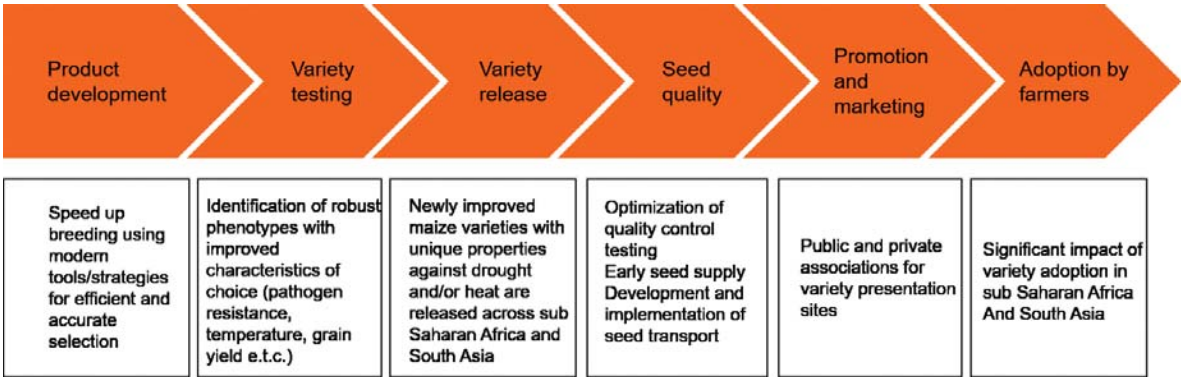

Fig. 2. Schematic representation that highlights the required key steps to facilitate enhanced adoption and impacts of improved climate-resilient maize varieties in the developing world. Increasing maize yields in stress-prone environments and reducing year-to-year variability is an important step in improving food safety, livelihoods and adaptation to the changing climate in the developing world (Cairns and Prasana, 2018).

breeding in elite germplasms when favored and stress environments are been examined (Crosbie *et al.,* 2006; Eathington *et al.,* 2007; Edgerton 2009). Most recently, the role of Abscisic Acid (ABA) pathway in drought resistance has been investigated and natural variants of ABA-(PYR1/PYL/RCAR) protein (PYL) receptors have been identified that can serve as potential molecular markers for breeding drought-resistant maize cultivars (He *et al.,* 2018).

Resistance against pathogens. Efforts to scale down maize losses from pathogen attacks through resistant crop varieties could provide tremendous opportunities for increasing and stabilizing maize productivity. QTL related to resistance to several diseases, such as downy mildew and rust, and insect-pests are known and mapped in maize, creating marker assisted choice as a potentially viable strategy to improve resistance to these biotic stresses (Ali and Yan 2012; García-Lara *et al.,* 2009; Krakowsky *et al.,* 2004; Wisser *et al.,* 2006).

Resistance against insect pests. The industry has made substantial progress with insect resistant maize through transformation with insecticidal proteins from *Bacillus thuringiensis* (Bt) which have been particularly successful in providing protection against several corn borers (Glaser and Matten 2003; Jiang *et al.,* 2018).

Quality traits. Quality traits, like oil content or high nutritional value molecules, have induced a shift in maize production far from strictly an identity-preserved cultivation to more a value-added product. The capability of changing cell membrane polysaccharides into possible sugars for grain ethanol production depends on cell membrane structure. Molecular markers can be a valuable tool when breeding for feed maize but with improved quality on grain ethanol.

QTLs with comparatively efficient results are found for feed maize including cell membrane composition and glucose release (GLCRel) (Lorenzana *et al.,* 2010), and some important constitutive and adaptive QTLs are identified by using meta-analysis (Hao *et al.,* 2010). (Torres *et al.,* 2015) presented the molecular progress that has been made in altering maize's cellulosic content in order to exploit useful biomass characteristics and design new breeding strategies.

Quality traits and tolerance to abiotic stress. There has been increasing interest in addressing advanced traits like grain quality and abiotic/biotic stress tolerances through recombinant DNA technology. Elite inbred South African transgenic corn plants were modified in 3 separate metabolic pathways to produce increased quantities of vitamin β-carotene, ascorbate and folate (Naqvi *et al.,* 2009). It has been demonstrated that engineering of the alkaloid synthesis pathway could have great impact on improving cold tolerance in maize (Quan *et al.,* 2004). Furthermore, genome-wide association analyses (GWAS) in temperate maize inbred lines is serving as a tool to find strategies for identifying genes for cold tolerance (Revilla *et al.,* 2016) and has been reported that the introduction of an antisense gene for pyruvate orthophosphate dikinase (PPDK) into maize with *Agrobacterium*-mediated transformation resulted in shifting the break point 3°C less than that of the wild type (Ohta *et al.,* 2004).

Drought is another stress factor that has been addressed in maize improvement. Nuclear Factor-Y (NF-Y) is a 3- subunit complex that has been shown to play major role in growth, development, and response to environmental stress. Except studies that have been performed for characterizing NF-Y gene families in maize (Zhang *et al.,* 2016), when ZmNF-YB2 or ZmNF-YB16 were constitutively expressed in elite maize inbred lines, the transgenic lines displayed improved drought tolerance compared to wild-type plants under water-stressed conditions in the field (Nelson *et al.,* 2007; Wang *et al.,* 2018). (Castiglioni *et al.,* 2008) demonstrated that transgenic maize lines recombinant with bacterial RNA chaperones resulted in not only abiotic stress tolerance but also improved grain yield under water-limited conditions. The application of this technology has the potential to considerably impact maize production systems that have drought. However, commercialization of transgenic maize for abiotic stresses like drought tolerance has been terribly restricted (Xu *et al.,* 2009).

Moreover, the past ten years we have witnessed extensive efforts toward the development of an efficient *Agrobacterium*-mediated transformation system for an array of maize developing organs with particular emphasis on increasing the efficiency and extending the range of amenable genotypes (Cao *et al.,* 2014; Lee and Zhang 2014; Shrawat and Lörz, 2006).

Validation of quantitative traits

In maize, a trait that has been extensively investigated as an indirect measure of drought tolerance is the capacity of ABA accumulation. The presence of a major QTL for root features (root-ABA1) was mapped on bin 2.04 in Os420 × IABO78. This major QTL affecting abscisic acid (ABA) concentration in the leaf, root traits and relative water content was further evaluated in maize using NILs (Landi *et al.,* 2005). Interestingly, the QTL allele for larger root mass and higher ABA concentration negatively affected grain yield (Landi *et al.,* 2006). Laurie *et al.* (2004) were able to detect 50 QTL accounting for genetic variance in maize oil content with a resolution of the order of a few centimorgans across generations.

QTL conditioning resistance to plant pathogens (rQTL) have been discovered and reviewed by several authors (Balint-Kurti and Johal, 2009; Redinbaugh and Pratt, 2009). To date only a few QTL conferring resistance to maize streak mastrevirus, *Cercospora zeae-maydis*, *Exserohilum turcicum* (Pass.) and *Peronosclerospora sorghiin* have been validated (Abalo *et al.,* 2009; Asea *et al.,* 2009; Nair *et al.,* 2005). For Cercospora resistance in maize, QTLs have been validated across genetic backgrounds (Pozar *et al.,* 2009) and environments (Juliatti *et al.,* 2009). Furthermore, a major QTL controlling maize streak virus resistance explains 50–70% of total phenotypic variation (Pernet *et al.,* 1999). Several microsatellite markers associated with this QTL were validated across populations and have been successfully used for the selection of resistant lines (William *et al.,* 2007).

Analyses for evaluating the significance of QTL x genetic background interactions in several diverse mapping populations, have been performed in maize for grain moisture, silking date and grain yield (Blanc *et al.,* 2006; Huo *et al.,* 2016). QTL meta-analysis is another approach to identify consensus QTL across studies, to validate QTL effects across environments/genetic backgrounds, and also to refine QTL positions on the consensus map (Goffinet and Gerber 2000). The concept of meta-analysis has been applied to the analysis of QTL/genes for flowering time (Chardon *et al.,* 2004) and drought tolerance in maize (Hao *et al.,* 2010). A meta-analysis of QTL associated with plant digestibility and cell wall composition in maize has been carried out and fifteen meta QTL with confidence interval (CI) smaller than 10cM were identified (Truntzler *et al.,* 2010).

Potato (*Solanum tuberosum,* L., Solanaceae)

Cultivated potato is the world's third most important human food crop (www.cipotato.org). It is also used as raw material for starch and alcohol production (Cantos-Lopes *et al.,* 2018). The basic chromosome number for potato species is 12. Even though one of the most widespread food crop around the world, the genetics of many potato traits is poorly understood.

Insights in genomic properties

An ultrahigh-density (UHD) genetic map composed of approximately 10,000 Amplified Fragment Length Polymorphism (AFLP) markers has been developed, which is most likely the densest map for a plant species ever constructed (Van Os *et al.,* 2006). Recently, the relationship between the genetic and chromosome map in potato was displayed and two linkage maps were integrated with potato genome sequence developing 8303 Single Nucleotide Polymorphism (SNP) for genome-guided breeding (Felcher *et al.,* 2012). Moreover, (Sharma *et al.,* 2013) elaborated 2469 marker loci in a linkage map which was integrated with potato reference genome (DM) and other physical and genetic maps of potato providing detailed information about chromosomal gene distribution. Using RFLP and AFLP markers, a QTL and linkage map of two segregating diploid populations previously evaluated for sugar content after cold storage, was generated. Ten potato genes with unknown function in carbon metabolism or transport were mapped and tested for their effects on sugar content. Results displayed linkage between glucose, fructose and sucrose QTLs and all of eight candidate gene loci (AGPaseS, AGPaseB, SbeI, GapC, Invap, Ppa1, Sut1, Sut2) (Menéndez *et al.,* 2002). Several QTLs affecting the ability to form tubers under long photoperiods (earliness) have been identified (Šimko *et al.,* 1999). A functional map for pathogen resistance, enriched with RGA (resistance gene analog) and DRL (defence related locus) sequences, SNPs and insertion-deletion polymorphisms (InDels) tightly linked or located within Nucleotide Binding Site - Leucine Rich Repeat (NBS-LRR) -like genes, has been developed on the basis of two potato populations (BC9162 and F1840) (Rickert *et al.,* 2003; Trognitz *et al.,* 2002). Recently, twenty-one QTL and eight reference published potato maps were merged together and the first consensus map was built. Individual QTLs for resistance to the late blight pathogen, *Phytophthora infestans* (Mont.) de Bary, and maturity traits were projected onto the consensus map and the first meta-analysis performed deals with both development trait and resistance to a biotic stress in potato (Danan *et al.,* 2011).

As a major follow-up, the genome of potato (850 Mb) was sequenced by the international Potato Genome Sequencing Consortium (PGSC), which was comprised by 13 countries [http://www.potatogenome.net/]. The new genome sequence data provides information about extensive copy number variation (CNV) which has great impact on 219.8 Mb (30.2%) of the potato genome. Almost 30% of genes are subjected to at least partial duplication or deletion which reveals the highly heterogeneous nature of the potato genome (Hardigan *et al.,* 2016). Comparative sequence analysis of *Solanum* and *Arabidopsis* in a hot spot for pathogen resistance on potato chromosome V has also been performed and revealed a patchwork of conserved and rapidly evolving genome segments (Ballvora *et al.,* 2007).

Several efforts to generate EST resources for potato have been performed (Flinn *et al.,* 2005). Potato cDNA microarray analysis was performed to assess the potential of transcriptomics to detect differences in gene expression due to genetic differences or environmental conditions (van Dijk *et al.,* 2009). A cDNA- AFLP approach and bulked segregate analysis (BSA) was used to identify genes co-segregating with earliness of tuberization in a diploid potato population. 81 candidate polymorphic transcript-derived fragments (TDFs) showing polymorphism between the early and late bulks were selected for further analysis (Fernández-del-Carmen *et al.,* 2007). Genetic engineering could enhance desirable characteristics of crops by modifying key regulatory steps for entire metabolic or developmental pathways. The optimal conditions for genetic transformation of Solanum spp mediated by *Agrobacterium tumefaciens* have been established (Chakravarty *et al.,* 2007). It has been demonstrated that transgenic katahdin plants containing the RB gene showed resistance to all tested *Pythophtora* isolates, including a super race that can overcome all eleven known R genes in potato. An RNA interference (RNAi)-based potato gene silencing approach using agroinfiltration, has been recently established (Bhaskar *et al.,* 2009).

How to design efficient breeding strategies

Tolerance to salt stress. Potato crop production is highly inversely connected to salt stress with substantial economic impacts (Katerji *et al.,* 2000). When potato is subjected to salt stress, increased activation of antioxidant enzymes, accumulation of proline, decrease in micro tubers and negative effects on physiological characteristics occur (Rahnama and Ebrahimzadeh 2004; Tang *et al.,* 2006a; Zhang *et al.,* 2005). Gene expression studies on potato cultivars under different stress conditions, such as cold, heat or salt, revealed that transcription factors, signal transduction factors and heat shock protein (HSP) are associated with abiotic stress responses (Rensink *et al.,* 2005; Tang *et al.,* 2016). In addition, when Δ-pyrroline-5-carboxylase synthetase, which is involved in proline production, is overexpressed, it confers salt tolerance to potato (Hmida-Sayari *et al.,* 2005).

Aghaei *et al.* (2008) examined closely in a protein level the differences between a salt tolerant and a salt sensitive potato culture. They pointed out that among the proteins that were differentially expressed photosynthesis- and protein synthesis-related proteins were drastically down-regulated, whereas osmotine-like proteins, type VI secretion immunity protein (TSI-1), heat-shock proteins, protein inhibitors, calreticulin, and five novel proteins were remarkedly up-regulated. Under salt conditions, major changes occur within the photosytem protein machinery and the Calvin cycle as demonstrated by an in-depth cDNA microarray map constructed from potato leaves (Legay *et al.,* 2009).

More recently, advances have been made in identifying several genes that play key roles to biotic and abiotic stress responses. A pathogen-related protein, named PR-10a, has been identified which is not only induced under biotic stress conditions in potato, but also exhibits significantly increased tolerance under salt and osmosis conditions (El-Banna *et al.,* 2010). Two different studies showed that the metal zinc finger protein St ZFP1 could participate to salt associated potato responses through the ABA- dependent pathway (Tian *et al.,* 2010) and also the cinnamyl alcohol dehydrogenase ibCAD1 may play a very important role in each abiotic and biotic stress resistance mechanisms (Kim *et al.,* 2010).

Tolerance to drought. Another major abiotic stress issue that ends up in crop losses in potato cultivars, is drought. The development of drought tolerant cultivars is of primary importance for maintaining yields beneath temperature change conditions and for the extension of cultivation to sub-optimal cropping areas. Extensive cDNA microarray analysis showed that a tolerant accession to drought, named 397077.16, presented differentially expressed genes when compared to a sensitive variety (Legay *et al.,* 2011). The genes belonged to groups of carbohydrate metabolism, cell protection and detoxification, meaning that the tolerant accession can respond more efficiently to stress and be more adaptive when compared to the sensitive one. Additionally, the work of other groups identified a transcription factor which is involved in the activation of drought related genes (Shin *et al.,* 2011) and showed the importance of the overexpression of the L-gulono-c-lactone oxidase (GLOase gene) gene to the resistance to various abiotic stress factors (Upadhyaya *et al.,* 2009).

Resistance to pathogens. The use of resistant varieties is taken into account to be the foremost appropriate approach for the management of *Phytophthora infestans.* Extensive examination of potato genotype SD20 revealed WRKY domain transcription factor (WRKY), single AP2/ERF domain transcription factor (ERF), MAP kinase (MAPK), and NBS-LRR gene families that play essential role in late blight (Yang *et al.,* 2018). Moreover, it has been suggested that the R8 gene, found in field trials, is responsible for late blight resistance and that its mapping on the long arm of chromosome IX along with the generation of markers would be a helpful tool for marker assisted breeding (Jo *et al.,* 2011). Nowadays, R8 gene is a worldwide tool for late blight resistance (Vossen *et al.,* 2016). The introduction of simultaneously three resistance genes from three potato accessions to a sensitive cultivar (Zhu *et al.,* 2012), the silencing of six S-genes in the susceptible potato cultivar Desiree (Sun *et al.,* 2016) or the contribution of R-gene dosage and biochemical pathways to resistance (Gao and Bradeen 2016), are good examples in the literature, considering transformation techniques for late blight resistance. On the other hand, since potato late blight resistance has been thoroughly studied, an extensive map of QTLs and Rpi-genes (resistance genes to *Phytophthora infestans*) has been generated (Danan *et al.,* 2011; Jiang *et al.,* 2018; Stefańczyk *et al.,* 2017).

Other efforts to increase potato resistance to pathogens include exploitation of inhibitor genes. (Khadeeva *et al.,* 2009) showed that transformation of potato plants with an inhibitor gene of buckwheat provides protection to the plants against pathogens. Furthermore, a gene family that function against nematode infections have been sequenced and characterized from *Solamun tuderosum* cv. Desiree (Turra *et al.,* 2009). Also, advances have been made in the identification of genes that are involved in the mechanisms controlling the arbuscular mychorrhizal establishment by the regulation of plant defense genes (Gallou *et al.,* 2012).

Molecular markers as a key tool for crop improvement

Tuber susceptibility to bruising. Diagnostic markers for tuber bruising and enzymatic discoloration, which are very crucial characteristics to crop quality of the cultivated potato, have been validated (Urbany *et al.,* 2011). The markers diagnostic for increased or decreased bruising susceptibility is expected to facilitate the combination of superior alleles in breeding programs.

Potato germplasm (use of sources of resistance to pests and diseases in order to breed varieties cheaper to grow). Although the actual copy number of the genes is not known, DNA markers located close to genes that encode resistance or hypersensitive response to the Potato virus Y (PVY), which can reduce yield up to 80 percent while being relatively symptomless, have been identified and validated (Fulladolsa *et al.,* 2015; Szajko *et al.,* 2014; Tomczyńska *et al.,* 2014). Furthermore, Cleaved Amplified Polymorphic Sequences (CAPs) and Sequence Characterized Amplified Regions (SCARs) have allowed the breeding of genotypes resistant to PVY (Kasai *et al.,* 2000).

The successful employment of four PCR-based diagnostic assays to combine the Ry adg gene for extreme resistance to PVY with Gro1 for nematode resistance and with Rx1 for extreme resistance to potato virus X (PVX, genus Potexvirus), or with Sen1 for wart resistance (*Synchytrium endobioticum*) has been reported (Gebhardt *et al.,* 2006).

The availability of DNA-based markers, which are easy to score, cost-effective and diagnostic for resistance to Pathotypes 2/3 (Pa2/3) of the most significant soilborne pests of potato, the potato cyst nematode (*Globodera pallida*), would greatly speed up the process of new variety development. A set of markers have been validated for QTL on linkage group IV (renamed GpaIV adg s) across a wide range of germplasm (Moloney *et al.*, 2010).

Field resistance to *Phytophthora infestans* has been characterized in a potato segregating family of 230 full-sub progenies derived from a cross between two hybrid *S. phureja x S. stenotomum* clones. QTLs have been identified and validated for the new genetic loci in this diploid potato family contributing to general resistance against late blight (Costanzo *et al.*, 2005).

Potato breeding widely exploits molecular techniques for generation and conservation of advanced clones, increasing the potato cultivar number every year (Fig. 3). Reliable maintenance of large culture collections is becoming more problematic and a rapid and robust method for variety differentiation is becoming highly desirable. The validation of a set of six SSRs markers that can be used to differentiate over 400 potato cultivars has been reported (Reid and Kerr, 2007).

Prospects

Genomic research allows high-throughput analysis for crop improvement. Genetic markers designed to cover a genome extensively allow not only identification of individual genes associated with complex traits by quantitative trait loci analysis but also the exploration of genetic diversity with regard to natural variations.

Wild relatives are valuable knowledge that can upscale with valuable traits the crop species. Nowadays, only a little fraction is exploited for crop improvement. One of the basic issues of crop improvement is to access the genetic variation from such wild species. This is particularly important to the transfer of valuable, novel genes from wild

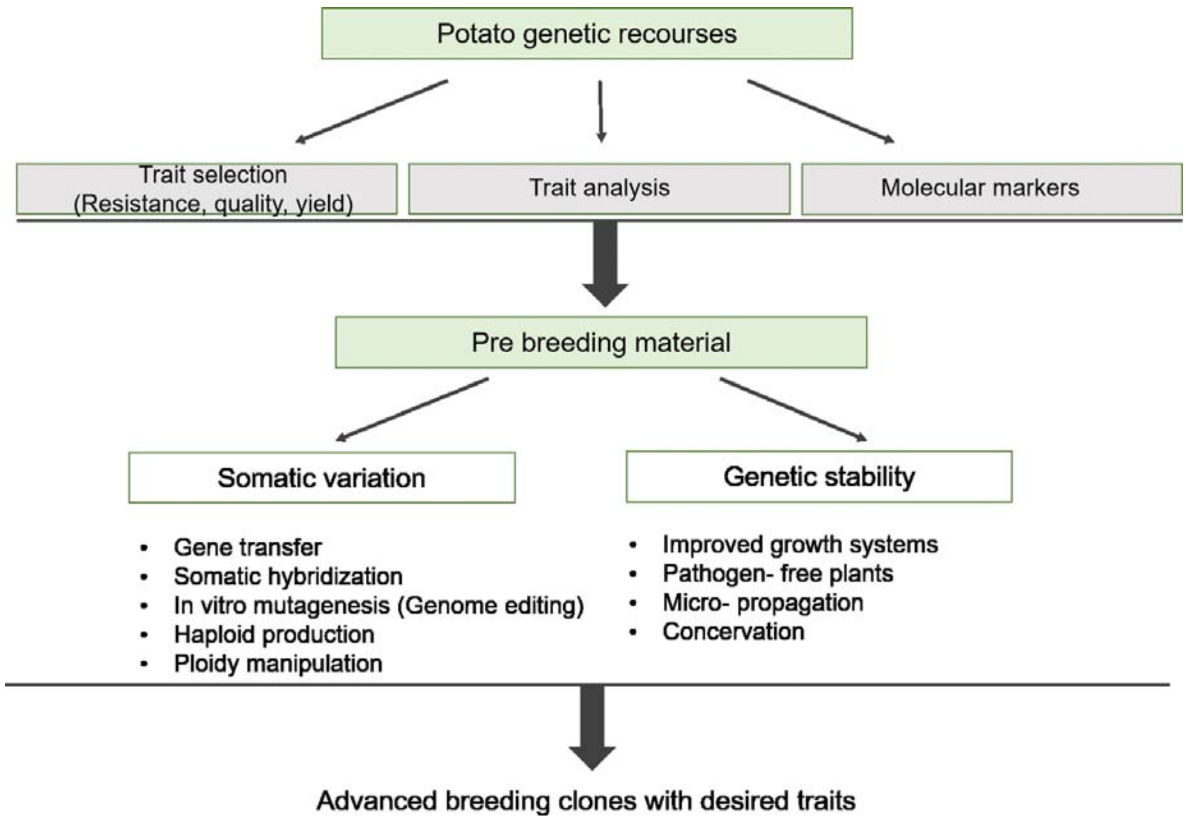

Fig. 3. Gene variants are a valuable tool for improving potato cultivars. Schematic overview of the individual sections that constitute the integrated management of potato genomic resources for the generation of elite breeding clones with improved agronomical traits of interest.

relatives to crops for non-food uses. Biotechnology offers the greatest potential in contributing solutions to problems that agriculture is facing now and the years to come.

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ΑΡΘΡΟ ΑΝΑΣΚΟΠΗΣΗΣ

Μοριακές πρόοδοι στη βελτίωση των γεωργικών καλλιεργειών για την κάλυψη των σύγχρονων απαιτήσεων στη γεωργία

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Περίληψη Ο ηλίανθος, ο αραβόσιτος και η πατάτα, είναι μεταξύ των σημαντικότερων καλλιεργειών στον κόσμο. Προκειμένου να βελτιωθούν διάφορα χαρακτηριστικά τους, οι καλλιέργειες έχουν υποστεί γενετική τροποποίηση σε μεγάλο βαθμό. Αν και οι μοριακοί δείκτες έχουν χρησιμοποιηθεί με επιτυχία για την ταυτοποίηση απλών χαρακτηριστικών, όπως η γονιμότητα, η ανοχή σε ζιζανιοκτόνα ή η αντίσταση στα παθογόνα, σημαντικά αγρονομικά χαρακτηριστικά, τα οποία είναι πολύπλοκα και πο-

σοτικά, όπως η απόδοση, η αντοχή σε συνθήκες στρες από βιοτικούς και αβιοτικούς παράγοντες και η ποιότητα του σπόρου, παραμένουν μία πρόκληση και απαιτούν προσεγγίσεις που περιλαμβάνουν τη μελέτη ολόκληρου του γονιδιώματος. Γενετικό υλικό για αυτές τις καλλιέργειες διατηρείται σε τράπεζες σε παγκόσμια κλίμακα και αντιπροσωπεύει πολύτιμους πόρους για τη μελέτη σύνθετων χαρακτηριστικών. Σήμερα, οι τεχνολογικές εξελίξεις και η δυνατότητα αλληλούχησης ολόκληρων γονιδιωμάτων έχουν καταστήσει εφικτές νέες προσεγγίσεις στο επίπεδο του γενώματος. Η μοριακή βελτίωση, συμπεριλαμβανομένων τόσο των διαγονιδιακών μεθόδων όσο και της βελτίωσης με τη βοήθεια γενετικών δεικτών, διευκόλυνε την ταυτοποίηση δεικτών για γενετικούς χάρτες υψηλής πυκνότητας και επέτρεψε μελέτες συσχέτισης ολόκληρου του γονιδιώματος και τη γονιδιακή επιλογή στον ηλίανθο, τον αραβόσιτο και την πατάτα. Η επιλογή μέσω γενετικών δεικτών σχετιζόμενων με τις αποδόσεις υβριδίων έχει δείξει ότι η γονιδιωματική επιλογή είναι μια επιτυχημένη προσέγγιση για την αντιμετώπιση σύνθετων ποσοτικών χαρακτηριστικών και μπορεί να διευκολύνει την επιτάχυνση των προγραμμάτων αναπαραγωγής σε αυτές τις καλλιέργειες στο μέλλον.

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