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Breeding potato for high yields: A review

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Abstract

This article overviewed important topics related to the importance of potatoes, potato taxonomy and its origin and domestication. It also provided participatory research approach in potato breeding, and farmers' trait preferences in potato breeding in Rwanda. Moreover, it went over potato genetics, conventional potato breeding for high yield, and molecular breeding applied to potato breeding such as maker-assisted breeding (MAB). In addition, gene action, and combining ability of potato yield were reviewed. Integration of MAB into conventional potato breeding program is promising for further research for crop improvement. This review may serve as a general frame work and important background information for potato breeders.

Keywords: Breeding for high yield, gene action, potato, Rwanda.
Abbreviation: MAB_maker-assisted breeding.

Introduction

Potato *(Solanum tuberosum* L.*)* is an important source of food globally. Potatoes are among the most widely-grown crop plants in the world, giving good yield under various soil and weather conditions (Lisinska and Leszczynski, 1989). Potato is the third most important food security crop in the world after rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) (Haverkort et al., 2009). Potato production growth rate is the highest among other main food crops such as wheat, maize, and rice, due to its high yield potential and excellent nutritional characteristics. Potato food quantity produced in one hectare is two to four fold than the food grain crops produced on the same unit area (FAO, 2008). In terms of water uptake, potato produces more food per unit water than any other major crop and seven times more efficient than cereals (CIP, 2008). According to Lachman et al. (2001), annual worldwide production of potatoes is approximately 350 million tons and more than one billion people worldwide eat potato (CIP, 2008). The world average per capita consumption in 2005 was estimated at 33.7 kg (FAO, 2008), while the Rwandan per capita consumption of potatoes is approximately 125 kg per person per annum. The highest potato consumption is in Europe with a per capita consumption of about 96 kg, followed by North America at 63 kg. The per capita consumption is low in Latin America (24 kg), Asia (12 kg) and Africa (8 kg) (FAO, 2008). However, in developing countries the per capita consumption and production is increasing where its production growth is more than any other food crops (FAO, 2013). The high consumption rate of potatoes is attributed to both their palatability and high nutritive value (Rytel et al., 2005). Potatoes serve as a major food source, as well as an inexpensive source of energy and good quality protein (Lachman et al., 2001). Potato is very rich in nutrients and can provide nutrition to the growing global population (Secor, 1999). It is a very low fat food with high content of carbohydrates. Also it has significant amounts of quality protein such as lysine, substantial amounts of vitamins, especially vitamin C, B and A (Kolasa et al., 1993; Lachman et al., 2001; Dale et al., 2003). Such important nutritional value makes potato an efficient crop in combating malnutrition (FAO, 2008). Kant and Block (1990) stated that potatoes are the third largest source of vitamin B_6 for adults (19-74 years of age). They also reported that potatoes were the second most important contributor of vitamin B_6 for the elderly, who are especially at risk of chronic disease. Vitamin B_6 is involved in amino acid, nucleic acid, glycogen, and lipid metabolism. It influences hormone modulation, erythrocyte production, and immune and nervous system functions. It is also proposed to play a major role in the etiology and/or treatment of various chronic diseases such as sickle cell anemia, asthma, and cancer (Kolasa et al., 1993). Potato tubers are also important sources of minerals including phosphorous, calcium, zinc, potassium, and iron and their value in the human diet is often understated or ignored, particularly as a source of ascorbic acid (Dale et al., 2003; Yilmaz et al., 2005; Andre et al., 2007). Potato has shown a steadily growth rate over other main crops in developing countries (CIP, 2008) and remains an important role in the food security, nutrition and combating hunger (FAO, 2013).

Taxonomy

The taxonomy of cultivated potatoes has been controversial with anywhere up to 20 species recognized (Huaman and Spooner, 2002). The word "potato" commonly refers to the potato of commerce belonging to the species *Solanum* *tuberosum* L. and other cultivated tuber-bearing species found in South America. These plants belong to the family *Solanaceae*, genus *Solanum*, section *Petota*. Most species in section *Petota* possess underground stolons bearing potato tubers at their tips, but some species lack these characteristic structures. Therefore, section *Petota* was divided into two subsections; subsection *Potatoe* containing both cultivated and wild tuber-bearing species, and subsection *Estolonifera* that contains non-tuber-bearing series (Hawkes, 1992). The tuber is the edible part of the potato, which is a part of the stem that stores food and plays a role in propagation. The tuber is also regarded as an enlarged stolon. Stolons are formed from lateral buds at the bottom of the stem (Beukema and Van der Zaag, 1990). Spooner et al. (2005) reported that all landraces of cultivated potato form a common gene pool and have a monophyletic origin from Andean and Chilean landrace complex. Using simple sequence repeat (SSR) DNA markers in combination with morphological analysis, Spooner et al. (2007) suggested classifying the cultivated potatoes into four species; *S. tuberosum*, *S. ajanhuiri*, *S. juzepczukii*, and *S. curtilobum*. According to Huaman and Spooner (2002), all landrace populations of cultivated potatoes are a single species, *S. tuberosum*, with eight cultivar groups. The landrace potato cultivars are highly diverse, containing diploids ($2n = 2x = 24$), triploids ($2n = 3x = 36$), tetraploids ($2n = 4x = 48$), and pentaploids ($2n = 5x = 60$). The tetraploids are the highest yielding and they are the sole cytotype of modern cultivars (Ames and Spooner, 2008).

Origin and domestication

Cultivated potato (*Solanum tuberosum L.*) originated in the Andes of Peru and Bolivia in South America. This species was first domesticated in Bolivia more than 8,000 years ago (Hawkes, 1994). It thereafter expanded to Mexico and Central America (Hawkes, 1994). Spanish explorers took it into Europe from where it reached North America, Asia and Africa (Beukema and Van der Zaag, 1990). In Rwanda, potato was introduced by the German missionaries at the end of 19th century (Monares, 1984). At that time, Rwandans did not appreciate this crop product and refused to grow and use it. However, potato cultivation became important when a serious famine occurred in Rwanda during the 1940s (Munyemana and Von Oppen, 1999). Subsequently, potato was adopted as one of the subsistence crop especially in the highland region, which is favourable for its successful production. In the country potato became a commodity crop and remained very popular so that in 1979, a national program was established geared towards potato improvement [(Programme National pour l'amélioration de la pomme de terre (P.N.A.P.)] within the Institut des Sciences Agronomiques du Rwanda (ISAR) to encourage and strengthen its production (Kidane-Mariam, 1987). Because of its significance as a staple food, the Government of Rwanda considers it as a food security crop and an important source of income to the growers and traders (Monares, 1984). Currently, potato is the second major food crop after cassava in Rwanda and it is also an important cash crop for growers and traders (FAOSTAT, 2013). It grows well throughout the country but the major production is localised in the high altitude zones, whose weather conditions favour it (Munyemana and Von Oppen, 1999).

Participatory research approach in potato breeding

Participatory rural appraisal (PRA) known as participatory learning and action has been extensively used in development research, action and evaluation (Narayanasamy, 2009). According to Rhodes and Booth (1982) a participatory rural appraisal research approach would involve both farmers and scientists when developing new technologies. Technologies should be adapted to local conditions with active farmer participation for successful research and development. However, the link between research and farmers is very weak or absent in developing countries (Ortiz et al., 2008). This results in a failure to adopt new technologies. In many cases when farmers were actively involved in plant breeding at various levels of the breeding process that led to successful adoption of new varieties. Participatory methods consider the value of farmers' knowledge, their preferences, ability and innovation, and their active exchange of information and technologies as was demonstrated during farmer field school approach at CIP (Ortiz et al., 2008). In the last decade at CIP, participatory research approach in potatoes provided a fruitful interaction on the benefits that can be generated to famers and thus promoted learning and innovation in many countries (Graham et al., 2001). For example, in Indonesia, farmer guided research on cultivation practices that was linked with integrated pest management (IPM) capacity built through farmer field school enabled farmers to learn, interact and implement new technologies with researchers. In Peru, participatory research was successful on combined use of varieties and fungicides within farmer field schools. In Bolivia farmers were involved in making crosses and selection in potato (Graham et al., 2001). In Kenya, farmers were involved in evaluating sweet potato varieties and selected four, due to their high yield and wide adaptation, which coincided with the breeders' selection (Ndolo et al., 2001). In Rwanda, farmers participated in screening materials distributed by CIP during on-farm trials and successfully released improved varieties with late blight resistance (Devaux and Tegera, 1981).

Farmers' potato trait preferences in Rwanda

Previous studies (Luthra et al., 2005) confirmed that genotypes with high tuber yields are promising candidate parents in a breeding program. Moreover, these genotypes might exhibit desirable tuber characteristics for consumer choice with productive flowers for sexual recombination for breeding. According to Kaushik et al. (2007), the use of accessions with high yield as parents in a breeding program is one of the most effective strategies to increase yield. It is therefore essential to consider farmers' knowledge and preferred traits to be included in cultivar development and variety selection. Subsequently, this would enhance the potential for adoption of new developed varieties. High yield, disease resistance and high dry matter content are the most important attributes preferred by farmers in Rwanda (Muhinyuza et al., 2012).

Potato genetics

Solanum tuberosum L. is tetrasomic with four different alleles at one locus (Bradshaw and Mackay, 1994; Carputo and Barone, 2005). The autotetraploid nature of potato makes the four set of chromosomes entirely homologous. Pairing is thus completely random within each group of four homologous chromosomes at meiosis and this results in tetrasomic inheritance (Sleper and Poehlman, 2006). Therefore, dominance or intra-locus interaction and inter-locus interaction (epistasis) occur, and all are factors important in potato breeding programs. The level of heterozygosity is influenced by the alleles within a locus and

Table 1. Multi-allelelism in an autotetraploid potato: the number of first, second and third order possible interactions for the five different tetrasomic conditions.

Tetrasomic condition	1st	2nd	3rd	Total
$a_1a_2a_3a_4$	6	4	1	11
$a_1a_1a_2a_3$	3	1	0	4
$a_1a_1a_2a_2$	1	0	0	1
$a_1a_1a_1a_2$	1	0	0	1
$a_1a_1a_1a_1$	0	0	0	0

$a_1a_1a_1a_1$: mono-allelic locus; all alleles are identical; balanced
$a_1a_1a_1a_2$: di-allelic locus; two different alleles in unequal frequency; unbalanced
$a_1a_1a_2a_2$: di-allelic locus; two different alleles occur with equal frequency; balanced
$a_1a_1a_2a_3$: tri-allelic locus; three different alleles
$a_1a_2a_3a_4$: tetra-allelic locus; four different alleles

the more diverse the alleles, the higher the heterozygosity (Acquaah, 2007). Five tetrasomic conditions are possible at an individual locus in an autotetraploid (Acquaah, 2007) (Table 1). Eleven different possible interactions are possible for the tetra-allelic condition whereas the mono-allelic has none. The tetra-allelic condition give the maximum heterosis due to inter-locus interactions of the tetrasomic potato (Sleper and Poehlman, 2006). The highest level of heterosis will occur as the frequency of tetra-allelic loci increase. Similarly, the number of inter-locus interactions will also occur as the frequency of tetra-allelic loci increases. In breeding potato for high yield, inter and intra-locus interactions are therefore all important (Sleper and Poehlman, 2006). Consequently, the segregation of heterotic seedling plants in a population is the highest when the parents are unrelated, have a very low inbreeding coefficient, and many loci with different alleles (Ross, 1986). In potatoes, heterosis is of great importance since genetic variation is achieved in the F_1 generation (seedlings) after hybridization (Bradshaw and Mackey, 1994; Sleper and Poehlman, 2006).

Breeding potato for high yield

Identification of superior parents with high yield and desirable traits is the basis of the potato breeding program. Potato breeders use various methods including conventional and molecular breeding to select the best progenitors and progenies (Acquaah, 2007). Conventional breeding uses hybridization, followed by clonal selection to improve potato for the desired character (Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). The selection procedure starts with identification of desirable parents among commercial cultivars, which are heterozygous, followed by crossing selected superior genotypes for the traits under consideration. The value of a hybridization is determined with mid-parent values and progeny test (Acquaah, 2007). Genetic variation is achieved in the F_1 generation after designed hybridization (Bradshaw and Mackay, 1994; Acquaah, 2007). After this, selected superior F_1 individuals are clonally propagated and maintained in their original genetic state (Bradshaw and Mackay, 1994; Acquaah, 2007). Tubers harvested from each superior F_1 plant are grown in rows for evaluation. Each row represents a clone from a single F_1 plant (Bradshaw, 1994). Selected and advanced clones are tested in multi-location trials for evaluation in relation to wide or specific adaptation and yield stability (Sleper and Poehlman, 2006). Molecular breeding is the use of genetic manipulation including genetic engineering, molecular marker-assisted selection, genomic selection performed at DNA molecular levels to improve traits under consideration. Marker-assisted breeding (MAB) is the application of molecular biotechnologies, specifically molecular markers, in combination with linkage maps and genomics, to improve plant traits on the basis of genotypic assays such as marker-assisted selection (MAS), marker-assisted backcrossing (MABC), marker-assisted recurrent selection (MARS), and genome-wide selection (GWS) or genomic selection (GS) (Ribaut et al., 2010). Marker-assisted selection (MAS) is a breeding procedure in which DNA marker detection and selection are integrated into a traditional breeding program. Genetic analysis using molecular makers helps to determine the variations present among genetic resources for breeding and strategic conservation. Although conventional breeding methodologies have been successful in new cultivars development, but evaluation and selection are subjective and empirical respectively. Since scientific breeding needs more science than experience, MAB has brought great challenges, opportunities and prospects for conventional breeding. However, MAB as transgenic breeding or genetic manipulation is a supplementary addition to conventional breeding. Moreover, MAB materials and equipments are very expensive and not easily affordable, especially in the developing countries (Collard and Mackill, 2008; Ribaut et al., 2010). Therefore, integration of MAB into conventional breeding programs is a promising strategy to be used for crop improvement in the future. It can be expected that further technology development will improve MAB theory and application and gradually overcome its negative aspects. MAB should thus be widely adopted.

Gene action controlling potato yield

A large base of germplasm with genetic variability can be used to develop high yielding potato cultivars, through selection and breeding (Bradshaw and Mackay, 1994). Crossing between two unrelated parents will generate genetic variation from which to practice phenotypic selection (Bradshaw and Mackay, 1994). Superior clones can then be selected from the segregating progeny. The general combining ability (GCA) gives an indication on the average performance of a parent into its progeny; it provides an estimation of the parental gametic contribution to its offspring by the mean performance of the progeny (Bradshaw and Mackay, 1994; Falconer and Mackay, 1996). Specific combining ability (SCA) is the deviation from the progeny mean from the expected on the basis of GCA (Bradshaw and Mackay, 1994). In this case, the performance of the progeny is either superior or inferior to the parents (Falconer and Mackay, 1996). Yield is a character quantitatively inherited (Falconer and Mackay, 1996). Additive would thus be more important than non-additive gene action (Falconer and Mackay, 1996). However, in the literature, it has been reported that both GCA and SCA are significant for potato yield with GCA being less important in magnitude than SCA (Bradshaw and Mackay, 1994; Ortiz and Golmirzaie, 2004; Ruiz de Galarreta et al., 2006, Gopal et al., 2008; Haydar et al., 2009). This implies that both additive and non-additive gene actions are important for potato tuber yield with non-additive gene action more predominant.

Conclusion

This review highlighted the importance of potatoes and major aspects of potato breeding for high yield. The integration of MAB into potato conventional breeding program would be a promising strategy for yield improvement in the future. Reviews on gene action and combining ability of potato yield showed that additive and non-additive gene actions are important for tuber yield. Non-additive gene action is reported to be more predominant for yield.

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