Review article

Reproductive biology and early generation's selection in conventional potato breeding

Jane Muthoni[1,2,*], Hussein Shimelis[1], Rob Melis[1] and Jackson Kabira[2]

[1]African Centre for Crop Improvement, University of KwaZulu-Natal, Private Bag X01, Scottsxille 3209, Pietermaritzburg, South Africa
[2]Kenya Agricultural Research Institute (KARI), National Potato Research Centre, Tigoni, Kenya

*Corresponding author: jayney480@yahoo.com

Abstract

This article gives an overview of potato reproductive biology as well as selection in early generations' in conventional breeding programmes. Potato is an autotetraploid ($2n=4x=48$, 4EBN) with tetrasomic inheritance. Both interlocus and intralocus interactions occur and the more they are, the greater the heterosis. Both additive and non-addititve gene actions are important in controlling various traits. Favourable traits are fixed in F_1 generation due to clonal propagation. Potato is predominantly self pollinated; flowering and fruiting are mainly affected by genotype, day length, and temperature. Continued self-pollination results in inbreeding depression; this results in reduction of germination percentage, plant vigour, flowering, male fertility, and open-pollinated fruit set. Hybrids are generally more vigorous than open-pollinated seeds; the open-pollinated seeds are generally selfs. The principal method of potato breeding is the conventional hybridisation followed by recurrent selection in the clonal generations. The choice of parents is determined by the breeding objective; crossability and unrelatedness should also be considered. The simplest method for predicting the value of cross combinations is to evaluate progenies at seedling stage. Conventional potato breeding takes long (about 10 years) before a cultivar is released, mostly due to the slow multiplication rate of the crop. This time can be reduced through use of marker assisted selection in identifying parents with desirable traits and selecting superior clones genotypically at seedlings stage.

Keywords: Early generations selection; Potato breeding; Reproductive biology.
Abbreviations: EBN-Endosperm balance number; GCA-General combining ability; SCA-specific combimimg ability.

Introduction

The genus *Solanum* contains over 2000 species, of which only 150 are tuber bearing (Sleper and Poehlman, 2006). The basic chromosome number in *Solanum* is x = 12, and the genus contain species that constitute a polyploid series ranging from diploids ($2n=2x = 24$) to hexaploids ($2n=6x=72$) (Douches and Jastrzebski, 1993; Carputo et al., 2003; Carputo and Barone, 2005). Generally, the even-numbered polyploids (4x and 6x) are sexually fertile, while the odd-numbered polyploids are male sterile (Douches and Jastrzebski, 1993). Nearly all of the diploid species are self-incompatible out-breeders while the tetraploids and hexaploids are mostly self-compatible polyloids that display disomic inheritance (Hawkes, 1990). A more or less regular meiosis is possible in the even-numbered tetraploids and hexaploids (Wolfgang et al., 2009). About 70% of tuber-bearing species are diploids, while 5%, and 8% are tetraploids and hexaploids, respectively (Sleper and Poehlman, 2006). There are four commonly cultivated diploid species: *Solanum stenotomum, Solanum phureja, Solanum goniocalyx,* and *Solanum ajanhuiri* (Sleper and Poehlman, 2006). *Solanum phureja* is widely used in bridegcrossing, and as a source of resistance to bacterial wilt (Fock et al., 2000; Fock et al., 2001). There are two cultivated triploid species, *Solanum chaucha,* and *Solanum juzepczukii,* and one cultivated pentaploid species *Solanum curtilobum.* A common wild hexaploid, *Solanum demissum*, is the source of the major R genes that confer resistance to late blight of potatoes (Carputo et al., 2003; Sleper and Poehlman, 2006). The cultivated potato, *Solanum tuberosum* L., is an autotetraploid ($2n=4x=48$, 4EBN) species that displays tetrasomic inheritance (Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). The species has a monophyletic origin, which means that it developed out of one wild plant, and hence it has a narrow genetic diversity. There are two major subspecies of *Solanum tuberosum*; *andigena* or Andean, and *tuberosum* or Chilean (Raker and Spooner, 2002). The Andean potato is adapted to the short-day conditions prevalent in the equatorial and tropical regions where it originated (Raker and Spooner, 2002). It is indigenous to Andean region from Venezuela to northern Chile and Argentina (Hawkes, 1990). The Chilean potato is adapted to the long-day conditions prevalent in the higher latitude region of southern Chile, especially Chiloé Island and Chonos Archipelago, where it is thought to have originated (Hawkes, 1990; Hijmans, 2001). The genetic relationship between subspecies *tuberosum* and *andigenum* is unresolved (Raker and Spooner, 2002). Grun, (1990) suggested that *tuberosum* was distinct from *andigenum* based on

cytoplasmic sterility factors, geographical isolation, and ecological differences. Hawkes, (1990) distinguished the two subspecies on the grounds that subspecies *tuberosum* has fewer stems, more horizontal foliage, less-dissected leaves, wider leaflets, and thicker pedicels than *andigenum*. In addition, subspecies *andigenum* has five chloroplast genotypes (A, C, S, T, and W) while subspecies *tuberosum* has only three (A, T, and W) (Hosaka and Hanneman, 1988). Conventional potato breeding involves initial crossing of parents possessing complementary traits followed by selection in the subsequent clonal generations (Sleper and Poehlman, 2006). Because the crop is generally vegetatively propagated, favourable traits are fixed in the F_1 generation. The clones are highly heterozygous and exploit heterosis. However, progenies produced by selfing of clones reveal strong inbreeding depression (Arndt and Peloquin, 1990). For effective potato breeding, there is need to understand the crop's reproductive biology as well as the breeding procedures. This review article gives an overview of reproductive biology of potato and selection in the early generations in a conventional breeding programme.

Genetics of *Solanum tuberosum*

Solanum tuberosum is an autotetraploid ($2n=4x=48$, 4EBN) and there can be four different alleles at a locus (Ross, 1986). The tetraploid nature of cultivated potato can be exploited by the breeder to improve desirable characteristics. It is well known that asexually propagated species such as potatoes have evolved taking advantage of nonadditive or epistatic gene action (Sleper and Poehlman, 2006). Because of the potato's autotetraploid nature, intralocus interactions (heterozygosity) and interlocus interactions (epistasis) occur, and are important when selecting breeding procedures to improve certain traits; it is assumed that increased heterozygosity leads to increased heterosis (Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). Heterosis in potato is when the progeny surpasses the value of the best parent or the parental mean. The exploitation of heterosis is by far the most important goal in potato breeding. The inheritance of heterosis is by minor genes or by the side effects of the major genes. Their action can proceed in an additive (general combing ability) or in a non-additive manner (specific combing ability): In most case both operate (Ross, 1986). Heterosis in potato is based mainly on non-additive interactions of genes and it comprises intralocus (overdominance) as well as interlocus (epistasis) interaction between genes and alleles (Ross, 1986). The level of heterozygosity is influenced by how different the four alleles are within a locus; the more diverse they are, the higher the heterozygosity and the greater the number of interlocus (epistatic) interactions and hence the greater the heterosis (Ross, 1986; Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). To see how increased heterozygosity can lead to more epistatic interactions, it is necessary to identify the allelic conditions possible in an autotetraploid (Caligari 1992; Sleper and Poehlman, 2006). Five tetrasomic conditions are possible at an individual locus in an autotetraploid (Table 1).
The $a_1a_1a_1a_1$ is a monoallelic locus where all alleles are identical.
$a_1a_1a_1a_2$ is an unbalanced diallelic locus where two different allele are present in unequal frequency.
$a_1a_1a_2a_2$ is a balanced diallelic locus where two different alleles occur with equal frequency.
$a_1a_1a_2a_3$ is a triallelic locus where three different alleles are present.

$a_1a_2a_3a_4$ is a tetraallelic locus where four different alleles are present.

It is hypothesized that the tetraallelic condition provides the maximum heterosis because more interlocus interactions are possible for this tetrasomic condition than for the other configurations (Ross, 1986; Sleper and Poehlman, 2006). For example, in the tetrallelic condition, the six first-order interactions are: a_1a_2, a_1a_3, a_1a_4, a_2a_3, a_2a_4, a_3a_4. The four second-order interactions are: $a_1a_2a_3$, $a_1a_2a_4$, $a_1a_3a_4$, $a_2a_3a_4$. The one third-order interaction is $a_1a_2a_3a_4$. There are a total of 11 different interactions possible for the tetraallelic condition. This is in contrast to the monoallelic condition, which has no interactions. The highest level of heterosis will occur as the frequency of tetraallelic loci increase. The greatest number of interlocus interactions will also occur as the frequency of tetraallelic loci increase. In breeding potatoes for higher tuber yields, inter- and intralocus interactions have been shown to be important; procedures that maximize the frequency of tetraallelic loci should be considered in breeding potato for increased yields (Ross, 1986; Bradshaw and Mackay, 1994; Sleper and Poehlman, 2006). Therefore, the segregation of heterotic seedlings in a population is likely to be greatest when three conditions are fulfilled: 1) the parents possess as low a coefficient of inbreeding as possible, 2) as many loci as possible have different alleles and, 3) the parents belong to different genepools which improves the chances of allelic diversity i.e. wide hybridisation (should be as unrelated as possible) (Ross, 1986). In potatoes, heterosis is of direct relevance for improving traits under consideration as it gets fixed in F_1 generation (seedling) due to vegetative propagation of the crop. Because potato is a highly heterozygous crop, an increase in heterozygosity results in heterosis. Distantly related genotypes are more complementary and they produce heterotic progenies (Ross, 1986).

Flowering in *Solanum tuberosum*

Potato has a terminal inflorescence consisting of 1 to 30 (but usually 7 to 15) flowers, depending on cultivar (Acquaah, 2007). The flower is 3-4cm in diameter and contains five sepals and petals, and a bilobed stigma (Acquaah, 2007). The five petals give the flower a star shape (Caligari, 1992). The petals vary in size with the cultivar, and the colour varies from white to a complex range of blue, red, and purple (Sleper and Poehlman, 2006; Acquaah, 2007). The petals are united and tubular. The stamens are attached to the corolla tube and bear erect anthers (Almekinders and Struik, 1996). The anthers are bright yellow except for those produced on male sterile plants, which are light yellow or yellow-green in colour; the stigma protrudes above a cluster of large, bright yellow anthers (Sleper and Poehlman, 2006). Flowers open starting with those nearest the base of the inflorescence proceeding upwards at a rate of about 2-3 flowers per day (Acquaah, 2007). At the peak bloom, there are usually 5-10 open flowers (Caligari, 1992; Acquaah, 2007). Flowers stay open for only 2-4 days, while the receptivity of the stigma and duration of pollen production is about two days (Sleper and Poehlman, 2006). Flowers open mostly in the early morning, although a few may continue to open throughout the day (Sleper and Poehlman, 2006). Genotype, day length and temperature are the main factors that determine flowering and fruiting in potato. Flowering in potato is best when long days (around 16 hours), abundant moisture, and cool temperatures prevail (Almekinders and Struik, 1996; Sleper

Table 1. The number of first, second and third-order possible interactions and their sums for the five different tetrasomic conditions in an autotetraploid.

| Tetrasomic Condition | Number of heteroallelic interaction | | | Total | Portion of Haploids(2x) conserving one first-order Interaction |
	First order	Second order	Third order		
$a_1a_2a_3a_4$	6	4	1	11	All
$a_1a_1a_2a_3$	3	1	0	4	5/6
$a_1a_1a_2a_2$	1	0	0	1	2/3
$a_1a_1a_1a_2$	1	0	0	1	1/2
$a_1a_1a_1a_1$	0	0	0	0	none

Adapted from Sleper and Poehlman, (2006)

and Poehlman, 2006). Photoperiod of 12-14 hours and night temperatures of 15-20°C has been shown to favour flower production and berry setting in potato (Almekinders, 1992; Gopal, 2006). Short days during flowering may lead to abscission of the floral bud, giving the impression that the cultivars do not flower well (Almekinders and Struik, 1996). Therefore, in tropics and sub-tropics, conditions conducive for flowering and fruiting are available only at high altitudes (>1500 m above sea level) (Gopal, 1994). A wide genetic variability has been observed for days to flowering, duration of flowering, flowering intensity, and berry setting (Gopal, 2006). Gopal (1994) conducted a survey of the flowering behaviour, male sterility, and berry setting in 676 accessions of tetraploid *Solanm tuberosum* from 25 countries. He conducted his studies outdoors at Kufri in India (32^0N, 70^0E, 2500 masl) during summer (12.1-14.1 hours of day length). He found that flowering intensity ranged from the dropping of floral buds just after initiation to profuse blooming. Majority of the accessions (58.3%) bloomed profusely, but 20.4 % did not bloom at all. Time to flowering ranged from 6 to 15 weeks and duration of flowering from 1 to 10 weeks. Pollen stainability (as an indicator of fertility) ranged from 0 to 90%, with 23 % of the accessions being completely male sterile. Berry setting ranged from zero to more than five berries per plant, with none in 31.8% of the flowering accessions. Therefore, only 54.3% of the accessions were found to be fertile in all respects and could be used as male and female parents. He also found that premature bud abscission was the major cause of sterility. In addition to genotype, temperature, and photoperiod, other factors such as inflorescence position (Almekinders and Wiersema, 1991), plant/stem density (Almekinders, 1991), competition between flower and tuber (Thijn, 1954), precipitation and date of planting (Jauhnl, 1954) and nutrient level (Bamberg and Hanneman, 1988) are also known to influence production of flowers and fruits in potato. Increasing stem density has been shown to decrease the number of flowers per plant, berry set and seed production from every inflorenscence (Mok, 1985; Almekinders, 1991; Almekinders and Wiersema, 1991). Increasing plant density was shown to increase the proportion of primary flowers in the total number of flowers per plant and reduced the proportion of flowers on lateral stems (Almekinders, 1991). However, increasing plant density was shown to increase the number of flowers and seed weight per m^2 (Mok, 1985). Luckily, flowering is no longer a serious handicap for breeders (Bradshaw and Mackay, 1994).

Flowering induction in *Solanum tuberosum*

Some techniques that are used by breeders to enhance flowering and seed set include shading of glasshouses to reduce temperature below 22^0C, girdling or constriction of the stem, and grafting of young potato shoots onto tomato or other compatible *Solananceous* plants (Caligari, 1992; Sleper

and Poehlman, 2006). However, the last method gives weaker growth (Gopal, 1994). Another method includes growing the seed tuber on a brick and the brick is covered with sand and peat. The roots grow over the brick and when they have penetrated the soil on which the brick is lying, the covering sand is washed away. The tips of the stolons, which would otherwise produce new tubers, are then removed. This promotes vigorous stem growth and enhances flowering (Gopal, 1994). Other methods which have been reported include foliar spray with GA_3 (El-Gizawy et al., 2006).

Pollination in *Solanum tuberosum*

Potato is predominantly self-pollinated, although some cross pollination is often accomplished by bumblebees (Caligari, 1992; Acquaah, 2007). Wind pollination plays a minor role in nature. Controlled pollination may be done in the field or in the greenhouse under controlled conditions. Crosses made in the field are liable to suffer losses from wind, rain, heat and drought and most breeders therefore prefer to work in the greenhouse. The best time for crossing is early morning when temperatures are not high (Acquaah, 2007). Prior to crossing, flower buds that are mature and plump with the petals ready to separate are selected for emasculation (Acquaah, 2007). If pollinations are done in the field, it is important to emasculate just prior to crossing as the wind can break off the stigma before pollination occurs if they are emasculated too far ahead of pollination. Normally, the unopened flowers of the female parent must be emasculated one to two days before crossing to avoid self contamination. For emasculation, choose the bud that has developed the petal colour but it is unopened. Pull back the petals carefully to expose the immature anthers; pull-off all the anthers carefully with a blunt scapel or tweezers. To facilitate emasculation of the selected buds, and to prevent contamination of the emasculated flowers by the open flowers, the remaining buds and open flowers in the inflorescence should be removed (Sleper and Poehlman, 2006; Acquaah, 2007). Removing the extra flowers increases the chance that pollination will be successful and reduces competition for photoassimilates (Almekinders and Struik, 1996). In the male plant, look for a newly opened flower and pull off the anthers. Slit open the anthers using a blunt scalpel to collect pollen; dab the pollen onto stigma of the emasculated female flower and label it; pollinate again the following day (Rick, 1980). Alternatively, open flowers are collected from the male plant and laid out to dry overnight (Almekinders and Struik, 1996). In the following morning, the pollen is collected from them by shaking into gelatine capsules or small tubes (Sleper and Poehlman, 2006). To pollinate, the stigma is dipped into the pollen and then the pollination tag is attached. The emasculated flowers do not need covering to avert contamination. Germination of the pollen is completed after 30 minutes, and the ovary is fertilized within 12 hours

490

(Bradshaw and Mackay, 1994). The berries appear within a few weeks and to prevent losses, they are bagged with nylon netting of large mesh. Potato fruits (berries) contain about 50 to 500 seeds with an average of 200 seeds (CIP, 1984). Pollinations can also be done on flowers attached to stems that have been cut and placed in jars of water with an anti-bacterial agent to reduce contamination (Peloquin and Hougas, 1959; Wolfgang et al., 2009).

Fertilization problems

Biological seed production in potatoes is low due to: failure of plants to flower, dropping of buds and flowers either before or after fertilization, low pollen production, failure to produce viable pollen, male sterility, and self-incompatibility (Sleper and Poehlman, 2006). Because open pollinated berries in potato result predominantly from self pollination, formation of open pollinated berries indicates that the genotype bearing them is both male and female fertile, self compatible, and that after fertilization, flowers do not drop, but develop into fruits. Non-formation of berries, on the other hand, can be due to any one or more of the causes listed above. Berry setting is the ultimate test of fertility if these berries carry seed in them, which is generally the case (Gopal, 1994). Hence, from practical point of view, genetic blockage at any stage from floral bud initiation to seed set should be considered as sterility. Male sterility is a very serious constraint in potato breeding (Gopal, 2006). The failure to produce pollen may be an inherent characteristic with sterility being dominant over fertility. Presence of a tetrasomic gene, which is lethal when present in a homozygous condition, or partly lethal when present in a heterozygous condition has also been reported (Sleper and Poehlman, 2006). Though both pollen and ovule sterility can occur, pollen sterility ranging from partial to complete absence of pollen grains is very common in potato (Pushkarnath and Dwivedi, 1961). Almost one third of the potato cultivars derived from *Solanum tuberosum* ssp. *tuberosum* do not form berries (Ross, 1986). Male sterility in potatoes is probably controlled by more than one gene, with partial dominance or by nuclear-cytoplasmic interactions (Howard, 1978) and depends partially on environmental factors. In cultivated *S. tuberosum* potato seven types of cytoplasmic factors exists each of which condition, in combination with a specific genotype, a specific type of sterility (Grun, 1970). These cytoplasmic factors are: indehiscence(Ins), sporads (Sp[s]), shrivelled microspores (SM[s]), anther style fusion (Af[s]), thin anthers (TA[s]), females sterility (Fm[s]), and deformed flower (df[s]) (Gopal, 2006). Variations, depending on the stage at which development is blocked have also been observed within a particular type of sterility. A block can occur at any place in the development process and depending on the particular gene-plasmon interaction involved, different kinds of blockage may occur (Grun, 1970; Grun, 1990). The prevalence of sterility to such a large extent limits the use of many germplasm clones as parents, but at the same time this is advantageous because males sterile clones do not require emasculation when used as females in controlled pollinations (Gopal, 2006). Crossability in a broad sense can be defined as any natural or artificial fusion of two genetically different cells leading to hybrid progeny. Cross-incompatibility can be bilateral (in both directions) or unilateral (in only one direction); both self- and cross incompatibility governed by a series of allelomorphs are widely prevalent in potato. The cultivated diploids are obligate outbreeders due to self incompatibility governed by the S locus system (Simmonds, 1997; Hosaka

and Hanneman, 1998). This incompatibility system does not operate in tetraploids. If effectively pollinated, the sequence of decreasing seed fertility (i.e. seed production per plant) goes: diploids>*andigena*>*tuberosum*. The least fertile class is certainly the 4x *Solanum tuberosum* subspecies *tuberosum*. Experience supports the assertion as to the superior fertility of andigena over tuberosum group. There is a widespread view that the cross *tuberosum x andigena* gives progeny superior to the reciprocal, *andigena x tuberosum*. However, the matter is still unresolved (Simmonds, 1997). In general the tetraploids bear fewer seeds per berry but larger than the diploids. Seed size in any potato has a large maternal element in its determination even though seed numbers per berry are bi-parentally controlled (Simmonds, 1995). While self-incompatibility does not operate in tetraploid *Solanum tuberosum*, 40 % (21 to 74%) natural cross pollination was estimated to occur in subsp. *andigena* in the Andes (Brown, 1993) and 20% (14 to 30%) in an artificially constructed *andigena* population (Glendining, 1976). The cultivated *Solanum tuberosum* is a tetraploid in which recombination among all the four homologs is possible (Bradshaw and Mackay, 1994). Such species do not exclusively self-fertilize in their natural habitats (Brown, 1993) and they maintain high levels of heterozygosity across generations (Hosaka and Hanneman, 1998). Another problem in pollinating potato is poor nicking (i.e. unsynchronized flowering of the parents). This can be prevented by planting both the male and female parents in a greenhouse. The luxuriant growth of plants in the greenhouse ensures a long period of pollen production. The pollen can be stored under appropriate conditions for later pollination. Pollen can be stored dessicated in the refrigerator for 1 to 2 weeks and in the freezer for 6 months to one year (Sleper and Poehlman, 2006).

Comparison of hand pollination (hybrids) versus open pollination

In dealing with autotetraploid parents, there is strong evidence of the superiority (heterosis) of hand pollinated (HP) hybrids over open pollinated (OP) progeny. This is because most open pollinated seeds in potatoes are actually selfs and selfing leads to reduction of heterozygosity and hence inbreeding depression (Ross, 1986). Previous studies have shown that hybrid progenies are more vigorous, more yielding, have a greater uniformity of tuber yields than the open pollinated progenies (Gisela and Peloquin, 1991). This is of importance in hybrid seed production as it can help identify open pollinated seeds from hybrids. There has been speculation that hybrid vigour might be promoted by selecting for large seeds on the grounds that crossed seeds are bigger than the inbred ones. However, experiments failed to reveal any useful response to selection; at most seedlings from large seeds were transiently larger (Simmonds, 1995).

Combining abilities in potato breeding

According to Griffing (1956a), the concepts of general combining ability (GCA) and specific combining ability (SCA) were introduced early (Sprague and Tatum, 1942). General combining ability is the average performance of a parental line in hybrid combinations and SCA is the contribution of an inbred line to hybrid performance in a cross with a specified inbred line, in relation to its contributions in crosses with an array of specified inbred lines (Sleper and Poehlman, 2006) i.e. the departure of a progeny mean from that expected on the basis of the GCAs of its parents is called the SCA. In potatoes both GCA and SCA

are important in conditioning traits, and both are fixed in the F_1 generation. This is because with clonal propagation, there is no further segregation. General combining ability represents mainly the additive and additive X additive type of genetic variance (Gopal, 1998). In potatoes, the SCA was reported to be more important than GCA in the inheritance of tuber yields (Plaisted et al., 1962; Tai, 1976; Killick, 1977, Gopal, 1998), while the opposite was reported to be the case by Maris (1989), and Brown and Caligari (1989). Galarreta et al. (2006) and Gopal (1998) found that SCA was more important than GCA in determining yields, tuber number per plant and average tuber weight in the seedling and the first two clonal generations. In addition, Gopal (1998) found that GCA for various characters varied from generation to generation; correlation coefficients between generations for GCA ranged from r=0.5 to r=0.8. General combining ability seems to be significantly larger than SCA for tuber yields and quality traits in crosses between non-related parents while SCA appears to be more important among related parents (Ortiz and Golmizaie, 2004). This is because in related material the number of different alleles is likely to be limited. Consequently, variation in additive gene action is limited as well while non-additive gene action, like episasis, can result in a relatively large between progeny variation. In such experiments the SCA effects are likely to be prominent (Neele et al., 1991). Plaisted et al. (1962) speculated that informal previous selection which narrowed the genetic base of the tested genotypes may be one of the possible causes for obtaining greater estimates of SCA variance for various characters. Killick and Malcolmson (1973), using a concept developed in evolutionary population genetics, suggested that traits subjected to directional selection would be expected to show little additive genetic variance, but a large degree of dominance and epistasis, whereas the reverse would be true for traits subjected to stabilising selection. General combining ability was found to be more important than SCA for maturity (Johansen et al., 1967; Killick, 1977; Maris, 1989), while SCA effects were found to predominate in determining resistance to late blight (Killick and Malcolmsom, 1973). In conditioning the after-cooking blackening in potatoes, it was reported that GCA was more important than SCA (Dalianis et al., 1966; Killick, 1977). Killick (1977) found SCA to be most significant for many traits of agricultural importance in potato. Tai (1976) reported that variation between progenies for tuber yields and number of tubers per plant was dominated by SCA while for average tuber weight and specific gravity GCA was more important. Another study showed that GCA was more important in determining the inheritance of number of stems, stolon length, plant appearance, skin colour, tuber shape, tuber yield, eye depth, number of tubers per plant, average tuber weight, harvest index, foliage weight, and total biomass (Neele et al., 1991). In yet another study, it was found that GCA dominated in determining total tuber yield, number of tubers per plant and plant appearance while the mean tuber weight depended on both GCA and SCA (Brown and Caligari, 1989). Tung et al (1992) found that SCA was more important than GCA in conditioning resistance to bacterial wilt, and there was a strong genotype x environment interaction. From the foregoing, it appears the literature on combining ability in potatoes is conflicting.

Conventional potato breeding

Potato breeding worldwide has traditionally involved making crosses between pairs of parents with complementary features based on phenotype in order to generate genetical variation on which to practise phenotypic selection over a number of vegetative generations, the aim being to identify clones with as many desirable characteristics as possible for release as new cultivars (Bradshaw and Bonierbale, 2010). Selection of parents and prediction of cross outcomeMaking crosses between pairs of parents with complementary features has traditionally been, and still is the main route for the development of new cultivars (Acquuah, 2007; Sleper and Poehlman, 2006; Caligari, 1992). The parents are usually chosen on the basis of their phenotypes (Bradshaw and Mackay, 1994; Caligari, 1992). The aim is to generate genetic variation on which to practice phenotypic selection over a number of vegetative generations for clones with as many desirable characteristics as possible for release as new cultivars (Acquaah, 2007; Sleper and Poehlman, 2006; Caligari, 1992). The choice of parents depends largely on the aims and objectives of the breeder (Caligari, 1992). An important criterion for the choice of parents is their crossability and unrelatedness (Wolfgang et al., 2009). Often the parents are chosen due to their performance *per se*. Theoretically, this cannot be secure in clonal crops like potatoes; clonal varieties are highly heterozygous hybrids and polyploids, so that segregation in crossings is almost unpredictable (Wolfgang et al., 2009). Suggestions that have been made for better assessment of parents is the offspring performance from test crosses; the other suggestion is to work on reduced polyploidy level, which has been especially proposed for breeding tetraploid potatoes (Ross, 1986). In general, parents should have a good combing ability and good performance over all traits. In potatoes, it has been observed that SCA is nearly as large as GCA, and in some cases SCA has been observed that is clearly larger than GCA (Tai, 1976; Killick, 1977). In situations where not much is known about the performance of a cross, the number of cross combinations should be increased to the maximum of the breeder's capacity and the number of genotypes per cross should be kept small (Wolfgang et al., 2009). This is based on selection theory which shows that if "the breeder has no prior knowledge on the cross, the breeder has to make as many crosses as possible"; this also minimizes the risk of raising genotypes with poor performance (Wricke and Weber, 1986). Potatoes are highly heterozygous so that dominance and epistatic effects contribute considerably to clone performance. Therefore, it should be assumed not much is known about the value of a cross combination until it has been made and the progeny tested. The simplest method for predicting the value of cross combinations is to evaluate progenies at seedling stage (Neele and Louwes, 1989; Neele et al., 1991). If a close relation between seedling performance and performance in subsequent field generations exists, as found by Brown and Caligari (1989) for tuber yield and plant appearance and by Neele and Louwes (1989) for crisp quality and dry-matter content, progeny selection could be carried out at the seedling stage. Progeny tests offer the means to replace phenotypic recurrent selection with a much more efficient, multitrait, genotypic recurrent selection programme, in which the generation cycle time can be reduced by several years, because parents with good GCA can be recognised shortly after each round of hybridization. Then their progeny can be used for subsequent crossing cycles and selection, whilst cultivars are being produced from resowings of the best progenies (Bradshaw and Mackay, 1994). Progeny means is therefore a reliable approach in identifying superior cross combinations (Brown and Caligari, 1989; Gopal, 1997). For highly heritable traits, the midparent value is a good predictor of the mean performance of the offspring, and a few carefully chosen crosses can be made (Bradshaw et al.,

2000). However, with an only moderately heritable trait such as yield, offspring mean is less predictable, and more crosses need to be made to ensure that they include the best possible cross for the trait (Bradshaw, 2007). For such a trait breeders still have rely on phenotypic data and the concepts of quantitative genetics to determine crossing strategies (Bradshaw, 2007). Mid parent values for yield and quality traits can complement the results of the seedling progeny tests. The mid-parent value is the predictor that is generally used in potato breeding programmes because the method is quick, cheap, and easy. No time is lost with the production of hybrid seed and seedlings, and the data are available from experiments already performed with the clones of interest. If additional information is required, the cost of trials is not likely to interfere with a large number of entries to be tested (Neele et al., 1991). Neele et al (1991) found the seed potato harvest prediction by the mid-parent value to be very good for most characters, with many correlation coefficients between progeny mean and miparent value exceeding r = 0.8. Moderate correlation coefficients were noted for foliage weight, number of stems, tuber shape and number of tubers. However, at ware potato harvest, the correlation coefficients were lower; tuber yield in particular was poorly predicted by the mid-parent value. Maris (1989) obtained moderate to good correlation coefficients (r=0.51 to r=0.85) between the mid-parent value and the actual progeny performance for various agronomically important characters. For yield and number of tubers, however, the correlations were moderate (r=0.51 and r=0.59 respectively). Brown and Caligari (1989) were not able to accurately predict the progeny performance by the mid-parent value. This suggests that a prediction based on the mean of the parental values might have limited value and might not result in progenies with the best prospects.

Selection in early generations for agronomic traits

The maximum genetic variation is exposed and is available for selection in the early generations i.e. seedling and first clonal generations. Therefore, any increases in efficiencies of selection in these stages are likely to result in major improvements in the quality of material advancing to the later stages of selection, and to increase the likelihood of genetic improvement in cultivar production (Bradshaw and Mackay, 1994). The programme at the Scottish Crop Research Institute (SCRI) before 1982 was typical of most relatively large programs in its handling of the early generations (Bradshaw, 2007; 2009; Bradshaw and Bonierbale, 2010): Visual selection of individual genotypes reduced the number of potential cultivars from 100,000 in the seedling generation (SG) in the glasshouse to 40,000 spaced plants at a high-grade seed site in the first clonal generation (FCG), then to 4,000 unreplicated three- or four-plant plots at the seed site in the second clonal generation (SCG) and finally to 1,000 clones in replicated yield trials at a ware site in the third clonal generation (TCG) (Bradshaw and Mackay, 1994; Bradshaw and Bonierbale, 2010). However, such intensive early-generation visual selection of individual clones was found to be very ineffective (Caligari, 1992; Tarn et al., 1992; Bradshaw et al., 1998). There are reports that repeatability of the performance of clones selected in early generations is low to very low in subsequent generations, and that selection of individual clones on the basis of general impression results at best in a random reduction in number of genotypes (Howard, 1963; Tai, 1975; Swiezynski, 1978; Brown et al., 1984; Brown et al 1987a; Brown et al., 1987b; Maris, 1988; Brown and Caligari, 1989; Gopal et al., 1992). Tai (1975) and Brown et al. (1987b) suggested that instead of individual

clonal selection, progeny selection should be carried out since the mean performance of a cross was found to have good repeatability in early generations. The progeny tests are used to discard whole progenies before starting conventional within-progeny selection (Bradshaw, 2007). Seedling progeny evaluation by breeders' visual preference scores can be used to reject entire crosses on the grounds that they were less likely than others to contain clones of commercial worth (Brown et al 1987a; Brown et al., 1988; Bradshaw et al., 1998). Mild clonal selection within the remaining crosses could then be practised in the first and second clonal generations to achieve the same target of 1,000 clones for replicated yield trials, but with a much improved frequency of superior clones. If necessary, the population sizes of the best crosses could be increased by sowing more true seed (resowings) of each (Bradshaw et al., 1998). Gopal (1997) found that population means improved for major characters of economic importance, i.e. tuber yield (g/plant), average tuber weight (g), tuber shape, and general impression as the generations advanced from seedling to second clonal generation. This implies that these characters cannot be efficiently selected for in seedling generation. In addition, plant vigour was higher in the clonal generations than in the seedling generation. More vigorous growth in clonal generations than in seedling generation (due to higher food reserves in the tuber for the young plant) indicated that raising the crop from tuber seeds is better than raising it from true potato seeds, with respect to plant vigour. The low to moderate correlation coefficients between seedling and clonal I generations and between clonal I and II generations for progeny means for most traits indicate that high selection pressure in these early generation would be detrimental (Gopal, 1997). For tuber yield, correlation coefficients between seedling generation and clonal II were low (r =0.34), whereas those between seedling and clonal I generation and between clonal I and clonal II were moderate (r=0.56 and 0.50, respectively). For general impression, plant vigour and tuber shape, all correlation coefficients were of moderate magnitudes (r=50 to r=69). Tuber colour and uniformity in tuber colour in seedling generation were highly correlated with those in clonal I (r=0.81, and r=0.92, respectively) (Gopal, 1997). Gopal (1998) found that the correlation coefficient between seedling generation and clonal I for uniformity of tuber colour was r=0.95 while that for average tuber weight between seedling and second clonal generation was r=0.18. In another study, Kumar and Gopal (2006) found that all inter-generation correlation coefficients (from seedling to third clonal generation) were high (r > 0.70) for predominant tuber shape, predominant tuber size, uniformity in tuber shape, uniformity in tuber size, and uniformity in tuber colour. In contrast, most of the intergeneration correlation coefficients for plant vigour, tuber yield, tuber number and average tuber weight were of low magnitude except between second and third clonal generations where these were high for tuber yield and its components (Kumar and Gopal, 2006). Neele et al. (1991) found that the correlation coefficients between the seedling progenies and the ware potato harvest performances in the subsequent years varied between r= -0.36 and r=0.07 for total tuber yield; r= -0.08 and r=0.14 for number of tubers, and r= -0.26 and r= -0.19 for mean tuber weight. These poor correlation coefficients show that seedling progeny performance is not likely to be a good measure of field performance. Maris (1988) also observed poor relationships between glasshouse seedlings and field performance for number of tubers and average tuber weight, while the correlation for tuber yield was moderate (r=0.44 to 0.52). In contrast, Brown and

Caligari (1989), using the progeny mean added to the within-progeny standard deviation, found a high correlation coefficient for tuber yield (r=0.90), moderate for mean tuber weight (r= 0.46) and poor for number of tubers (r = 0.11). Gopal et al. (1992) found that the correlation coefficients of seedling generation with clonal generations were higher for progeny means than those for individual genotypes for characters like tuber yield and tuber number; for average tuber weight these were more or less of similar magnitudes. Brown et al. (1987a) reported that progeny means have higher repeatabilities than individual clones in the early generations for general impression. It appears that, in general, for seedling versus clonal generations, the repeatability of the progeny mean is better than that of individual genotypes' performance. Gopal et al. (1992) reported that seedlings of poor vigour may be rejected prior to transplanting in the field as they represent inferior genotypes. In addition, clones with undesirable tuber colour, tuber shape, eye depth and tuber cracking may be rejected from the seedling stage onwards as these characters have a high repeatability over generations. No rejection should be done on the basis of tuber yield, average tuber weight or number of tubers in the seedling generation; a negative selection (rejection of poor phenotypes) for tuber yield and tuber weight can be initiated from the clonal 1 generation onwards, whereas a negative selection based on number of tubers can be initiated from clonal 2 generation onwards (Gopal et al., 1992). These results agree with those of Swiezynski (1978), who reported that selection for tuber shape and deep eyes is effective in the seedling generation. However, Howard (1963) reported that selection for tuber shape in the seedling generation is not effective. Although selection on the basis of plant appearance (breeder's visual preference) in seedling, clonal I and II generations looks attractive, it has been reported that the heritability of visual preference is sufficiently low to warrant using cross means to reject entire crosses on the grounds that they are less likely than others to contain outstanding individual clones; especially when based on glasshouse-raised seedling progenies (Brown and Caligari, 1989). The report also supports the application of mild clonal selection within the selected progenies in the clonal I generation, and then the assessment of the clonal II generation under ware conditions because of strong clone-harvest date interactions (Bradshaw and Mackay, 1994). In the early stages, it is nearly always the best resource allocation to test as many clones as possible at one location without replications (Wolfgang et al., 2009). Although early selection does not always appear to pay off in breeding potato clones (Tai and Young, 1984), selecting for vigorous seedlings in the nursery (Gisela and Peloquin, 1991; Golmirzaie and Ortiz, 2002a), or in the field (Ortiz and Golmirzaie, 2004), results in high yielding potato hybrid TPS offspring. It seems that highly heterozygous genotypes show their vigour in early stages of growth (Altin and Wiersema, 1988; Arndt and Peloquin, 1990), which may facilitate tuber set. .Evaluation of clones in early breeding stages should be based on traits with high heritability (i.e. quality traits such as skin and tuber colour, and possibly eye depth and tuber shape) and for tolerance and resistance to pathogens; while the evaluation at later stages should be conducted in many target environments and based on traits with a lower heritability (i.e. quantitative traits such as yield and yield components, dormancy, dry matter and starch content, tuberization, resistance to *Erwinia*)(Bradshaw, 2007). However, even in the early generations breeders are greatly influenced by tuber yield and yield components when visually assessing breeding material (Maris, 1969; Tai, 1975; Brown and Caligari, 1986).

Bradshaw et al. (1998) found that yield was an important component of visual preference in the second and third clonal generations while Brown and Caligari (1986) found it to be an important component in the seedling and first clonal generation. Likewise, Neele et al. (1991) found that tuber yield was the principal component of plant appearance (equivalent to visual preference) in an experiment with 600 clones from 20 progenies over the first two clonal generations. However, selection for yield and yield components appears to be more effective in the second clonal generation (Caligari et al., 1986).

Marker assisted selection in potato breeding

In potato, molecular markers have been used for construction of genetic linkage maps (Bonierbale et al., 1988; Gebhardt et al., 1991; Bonierbale et al., 1994), trait tagging (Gebhardt et al., 1993; Bryan et al., 2002), fingerprinting analysis (Milbourne et al., 1997; McGregor et al., 2000b; Norero et al., 2004), phylogeny studies (Debener et al., 1990; Raker and Spooner, 2002), and characterization of accessions from germplasm banks (Gebhardt et al., 2004; Ghislain etal., 2006). Powell et al. (1991) have suggested using genetic distance based on molecular markers to select diverse parents capable of producing high-performing progeny. Molecular markers have been identified for resistance against late blight (Colton et al., 2006), nematodes (Gebhardt et al., 2006; Zhang et al., 2007) and viruses (Gebhardt et al., 2006) in potatoes. There are three major types of genetic markers: (1) morphological (also 'classical', 'phenotypic' or 'visible') markers which themselves are phenotypic traits or characters; (2) biochemical markers, which include allelic variants of enzymes called isozymes; and (3) DNA (or molecular) markers, which reveal sites of variation in DNA sequence (Winter and Kahl, 1995; Jones et al., 1997). The major disadvantages of phenotypic and biochemical markers are that they may be limited in number and are influenced by environmental factors or the developmental stage of the plant (Winter and Kahl, 1995). In addition, biochemical markers are expensive. Despite these limitations, these markers have been extremely useful to plant breeders (Weeden et al., 1994; Eagles et al., 2001). Molecular markers are the most widely used mainly due to their abundance. They are also environmentally neutral and independent, and therefore more robust and unbiased compared to phenotypic descriptors. They arise from different classes of DNA mutations such as substitution mutations (point mutations), rearrangements (insertions or deletions) or errors in replication of tandemly repeated DNA (Paterson, 1996). The most widely used molecular markers in potatoes are restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and simple sequence repeats (SSR) or microsatellites (Collard et al., 2005). Single nucleotide polymorphisms (SNP) are the latest markers (Hamilton et al., 2011).

Conclusions and Recommendations

Potato is easy to breed because it is clonally propagated; once variation is released through crossing, there is no problem with stabilizing (fixing) any desirable combination that arises, as any clone can be multiplied unchanged by asexual reproduction. However, generating TPS is a problem due to various infertility systems operating in potatoes. Conventional potato breeding takes long (about 10 years) before a cultivar is released, mostly due to the slow multiplication rate of the crop. This time can be reduced by

use of progeny tests to discard whole families before starting the within family selection; use of modern methods of rapid multiplication may shorten the time even further. A big impact on the efficiency and rate of progress would be the identification of superior clones genotypically as seedlings in the glasshouse. This will require molecular marker assisted selection or preferably direct recognition of the desired allele at a genetic locus. Molecular makers have been used extensively in potatoes in genetic studies; they could be used in identifying parents with desired traits and hence shorten the breeding cycle.

References

Acquaah G (2007) Principles of plant genetics and breeding. Blackwell Publishing Ltd., 350 Main Street, Malden, MA, USA

Almekinders CJM (1991) Flowering and true seed production in potato (*Solanum tuberosum* L.) 2. Effects of stem density and pruning of lateral stems. Pot Res. 34:379-388

Almekinders CJM (1992) The effect of photoperiod on flowering and TPS production in the warm tropics. Pot Res. 35:433-442.

Almekinders CJM, Wiersema SG (1991) Flowering and true seed production in potato (*Solanum tuberosum* L.) 1. Effects of inflorescence position, nitrogen treatment and harvest date of berries. Pot Res. 34:365-377

Almekinders CJM, Struik PC (1996) Shoot development and flowering in potato (*Solanum tuberosum* L). Pot Res. 39:581-607

Altin GN, Wiersema SG (1988) Selection against inbred seedlings in mixtures of inbred lines and hybrid true potato seed. Pot Res. 31:105-112

Arndt, GC, Peloquin SJ (1990) The identification and evaluation of hybrid plants among open pollinated true seed families. Am Pot J. 67:293-304

Bamberg JB, Hanneman RE (1988) Enhanced production of botanical seed of tuber bearing *Solanum* species via supplemental fertilizer applications. Am Pot J. 65:470

Bonierbale MW, Plaisted RL, Tanksley SD (1988) RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. Genet. 120:1095-1103

Bonierbale MW, Plaisted RL, Pineda O, Tanksley SD (1994) QTL analysis of trichome-mediated insect resistance in potato. Theor Appl Gen. 87:973–987

Bradshaw J (2009) Potato breeding at the Scottish Plant Breeding Station and the Scottish Crop Research Institute: 1920-2008. Pot Res. 52:141-172

Bradshaw JE (2007) Breeding potato as a major staple crop. p. 277-332. In: M.S. Kang and P.M. Priyadarshan (ed.) Breeding major food staples. Blackwell Publishing professional, Ames, Iowa, USA

Bradshaw JE, Mackay GR (1994) Breeding strategies for clonally propagated potatoes. p. 467-497. In: J.E. Bradshaw and G.R. Mackay (ed.) Potato genetics. CAB International, Wallingford, UK

Bradshaw JE, Bonierbale M (2010) Potatoes. p. 1-52. In Bradshaw JE (ed) Root and tuber crops, Handbook of plant breeding 7. Springer Science +Business Media, New York.

Bradshaw JE, Todd D, Wilson RN (2000) Use of tuber progeny tests for genetical studiesas part of a potato (*Solanum tuberosum subsp. tuberosum*) breeding programme Theor Appl Gen. 100:772-781

Bradshaw JE, Dale MFB, Swan GEL, Todd D, Wilson RN (1998) Early-generation selection between and within pair crosses in a potato (*Solanum tuberosum subsp. tuberosum*) breeding programme. Theor Appl Gen. 97:1331-1339

Brown CR (1993) Outcrossing rate in cultivated autotetraploid potato. Am Pot J. 70:725-734

Brown J, Caligari PDS (1986) The efficiency of seedling selection for yield and yield components in a potato breeding programme. Pflanzenzucht 96

Brown J, Caligari PDS (1989) Cross prediction in a potato breeding programme by evaluation of parental material. Theor Appl Gen. 77:246-252

Brown J, Caligari PDS, Mackay GR (1987a) The repeatability of progeny means in the early generations of a potato breeding programme. Ann Appl Bio. 110:365-370

Brown J, Caligari PDS, Mackay GR, Swan GEL (1984) The efficiency of seedling selection by visual preference in a potato breeding programme. J Agric Sci. 103:339-346

Brown J, Caligari PDS, Mackay GR, Swan GEL (1987b) The efficiency of visual selection in early generations of a potato breeding programme. Ann Appl Bio. 110:357-363

Brown J, Caligari PDS, Dale MFB, Swan GEL, Mackay GR (1988) The use of cross prediction methods in a practical potato breeding programme. Theor Appl Gen. 76:33-38

Bryan GJ, McLean K, Bradshaw JE, De Jong WS, Phillips M, Castelli L, Waugh R (2002) Mapping QTLs for resistance to the cyst nematode *Globodera pallida* derived from the wild potato species *Solanum verneii*. Theor Appl Gen.105:68-77

Caligari PDS (1992) Breeding new varieties .p. 334-372. In: P. Harris (ed.) The potato crop. 2nd ed. Chapman and Hall, London

Caligari PDS, Brown J, Abbott RJ (1986) Selection for yield and yield components in the early generations of a potato breeding programme. Theor Appl Gen.73:218-222

Carputo D, Barone A (2005) Ploidy level manipulations in potato through sexual hybridisation. Ann Appl Bio. 146:71-79

Carputo D, Frusciante L, Peloquin SJ (2003) The role of 2n gametes and endosperm balance number in the origin and evolution of polyploids in the tuber-bearing *Solanums*. Genet. 163:287-294

CIP (1984) Potato for the developing world. A collaborative experience. Centro Internacional de la Papa, Lima, Peru

Collard BCY, Jahufer MZZ, Brouwer JB, Pang ECK (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: The basic concepts. Euphyticaytica. 142:169-196

Colton LM, Groza HI, Wielgus SM, Jiang (2006) Marker-Assisted Selection for the broad-spectrum potato late blight resistance conferred by gene RB derived from a wild potato species. Crop Sci. 46:589-594

Dalianis CD, Plaisted RL, Peterson LC (1966) Selection for freedom from after cooking darkening in a potato breeding program. Am Pot J. 43:207-215

Debener T, Salamini F, Gebhardt C (1990) Phylogeny of wild and cultivated *Solanum* species based on nuclear restriction fragment length polymorphisms (RFLPs). Theor Appl Gen.79:360-368

Douches DS, Jastrzebski K (1993) Potato, *Solanum tuberosum* L. p. 605-644. In: G. Kalloo G, Bergh BO (eds) Genetic improvement of vegetable crops. Pergamon Press, Oxford, U.K

Eagles H, Bariana H, Ogbonnaya F, Rebetzke G, Hollamby G, Henry R, Henschke P, Carter M (2001)

Implementation of markers in Australian wheat breeding. Aust J Agric Res. 52:1349-1356

El-Gizawy AM, El-Yazied AA, Tawfik AA, El-Kaddour AA (2006) Effect of Gibberellic acid (GA$_3$) on enhancing flowering and fruit setting in selected potato cultivars. Annals of Agricultural Science, Ain Shams University, Cairo 51:173-189

Fock I, Collonnier C, Purwito A, Luisetti J, Souvannavong V, Vedel F, Servaes V, Ambroise A, Kodja H, Ducreux G, Sihachakr D (2000) Resistance to bacterial wilt in somatic hybrids between *Solanum tuberosum* and *Solanum phureja*. Plant Sci. 160:165-176

Fock I, Collonnier C, Luisetti J, Purwito A, Souvannavong V, Vedel F, Servaes A, Ambroise A, Kodja H, Ducreux G, and Sihachakr D (2001) Use of *Solanum stenotomum* for introduction of resistance to bacterial wilt in somatic hybrids of potato. Plant Physiol Biochem. 39:899-908

Gebhardt C, Mugnieri D, Ritter E, Salamini F, Bonnel E (1993) Identification of RFLP markers closely linked to the H1 gene conferring resistance to *Globodera rostochiensis* in potato. Theor Appl Gen. 85:541-544

Gebhardt C, Ballvora A, Walkenmeier B, Oberhagemann P, Schuller K (2004) Assessing genetic potential in germplasm collections of crop plants by marker-trait association: A case study for potatoes with quantitative variation of resistance to late blight and maturity type. Mol Breed. 13:93-102

Gebhardt C, Ritter E, Barone A, Debener T, Walkemeier B, Schachtschabel U, Kaufmann H, Thompson RD, Bonierbale MW, Ganal MW, Tanksley SD, Salamini F (1991) RFLP maps of potato and their alignment with the homologous tomato genome. Theor Appl Gen. 83:49-57

Gebhardt C, Bellin D, Henselewski H, Lehmann W, Schwarzfischer J, Valkonen JPT (2006) Marker-assisted combination of major genes for pathogen resistance in potato. Theor Appl Gen. 112(8):1458-1464

Ghislain M, Andrade D, Rodríguez F, Hijmans RJ, Spooner DM (2006) Genetic analysis of the cultivated potato *Solanum tuberosum* L. Phureja Group using RAPDs and nuclear SSRs. Theor Appl Gen. 113:1515-1527

Gisela CS, Peloquin SJ (1991) Performance of true potato seed families. II. Comparison of transplants versus seedling tubers. Pot Res. 34:409-418

Glendining DR (1976) Neo-Tuberosum: New potato breeding material. 4. The breeding system of Neo-Tuberosum, and the structure and composition of the the Neo-Tuberosum genepool. Pot Res. 19:27-36

Golmirzaie AM, Ortiz R (2002a) Inbreeding and true seed in tetrasomic potato. III. Early selection for seedling vigor in openpollinated populations Theor Appl Gen. 104:157-160

Gopa J (1994) Flowering behaviour, male sterility, and berry setting in tetraploid *Solanum tuberosum* germplasm. Euphytica. 72:133-142

Gopa J (1997) Progeny selction for agronomic characters in early generations of a potato breeding programme. Theor Appl Gen. 95:307-311

Gopa J (1998) General combining ability and its repeatability in early generations of potato breeding programmes. Pot Res. 41:21-28

Gopa J (2006).Considerations for successful breeding. p. 77-108. In: Gopal J, Khurana SMP(eds) Handbook of potato production, improvement, and postharvest management. Food Products Press, New York

Gopal J, Gaur PC, Rana MS (1992) Early generation selection for agronomic characters in a potato breeding programme. Theor Appl Gen. 84:709-713.

Grun P (1970) Cytoplasmic sterilities that separate the cultivated potato from its putative diploid ancestors. Evol. 24:750-758

Grun P (1990) The evolution of cultivated potatoes. Econo Bot. 44:39-55

Hamilton JP, Hansey CN, Whitty BR, Stoffel K, Massa AN, Deynze AV, De Jong WS, Douches DS, Buell CR (2011) Single nucleotide polymorphism discovery in elite north american potato germplasm. BMC Genomics 12:302 http://www.biomedcentral.com/1471-2164/12/302

Hawkes JG (1990) The potato: Evolution, biodiversity, and genetic resources. Belhaven Press, London

Hijmans R (2001) Global distribution of the potato crop. Am. J Pot Res. 78:403-412.

Hosaka K, Hanneman RE (1988) Origin of chloroplast DNA diversity in andean potatoes. Theor Appl Gen. 76:333-340

Hosaka K, Hanneman RE (1998) Genetics of self-incompatibility in a self-incompatible wild diploid potato species *Solanum chacoense* .I. Detection of an S locus inhibitor (Sli) gene. Euphytica. 99:191-197

Howard HW (1963) Some potato breeding problems. p.5-21. In: Annual report plant breeding institute, Cambridge

Howard HW (1978) The production of new varieties. p.607-644. In: Harris PM (ed) The potato crop. Chapman and Hall, London

Jauhnl G (1954) Zur Kenntnis des Bluuhverhaltens der Kartoffel . Verouff. Bundesanst. alp. Landw Admont 9:40-74

Johansen RH, Miller JC, Newsom DW, Fontenot JF (1967) The influence of environment on the specific gravity, plant maturity, and vigour of potato progenies. Am Pot J. 14:107-122

Jones N, Ougham H, Thomas H (1997) Markers and mapping: We are all geneticists now. New Phytology 137:165-177

Killick RJ (1977) Genetic analysis of several traits in potatoes by means of a diallel cross. Ann Appl Biol. 86:279-289

Killick RJ, Malcolmsom JF (1973) Inheritance in potatoes of field resistance to late blight (*Phytophthora infestans*). Physiol Plant Path. 3:121-131

Kumar R, Gopal J (2006) Repeatability of progeny mean, combining ability, heterosis and heterobeltiosis in early generations of a potato breeding programme. Pot Res. 49:131-141

Maris B (1969) Studies on maturity, yield, under water weight, and some other characters of potato progenies. Euphytica. 18:279-319

Maris B (1988) Correlations within and between characters between and within generations as a measure for the early generation selection in potato breeding. Euphytica. 37:205-224

Maris B (1989) Analysis of an incomplete diallel cross among three ssp. *tuberosum* varieties and seven long-day adapted ssp. *andigena* clones of the potato (*Solanum tuberosum* L.). Euphytica. 41:163-182

Mc Gregor CE, Lambert CA, Greyling M, Louw JH, Warnich L (2000b) A comparative assessment of DNA fingerprinting techniques (RAPD, ISSR, AFLP and SSR) in tetraploid potato (*Solanum tuberosum* L.) germplasm. Euphytica. 113:135-144

Milbourne D, Meyer R, Bradshaw JE, Baird E, Bonar N, Provan J, Powell W, Waugh R (1997) Comparison of PCR based marker systems for the analysis of genetic relationships in cultivated potato. Mol Breed. 3:127-136

Mok G (1985) TPS research in Korea. p. 215-219. In: Innovative methods for propagating potatoes. CIP, Lima, Peru

Neele AEF, Louwes KM (1989) Early selection for chip quality and dry matter content in potato seedling populations in greenhouse or screenhouse. Pot Res. 32:293-300

Neele AEF, Nab HJ, Louwes KK (1991) Identification of superior parents in apotato breeding programme. Theor Appl Gen. 82:264-272

Norero N, Malleville J, Huarte M, Feingold S (2004) Cost efficient potato (*Solanum tuberosum* L.) cultivar identification by microsatellite amplification. Pot Res. 45:131-138

Ortiz R, Golmirzaie AM (2004) Combining ability analysis and correlation between breeding values in true potato seed. Plant Breed. 123:564-567.

Paterson AH (1996) Making genetic maps.p. 23-39. In: Paterson AH(ed) Genome Mapping in Plants. R. G. Landes Company, San Diego, California. Academic Press, Austin, Texas

Peloquin JS, Hougas RW (1959) Decapitation and genetic markers as related to haplidy in in *Solanum tuberosum*. Eur Pot J. 2:176-183

Plaisted RL, Sanford L, Federer WT, Kehr AE, Peterson LC (1962) Specific and general combining ability for yield in potatoes. Am Pot J. 39:185-197

Pushkarnath, Dwivedi RS (1961) Potato floral biology series. II. Pollen and pollination. Ind Pot J. 3:76-85

Raker CN, Spooner DM (2002) Chilean tetraploid cultivated potato *Solanum tuberosum* is distinct from Andean populations: Microsatellite data. Crop Sci. 42:1451-1458

Rick CM (1980) Tomato. p. 669-680. In: Fehr WR, Hadley HH (eds) Hybridization of crop plants. American Society of Agronomy and Crop Science of America, Wisconsin

Ross H (1986) (ed) Potato breeding: Problems and perspectives. Verlag Paul Parey, Berlin and Hamburg

Simmonds NW (1995) Potatoes. p. 466-471. In: Smartt J, Simmonds NW (eds) Evolution of crop plants. 2nd ed. Longman, London

Simmonds NW (1997) A review of potato propagation by means of seed, as distinct from clonal propagation by tubers. Pot Res. 40:191-214

Sleper DA, Poehlman JM (2006) Breeding field crops, 5th ed. Blackwell Publishing Professional. 2121 State Avenue, Ames, Iowa

Sprague GF, Tatum LA (1942) General versus specific combining ability in single crosses of corn. J Amr Soci Agron. 34:923-932

Swiezynski KM (1978) Selection of individual tubers in potato breeding. Theor Appl Gen. 53:71-80

Tai GCC (1975) Effectiveness of visual selection for early clonal generation seedlings of potato. Crop Sci. 15:15-18

Tai GCC (1976) Estimation of general and specific combing abilities in potato Can J Genet Cytol. 18:463-470

Tai GCC, Young DA (1984) Early generation selection for important agronomic characteristics in a potato breeding population. Am Pot. J. 61:419-434

Tarn TR, Tai GCC, Jong HD, Murphy AM, Seabrook JEA (1992) Breeding potatoes for long-day, temperate climates. Plant Breed Rev. 9:219-332

Thijn GA (1954) Observations on flower induction with potatoes Euphyticaytica 3:28-34

Weeden N, Timmerman G, Lu J (1994) Identifying and mapping genes of economic significance. Euphytica. 73:191-198

Winter P, Kahl G (1995) Molecular marker technologies for plant improvement. World J Microbio Biotech. 11:438-448

Wolfgang J, Mwanga R, Andrade M, Espinoza J (2009) Selection methods. Part 5: Breeding clonally propagated crops. p. 275-322. In: Ceccarelli S, Guimaraes EP, Weltzien E (eds) Plant breeding and farmer participation, FAO, Rome

Wricke G, Weber WE (1986) Quantitative geentics and selection in plan breeding. de Gruyter, Berlin

Zhang LH, Mojtahedi H, Kuang H, Baker B, Brown CR (2007) Marker-assisted selection of Columbia root-knot nematode resistance introgressed from *Solanum bulbocastanum*. Crop Sci. 47: 2021-2026