

Production of hybrid potatoes: Are heterozygosity and ploidy levels important?

Jane Muthoni^{*1}, Hussein Shimelis², Rob Melis²

¹Kenya Agricultural and Livestock Research Organization (KALRO), Kenya

²African Centre for Crop Improvement, University of KwaZulu-Natal, College of Agriculture, Engineering and Science, School of Agricultural, Earth and Environmental Sciences, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa

*Corresponding author: jayne480@yahoo.com

Abstract

It has been proposed that maximizing heterosis for yield in potato may be achieved by maximizing heterozygosity and associated intra and interlocus interactions. Tetraploids offer more opportunities to create such interactions than diploids hence the general observations that tetraploids are higher yielding than diploids. Consequently, efforts have been made to increase heterozygosity in tetraploids by introgressing allelic diversity from other *Solanum* species into cultivated potato. However, conventional potato breeding is difficult because the cultivated potato is an autotetraploid with tetrasomic inheritance and it comprises highly heterozygous individuals which suffer inbreeding depression upon selfing; breeding at the tetraploid level is slow and less efficient than at diploid level. At the diploid level, it is possible to breed for and fix traits under recessive genetic control; it is nearly impossible to do so at the tetraploid level. There is also rapid response to selection due to greater variation in diploids than tetraploids. Consequently, there have been efforts to convert potato from an asexually propagated tetraploid crop into an inbred seed-propagated diploid; this is by production of inbred lines through selfing of the tetraploids to assemble desirable combinations of genes in the inbreds. These efforts are at the experimental stages and a lot of research needs to be done before they are confirmed. Because currently there is little experimental evidence to support superiority of the inbred seed-propagated diploid strategy, it appears the theory that heterosis for yield in potato may be achieved by maximizing heterozygosity and associated intra and interlocus interactions remain unchallenged; these interactions are more in tetraploids than in diploids. This paper therefore looks at genetic basis of yield heterosis in cultivated potato and the role of heterozygosity and ploidy level in production of hybrid potatoes.

Keywords: Breeding, Diploid, Heterozygosity, Heterosis, Hybrid potatoes, Tetraploid.

Introduction

The commonly cultivated potato (*Solanum tuberosum* L.) is an autotetraploid ($2n = 4x = 48$) that displays tetrasomic inheritance and hence has complex inheritance patterns (Bradshaw, 2006). The crop exhibits heterosis due to multi-allelic gene action; selfing leads to inbreeding depression for a number of characters including fertility and tuber yield while an increase in heterozygosity and multi-allelic loci results in more tuber yields (Gopal, 2014). Because of the potato's autotetraploid nature, intralocus interactions (heterozygosity) and interlocus interactions (epistasis) occur; it is assumed that increased heterozygosity leads to increased heterosis (Bradshaw and Mackay 1994; Sleper and Poehlman 2006). The exploitation of heterosis is by far the most important goal in potato breeding. Selection based on maximum heterozygosity rather than additive genetic variance is critical in potato breeding especially for quantitative traits. 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 combining ability) or in a non-additive manner (specific combining ability); in most case both operate (Ross 1986). Major theories explaining the

genetic basis of heterosis include dominance, overdominance and epistasis (Crow, 2000; Jinks, 1983; Birchler et al, 2010). Heterosis in potato is based mainly on non-additive interactions of genes and it comprises intralocus (over dominance) as well as interlocus (epistasis) interaction between genes and alleles (Ross 1986). Tetraploid potatoes can be very productive and stable in various environments.

This review paper looks at genetic basis of yield heterosis in cultivated potato and the role of heterozygosity and ploidy level in production of hybrid potatoes.

Role of ploidy level and heterozygosity in yield determination in cultivated potato

Tetraploid potatoes have greater yield potential than diploids (Mendiburu et al., 1977; Mendoza and Haynes, 1974). This is attributed to the greater number of alleles per locus possible in the polyploid form; colchicine-doubling experiments have revealed no advantage in higher ploidy *per se* (Rowe, 1967b). Tetraploid potatoes can have high

degree of intralocus interactions (dominance) due to the four alleles as well as interlocus interactions (epistasis) which can result in high yield. According to theory of heterosis in potatoes, these genic interactions are very important in determining yield (Mendoza and Haynes, 1974); tetraploidy offers more opportunities to create such interactions (Jansky, 2009) than diploidy. Multiallelism is an important factor in determining the vigour of tetraploid cultivars (Douches and Jastrzebski, 1993); potato genotypes with multi-allelic interactions are superior to those that are mono- or di-allelic depending upon the genetic background of the material (Bonierbale et al., 1993). Understanding the genetical basis of yield heterosis (hybrid vigour) and inbreeding depression in cultivated potatoes requires a consideration of the complexities of gene expression. These arise from the possibility of four different alleles at each locus and hence more allelic and non-allelic (between genetic loci) interactions than in diploids (Bradshaw, 2007). It has been proposed that maximizing heterosis for yield in potato may be achieved by maximizing heterozygosity and associated intra and interlocus interactions (Mendoza and Haynes, 1974). Several studies support this hypothesis (Mendiburu and Peloquin 1971; Mok and Peloquin 1975; De Jong and Tai 1977; Buso et al. 1999), and efforts have been made to increase heterozygosity by introgressing allelic diversity from other *Solanum* species into cultivated potato (Bradshaw and Ramsay 2005; Jansky and Peloquin 2006). It has long been assumed that the tetraploid state is optimal for superior agronomic performance in cultivated potato. The assumption that tetraploid potatoes are higher yielding than diploid potatoes is based largely on hypothesis that four allelic variants per locus contribute to yield superiority (Bani-Aameur et al., 1991; De Jong and Tai, 1991; Werner and Peloquin, 1991; Buso et al., 1999, 2000). It is hypothesized that the tetraallelic condition ($a_1a_2a_3a_4$) provides maximum heterosis because more intralocus and interlocus interactions are possible for this tetrasomic condition than for the other configurations (Ross 1986; Sleper and Poehlman 2006). The possibility of involvement of four alleles at each tetraallelic locus in tetraploid potato may result in six first-order, four second-order and one third-order allelic interactions at each locus (Sleper and Poehlman 2006). 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: $a_1a_2a_3$, $a_1a_2a_4$, $a_1a_3a_4$, $a_2a_3a_4$ while the one third-order interaction is $a_1a_2a_3a_4$. Therefore, there are a total of 11 different interactions possible for the tetraallelic condition; this is in contrast to the monoallelic condition ($a_1a_1a_1a_1$) which has no interactions. Consequently, the highest level of heterosis will occur as the frequency of tetraallelic loci increase and the greatest number of interlocus interactions will also occur as the frequency of tetraallelic loci increase. It has also been shown that yield stability in different environments can be achieved by increasing heterozygosity (Mendoza and Haynes, 1974); tetraploids exhibit high levels of yield stability across environments, presumably due to the buffering provided by allelic diversity (Darmo and Peloquin, 1990; Ortiz et al., 1991). The high productivity of potato in wide environments among major crops in the world is due to its tetraploid nature; diploid species such as *Solanum stenotomum* and *S. phureja* would not compete well with other crops for productivity and yield stability (Iwanaga, 1980).

Earlier studies conducted to test the importance of genetic interactions at multi-allelic loci in determining the vigour of autopolyploids such as alfalfa and potato suggested that heterosis for forage yield, fertility, and tuber yield increased progressively with the theoretical levels of heterozygosity of populations in these crops (Mendiburu et al. 1974; Mendoza and Haynes, 1974; Mendiburu and Peloquin 1977). However, one investigation concluded that there is a possible threshold to this diversity-based heterosis in potato based on diminishing returns observed beyond a certain level of theoretical heterozygosity (Sanford and Hanneman 1982). Another study indicated that the value of maximum heterozygosity is not universal but dependent on the genetic background of the material under evaluation (Bonierbale et al., 1993). It also reported that in a cross between adapted potato breeding lines, homozygosity was negatively correlated with tuber yield and maximum heterozygosity was positively correlated with the proportion of large-sized tubers; in crosses between adapted and unadapted parents, maximum heterozygosity had no detectable effect on any character. In addition, the study reported that regardless of the genetic background, additive genetic effects are more strongly correlated with the components of yield than are any measures of heterozygosity (Bonierbale et al., 1993). Observations that tetraploid cultivars were higher yielding than diploid cultivars drove the bulk of the research into true potato seeds (TPS) arising from biparental crosses between tetraploids (Kidane-Mariam et al., 1985b; Golmirzaie et al., 1994). A comparison of diploid and tetraploid lines revealed substantially lower heterozygosity in diploids compared with tetraploids suggesting that greater ploidy may be associated with greater heterozygosity (Hirsch et al., 2013). Uijtewaal et al. (1987) demonstrated that polyploidy itself, or gene dosage regardless of heterozygosity, affects potato performance to a degree that varies with the genotype examined. Research have shown that diploids usually have lower yields than tetraploids although some diploids may outyield tetraploid standards (Hutten et al., 1994). In a previous study, potato dihaploids exhibited inbreeding depression including poor vigour and low fertility (Peloquin and Hougas, 1960). Furthermore, severe inbreeding depression has been observed when cultivated potato is self-pollinated, a phenomenon attributed to the retention of deleterious and dysfunctional alleles (Mullin and Lauer 1966). This hypothesis is consistent with genome analyses that revealed a higher frequency of frameshift mutations in a vigorous heterozygous diploid line compared with a low-vigour, homozygous doubled monoploid line (PGSC, 2011). However, evidence is currently inconclusive over whether or not interactions between three or four different alleles are important and should be sort to maximize yield heterosis in breeding tetraploid cultivars for both clonal and True Potato Seed (TPS) propagation (Bradshaw, 2007). In a study comparing tetraploid three-way hybrids with two-way hybrids, the three-way hybrids were never higher yielding (Sanford and Hanneman, 1982). This suggests that increased levels of heterozygosity do not necessarily translate to improved yield. In addition, recent genomics data indicate that, at least at the single nucleotide level, tri-allelic and tetra-allelic loci are rare (Uitdewilligen et al., 2011; Hirsch et al., 2013). The contribution of multiple alleles per locus to yield superiority may be questioned in light of the observation that diploids have been repeatedly shown to

have high yield potential (Rowe, 1967a; Maris, 1990; Hutten, 1994; Simmonds, 1997). Recently, researchers reported that diploid wild potato relatives and their hybrids with cultivated potato often produce plants that are as vigorous as potato cultivars (Jansky et al., 2016) while other scientists are of the opinion that there is no fundamental knowledge on the performance of diploids versus tetraploids and at this moment, commercial tetraploids perform better than diploids (Lindhout et al., 2011). In addition, it is often difficult to distinguish between tetraploid and diploid potato plants on the basis of vine and tuber appearance; studies have shown that diploids grow faster and mature earlier than tetraploids (Rowe, 1967b; Maris, 1990). Some researchers are of the opinion that the long-held concept that homozygosity implies low vigour, is not always true (Jansky et al., 2016). However, it is important to consider, though, that heterozygosity at some loci may be more important than overall heterozygosity (Bonierbale et al., 1993).

Efficiency of breeding diploids vs tetraploids

The traditional system of potato breeding is laborious and the probability of finding superior cultivars is very low partly due to the complexity of tetrasomic inheritance in the cultivated potato (Douches and Jastrzebski, 1993). The cultivated potato is an autotetraploid with tetrasomic inheritance and it comprises highly heterozygous individuals which suffer inbreeding depression upon selfing (Bradshaw, 2006). The complexities of tetrasomic inheritance arise from diploid gametes in which diallelic interactions (dominance effects) can be transmitted to the next generation, sister chromatids can occur as a result of double reduction and two alleles can be identical by descent. Furthermore, one generation of random mating does not achieve the single locus equilibrium of genotype frequency following the Hardy-Weinberg equilibrium nor does it remove the effects of inbreeding (Bradshaw, 2007). Most potato research and traditional breeding is done at the tetraploid level. The most significant hindrance to breeding gain in potato at the tetraploid level is likely the abundance of deleterious alleles that can be tolerated within a polyploid genome; traditional tetraploid potato breeding allows maintenance of a high level of unfavourable alleles (Douches and Jastrzebski, 1993). Consequently, it is expected that a high proportion of inferior genetic combinations would result when crosses are made between heterozygous tetraploid parents (Jansky et al., 2016). This is commonly observed in traditional potato breeding programs where 90% or more of progeny from crosses between elite lines are discarded because they are not superior to their parents for the vast array of characteristics required for a potato cultivar. This problem was clearly identified by Allard (1999) who stated that “nearly all vegetatively propagated plants are open-pollinated, and highly heterozygous. When they reproduce sexually, the extensive segregation and recombination that occur during sexual reproduction lead to very large numbers of novel genotypes, nearly all of which are inferior to the parental genotype. Thus, improvement tends to be slow in nature and in cultivation.”

Tetrasomic inheritance has advantages and disadvantages for conventional breeding compared to the regular disomic inheritance. As stated previously, the main advantage of the

tetraploid potato is that this ploidy level is most productive and heterosis for tuber yields is primarily the result of exploitation of intralocus and interlocus interactions (Mendoza and Haynes, 1974), consequently, breeding schemes should aim to maximize heterozygosity in the tetraploid cultivars which will maximize heterosis (Douches and Jastrzebski, 1993). In addition, because of vegetative propagation, a promising clone can be multiplied with all its inter- and intraallelic gene actions intact and be adopted as a variety for commercial cultivation (Gopal, 2014). However, tetrasomic inheritance makes genetic studies and potato breeding programmes complicated; tetrasomic inheritance has hampered the breeders' ability to elucidate the genetic basis of many characters and has also made it difficult to accumulate favourable genes in a homozygous state (Douches and Jastrzebski, 1993). First, studies for genetic control of a certain character such as disease resistance cannot be done easily due to the complicated hereditary patterns and large sample size of progeny required for genetic analyses. Therefore breeders sometimes have to work with a vague knowledge of the inheritance of the characters they want to improve. Secondly, it is more difficult to improve potatoes at the tetraploid (4x) level than at the diploid (2x) level. For example, if one wanted to accumulate a dominant gene (X) for resistance to potato virus X, plants with dominant gene X are selected and intermated to increase the gene frequency. At the 2x level, selected plants are either XX or Xx. At the 4x level, XXXX, XXXx, XXxx and Xxxx plants would be selected as resistant. Even the simplex Xxxx plants with three recessive genes are selected and intermated. Consequently, breeding work for increasing gene frequency at the 4x level is slower than at the 2x level (Iwanaga, 1980). Another disadvantage of tetrasomic inheritance is the difficulty of combining two or more recessive genes; if one wanted to get *aaaabbbb* genotype from *AAAA bbbb* and *aaaaBBBB* crosses, one would need to grow a large number of F₂ progeny because the frequency of *aaaabbbb* is 1 out of 1296 while 1 out of 16 is expected to be *aa bb* at the 2x level. If a character is polygenically controlled, the complication and inefficiency of tetrasomic inheritance is even greater. In addition, tetraploid potato plants with recessive characters may appear less frequently than they would in a diploid species. This requires that the breeder grow a larger population of the autotetraploid to recover a certain number of recessive phenotypes following a cross than would be necessary with an ordinary diploid (Bamberg and del Rio, 2004). Furthermore, recessive mutations that are deleterious to the parent may be masked by their dominant alleles to a greater extent in autotetraploid so that they are not expressed as frequently in the phenotype of the plant (Sleper and Poehlman, 2006).

One of the most significant advantages of working at the diploid level is that it is possible to breed for and fix traits under recessive genetic control, whereas it is nearly impossible to fix recessive alleles at the tetraploid level (Jansky et al., 2016). Another advantage of using diploids in breeding is rapid response to selection due to greater variation in diploids. Genetic gains are more easily realized at the diploid level (Jansky et al., 2016; Maris, 1990); it has been indicated that response to selection would always be greater in diploid than in autotetraploid populations when gene frequency was the same in both, and that

situations in which little or no response to selection could be expected would be more frequent in autotetraploids (Hill, 1971). Theoretically, the variation of a segregating diploid population will be three times that of an equivalent autotetraploid population (assuming complete chromosome segregation) (Stebbins, 1956). The tetraploid population will consist of a greater proportion of individuals grouped about the mean while there will be more individuals at each extreme of the diploid distribution; since plant breeders are usually concerned with selecting the extreme segregates, the diploid distribution has obvious value (Rowe, 1967a; Rowe, 1967b). In addition, haploids of tetraploid potatoes can be hybridized directly with the diploid species and more efficiently selected by taking advantage of disomic inheritance; when superior diploid genotype has been generated, $2n$ gametes can be used through $4x \times 2x$ or $2x \times 2x$ crosses to obtain $4x$ progeny (Douches and Jastrzebski, 1993).

In order to achieve continuous progress in potato breeding, an alternative system should be developed that is based on the structural removal of unfavourable alleles (Lindhout et al., 2011). This is most efficiently achieved at the diploid (or even haploid) level as the chance that unfavourable alleles are homozygously present is much higher in diploids than in tetraploids. Such genes may be identified and eliminated in a breeding programme based on selfed generations. Tetraploids are much more tolerant of unfavourable alleles as the chance to get a completely homozygous locus is far lower than for diploids (Lindhout et al., 2011). However, diploids usually have lower yields than tetraploids, although some diploids may outyield tetraploid standards (Hutten, 1994); this yield gap between diploids and tetraploids may be bridged by breeding at the diploid level (Lindhout et al., 2011). Because breeding at the diploid level is more efficient than at the tetraploid level, an efficient breeding programme may be executed at the diploid level while tetraploid F_1 hybrids may be generated by oryzalin treatment of diploid parents or from diploid crosses by using unreduced gametes (Carputo et al., 2000; Chauvin et al., 2003).

Production of hybrid potato seeds

The basic technique of potato breeding is hybridisation to combine traits from two complementary parents or to increase the frequency of favourable genes (Douches and Jastrzebski, 1993). The conventional means of hybridisation is cross pollination; this is followed by phenotypic recurrent selection for traits of interest in the subsequent clonal generations (Howard, 1970; 1978). This can be improved by breeding technologies that allow genotypic recurrent selection along with selection for combining ability (Jansky et al., 2016).

There has been a suggestion to create inbred lines at the tetraploid level because tetraploid cultivated potato is self-compatible. This is based on the premise that creation of homozygous sets of additive loci through recombination and inbreeding is important for genetic gain (Fasoula and Fasoula, 2002). However, the approach to homozygosity is slow at the tetraploid level than at diploid (Haldane, 1930). In theory, it takes about 3.8 times as many generations of selfing tetraploids to reach the same degree of homozygosity as in a diploid genome; consequently, it is

difficult to produce homozygous inbreds or purelines through selfing in tetraploids (Douches and Jastrzebski, 1993). In addition, tetraploid potatoes are highly heterozygous individuals which display inbreeding depression on selfing (Bradshaw, 2007); the inbreeding depression is further compounded by the male sterility associated with the process of selfing (Douches and Jastrzebski, 1993). Krantz (1951) reported that self-pollination in potato leads to loss of fertility; unless the tetraploids carry dominant self-incompatibility inhibitor alleles, which are difficult to select at the tetraploid level, they will likely lose their ability to self-pollinate as they approach homozygosity. In tetraploids, pollen tube growth is inhibited when pollen is homozygous for S alleles but not when it is heterozygous (Lewis, 1943, 1947). Consequently, production of inbreds at tetraploid level through selfing is yet to be realized (Gopal, 2014). Efforts to self-pollinate potato at the tetraploid level were initiated in the mid-twentieth century in response to the success of the inbred-hybrid methods developed in maize (*Zea mays* L.) (Shull, 1909; Guern, 1940). In crops such as maize and beet, successful F_1 hybrid breeding has been achieved by consistent breeding for high-performing inbred lines (Crow 1998).

In potatoes, low yield and poor fertility were observed in S_5 and S_6 generations (Jansky et al., 2016). Iwanaga and Atlin (1986) reported that after two generations of selfing (S_2), only 22 % as much stainable pollen was produced per family in comparison with genetically comparable hybrids (S_0). De Jong and Rowe (1971) reported that the S_2 yielded only 36 % of the S_0 in the cultivated diploid hybrids while Krantz (1946) reported that the S_2 yielded 82 % of the S_0 in tetraploids. The difference can be attributed to the more rapid increase in homozygosity at the diploid level. Grun (1990) noted that inbreeding caused a sudden reduction in vigour and yield even in initial stages of selfing, and crosses between inbred lines of potato did not produce higher yields than the parental varieties. Golmirzaie et al. (1998a) demonstrated strong inbreeding depression in selfed progeny of tetraploids with respect to pollen viability, number of flowers and berries/plant, number of seeds/berry, pollen and seed production and tuber yield/plant; among these traits, pollen viability and tuber yield were strongly influenced by inbreeding depression (Golmirzaie et al., 1998b). This is because tuber yield reduction and loss of fertility are controlled largely by heterotic genetic effects (Mendiburu and Peloquin 1977; Golmirzaie et al. 1998a; 1998b). Accumulation of deleterious recessives, as a consequence of inbreeding, could explain poor pollen fertility of inbreds (Ortiz and Peloquin, 1994; Salaman and Lesley, 1922). Previous attempts to develop tetraploid TPS-based cultivars revealed that one to two generations of self-pollination does not always result in inbreeding depression (Kidane-Mariam et al., 1985; Golmirzaie et al., 1998a). Consequently, partial inbreds are likely to be components of the potato breeding system, especially in the near term when the vigour of inbred germplasm is likely to be lower than that of parental lines and hybrids. Hybridization of partial inbreds could lead to the selection of clones that are asexually propagated as cultivars using methods of traditional potato breeding. Such an approach would benefit from the reduction in deleterious alleles that is expected to

occur as individual lines approach homozygosity (Jansky et al., 2016).

Another suggestion is to convert potato from an asexually propagated tetraploid crop into an inbred seed-propagated diploid (Jansky et al., 2016) because the approach to homozygosity is slow at the tetraploid level than at diploid (Haldane, 1930). However, previous research showed that direct-seeded TPS produced lower yields than crops started from tubers (Almekinders et al., 2009; Malagamba et al., 1983). While the reinvention of the potato as a seed-propagated diploid crop will be facilitated greatly by a reduction in ploidy, it will also benefit from the production of inbred lines to systematically assemble desirable combinations of genes and exploit heterosis (Jansky et al., 2016). However, in transitioning potato from tetraploid to a diploid crop, it is important to consider the effect of the ploidy level on agronomic traits. Diploids typically produce smaller cells than tetraploids; little is known on how reduction of ploidy level might affect starch granule size, tuber sugar content, potato texture, and other quality characteristics (Jansky et al., 2016). In addition, homozygous potato clones generated through repeated selfing of diploids showed poor agronomic performance as tuber quality and yield were extremely low (Phumichai et al., 2005; Phumichai and Hosaka, 2006; Phumichai et al. 2006). This could be considered as evidence of severe inbreeding depression in potato; inbreds may never have commercial value (Uijtewaal et al. 1987; Almekinders et al., 2009).

How efficiently inbred lines will produce hybrid seed is a matter of speculation, it is impossible to know whether the inbred seed-propagated diploid strategy is feasible until it is tested on a large scale, which will require significant resources and buy-in from the potato-breeding community (Jansky et al., 2016). In potato, it is relatively easy to generate dihaploids from tetraploid cultivars through anther culture or through pollination by specific “pollinator” lines of *S. phureja* (Hougas et al., 1958; Peloquin et al., 1996). However, potato dihaploids exhibit inbreeding depression including poor vigour and low fertility (Peloquin and Hougas, 1960). Most dihaploids are male sterile, but many are female fertile. The frequent expression of male sterility at the diploid level might be a challenge for diploid breeding, at least initially. As with other allogamous plants that have been forced to self-pollinate, inbreeding depression occurs when diploids are self-pollinated in potato (De Jong and Rowe, 1971; Phumichai et al., 2005; Lindhout et al., 2011). Reductions in vigour are observed, but the main challenge is maintaining male fertility. In early generations of selfing, inbreeding depression is likely due in part to the expression of deleterious recessive alleles; male sterility in F_4 and F_5 populations derived from interspecific F_1 hybrids is still a barrier (Jansky et al., 2016). This may be due to hybrid breakdown (Jansky et al., 2016). In recent years, both public and private breeders have taken up the challenge of developing diploid hybrid potatoes from inbred lines. For example, Solynta (a private company) has developed a true hybrid breeding system in diploid potato whereby homozygous parent lines are developed by several rounds of inbreeding and hybrid cultivars are generated by crossing these parent lines (Lindhout et al., 2011); the resulting true potato seeds were sown in seed boxes and later seedlings were transferred in the field. From their initial trial, the seedlings gave a maximum yield of 26 ton/ha and 29 ton/ha

in Netherlands and DR Congo respectively (de Vries et al., 2016). However, these yields are far below the world average which stands at approximately 40 ton/ha (CSO, 2016); this is despite the intense care given to the delicate seedlings in this trial. The yields recorded in this trial were higher than the average yield in East African countries which ranges between 5 and 15 ton/ha (Gildemacher et al., 2009; Janssens et al., 2013; FAOstat, 2016). However, it should be understood that most potato farmers in the east African countries are generally small scale, resource-poor and mainly depend on rainfed agriculture. In addition, these farmers use poor quality seeds and apply farm inputs below the recommended rates hence the low potato yields (Muthoni and Nyamongo, 2009). From our experience, yields of up to 80 ton/ha have been achieved at potato research centre at Tigoni, Kenya when certified seeds and correct agronomic practices were employed (Muthoni and Kabira, 2011). Therefore, increasing potato yields in east Africa may involve planting of superior cultivars, availing good quality seeds at an affordable price and use of recommended rates of fertilizers and pesticides among other cultural practices. Although the number of tubers reported in this trial by Solynta was high, up to 37 tubers/plant, the tuber size was small (17-48 gr/tuber) compared to 50-100 gr/tuber for usual tuber weight range (Struik and Wiersema, 2012). Previous studies have shown that seedling transplants produce lower tuber yields (ton/ha) and percentage of ware-sized tubers than a crop propagated from conventional tubers (Almekinders et al., 2009; Muthoni et al., 2014). The low yields reported in this trial could be due to three confounded factors: diploid versus tetraploid, experimental hybrid versus commercial cultivar and seedlings versus seed tubers (de Vries et al., 2016). Further tests with plants grown from conventional tubers and tetraploid experimental hybrids are needed to dissect these factors.

Conclusion

From the review, it is difficult to conclude whether higher ploidy level and the associated heterozygosity are important in determining heterosis in cultivated potatoes due to conflicting reports. Most researchers, however, are of the opinion that indeed higher ploidy level and the associated heterozygosity are important in determining heterosis in cultivated potatoes. Tetraploids have more intralocus and interlocus interactions than diploids and hence more yielding. However, breeding at the tetraploid level is slow and less efficient than at diploid level. In recent times, there have been efforts to develop diploid hybrid potatoes from inbred lines. Conversion of asexually propagated tetraploid crop into an inbred seed-propagated diploid will be facilitated greatly by a reduction in ploidy, it will also benefit from the production of inbred lines to systematically assemble desirable combinations of genes and exploit heterosis. Efforts to produce diploid hybrid potatoes from inbred lines are in experimental stages; a lot of research needs to be done before they are commercially recommended.

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