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Tetrasomic inheritance in cultivated potato and implications in conventional breeding

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Abstract

The commonly cultivated potato (*Solanum tuberosum* L.) is an autotetraploid (2n=4x=48) that displays tetrasomic inheritance. The potato comprises highly heterozygous individuals which suffer inbreeding depression upon selfing. Due to their tetrasomic inheritance and high level of heterozygosity, tetraploid potatoes can be very productive and stable in various environments compared with their diploid counterparts. However, tetrasomic inheritance makes genetic studies and potato breeding programmes complicated. First, studies for genetic control of a certain character such as disease resistance cannot be done easily due to the complicated hereditary patterns and a large sample size of progeny is required for analyses. Secondly, it is more difficult to improve potatoes at the tetraploid (*4x*) level than at the diploid (*2x*) level. In addition, most useful wild and cultivated diploid species which are good sources of pest and disease resistance are not easily crossed with the tetraploid potatoes to recover new individuals with recombined traits. These ploidy differences can be overcome through sexual polyploidization (unreduced gametes), somatic fusion and use of dihaploid technology among other methods.

Keywords: Dihaploidy, Heterozygosity, Potato, Tetraploid, Tetrasomic inheritance.

Introduction

The potato 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).One hundred and eighty one tuber-bearing species of *Solanum* have known ploidy levels: 76% are diploids, 3% triploids (2n=3x=36), 12% tetraploids (2n=4x=48), 2% pentaploids (2n=5x=60) and 7 % hexaploids (2n=6x=72) (Hawkes, 1990; Spooner etal., 2004). The diploid species are obligate outbreeders with a gametophytic self-incompatibility system which becomes inoperative at higher levels of ploidy. The commonly cultivated potato (*Solanum tuberosum* L.) is a tetraploid that displays tetrasomic inheritance and hence has complex inheritance patterns (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, 2007a). The potato crop is highly heterozygous in nature and suffers inbreeding depression upon selfing (Bradshaw, 2006). Cultivated tetraploids, if pollen fertile, are self fertile but will exhibit the usual symptoms of inbreeding depression on selfing and the potato is regarded as an outbreeder. Consequently, potato cultivars and breeders' clones are usually highly heterozygous. Understanding the complexities of tetrasomic inheritance in the cultivated potato and their implications in potato breeding will go along way in enhancing efficiency ina conventional potato breeding programme. This article looks at tetrasomic inheritance in the cultivated potato (*Solanum tuberosum* L.) and the implication of this inheritance in conventional potato breeding.

Conventional potato breeding scheme

The principal basis of developing a potato cultivar is through crosses involving complementary parents of contrasting traits such as yield, quality and disease resistance. This will enable to isolate recombinants with combined traits of high yield, better quality and disease resistance. Phenotypic recurrent selection as implied here remains important during cultivar development (Howard, 1970; 1978). In a typical breeding programme, parental clones may be selected on the basis of their combining ability and phenotype on the assumption that complementary phenotypes will produce recombinants with the desirable traits of both parents in the ensuing populations (Mackay, 2005). Mid-parental values may provide good indicators of the likely average value of their progeny and thus serve as a useful means of cross prediction in some instances(Brown and Caligari, 1989).Some breeders choose to cross a potentially new source of parental clones with tester clones whose value as parents is already known (Mackay, 2005). It is also possible by the use of progeny tests to estimate breeding value or combining ability of parents (Wastie et al., 1993). Whatever the method of identifying potentially useful parents, the probability of finding recombinants in ensuing progenies possessing all the desirable attributes of an improved cultivar is very low. Consequently, traditional breeders tend to raise many thousands of seedlings from among which individual clones are selected. Though the phenotype and mid-parental value of the phenotypes of any two parents may provide a guide to their selection, the complexity of tetrasomic inheritance and low heritability of some traits renders this only a partially effective predictor of performance. However, there are some traits governed by simply inherited major dominant genes such as H_1gene (in *andigena*)which conveys total resistance to strains RO_1 and RO_4 of *Globodera rostochiensis* and the genes Ry_{sto} and Rx_{adg} that confer almost total resistance to viruses PVY and PVX respectively (Cockerham, 1970). A parental clone simplex (Aaaa) for one such gene will guarantee that 50% of its progeny from a cross to a susceptible clone will inherit that resistance. If the parental clone is duplex (AAaa), the probability is raised to more than 80% (Mackay, 2005). What is true in simple inheritance of major dominant genes is also true for traits of more complex inheritance and has been attempted by use of seedling progeny tests (Caligary et al., 1985; Bradshaw et al., 1995). The use of progeny tests for other traits permits identification of genetically superior parents whose application in breeding significantly raises the probability of their progeny inheriting some important traits (Mackay, 2005). By using proven progeny tested parents it is possible to accelerate the breeding process from seedling to cultivar (Mackay, 2007). This approach relies heavily on discarding entire progenies and subsequently all clones which fail to meet the very specific criteria and select/retain only those which possess the particular trait desired. In a bid to hasten the breeding process, the best clones from the best families are crossedto produce a new segregating population upon which to practice selection at a much earlier stage.

Improvements to the conventional potato breeding scheme

In a conventional potato breeding scheme, clones would seldom be used as parents until they successfully reached the final stage of selection as potential varieties or indeed were declared varieties. Moreover, based on appropriate crossing schemes, it is possible to determine the heritable potential of various traits for selection and breeding values or combining abilities of the parents thus enabling more emphasis on genotypic versus phenotypic selection (Bradshaw and Mackay, 1994; Bradshaw et al., 1995; Bradshaw et al., 1999). The improved breeding programme at Scottish Crop Research Institute (SCRI) has been making use of progeny tests (Bradshaw et al., 2003)and involves cycles of crossing, selection between progenies (full-sib families) and clonal selection within the selected progenies. It has been shown that recurrent selection based on progeny testing, with limited within progeny selection, can operate on a3-year cycle and full combined selection between and within progenies on a 6-year cycle. These cycle lengths are much shorter than the time from making a cross to releasing a new cultivar which has averaged 13 years since 1975, a year longer than the target of 12 years (Mackay, 2005). This would be the time taken if one waited for release of a cultivar before using it as a parent. Furthermore, it has previously been shown that progeny testing provides a solution to the common but ineffective practice in potato breeding of intense visual selection for quantitative traits between seedlings in a glasshouse and spaced plants at a seed site (Bradshaw and Mackay, 1994; Bradshaw et al., 1998). Conventional potato breeding is difficult because the cultivated potato is tetraploid with tetrasomic inheritance and it comprises highly heterozygous individuals which suffer inbreeding depression upon selfing (Bradshaw, 2006).

Tetrasomic inheritance in potatoes

The principal cultivated potato (*Solanum tuberosum* subsp. *tuberosum*) is an autotetraploid (2n=4x=48) that displays tetrasomic inheritance. There are four homologous chromosomes instead of two and, subsequently, there are four alleles per locus. With autotetrasomic inheritance, all possible allelic combinations are produced in equal frequencies (Muller, 1914); this is generally considered indicative of autotetraploidy (Soltis and Soltis, 1993). Understanding tetrasomic inheritance requires an appreciation of chromosome behaviour during meiosis: DNA synthesis takes place before the start of the first division so that each homologous chromosome comprises two identical sister chromatids which are joined at the centromere. Each chromosome may then pair randomly with any of its homologs in bivalents or quadrivalents (Marc et al., 2008).Although low frequencies of quadrivalents, trivalents (associations of three chromosomes), and univalents (unpaired chromosomes) occur, cytological evidence suggests that bivalents predominate in potato (Bradshaw, 2007a). The simplest situation is where four homologous chromosomes pair at random to give two bivalents in both the male and female parents. The two cellular divisions of meiosis proceed normally and produce equally viable diploid gametes, and male and female gametes unite at random to form tetraploid offspring. The results are the well-known Mendelian segregation ratios for autotetraploids (e.g. AAaa×aaaa giving 1 AAaa : 4 Aaaa : 1 aaaa offspring and AAaa×Aaaa producing1 AAAa : 5 AAaa : 5 Aaaa : 1 aaaa) (Bradshaw, 2007a). Tetrasomic inheritance has advantages and disadvantages for conventional breeding compared to the regular disomic inheritance. Tetraploid potatoes can be very productive and stable in various environments. They can have high degree of intralocus interactions (dominance) due to the four alleles as well as interlocus (epistasis) interactions 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). It has also been shown that yield stability in different environments can be achieved by increasing heterozygosity (Mendoza and Haynes, 1974). The high productivity of potato in wide environment 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). Despite its advantages, tetrasomic inheritance makes genetic studies and potato breeding programmes complicated. 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 F_2 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, most useful wild and cultivated species which are good sources of pest and disease resistance are diploids and are not easily crossed with the tetraploid potatoes. As with other autopolyploid species, 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. In addition, 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). This ploidy difference has caused serious problems for incorporation of useful diploid germplasm into the tetraploid potatoes through conventional breeding. This is a major challenge especially in developing countries where conventional potato breeding programmes are in formative stages.

Implications of tetrasomic inheritance in conventional potato breeding

As a consequence of tetrasomic inheritance, genetic analysis has proved to be difficult particularly for quantitative traits. For qualitative traits (e.g. flower and tuber colour and presence or absence of molecular markers), individuals can be classified into distinct categories and the number of individuals in each category can be counted. One can look for simple Mendelian ratios in order to understand the inheritance of these traits, whether in diploid or tetraploid potatoes. In addition, one can look for association between traits and build up linkage maps of the underlying genes (Bradshaw, 2006). For quantitative traits, however, measurements can be made but individual genes cannot be recognised by Mendelian analysis because discrete classes cannot be discerned. Genetic information can be inferred from measurements on related individuals on the supposition of Mendelian inheritance. Biometrical methods have been developed and refined to undertake genetic analyses for quantitative traits (Bradshaw and Mackay, 1994). A statistically significant offspring-mid-parent regression is evidence of heritable variation and the slope of the regression line is a measure of heritability. Therefore, for many economically important traits, it has only been possible to partition genetic variation into components due to general combining ability (GCA) and specific combining ability (SCA) (Bradshaw and Mackay, 1994). Nevertheless, such information is of value to breeders, particularly at the start of a new breeding programme (Bradshaw et al., 1995). Combining ability analysis has become popular in both diploid and tetraploid potatoes because no random mating population in equilibrium has been assumed (Bradshaw, 2006). The general combining ability (GCA) of a parental clone provides an assessment of its genetic output as judged by the mean performance of its progenies from crosses with other clones. In order to make valid inferences, these latter clones should be either all those of interest or a random sample of them. Two types of factorial crossing designs are commonly used to determine combining abilities. In the first, one set of clones is crossed with another set that complements it for desirable traits. This is called North Carolina II matng design (NCII). In the second, a diallel set of crosses is made among clones showing a range of values for the trait(s) of interest. Where possible, reciprocal crosses are made and, ideally, the subsequent progenies assessed in more than one environment in order to study the genotype x environment interaction. The departure of a progeny mean from that expected on the basis of the GCA of the parents is called specific combining ability (SCA)(Bradshaw, 2006).

$$\text{Progeny}_{ij} - \mu = \text{GCA}_i + \text{GCA}_j + \text{SCA}_{ij}$$

The total genetic variation between families for an NCII design is

$$\sigma^2_G = \sigma^2_{GCA}\,(\text{set } 1) + \sigma^2_{GCA}\,(\text{set } 2) + \sigma^2_{SCA}$$

and for a diallel design it is

$$\sigma^2_G = 2\,\sigma^2_{GCA} + \sigma^2_{SCA}$$

Should the parents come from a random mating population in equilibrium, the total genetic variation can be partitioned into uncorrelated components that are attributable to different causes and can be used to determine the covariance of relatives (FS: full sib, HS: half sib) and to predict the response to selection.

$$\sigma^2_{GCA} = \text{COV(HS)}$$
$$\sigma^2_{SCA} = \text{COV (FS)} - 2\text{COV(HS)}$$

In NC II design in tetraploids assuming no maternal effects, no linkage equilibrium, no epistasis, no selection of parental plants, and tetrasomic inheritance with random chromosomal segregation (i.e. $\alpha = 0$),

$$\sigma^2_m = \sigma^2_f = \text{COV(HS)} = 1/4\ \sigma^2_A + 1/36\ \sigma^2_D$$

$$\sigma^2_{fm} = \text{COV(FS)} - 2\text{COV(HS)} = 1/6\ \sigma^2_D + 1/12\ \sigma^2_T + 1/36\ \sigma^2_Q$$
$$\text{COV(parent-offsring)} = 1/2\ \sigma^2_A + 1/6\ \sigma^2_D$$

where σ^2_A and σ^2_D are the additive and diallelic (digenic interaction) components of variance and σ^2_T and σ^2_Q are those for triallelic (trigenic) and tetra-allelic (quadrigenic) intralocus interactions in tetraploids. In autotetraploids the dominance variance arising from intralocus interaction includes variances due to digenic. trigenic and quadrigenic effects (Le Clerg, 1966).

Breeding potatoes at tetraploid level Ploidy manipulation (sexual polyploidization)

Crossing between the tetraploid (*4x*) and diploid (*2x*) potatoes has been achieved through use of unreduced gametes produced by the diploid parent. The formation of *2n* pollen from a diploid potato is under genetic control. Specific genes have been identified in wild and cultivated species that produce unreduced male gametes by at least three different mechanisms (Mok and Peloquin, 1975b). Several meiotic mutants have been discovered that lead to the formation of *2n* pollen with the most useful being the formation of parallel spindles controlled by the recessive *ps* gene. When unreduced gametes are formed from the diploid in the presence of *ps* allele, it is genetically similar to first division restitution (FDR). Several mutations leading to 2*n* egg formation have also been found (Werner and Peloquin, 1991). Formation of unreduced eggs is most commonly the result of omission of the second meiotic division which is genetically similar to second division restitution (SDR) mechanism. The recessive gene *os* controls formation of unreduced gametes by this mechanism. Formation of unreduced gametes by FDR and SDR-like mechanisms allows the transfer of large portions of intralocus (heterozygous) and interlocus (epistasis) interactions from the *2x* parent to the resulting 4*x* progeny. This is in contrast with normal meiosis in *2x* parents which would transfer little or no intralocus and interlocus interactions. In FDR, all loci from the centromere to the first crossover that are heterozygous in the parent will be heterozygous in the gametes, and half the heterozygous parental loci between the first and second crossover will be heterozygous in the gametes (Sleper and Poehlman, 2006). Since potato chromosomes are small, there is typically only one crossover per chromosome (Yeh et al., 1964; Carputo et al., 2003).The result of FDR is formation of unreduced and highly heterozygous male gametophytes that grow vigorously down the style (Simon and Peloquin, 1976). The heterozygosity of the male unreduced gametes in turn results in high vigour of the offspring plants (Mok and Peloquin, 1975a). In contrast, in SDR, all heterozygous loci from the centrometre to the first crossover in the parent will be homozygous, and those between the first and second crossover will be heterozygous in the resulting gametes. It has been estimated that FDR can transfer 80% of the heterozygosity and a significant portion of epistasis from parent to progeny. The SDR is less efficient and transfers less than 40% of the heterozygosity of the *2x* female parent to the *4x* progeny. Both FDR and SDR allow breeders to transfer desirable linkage groups and gene interactions intact from parent to offspring without having them broken up through the normal meiosis (Sleper and Poehlman, 2006). This is important because the potato is clonally propagated; once heterosis if fixed in F1, it is not broken up again. Formation of unreduced gametes by either male or female parent is called unilateral sexual polyploidization (USP) and allows for crosses between *2x* X *4x* or *4x* X *2x* parents to produce *4x* progeny. Simultaneous occurrence of unreduced gametes in the male and female parent is called bilateral sexual polyploidization (BSP) and allows for production of *4x* progeny from *2x* X *2x* crosses (Sleper and Poehlman, 2006). Unilateral sexual polyploidization offers a modified form of conventional breeding that can maximize the effects of heterosis. Exceptionally high tuber yields have been observed in tetraploid ($2n = 4x = 48$) progenies obtained from *4x* X *2x* matings in potatoes (Hanneman Jr and Peloquin, 1967; Hanneman Jr and Peloquin, 1968; Mok and Peloquin, 1975a). The progeny of *4x* X *2x* crosses are typically vigorous and relatively uniform for high tuber yield, which may at first seem surprising, considering the heterozygosity of the parents. The heterotic response is most commonly observed when the tetraploid is used as the female parent and the diploid parent produces 2*n* pollen by FDR (Jansky, 2006). In addition, families from *4x* X *2x* (FDR 2n pollen) crosses outyield *4x* X *2x* (SDR 2n pollen) and *4x* X *4x* families by about 50% (Mok and Peloquin, 1975b). Because intralocus and interlocus interactions contribute to high yield in potato, this significant increase in yield by *4x* X *2x* (FDR 2*n* pollen) hybridization is most likely due to the increase in transmission of heterozygosity and epistasis by *2n* FDR gametes (Mendiburu and Peloquin, 1977). Tetraploid progeny from BSP are highly heterotic and typically outyield their diploid full-sibs (Mandiburu and Peloqun, 1977) and even tetraploid commercial cultivars (Werner and Peloquin, 1991). The yield gains from BSP are typically higher than those from USP presumably due to the contributions of heterozygosity from both parents (Werner and Peloquin, 1991). Ploidy manipulations are commonly used in potato to access wild species germplasm. One of the most effective breeding techniques for the capture of exotic genetic diversity is USP in which a *4x* plant is crossed with a *2x* plant that produces *2n* pollen or *2n* eggs. The diploid plant could be *S. phureja* or *S. stonotomum*.

Somatic fusion

Diploid hybrids can be somatically doubled through chemical means such as colchicine (Ross et al., 1967) or through tissue culture (Sonnino et al.,1988) to bring them to teraploid level. However, tetraploids produced by this method do not exhibit a yield increase because new interlocus and intralocus interactions are not created (Rowe, 1967; Maris, 1990; Tai and Jong, 1997). Somatic doubling can produce only one type of heterozygote (duplex- AAaa) and a maximum of two alleles per locus while sexual polyploidization can produce three types of heterozygotes (simplex, duplex and triplex) and up to four alleles per locus. In addition, a wider array of complex epistatic (inter-locus) interactions results following sexual polyploidization (Jansky, 2006). A common somatic fusion strategy fuses protoplasts of tetraploid cultivars with those of sexually incompatible diploid wild species. The resulting hexaploid hybrids are often fertile and crossable with the tetraploid cultivars (Carputo et al., 1997). Most somatic fusions have been carried out to capture disease resistance genes; somatic fusion hybrids with improved salt tolerance have also been developed (Bidani et al., 2007).

Breeding at 2x level

Utilization of haploids (dihaploids) ($2n=2x=24$) extracted from tetraploid potato can solve some of the breeding problems. Most of the diploid species are easily crossed with haploids; incorporation of diploid germplasm is therefore facilitated (Iwanaga, 1980).Selection progress ismore rapid with diploids than tetraploids due to simple disomic inheritance at *2x* level (Jansky, 2009). Disomic genetic ratios are easier to interpret and work with than tetrasomic genetic ratios. Haploids can also be used to measure the genetic load in the tetraploids from which they are derived since deleterious alleles hidden in tetraploids are often expressed in haploids. Haploids can be produced from tetraploid cultivars and breeding clones via parthenogenesis (Hougas and Peloquin, 1957). As a result of segregation, haploids may express traits that were not found in their tetraploid parents. Populations of haploids provide unique opportunities for the genetic analysis of polygenic traits. They have been used to characterize the genetic basis of total tuber yield, average tuber weight, tuber number, dry matter content, tuber dormancy, vine maturity, and tuber glucose levels (Kotch et al., 1992). However, tetraploid potatoes are typically more vigorous and higher yielding than their haploid offspring (Peloquin and Hougas, 1960; DeMaine, 1984; Kotch and Peloquin, 1987). The loss of vigour and yield in haploids is due to ploidy reduction and inbreeding depression. The magnitude of this loss at the diploid level differs depending on the tetraploid clone from which the haploids were derived (Kotch and Peloquin, 1987).

Conclusions

The commonly cultivated potato (*Solanum tuberosum* L.) is a tetraploid that displays tetrasomic inheritance and hence has complex inheritance patterns. This makes genetic studies on potato and conventional potato breeding programmes complicated. This can be partially alleviated through sexual polyploidization (unreduced gametes), somatic fusion and use of dihaploids among other methods.

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