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Cytological and breeding behavior of pentaploids derived from 3x × 4x crosses in potato

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Abstract Cytology and breeding behavior of *Solanum commersonii* – *S. tuberosum* hybrids derived from $3x \times 4x$ crosses was examined. The chromosome number of hybrids ranged from hypo-pentaploid ($2n=5x–8=52$), to hyper-pentaploid ($2n=5x+7=67$), with the euploid pentaploid $2n=5x=60$ class predominant. The high variability in chromosome number of the $3x \times 4x$ hybrids was attributed to the fact that meiotic restitution during megasporogenesis of the $3x$ female may have involved poles with various chromosome numbers, resulting in $2n$ eggs with 24–48 chromosomes. Microsporogenesis analyses provided evidence that chromosome pairing between *S. commersonii* and *S. tuberosum* genomes occurred. In addition, chromosome distribution at anaphase I and anaphase II revealed an average chromosome number of 29.5 and 29.1 per pole, respectively. To further study the extent of transmission of extra genome chromosomes from pentaploids, $5x \times 4x$ and $4x \times 5x$ crosses were performed, and the chromosome number of resulting progeny was determined. Ploidy ranged from $2n=4x=48$ to $2n=5x=60$ following $5x \times 4x$ crosses, and from $2n=4x+1=49$ to $2n=5x=60$ following $4x \times 5x$ crosses. These results provided indirect evidence that the pentaploid hybrids produced viable aneuploid gametes with a chromosome number ranging from 24 to 36. They also demonstrated that gametes with large numbers of extra chromosomes can be functional, resulting in sporophytes between the $4x$ and $5x$ ploidy level. Fertility parameters of crosses involving various (aneuploid) pentaploid genotypes were not influenced by chromosome number, suggesting a buffering effect of polyploidy on aneuploidy. The possibility of successfully using (aneuploid) pentaploid genotypes for further breeding efforts is discussed.

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Introduction

The numerous species of the *Solanum* genus are a valuable source of germplasm for the genetic improvement of the tetraploid ($2n=4x=48$) cultivated potato *Solanum tuberosum* Group Tuberosum (tbr). They occur mainly as diploids ($2n=2x=24$), but species up to the hexaploid level also exist. *Solanum* species differ not only in the ploidy level but also in the endosperm balance number (EBN), which varies from one to four (Johnston et al. 1980). Diploid species can be either 1 or 2EBN, triploids 2EBN, tetraploids 2 or 4EBN, pentaploids and hexaploids 4EBN. The cultivated *S. tuberosum* Group Tuberosum is 4EBN. EBN differences between parents prevent hybridization between different ploidies within a species and between species. In fact, normal endosperm development occurs when there is a 2:1 maternal to paternal EBN ratio. In all the other cases the endosperm usually degenerates (Johnston et al. 1980).

Potato breeding has generally been directed at two ploidy and EBN levels. These are: (1) the tetraploid 4EBN level, involving crosses between selected $4x$(4EBN) tbr varieties and/or clones; (2) the diploid (2EBN) level, involving crosses between tbr haploids ($2n=2x=24$, 2EBN) and $2x$(2EBN) wild species. This latter approach has the great advantage of disomic rather than tetrasomic inheritance patterns and allows the transmission of useful genes as well as high levels of allelic diversity and allelic interactions from wild germplasm into the cultivated potato (Peloquin et al. 1999). Unfortunately, a number of diploid species with valuable traits and EBN=1 cannot be exploited using the diploid (2EBN) approach due to EBN differences with tbr haploids. Thus, alternative strategies have been proposed to efficiently use these incongruent sources of germplasm (Masuelli et al. 1992; Watanabe et al. 1995; Janssen et al. 1997; Thieme et al. 1997).

A ploidy bridge approach was developed by Carputo et al. (1997) to introgress resistance genes from the 2*x*(1EBN) species *S. commersonii* (cmm) into the tbr gene pool. It was based on a series of ploidy manipulations leading to the production of F_1 triploid and BC_1 pentaploid bridges. This breeding approach is quite straightforward and easy to carry out. One main disadvantage is related to the fact that, due to the presence of odd ploidies, the gametes produced may be sterile, and so the bridge genotypes produced may become genetic "dead ends". However, previous studies provided evidence that F_1 triploids produce 2*n* eggs, which represent balanced functional gametes. This made it possible to perform 3*x* × 4*x* crosses with tbr varieties to produce a fertile BC_1 pentaploid generation (Carputo et al. 1997). Subsequent studies demonstrated the potential for recombination between cmm and tbr (Barone et al. 2001) as well as the transmission of resistance traits from the wild parent to the cultivated gene pool (Carputo et al. 2000). The unique ploidy of bridge genotypes produced and their fertility make this material suitable for broadening our understanding of the cytological and breeding behavior of genotypes with odd ploidies. This seems very interesting in the potato where in nature a ploidy series (including triploids and pentaploids) exists and, especially at the pentaploid level, few data are available.

In this paper, a detailed cytogenetic analysis of the pentaploid BC_1 cmm-tbr hybrids and their BC_2 offspring is reported that provides insight into the selective mechanisms influencing the transmission of extra chromosomes in gametes of oddploid potato genotypes.

Materials and methods

Plant material

BC_1 hybrids

Thirty-eight BC_1 hybrids from 3*x* × 4*x* crosses generated as reported by Carputo et al. (1997) were used for mitotic analysis to determine their exact somatic chromosome number. A sample of these 38 hybrids was also examined cytologically at microsporogenesis to characterize some key features of pentaploid meiosis. To study pollen fertility and crossability of BC_1 hybrids, reciprocal crosses were performed between BC_1 hybrids and tbr vars. *Blondy*, *Carmine* and *Tollocan*. Crosses were made under screenhouse conditions at Camigliatello Silano (southern Italy). Fresh pollen, collected 1–2 h before pollination, was applied to the stigmas after emasculation of the flowers. For each cross combination, 15–30 flowers were pollinated. Fruits were allowed to ripen for about 6–8 weeks, and then seeds were extracted.

BC_2 hybrids

Four BC_2 progenies derived from reciprocal crosses between two euploid pentaploids (MCPH-1 and MCPH-3) and tbr var. *Carmine* were also utilized for mitotic analysis to indirectly determine the extent of transmission of extra genome chromosomes from pentaploids. The somatic chromosome number of 54 hybrids was compared with that expected following a random segregation of chromosomes to the poles, which was obtained by expanding the binomial $(0.5 + 0.5)^{12}$.

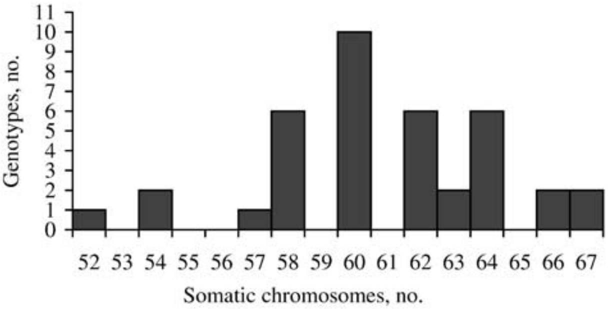

Fig. 1 Chromosome number of hybrids derived from 3*x* × 4*x* crosses

Mitotic analysis

Root tips of each BC_1 and BC_2 genotype were collected from plants propagated in vitro on Murashige and Skoog (1962) salts, 10% sucrose, and 8% agar. Root tips were treated for 4–5 h in 0.29 g/l 8-hydroxyquinoline, fixed in alcohol-acetic acid (3:1) for 48 h and finally kept at 4 °C in 70% alcohol. To prepare the slides, root tips were hydrolyzed in 5*N* HCl for 55 min, stained in Shiff's reagent for at least 2 h and then squashed in 45% acetic acid.

Meiotic analysis

Buds from emerging fluorescences were collected from BC_1 plants grown under screenhouse conditions at Camigliatello Silano. The buds were fixed in a 3:1 alcohol: propionic acid solution for at least 3 weeks. The anthers were dissected out, and the meyocites were squeezed out in 1% aceto-carmine.

Results

The results of mitotic analysis of 38 BC_1 genotypes from 3*x* × 4*x* crosses are shown in Fig. 1. Chromosome numbers ranged from hypo-pentaploid, $2n{=}5x{-}8{=}52$, to hyper-pentaploid, $2n{=}5x{+}7{=}67$, with the euploid pentaploid $2n{=}5x{=}60$ class predominant (26% of genotypes). The overall mean for BC_1 genotypes was $2n{=}60.9$ chromosomes, a value very close to the euploid pentaploid chromosome number.

Significant events during microsporogenesis of a sample of euploid and aneuploid pentaploid hybrids were also studied (Fig. 2). At diakinesis, pairing was mainly as bivalents. However, in most of the pollen mother cells examined multivalents were also found (both as rings and as chains). Chromosome distribution at anaphase I revealed an average chromosome number of 29.5 per pole, with a range of 24 to 35 chromosomes (data not shown). In particular, the average chromosome numbers per pole of hybrids analyzed were 29.5 for MCPH-1, 30.4 for MCPH-3, 29.9 for MCPH-8, 30.2 for MCPH-10 and 28.7 for MCPH-5. For all hybrids analyzed, the distribution of chromosomes at anaphase I was not random. Anaphase-II analysis of hybrid MCPH-3 confirmed the non-random distribution of chromatids to the poles, and the average chromosome number per pole was 29.1.

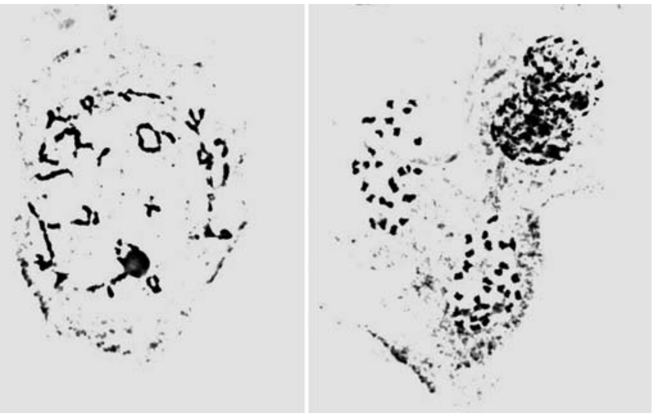

Fig. 2 Chromosome pairing at diakinesis and anaphase-I chromosome distribution of $3x \times 4x$ hybrids MCPH-5 ($2n=5x-2=58$) and MCPH-8 ($2n=5x+2=62$), respectively

The chromosome number of $5x \times 4x$ hybrids produced by crosses involving euploid $5x$ genotypes is reported in Table 1. It ranged from $2n=4x=48$ to $2n=5x=60$ following $5x \times 4x$ crosses, and from $2n=4x+1=49$ to $2n=5x=60$ following $4x \times 5x$ crosses. According to these results, it seems that pentaploid MCPH-3 tolerated a higher number of extra chromosomes in the gametes than MCPH-1. Indeed, progeny means of $5x$–$4x$ crosses were $2n=54.0$ and $2n=53.8$ when MCPH-3 was the $5x$ parent (*Carmine* × MCPH-3 and MCPH-3 × *Carmine* cross combinations, respectively). In contrast, when the $5x$ parent was MCPH-1, progeny means were lower – $2n=50.8$ (MCPH-1 × *Carmine*) and $2n=51.8$ (*Carmine* × MCPH-1). Each cross was tested so as to fit the distribution expected assuming random transmission of extra chromosomes. Chi-square values were significant at $P<0.01$ for both $5x \times 4x$ ($\chi^2=466.5$) and $4x \times 5x$ ($\chi^2=205.7$) crosses. These results confirmed anaphase analyses, which suggested a non-random transmission of chromosomes during the microsporogenesis of $3x \times 4x$ genotypes.

Most (aneuploid) pentaploid hybrids flowered profusely and shed stainable pollen with a variable diameter, probably reflecting the various chromosome number (from 24 to 36) of each pollen grain. Some hybrids also produced $2n$ pollen. Meiotic analysis provided evidence that all of the hybrids analyzed had high frequencies of parallel spindles (Table 2). While for some genotypes (e.g. MCPH-1) the frequency of dyads expected on the basis of parallel spindle frequency was similar to the observed value, for other genotypes (e.g. MCPH-10) high frequencies of parallel spindles resulted in only a few dyads. The results of metaphase-II analysis of pentaploids confirmed the previous analysis of their triploid parents that showed high frequencies of parallel spindles but no dyads (Carputo et al. 1995).

Flower profusion and the availability of stainable pollen allowed the use of some hybrids in crosses with tbr (Table 3). $4x \times 5x$ crosses performed better than $5x \times 4x$ crosses in terms of berry set (69% vs. 49%), but many berries were parthenocarpic. In contrast, $5x \times 4x$ crosses gave a higher average number of seeds/pollination (11.0 vs 4.6) and seeds/berry (47.2 vs. 13.8). Genotypes displaying the best results in terms of fertility parameters were MCPH-10 ($2n=5x+4=64$) and MCPH-7 ($2n=5x+7=67$) following $5x \times 4x$ and $4x \times 5x$ crosses, respectively.

Table 1 Somatic chromosome number of four BC_2 progenies from $5x \times 4x$ and $4x \times 5x$ crosses involving pentaploid ($2n=5x=60$) genotypes MCPH-1 and MCPH-3 and tetraploid ($2n=4x=48$) cultivar Carmine

Cross combination	Number of genotypes analyzed	Number of genotypes with 48–60 somatic chromosomes, respectively												
		48	49	50	51	52	53	54	55	56	57	58	59	60
$5x \times 4x$														
MCPH-1 × Carmine	10	1	1	4	0	2	1	1	0	0	0	0	0	0
MCPH-3 × Carmine	15	0	0	1	2	1	2	5	1	2	0	0	0	1
$4x \times 5x$														
Carmine × MCPH-1	14	0	1	3	2	2	4	1	1	0	0	0	0	0
Carmine × MCPH -3	15	0	0	0	1	3	4	2	1	3	0	0	0	1

Table 2 Frequency of parallel spindle (ps) and normal spindle (ns) orientation at metaphase II and frequency of dyads and tetrads in microsporogenesis of pentaploid and near-pentaploid hybrids

Genotype	Number of chromosomes	Number of cells	Spindle orientation		Number of cells	Dyads (%)	Tetrads (%)
			ps (%)	ns (%)			
MCPH-3	60	615	22.3	77.7	217	3.7	96.3
MCPH-10	63	373	22.2	77.8	214	0.8	99.2
MCPH-1	60	345	40.6	59.4	565	34.5	65.5
MCPH-5	58	142	19.0	81.0	363	2.2	97.8
MCPH-2	60	314	10.8	89.2	187	1.1	98.9

Table 3 Results from 5*x* × 4*x* and 4*x* × 5*x* crosses involving pentaploid/near-pentaploid genotypes and *Solanum tuberosum* Group Tuberosum (tbr) 4*x* varieties

Cross combination	Chromosome no. of the 5*x* parent	Berry set %	Average no. of seeds per	
			Pollination	Berry[a]
5*x* × 4*x*				
MCPH-10 × tbr[b]	$2n$=64	33.3	23.0	69.0
MCPH-5 × tbr	$2n$=58	100	0.0	0.0
MCPH-1 × tbr	$2n$=60	50.3	15.6	38.7
MCPH-3 × tbr	$2n$=60	64.7	27.4	42.3
MCPH-7 × tbr	$2n$=67	0.0	0.0	0.0
MCPH-12 × tbr	–[c]	43.7	0.0	0.0
Mean		48.9	11.0	47.2
4*x* × 5*x*				
tbr × MCPH-5	$2n$=58	100	0.0	0.0
tbr × MCPH-7	$2n$=67	100	23.6	16.5
tbr × MCPH-13	$2n$=58	100	0.0	0.0
tbr × MCPH-1	$2n$=60	29.6	2.8	9.5
tbr × MCPH-3	$2n$=60	47.1	3.9	8.4
Mean		69.0	4.6	13.8

[a] Only berries with seeds were considered
[b] Composite involving vars. *Blondy*, *Carmine* and *Désirée*
[c] Not available

Discussion

The variability in chromosome number of the 3*x* × 4*x* progeny we produced is much higher than that reported by Adiwilaga and Brown (1991) in 4*x* × 3*x* crosses where the triploid parent produces 2*n* pollen. Indeed, these authors found mainly euploid pentaploids, and few aneuploids, mostly with 59 chromosomes. The high variability in chromosome number of our 3*x* × 4*x* hybrids is probably the result of two key features of meiosis of the triploid females. First, after anaphase-I in a triploid genotype with 36 chromosomes, telophase-I poles with various chromosome complements may be theoretically produced (e.g. 12+24, 13+23, 14+22 … 18+18). Second, the meiotic mutation responsible for 2*n* egg production in the triploids is the omission of second meiotic division (Carputo et al. 1999), and thus meiotic restitution involved poles that after meiosis I had various chromosome numbers, from 12 to 24. As a result, 2*n* eggs with from 24 to 48 chromosomes were theoretically produced. Following fertilization by pollen with n=24 chromosomes after 3*x* × 4*x* crosses, 2*n* eggs gave a BC_1 progeny with a variable chromosome number, from 52 to 67. In a larger sample size, plants with chromosome numbers not represented (e.g. 48, 56) would have been found. The occurrence of genotypes with odd chromosome numbers (e.g. 57, 63) is probably due to the occasional omission of chromosomes from the restitution nuclei.

Interestingly from the breeding standpoint, 3*x* × 4*x* crosses may potentially generate hybrids with 48 chromosomes. This happens when the 2*n* eggs involved have 24 chromosomes, which guarantees the re-establishment of the tetraploid level of the cultivated potato after one single backcross, thereby avoiding the production of a second odd ploidy bridge. To have a good chance of identifying 3*x* × 4*x* hybrids with 48 chromosomes a large 3*x* × 4*x* progeny sample has to be screened. In fact, especially if chromosomes segregate randomly, at anaphase I the frequency of poles with a chromosome distribution "12+24" of the 3*x* parent (and consequently the frequency of 2*n* eggs with either 24 or 48 chromosomes) is low. 2*n* eggs with 24 chromosomes may also be produced through chromosome elimination from 2*n* eggs with higher chromosome numbers. Independently of the process leading to the production of 2*n* eggs with 24 chromosomes, a necessary condition is that 2*n* eggs with 24 chromosomes have an EBN of 2 in that it will give a hybrid endosperm with a 2:1 EBN ratio.

Most of data available in the literature is on the production and use of triploid bridges producing 2*n* pollen (Brown 1988; Brown and Adiwilaga 1990; Adiwilaga and Brown 1991; Louwes et al. 1992). The use of 2*n* pollen producing triploids guarantees the development of euploid pentaploid progenies when the meiotic mutation responsible for 2*n* pollen formation is parallel spindles. In fact, after the chromosomes of the triploid distribute randomly into the telophase-I nuclei, the parallel spindle mechanism in the second division ensures a symmetric incorporation of 36 chromosomes in each pair of 2*n* microspores. In contrast, 2*n* eggs producing triploids generate, as in our case, a high frequency of aneuploid pentaploids. Even though this may be a disadvantage of 2*n* eggs vs. 2*n* pollen, the production of a large 3*x* × 4*x* progeny may lead to the identification of BC_1 hybrids with 48 chromosomes, which is highly desirable.

Diakinesis analysis of microsporogenesis of a sample of (aneuplopid) pentaploids provided evidence that bivalents as well as multivalents were present in most of meyocites. The high frequency of bivalents does not exclude homeologous pairing since short chromosomes, like those of the potato, may not allow the multiple chiasmata needed for an association of multivalents (Obajimi and Bingham 1973). Recent analysis based on the use of markers with restriction fragment length polymorphism (RFLP) known location on the potato RFLP map confirmed not only the possibility of pairing, but also of recombination, between cmm and tbr chromosomes (Barone et al. 2001). In particular, it provided evidence for recombination on 5 out of 12 chromosomes in a sample of hybrids. Interesting results were also given by anaphase-I and -II analyses. It indicated that for all (aneuplopid) pentaploid hybrids analyzed, the distribution of chromosomes was not random, and suggested that some chromosomes may be lost during meiosis and that others may be transmitted all together. Pioneering work by Satina and Blackslee (1937) in pentaploid genotypes showed that normally, due to a process of chromosome elimination, there is a shift in chromosome distribution at anaphase-I poles in such a way that the poles with theoretically higher numbers tend to lose chromosomes and those with lower numbers tend to gain chromosomes.

To further study the extent of the transmission of extra genome chromosomes from pentaploids, the chromosome number of hybrids produced by crosses involving euploid 5*x* genotypes was determined. The results confirmed the non-random transmission of chromosomes during microsporogenesis of 3*x* × 4*x* genotypes and provided indirect evidence that the pentaploid hybrids produced viable aneuploid gametes with chromosome numbers ranging from 24 to 36. They also demonstrated that gametes with large numbers of extra chromosomes were functional, resulting in sporophytes between the 4*x* and 5*x* ploidy level. The tolerance to a high chromosome imbalance in gametes of pentaploids and sporophytes resulting from 5*x*–4*x* crosses is probably due to the buffering effect of polyploidy on aneuploidy, as has also been reported in blueberry (Timothy and Vorsa 1991). Some authors have reported that extra chromosome transmission is genotype-dependent (Zhirov and Ternovskaya 1979). According to Rick and Notani (1961), the tolerance to several extra chromosomes also depends on the primitiveness of the genotypes. Different hypotheses can be formulated to explain the non-random transmission of chromosomes from (aneuplopid) pentaploids to their offspring. In addition to chromosome elimination during meiosis, one possible explanation is that there is a selection against certain aneuploid gametes and seeds. In the potato the EBN system operates in interploidy crosses. It is possible that certain aneuploid gametes/seeds may lack the chromosomes controlling the EBN system, and in 5*x*–4*x* crosses this may give an unbalanced male to female EBN ratio after fertilization with 1*n*(2EBN) gametes produced by tetraploid varieties.

Most (aneuploid) pentaploid hybrids flowered profusely and shed stainable pollen, thereby allowing the use of some hybrids in crosses with tbr. On average 5*x* × 4*x* crosses gave a higher average number of seeds/pollination and seeds/berry than 4*x* × 5*x* crosses, suggesting that egg cells can withstand chromosome imbalance better than pollen. Interestingly, the genotype that gave the highest number of seeds/berry was aneuploid (MCPH-10, $2n=5x+4=64$), and this confirms the buffering effect of polyploidy on aneuploidy. The possibility of successfully using genotypes from 5*x*–4*x* crosses indicates that there should be no barrier to further breeding efforts for gene transfer. This is particularly true if, in a larger sample size, genotypes with 48 chromosomes are recovered.

In conclusion, the analyses performed provided evidence that the unique features of triploid meiosis led to the production of 2*n* eggs with various chromosome complements, which subsequently gave rise to euploid/aneuploid pentaploid genotypes following 3*x* × 4*x* crosses. These genotypes produced fertile gametes with various chromosome numbers, representing the entire series between 2*x* and 3*x*. Consequently, 5*x*–4*x* progenies with the tetraploid chromosome number of the cultivated potato may be potentially produced and selected for use in further backcrosses.

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