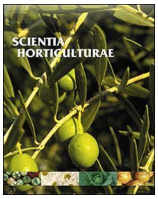
Scientia Horticulturae 234 (2018) 101–109

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti



Phenotypic and epigenetic variation induced in newly synthesized allopolyploids and autopolyploids of potato

Carlos F. Marfil[1], Paola F. Duarte[1], Ricardo W. Masuelli*

Instituto de Biología Agrícola de Mendoza, Consejo Nacional de Investigaciones Científicas y Técnicas (IBAM-CONICET), Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo, A. Brown 500 (M5528AHB) Chacras de Coria, Mendoza, Argentina

ARTICLE INFO

Keywords:
Allopolyploid
Autopolyploid
DNA methylation
Heterosis
Solanum kurtzianum
Solanum tuberosum

ABSTRACT

Polyploidy is one of the most important events in plant evolution: the evidence suggests that more than 70% of the angiosperms underwent some event of genomic duplication during their diversification. In potato, the third more important crop worldwide, the effects of autopolyploidization at morphological, physiological and molecular levels have been explored and no evident phenotypic superiority of polyploid lines respect to the parental diploid lines has been found. On the other hand, the consequences of allopolyploidization have not been analysed so far in potato from a molecular point of view. In this work we study the variability induced by whole genome duplication in potato auto and allotetraploids obtained by chromosomal duplication of a *S. kurtzianum* genotype (autopolyploid model) and by chromosomal duplication of a diploid interspecific hybrid between *S. tuberosum* and *S. kurtzianum* (allopolyploid model). Polyploid lines in both models showed a tendency to increase the vigor in phenotypic characters compared with diploid parent they derived from. AFLP analysis showed no polymorphism between parental diploid and derived polyploids lines. However, there were DNA methylation changes between diploids and polyploids, indicating that polyploidization alters the epigenetic patterns in potato. It is possible that the superiority of the tetraploid can be explained as a heterotic response dependent on the presence of heterozygous loci and epistatic interactions inducing alterations in the gene regulation of the polyploid genomes.

1. Introduction

Polyploidy is one of the most important events in plant evolution and several authors refer that more than 70% of angiosperms have experience genome duplication during their evolution (Soltis et al., 2009). Whole-genome duplication of the same or very similar genomes results in autopolyploidy (polysomic polyploidy) and the duplication of two or more divergent genomes in allopolyploidy (disomic polyploidy). Polyploidization can be achieved mainly in two ways, by somatic doubling of the chromosomes (asexual polyploidization) or by 2n gametes with the sporophytic chromosome number (sexual polyploidization) (Iwanaga and Peloquin, 1982; De Storme and Geelen et al., 2013; Spoelhof et al., 2017).

The advantages of polyploids over diploids, such as higher yields, enhanced vigour and novel variation were thoroughly states by several authors (Leitch and Bennett, 1997; Wendel, 2000; Comai, 2005). Genome duplication entails the reorganization of two divergent subgenomes in the allopolyploid or the similar duplicated genome in the autopolyploid inducing gene expression modifications. Investigations on synthetic autopolyploids showed that modifications are not as intense as in allopolyploids, and it has been proposed that differences could be originated by the presence of diverged regulatory hierarchies in allopolyploids (Comai, 2005; Yu et al., 2010). Tan et al. (2015) found that tetraploidization of citrus (*Citrus junos* Sieb. ex Tanaka) had a limited effect on transcriptome changes when diploid parent and tetraploid derived lines were compared. Results obtained in *Arabidopsis* suggested that doubling the same genome in autopolyploids has much smaller effects on gene regulation than combining divergent genomes in allopolyploids (Wang et al., 2006). In cabbage, leaf and stem proteomes remained globally unchanged between diploid and autopolyploid lines (Albertin et al., 2005). Additional examples of changes in gene expression induced by allopolyploidization in vegetable crops have been reported in *Brassica* (Xu et al., 2009) and in wheat (Kashkush et al., 2002; He et al., 2003).

The cultivated potato (*Solanum tuberosum* L., tbr, $2n = 4x = 48$), the third most important food crop after rice and wheat, is considered an autotetraploid with a chromosome base number of 12 (Iwanaga and Peloquin, 1982). However, Cribb and Hawkes (1986) provide evidences

---

* Corresponding author.
E-mail addresses: cmarfil@fca.uncu.edu.ar (C.F. Marfil), pduarte@mendoza-conicet.gob.ar (P.F. Duarte), rmasuelli@fca.uncu.edu.ar (R.W. Masuelli).
[1] These authors contributed equally to the paper.

https://doi.org/10.1016/j.scienta.2018.02.022
Received 16 November 2017; Received in revised form 3 February 2018; Accepted 7 February 2018

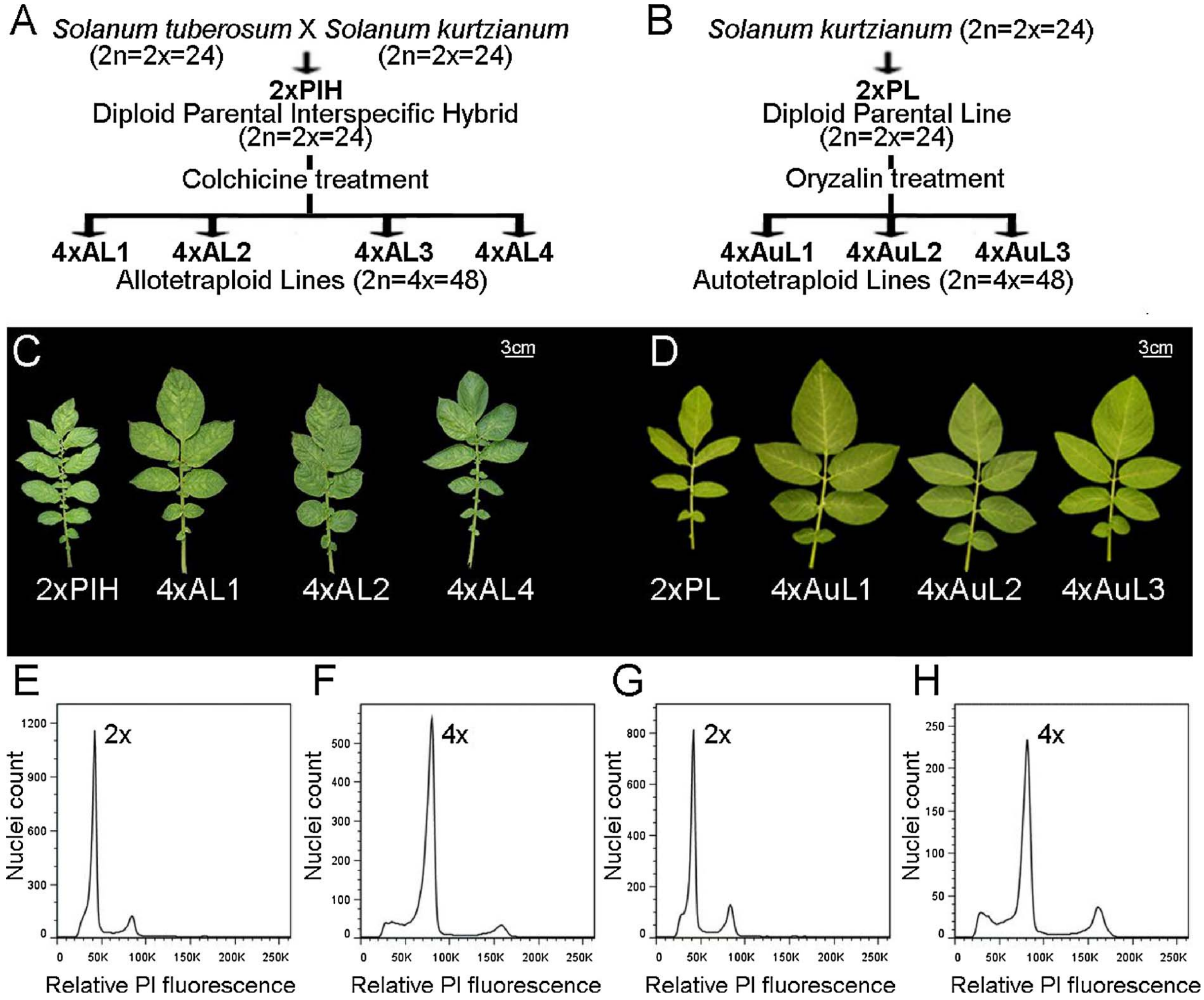


Fig. 1. Outline of the assayed experimental models, leaves and flow cytometry analyses of diploid and tetraploid lines. (A), allopolyploid model: a diploid parental interspecific hybrid was compared with four tetraploid lines derived from it after colchicine treatment. (B), autopolyploid model: a diploid *Solanum kurtzianum* genotype was compared with three tetraploid lines derived from it after oryzalin treatment. (C) and (D), photography of the sixth leaf of the diploid and three derived tetraploid lines in the allopolyploid and autopolyploid models, respectively. (E–H), representative analysis by flow cytometry of nuclei stained with propidium iodide (PI) of the diploid parental interspecific hybrid 2xPlH (E), the allotetraploid line 4xAL2 (F), the diploid parental line 2xPL (G) and the autotetraploid line 4xAuL3 (H).

that support the allotetraploid origin of tbr. Matsubayashi (1991), based on cytological analysis, propose that tbr is a segmental polyploid with two subgenomes (AAA^tA^t). Martinez-Zapater and Oliver (1984), analysing isoenzyme segregation suggested that autopolyploidy or amphidiploidy with lack of chromosome differentiation of the parental species may explain the tetrasomic segregation in potato. Therefore, it is possibly that divergent genomes participated in the origin of the tetraploid potatoes through the spontaneous doubling of a diploid hybrid (Ugent, 1970) or by functioning of 2n gametes (Iwanaga and Peloquin, 1982).

Previous studies of phenotypic, genetic, epigenetic and transcriptomic changes in three potato species (*S. bulbocastanum* Dun., *S. commersonii* Dun. and *S. phureja* Juz. et Buk.) were focused on newly synthesized autotetraploids, in which subtle transcriptomic changes were observed between the autotetraploids and the diploid parent they derived from; and no clear superiority of tetraploids was observed in terms of leaf thickness and area, vessel number, lumen size and vessel wall thickness, stomata pore length and width, guard cell width, and stomatal density compared with their diploid progenitors (Stupar et al., 2007; Caruso et al., 2011; Aversano et al., 2013, 2015b). However, hundreds of cultivated and wild potato species have been described (Spooner et al., 2014); therefore, the explored autopolyploid model in the three species above mentioned could be not representative of the induced variability nor the evolutionary relevance of genome duplication in potato. In addition, there are no studies focused on the effect of allopolyploidization in tuber-bearing *Solanum* species.

Extensive genetic and epigenetic modifications have been described in newly synthesized allopolyploids. Genetic changes include chromosomal rearrangements, transpositions and deletions (Shaked et al., 2001; Pontes et al., 2004). Epigenetic changes include alteration in DNA methylation, histone modifications and differential sRNAs accumulation (Comai, 2005). Rapid sequence rearrangements derived from autopolyploidization also has been reported (Martelotto et al., 2007). Scarce experiments have addressed direct comparisons between closely related allo and autopolyploid models. Most findings reported in the literature, seems to corroborate the hypothesis that, due to the absence of hybridization, autopolyploids experience less dramatic genetic and genomic alterations than those induced by allopolyploidization (Spoelhof et al., 2017).

Our aim was to study the phenotypic, genetic and epigenetic changes induced by allopolyploidization and autopolyploidization in potato and to compare the magnitude of the variability generated between these two models. The hypotheses of the research were that allopolyploids would have higher rates of genetic and epigenetic changes than autopolyploids and that the polyploidization in potato would not generate a phenotypic superiority respect to the diploid counterpart. To