Ciência Rural, Santa Maria, v.53:7, e20210742, 2023

http://doi.org/10.1590/0103-8478cr20210742

ISSNe 1678-4596
BIOLOGY

Origin, evolution and strategies for the genetic improvement of physalis

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ABSTRACT: *Physalis peruviana* L. (physalis) has significant economic potential by virtue of the unique flavor of its fruit. However, the productivity of Brazilian plantations is low because of the limited number of varieties or cultivars available. The main obstacle in the selection of superior genotypes is the lack of information about genetic variability within- and between- populations and limited genetic basis that has likely resulted from evolutionary, domestication and selection processes of the natural or artificial populations. Physalis currently cultivated in Brazil is tetraploid, and such polyploidy may have led to the reproductive isolation of the species, preventing the occurrence of intraspecific hybridization. Moreover, cultivated populations derive from a common gene pool and have undergone a long process of domestication and selection carried out empirically by farmers. In Colombia and other Andean countries there are wild populations that exhibit genetic diversity which; although, fundamental for the conservation of the species, have low potential for the development of genotypes with superior agronomic traits. In order to create and expand the genetic variability of physalis, breeders have employed various strategies including induction of mutation, chromosome duplication, and interspecific and intraspecific hybridization. Furthermore, the production of double haploid lines from *in vitro* anther cultures has shown good results in the selection of hybrids. The mutant genotypes and/or hybrids obtained using these methods in association with those of wide genomic selection can generate cultivars with superior agronomic traits.

Key words: Solanaceae, genetic improvement, mutagenesis, chromosomal duplication, interspecific and intraspecific hybridization.

Origem, evolução e estratégias para o melhoramento genético de fisális

RESUMO: *Physalis peruviana* L. (fisális) apresenta grande potencial econômico devido ao sabor diferenciado de seus frutos. A produtividade dos pomares brasileiros é baixa em função do número limitado de variedades ou cultivares disponíveis. O principal entrave na seleção de genótipos superiores é a falta de informação sobre a variabilidade genética dentro e entre as populações de fisális e, possivelmente, a base genética limitada das mesmas, que pode ser explicada pelos processos evolutivos, de domesticação e de seleção das populações naturais ou artificiais. A fisális cultivada atualmente no Brasil é tetraploide e tal poliploidia pode ter levado ao isolamento reprodutivo da espécie, o qual impede a ocorrência de hibridação intraespecífica. As populações cultivadas provêm de um *pool* genético comum e, além disso, sofreram um longo processo de domesticação e seleção realizadas empiricamente pelos agricultores. Porém, na Colômbia e em outros países andinos existem populações silvestres que exibem diversidade genética que, embora sejam fundamentais para a conservação da espécie, apresentam baixo potencial para o desenvolvimento de genótipos com características agronômicas superiores. A fim de criar e ampliar a variabilidade genética de fisális, os melhoristas tem empregado várias estratégias incluindo a indução de mutação, a duplicação cromossômica e a hibridação inter e intraespecífica. Além disso, a produção de linhagens duplo-haploides a partir da cultura de anteras *in vitro* vem demonstrando bons resultados para a seleção de híbridos. Os genótipos mutantes e/ou híbridos obtidos através dos métodos citados em associação com os de seleção genômica ampla podem gerar cultivares com características agronômicas superiores.

Palavras-chave: Solanaceae, melhoramento genético, mutagênesis, duplicação crômossomica, hibridação interespecífica e intraespecífica.

INTRODUCTION

Physalis peruviana L. (Solanaceae), commonly known as physalis or fisális in Brazil, is an exotic plant of considerable economic potential by virtue of the remarkable flavor and aroma of the fruits in conjunction with their important nutritional and medicinal properties (LONDOÑO, 2013; FISCHER et al., 2014). Physalis can be consumed *in natura* or in the form of juice, ice cream or liqueurs, and is

Received 10.18.21 Approved 08.09.22 Returned by the author 10.26.22
CR-2021-0742.R1
Editors: Leandro Souza da Silva Maria do Céu Monteiro Cruz

also used in the confectionery industry for decorating cakes and desserts (FISCHER et al., 2014).

Colombia is the largest global producer of physalis with annual fruit production estimated at 18,134 t, some 80% of which is exported *in natura* generating revenue of US$ 32 million (AGRONET, 2019). Commercial plantations of physalis have also been established in India, the United States of America, Portugal, France, Bulgaria, Brazil and South Africa. However, while the productivity in Colombia ranges from 9 to 28 t ha^{-1}, in the other growing regions productivity is much lower and varies between 2 and 6 t ha^{-1} (GOULART JUNIOR et al., 2017). In addition, countries outside the Andean region tend to produce fruits that are of inferior quality, with low concentrations of total soluble sugars (TSS), and they cannot compete in the marketplace with fruits of Colombian origin.

The major problem in expanding fruit production in non-Andean countries is the lack of improved cultivars. Currently, only two cultivars are available, namely Corpoica Andina and Corpoica Dorada, but both were selected for the climatic conditions in Colombia and may not perform satisfactorily in other regions (SÁNCHEZ-BETANCOURT et al., 2016a, 2016b). Genetic improvement of physalis is necessary in order to obtain genotypes that are more tolerant to pests and diseases while having the capacity to produce high yields of perfectly formed fruits. According to ALLARD (1999), the success of a breeding program is directly dependent on the existence of genetic variability. However, preliminary investigations have shown that cultivated physalis populations exhibit a somewhat restricted genetic base with respect to agronomic traits of interest (GARZÓN-MARTÍNEZ et al., 2012; TREVISANI et al., 2016a; MORILLO-CORONADO et al., 2018; DELGADO-BASTIDAS et al., 2019).

The presence of a limited genetic base may be related to the processes of evolution, domestication and selection (natural or artificial) of a species. In the case of physalis, domestication dates from the pre-Inca period and the species was subsequently disseminated through North America, Europe and Africa. In 1980, superior genotypes of physalis that had been created through natural chromosomal duplication followed by mass selection were found in South Africa. It is likely that Colombian growers performed empirical crossings between African and local genotypes and propagated the derived populations over the years, thereby reducing genetic variability through parental crosses (WILF et al., 2017).

According to ALLARD (1999), the main strategies used in plant breeding to overcome the limited genetic base of valuable plant species are induced mutation, interspecific and intraspecific hybridization and chromosomal duplication, including recombination and amplification of plant variability. The use of such approaches, alongside appropriate application of conventional and biotechnological breeding techniques, can accelerate the development of physalis variants (ALLARD, 1999; TREVISANI et al., 2018). In this manner, breeders could create new cultivars by screening the best-adapted mutants and hybrids, and subsequent directed crossings between plants.

The present review describes the evolutionary process and the existing genetic variability in *P. peruviana* with the aim of understanding the key issues involved in the design of efficient breeding strategies for this valuable resource.

Botanical characterization and origin of Physalis

Physalis is one of the many economically important genera belonging to the family Solanaceae, and encompasses approximately 100 species, several of which produce edible fruits and bioactive compounds (OLMSTEAD, 2013). Along with *P. peruviana*, the species most frequently cultivated are *Physalis pubescens* L. (syn. *Physalis floridana* Rydb.*;* hairy groundcherry) and *Physalis ixocarpa* Brot. ex. Hornem (tomatillo).

Physalis peruviana has many common names around the world as, for example, fisális or physalis in Brazil, uchuva in Colombia, uvilla in Ecuador, tepareey makowi in India, groselha-do-Peru in Portugal, kapstachelbeere in Germany and Cape gooseberry or goldenberry in the United States of America. Although, the exact Andean origin of physalis is uncertain, it is known that the species was acclimatized and domesticated in the highlands of Peru and Chile prior to the formation of the Inca Empire (RODRÍGUEZ & BUENO, 2006).

Physalis is an herbaceous species with an indeterminate growth habit; although plants do not normally exceed 2 m in height. The life cycle can be annual or biennial depending on climatic conditions (DUARTE et al., 2013; FISCHER et al., 2014), with some varieties displaying short-day photo periodism and others exhibiting neutral-day behavior. The leaves bear numerous trichomes and present a soft velvety texture. The roots are fibrous and pivotal and may reach up to 80 cm in length,but the species does not tolerate waterlogged soils (FISCHER et al., 2014). The flowers are hermaphrodite and can be either insect-pollinated or self-pollinated depending on the climatic conditions of the region and the planting regime employed (LAGOS et al., 2008; PUENTE et al., 2011). Although, vegetative reproduction is rather common in this species, it is not used for commercial propagation (FISCHER et al., 2005). The fruits of physalis have a distinct morphology characterized by a spherical orange/yellow berry (diameter 1.25 to 2.5 cm; mass 4 to 10 g) enclosed in a papery husk (inflated fruiting calyx), the function of which is to protect against microbial degradation and physico-mechanical damage. Some authors have claimed that fruits encased in the calyx can have a shelf life of approximately one month (GALVIS et al., 2005).

Genetic variability and evolution of physalis

The primary sources of variability in *P. peruviana* are the native plant populations present at the original sites followed by those conserved in active germplasm banks (AGBs). Most of the physalis AGBs are located in Latin America (DUARTE et al., 2013) with the largest collection, comprising 222 accessions, being housed in the germplasm bank of the Universidad Nacional de Colombia at Palmira. Other important physalis AGBs in Columbia are maintained by the Corporación Colombiana de Investigación Agropecuaria, (AGROSAVIA) with 98 accessions (LIGARRETO et al., 2005) and the Universidad de Nariño (UDENAR) with 50 accessions. In addition, the Departamento Nacional de Rescursos Fitogenéticos/Instituto Nacional Autónomo de Investigaciones Agropecuarias (DENAREF/INIAP) preserves 23 traditional varieties of *P. peruviana* from Ecuador and one each from Colombia and Bolivia at the Estación Experimental Santa Catalinain Quito, Ecuador (RAMÍREZ & DAVENPORT, 2021).

The use of molecular markers and gene mapping techniques has facilitated studies concerning the evolution process and genetic variability of plant species, particularly with regard to loci for quantitative traits (WHITE et al., 2007).Various molecular markers are available for the analysis of plant genetic diversity (WHITE et al., 2007) and several have been used in the analysis of *P. peruviana*, including single sequence repeat (SSR; also known as microsatellites) (LAGOS et al., 2007; SIMBAQUEBA et al., 2011; CELY et al., 2015; CHACÓN et al., 2016) and single nucleotide polymorphism (SNP) (GARZÓN-MARTÍNEZ et al., 2015; OSORIO-GUARÍN et al., 2016; GARCÍA-ARIAS et al., 2018a) markers (Table 1). Since these markers are highly polymorphic and co-dominant, they enable alterations in sets of chromosomes, as well as in specific nitrogen bases, to be identified so that the presence of heterozygotes and/or hybrids can be readily observed.

Studies have shown that the index of heterozygosity in physalis varies between 0.17 and 0.73 with polymorphism in the range of 22 to 35.8%, indicating that DNA-based techniques are efficient in detecting genetic variability among plant populations. Hence, it is possible to discriminate ecotypes of physalis according to level of ploidy, geographical origin and

Table 1 - Molecular markers used in studies on the genetic variability of *Physalis peruviana.*

Reference	Population	Marker	Number of markers used	Observed heterozygosis	Polymorphism (%)
SIMBAQUEBA et al. (2011)	Native and commercial	Quantitative: SSR[1]	138	NA[3]	22
CELY et al. (2015)	Intraspecific hybridization	Quantitative and qualitative: mass DNA ladder	482	0.73	35.8
GARZÓN-MARTÍNEZ et al. (2015)	Cultivated and non-cultivated	SNP[2]	454	0.47	33
GARCÍA-ARIAS et al. (2018a)	Various parts of the world	Quantitative:SNP[2]	27.982	0.72	34
CHACÓN et al. (2016)	Cultivated and non-cultivated	Quantitative: SSR[1]	16	0.17	12
MORILLO et al. (2018)	Accessions	Quantitative: SSR[1]	6	0.44	NA[3]
DELGADO-BASTIDAS et al. (2019)	Accessions	Quantitative: SSR[1]	6	0.17	0.12

[1] Simple-sequence repeat.
[2] Single nucleotide polymorphism.
[3] Not available.

degree of domestication (i.e. wild or domesticated) (LEIVA-BRONDO et al., 2001). According to earlier studies, the number of chromosomes in populations of *P. peruviana* is variable, and three distinct ecotypes or cytotypeshave been recognized, namelywild (2n = 24), Colombian (2n = 32) and Kenyan or African (2n = 48) (MENZEL, 1951; GANAPATHI et al., 1991; LAGOS et al., 2008). The Colombian ecotype is probably a hybrid resulting from crossings between individuals from different cultivated populations of physalis (RODRIGUES & BUENO, 2006).

More recent analyses of wild and cultivated populations of *P. peruviana*in Colombia, Brazil and Spain have revealed the existence of a limited genetic base since observed heterozygosis indices werein the region of 17% and polymorphism around 12% (LEIVA-BRONDO et al., 2001; TREVISANI et al., 2018). SIMBAQUEBA et al. (2011) identified 83 perfect SSR loci in the coding regions from the physalis leaf transcriptome, from which 162 primers were developed for use in the evaluation of seven physalis ecotypes from Colombia, Kenya and Ecuador in addition to a related species (*P. floridana*). These authors reported that the genetic diversity among the ecotypes was low with a polymorphism rate of 22%. In a later study, CHACÓN et al. (2016) found substantial similarity in the genetic structures of 85 native and cultivated physalis accessions from the central, western and eastern regions of the Andes. Low variability has also been reported for wild and cultivated physalis genotypes from Boyacá, Colombia (MORILLO-CORONADO et al., 2018) and for 40 accessions and lineages maintained by UDENAR and AGROSAVIA (DELGADO-BASTIDAS et al., 2019).

Disparities between the findings of these studies can be explained by the difficulties in evaluating the genetic variability that is inherent to the species, which include limitations regarding phytosociological surveys and the lack of definition of the parameters to be evaluated. In addition, selection of the site of the studied population may in sampling error known as the “founder effect”, which occurs when a new population is formed by a small number of migrants that are not representative of the parent population. This phenomenon gives rise to fluctuations in the frequency of particular version of alleles (genetic drift). Another problem is that the available molecular marker shave not been fully validated for *Physalis* species. Until specific markers and a reference genome (there is currently no reported genome sequence for *Physalis*) are forthcoming, genetic variability may be overestimated or its assessment may be affected by bias (OSORIO-GUARÍN et al., 2016; MORILLO-CORONADO et al., 2018; DELGADO-BASTIDAS et al., 2019).

As is the case for many plant species, the genetic similarity among physalis populations is associated with evolutionary processes, domestication and selection of genotypes (either natural or artificial) (VEASEY et al., 2011). Physalis has developed competent mixed (autogamous and allogamous) reproductive systems and/or efficient cell repair mechanisms. Autogamous plants generally exhibit lower genetic diversity (ALLARD, 1999) and, in the case of physalis, autogamy may have become predominant (MORILLO-CORONADO et al., 2018). In addition, physalis produces large amounts of pollen such that the chances of gene flow between and within populations are very much reduced.

Polyploidy in physalis may cause inbreeding depression and restrict the genetic base in a short space of time. According to FISCHER et al. (2005), tetraploidy in cultivated physalis arose in South African populations that underwent natural chromosomal duplication. This event may have led to some reproductive isolation and an associated decline in the number of parental genotypes. Reproductive isolation mechanisms can prevent crossbreeding between populations with different chromosome levels that would likely result in the formation of non-viable embryos or render the survival of plants in the natural environment more difficult (PELÉ et al., 2018).

Populations of polyploid physalis were introduced into Colombia by researchers and disseminated by farmers since 1980, an actuality that promoted crosses between related individuals with a common background and a shared gene pool (DELGADO-BASTIDAS et al., 2019). In this sense, the farmers themselves contributed, intentionally or not, to the restriction of the genetic base by selecting and multiplying the populations of interest, thereby preventing genetic recombination with non-domesticated populations (GUPTA & ROY, 1981).

Genetic improvement of Physalis

Genetic improvement of plants is the most viable and ecologically sustainable method of increasing agricultural production. Selective breeding of physalis has, for many years, been performed by farmers in an empirical manner (LONDOÑO, 2013) but research programs have intensified recently in some countries in order to improve the productive performance of the culture (MIRANDA et al., 2020). The most advanced genetic improvement program for physalis is currently being conducted in Colombia (CHACÓN et al., 2016), but in most other producing countries, the culture continues to be propagated by seeds of unknown genetic structure and only a few improved cultivar shave been registered (LAGOS et al., 2008).Two of the cultivars that are available, namely Corpoica Andina and Corpoica Dorada, were obtained through mass selection and hybridization between cultivated populations (Caldas, Cundinamarca and Nariño) and new accessions from Guatemala and the Netherlands that were introduced into the AGROSAVIA breeding program (SÁNCHEZ-BETANCOURT et al., 2016a, 2016b; NUNEZ ZARANTES, 2020).

The genetic improvement of physalis would involve the selection of genotypes with superior traits such as enhanced productivity and resistance to biotic and abiotic stresses. The biggest problems with physalis culture worldwide relate to post-harvest depreciation caused by fruit cracking (FISCHER et al., 2005) and to viral diseases caused by tomato severe rugose virus (ToSRV) and *Fusarium oxysporum* Schlecht. (ENCISO-RODRÍGUEZ et al., 2013). In addition, development of cultivars that produce bioactive principles with nutraceutical, pharmaceutical and medicinal applications would be an added bonus.

However, the limited genetic base of physalis represents a significant obstacle in the development of cultivars with enhanced traits, especially in countries such as Brazil (TREVISANI et al., 2018). According to ALLARD (1999), the success of a plant-breeding program is positively correlated with the existence of a broad genetic base since adaptation and selection of the species over the generations depends on the existence of variability upon which the improvement can act. Thus, the job of the plant breeder is to increase the frequency of evolutionary forces that create, amplify and regulate genetic variability.

Main approaches for the amplification of genetic variability in Physalis

There are three main strategies available for overcoming and augmenting the limited genetic base of physalis. The first is the introduction of new accessions and production of intraspecific hybrids, the second is the induction of mutation followed by mutant selection, while the third possibility is the development of polyploids through chromosomal duplication or of amphipolyploids via interspecific hybridization followed by chromosomal duplication.

Introduction of germplasm

It is likely that genetic variability associated with agronomic traits of interest has been exhausted in physalis by the continuous selection performed by farmers or has already been exploited by breeders in the development of new cultivars. Under these circumstances, the low level of diversity still available in cultivated populations may be of limited agronomic importance. However, there are reports of native germplasm from other species of *Physalis*, or from interspecific hybrids within the genus, being used for hybridization inasmuch as they represent a source of alleles conferring resistance to viral diseases (CELY et al., 2015; SILVA-JÚNIOR et al., 2022). In addition, some studies have shown that variability within-populations is greater than between-populations; therefore, it is important to design tools that allow the evaluation of individual plants in order better to exploit intrapopulation resources (CHACÓN et al., 2016).

Induction of mutation

Mutagenesis is the only mechanism that generates genetic variations by changing the nucleotide sequence in the DNA of a particular gene, thereby creating a new allele with the potential to modify phenotypic expression. However, the rate of natural mutation is low and the majority (99%) of point mutations are in recessive alleles or are deleterious to plants (ORTON, 2019). Moreover, it is difficult to observe phenotypic alterations induced by natural mutations and, for this reason, chemical and physical agents are used to increase the frequency of mutations in plants. The mutagenic compounds most commonly employed are the low-cost alkylating agents ethylmethanesulfonate (EMS) and methylmethanesulfonate (MMS). These mutagens add ethyl or methyl groups to the nitrogenous bases of DNA, thereby altering the pairing capacity or even blocking the action of DNA polymerase (ORTON, 2019). According to GUPTA et al. (2018), the use of EMS in physalis increased the rate of genetic variability to 4.5%.

Studies involving the use of physical mutagenic agents in physalis have been ongoing since 1970 (FOOD AND AGRICULTURE ORGANIZATION/INTERNATIONAL ATOMIC ENERGY AGENCY, 2019). Gamma radiation is the most common agent employed in physalis breeding research because it is safe, does not generate toxic residues after irradiation and is highly efficient in penetrating cell tissues resulting in chromosomal breakages or point alterations in the nitrogenous bases (ALLARD et al., 1999). Various doses of gamma rays produced by^{60} Co sources have been evaluated (ANTÚNEZ-OCAMPO et al., 2017;

GUPTA et al., 2018) and levels between 300 and 350 Gy were reported to produce the best responses, with the highest frequency of observed mutations ranging between 3 and 5% (CARO-MELGAREJO et al., 2012; GUPTA et al. 2018). It would appear that mutagenesis of axillary buds of physalis followed by growth of the irradiated material under *in vitro* conditions is more effective than mutagenesis of seeds (CARO-MELGAREJO et al., 2012).

Although, increases in genetic variability have been observed in physalis after induction of mutagenesis, more information is required concerning the segregation of populations in the field with respect to traits of economic importance. The only two trials of this type reported in the literature (TREVISANI et al., 2016b; ANTÚNEZ-OCAMPO et al., 2020) described vegetative changes in plants and physiological alterations in fruits such as increased diameter and weight. Nevertheless, the genetic gain derived was insufficient to increase production or to allow the exploitation of heterosis in crossings. Despite the difficulties, genetic variability in physalis can be enhanced by increasing the frequency of mutations, either by adjusting the dose-response relationship or by increasing the number of individuals exposed to mutagens (ORTON, 2019).

Induction of polyploidy

Polyploidy refers to the variation in the number of chromosomes that occurs in somatic or germ cells as a result of whole-genome duplication under natural or induced conditions (VAN DE PEER et al., 2017), whereas aneuploidy is the condition were one or more chromosomes in a set are missing or present in an abnormal copy number (GRIFFITHS, 2009; SATTLER et al., 2016). Euploidy is the state in which the duplication of an entire set of chromosomes occurs once or several times generating diploids (2x), triploids (3x) and so forth (ALLARD, 1999). Euploids may be classified as autopolyploids that arise within a single species as a result of the doubling of one chromosome (represented by a genome AAAA, for example), or allopolyploids that arise through the merging of chromosome sets of different parental species (hybridization) followed by chromosomal duplication (represented by a genome AABB, for example) (GRIFFITHS, 2009).

Polyploidy can be induced artificially through the application of mitotic inhibitors, the most commonly used of which is colchicine, an alkaloid extracted from the seeds or shoots of saffron (*Colchicum autumnale* L.) (PEREIRA et al., 2017; SATTLER et al., 2016). Colchicine interferes with spindle formation during cell division by impeding polymerization or promoting depolymerization, thereby preventing chromosome segregation during the anaphase and effectuating doubling of the number of chromosomes in the treated cell tissues (WITTMANN & DALL'AGNOL, 2003). In addition to the use of chemical agents, a sophisticated method of producing polyploids is the induction of doubled haploid via anther culture, a technique that has been employed in the development of new varieties of crops including *P. peruviana* (GARCÍA-ARIAS et al., 2018b).

Polyploidy is important in the genetic improvement of plants because it allows the possibility of expanding the genetic base, increasing heterosis and obtaining new lineages in a short space of time without the need for self-fertilization. According to ALLARD (1999), the presence of a single dominant allele in a polyploid is already sufficient for expressing dominance, thereby masking or buffering the effects of deleterious alleles and resulting in improved performance of the individual plant. Moreover, the induction of polyploidy is more effective than other methodologies for inducing expression of quantitative traits. For example, in polyploids (mainly the autotetraploids) there is expansion of the cell owing to the increase in nuclear content and, consequently, enlargement of organs as well. This phenomenon, known as the Gigas effect, results in fitness advantages such as thickened leaves and stems, bigger grains, tubers and fruits.

Polyploidy is common in perennial species and natural populations of *P. peruviana* with diploid and tetraploidy genotypes have been reported (RODRÍGUEZ & BUENO, 2006), while polyploidy has been induced successfully in *P. ixocarpa* and *P. peruviana* (DÍAZ et al., 2008; ROBLEDO-TORRES et al., 2011; LIBERATO et al., 2014; GARCÍA-ARIAS et al., 2018b). According to ROBLEDO-TORRES et al. (2011), treatment of young *P. ixocarpa* seedlings with 0.12% or 0.16% colchicine for 24h induced autotetraploidy ($2n = 4x = 48$) with an average efficiency of 66%. GARCÍA-ARIAS et al., (2018b) employed axillary buds from four haploid *P. physalis* genotypes to evaluate the effects of colchicine-induced chromosome doubling on ploidy level and pollen fertility. Optimal chromosome doubling of the haploids was obtained with 5 mM colchicine solution and a 2h exposure time, with more than 60% of the regenerants presenting chromosome doubling and high levels of fertility. Other studies have reported lower success rates in the range of 4 to 58% when using seeds (KUMAR, et al., 2019; COMLEKCIOGLU & OZDEN, 2019).

The main disadvantages of autopolyploidy are the low fertility of the generated plants and, more especially, their genetic instability, which may give rise to high frequencies of mixoploids or chimeras presenting different ploidy levels in the same tissues (PEREIRA et al., 2017). Indeed, chromosome doubling may confer partial or total sterility owing to the formation of unreduced gametes arising from meiotic anomalies. GARCÍA-ARIAS et al., (2018b) reported that the induction of autopolyplody in *P. peruviana* resulted 60% of duplication with most individuals high frequency of chimeras. Furthermore, these researchers observed that, after a few generations, the autopolyplody populations had returned to their initial chromosomal constitution owing to the occurrence of chromosome losses or deletions. According to TAYALÉ & PARISOD (2013), successful nascent polyploids have to overcome incompatibilities associated with the drastic reorganizations that are commonly observed in the genome of the newly formed polyploid.

Some studies have shown that the induction of polyploidy in *P. peruviana* can lead to the formation of deformed and pulpless fruit (GARCÍA-ARIAS et al., 2018b). Moreover, the reproductive cycle of some plants increased by more than one month in comparison with the tetraploids, and other morphological changes were observed including leaves that were wrinkled and dark-green and flowers of reduced size with petals exhibiting an intense yellow color (KUMAR, et al.,2019; GARCÍA-ARIAS et al., 2018b). However, the advantage of physalis genotypes is that they can be propagated through cuttings, which not only fixes genetic instability problems but also reduces the stages of genetic improvement.

Intraspecific and interspecific hybridization

In comparison with other cultivated species, reports that describe controlled intraspecific and interspecific crossings in physalis and subsequent selection to obtain superior genotypes are somewhat scarce. Indeed, intraspecific hybridizations experiments aimed to assess the general and specific combining ability of physalis only commenced some two decades ago. Nevertheless, physalis plants with elevated combining ability, which is defined as the capacity of an individual to transmit superior performance to its offspring, have been obtained in respect of various important agronomic traits, indicating that it is possible to select promising hybrids (LEIVA-BRONDO et al., 2001; LAGOS-BURBANO et al., 2021a, 2021b). These hybrids produced fruits of superior quality, larger size, higher maturation index and increased levels of total soluble solids (TTS) and vitamin C, along with a lower percentage of cracked fruit. LAGOS et al. (2007) also observed the superior combining abilities of intraspecific hybrids of physalis with the best exhibiting TSS values ranging between 15.73 and 16.25 °Brix (2% higher than the parents) and fruit/husk masses varying in the range 6 and 7 g (2g more than the parents). However, significant differences were observed between reciprocal crosses with respect to the character fruit diameter, indicating the occurrence of maternal effects regarding this variable. Thus, it is important to determine which of the parents should be used as male and female genitors in the hybridizations. In contrast to the above, the populations employed in hybridization experiments performed by TREVISANI et al. (2018) presented unsatisfactory specific combining abilities making it difficult to attain hybrids,most likely because of the varying degrees of polyploidy. These authors emphasized that the limited genetic base was another factor that made the production of superior hybrids more difficult, and that many more self-fertilizations would be required to obtain divergent lineages.

The double haploid technique has hastened the development of physalis lines exhibiting increased genetic gains by minimizing the problems posed by the differential levels of ploidy that impede crossings between varieties. Recently, LAGOS-BURBANO et al. (2021b) evaluated 36 physalis hybrids obtained from crossings between nine double haploid lines and described their combining ability as generally high. The selected hybrids exhibited encouraging potential since they produced fruits with high TSS values (> 14ºBrix),high fruit/husk weight (> 7 g) and low cracking percentage. Studies have shown that, in general, better hybrids can be obtained from crossings between Colombian ecotypes with Kenian/African ecotypes and/or populations from Guatemala and the Netherlands. However, it is important to highlight that the interaction genotype × environment also affects the performance of the plants, and this may explain the restricted phenotypic variations reported in populations cultivated in Brazil.

Interspecific or intergeneric hybridization involves crossing distinct but related species such as a domesticated species and its wild parent. Intergeneric hybridizations have allowed the selection of fruits with interesting characteristics, as exemplified by the different combinations of color, shape and taste that have been obtained with strawberry (*Fragaria* x *ananassa* Duch.).

In the case of the genus *Physalis*, species with the same level of ploidy interbreed readily in nature (PANDEY, 1957). Thus, hybridization of *P. Peruviana* with wild species such as *P. angulata* and *P. ixocarpa* can broaden the genetic base and, if accompanied by repeated backcrossing, could result in the introgression of genes of agronomic interest into the domesticated species. Introgressive breeding allows the selection of progenies with superior traits such as increased productivity and disease resistance (ENCISO-RODRÍGUEZ et al., 2013).

MENZEL (1951) pioneered interspecific hybridizations between *P. peruviana* and *P. angulata, Physalis heterophylla* Nees, *Physalis virginiana* Mill., *Physalis mollis* Nutt. and *Physalisviscosa* L.; although, viable seeds were obtained solely from the crossing *P. peruviana* and *P. angulata*. AZEEZ & FALUYI (2018) performed crossings between *P. peruviana*, *P. angulata*, *Physalisminima* L. (syn. *P. micrantha* Link) and *P. pubescens*, but only one F1 hybrid derived from *P. angulata* x *P. pubescens* was viable. Additionally, GANAPATHI et al. (1991) reported that attempted hybridizations between *P. pubescens*, *P. peruviana* and *P. angulata* were unsuccessful, including their reciprocal crossings. Conversely, PAL et al. (1993) were able to produce successful interspecific hybrids between *P. Minima* and *P. peruviana* by culturing excised embryos *in vitro* on Murashige & Skoog medium at 20-25 days post-pollination. The majority of the regenerated seedlings (64%) survived after transferring them to pots and watering with nutrient solution. The hybrid fruits were similar in color to those of the wild male parent but with varying color intensity.

The interspecific crossings between *P. floridana* and *P. peruviana* performed by CELY et al. (2015) yielded hybrids with around 50% pollen viability and the formation of normal fruits with viable seeds. These results indicate likely sequence homology between the genomes of the two species. Nonetheless, such outcomes were observed only when *P. floridana* was used as a pollen receptor, while in reciprocal crossings with *P. peruviana* as female genitor, the capacity for fruit formation was reduced and the fruits (when formed) were small, misshapen and seedless.

According to these researchers, this finding may be explained by a phenomenon known as unilateral interspecific incompatibility, which probably occurred during the speciation process. This situation is prevalent within members of the Solanaceae, particularly among species of *Solanum* and *Capsicum*, and gives rise to a form of reproductive isolation. Unilateral incompatibility is a reproductive barrier generally resulting from the delay or inhibition of growth of the pollen tube and the lack of germination of the pollen grain. LUIS (2016) also observed pollen incompatibility between *P. peruviana* and *P. ixocarpa* and, in this case, the single hybrid produced three fruits with only one survivor, demonstrating that the hybrid seeds were viable. It was not possible to confirm whether this hybrid was amphipolyploid because the amount of DNA in the seeds was too smallto allow analysis by flow cytometry.

Very recently, SILVA-JÚNIOR et al. (2022) reported encouraging results from hybridization experiments carried out between *P. angulata*, *P. ixocarpa*, *Physalis pruinosa* L., *P. peruviana*, *P. pubescens*, *P. minima* and *Physalis daturifolia* Lam. The 29 interspecific hybrids so obtained could be classified into five distinct groups that produced fruit with enhanced qualitative (level of TSS) and/or quantitative (productivity, diameter, fresh and dry mass) characteristics in comparison with those of the parent plants. Such hybrids may contribute to the improvement of physalis in the future.

The main problems encountered with intraspecific hybridization of *Physalis* are the reduction of pollen viability (pre-zygotic), malformation of pollen grains, embryo death and aborted seeds, resulting in the sterility of hybrids (post- zygotic)(AZEEZ & FALUYI, 2018). Regarding interspecific hybridization, the principal issue is the sterility of hybrids related to meiotic defects originating from the inheritance of only one genome from each of the parents. During meiotic division, chromosome pairing is hindered owing to the lack of homology between the copies of parental DNA, and such faults results in sterility. In order to overcome this problem and restore fertility to interspecific hybrids, chromosome duplication can be induced to generate polyploids that have homologous chromosomes (amphidiploids or amphipolyploids).

Future perspectives and strategies

In order to face the challenges currently encountered in the genetic improvement of physalis and to accelerate the expansion of the genetic base, breeders must adopt more efficient approaches and fully exploit the existing genetic resources between- and within-populations. It will be essential to employ advanced biotechnological techniques such as genome-wide selection (GWS) assisted by molecular markers to design novel breeding programs, as well as high-through put next-generation sequencing (NGS) and gene editing. In this context, the clustered regularly inter spaced short palindromic repeats/associated enzyme Cas 9 (CRISPR/Cas 9) genome editing system offers a high precision approach for the insertion and/or deletion genes of interest in physalis and for the performance of site-directed mutagenesis. Once the restricted genetic base of physalis has been surmounted using these techniques, artificial crosses must be carried out. The use of the doubled haploid technique from anther culture is of great value in the selection of physalis hybrids with good combinations of characteristics for use in experimental crosses of the species.

In the long-term, the mutants and hybrids so obtained may generate physalis cultivars with superior traits, and these must be finally tested in the field for phenotypic stability prior to release and commercialization. In this regard, and as a part of the GWS approach, it is worth mentioning the best linear unbiased prediction (BLUP) method, a statistical procedure used in linear mixed models that has proved successful in the complete analysis of the phenotypic performance of parents and their progenies.

ACKNOWLEDGMENTS

The authors wish to thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Programa de Bolsas Universitárias de Santa Catarina/Fundo de Apoio à Manutenção e ao Desenvolvimento da Educação Superior (UNIEDU/FUMDES) for provision of scholarships. We are also grateful to Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina (FAPESC) for financial support.

DECLARATION OF CONFLICT OF INTEREST

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analysis, or interpretation of the data; in the writing of the manuscript, and in the decision to publish the results.

AUTHORS' CONTRIBUTIONS

All authors contributed equally to the manuscript.

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