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TAKING ADVANTAGE OF ORGANELLE GENOMES IN PLANT BREEDING: AN INTEGRATED APPROACH

APROVECHANDO LOS GENOMAS DE LAS ORGANELAS EN EL MEJORAMIENTO GENÉTICO DE PLANTAS: UN ENFOQUE INTEGRADO.

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ABSTRACT

Plant cells carry their genetic information in three compartments: the nucleus, the plastids and the mitochondria. In last years, next-generation sequencing has allowed the development of genomic databases, which are increasingly improving our knowledge about the role of nuclear and cytoplasmic genes as well as their interactions in plant development. However, most plant breeding efforts consider the utilization of the nuclear genome, while less attention is given to plastid and mitochondrial genomes. The objective of this review is to present current knowledge about cytoplasmic and cytonuclear effects on agronomic traits bearing in mind the prospective utilization of all the genomes in plant breeding.

Key words: Cytoplasmic genes, cytoplasmic-nuclear interactions, plant breeding methods.

RESUMEN

La información genética de las células vegetales está contenida en tres compartimentos: el núcleo, los plástidos y las mitocondrias. En los últimos años, la secuenciación de última generación ha permitido desarrollar bases de datos genómicas que están aumentando progresivamente nuestro conocimiento sobre el rol de los genes nucleares y citoplásmicos y de sus interacciones durante el desarrollo de la planta. Sin embargo, la mayoría de los esfuerzos de la mejora vegetal se basan en el aprovechamiento del genoma nuclear y relegan a los genomas de los plástidos y las mitocondrias. El objetivo de esta revisión es actualizar el conocimiento sobre de los efectos citoplásmicos y las interacciones núcleo-citoplásmicas sobre caracteres interés agronómico, asumiendo la utilización potencial de todos los genomas en el mejoramiento vegetal.

Palabras clave: genes citoplásmicos, interacciones núcleo-citoplásmicas, métodos de mejoramiento vegetal.

PLANT ORGANELLE GENOMES

The plant cell is the result of endosymbiotic events which resulted in the evolution of the mitochondrion from an α-proteobacterium and, somewhat later, the evolution of the chloroplasts from a cyanobacterium. During co-evolution, the three genomes of plant cells have undergone significant structural changes that resulted in an optimized expression of the compartmentalized genetic material and cross-talk between the nucleus and the organelles. As a result of co-evolution, most genes from the symbionts were transferred to the nucleus of the host cell. Although mitochondria and plastids still retain their own, ancestral DNA, most proteins required for organelle function are encoded in the nucleus and must be imported (Allen, 2015; Archibald, 2015; Grainer and Bock, 2013; Smith and

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Keeling, 2015). There are multiple copies of both plastid and mitochondrial DNA inside each organelle. The number of copies varies depending on the tissue type and it changes notably during development (Kumar *et al.*, 2015; Oldenburg and Bendich, 2015). Regarding their mode of inheritance, while nuclear genetic information is inherited biparentally, plastid and mitochondrial genomes of most land plants show predominantly maternal inheritance, with some cases of paternal and biparental inheritance (Birky, 1995; Xu, 2005; Greiner *et al.*, 2014).

High-throughput sequencing technologies have allowed rapid advance in organelle genetics and genomics. To date, 2257 complete chloroplast genomes and 246 plant mitochondrial genomes are available (https://www.ncbi.nlm.nih.gov/genome/browse#!/organelles).

The chloroplast genomes (plastomes) of land plants range between 107 kb (*Cathaya argyrophylla*) to 403 kb (*Codonopsis lanceolata*). They have highly conserved structures and organization of content, consisting of a single circular molecule with two copies of an Inverted Region (IR) that separate large and small single-copy (LSC and SSC) regions. Recent studies have identified considerable diversity within non-coding intergenic spacer regions, which often include important regulatory sequences. The chloroplast genome includes 120-130 genes, mainly participating in photosynthesis, transcription, and translation (Daniell *et al.,* 2016).

Plant mitochondria genomes range between 200 and 750 kb in angiosperms, but extreme sizes of 6.7 Mb and 11.3 Mb are found in *Silene noctiflora* and *Silene conica* respectively, resulting from massive proliferation of non-coding content. The number of genes usually ranges between 50 and 60, with multiple cis- or trans-spliced introns and large intergenic regions. Protein genes encode subunits of the oxidative phosphorylation chain complexes proteins involved in the biogenesis of these complexes and several ribosomal proteins. The physical organization of the plant mitochondrial DNA includes a set of sub-genomic forms resulting from homologous recombination between repeats, with a mixture of linear, circular and branched structures. Recombination appears to be an essential characteristic of plant mitochondrial genetic processes, both in shaping and maintaining the genome. In addition, autonomous plasmids of essentially unknown function are found, increasing the complexity of the genome (Gualberto *et al.*, 2014; Morley and Nielsen, 2017).

THE ROLES OF PLANT ORGANELLES

Chloroplasts and mitochondria are mainly known by their involvement in photosynthesis and ATP production, respectively. However, both organelles play a part in multiple metabolic pathways and are essential for normal growth and development of plants (van Dingenen *et al.*, 2016). Chloroplasts are part of the family of plastids, in which some components are interconvertible during development: proplastids, etioplasts, chloroplasts, chromoplasts, leucoplasts, elaioplasts, amyloplasts, proteinoplasts and gerontoplasts. All plastids perform house-keeping functions and basal metabolic functions essential to the cell metabolism and specific roles according to their differentiated type. Plastids are the site of carbon oxidation via photorespiration, chlorophyll synthesis, carotenoid, α-tocopherol (vitamin E), plastoquinone and phylloquinone (vitamin K) synthesis, fatty acid and lipid synthesis, nitrogen assimilation and aminoacid synthesis, sulfur metabolism, oxygen metabolism and chlororespiration (Wise, 2007; Rolland *et al.*, 2018).

Mitochondria are dynamic organelles, changing shape, number, size, composition and distribution inside the cell depending on developmental stage, type of tissue, cell cycle phase, energetic cell demand, and external stimuli. Mitochondria are involved in the synthesis of nucleotides, vitamins and cofactors, the metabolism of amino acids and lipids, the photorespiratory pathway and the export of organic acid intermediates for wider cellular biosynthesis (Welchen *et al.*, 2013; Rao *et al.*, 2017).

Results obtained in last years demonstrated that mitochondria and chloroplasts also play a crucial role in perceiving and responding to biotic and abiotic stress conditions and that both organelles participate in programmed cell death (Chi *et al.*, 2015;Liberatore *et al.*, 2016; Wang *et al.*, 2018; Beltrán *et al.,* 2018; Rolland *et al.,* 2018; Zhao *et al.*, 2018). Thousands of plastid and mitochondrial proteins needed to perform such a variety of functions are nuclear encoded and targeted to the organelles, making it crucial to ensure the coordinated expression of different genomes. A complex signaling network between the nucleus and the organelles, including both anterograde signaling (from the nucleus to the organelles) and retrograde signaling (from the organelles to the nucleus) as well as inter-organelle signaling mediates the communication between genomes and ensures proper gene expression (Blanco *et al.*, 2014; Kleine and Leister, 2016; van Aken and Pogson, 2017; de Souza *et al.*, 2017; Brunkard and Burch-Smith, 2018; Crawford *et al.*, 2018).

ORGANELLES GENOMES IN PLANT BREEDING

Breeders have been regularly aware of the contribution of cytoplasmic genomes to plant phenotype and have therefore chosen certain particular combinations of cytoplasmic and nuclear donor genetic materials. The most direct way to uncover cytoplasmic genetic effects on a trait is by the use of reciprocal crosses, in which each individual is used both as a male and as a female parent. For any trait, differences observed between hybrids obtained from the same parents suggest that the cytoplasm plays a role in the considered trait. Reciprocal crosses included in some of the traditional mating designs have been used to estimate genetic effects in quantitative genetics (Hayman, 1954; Griffing, 1956). Fan *et al.* (2014) compared the results obtained using a diallel experiment with or without reciprocal crosses and found that including reciprocal crosses allowed for the recovery of more high yielding hybrids and influenced both the estimates of general combining ability (GCA) and specific combining ability (SCA) effects and the heterotic group classification in maize.

However, differences between direct and reciprocal hybrids may be also due to genomic imprinting and maternal effects, like endosperm dosage effects and maternal phenotypic effects resulting from the environment or genotype of the maternal parent. In order to avoid these confounding effects, new populations for QTL analysis have been proposed, like F2 reciprocal populations and their F2:F3 families (Tang *et al.*, 2013) or reciprocal RILs (McKay *et al.*, 2008).

Another reliable approach extensively used to identify independent cytoplasmic effects, consists in developing nuclear substitution lines or cytolines by backcrossing several times a cytoplasm donor by the recurrent male parent, in order to obtain isonuclear lines differing only in the cytoplasm type. Allen (2005) used a set of cytolines carrying the nuclear genome of a maize inbred line and the cytoplasm from different teosintes belonging to the sections *Zea* and *Luxuriantes*, and found that cytolines with cytoplasm from the more distantly related *Z. luxurians*, *Z. diploperennis*, or *Z. perennis* presented significant differences for 56 of the 58 characters studied, affecting growth, development, morphology, and function. Besides their usefulness to uncover cytoplasmic effects on agronomic traits, cytolines are also valuable tools to diversify the genetic basis of crops (Calugar *et al.,* 2016).

Sometimes it is necessary to bypass post- and pre-zygotic sexual incompatibilities that prevent the use of wide crosses. In this case, somatic hybrids can be developed via protoplast fusion, thus allowing the combination of nuclei and organelles from different origin. Practical results using somatic hybrids to improve agronomic traits have been recently reported in model families *Rutaceae, Brassicaceae* and *Solanaceae* (Xia, 2009; Eeckhaut *et al.*, 2013).

The magnitude of cytoplasmic genetic effects on phenotypic expression is still a matter of debate. Cytoplasmic genetic effects can be additive, due to mutations in organelle genes, or epistatic, resulting from interactions between organelle and nuclear genes. In a meta-analytic review Dobler *et al.* (2014) evaluated 521 effect-size estimates reported in 66 publications including animals, fungi and plants. These authors found that cytoplasmic effect sizes are generally moderate in size and associated with variation across a range of factors, like the analyzed trait type, the experimental design used, the gene action associated with the reported cytoplasmic effect (additive or epistatic) and the experimental scale (intrapopulation, interpopulation or interspecies).

A growing set of data obtained following different approaches show that organelle genomic variation can modulate the effects of nuclear genomic variation in plants. Cytonuclear genetic interactions are predictable considering the complex network of retrograde signaling existing between organelles and nuclear genomes which ensures normal plant development. Joseph *et al.* (2013) analyzed the effect of cytoplasmic genomes on quantitative variation within the metabolome using a reciprocal recombinant RILs population in *Arabidopsis*. These authors demonstrated that genetic variation in the organelles influenced the accumulation of over 80% of the detectable metabolites and that cytoplasmic background affected epistatic interactions between nuclear loci. Other studies using phenotypic, microarray, and metabolomics analyses as well as whole transcriptome sequencing of cytolines revealed cytonuclear effects in rice, maize and wheat (Tao *et al.*, 2004; Crosatti *et al.*, 2013; Soltani *et al.*, 2016; Miclaus *et al.*, 2016).

So far, the traits with major impact in plant breeding showing cytoplasmic effects have been cytoplasmic male sterility (CMS), caused by mitochondrial genes (Bohra *et al.*, 2016; Chen *et al.*, 2017) and herbicide resistance, codified by mutations in the chloroplast gene *psbA* (Greiner, 2012). However, many other characters like yield and quality parameters, disease resistance, chilling tolerance, tissue culture response and regeneration, combining ability and plant adaptation have been found to be associated with the effect of cytoplasmic genes and cytonuclear interactions (Chandra-Shekara *et al.*, 2007; Gordon and Staub, 2011; Reddy *et al.*, 2011; Bock *et al.*, 2014; Shen *et al.*, 2015; Roux *et al.*, 2016; Satyavathi *et al.,* 2016; Dey *et al.*, 2017b; Boussardon *et al.*, 2019). The most recent reviews on this subject have been published several years ago (Frei *et al.*, 2003; Dhillon *et al.*, 2008; Mackenzie, 2010) creating the need to bring together the new data obtained to date. In the next sections, an update on the effects of cytoplasmic genomes and their interactions on agronomic traits in different crops is presented, emphasizing the methodologies and plant materials employed.

Maize

In maize (*Zea mays* L.) male sterile cytoplasms have been classified in three major groups by their response to specific restorer genes: T (Texas), S (USDA), and

C (Charrua) (Gabay-Laughnan and Laughnan, 1994; Allen *et al*., 2007; Su *et al*., 2016; Li *et al*., 2017). As in other species in which CMS is used to produce hybrid seeds, importance has been given to evaluate the effects associated to male sterile cytoplasms on agronomic traits. Cytoplasm T constitutes a typical case of the risks of genetic uniformity. This source of male sterility had been extensively adopted by breeders due to its reliability since the 1960's. However, cytoplasm T resulted susceptible to Southern Corn Leaf Blight caused by *Bipolaris maydis* (Nisikado and Miyake) Shoemaker; race T. As a result of the severe losses caused by the epidemic of 1970–1971 in USA and southern Canada, with >85% of the hybrids grown carrying cytoplasm T, this cytoplasm has been banned from hybrid seed production (Bruns, 2017). After cytoplasm T withdrawal, cytoplasms S and C have been adopted for hybrid seed production. Although cytoplasm C shows higher stability than cytoplasm S (Weider *et al*., 2009), it should be kept in mind that C is also specifically susceptible to race C of *B. maydis*, which is only known to occur in China (Gao *et al.,* 2005). As in other crops, introduction of male sterile cytoplasms in maize breeding programs must be preceded by a careful evaluation of their associated defects on agronomic traits (Jovanovick *et al*., 2017).

Apart from the case of male sterile cytoplasms, several studies have found cytoplasmic and cytonuclear effects in maize. A diallel analysis using nine quality protein maize (QPM) inbred lines evaluated over seven environments detected significant reciprocal effects for quality index, tryptophan, and anthesis date, which on the average accounted for <13% of the variation among hybrids (Machida *et al.,* 2010).

Tang *et al.* (2013) evaluated the cytoplasmic effects and cytonuclear interactions on plant height (PH) and ear height (EH), by using the joint analysis approach to both reciprocal F2 and F2: 3 families and incorporating the cytonuclear interaction mapping method. These authors identified six cytonuclear epistatic QTL affecting PH and five affecting EH. The average phenotypic variance explained by the genetic components of the QTL x cytoplasm interaction for each QTL was 18% for PH and 9% for EH. Regarding cytoplasmic effects, they reached 9% and 40% of the phenotypic contributions to PH and EH, respectively.

Flowering time in maize was analyzed applying the same approach (Tang *et al*., 2014). In this case, the authors evaluated the days to tassel (DTT) and the days to pollen shed (DPS) and found that although the cytoplasmic effects were not significant between the direct and reciprocal populations, four and eight cytonuclear epistatic QTL significantly contributed to the variation in DTT and DPS, respectively. Most of the cytonuclear epistatic QTL cannot be detected when using the interval mapping method, evidencing the importance of proper statistical modeling. In a study carried out by Calugar *et al.* (2016) a set of cytolines, obtained after transferring the nucleus of five inbred lines on four cytoplasm sources by backcrossing for ten generations, was used to determine the cytoplasmic effect on the plant height, ear height, number of leaves/plants, leaf area and the tassel length on some maize inbred lines. Two cytoplasms (T 248 and TC 221) showed significant effect on plant and ear height, leaf area and the tassel length. Besides, the authors detected some interaction between the cytoplasm and the nucleus that caused significant differences in the analyzed traits when the cytoline was compared to the original inbred.

Several reports noted differential expression between reciprocal F1 hybrids in maize for various kernel and germination traits (Cervantes Ortiz *et al*., 2007; Cabral *et al*., 2013; de la Torre and Biasutti, 2015; Santos *et al*., 2017; de Abreu *et al*., 2019). In Angiosperms, double fertilization results in the development of the diploid embryo and triploid endosperm that are surrounded by the maternal seed coat derived from the ovule integuments. Therefore, communication between these three genetically distinct structures ensures viable seed development (Figueiredo and Kohler, 2016; Chettoor *et al*., 2016). Differences observed in reciprocal F1 crosses may thus be due to epigenetic phenomena (imprinting and xenia), dosage effects (in case of triploid tissue such as endosperm) and cytoplasmic effects (associated to mitochondrial and chloroplast genomes). Interestingly, phenotypic and differential expression profiling carried out using reciprocal F1 hybrids to determine the genes associated to seed size (Zhang *et al.,* 2016), cold germination and desiccation tolerance (Kollipara *et al*., 2002), suggest the role of gene imprinting and not cytoplasmic genetic effects as a molecular mechanism underlying the observed reciprocal effects.

Wheat

Pioneer research on alloplasmic lines in wheat (*Triticum aestivum* L.) led to the discovery of cytoplasmic male sterility associated to *Aegilops caudata* (Kihara, 1959). At present, wheat has a large set of alloplasmic lines providing an excellent tool for evaluating the genetic effects of different cytoplasms (Tsunewaki, 2009). Three alloplasmic wheat series involving *T. aestivum* nuclear genome and cytoplasms from *T. aestivum* subsp. *macha*, *Ae. ventricosa*, *Ae. squarrosa*, *Ae. uniaristata* and *Hordeum chilense,* were used by Atienza *et al.* (2007) who observed that plant height, flowering date and yield per plant were least affected by the donor cytoplasm of the *Triticum–Aegilops* complex than by *Hordeum chilense* cytoplasm, with the latter being associated with detrimental effects on agronomic traits. On the other hand, all the alloplasmic lines studied showed significant differences for seed lutein content relative to euplasmic controls, thus revealing the role of cytoplasm genes on seed carotenoid content in wheat.

Soltani *et al.* (2016) used wheat alloplasmic lines carrying the cytoplasm of *Aegilops mutica* along with an integrated approach utilizing comparative quantitative trait locus (QTL) and epigenome analysis in order to evaluate the role of nuclear-cytoplasmic interactions upon interspecific hybridization. Results showed that cytoplasmic genomes modified the magnitude of QTL controlling plant height, dry matter weight and number of spikes per plant. Strikingly, when the methylation profiles were compared between alloplasmic and euplasmic lines, eight polymorphic regions associated with transposable elements, stress responsive, and metabolite pathways resulted affected by the cytoplasm type. Taken together, results suggest that novel nuclear-cytoplasmic interactions can trigger a potential epigenetic modification in the nuclear genomes and eventually change the genetic network controlling physiological traits.

In order to evaluate the effect of cytoplasmic diversity on traits related to heat tolerance during the reproductive stage Talukder *et al.* (2014) developed cytoplasmic near isogenic lines (NIL) using ten different cytoplasms and four different recurrent parents. Results showed that cytoplasmic variations can contribute to an increase in chlorophyll content and quantum efficiency of photosystem II during heat stress and detected interactions between cytoplasmic and nuclear genes, thus emphasizing the potential of cytoplasmic sources as components of any strategy to improve heat tolerance in wheat.

In a recent work Takenaka *et al.* (2018) studied cytoplasmic genetic diversity affecting seedling emergence and growth under submergence stress. Using a set of 37 nucleo-cytoplasmic hybrids carrying the nuclear genome of the wheat cultivar Chinese Spring and different cytoplasms of the *Triticum-Aegilops* complex they found a significant diversity with divergent cytoplasmic effects on submergence response. While T^2 cytoplasm of *Aegilops mutica* showed a positive contribution to submergence tolerance, cytoplasms of *Aegilops umbellulata* and related species caused a greater inhibition. Evaluation of more nuclear genetic backgrounds is needed to detect nuclear-cytoplasmic interactions affecting this trait.

Using a different experimental approach, Bnejdi *et al.* (2010) studied cytoplasmic effects affecting grain resistance to yellow berry, a serious physiological disorder in wheat and triticale, characterized by softer, light colored and starchy endosperm, which lacks the vitreous texture characteristic of normal grains (Ammiraju *et al.*, 2002). In this case, the authors employed parental, F1, reciprocal F1 (RF1), F2, reciprocal F2 (RF2), BC1P1 and BC1P2 generations of four crosses involving four cultivars of durum wheat. Significant cytoplasmic genetic effects were found in all crosses, indicating that the choice of the female parent resistant to yellow berry could significantly contribute to an increase in resistance level.

Reciprocal crosses and the F1, F2, F3, BC1, and BC1F1 offspring were also used by Guo *et al.* (2017) to assess the effect of an *Aegilops* cytoplasm on the expression of the multi-ovary gene. Results showed that the heterogeneous cytoplasm could suppress the expression of the heterozygous, but not homozygous, dominant multi-ovary gene. In a subsequent research, Guo *et al.* (2018) used methylation-sensitive amplification polymorphisms (MSAP) to assess the DNA methylation status of the reciprocal crosses between *Aegilops* and common wheat. The authors found that heterogeneous cytoplasm significantly changed DNA methylation patterns between the reciprocal crosses and suggested that this epigenetic control plays a role in the suppression of the multi-ovary gene.

Rice

Although several CMS types have been described in rice (*Oryza sativa* L.), the majority of hybrids were developed using mainly WA (wild abortive type) and to a lesser extent, BT (Boro type) and HL (Hong-Lian type) male sterile cytoplasms (Tang *et al.*, 2017). In a study designed to analyze DNA methylation as affected by male sterile cytoplasms in rice, Xu *et al.* (2013) compared the extent and polymorphism of DNA methylation between male sterile lines (A) carrying four different cytoplasms and their maintainer lines (B) using the MSAP technique. Results showed identical differences in methylation between A and B lines at three sites in all the analyzed cytoplasms, suggesting a relationship of DNA methylation at these sites specifically with male sterile cytoplasms, since cytoplasm is the only difference between the A and B lines. Interestingly, it was also found that different cytoplasms affected DNA methylation to different levels, depending on the genetic distance between the nucleus and the cytoplasm of each cytoplasm type donor. Evidence of the effect of male sterile cytoplasms on nuclear gene expression has also been obtained by Hu *et al.* (2016) who analyzed the anther transcript profiles of three *indica* rice alloplasmic CMS lines and their maintainer line and found a set of differentially expressed genes (DEGs) involved in anther development.

A common drawback associated with different CMS in rice is panicle enclosure, in which part of the panicle fails to exert from the sheath of the flag leaves, leading to lower seed-setting rates and yield loss and demanding gibberellin application for hybrid seed production (Chen *et al.*, 2013). The effects of male sterile cytoplasms on quality traits of rice has been examined by Waza and Jaisbal (2015) who compared the difference in performance between 20A (WA-CMS line) x R (Restorer line) hybrids and the corresponding B (Maintainer line) x R (Restorer line) hybrids. In this study, WA cytoplasmic influence for different traits was found to be highly cross-specific, depending on the nuclear background of the CMS line and the fertility restorer. Results showed that WA cytoplasm had no significant influence on some traits (head rice recovery, elongation ratio and aroma) but it negatively affected others (hulling recovery, milling recovery, kernel length before cooking, kernel breadth before cooking, kernel length after cooking, kernel breadth after cooking, alkali spread value and amylose content) and exhibited both favorable and unfavorable cytoplasmic effects depending upon the parental combination (kernel length/breadth ratio before and after cooking). The most significant effect of WA cytoplasm was reduction in length of cooked kernel followed by decrease in amylose content, which are two undesirable quality traits.

Narrow cytoplasmic genetic diversity observed both in rice hybrids and varieties has led breeders to look for new cytoplasmic resources and to characterize their effects on traits of agronomic value (Huang *et al.*, 2013; Kumar *et al.*, 2013; Toriyama and Kazama, 2016; El-Namaky, 2018). In order to study the effects of cytoplasm, nucleus, and interaction between nucleus and cytoplasm on agronomic traits in rice, Tao *et al.* (2004) evaluated fifteen isolines obtained by crossing five widely used *japonica* cytoplasm resources as females by three distinct *japonica* rice cultivars followed by several backcrosses to the male recurrent parent. Analysis of the results showed that cytoplasms had significant effects on yield, width of flag leaf, and low temperature tolerance. Besides, significant effects of cytoplasm-nucleus interaction on yield, plant height, and low temperature tolerance were also found. In a similar research undertaken to analyze eighteen isolines of *indica* rice obtained by backcrossing six different cytoplasmic sources with three cultivars as recurrent male parents, Tao *et al.* (2011) detected significant effects of cytoplasms on 1000-grain weight, which is a major component of yield and grain quality in rice production. Additionally, a three-way interaction between cytoplasms, nuclei and locations was found for filled-grain ratio, emphasizing the need to evaluate cytoplasmic effects in the nuclear backgrounds of interest and at multiple locations.

Sorghum

Evidence about cytoplasmic effects on agronomic traits in sorghum (*Sorghum bicolor* L. Moench) has been mainly obtained from research on male sterile cytoplasms. Although several types of male sterile cytoplasms are known in sorghum -A1, A2, A3, A4, A4M, A4VZM, A4G1, A5, A6, 9E, M35 and KS- A1 is the most widely used for commercial hybrid seed production followed by A2, due to adverse effects on agronomic traits and poor environmental stability of male fertility restoration observed in the other types (Reddy *et al.*, 2007; Kumar *et al.*, 2011; Elkonin and Tsvetova, 2012; Kozhemyakin *et al.*, 2017; Kante *et al.*, 2018). The effect of cytoplasms on performance of grain sorghum hybrids varies according to different authors, although A3 hybrids consistently showed reduced grain yield compared to A1 and A2 hybrids. On the other hand, no adverse effects associated with male sterile cytoplasms were observed in biomass sorghum hybrids (Hoffman and Rooney, 2013). Recently, Vacek and Rooney (2018) evaluated 16 isocytoplasmic bio-energy sorghum hybrids, each of them carrying three different male sterile cytoplasms A1, A2 and A3, to assess the effect of cytoplasm type on the agronomic performance and quality. Results showed that cytoplasms "per se" did not influence any agronomic or composition trait; however, hybrid by cytoplasm interactions were significant for several traits, showing the importance to identify the best cytoplasm and hybrid combination for sorghum use as a biomass source.

The effect of male sterile cytoplasms on resistance to diseases and insect pests in sorghum has been studied following different approaches. Durga *et al.* (2008) studied the influence of male sterile cytoplasm on the occurrence of leaf blight caused by *Exserohilum turcicum* (Pass) using paired cytoplasmic male-sterile (CMS) A lines and maintainer (B) lines, which were crossed with R-lines (restorers) to produce two types of hybrids: (A x R) and (B x R), differing only in the cytoplasm type. Although significant cytoplasmic effects were detected for some disease related parameters (reduced lesion length and lesion area), the overall disease damage was not significantly different between genotypes with male fertile and male sterile cytoplasm. Reddy *et al.* (2011) evaluated the effect of cytoplasms A1, A2, A3, A4M, 4G, 4VZM on grain mold resistance using a set of 72 hybrids obtained from the cross of 36 isonuclear alloplasmic lines (A lines) by two restorer lines (R). Results showed significant effects due to cytoplasms "per se" and to their interactions with A lines, R lines and years. A1 cytoplasm contributed to grain mold resistance, followed by A4VZM and A2, indicating that introduction of these two alternative cytoplasm to hybrid sorghum production should not increase the risk of grain mold. Insect resistance has also been evaluated as influenced by different cytoplasm types in sorghum, taking into account that A1 is highly susceptible to insect pests (Dhillon *et al.*, 2008). In the case of sorghum shoot fly (*Atherigona soccata* (Rondani)) Sharma *et al.* (2006) found that the expression of traits associated with resistance in the F1 hybrids depends on the interactions between cytoplasmic and nuclear genes and concluded that resistance to shoot fly is needed in both parents to develop shoot fly resistant hybrids. Akula *et al.* (2012) evaluated four isogenic lines in four male-sterile backgrounds, A1, A2, A3 and A4, and their corresponding maintainer (B lines) lines. Results showed that the A4 cytoplasm was the least susceptible to sorghum shoot fly as it was comparatively less preferred for oviposition and had lower dead heart incidence than the other cytoplasms tested. Mohammed *et al.* (2016) studied the nature of gene action involved in shoot fly resistance using a complete diallel design and found significant reciprocal effects of combining abilities for oviposition, leaf glossy score and trichome density, thus supporting the influence of cytoplasmic factors in inheritance of shoot fly resistance.

Potato

A PCR-based classification method using chloroplast and mitochondrial DNA markers (Hosaka and Sanetomo, 2012; Sanetomo and Hosaka, 2013) distinguishes cytoplasms of cultivated potatoes and closely related wild species into six distinct types: M (an ancestral type of Andean cultivated potatoes), P (derived from *Solanum phureja*), A (the most prevalent *Solanum tuberosum* ssp. *andigena* type), W (wild species), T (the most prevalent *Solanum tuberosum* ssp. *tuberosum* type), and D (derived from *Solanum demissum*). Besides, potato mitochondrial genomes have been classified in five types: α, β, γ, δ, and κ (Lössl *et al.*, 2000). Cytoplasmic male sterility has been reported in T/β cytoplasm, as well as in D and W/γ-type derived from *S. stoloniferum*. T/β is the most extended cytoplasm type in potato cultivars all over the world except in German cultivars, due to the fact that *S. demissum* and *S. stoloniferum* were broadly used in German breeding programs for their resistance to late blight and potato virus Y, respectively. Knowledge of the cytoplasm types is necessary to prevent the cytoplasmic invasion of male sterile types, which severely limits the selection of male parents in breeding programs (Hosaka and Sanetomo, 2012; Mihovilovich *et al.*, 2015; Anisimova and Gabrilenko, 2017).

Sanetomo and Gebhardt (2015) estimated the correlation of cytoplasmic genomes with complex agronomic traits using 1,217 cultivars and breeding clones of 6 different populations. Results showed significant effects of cytoplasm type on traits such as resistance to late blight and tuber bruising, plant maturity, tuber shape, starch content and yield. On the contrary, no cytoplasmic difference was found for processing quality traits such as chip color and reducing sugar content. In particular, it was shown that the W/γ-type cytoplasm was correlated with increased tuber starch content and later plant maturity, while the D-type cytoplasm was correlated with increased foliage resistance to late blight. W/γ cytoplasm type was also found to be associated with potato tuber yield, starch content and/or starch yield when reproducibility of diagnostic nuclear DNA markers was evaluated using an association mapping approach (Schönhals *et al.*, 2016).

Reciprocal crosses between cultivated potatoes and diploid wild related species have been frequently used to evaluate the cytoplasmic effects on agronomic traits. Jansky (2011) found improved male fertility when *S. brevicaule* and *S. microdontum* were used as females instead of *S. tuberosum*, but lower percentages of selected clones and clones that tuberized when *S. chacoense* and *S. microdontum* were used as the female parents.

In the case of the crosses between *S. tuberosum* (T) and the hexaploid *S. demissum* (D), non-complete unilateral incompatibility determines that seed is obtained preferentially when the cultivated potato is used as pollen donor. Moreover, apparent size differences between DT and TD seeds are observed, the former being significantly larger than the latter (Sanetomo *et al.*, 2011). In order to shed light on the mechanisms involved in such behavior, Sanetomo and Hosaka (2011) compared reciprocal F1 hybrids TD and DT using methylation-sensitive amplified polymorphism (MSAP) analysis. Their results showed differences both in DNA sequences and in the DNA methylation level between TD and DT.

Somatic hybridization is a powerful tool to overcome the sexual barriers between the cultivated and wild species. In a recent review, Tiwari *et al.* (2018) examined research in somatic hybridization in potato during the past 40 years. Data show that majority of somatic hybrids follow recombination of mitochondrial genome from both parents, and chloroplast pattern from only one, except the recombination of the chloroplast genome observed once in *S. tuberosum*-*S. vernei* somatic hybrid. Given that the interaction between nuclear and cytoplasmic genes from different species can affect fertility and agronomic traits of somatic hybrids and progenies, information on such interactions could be useful when using somatic hybrids in breeding.

Brassicaceas

This family includes several vegetable crops: cabbage, cauliflower and broccoli (*Brassica oleracea* var. *capitata* L., *var. botrytis* L. and *var. italica* Plenck, respectively), turnip (*Brassica rapa* L. spp. *rapa*) and radish (*Raphanus sativus* L.) and an important oil crop, oilseed rape (*Brassica napus* L.). Hybrid seed production in these crops has been developed worldwide using Ogura male sterile cytoplasm discovered in a Japanese radish (*Raphanus sativus* L.) and introgressed in *B. oleracea* by repeated backcrosses (Yamagishi and Bhat, 2014; Kaminski *et al.*, 2016; Sekhon *et al.*, 2018). However, these initial alloplasmic male sterile lines carrying Ogura cytoplasm presented chlorophyll deficiency at low temperatures, underdeveloped nectaries and malformed ovaries and pods which reduced the seed set. Additionally, the same defects were observed after Ogura cytoplasm transfer into *B. napus*. It was then assumed that undesirable effects were due to negative interactions between the *Brassica* nucleus and the *Raphanus* chloroplasts. Protoplasts from a normal *B. napus* line were fused with protoplasts from a CMS (Ogura radish cytoplasm) *B. napus*, and protoplasts from a normal *B. oleracea* line were fused with protoplasts from a CMS (Ogura radish cytoplasm) *B. oleracea*, in order to select cybrids carrying only *Brassica* chloroplasts that grew normally. These improved CMS lines are known as Ogu-INRA and are widely used to produce hybrids in *Brassicaceae* (Pelletier and Budar, 2015). Similar advances have been achieved by Indian breeders who developed and characterized several Ogu-CMS lines in cauliflower and cabbage (Dey *et al.*, 2017a; Bathia *et al.*, 2015; Parkash *et al.*, 2015). Recently, Dey *et al.*, (2017b) reported that the introgression of Ogura cytoplasm into the nuclear background of cauliflower genotypes significantly affected nutritional traits. However, the effects were genotype specific suggesting the role of nuclear–cytoplasmic interaction in expression of different quality traits. Thus, Ogura cytoplasm interacted favorably in particular nuclear backgrounds in expression of antioxidant capacities. On the other hand, it had adverse effects for anthocyanin, total chlorophyll content in most of the genotypes, which is desirable in cauliflower but not in cabbage. Besides, while ascorbic acid concentration was adversely affected, total carotenoids and β-carotene concentration were higher in most of the genotypes after introgression of Ogura cytoplasm. Following a novel approach Singh *et al.* (2018) combined CMS and doubled haploid inbred lines to determine heterotic combinations for important antioxidant compounds such as CUPRAC, FRAP, phenols, carotenoids, anthocyanins and ascorbic acid in cauliflower.

Interspecific and intergeneric crosses are commonly used to exploit alloplasmic effects in plant breeding. Chang *et al.* (2015) investigated the alloplasmic effect of the cytoplasm of *B. juncea* and *B. napus* on heat and cold toleranceof *B. carinata*, by comparing the performance of alloplasmic and euplasmic lines of *B. carinata* for a variety of physiological parameters. While plants with cytoplasm of *B. napus* showed little difference inheat tolerance, those with the cytoplasm of *B. juncea* displayed higher heat injury than the euplasmic lines. Moreover, both alloplasmic lines showed decreased cold tolerance than the euplasmic lines. Results suggested that tolerance of extreme temperature stress was controlled by the nucleus, the cytoplasm and the interaction between maternal and nuclear genomes.

In the case of oilseed rape, recent data have revealed cytoplasmic effects on yield related traits and quality traits, like number of seeds per pod, oil content, protein content, glucosinolates, oleic acid, linolenic acid and erucic acid (Ishaq *et al.*, 2016; Guo *et al.*, 2017; Szała *et al.*, 2018).

Cucumber

In cucumber (*Cucumis sativus* L.) plastids and mitochondria are inherited maternally and paternally, respectively (Corriveau and Coleman, 1988; Havey 1997). Chilling tolerance was reported to display maternal inheritance (Chung *et al.*, 2003) so it was postulated that chilling tolerance was associated with the plastid genome. In order to identify candidate plastid genomic regions, Chung *et al.* (2007) carried out a comparative complete sequencing of chloroplast DNA of a susceptible and a tolerant cucumber line and found three polymorphic sites associated with the trait. Afterwards, sdCAPS (simply derived cleaved amplified polymorphic sequence) were developed converting sequence data in PCR-based markers that were successfully used to distinguish plastid types (Ali *et al.*, 2013; 2014). Therefore, breeding chilling tolerance into elite cultivars by backcrossing may be effective for the rapid introduction of plastomes conferring a tolerant phenotype (Gordon and Staub, 2011; 2014).

Diallel mating designs have been used to estimate GCA, SCA, and reciprocal-cross effects for agronomic traits in cucumber. Significant reciprocal effects were reported for fresh and dry weight per plant (Shen *et al.*, 2015) and for internode length, leaf length, leaf width, fruit length, fruit diameter, number of fruits per plant, yield per fruit and yield per plant (Golabadi *et al.*, 2015).

Organelle omics generate a novel and promising field for cucumber breeding. In this regard, a tiling microarray comprising the whole cucumber chloroplast genome has been developed and it has been used to study chloroplast responses to abiotic stresses (Żmieńko *et al.*, 2011). Besides, cucumber plants regenerated from cell cultures occasionally originate paternally transmitted mosaic (MSC) phenotypes, characterized by slower growth, chlorotic patterns on the leaves and fruit, lower fertility, and rearrangements in their mitochondrial DNAs (Malepszy *et al.*, 1996; Lilly *et al.*, 2001; Bartoszewski *et al.*, 2004; 2007; Del Valle-Echeverria *et al.*, 2015). Analysis of nuclear gene expression in MSC mutants will help to understand mitochondrial retrograde signaling and will allow to identify genes associated with stress responses and use them as potential selection targets for breeding (Pawełkowicz *et al.*, 2016; Mróz *et al.*, 2018).

Onion

In onion (*Allium cepa* L.) two main sources of CMS -S and T- have been mainly used in hybrid seed production. S type results from the interaction of a cytoplasmic factor S and a single nuclear restorer gene Ms (Jones and Emsweller, 1936; Jones and Clarke, 1943). T type is determined by the interaction of the cytoplasmic factor T and two to three complementary restorer genes

(Berninger, 1965; Schweisguth, 1973). While S type is the most widely used due to the relatively common occurrence of the recessive allele at Ms, the stability of male sterility over environments and no reduction of female fertility (Goldman *et al.*, 2000; Leite *et al.*, 1999), T cytoplasm is commercially used in Europe and Japan (Havey, 2000) and is present in Brazilian onion populations (Fernandes Santos *et al.*, 2010). Moreover, new sources of CMS from *Allium galanthum* (Havey, 1999) and *Allium rolyei* (Vu *et al.*, 2012) have been identified making it possible to diversify the cytoplasms used in hybrid seed production, to reduce the risks of genetic uniformity associated to the major use of S type (Havey, 2018). Recently, complete sequencing of mitochondrial genomes of S, T and normal cytoplasms has been achieved and a chimeric gene encoded by *orf 725* has been postulated as the common causal gene for CMS induction in onions (Kim *et al.*, 2016; Kim *et al.*, 2019).

Carrot

The main types of CMS in carrot (*Daucus carota* ssp. *sativus* L.) are "brown anther" (Sa), characterized by shriveled, yellow-to-brown anthers with no pollen (Welch and Grimball, 1947) and "petaloid" (Sp), in which anthers are replaced by a whorl of petals (Thompson 1961; Peterson and Simon, 1986). While "brown anther" type was found in a lot of cultivars as well as in wild relatives, "petaloid" type was only identified in wild relatives and has been introduced into the nuclear genetic background of the cultivated carrot (Linke *et al.*, 2019). In addition to the two main types, CMS-GUM, CMS-MAR and CMS-GAD (from *D. carota subsp. gummifer, D. carota subsp. maritimus and D. carota subsp. gadecaei, respectively)* have been described (Linke *et al.*, 1999; Nothnagel *et al.*, 2000).

Different hypotheses have been postulated to explain restoration of fertility in carrot involving single or multiple nuclear genes with complex interactions (Thompson, 1961; Hansche and Gabelman, 1963; Börner *et al.*, 1995; Wolyn and Chahal, 1998). Alessandro *et al.* (2013) found that restoration of "petaloid" cytoplasmic male sterility was due to a single dominant gene, *Rf1*, and developed a linkage map using molecular markers, some of which can be applied in marker assisted selection (MAS) in hybrid breeding programs.

Both "brown anther" and "petaloid" systems show instability due to high temperatures, dry conditions, growing time or long day conditions. Although hybrid seed production is mainly based on the use of petaloid CMS type because of less frequent reversion to male fertility, seed yields on the brown-anther CMS are generally higher (Havey, 2004; Dhall, 2010).

In a recent study carried out to determine the genetic basis of carrot shoot growth, Turner *et al.* (2018) analysed a diallel mating design and found highly significant reciprocal effects in all the evaluated traits: canopy height and width, shoot biomass, root biomass, and the ratio of shoot: root biomass. Besides, significant Reciprocal x E interactions were observed for canopy height at harvest and fresh shoot biomass.

Sunflower

Although 72 sources of cytoplasmic male sterile cytoplasm have been described by different authors in sunflower (*Helianthus annuus*), nearly all hybrid seed production relies on the use of a single male sterile cytoplasm, PET1, derived from *Helianthus petiolaris* ssp. *petiolaris* (Leclerq, 1969; Sabar *et al.*, 2003; Serieys and Christov, 2004). In this context, diversification of the cytoplasmic background is desirable to avoid the risks of genetic uniformity (Jan and Vick, 2007; Zhang *et al.*, 2010; Christov, 2013; Reddermann and Horn, 2018; Makarenko *et al.*, 2019).

Several reports have discussed the effects of different cytoplasm sources on agronomic traits as a prerequisite to their introgression in sunflower breeding programs. Jan *et al.* (2014) evaluated twenty diverse cytoplasmic substitution lines from six annual and six perennial wild diploid *Helianthus* species for agronomic and oil traits. Results showed that cytoplasms of perennial species *H. mollis*, *H. grosseserratus*, *H. divaricatus* and *H. angustifolius* had more adverse cytoplasmic effects affecting agronomic traits. In contrast, cytoplasms from annual species had no adverse effects. Additionally, ten alien CMS sources from annual species, wild *H. annuus* accessions and perennial species were tested and yield-reducing cytoplasmic effects were only observed in perennial *H. maximiliani* and annual *H. annuus* PI 413178 and PI 413024. No significant cytoplasmic effects were detected in oil percentage and fatty acid composition. These data support the exploitation of wild annual *Helianthus* species to broaden cytoplasmic diversity in sunflower breeding.

Tyagi *et al.* (2015a) used nine CMS sources to develop CMS alloplasmic lines, here designated as CMS analogues, by crossing them by a common maintainer line followed by repeated backcrossing. The CMS analogues, carrying the same nuclear genotype and different cytoplasmic genomes, were evaluated in the field for 21 morphological, agronomic, physiological and quality traits. Significant differences between CMS analogues were detected for all the traits. The genetic parameters analysis indicated that selection for grain yield accompanied with high harvest index, large head size and biological yield can be effectively used from these sources for genetic improvement in sunflower. The same CMS sources were evaluated under water stress conditions (Tyagi *et al.*, 2015b) and it was found that CMS-XA (unknown origin), E002-91 (*H. annuus*), ARG-3A (*H. argophyllus*) PHIR-27A (*H. praecox* ssp *hirtus*) and PRUN-29A (*H. praecox* ssp. *runyonii*) presented significantly higher yield than the common maintainer line, making them potentially useful to develop efficient water use CMS lines. Furthermore, the effects of cytoplasmic sources on the estimation of combining ability for agronomic traits and stability under different environments were also evaluated (Tyagi and Dhillon, 2017; Tyagi *et al.*, 2018).

A research by Velasco *et al.* (2007) analyzed the relationships between fatty acid profile and seed oil content in F1s and F2s of reciprocal crosses between CAS-3, a high stearic acid mutant and ADV-37, a high seed oil content inbred line. Results demonstrated the existence of cytoplasmic effects in the genetic control of oil content both at the F1 and F2 plant level. On the contrary, cytoplasmic effects on stearic acid content were only observed at the F1 but not at the F2 plant level, a difference which may be due to small environmental influence, sampling deviations or to the effect of maternal rather than cytoplasmic genetic effects. Ferfuia and Vannozzi (2015) studied seed fatty acid composition in seeds from reciprocal F1s, F2s and BC populations between two high oleic inbred lines under different environmental conditions. Results showed that oleic acid percentage was affected by cytoplasmic or cytoplasmic x nuclear interaction. In particular, the expression of nuclear genes affecting oleic acid percentage, *OLs* and/or *Olm*, was modified by temperature and cytoplasm genotype.

Another trait of interest for sunflower breeding is the regeneration ability for "*in vitro*" culture. In order to evaluate the effect of different cytoplasmic background on the regeneration ability in sunflower, Cravero *et al.* (2012) tested seven alloplasmic CMS lines introgressed into the inbred line HA89 and one fertile cytoplasm (*H. annuus*) under different *in vitro* culture conditions, detecting cytoplasm by culture media interaction for the regeneration percentage and productivity rates. The authors concluded that the non-nuclear genome could be considered as another source of variability modifying the regeneration ability of recalcitrant sunflower genotypes.

Soybean

Several sources of CMS have been described in soybean (*Glycine max* L. Merr): RNTED, ZD 83-19, N8855, N21566, N23168 and N23661. Several hybrid soybean cultivars developed in China using CMS yielded 20% more than control varieties. However, both a low out cross pod-set rate in the existing CMS lines and the influence of day length and temperature on male sterility of some CMS lines and male fertility of F1 hybrids have delayed hybrid seed production in soybean to date (Bai and Gai, 2006; Zhao and Gai, 2006; Dong *et al.*, 2012; Nie *et al.*, 2017).

Stay-green mutants show impaired chlorophyll degradation during leaf senescence and seed maturation and they can affect seed maturation, seed oil quality, and meal quality in oil crops (Delmas *et al.*, 2013). Among the stay-green mutants described in soybean, green cotyledon gene *cytG* is maternally inherited (Terao, 1918). Sequencing of the chloroplast genome revealed a 5-bp insertion causing a frame-shift in *psbM* gene, which encodes one of the small subunits of photosystem II, thus linking photosynthesis in pre-senescent leaves with chlorophyll degradation during leaf senescence and seed maturation (Kohzuma *et al.*, 2017).

Significant reciprocal effects on physiological characters such as CO_2 exchange rates, intercellular CO_2 concentration, stomatal conductance, transpiration, plant height, number of branches, fertile nodes, filled pods, seeds per plant, weight of seeds per plant and weight of 100 seeds were detected in soybean by diallel analysis (Karyawati *et al.*, 2015). Using the same analysis Cruz *et al.* (2011) found significant reciprocal effects on resistance to Asian soybean rust (*Phakopsora pachyrhizi*) and suggested the involvement of cytoplasmic or maternal effects on this trait.

Xu *et al.* (2011) looked for QTLs for the seed size traits in soybean using F2:3, F2:4 and F2:5 populations from the direct and reciprocal crosses and employing a multi-QTL joint analysis (MJA) along with composite interval mapping (CIM). These authors detected cytoplasmic effects on seed length, seed width, seed thickness and the ratios length to thickness and width to thickness, but not on the ratio length to width. Besides, 92 cytoplasm-by-QTL interactions were detected, 28 of which were consistent with main effect QTLs detected by CIM.

Cotton

Most recognized CMS systems in cotton are CMS-D2 and CMS-D8, that were developed by transferring the cytoplasm of wild species *Gossypium harknessii* Brandegee and *Gossypium trilobum* (DC) Skovst, respectively, into tetraploid upland cotton *Gossypium hirsutum* (Wang *et al.,* 2010; Wu *et al.*, 2017; Yang *et al.*, 2018). Regarding the effect of male sterile cytoplasms on agronomic traits Tuteja and Banga (2011) evaluated four D2 type male sterile lines (A) and their corresponding maintainer lines (B) crossed as paired crosses with eight restorer lines (R). Cytoplasmic effects were estimated by comparing (A × R) and (B × R) hybrids combinations. Results indicated that although male sterile cytoplasm had a significant unfavorable effect on number of bolls, boll weight, yield and fiber quality traits in some of the cross combinations, performance of male sterility-based hybrids in cotton is governed by the interaction of nuclear genes with the sterility-inducing cytoplasm, making it more appropriate to test the CMS lines in newer combinations rather than converting the female parents of released hybrids into male sterile lines. Recently, a comparison between cytoplasmic effects of D2 and D8 on lint yield and fiber quality was done by Zhang *et al.* (2019) using eight pairs of reciprocal hybrids obtained from crosses between two restorer lines carrying D2 and D8 cytoplasm and four commercial cotton cultivars. Analysis of results demonstrated that D2 cytoplasm had mild negative effects on lint yield and its component, but it had beneficial effects on most of the fiber quality traits. On the other hand, the negative effects of D8 cytoplasm on lint yield and its components were more profound than D2 cytoplasm, with no effect on quality traits (except for a reduction in micronaire), thus presenting important challenges for hybrid cotton breeding.

Complete diallel designs have frequently been used to determine the mode of gene action for agronomic traits in cotton. Using this approach, significant reciprocal effects have been detected for fiber length, fiber strength, fiber elongation and fiber fineness and lint percentage (Shaukat *et al.*, 2013), monopodia branch length (Zangi *et al.*, 2010), days to first flowering, seeds, locule^{-1} and lint percentage (Khan *et al.*, 2011).

Using another approach, Wu *et al.* (2010) designed an additive and dominance (AD) genetic model with cytoplasmic effects to estimate genetic effects on several seed traits in F3 hybrids of 13 cotton chromosome substitution lines crossed with five elite cultivars. Significant cytoplasmic effects were detected for seed oil content, oil index, seed index, seed volume, and seed embryo percentage.

PERSPECTIVES

Current knowledge and methods available make it possible to envisage greater opportunities to select not just the best nuclear genotypes but also the best cytonuclear interactions, by considering the information of all the genomes present in different plant cell compartments. Characterization of genetic diversity of chloroplast and mitochondrial genomes can be easily achieved by modern "omics" technologies. Besides, assessment of the additive and epistatic effects of cytoplasmic genes on traits of interest is facilitated by the development of specific genetic designs and statistical models. In addition, molecular markers associated with cytoplasm types can be applied in Marker Assisted Selection (MAS) schemes to increase the efficiency of their incorporation in breeding programs. As it has been suggested by Kersten *et al.* (2016), the availability of the genomic information of all three DNA-containing cell organelles will allow a holistic approach in plant breeding in the future. This perspective will contribute to optimize the use of genetic resources and will allow increasing genetic cytoplasmic diversity to reduce the vulnerability of crops to potential biotic and abiotic risks.

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