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NOTE

Meiotic irregularities in *Capsicum* L. species

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Abstract – *Cytogenetic and pollen viability (PV) studies were performed in pepper accessions,* Capsicum chinense *and* Capsicum baccatum*. Irregularities such as laggard and univalent chromosomes, bridges, problems in the spindle fibers and cytomixis were observed, especially in* C. baccatum *which was the most unstable genotype. In the post-meiotic products, irregularities were observed, on average, at 20 % of the microspores in* C. baccatum *and 17 % in* C. chinense*. PV in* C. baccatum *was below 70 %, while in* C. chinense*, it was above 80 %. Meiotic irregularities in* Capsicum*, mainly in* C. baccatum*, considering the low PV estimated, were significant but not impeditive for fertilization.*

Key words: *pepper, microsporogenesis, cytomixis, pollen viability.*

INTRODUCTION

Capsicum baccatum L. and *C. chinense* Jacq. are native to tropical and temperate regions in America, and were domesticated by native Americans (Moscone et al. 2007). The domesticated types are found around the world, while wild species have more limited distribution (Lanteri and Pickersgill 1993). *Capsicum* phylogenetic relationships, using evidences of chloroplastidic and nuclear DNA showed that, although being close, the species were grouped in different clades. *Capsicum baccatum* was included in the clade *baccatum* while *C. chinense* was included in the clade *annuu*m, and such results agree with groupings obtained based in morphology and isoenzymes (Choong 1998). *Capsicum chinense* presents great intraspecific genetic diversity (Fonseca et al. 2008).

Interspecific crossings have been performed in *Capsicum* species to elucidate the genetic relationships between them, and, mainly, to permit the genetic improvement of cultivars by introducing valuable alleles from wild accessions that are responsible, for example, for the resistance to pathogens, as obtained by Boiteux et al. (1993). The success of interspecific crossings is related to the genomic homology of parent species. For this kind of analysis, cytogenetic studies in domesticated or semi-domesticated *Capsicum* species and their ancestors have been performed (Lanteri and Pickersgill 1993). Cytogenetic investigations may reveal the proximity between species and genotypes through the observation of uniformity in chromosome pairing, or the distance between them, as observed in *C. tovarii* x *C. baccatum* hybrids that presented reciprocal translocations certifying the genetic distance between the parent species (Tong and Bosland 1999).

Meiosis is considered an event of high evolutional stability (Caetano-Pereira et al. 1998), but the occurrence of failures in the meiotic process, such as laggard chromosomes or the disorganization of the spindle fibers, are undesirable factors in the production of hybrids, as in *Passiflora* (Souza and Pereira 2011). Many times, the meiosis irregularities impinge a chromosome variation to new generations due to the loss or gain of chromosomes that generate unviable gametes, and it is not desirable when the parents are selected. In *Solanum*, pollen viability, a consequence of the regular meiosis, was used to identify the most appropriate genotypes for breeding programs (Tomé et al. 2007).

In *Capsicum*, meiotic and PG stainability analysis were performed to infer about the genetic relationship between two species (Kumar et al. 1988). *Capsicum baccatum* and

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C. chinense ($2n = 24$) are considered self-compatible, and usually these species do not present unilateral or crossed incompatibility (Nacio Onus and Pickersgill 2004). However, artificial crossings, performed between *Capsicum baccatum* L. and two accessions of *Capsicum chinense* Jacq., have resulted in very low fertilization rates. Thus, this work was performed to analyze the development of meiocytes, microspores and the pollen viability in *Capsicum* species for use in breeding programs.

MATERIALS AND METHODS

The studies were performed in three *Capsicum* L. accessions, *C. baccatum* L. (accession UENF-1417) and *C. chinense* Jacq. (accessions UENF-1418 and UENF-1419), conserved in the *Capsicum* collection maintained by Universidade Estadual do Norte Fluminense Darcy Ribeiro - UENF (Campos dos Goytacazes, RJ). These accessions were donated by Universidade Federal de Viçosa and have been used in the breeding program conducted by UENF.

Meiotic and post-meiotic behavior

For microsporogenesis studies, flower buttons were fixed in Carnoy I for 2 to 3 hours at room temperature and maintained at -20 ºC. The slides were prepared with the squashing technique and cells were stained with 1 % carmine. Five plants randomly sampled of each accession were analyzed; at least 50 cells of each meiotic phase analyzed were observed, per accession. The observation of chiasmata was performed in 20 cells per accession and used to obtain the recombination index (RI = [∑ total number of chiasmata ÷ number of cells analyzed] + *n* value; Darlington 1958). The bivalents were united by one or two chiasmata - the bivalent rods were scored as containing one chiasma while the bivalent rings as having two chiasmata (Senda et al. 2005). Then numbers of the post-meiotic products as monads, dyads, triads, tetrads and polyads were registered in order to calculate the meiotic index (%MI = [number of normal tetrads x 100] ÷ number of post-meiotic products counted; Love 1951) and to analyze the variance (Anova). Data were analyzed using the software Genes (Cruz 2006).

Pollen Viability

Pollen grains (PG) from recently opened flowers were collected and tested using the Alexander solution (Alexander 1969). The PG whose cytoplasm had stained and remained intact was considered viable. To prepare the slides, PG were delicately placed on a drop of stain, and after 5 minutes at room temperature, they were observed regarding to the morphological aspect and stainability, counted and measured. Five plants were analyzed (repetitions) per accession, and at least 500 PG were counted per repetition/accession. The PG were classified into two types (Souza et al. 2003): type 1 (T1), empty (absence of cytoplasm), and type 2 (T2), contracted cytoplasm. The lengths of 50 viable and unviable PG per accession were measured using a micrometric ocular. Descriptive statistics and Anova were performed using the software Genes.

RESULTS AND DISCUSSION

Meiotic behavior

Meiotic irregularities were observed in accessions of pepper in all the analyzed phases. After the zygotene stage, groupings were observed characterizing pycnosis in the chromatin, sometimes near the cell wall of meiocytes, facilitating the intercell chromatin flow, cytomixis. In this stage, cytoplasmic connections between meiocytes and the passing of chromatin between cells were observed (Figure 1a), resulting in anucleate or two nuclei cells, and also cells with unbalanced number of chromosomes. As observed in *C. baccatum* and *C. chinense*, *C. pubescens* also presented pycnosis, however, leading to the degeneration of nuclear material in this species.

Cytomixis is an important factor to be considered in crossability analysis, because it alters the chromosomes number and leads to pairing irregularities and pollen sterility. Cytomixis is also considered a way to conserve genetic heterozygozity of the gametes (Veilleux 1985) and, according to Falistocco et al. (1995), it is important for the phylogenetic evolution of karyotypes due to the reduction or increase of ploidy, creating aneuploids and polyploids that, if successful, result in variability. Cytomixis may occur for many reasons, one of them is the action of genes (Kaul and Nirmala 1991). In *Arabidiopsis* thaliana, genes like the *DIF1* (Bhatt et al. 1999), responsible for irregular meiotic chromosome segregation, have also been related to the cytomixis regulation (Bellucci et al. 2003).

The chromosome pairing expected for *C. baccatum* and *C. chinense* is 12 bivalents ($2n = 24$; $n = 12$) because they are diploid species, however univalents were observed, especially in *C. baccatum*; in *C. chinense* this percentage was lower (Figure 1b-c). Average percentages of chromosome pairing configurations 12 II and 10 II + 2 I were, respectively: a) *C. baccatum* – 81.0 and 19.0; b) *C. chinense* UENF 1418 – 94.0 and 6.0; c) *C. chinense* UENF 1419 – 96.0 and 4.0. The species presented different percentages of laggard or precocious chromosomes (irregular segregation), univalents and bivalents, in all stages of meiosis (Figure 1d-f). Average percentage of cells with irregular segregation of univalents

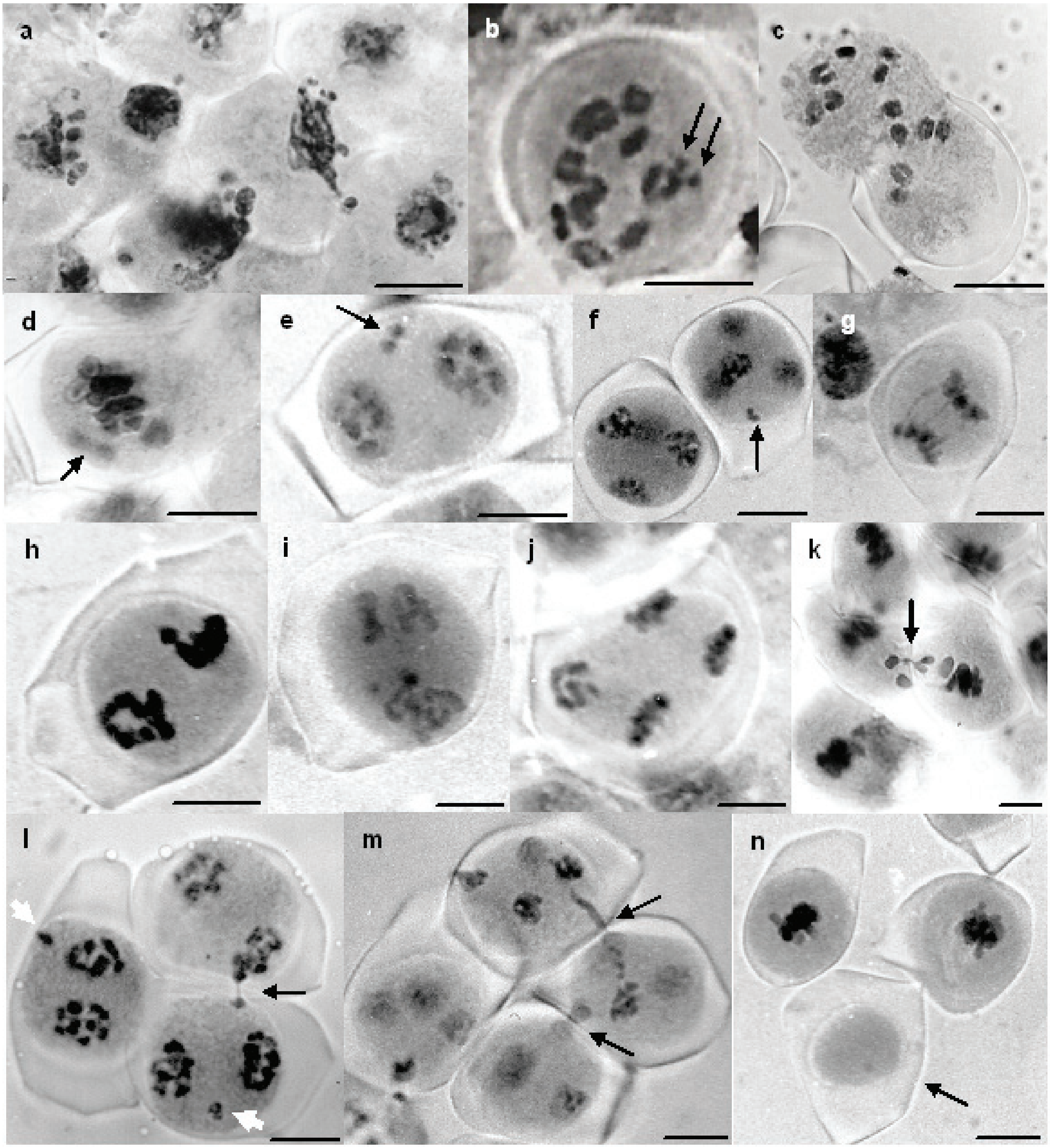

Figure 1. Meiotic irregularities in *Capsicum* species. **a)** Pycnosis after zygotene in *C. chinense*; **b)** Diakinesis with 11 B + 2 U (arrow) in *C. baccatum*; **c)** Diakinesis with *n* = 12 in *C. chinense*; **d)** Irregular segregation at M I in *C. baccatum*; **e)** Univalents (arrow) at T I in *C. chinense*; **f)** Irregular segregation (arrow) persisting at T II in *C. baccatum*; **g)** Chromosome bridges at A I in *C. chinense*; **g)** Asynchrony at M II in *C. baccatum*; **i)** Asynchrony in *C. baccatum* showing anaphase and pre-metaphase in the same cell at meiosis II; **j)** A II in *C. chinense* with a chromosome set disorganized; **k)** Cytomixis (arrow) at M I in *C. chinense*; **l)** Cytomixis (black arrow) at early T I in *C. baccatum*; disjointed chromosomes are observed (white arrow); **m)** Cytomixis (arrows) at T II in *C. chinense*; **n)** Anucleate cell (arrow) during M I in *C. baccatum*. Bar = 10µm.

and bivalents were, respectively: a) *C. baccatum* – metaphase I (M I) with 19.57 and 15.11, anaphase I (A I) with 18.10 and 12.32, telophase I (T I) with 17.28 and 11.11, M II with 18.48 and 8.43, A II with 15.61 and 8.81, T II with 9.42 and 5.32; b) *C. chinense* UENF 1418 – M I with 8.39 and 3.36, A I with 8.22 and 2.98, T I with 12.11 and 2.94, M II with 12.54 and 3.13, A II with 6.10 and 3.05, T II with 4.33 and 2.47; c) *C. chinense* UENF 1419 – M I with 10.93 and 6.25, A I with 11.12 and 2.45, T I with 13.83 and 1.16, M II 12.07 and 2.25, A II with 14.42 and 2.56, T II with 4.58 and 2.38.

C. baccatum obtained a higher percentage of irregular segregation, especially in meiosis I, while among *C. chinense* accessions the percentages of irregular segregation were lower in telophase II. During anaphase and telophase II, the percentage of lagging chromosomes decreased, suggesting that many of these chromosomes were reincorporated during meiosis II, probably due to the action of genes regulating nuclear restitution, which does not guarantee a viable final meiotic product.

Univalents were observed by Tong and Bosland (2003) in *C. buforum* and in *C. lanceolatum*, the latter in 33 % of meiocytes in diakinesis, although no laggard chromosomes were observed in the following phases. Cawood and Jones (1980) observed not paired centrometers in bivalents of *C. annuum* that were still in diplotene, which can be an indication of precocius segregation of homologous, resulting in univalents in the other meiotic phases. According to Kumar et al. (1987), the presence of univalents can be a mechanism of genetic isolation in *Capsicum*. Shopova (1966) attributed the irregular segregation observed in *C. annuum*, *C. frutescens* and *C. pubescens* to DNA breaks which occurred during pycnosis in these species.

Interstitial chiasmata were predominant in all cells from all accessions studied. Average number of terminal, interstitial and total chiasmata per cell observed in diakinesis were, respectively: a) *C. baccatum* – 3.1, 9.0 and 12.05; b) *C. chinense* UENF 1418 – 3.2, 8.8 and 12.1; c) *C. chinense* UENF 1419 – 8.7, 6.9 and 15.6. The RI varied between *C. chinense* accessions. Average number of recombination index were 24.05 in *C. baccatum*, 24.1 in *C. chinense* UENF 1418 and 27.6 in *C. chinense* UENF 1419. According to the variance analysis, there was a significant difference at the 1 % ($P < 0.01$) probability level by test F between the accessions for the following characteristics: number of terminal chiasmata, number of interstitial chiasmata and total number of chiasmata. Kumar et al. (1987, 1988) observed, on average, 19.64 chiasmata per nucleus in *C. chinense*, with minimum and maximum values between 17 and 24. Different numbers of chiasmata per nucleus were observed in *C. baccatum*, 18.1 to 20.5 (Rao et al. 1992), 17 to 22 (Kumar et al. 1987) and 10 to 22 (Tong and Bosland 1999). In *C. baccatum* and *C. chinense* genotypes studied, the average number of chiasma per nucleus observed was lower than the ones reported by other authors, varying from 11 to 13 in *C. baccatum* and from 9 to 17 in *C. chinense*.

Interstitial chiasmata (one per bivalent) prevailed in all accessions of both species, which decreases the recombination index. In the accessions studied, the low number of chiasmata may have been the cause for the univalents observed. Lein and Lelley (1987) have reported that the chiasmata frequency and location are under polygenic control. If a genic segregation occurs, different frequencies of chiasmata may be observed (Defani-Scoarize et al. 1996), but a little is known about the genetic control of chiasmata. In *C. baccatum* and *C. chinense* accessions analyzed, the low frequency of chiasmata and the transfer of portions of chromatin from one cell to another in different phases of meiosis may have been the cause of laggard chromosomes and, consequently, of micronuclei in microspores, and of binucleate pollen grains.

Chromosome bridges were observed (Figure 1g) in meiocytes of *C. baccatum* and in *C. chinense* UENF 1418 and UENF 1419 accessions. Average percentage of cells with bridges were: a) *C. baccatum* – 5.28 in A I, 3.65 in A II; b) *C. chinense* UENF 1418 – 4.71 in A I, 1.92 in A II; c) *C. chinense* UENF 1419 – 3.98 in A I, 2.34 in A II. Asynchrony was observed in all phases of meiosis II, when in the same cell both chromosome sets presented different arrangements (Table 3; Figure 1h-j). Average percentage of cells with asynchrony were: a) *C. baccatum* – 22.55 in M II, 15.74 in A II, 5.28 in T II; b) *C. chinense* UENF 1418 – 14.20 in M II, 11.29 in A II, 2.26 in T II; c) *C. chinense* UENF 1419 – 19.58 in M II, 12.66 in A II, 3.19 in T II. In over 30 % of cells at meiosis I and II in *C. baccatum* and *C. chinense*, cytoplasmic connections and the exchange of chromosome material between meiocytes were observed (Figure 1 k-m), most of the time involving chromosomes located next to the walls, as well as empty meiocytes (Figure 1n), due to cytomixis observed in these species.

According to Lanteri and Pickersgill (1993), rearrangements in the genome seem to be associated with the evolution and differentiation of many *Capsicum* species when the chromosome exchanges are reciprocal. Only one persistent bridge, without fragments, was observed in each *C. baccatum* and *C. chinense* meiocyte with this irregularity, suggesting heterozygote inversion (Kumar et al. 1987), probably because these accessions come from improved generations.

Abnormality in the formation of the spindle and asynchrony in meiosis II affected the post-meiotic products. Depending on which type of irregularity that occurs in the cell, the spindles may group or separate homologous chromosomes (Caetano-Pereira et al. 1998), and result in meiocytes with trinucleate telophase II, or even with cells presenting the division of non-equational cytoplasm due to the unbalanced number of chromosomes, as observed in the studied accessions. In *Zea*, irregularities in the spindle are caused by genetic factors, and in some populations, mutants with genes *dv* (divergent spindle) (Golubovskaya and Mashnenkov 1981), *ms43* (absence of the second meiotic division due to a disturbance in the spindle orientation) and *ms28* (late depolymerization of the spindle fibers) (Golubovskaya 1989) were observed.

Post-meiotic behavior

At the end of meiosis, irregularities (Figure 2) and MI (%) in *C. baccatum* and *C. chinense* UENF 1418 and UENF 1419 accessions were also observed, respectively: a) monads – 0.8, 0.2 and 0.3; b) dyads – 0.5, 0.4 and 0.4; c) triads – 12.7, 9.7 and 10.9; d) polyads – 9.3, 7.2 and 6.6; MI – 76.5, 82.4 and 81.7. Triads were the most observed irregular product, probably due to the asynchrony during meiosis II, which disturbs chromosome segregation (Souza and Pereira 2011).

While tetrads of the tetrahedral type were normally observed, some linear tetrads were found only in *C. baccatum* (Figure 2c). Some microspores presented one or more micronuclei, while others were bi-nucleated (Figure 2d). Irregular chromosome segregation in meiosis I and II could be the result of the non-oriented chromosomes, which show an inability to congregate on the equatorial plate, resulting in the grouping of the many sets of chromosomes in telophase II, as well as micronuclei, incorrect cytoplasm division and polyads (Souza and Pereira 2011).

Pollen viability

The pollen viability in *C. baccatum* was below 70 %, while in *C. chinense*, both accessions presented pollen viability above 80 %. The frequency of viable and unviable PG in relation to the pollen length is presented in the Figure 3. In the analyzed species, the highest frequency of viable PG was measured between 32-34 µm, while for the unviable PG there was a size variation (20-28 µm) between types T1 and T2 and between the accessions. The PG average length between unviable T1 and T2 varied 5 % in *C. baccatum*, 17.8 % in *C. chinense* UENF 1418 accession, and 6.1 % in *C. chinense* UENF 1419. The difference in percentage between the average length of unviable and viable PG was higher, being 29.7 % in *C. baccatum*, 22.8 % in *C. chinense* UENF 1418 accession, and 33.5 % in *C. chinense* UENF 1419. Some binucleate PG was observed (Figure 2e).

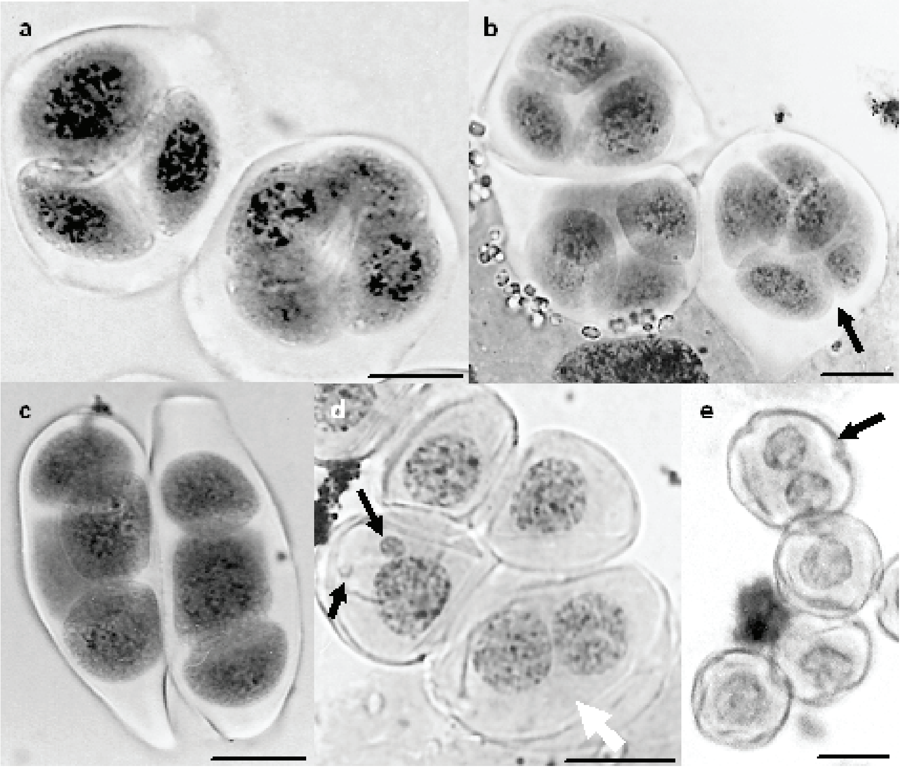

Figure 2. Irregular post-meiotic products in *Capsicum* species. **a)** Normal tetrad and triad in *C. chinense*; **b)** Normal tetrad and polyad (arrow) with cell of different sizes in *C. baccatum*; **c)** Linear tetrads in *C. baccatum*; **d)** Microspore with micronuclei (arrow) and binucleate (white arrow) in *C. baccatum*; **e)** Normal microspores and PG binucleate (arrow) in *C. chinense*. Bar = 20µm..

The MI in *C. baccatum* (76.5 %) was lower than in *C. chinense* accessions (80 %). However, the pollen viability (PV) was even lower in *C. baccatum*, 65.7 %, while in *C. chinense* were above 88 %. The percentage of the PV is different between accessions of *Capsicum* species. Tong and Bosland (1999, 2003) observed PV above 96 % in accessions of *C.*

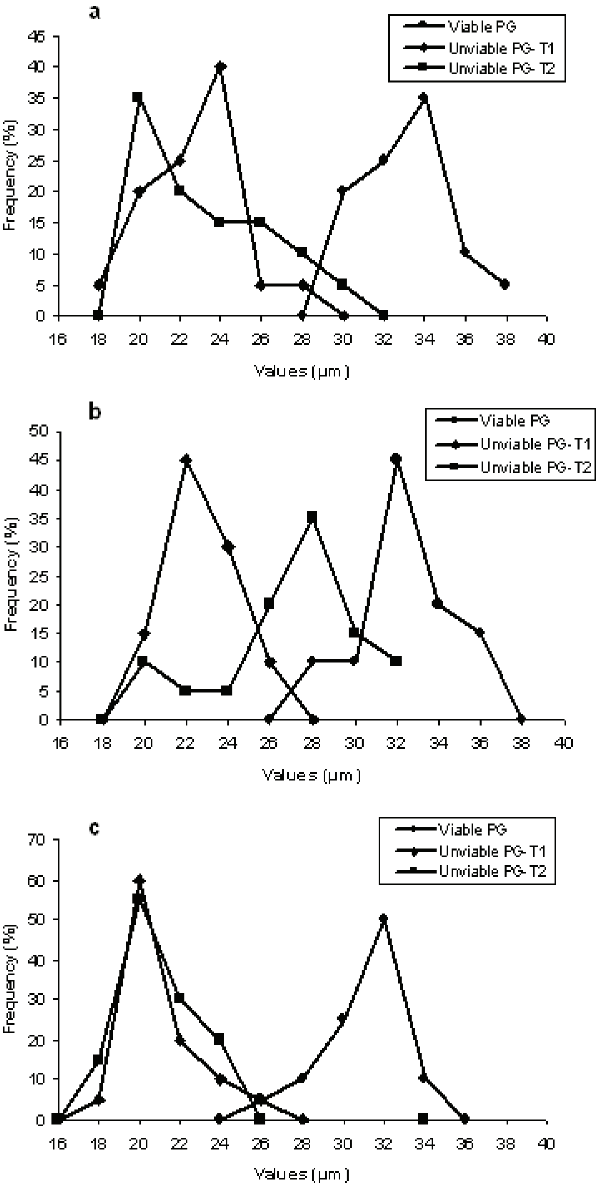

Figure 3. Viable and sterile pollen grains (PG) in relation to PG size in *Capsicum* accessions. **a)** *C. baccatum*; **b)** *C. chinense* UENF 1418; **c)** *C. chinense* UENF 1419.

baccatum, and regular meiosis. In *C. chinense*, PV percentages were between 84 to 87 %, being 60 % from unviable PG, type T1, however, multivalents were observed during the chromosome pairing (Lanteri and Pickersgill 1993). Dharamadhaj and Prakash (1978) attributed the variation found in the PV percentage in *Capsicum* species to environmental influence and observed pollen fertility above 90 % in the summer, while in the winter the same accessions presented a maximum pollen fertility of 31 %.

In the accessions studied, the values of MI and PV observed suggest that in *C. baccatum* the low PV occurred, mainly, due to meiotic irregularities, since the majority of unviable PG is type T1, empty, with a maximum of 24 µm and 30 % of the size of the viable PG. The pollen sterility deserves attention in breeding programs because in some cases the unviable T1 PG may occur due to genic mutations (Twell 1995). However, not only the irregularities observed during meiosis, but also post-meiotic factors were responsible for the pollen sterility. In both *C. chinense* accessions, the percentages observed of unviable T2 PG, contracted, were higher than those of T1 PG, measuring up to 34 µm. Thus, it is suggested that the sterility of type 2 occurred during the gametophytes development, probably starting in the microspore stage, while those of type 1 are aborted in the beginning of their development.

Among the three accessions analyzed, *C. baccatum* demonstrated higher meiotic instability. The irregular chromosome pairing, univalents, chromosome bridges and laggards in anaphase I resulted in a lower meiotic index and higher pollen non-viability. These results indicated that the analyzed *C. baccatum* accession suffered small chromosome alterations in the process of domestication and improvement, and that its genome is structurally different from the analyzed *C. chinense* accession.

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Irregularidades meióticas em espécies de *Capsicum* L.

Resumo – *Estudos citogenéticos e de viabilidade polínica (VP) foram realizados em acessos de pimenta de* Capsicum chinense *e* Capsicum baccatum*. Irregularidades tais como cromossomos retardatários e univalentes, pontes, problemas na formação das fibras dos fusos e citomixia foram observados, especialmente em* C. baccatum*, que foi considerado o genótipo mais instável. Nos produtos pós-meióticos foram observadas irregularidades tais como tríades e políades em 20 % dos micrósporos de* C. baccatum *e em 17 % dos micrósporos de* C. chinense*, em média. VP em* C. baccatum *foi abaixo de 70 %, enquanto* C. chinense *apresentou VP acima de 80 %. Irregularidades meióticas em* Capsicum*, principalmente em* C. baccatum*, considerando a baixa VP estimada, foram significativas, mas não impeditivas para ocorrência de fertilização.*

Palavras-chave: *pimenta, microsporogênese, citomixia, viabilidade polínica.*

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