
Cytomixis impairs meiosis and influences reproductive success in *Chlorophytum comosum* (Thunb) Jacq. – an additional strategy and possible implications

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Spontaneous intercellular chromatin migration/cytomixis was observed to occur in the pollen mother cells (PMCs) of the *Chlorophytum comosum* for the first time. The migration through cytotoxic channels was more pronounced in meiosis-I and very rare in meiosis-II. The process was associated with erratic meiosis, which was characterized by defects in chromosome organization and segregation. Cytomixis was more intense in the month of April than in July and consequently the frequency of meiotic irregularities was much more pronounced during the month of April. As a consequence of abnormal meiosis, fertility was drastically reduced resulting in meager seed efficiency of 17% only. Recombination system also does not guarantee the release of sufficient variability. We view the phenomenon of cytomixis as genetically controlled mechanism involving meiotic genes and operating through signal transduction pathway triggered by the environmental stimuli. The evolutionary significance and tenable hypothesis in the backdrop of existing literature is also proposed.

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1. Introduction

The phenomenon of cytomixis is characterized by the migration of chromatin/chromosomes between the proximate meiocytes through cytoplasmic channels or intercellular bridges. This striking phenomenon was first recorded by Koernicke (1901) in the pollen mother cells of *Crocus sativus* and subsequently reported by Gates (1911) in *Oenothera gigas* and *O. biennis*. Though an infrequent cytological phenomenon, it has been reported to occur in large array of plant species (Gottschalk 1970; Cheng *et al* 1975; Omara 1976; Guochang *et al* 1987; Bedi *et al* 1990; Bellucci *et al* 2003). Cytoplasmic connections preexist between meiocytes in the form of plasmodesmata within the syncytium and then become severed as a result of insulation of meiocytes by the progressive deposition of callose (Heslop-Harrison 1966). In some cases, however, the plasmodesmata still persist during meiosis and increase in size to generate cytotoxic connections. These are

termed as cytotoxic channels and are large enough to permit the transfer of cytoplasmic organelle and in some cases chromatin material also (Risueno *et al* 1969). The preexistence of plasmodesmata may help to achieve the uniform and better gamete quality through intercellular exchange of molecular signals and also the mixing of protoplasm between the connected cells so that they have similar levels/states of mRNA's proteins and organelles etc. through cytotoxic channels (Guo and Zheng 2004). Nevertheless, the persistence of cytotoxic channels have profound influence on the meiotic process, its end products and overall sexuality of the species. This process seems to be of evolutionary significance which is endorsed by many authors (Srivastav and Raina 1980; Zheng *et al* 1983), and is more frequent in species with unbalanced genomes such as haploids, aneuploids, hybrids (de Nettancourt and Grant 1964), mutants (Gottschalk 1970), triploids (Salesses 1970) and apomicts (Mantu and Sharma 1983). There are some instances where the polyploid forms seem to display more

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cytomixis than their diploid counterparts (Semyarkhina and Kuptsou 1974).

Cytomixis is generally associated with erratic meiosis and consequently low fertility. Meiosis seem to be highly evolved but complex process to produce gametes genetically and structurally different from the meiotic mother cells. This process is made necessary by the biparentalism as the main counterpart of fertilization. All the organisms, irrespective of their evolved complexity, meiotically reduce the chromosome number at the start of sexual reproduction, compensating for fertilization and maintaining the diploid chromosome set from generation to generation (Golubovskaya 1979). Besides mutation and hybridization, meiosis is a potential means for increasing the genetic variability within a species through the process of chromosome segregation and gene recombination.

Meiosis is highly coherent and genetically programmed process and comprises pairing of homologous chromosomes, crossing over, the reduction in chromosome number, the requirement of two cell divisions and the lack of S period between the two divisions. Like any other biological process, all the sequential steps involved in meiosis are controlled by a large array of genes (Ramana 1974; Mok and Peloquin 1975; Mok *et al* 1976; Koduru and Rao 1981; Falistocco *et al* 1994). Mutation in any of these genes that govern micro or megasporogenesis from pre-meiotic to post meiotic events can lead to serious anomalies in the whole process resulting in the genetically aberrant end products having adverse impact on fertility and overall reproductive efficiency of the species.

In the present study cytomixis was recorded for the first time in a widely used ornamental, *Chlorophytum comosum*, belonging to family liliaceae. Our interest in the species is from the medicinal point of view as its tubers are shown to possess inhibitory activity on tumour promoter-induced phospholipids metabolism of HeLa cells (Mimaki *et al* 1996). The present investigation deals with the consequences of cytomixis in relation to meiotic behaviour and reproductive success of the species. The evolutionary significance and tenable hypothesis in the backdrop of existing literature is also proposed.

2. Materials and methods

The materials used for the present study consisted of a population of 75 plants procured from various commercial and non-commercial sources in India. The plants were grown in a well-drained sandy loam soil with periodic organic manuring under uniform cultivation conditions in the experimental plots at Regional Research Laboratory, Jammu, India (32° 44' N, 75° 55' E; 305 m in altitude). During first year of cultivation experiment (2003), we observed meager seed production and pronounced vegetative vivipary in all

the plants of the population. These observations prompted us to undertake cytological studies in the species. For meiosis fourteen plants at random were selected and their young inflorescences at an ideal stage were fixed in ethanol: chloroform: acetic acid (6:3:1) for 24 h, transferred to 70% alcohol and stored under refrigeration at 4°C. Squash preparations were made following La cour's 2% aceto-carmine method for meiotic studies. Pollen stainability was scored from freshly prepared aceto-carmine mounts of pollen and the pollen dimensions from these mounts using ocular and stage micrometer (Sharma *et al* 1993). Pollen stainability often does not correspond closely to viability. Hence *in vitro* germination test (hanging drop culture) was used, employing Brewbaker and Kwack's medium (1963).

Mitotic chromosome counts were made from 4–5 mm long excised root tips from the field grown plants. Root tips were pre-treated with 0.05% colchicine for 2–3 h at 4°C. Pretreated material was thoroughly washed with tap water, fixed in ethanol: chloroform: acetic acid (6:3:1) for 24 h and stored in 70% ethanol at 4°C. For karyotype analysis, root tips were hydrolysed in 1 N HCl and stained and squashed with 2% aceto-orcein. Observations were made from metaphase stage of cells and chromosome measurements were recorded from freshly prepared mounts using ocular and stage micrometer. Based on the chromosome metrics and position of centromere, Battaglia's (1955) scheme was employed for classifying the somatic chromosomes for deriving the karyotype formula. Cumulative sum of the haploid chromosome complement at metaphase was taken as total chromatin length. At least 53 preparations from different plants in metaphase were used for observations.

Pollen output per flower was calculated by estimating the number of pollen grains per anther and multiplying by six, pollen-ovule ratio was obtained by dividing the number of pollen grains by number of ovules per flower (Cruden 1977).

For estimation of seed efficiency, few individual inflorescences were selected at random, tagged and scored, first for number of flowers and ovules and then the number of seed set. Seed efficiency was calculated as the number of filled seeds, divided by seed potential multiplied by 100.

Reproductive success is the product of the fruit to flower ratios (Fr/FI) and the seed to ovule ratio (S/O) (Weins *et al* 1987). Eighteen individual inflorescences from 9 plants were tagged to measure the reproductive efficiency.

3. Results

3.1 *Cytomixis in pollen mother cells*

Cytomixis was observed to occur in pollen mother cells (PMCs) of *C. comosum*. The process involved 2 to 3 meiocytes (figure 1b,c) and manifested in the form of

cytomictic channels. Occasionally proximate PMC's were connected by two or more conjugating channels of varying breadth (figure 1e). In some situations, the connections enlarged to such an extent that the adjacent meiocytes tended

to fuse together to facilitate the chromatin transfer, and in some instances, direct fusion of PMC's in the aggregates of twos and threes were also observed (figure 1c,d). Spontaneous chromatin migration was more pronounced in

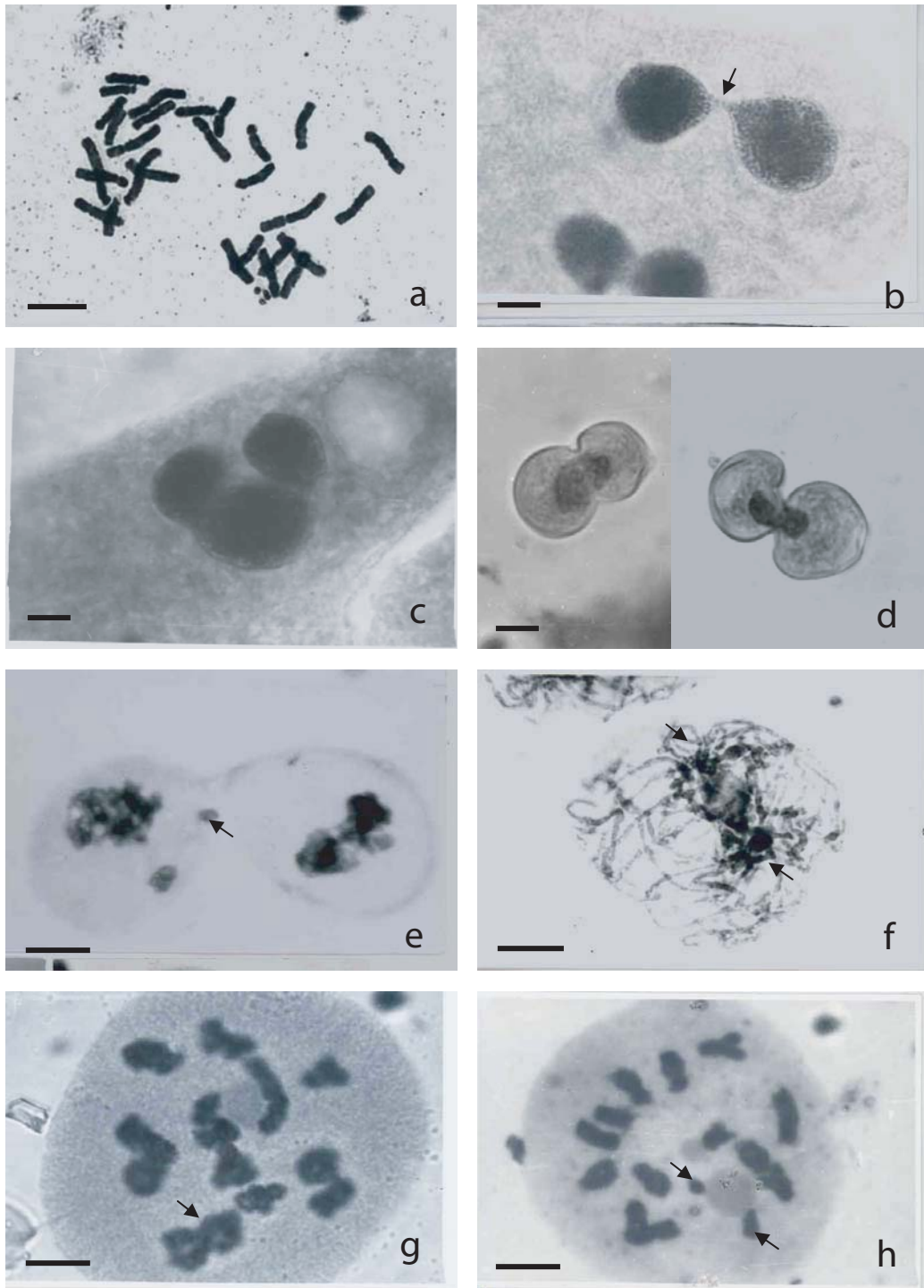


Figure 1. For caption, see p. 632.

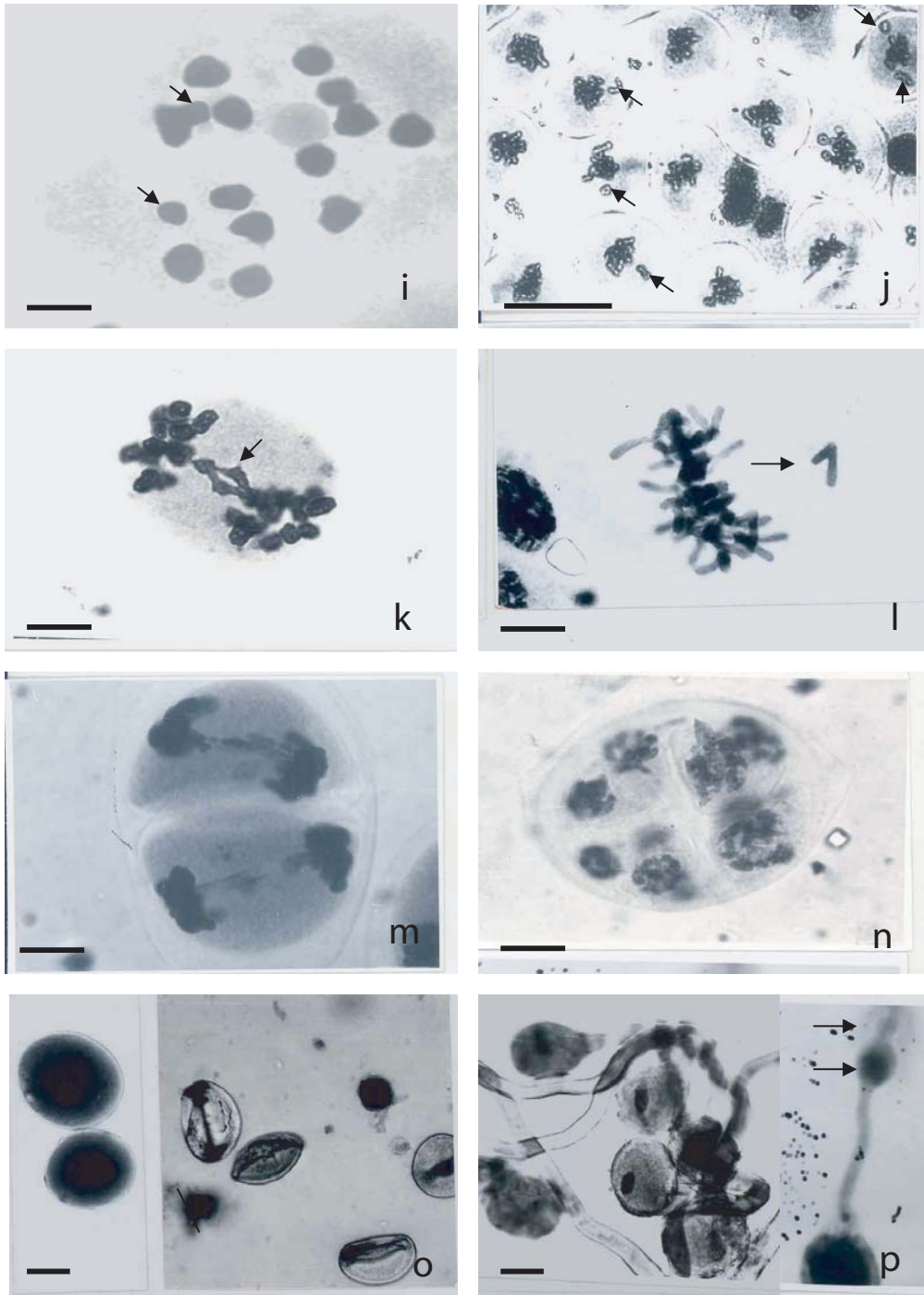


Figure 1. (a) Somatic metaphase depicting $2n=28$. (b,c) Two and three meiocytes showing cytomixis; note prominent cytomictic channel (b). (d) Two meiocytes involved in cytomixis by direct fusion. (e) Enlarged cytomictic channels showing cytomixis at metaphase-I-note chromosomes clumped by stickiness in two meiocytes. (f) Densely staining additional pycnotic accumulations at pachytene. (g) Meiocyte at diplotene with $1^{IV} + 12^{II}$. (h) Meiocyte at diakinesis showing $13^{II} + 2^I$. (i) Meiocyte showing $13^{II} + 2^I$ at diakinesis. (j) Meiocyte at metaphase-I showing precociously ascending chromosomes. (k) Abnormal anaphase-I showing double dicentric bridge. (l,m) One unoriented chromosome at metaphase-II- note also the pycnosis, giving the metaphase plate a sticky appearance, (l) and chromatin bridge at anaphase-II (m). (n) Polyad with two microspores and four micronuclei. (o) Stainable (dark) dimorphic pollen grains and sterile oblong (transparent) pollen grains. (p) *In vitro* pollen germination showing abnormal pollen tube with a bulge and callose plug at the tip. (Bars = $10 \mu\text{m}$).

Table 1. Percentage of microsporocytes with abnormalities during April/July months in *C. comosum**.

Pachytene	Diakinesis	Metaphase-I	Anaphase-I	Abnormalities (%)				
				Telophase-I	Metaphase-II	Anaphase-II	Telophase	Tetrad
1/1	68/43	54/40	59/32	41/33	43/30	38/27	32/24	27//20

*Number of microsporocytes and tetrads studied:
 Microsporocytes – 5668 (April); 4630 (July).
 Tetrads – 9244 (April); 8743 (July).

Table 2. Some reproductive features depicting reproductive success and seed efficiency in cytotoxic *C. comosum*.

Number of pollen grains / anther	9913 ± 733*	(21)**
Number of pollen grains / flower	59478	
Number of ovules/flower	22 ± 0.8	(85)
Pollen/ovule ratio / flower	2703	
Pollen stainability (%)		
April	89 ± 12.4	(6788)
July	92 ± 9	(7040)
<i>In vitro</i> pollen viability (%)		
April	30 ± 4.2	(2817)
July	48 ± 5.1	(2900)
Pollen size		
Small	14 μm ± 2	(2110)
Large	29 μm ± 1.8	(1983)
Pollen load / stigma	46 ± 5.7	(42)
<i>In situ</i> pollen germination at peak stigma receptivity	4 ± 0.3	(56)
Number of flowers / plant	1265 ± 178	(48)
Number of capsules / plant	123 ± 16	(48)
Number of seeds / capsule	3.4 ± 0.4	(538)
Reproductive success (Fr/FlxS/O)	0.014	
Seed efficiency (%)	17	

*Mean ± SE.

**Number of observations.

meiosis I and very rare in meiosis II. It was more intense in early stages at leptotene and metaphase-I. Migration was exclusively unidirectional and proceeded from donor to recipient cell. In majority of the cells migration was incomplete and very rarely did we observe meiocytes empty.

No cytoplasmic connections were found between the PMC's at different stages of meiosis.

3.2 Meiotic irregularities

Comparison of cytotoxicity in the PMC's for the months of April and July revealed that the event was more pronounced (9%) in April than in July (3%). Comparative frequency of the meiotic abnormalities from pachytene to tetrad stage, exhibited higher preponderance of aberrations during the month of April (table 1). The frequency of aberrant meiocytes at diplotene/metaphase, anaphase-I and anaphase-II was higher than the frequency of normal meiocytes. The various structural chromosome aberrations were recorded and pachytene presented as a first stage to show densely staining pycnotic accumulations (1%) (figure 1f). Diakinesis showed the presence of single quadrivalent (1.3%) and more frequently two univalents (5%) (figure 1g,h,i). In some cells an additional bivalent, 15 in number were observed instead of 14 bivalents at diakinesis and metaphase-I (3%). Precocious chromosome ascension and non-congressed bivalents at equatorial plate were also discernible (figure 1j,l). Non-disjunction was also observed in some cases. Anaphase-I and anaphase-II were characterized by the lagging chromosomes, bridges, fragments and some dicentric bridges (19%) (figure 1k,m). Unequal distribution of chromatin was also discernible in small percentage of cells (3%) at telophase-II. High incidence of chromosome stickiness was another manifestation visible in all the phases of meiosis I and meiosis II. The result of all these irregularities at different stages of microsporogenesis showed abnormal end products in the form of microspores with micronuclei (24%). The abnormal microspores gave rise to pollen grains differing in size and apparently in chromatin content also.

3.3 Chromosome complement and chiasmata frequency

C. comosum has a chromosome number of $2n = 28$ (figure 1a). Total chromatin length is 169 μm. The karyotype formula of the species is: 1 M + 7 SM^{1sc} + 6 ST. The number

Table 3. Features of meiotic system in *C. comosum*.

Somatic chromosome number	Xta frequency per pmc at		Recombination index
	Diplotene	Metaphase-I	
28	24 ± 2	18 ± 2	38

of chiasmata per bivalent ranged from 1–3 with an average of 1.7 chiasmata per bivalent. The mean chiasmata frequency at diplotene and metaphase-I varied with an average of 24 ± 2 and 18 ± 2 chiasmata per meiocyte respectively (table 3). However, there were no significant differences between chiasmata frequencies during the two months i.e. April and July.

3.4 Seed efficiency and reproductive success

In open pollination, various reproductive parameters to evaluate the seed efficiency and reproductive success are depicted in table 2. Pollen grains differentiating per anther averaged 9913 ± 733. The ovules per ovary ranged between 21–25 (\bar{X} = 22 ± 0.8). The pollen ovule ratio per flower averaged 2655. Seed to ovule ratio (S/O) in open pollination was 0.06 and 0.14 in April and July respectively. Reproductive success (Fr/FI X S/O) was extremely low in both the months (0.007 and 0.014). Though the seed to ovule ratio and fruit to flower ratio in the month of July was comparatively better than in the month of April. Seed frequency per fruit ranged from 1–4 only. There were no significant differences in the seed set per fruit between the two months.

3.5 Pollen stainability, in vitro pollen viability and abnormalities of pollen-tube growth

Pollen stainability with aceto-carmines averaged 89% and 92% for the months of April and July respectively. However, *in vitro* pollen viability test using Brewbaker and Kwack's solution showed only 30% and 48% viability for months of April and July respectively. Pollen germination commenced within 2 h with an average tube growth of 26 $\mu\text{m h}^{-1}$. Viable pollen grains had straight, thin walled pollen tubes with tapering tips whereas the non-viable pollen grains either failed to germinate or manifested some abnormalities and callose deposition at tips (figure 1o,p). All these abnormalities are in conformity with the genetically imbalanced nature of pollen. Though, the stainability percentages were high, yet these did not correspond with the fertility level of pollen grains. The pollen varied in size from 14 μm to 29 μm . Smaller pollen grains were generally nonviable but the larger size was no guarantee for being viable. Under *in vivo* conditions stigma at its peak receptivity had a moderate pollen load

of about 46 ± 5.7, with only 2–5 germinating pollen grains available for siring of about 22 ± 0.8 ovules per flower.

4. Discussion

Cytomixis, the migration of chromatin material between and among the meiocytes, meristematic, tapetal, integumental, nucellar and ovary cells through cytotoxic channels or direct adhesion is a well established phenomenon reported in large array of plants (Rieger *et al* 1976; Bobak and Herich 1978; Guochang *et al* 1987; Consolaro and Pagliarini 1995; Bellucci *et al* 2003). Cytomixis is a potential means to conserve the genetic heterozygosity of gametes (Villeux 1985) and additional means of phylogenetic evolution of karyotypes by reducing or increasing the basic series (Cheng *et al* 1980, 1987), creation of aneuploids and polyploids (Sarvella 1958; Falistocco *et al* 1995). In recent years there is an accumulating evidence to suggest that cytomixis is a normal genetically controlled phenomenon influenced by physiological and environmental factors (Brown and Burtke 1974; Omara 1976; Mantu and Sharma 1983; Falistocco *et al* 1994; Bellucci *et al* 2003) rather than due to fortuitous causes such as artifacts produced by fixation, mechanical injuries or pathological anomaly (Takats 1959; Gottschalk 1970; Morisset 1978). Cytomixis in *C. comosum* revealed that the spontaneous transfer of chromatin material is more frequent in meiosis I and very rare in subsequent division. Preponderance of cytomixis in early stages of meiosis has also been observed in many other species (Mantu and Sharma 1983; Cheng *et al* 1987; Feijo and Paris 1989; Yen *et al* 1993; Bellucci *et al* 2003). Nevertheless, the transfer of chromosomes is not necessarily restricted to early phases of meiosis but may continue even until tetrad stage (Sen and Bhattacharya 1988; Koul 1990). Genes like *DIF1* in *Arabidopsis thaliana* (Bhatt *et al* 1999) responsible for aberrant meiotic chromosome segregation have also been implicated in the regulation of cytomixis (Bellucci *et al* 2003).

In case of *C. comosum* cytomixis was more intense in the month of April than in July and consequently the frequency of meiotic irregularities were also much more frequent during the month of April. During the months of April and July, the mean temperature fluctuate between 40°C and 32°C with relative humidity around 50% and 90% respectively in Jammu (India). These results suggest that there exists a positive correlation between the extent of cytomixis and preponderance of meiotic disturbances during the two phases of growth.

Erratic meiosis and various structural chromosome aberrations like pycnosis, precocious chromosome ascension, laggard, non-congressed bivalents at equatorial plates, univalents at diakinesis, unoriented chromosomes at metaphase-II, quadrivalents, irregular disjunction

at anaphase-I and anaphase-II, unequal distribution of chromatin material at telophase-II and microspores with micronuclei and few instances of pycnotic micronuclei were observed. Some of these meiotic irregularities have also been described by Pagliarini *et al* (1993) but they did not observe any cytomixis in *C. comosum*. Two of the anomalies, one additional bivalent at diakinesis and one quadrivalent at diplotene has implications for the origin of aneuploids in this species. The low frequency of quadrivalents suggest it as an outcome of translocation rather than segmental allopolyploid. High incidence of chromosomal irregularities may be genetic in nature and modified by the environment as there exists a plethora of experimental evidence that each and every step of meiosis is genetically regulated (Gottschalk and Kaul 1974; Baker *et al* 1976; Golubovskaya 1979; Kaul and Murthy 1985; Dawson *et al* 1993; Taschetto and Pagliarini 1993).

Persistence of meiotic anomalies during the microsporogenesis has an adverse effect on the fertility level of *C. comosum*. On an average only about 4 ± 0.3 viable pollen are available for siring of about 22 ± 0.8 ovules per flower, though the pollen ovule ratio per flower averages 2703, indicating that cytomixis and its genetic consequences have no effect on pollen production. Cytomixis and its downstream effects on meiosis result in aberrant end products and as a consequence, the number of flowers per plant that mature into fruits averages 123 ± 16 and the number of ovules that are sired into seeds per fruit averages 3.4 ± 0.4 . Perusal of literature suggests that erratic meiosis, inherent in many plant species may preclude cytomixis but cytomixis is invariably associated with anomalous microsporogenesis. It seems likely that genes responsible for aberrant meiosis and cytomixis may be the same. Nevertheless, the key to understand this lies in molecular dissection of the phenomenon. Preponderance of chromosomal aberrations and frequency of micronuclei at tetrad stage could serve as an important index for pollen fertility and reproductive success. Moderate chiasmata frequency (1.7 chiasmata/bivalent) coupled with meager reproductive success (0.014) in *C. comosum* indicates towards the generation of limited variation through meiotic recombination and breeding system.

Cytomixis in *C. comosum* has not been previously recorded in literature. Extremely low reproductive success in this species is compensated by its perennial behaviour and aggressive asexual reproduction through vegetative vivipary, a phenomenon where the florets transform into asexual propagules. Perusal of literature also reveals that this phenomenon though rare may occur under diverse environmental conditions. It seems plausible to propound that in addition to three chief sources of variation i.e. mutation, hybridization and recombination, cytomixis could be an additional strategy employed by plants to

generate variability either by reducing the self-fertility thus promoting shift in the breeding system from selfing to crossing over a period of time or by generating the high levels of heterozygosity through male track. It also has implications in the evolution of karyotypes and the process of speciation. We also view the phenomenon of cytomixis as a genetically controlled mechanism involving the meiotic genes and operating through signal transduction pathway triggered by the environmental stimuli.

C. comosum is also very unusual in that its pollen grains show traits of different modes of plastid inheritance. About 50% of the pollen grains exhibit the potential for biparental plastid inheritance, where as the rest exhibit maternal plastid inheritance (Liu *et al* 2004). In fact this species represents transitional type between the biparental and maternal modes of plastid inheritance. Could there be any evolutionary significance and interrelationship between the cytomixis and biparental mode of plastid inheritance in relation to inadequacy of breeding and meiotic systems as in case of *C. comosum* to generate sufficient variation? These unusual phenomenon i.e. cytomixis and biparental mode of plastid inheritance could be additional strategies to enhance the survival value of plant species by releasing more variation. To test experimentally some of our explanations we intend to evaluate the F_1 and subsequent progenies through molecular and cytological analysis for the level of heterozygosity and variation in chromosome numbers in cytomicitic and non-cytomicitic populations under different environments.

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