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RESEARCH ARTICLE

CYTOMIXIS – A WELL KNOWN BUT LESS UNDERSTOOD PHENOMENON IN PLANTS

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ABSTRACT

A review of cytomixis, a cytological anomaly mostly prevalent during microsporogenesis in flowering plants, is given. The phenomenon is more prevalent in genetically, physiologically and biochemically imbalanced plants such as, haploids, aneuploids, triploids, hybrids and apomicts. There are conflicting opinions and explanations regarding the causes and significance of cytomixis. Recent evidences suggest that it is a natural genetically controlled phenomenon influenced by physiological and environmental factors, and the anomaly may have some evolutionary significance.

INTRODUCTION

The phenomenon of cytomixis, defined as the migration of chromatin material/chromosomes, cell organelles especially nuclei, or cytoplasm between proximate meiocytes through cytomictic channels or intercellular bridges or occasionally by direct fusion, has been reported in numerous plant species. The phenomenon was first described by Arnoldy (1900) in reproductive organs of gymnosperms and then by Körnicke (1901) in pollen mother cells (PMCs) of *Crocus vernus* and by Miehe (1901) in the leaf epidermis of *Allium cepa*. Gates (1911) observed this striking phenomenon during microsporogenesis in *Oenothera gigas* and *O. biennis* and coined the term cytomixis. Since then, this phenomenon was reported mainly during microsporogenesis by many researchers in a wide range of flowering plants (Levan 1941; Sarvella 1958; Tarkowska 1960, 1965; Bell 1964; Heslop-Harrison 1966; Gottschalk 1970; Cheng *et al* .,1975; Shnaider 1975; Omara 1976; Saggoo and Bir 1983; Singhal and Gill 1985; Guochang 1987; Soodan and Wafai 1987; Bahl and Tyagl 1988; Sen and Bhattacharya 1988; Wang 1988; Bedi 1990; Koul 1990; Kostritsyna and Soldatov 1991; Consolaro and Pagliarini 1995; Haroun 1995; De Souza and Pagliarini 1997; Bellucci *et al.,*2003; Bione *et al.* 2000; Ghanima and Talaat 2003; Wu *et al.,*2003; Datta *et al.,* 2005; Ghaffari 2006; Lattoo *et al.* 2006; Sheidai and Bagheri-Shabestarei 2007; Singh *et al* .,2007; Sheidai 2008; Singhal and Kumar 2008; Maity and Datta 2009; Song and Li 2009; Kumar *et al.* 2010; Mursalimov and Deineko 2011; Ranjbar *et al.,*2011; Guan *et al.,* 2012). However, cytomixis is also known to occur, although rarely, in somatic cells such as root meristematic cells (Jacob 1941; Sarvella 1958; Tarkowska 1960; Kostritsyna and Soldatov 1991), leaf epidermal and subepidermal layers (Cooper 1952; Tarkowska 1960), ovary cells (Koul 1990), tapetal cells (Cooper 1952) and shoot apex (Guzicka and Wozny 2005), or between mitotic (tapetal) and meiotic cells (Cooper 1952). Besides in natural species, cytomixis has also been observed in artificially synthesized interspecific/generic hybrids (Li *et al.,* 2005, 2009). The phenomenon has also been reported in spermatogenesis in animals (Ventela *et al.,* 2003), lower plants (Kwiatkowska *et al.,* 2003) and gymnosperms (Guzicka and Wozny 2005). Recently, it has also been reported in transgenic plants of *Nicotiana tabacum* (Sidorchuk *et al.,* 2007). The migration of nuclei during cytomixis is believed to be due to actin cytoskeleton because the migration of cell contents through cytomictic channels is stopped due to cytochalasin B, a chemical that prevents the growth of actin filaments (Zhang *et al.,* 1985).

Origin of cytomictic channels

Cytoplasmic connections between meiocytes originate from the preexisting system of plasmodesmata which develops in anther tissues and then, in general, becomes obstructed by the progressive deposition of callose (Heslop-Harrison1966). However, the plasmodesmata may sometimes persist during meiosis and either increase in size (Mursalimov *et al.,* 2010) or several closely located plasmodesmata join together (Wang *et al.,* 2004) to generate intermeiocytic connections known as cytomictic channels. Sometimes such channels are formed de novo during cell wall dissolution (Wang *et al.,* 1998; Yu *et al.,* 2004). Through these channels, which look like stretched strands, not only chromatin but even cytoplasmic organelles may also pass (Risueño *et al.,* 1969; Mursalimov and Deineko 2011). Sometimes the PMCs are directly fused to facilitate the transfer of chromatin by dissolution of their cell walls without involving the formation of channels (Lone and Wafai 2009; Ranjbar *et al.,* 2011).

Prevalence

Cytomixis occurs with equal or different intensity in all phases of meiosis (Basavaiah and Murthy 1987; Bauchan 1987; Sapre and Deshpande 1987; De Souza and Pagliarini 1997; Shamina *et al.* 2000; Ressayre *et al.* 2003), however others (Maheshwari 1950, Kundu and Sharma 1988, Sen and Bhattacharya 1988, Haroun

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1995, Singhal and Kumar 2010, Kumar and Singhal 2011) are of the opinion that early stages of meiosis-I are more favourable for cytomixis. Song and Li (2009) in their communication on *Salvia miltiorrhiza*, a well-known Chinese herb, reported that cytomixis was observed mainly during early prophase I in PMCs and the frequency was highest during pachynema. Cytomixis also occurs during metaphase and anaphase I, but very rarely in meiosis II. Liu *et al* .,(2012) while working on *Pinellia ternata* observed cytomixis between meiocytes only during diakinesis or in early stages of first division. Chromatin migration does not only happen among cells that are in the same stage, but also cells in different stages of meiosis. Further, the migration of chromatin occurs through the formation of a single strand or multiple strands (Belluci *et al* .,2003; Singhal and Kumar 2008) and that a simultaneous transfer of chromatin from a single PMC to two or more different PMCs has also been recorded (Bhat *et al* .,2006; Singhal and Kumar 2008). The transfer of chromatin is either partial, involving a small part, or complete, involving the entire chromosome complement as a result PMCs with little or no chromatin and PMCs with additional chromatin are observed (Singhal and Kumar 2008). The extra chromatin masses present in the PMCs do not pair with the main chromatin and remain in the cell as a separate mass (Singhal and Kumar 2008, Ranjbar *et al* .,2011). The fate of such additional masses of chromatin is not known, but they probably form micronuclei or micro pollen as suggested by Bhat *et al* .,(2006) and Ranjbar *et al* .,(2011).

The process is more prevalent in genetically, physiologically and biochemically imbalanced plants such as, haploids, aneuploids, hybrids (De Nettancourt and Grant 1964), triploids (Salesses 1970), mutants (Gottschalk 1970), and apomicts (Mantu and Sharma 1983) than their diploid counterparts. While commenting on the prevalence of cytomixis in tetraploid cytotypes of *Ranunculus hirtellus* and absence of such anomaly in diploid cytotypes Kumar and Singhal (2011) attributed it to genetic imbalance in tetraploid cytotypes, high altitude and low temperature stress conditions prevailing in cold deserts. Semyarkhinaand Kuptsou (1974) and Singhal *et al* .,(2007) also inferred in "sugar beet" and "jamun" that polyploid taxa are more prone to cytomixis than their diploid counterparts. However, Singhal and Kumar (2008) while working with *Withania somnifera* got contradictory results. They found that cytomixis was much higher in the diploid as compared to their tetraploid counterparts. In the diploid chromatin transfer was observed to occur during the first and second meiotic divisions compared with tetraploid where it existed only during the first meiotic division. Presence of cytomixis has been observed by Lone and Wafai (2009) in some cultivars of *Prunus avium* (diploid), *Prunus cerasus* (tetraploid) and *P. domestica* (hexaploid), under cultivation in Kashmir, in almost equal frequency.

Causes

Although transfer of chromatin material has been reported in countless species, there are conflicting opinions and explanations regarding the causes of cytomixis. Possible causes suggested earlier include the action of chemical agents such as colchicines (Dwivedi *et al*. 1988), the use of herbicides (Bobak and Herich 1978, Ajay and Sarbhoy 1987, Haroun 1995), pathological conditions (Bobak and Herich 1978, Morisset 1978), physiological changes (Bell 1964, Bahl and Tyagi 1988), mechanical injury (Sarvella 1958), temperature (Narain 1976), the partial or total inhibition of cytokinesis during microsporogenesis (Risueno *et al*. 1969), changes in the biochemical processes that involve microsporogenesis modifying the microenvironment of affected anthers (Koul 1990). Pressure difference (Tarkowska 1965, Morisset 1978) and clumped chromatin bridges during premeiotic anaphase (Mendes and Rijo 1951) are other explanations put forth by some researchers. Many authors suggest that cytomixis is an artifact of fixation (Woodworth 1931; Jacob 1941; Takats 1959; Gottschalk 1970; Ahadi and Sharma 1988), however, Haroun (1995) while working with *Polygonum tomentosum* noticed the phenomenon at an equal frequency in fixed and freshly stained material. Some researchers found that cytomixis could be induced by chemicals like methyl methane sulphonate (Bhat *et al* .,2006), ethyl methane sulphonate (Srivastava and Kumar 2012) and sodium azide (Kumar and Yadav 2012). Bell (1964) while working with *Tauchia nudicaulis* reported that cytomixis is not a regular or constant aspect of meiosis of a species but is, as in most other reported cases, of limited occurrence, as no such phenomenon was observed by him in earlier collections of the species from the same locality. Recent evidence suggests that it is a natural genetically controlled phenomenon influenced by physiological and environmental factors (Gottschalk 1970, Bhagvandoss *et al* .,1973, Brown and Bertke 1974, Omara 1976; Mantu and Sharma 1983; Singhal and Gill 1985, Zheng *et al*. 1987; Chatha and Bir 1988; Bedi 1990; Boldrini *et al* .,2006; Singhal *et al* .,2007; Singhal and Kumar 2008; Ranjbar *et al* .,2011) rather than being due to fortuitous causes such as fixation, mechanical injuries or pathological anomaly etc. Lattoo *et al.,* (2006) in their study on *Chlorophytum cosmosum* suggested that cytomixis is invariably associated with anomalous microsporogenesis and that the genes responsible for aberrant meiosis and cytomixis may be the same. The authors viewed that these genes are operating through signal transduction pathway triggered by the environmental stimuli. Bellucci *et al*. (2003), on the basis of observation in *Medicago sativa* that cytomixis occurs during a definite phase of meiosis (prophase I) and persists in S_1 and F_1 progenies, concluded that cytomixis is under direct genetic control, although physiological factors certainly influence its manifestation but the authors ruled out the effect of environment on this phenomenon. According to Nirmala and Kaul (1994), cytomixis as observed in *Pisum sativum,* is caused by a male-sterile mutant gene and its frequency is altered by environmental factors.

Consequences

Whether a spontaneous or an induced process, cytomixis may have serious genetic consequences, such as the formation of PMCs with anomalous chromosome numbers or binucleated/anucleated PMCs (Gottschalk 1970; Ashraf and Gohil 1994; Dagne 1994; Poggio *et al* .,1997; de Souza and Pagliarini 1997), and of aberrant microspores (triads, pentads, hexads), pollen sterility (Soodan and Wafai 1987), and chromosome stickiness, unorganized and pyknotic chromatin (Puneet *et al* .,2011), interbivalent connections, laggards and chromatin bridges, desynapsis, and late disjunction (Mary 1979; Chauhan 1981; Mary and Suvarnalatha 1981; Singhal and Gill 1985; Patra *et al*. 1986; Singhal and Kumar 2008; Ranjbar *et al* .,2011) and low pollen stainability and poor seed set (Liu *et al* .,2012). In addition to these anomalies Massoud *et al.,* (2011) have reported the formation of coenocytes in early prophase I of *Astragalus cyclophyllos* as a result of cytomixis. The coenocytes formed due to cytomixis lead to the formation of abnormal-sized pollen grains as suggested by Mendes-Bonato *et al.,* (2001). The role of cytomixis in inducing such meiotic irregularities has been reported in various plants such as *Althea rosea* (Mary 1979), *Papaver rhoeas* (Chauhan 1981), *Gossypium* (Mary and Suvarnalatha 1981), *Crotolaria* (Akpabio 1990), *Capsicum* (Falusi 2006), *Meconopsis* (Singhal and Kumar 2008), and *Vicia faba* (Haroun *et al.,* 2004, Bhat *et al.,* 2006). However, these workers are of the opinion that with the advancement of meiosis there is a reduction in the frequency of interbivalent connections.

Significance

Although opinions about the significance of cytomixis are varied and conflicting, most researchers agree that it must have evolutionary significance (Falistocco *et al.,* 1995; Srivastav and Raina 1980; Ghanima and Talaat 2003; Boldrini *et al.,* 2006). But so far no consensus regarding its importance has been developed due to different opinions and explanations. Although some considered it a possible cause of aneuploidy and polyploidy (Bell 1964; Lattoo *et al*. 2006), and even as one of the modes of origin of B chromosomes (Cheng *et al*. 1975). It has also been propounded to promote a 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 (Lattoo *et al.,* 2006). The work of Singhal and Kumar (2008) on *Meconopsis* and works of several other authors (Soodan and Wafai 1987 on almonds; Kumar and Singhal 2011 on *Ranunculus hirtellus*) reveal that cytomixis is directly responsible for abnormal meiotic behavior, development of different sized pollen grains and even for the induction of pollen sterility. Similar findings have been reported in *Coix* (Sapre and Deshpande 1987), *Alopecurus arundinaceus* (Koul 1990), *Polygonum tomentosum* (Haroun 1995), *Hordeum vulgare* (Haroun 1996), *Brassica napus* var. *oleifera* and *Brassica comprestris* var. *oleifera* (Alice and Maria 1997), and *Vicia faba* (Haroun *et al.,* 2004). Inversely, the cytomictic plants of diploid *Dactylis* are reported to have high pollen viability as the cytomixis is thought to be one of the origins of 2n gametes (Falistocco *et al.,* 1995). In *Houttuynia cordata* cytomixis is believed to have produced a range of cytotypes (2n = 24-128) with x = 8,9,12 (Wu *et al .,*2003; Gua *et al .,*2012) because it has been shown to be a potential means to conserve the genetic heterozygosity of gametes (Veilleux 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). Therefore, the relationship between cytomixis and pollen viability varies from species to species (Guan *et al.,* 2012).

References

Ahadi, K.K. and Sharma, A.K. 1981. Cytomixis in Laminaceae. *Cytologia*, 53: 167-174.

Ajay, K.J and Sarbhoy, R.K. 1987. Cytogenetical studies on the effect of some chlorinated pesticides II. Effect on meiotic chromosomes of *Lens* and *Pisum*. *Cytologia* 52: 55-61.

Akpabio, K.E. 1990. Chromosomal interconnections and metaphase 1 clumping in meiosis of four species of *Crotalaria* L. *Nig*. *J.Bot*. 3: 191–195.

Alice, M.S and Maria, S.P. 1997. Cytomixis in *Brassica napus* var.*oleifera* and *Brassica campestris* var. *oleifera* (Brassicaceae). *Cytologia* 62: 25–29.

Arnoldy, W.1900. Beiträge zur Morphologie der Gymnospermen. IV. Was sind die "Keimbläschen" oder "Hofmeisters-Körperchen" in der Eizelle der Abietineen? *Flora* 87: 194-204.

Ashraf, M. and Gohil, R.N. 1994. Cytology of legumes of Kashmir Himalaya V. Cytomixis and chromosome migration in *Astragalus subuliformis* DC. *Nucleus* 37: 119–122.

Bahl, J.R. and Tyagi, B.R. 1988. Cytomixis in pollen mother cells of *Papaver dubium* L. *Cytologia* 53: 771–775.

Basavaiah, D. and Murthy, T.C.S. 1987. Cytomixis in pollen mother cells of *Urochloa panicoides* P. Beauv. (Poaceae). *Cytologia* 52: 69-74.

Bauchan, G.R. 1987. Cytomixis in *Agropyron cristatum. Genome* 29: 765-769.

Bedi, Y.S. 1990. Cytomixis in woody species. *Proc*. *Indian Natl*. *Sci*. *Acad*. (*Plant Sci*.) 100: 233–238.

Bell, C.R. 1964. Cytomixis in *Tauschia nudicaulis* Schlecht (Apiaceae). *Cytologia* 29: 369–398.

Bellucci, M., Roscini, C. and Mariani, A. 2003. Cytomixis in pollen mother cells of *Medicago sativa* L. *J. Hered.* 94: 512-516.

Bhagvandoss, M., Jayaraman, N. and Ramakrishnaa, P. 1973. A preliminary note on cytomixis in cotton. *Madras Agr. J.* 60: 269-270.

Bhat, T.A., Parveen, S. and Khan, A.H. 2006. MMS-induced cytomixis in pollen mother cells of broad bean (*Vicia faba* L.). *Turk*. *J. Bot*. 30: 273–279.

Bione, N.C.P., Pabliarini, M.S. and de Toledo, J.F.F. 2000. Meiotic behaviour of several Brazilian soybean varieties. *Genet. Mol. Biol*. 23: 623-631.

Bobak, M. and Herich, R. 1978. Cytomixis as a manifestation of pathological changes after the application of trifuraline. *Nucleus* 21: 22–26.

Boldrini, K.R., Pagliarini, M.S. and Valle, C.B. 2006. Cell fusion and cytomixis during microsporogenesis in *Brachiaria humidicola* (Poaceae). *South Afr. J. Bot.* 72: 478-481.

Brown, W.V. and Bertke, E.M. 1974. *Textbook of cytology* 2nd edition (Saint Louis: C V Mosby).

Chatha, G.S. and Bir, S.S. 1988. Cytomixis in some Indian woody species. *Nucleus* 31: 8-13.

Chauhan, A. K. S. 1981. Cytomixis in *Papaver rhoeas*; Perspectives in cytology and genetics*;* in *Proceedings of the third All India Congress of Cytology and Genetics* (eds) G K Manna and U Sinha (New Delhi: Hindasia Publishers) pp 309–312.

Cheng, K.C., Nieh, H.W., Yang, C.L., Wang, I.M., Chou, I.S., and Chen, J.S. 1975. Light and electron microscopial observations on cytomixis and the study of its relation to evolution; *Acta. Bot.Sin.* 17 60–69

Cheng, K.C., Nie, X.W., Wang, Y.X. and Yang, Q.L. 1980. The relation between cytomixis and variation of chromosome numbers in pollen mother cells of rye (*Secale cereals* L.). *Acta Bot. Sin.* 22: 216-220.

Cheng, K.C., Quiglan, Y. and Yongsen, Z. 1987. The relationship between cytomixis, chromosome mutation and karyotype evolution in Lily. *Caryologia* 40: 243-259.

Consolaro, M.E.L. and Pagliarini, M.S. 1995 Cytomixis in pollen mother cells of *Centella asiatica* L. *Nucleus* 38: 80–85.

Cooper, D.D. 1952. The transfer of deoxyribose nucleic acid from the tapetum to the microsporocytes at the onset of meiosis. *Cytologia* 86: 271–274.

Dagne, K. 1994. Meiosis in interspecific hybrids and genomic interrelationships in *Guizotia* Cass. (Compositae). *Hereditas* 121: 119–129.

Datta, A.K., Mukherjee, M. and Iqbal, M. 2005. Persistent cytomixis in *Occimum basilicum* L. (Lamiaceae) and *Withania somnifera* (L.) Dun (Solanaceae). *Cytologia* 70 309–313.

de Nettancourt, D. and Grant, W.F. 1964. Lacytogénétiquede *Lotus* (Leguminosae) III. Un cas de cytomixie dans un hybride interspécifi que. *Cytologia* 29 191–195.

de Souza, A. and Pagliarini, M. 1997. Cytomixis in *Brassica napus* var. *oleifera* and *Brassica campestris* var. *oleifera* (Brassicaceae). *Cytologia* 62 25–29.

Dwivedi, N.K., Ksikdar, A.K., Jolly, M.S., Susheelamma, B.N. and Suryanarayana, N. 1988. Induction of tetraploidy in colchicine-induced mutant of mulberry. I. Morphological and cytological studies in cultivar Kanva *2*. *Indian J. Genet*. 48: 305-311.

Falistocco, E., Tosti, N. and Falcinelli, M. 1995. Cytomixis in pollen mother cells of diploid *Dactylis*, one of the origins of 2n gametes. *J. Hered.* 86: 448-453.

Falusi, O.A. 2006. Interchromosomal connections and metaphase 1 clumping in meiosis of two *Capsicum* Linn. species in Nigeria. *Afr. J. Biotechnol*. 5: 2066–2068.

Gates, R.R. 1911. Pollen formation in *Oenothra gigas*. *Ann. Bot.* 25 909–940.

Ghaffari, G.M. 2006. Occurrence of diploid and polyploidy microspores in *Sorghum bicolor* (Poaceae) is the result of cytomixis. *Afr. J. Biotechnol.* 5: 1450-1453.

Ghanima, A.M. and Talaat, A.A. 2003. Cytomixis and its possible evolutionary role in a Kuwaiti population of *Diplotaxis harra* (Brassicaceae). *Botanical Journal of the Linnean Society*, 143: 169-175.

Gottschalk, W. 1970. Chromosome and nucleus migration during microsporogenesis of *Pisum satium*. *Nucleus* 13: 1–9.

Guochang, Z., Qinglan, Y. and Yongren, Z. 1987. The relationship between cytomixis, chromosome mutation and karyotype evolution in Lily. *Caryologia* 40: 243-259.

Guzicka, M. and Wozny, A. 2005. Cytomixis in shoot apex of Norway spruce [*Picea abies* (L.) Karst.]. *Trees* 18: 722–724.

Guan, J.Z., Wang, J.J., Cheng, Z.H. and Li, Z.Y. 2012. Cytomixis and meiotic abnormalities during microsporogenesis are responsible for male sterility and chromosome variations in *Houttuynia cordata*. *Genet. Mol. Res.* 11(1): 121-130.

Haroun, S.A.1995. Cytomixis in pollen mother cells of *Polygonum tomentosum* Schrank. *Cytologia* 60: 257-260.

Haroun, S.A. 1996. Induced cytomixis and male sterility in pollen mother cells of *Hordeum vulgare* L. *Delta J. Sci.* 20: 172-183.

Haroun, S.A., Al Shehri, A.M. and Al Wadie, H.M. 2004. Cytomixis in the microsporogenesis of *Vicia faba* L. (Fabaceae). *Cytologia* 69: 7-11.

Heslop-Harrison, J. 1966. Cytoplasmic connexions between angiosperm meiocytes. *Ann. Bot*. 30 221–234.

Jacob, K.T. 1941. Certain abnormalities in the root tips of cotton. *Curr. Sci.* 10 174–175.

Kornicke, M. 1901. Über Ortsveränderung von Zellkarnern S B Niederhein. *Ges. Nat. Heilk. Bonn.* 14-25.

Kostritsyna, T.V. and Soldatov, I.V. 1991. Cytomixis in the shoot apical meristem of hybrids of *Prunus domestica* L. *Persica vulgaris* Mill. *Genetika*,27: 1790-1794.

Koul, K.K. 1990. Cytomixis in pollen mother cells of *Alopecurus arundinaceus* Poir. *Cytologia* 55: 169-173.

Kumar, P. and Singhal, V.K. 2011. Male meiosis, morphometric analysis and distribution pattern of 2x and 4x cytotypes of *Ranunculus hirtellus* Royle, 1834 (Ranunculaceae) from the cold regions of northwest Himalayas (India). *Comp. Cytogen*. 5: 143-161.

Kumar, P., Singhal, V.K., Kaur, D. and Kaur, S. 2010. Cytomixis and associated meiotic abnormalities affecting pollen fertility in *Clematis orientalis*. *Biologia Plantarum* 54: 181-184.

Kumar, G. and Yadav, R.S. 2012. Induction of cytomixis affects microsporogenesis in *Sesamum indicum* L. (Pedaliaceae). *Russian Jr. Dev. Biol*. 43: 209-214.

Kundu, A.K. and Sharma, A.K. 1988. Cytomixis in Lamiaceae. *Cytologia* 53: 469-474.

Kwiatkowska, M., Poplónska, K. and Wojtczak, A. 2003. *Chara tomentosa* antheridial plasmodesmata at various stages of spermatogenesis. *Biologia Plantarum* 46: 233-238.

Lattoo, S.K., Khan, S., Bamotra, S. and Dhar, A.K. 2006. Cytomixis impairs meiosis and influences reproductive success in *Chlorophytum comosum* (Thunb.) Jacq. - an additional strategy and possible implications. *J. Biosci.* 31: 629-637.

Levan, A. 1941. Syncyte formation in the pollen mother cells of haploid *Pheleum pratense*. *Hereditas* 27: 243-252.

Li, X.F., Liu, S.B., Gao, J.R., Lu, W.H., et al. 2005. Abnormal pollen development of bread wheat - *Leymus mollis* partial amphiploid. *Euphytica* 144: 247-253.

Li, X.F., Song, Z.Q., Feng, D.S. and Wang, H.G. 2009. Cytomixis in *Thinopyrum intermedium*, *Thinopyrum ponticum* and its hybrids with wheat. *Cereal Res. Commun.* 37: 353-361.

Li, Z., Liu, H.L. and Luo, P. 1995. Production and cytogenetics of intergeneric hybrids between *Brassica napus* and *Orychophragmus violaceus*. *Theor. Appl. Genet.* 91: 131-136.

Linnert, G. 1955. Cytologische Grundlagen fur sterilitatscheinung en in der Gattung *Salvia. Der Zuchter.* 25: 237-241.

Liu, Y., Hui, R.K., Deng, R.N., Wang, J.J., et al. 2012. Abnormal male meiosis causes pollen sterility in medicinal polyploidy plant *Pinellia ternate*. *Genet. Mol. Res.* 11: (in press).

Lone, F.A. and Wafai, B.A. 2009. Chromsome conspectus and cytogenetic appraisal of some commercial cultivars of cherry (*Prunus avium* L., *P. cerasus* L.) and plum (*P. domestica* L.) using a partially modified staining technique. *Phytomorphology* 59: 29-34.

Maheshwari, P. 1950. An introduction to the embryology of angiosperms. McGraw-Hill Book Co. Inc., New York, 453 pp.

Maity, S. and Datta, A.K. 2009. Meiosis in nine species of jute (*Corchorus*). *Indian J. Sci. Tech.* 2: 27-29.

Malallah, G.A. and Attia, T.A. 2003. Cytomixis and its possible evolutionary role in a Kuwaiti population of *Diplotaxis harra* (Brassicaceae). *Bot. J. Linn. Soc.* 143: 169-175.

Mantu, D.E. and Sharma, A.K. 1983. Cytomixis in pollen mother cells of an apomictic ornamental *Ervatamia divaricata* (Linn.) Alston. *Cytologia* 48: 201-207.

Mary, T.N. 1979. Cytomixis in *Althea rosea* L. *Indian J. Bot*. 2: 80–82.

Mary, T.N. and Suvarnalatha, B. 1981. Cytomixis and deviation of chromosome numbers in pollen mother cells of *Gossypium* species; *J. Indian Bot. Soc*. 60: 74.

Mendes, E.J. and Rijo, L. 1951. A new interpretation for cytomixis. *Portug. Acta. Biol*. A-3: 211-288.

Miehe, H. 1901. Ueber die Wanderungen des pflanzlichen Zellkernes. *Flora* 88: 105-142.

Morisset, P. 1978. Cytomixis in pollen mother cells of *Ononis* (Leguminosae). *Can. J. Genet. Cytol*. 20: 383.

Mursalimov, S. R., Baiborodin, S. I., Sidrochuk, Yu. V., Shumny, V. K. and Deineko, E. V. 2010. Characteristics of the cytomictic channel formation in *Nicotiana tabacum* L. pollen mother cells. *Cytol. Genet.* 44: 14-18.

Mursalimov, S. R. and Deineko, E. V. 2011. An ultrastructural study of cytomixis in tobacco pollen mother cells. *Protoplasma* 248: 717-724.

Narain, P. 1976. Cytomixis in pollen mother cells of *Hemerocallis* Linn. *Curr. Sci*. 48 996–998.

Nirmala, A. and Rao, P.N. 1996. Genesis of chromosome numerical mosaicism in higher plants. *Nucleus* 39: 151-175.

Nirmala, C. and Kaul, M.L.H. 1994. Male sterility in pea. VI. Gene action duplicity. *Cytologia* 59: 195-201.

Oginuma, K., Sato, H., Kono, Y., Chen, S., *et al.* 2007. Intraspecific polyploidy of *Houttuynia cordata* and evolution of chromosome number in the Saururaceae. *Chromosome Bot.* 2: 87-91.

Omara, M.K. 1976. Cytomixis in *Lolium perenne*. *Chromosoma* 55: 267-271.

Patra, N.K., Chauhan, S.P. and Srivastava, H.K. 1986. Syncites with premeiotic mitotic and cytomictic comportment in opium poppy *(Papaver somniferum L.)*. *Indian J. Genet*. 47: 49-54.

Peng, Z.S., Yang, J. and Zheng, G.C. 2003. Cytomixis in pollen mother cells of new synthetic hexaploid amphidiploid *(Aegilops tauschii, Triticum turgidum*). *Cytologia* 68: 335-340.

Poggio, L., Rosoto, M., Mazoti, L.B. and Naranjo, C.A. 1997. Variable meiotic behavior among plants of an alloplasmic line of maize. *Cytologia* 62: 271-274.

Premchandran, M.N., Sachan, J.K.S. and Sarkar, K.R. 1988. Cytomixis in a Maize trisomic. *Curr. Sci.* 57: 681-682.

Puneet, K., Singhal, V.K., Kumar, R.P., Shubhpreet, K. and Kaur, D. 2011. Cytology of *Ranunculus laetus* Wall. ex Royle from cold desert regions and adjoining hills of North-west Himalayas (India). *Caryologia* 64: 25-32.

Ranjbar, M., Karamian, R. and Nouri, S. 2011. Impact of cytomixis on meiosis in *Astragalus cyclophyllos* Beck (Fabaceae) from Iran. *Caryologia* 64(3): 256-264.

Ressayre, A., Mignota, A., Siljak-Yakovlev, S. and Raquin, C. 2003. Post meiotic cytokinesis and pollen aperture number determination in eudicots: Effect of the cleavage wall number. *Protoplasma* 221: 257-268.

Risueño, M.C., Giménez-Martin, G., López-Sáez, J.F., R-Garcia, M.I. 1969. Connexions between meiocytes in plants. *Cytologia*. 34:262-272.

Saggoo, M.I.S. and Bir, S.S. 1983. Cytomixis in some members of Acanthaceae and Labiateae. *Jr. Cyto. Genet*. 18: 92-99.

Salesses, G. 1970. Sur le phénomène de cytomixie chez des hybrides triploïdes de prunier. Conséquences génétiques possibles. *Ann Amélior Plant*. 20:383-388.

Sapre, A.B. and Deshpande, D.S. 1987. A change in chromosome number due to cytomixis in an interspecific hybrid of *Coix* L. *Cytologia* 52: 167-174.

Sarvella, P. 1958. Cytomixis and loss of chromosomes in meiotic and somatic cells of *Gossypium*. *Cytologia* 23: 14-24.

Semyarkhina, S.Y.A. and Kuptsou, M.S. 1974. Cytomixis in various forms of sugarbeet; *Vests I ANBSSE Ser. Biyal*. 4 43 - 47.

Sen, O. and Bhattacharya, S. 1988. Cytomixis in *Vigna glabrescens* TTK (Wild.). *Cytologia* 53: 437-440.

Shamina, N.V., Dorogova, N.V., Zagorskaya, A.A., Deineko, E.V. and Shumnyi, V.K. 2000. Disturbances of male meiosis in tobacco transgenic line res 91. *Tsitologiya*, 42: 1173-1178.

Sheidai, M. and Bagheri-Sabestarei, E.S. 2007. Cytomixis and unreduced pollen in some *Festuca* L. species of Iran. *Caryologia* 60(4): 364-371.

Sheidai, M. 2008. Cytogenetic distinctiveness of sixty-six tetraploid cotton (*Gossypium hirsutum* L.) cultivars based on meiotic data. *Acta Bot. Croat.* 67: 209-220.

Shibata, K. and Miyake, H. 1908. Ueber Parthenogenesis bei *Houttuynia cordata*. *Bot. Mag. Tokyo* 22: 141-144.

Shnaider, T. 1975. About the issue of cytomixis in plants. *Izv. An. Est. SSR*, 24: 199-209.

Singhal, V.K. and Gill, B. 1985. Cytomixis in some woody species. *Biologica* 1: 168–175.

Singhal, V.K. and Kumar, P. 2008a. Impact of cytomixis on meiosis, pollen viability and pollen size in wild populations of Himalayan poppy (*Meconopsis aculeata* Royle). *J. Biosci.* 33: 371-380.

Singhal, V.K. and Kumar, P. 2008b. Cytomixis during microsporogenesis in the diploid and tetraploid cytotypes of *Withania somnifera* (L.) Dunal, 1852 (Solanaceae). *Comp. Cytogenet.* 2: 85-92.

Singhal, V.K. and Kumar, P. 2010. Variable sized pollen grains due to impaired male meiosis in the cold desert plants of North West Himalayas (India). In: Benjamin JK (Ed) Pollen: structure, types and effects. New York, USA, Nova Science Publishers, 101-126.

Singhal, V.K., Gill, B.S. and Dhaliwal, R.S. 2007. Status of chromosomal diversity in the hardwood tree species of Punjab State. *J. Cytol. Genet.* 8: 67-83.

Song, Z.Q. and Li, X.F. 2009. Cytomixis in pollen mother cells of *Salvia miltiorrhiza*. *Caryologia* 62(3): 213-219.

Souza, A.M. and Pagliarini, M.S. 1997. Cytomixis in *Brassica napus* var. *oleifera* and *Brassica campestris* var. *oleifera* (Brassicaceae). *Cytologia* 62: 25-29.

Srivastav, P.K. and Raina, S.N. 1980. Cytomixis in *Clitoria termatea* L. var. Pleniflora Fantz. f. Pleniflora. *Curr. Sci.* 49: 824–835.

Takats, S.T. 1959. Chromatin extrusion and DNA transfer during microsporogenesis. *Chromosoma* 10: 430–453.

Tarkowska, J. 1960. Cytomixis in the epidermis of scales and leaves and in meristems of root apex of *Allium cepa* L. *Acta Soc. Bot. Pol.* 29: 149–168.

Tarkowska, J. 1965. Experimental analysis of the mechanism of cytomixis I. Cytomixis in vegetative tissues. *Acta Soc. Bot. Pol.* 34: 27–44.

Veilleux, R. 1985. Diploid and polyploid gametes in crop plants: mechanisms of formation and utilization in plant breeding. *Plant Breed. Rev.* 3: 253-288.

Ventela, S., Toppari, J. and Parvinen, M. 2003. Intercellular organelle traffic through cytoplasmic bridges in early spermatids of the rat: mechanisms of haploid gene product sharing. *Mol. Biol. Cell* 14: 2768-2780.

Wang, R.R.C. 1988. Coenocytism, ameiosis, and chromosome diminution in intergeneric hybrids in perennial Triticeae. *Genome* 30: 766-775.

Wang, X. Y. Guo, G. Q., Nie, X. W. and Zheng G. C. 1998. Cytochemical localization of cellulose activity in pollen mother cells of David lily during meiotic prophase I and its relation to secondary formation of plasmodesmata. *Protoplasma* 204: 128-138.

Wang, X. Y. Yu, C. H. Li, X., Wang, C. Y. and Zheng, G. C. 2004. Ultrastructural aspects and possible origin of cytomictic channels providing intercellular connection in vegetative tissues of anthers. *Russ. J. Plant Physiol.* 51: 110-120.

Woodworth, R.H. 1931. Cytomixis. *Jour. Arnold Arb.* 12: 23-25.

Wu, W., Zheng, Y.L., Yang, R.W., Chen, L., et al. 2003. Variation of the chromosome number and cytomixis of *Houttuynia cordata* from China. *J. Syst. Evol.* 41: 245-257.

Yu, C. H., Guo, G. Q., Nie, X. W. and Zheng, G. C. 2004. Cytochemical localization of pectinase activity in pollen mother cells of tobacco during meiotic prophase I and its relation to to the formation of secondary plasmodesmata and cytomictic channels. *Acta Bot. Sin.* 46: 1443-1453.

Zhang, W. C., Yan, W. M. and Lou, C. H. 1985. Mechanism of intercellular movement of protoplasm in wheat nucellus. *Sci. China* 28: 1175-1183.

Zheng, G.C., Yang, Q.L., and Zheng, Y.R. 1987. The relationship between chromosome mutation and karyotype evolution in Lily. *Caryologia* 40: 243-259.

Zhou, S.Q. 2003. Viewing the difference between diploid and polyploid in the light of the upland cotton aneuploid. *Hereditas*, 138: 65-72.

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