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The Mechanism of the Origination of Auto-allopolyploidy and Aneuploidy in Higher Plants Based on the Cases of *Iris* and *Triticeae*.

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ABSTRACT

Cytomixis is a natural process of chromatin exchange among cells. In *Iris confusa* and *I. japonica*, the synchronized cytomixis takes place between PMC's during a stage just before meiosis. This process produces euploid and aneuploid offspring. The chromosome number of a fertile diploid plant is 30 (2n). Most accessions of *I. confusa* and *I. japonica* are sterile aneuploids. The chromosome numbers are varied, ranging 2n = 28 to 60. In Triticeae cytomixis plays an important role in spontaneous chromosome doubling or redoubling, resulting in the origin of auto-allopolyploidy and aneuploidy. We have obtained amphidiploid plants by spontaneous chromosome doubling. These plants indicate indirectly that cytomixis takes place in the macrosporocytes, giving rise to high level auto-allopolyploid Triticeae species.

INTRODUCTION

The phenomenon of cytomixis was discovered by Arnol'de in 1900. Gates (1911) studied this phenomenon in *Oenothera* and designated the term "cytomixis" to describe chromatin material migrating through the plasmodesmata into neighboring cells. The question of whether cytomixis is an abnormal artificial behavior or a natural behavior of chromatin material has long been debated. Lou et *al.* (1962) observed cytomixis in living cells, Cheng et *al.* (1956) observed cytomixis using electronmicroscopy, and Yen et *al.* (1993) observed cytomixis taking place between two untreated fresh pollen mother cells of the *Roegneria ciliaris x Psathryostachys huashanica* F_1 hybrid under phase contrast microscopy. These workers proved that cytomixis is a natural process where chromatin exchange occurs among cells. Yen et *al.* (1993) and Sun et *al.* (1993) reported that intergeneric hybrids of Triticeae had some special cell structure formations, including the conjugation opening and conjugation tube besides the plasmodesma. The resting stage nuclei, chromatin masses, chromonemata, or chromosomes can migrate through these structure into immediate neighboring cells before, during or after meiosis in the hybrids of *Roegneria ciliaris x Psathyrostachys huashanica* and *Triticum aestivum x Psathyrostachys huashanica*. Multipolar division and coenocytes also occurred in these hybrids. Yen et *al.* (1992) pointed out multipolar division might be caused by the multipolar zones of synchronized nuclei in the coenocyte. We speculate that this kind of PMCs can not form normal tetrads and degenerates. Conversely, synchronized nuclei in some PMCs fuse together first, then it is followed by normal bipolar division in a few PMCs, where the normal tetrad might be produced. If this is true, the spontaneous chromosome doubling or redoubling might have occurred. If this process takes place in the macrosporocyte, a fertile egg cell and synergid nuclei should be produced. Fertile pollen grains are produced by the same spontaneous chromosome doubling or redoubling in the microsporocyte of the same floret. There is a chance that chromosome doubled or redoubled egg cells could develop a plant by parthenocarpy. The present paper reports on the origin of allopolyploidy, euploidy, and aneuploidy in *Iris* and Triticeae taxa.

MATERIALS AND METHODS

The accessions of *Iris confusa* Sealy and *I. japonica* Thunberg collected in China and Japan are shown in Table 1. The hybrids of Triticeae are shown in Table 2. Root tips were collected at 11 o'clock in the morning, and keep in the refrigerator at 4° C overnight, then fixed in Carnoy's fluid for 48 hours. Root tips were then transferred to 70% alcohol and stored until analyzed. PMC's for cytology were collected and treated in the same way as the root tips. Slides were prepared for cytological studies by means of

Table I: Observation on evansia irises of Far East, Asia.

species	accession number	locality	chromosome number	fertility
Iris confusa	1	Baimaqiao, Rongjing, Sichuan, China	42	-
	2	Siping, Rongjing, Sichuan, China	30	+
	3	Siping, Rongjing, Sichuan, China	34	-
	4	Jizigang, Yaan, Sichuan, China	28	-
	5	Juejiping, Tianquan, Sichuan, China	30	+
	6	Juejiping, Tianquan, Sichuan, China	36	-
	7	Xingou, Tianquan, Sichuan, China	30	+
	8	Xingou, Tianquan, Sichuan, China	34	-
	9	Dechang, Sichuan, China	28	-
	10	Kunming, Yunnan, China	30	-
Iris japonica	11	Kyoto, Japan	54	-
	12	Kyoto, Japan	36	-
	13	Kyoto, Japan	56	-
	14	Okayama, Japan	34	-
	15	Yokahama, Japan	28	-
	16	Laobanshan, Yaan, Sichuan, China	60	-
	17	Jinjiguan, Yaan, Sichuan, China	36	-
	18	Dujiangyan, Sichuan, China	32	-
	19	Jiuionggou, Chongqing, Sichuan, China	42	-
	20	Neijiang, Sichuan, China	38	-
	21	Zigong, Sichuan, China	46	-
	22	Wanxian, Sichuan, China	36	-
	23	Dali, Yunnan, China	30	+
	24	Changsha, Hunan, China	34	-
	25	Nanjing, Jiangsu, China	52	-
	26	Hangzhou, Zhejiang, China	42	-

Table 2: Observation on somatic chromosome number of the F_1 hybrid of *Elymus caninus* x *Hordeum vulgare*.

F_1 hybrid	number of chromosomes per cell												
	30	40	41	42	43	44	45	56	47	48	49	50	51
1	-	1	-	4	-	-	-	-	-	-	-	-	-
2	-	-	6	3	-	-	-	-	-	-	-	-	-
3	-	2	1	9	-	-	-	-	-	-	-	-	-
4	-	-	-	1	-	-	-	-	-	-	8	-	1
5	1	-	-	6	-	1	1	-	-	-	-	-	-

acetocarmine smear. Before squashing the root tips, the intercellular substance between the cells is dissolved by 1N hydrochloric acid solution, in a 60° C incubator for 5 minutes.

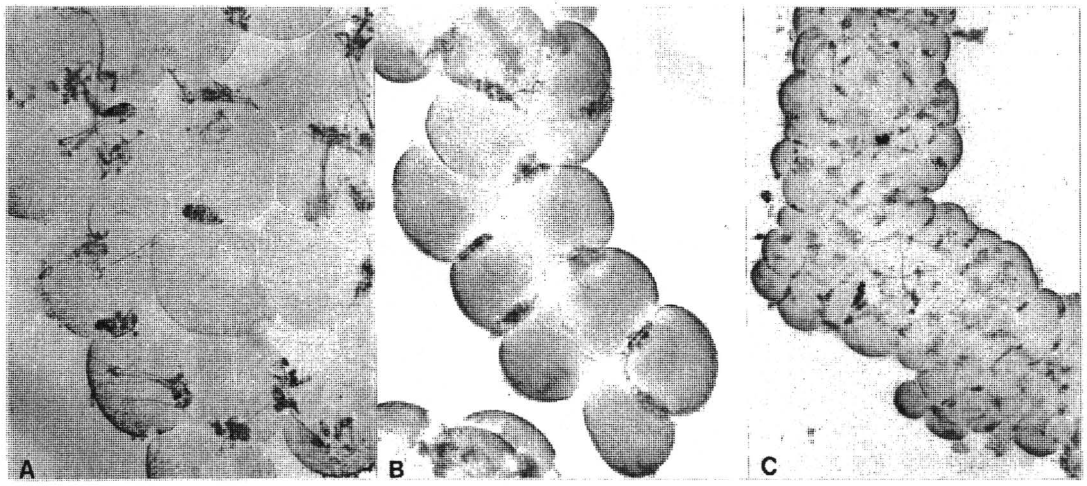
RESULTS AND DISCUSSION

Iris japonica Thunberg and *I. confusa* Sealy

Iris japonica is native to China and Japan. *Iris confusa* has an erect cane-like stem which is different from *I. japonica*. It is a native plant of southwest China, where it inhabits high mountain meadows. All accessions of *I japonica* observed were sterile, with only a few abnormal capsules found. All the accessions were studied cytologically. They are all aneuploids except one autotetraploid accession found from Yaan (Table I). All plants have a cytomixis stage just before meiosis. The synchronized cytomixis takes place among PMCs evenly (Fig. 1:A. B. C.). Sinoto (1921) and Yasui (1939) observed cytomixis in *I. japonica*. Yasui believed that *I. japonica* was a triploid, she followed Kazo (1929), and Simonet (1934). Kihara (1982) also agreed with them. They did not point out the universality of cytomixis in this species and did not point out how cytomixis caused the chromosome number to vary among different accessions. We observed cytomixis in microsporocytes. The normal pollen grains accompanied many abnormal and functionless pollens in the same anther lobe. However, the diploid plants produced normal capsules and bore normal seeds. Most seedlings from these seeds are aneuploids. In natural vegetation, more than 90 percent of accessions were aneuploids. Our results of cytological observations are shown in Table I. Between *I. confusa* and *I. japonica*, there were intermediate forms observed in morphology and cytology. Diploid *I. confusa* has a small geographical distribution on the high mountain meadows of Sichuan, Yunan and Guangxi Provinces. The distribution of the aneuploid *I. japonica* is much larger. It occupies all the subtropic regions of the Far East, from the Himalaya valley to Japan. An accession of *I. japonica* from Dujiangyan City was found to have two normal and five abnormal seeds in 0.35% of its capsules. The normal seeds proved to be aneuploids with chromososome number of 36 and 40. Cytomixis plays an important role in chromosomal aberrations, which is bound to create cytological and morphological diversity in these evansia irises. Natural selection seeks out the adaptive accessions.

Triticeae

Within the Triticeae taxa there exists a high level of auto-allopolyploids which have multiple genomes, such as *Leymus angustus* (Trin.) Pilger. Chromosome numbers of 2n=28, 42, 56, 70 and 84 have been reported for this species (Bowden, 1957; Sun *et al.*, 1990). In the hexaploid plant of *L. angustus*, the genomes must be unevenly doubled, although the origin of these various cytotypes could be quite different, they could be accomplished much easier through cytomixis of complete nuclei which fuse together. This mechanism was suggested earlier (Yen *et al.*, 1993; Sun *et al.*, 1993). Recently, we obtained F_2 hybrid plants, which were derived from a cross of *Elymus caninus* (L.) L. x *Hordeum vulgare* L. The F_1 hybrid is a normal amphihaploid which has 21 chromosomes comprised of the S, H and I genomes. Cytomixis took place in PMCs (Fig. 2B. C.). Fig. 2A shows that a PMC has an outgrowth. We can see a new bud developing again on the old one. As a result of cytomixis, chromosome numbers varied among PMCs. Fig. 2D shows that only 4 chromosomes are present in a small PMC. Fig. 2E, shows 14 chromosomes in the PMC, and Fig. 2F shows that it has 19 chromosomes slightly less than the normal cell. Fig. 2G, shows a small pollen grain which has no chromatin material (arrowed). Pollen has more chromatin bodies than usual. Every year, this plant bears some seeds (30%). Most of these seeds are shrunken and have no viabity. The normal seeds and seedlings had mainly 42 chromosomes (Table 2). The endosperm of these seeds were well-developed, but most of the seeds had no embryo. F_1 and F_2 plants had dehiscent anthers, which contained some viable pollen grains when stained with iodine. The F_2 plant looked like an amphidiploid which had 42 chromosomes. If the F_2 is an amphidiploid and breeds true, its origin is either by nondisjunction division of anaphase I followed by normal fertilization or by cytomixis followed by parthenogenetic reproduction. Fortunately, this perennial hybrid produces seed every year. Most of the F_2 plants proved to be euploids with 42 somatic chromosomes (Fig. 2H), along with fewer aneuploids formed. Some F_2 plants, had many univalents (Fig. 3A) and multivalents in their PMCs at MI (Fig. 3B). This kind of F_2 euploid is frequently produced (more than 0.3%). Thus, *Elymus caninus x Hordeum vulgare* is a good example to demonstrate that cytomixis plays an important role in chromosome multiplication, aberration and production of euploid and aneuploid offspring. Sarvella (1958), Bell (1964), Marechal (1963), Salesses (1970), and Kundu *et al.* (1988) noted that cytomixis contributed to the production of aneuploidy gametes, but they did not discuss the chance for amphipolyploid to be originated through the process of cytomixis. Cheng *et al.* (1975) pointed out that cytomixis could be caused by chromosomal aberration and chromosome multiplication or diminution. Kundu and Sharma (1988) wrote, "however, this is of limited significance because of the absence of viable seed setting". But, our observation of *Iris confusa, Iris japonica* and the hybrids of *Triticum aestivum* L. cv. 'Xiaoyuermai' x *Secale cereal* L. winter rye (Luo, Yen and Yang, 1992) and *Elymus caninus* L. x *Hordeum vulgare* L. showed that they did bear good viable seeds in nature. These cases suggested the evolutionary significance of cytomixis.



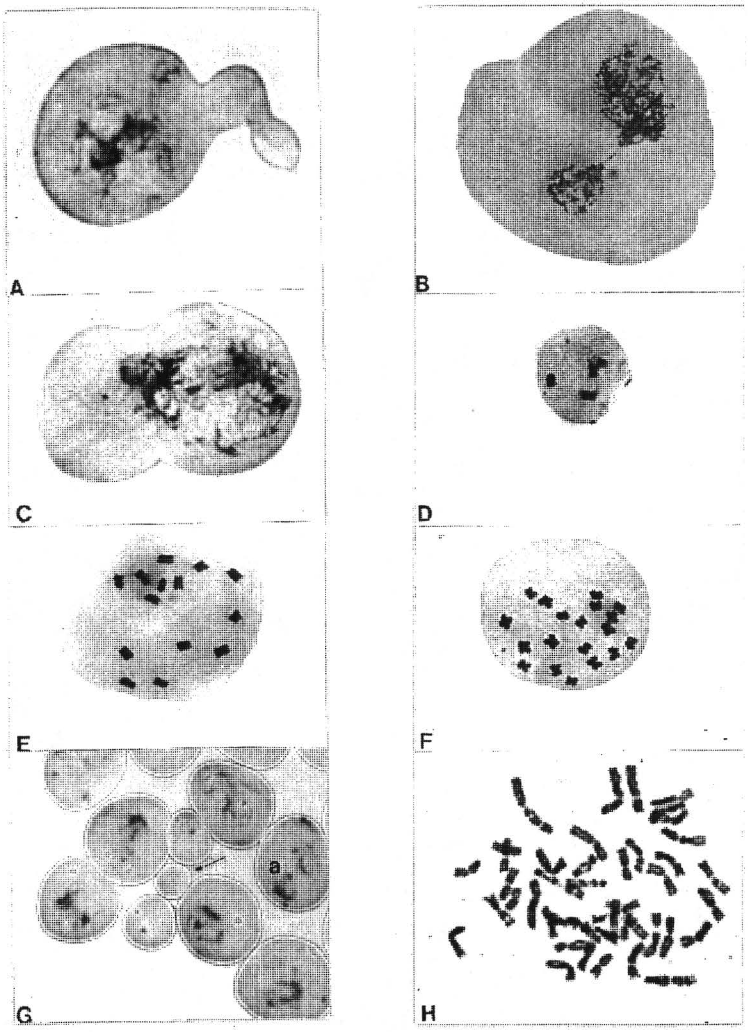


Figure 1. The cytomixis stage of PMCs in *Iris japonica* Thunberb. (A). *I. japonica* from Kyoto, Japan. (B). *I. japonica* from Dujiangyan City, Sichuan, China. (C). *I. japonica* from Nanjing, China.

Figure 2. Cytological observation on the hybrid of *Elymus caninus* (L.) *L. x Hordeum vulgare* L. (A). A PMC of hybrid shows secondary budding (conjugation tube). (B). Cytomixis takes place through plasmodesma between two PMCs. (C). Cytomixis takes place through a big conjugation opening it seems to be cell fusion. (D). A small PMC of F_1 cybrid has 4 chromosomes. (E). A PMC of F_1 hybrid has 14 chromosomes. (F). a PMC of F_1 hybrid has 19 chromosomes. (G). A group of young pollen grains have diferent amount of chromatin materials. A small one has no chromatin material (arrowed). Pollen grain a, has a large amount of chromatin materials much more than usual. (H). A somatic cell has 42 chromosomes which was observed in the root tip of F_2 hybrid plant.

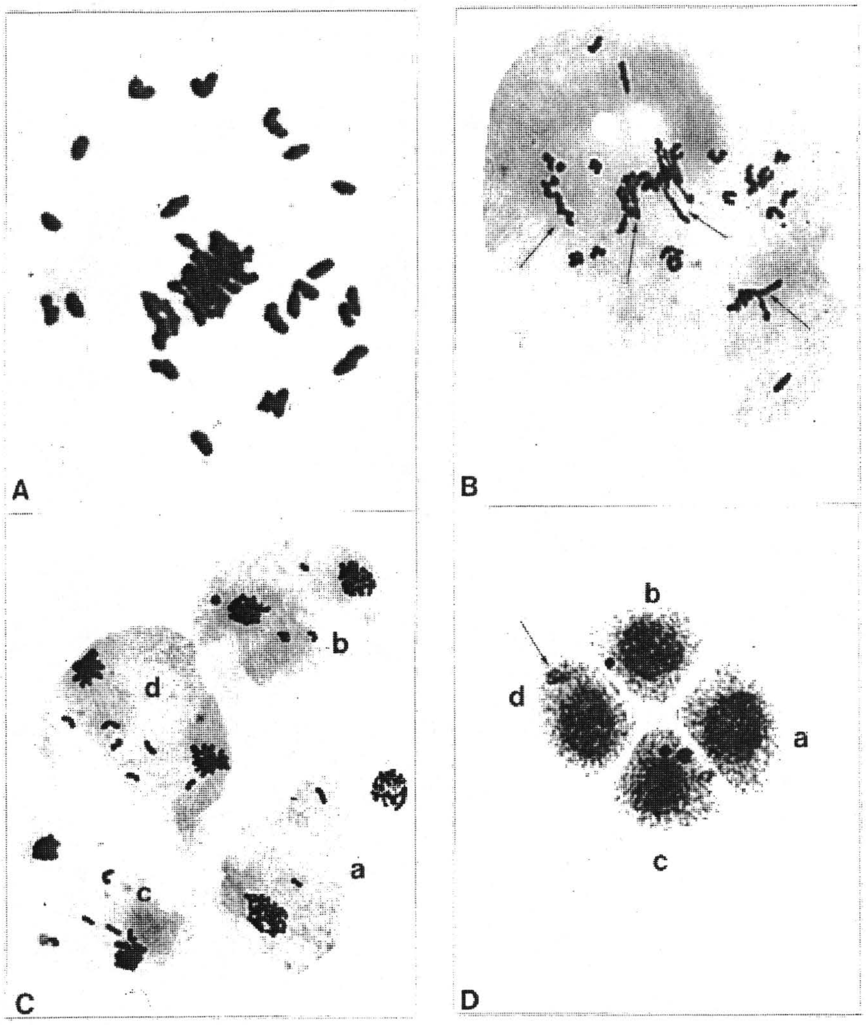


Figure 3. Meiotic behavior of F_2 hybrid of *Elymus caninus* (L.) *L. x Hordeum vulgare* L. (A). A PMC at MI, it has 26 univalents. (B). A PMC at MI, it has multivalents (arrowed), they are separated in the cell. (C). The PMCs at anaphase I show different amount of lagging chromosomes. The cell a, has one pair; cell b and c have two pairs and cell d, has three pairs. (D). The tetrad of F_2 hybrid, a is normal cell, b has one micronucleous, c has two micronuclei and d has a small group of extra late concentrated chromonemata.

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