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## Meiotic Irregularities in Interspecific Crosses Within Edible Alliums

Agnieszka Kielkowska  
University of Agriculture in Krakow,  
Poland

### 1. Introduction

The economically most important edible alliums are onion (*Allium cepa* L.), Japanese bunching onion (*A. fistulosum* L.), leek (*A. ampeloprasum* spp. *porrum* L.), and garlic (*A. sativum* L.). These species are mostly used as condiments, but also have medicinal value (Keusgen, 2002). Onion and garlic are grown worldwide, leek is predominantly grown in Europe, and Japanese bunching onion in East Asia (Kik, 2002). Hybridization of certain genotypes, increasing genetic variability, is the predominant breeding method used for onion, leek and Japanese bunching onion. Garlic breeding is accelerated by clonal selection (Etoh & Simon, 2002).

Interspecific hybridization within the genus *Allium* has a long history, and has been an important tool for increasing genetic variation. It was used for creating new varieties as well as for transferring agronomically useful traits from wild relatives (Brewster, 1994; Kielkowska & Adamus, 2010; Kik, 2002). However, techniques of sexual hybridization very often have been accompanied by several difficult to overcome pre- and post-fertilization barriers, resulting in a limited number of obtained F1 hybrids, as well as difficulties with back-crossing. Meiotic studies of hybrids and back-cross progenies within *Allium* revealed interesting information about the nature of alien introgression and improved our understanding of “foreign” chromatin transmission into cultivated species (Kik, 2002; van Heusden et al., 2000).

The purpose of the present paper is to give a concise review of meiosis in pollen mother cells (PMC) and pollen fertility in *Allium cepa* and its crosses with *A. fistulosum*, *A. ampeloprasum*, and *A. sativum*.

### 2. Chromosome number and meiosis

Most alliums are diploids ( $2n=2x$ ), with basic chromosome numbers  $x=7$  (North America),  $x=8$  (Eurasia and Mediterranean basin), or  $x=9$  (Eurasia) (Havey, 2002; Ved Brat, 1965a). Polyploids such as triploids (*A. rupestre*, *A. scordoprasum*), tetraploids (*A. ampeloprasum*, *A. chinense*, *A. nutans*), pentaploids (*A. splendens*), hexaploids (*A. lineare*), and octoploids (*A. nutans*) also occur (Jones R.N., 1990; Jones R.N & Rees, 1968; Ved Brat, 1965a).

Accessory chromosomes (B-chromosomes, supernumerary) have been documented (Bougourd and Plowman 1996). Their size and centromere position is variable within species (Ved Brat, 1965a, 1965b). B-chromosomes found in *A. paniculatum* never undergo pairing with

other chromosomes during meiosis, however, occurrence of chiasmata associations among B-chromosomes in *A. schoenoprasum* was observed (Bougourd & Parker 1979).

The majority of species within the genus carry meta- or submetacentric chromosomes (Ved Brat, 1965a). Levan (1932, 1935) noted that species with  $x=7$  had larger chromosomes than those with  $x=8$  or  $x=9$  and that arm-length asymmetry was more frequent in the "16" and "18"-chromosomes types and that the "14"-chromosome types were the most primitive. Ved Brat (1965a) estimated, that 40% of the forms within the genus possessing eight chromosomes had varying number of asymmetrical chromosomes, often carrying the nucleolar organizer regions (NOR), whereas remaining 60% had symmetrical chromosomes. Reports about differences in telomeric sequences in *Allium* (Fuchs et al., 1995) and stabilization of chromosome ends by highly repetitive satellites and rDNA (Pich et al., 1996) were also published.

Length of the alliums chromosomes also varies; the shortest ( $\sim 7 \mu\text{m}$ ) chromosomes were found in *A. yunnanense* ( $x=8$ ), the longest ( $\sim 22 \mu\text{m}$ ) in *A. fragrans* ( $x=9$ ) (Levan 1935). Investigation of the nuclear DNA content revealed that evolution of alliums was associated with variation in DNA amounts. Nuclear DNA content was proportional to chromosome 'volume' in the cell, and changes in the DNA amount were distributed between chromosomes within complements (Jones R.N. & Rees, 1968). *Alliums* with  $n=8$  have in general the lowest; mean 28,9 pg/2C nuclear DNA amounts, while those with  $n=9$ , the highest; mean 42,2 pg/2C (Bennett & Leitch, 2010).

Breeding systems in alliums are variable; some are reproduced sexually as outbreeders or inbreeders, some asexually with vivapory or apomixis and some are vegetatively propagated (Ved Brat, 1965b). An overwhelming majority of the genus is propagated sexually, which allows for gene exchange and, in consequence, more genetic variability. However, in the vegetatively reproduced *A. sativum* the main source of variation is the occurrence of alterations in the number and morphology of chromosomes in somatic cells of the clone (Konvička & Levan, 1972).

Meiosis in alliums was reviewed by Levan (1931, 1935). In prophase I of the diploid forms chiasmata are visible at early diakinesis. Terminalization of chiasmata causes a decrease in their number from 10-15 to 2-3 in each conjugating pair. The most common types of chromosome shape in metaphase are rings and rods. In some cases i.e. *A. nutans*, pairing in meiosis is incomplete in certain chromosome pairs (Levan, 1931). During meiosis in the polyploid forms, associations of chromosomes are common. Appearance of trivalents in *A. nutans* was reported (Levan, 1935). Observed trivalents had different forms, i.e V-shaped trivalents with one rod on each arm or with two rods on one arm. In anaphase I trivalents are distributed randomly, usually twelve to the pole, however, formation 8 to one pole and 16 to other was also observed (Levan, 1931). Occurrence of lagging chromosomes developing micronuclei, as well as formation of unreduced gametes was reported in triploids (Ved Brat, 1967). Quadrivalents were formed in meiosis I in the PMC of *A. schoenoprasum* and *A. porrum*. The most frequent types of quadrivalents were rings and chains (Levan, 1935). In polyploid *A. oleraceum* ( $2n=24, 32, 40$ ) elimination of chromosomes during meiosis was observed, thus pollen grains with 13, 15, 17, and other number of chromosomes were noted (Levan, 1931).

## 2.1 *A. cepa*

*Allium cepa* L. belongs to the genus *Allium*, subgenus *Rhizirideum*, section *Cepa* (Mill.) (Fritsch & Friesen, 2002). It is a diploid ( $2n=2x=16$ ) and possesses one of the largest genomes among

cultivated plants (Havey, 2002). The nuclear genome of onion contains 35,8 pg per 2C (Labani & Elkington, 1987), which is reflected by very large chromosomes. Onion has a complement of eight pairs of metacentric and submetacentric chromosomes including one set of terminal satellite chromosomes. Meiosis in onion is regular with eight bivalents (R.N. Jones, 1990). Chiasmata during metaphase I in PMC in onion are distributed at random in each bivalent and by the mid-metaphase they become terminal or sub-terminal and either rod or ring bivalents are formed (Fig. 1 & Fig. 2) (Emsweller & H.A. Jones, 1945; Levan, 1936). The cross-over points are therefore located mainly in distal and interstitial regions of the chromosome arms (Koul & Gohil, 1970; Levan, 1933). There is no information about localized chiasmata in onion (Emsweller & H.A. Jones, 1945).

## 2.2 Hybrids with introgression from *A. fistulosum*

*Allium fistulosum* L. (Japanese bunching onion, Welsh onion) is a diploid species ( $2n=2x=16$ ). *A. fistulosum*, similarly to onion, belongs to section *Cepa* of the genus *Allium* (R.N. Jones, 1990). Nuclear DNA content is 26,3 pg (2C), what is about 20% less than in onion (R.N. Jones & Rees, 1968).

During meiosis I in *A. fistulosum* eight bivalents are formed. Bivalents are held together by two chiasmata, one on each side of the centromere, thus in the metaphase plate they appear like a cross (Fig. 2). Chiasmata in the bivalent are usually localized proximally, adjacent to the centromere, however, occasional formation of more interstitial and randomized chiasmata were observed (R.N. Jones, 1990; Levan, 1933; Maeda, 1937).

Progenies from generative hybridization of onion with *A. fistulosum* have been studied most extensively among all interspecific crosses in the genus *Allium*. Those two species can be easily hybridized in the greenhouse and the success rate can be enhanced by the use of embryo-rescue in tissue cultures (Doležel et al., 1980). First hybrids between *A. cepa* and *A. fistulosum* were reported in 1935 by Emsweller and Jones. Meiotic studies showed that in early prophase I the hybrid chromosomes appear to be single threads, like in the parents. Abnormalities in the cell division start at late prophase, what was confirmed by Maeda (1937). In pachytene, single threads are doubled and chiasmata are visible between some conjugating partners, whereas other chromosomes probably just overlapped each other at entire length of the arms. When the bivalents were formed by chromosomes of different length, they sometimes separated in association long plus long chromatid, as well as long plus short chromatid. Emsweller and Jones (1935b) observed extension of long arm of conjugated chromosomes well beyond the end of the other. That condition depends on the arrangement of chiasmata at the ends of a bivalent (Emsweller & H.A. Jones, 1935a). In diakinesis, chromosomes were usually well-separated and their configuration could be easily determined. In *A. cepa*, chiasmata are predominantly terminal, in *A. fistulosum* chiasmata are localized near the centromere region (Fig. 1). The hybrids have chiasmata localized randomly (Emsweller & H.A. Jones, 1945; Maeda, 1937). Hybrids had high frequency of complete bivalent pairing, but unpaired chromosomes were also observed (Emsweller & H.A. Jones, 1935a, 1938). In anaphase I, when the separations of chromosomes occur, occasional chromosome bridges were present (Emsweller & H.A. Jones, 1938).

Emsweller and Jones (1935a, 1935b, 1938) as well as Peffley (1986) and Maeda (1937) reported regular bivalentization (Fig. 2) in about 70% of tested cells, whereas Levan (1941) reported regular bivalent formation in only 2% of the tested PMC in his *A. cepa* x *A. fistulosum* hybrids. Early stages of meiosis in that plant material showed a number of

unpaired threads, the maximal pairing was found before diplotene. Few pachytene chromosomes had threads longer than their pairing partner, what in consequence lead to occurrence of loop shape formations. Loops were localized on one side of the pairing complex, but in some cases the longer thread folded and paired with itself. Ring (Fig. 2.) and chromosome configurations with three chiasmata were also found (Levan, 1935). Inter-chromosomal differences, resulting in pairing of more than two chromosomes were observed. Levan (1941) observed frequent trivalents (14%), forming rings in metaphase. Seldom quadrivalents, pentavalents, hexavalents, were reported (Emsweller & H.A. Jones, 1935b, 1938; Levan, 1936; Peffley, 1986). However, Maeda (1937) reported absence of associations higher than bivalents in his hybrids. Abnormalities observed by Peffley (1986) in anaphase I included bridge formation in 28% and lagging chromosomes in 10% of the cells. Deficiencies, translocations, and inversions were reported (Emsweller & H.A. Jones, 1938; Levan, 1935, 1941; Peffley, 1986). Presence of heteromorphic pairing in F<sub>1</sub> interspecific hybrids was observed (Emsweller & H.A. Jones, 1935b; Maeda, 1937). Peffley (1986) suggested that heteromorphic bivalents were the consequence of pairing between chromosomes with translocation or inversion at the centromeric region.

The above-described discrepancies in meiotic events in F<sub>1</sub> *A. cepa* x *A. fistulosum* hybrids may be explained by a different origin of *A. cepa* and *A. fistulosum* used in the discussed studies. Maeda and Emsweller and Jones used the same variety of *A. cepa* (Yellow Danvers) and *A. fistulosum* in Japanese form (Nebuka, Hidanegi), whereas Levan mentioned the use of a commercial onion variety 'Braunschweiger' and as a source of *fistulosum* points one of the European botanical gardens. Peffley (1986) used onion cv. 'Yellow Grano' and ten different accessions of *A. fistulosum* supplied by International Plant Breeders. Thus, it can be concluded that the cytological behavior during meiosis in F<sub>1</sub> interspecific hybrids seems to be accession-specific. Moreover, chromosomal variants (multivalents) and changes in the chromosome structure (bridges) offer an explanation of the low pollen fertility of the F<sub>1</sub> hybrids (H.A. Jones & Mann, 1963; Levan, 1941; Peffley, 1986).

Using GISH (Genomic *In Situ* Hybridization) Stevenson et al. (1998) detected reciprocal crossover events in F<sub>1</sub> interspecific hybrids. The frequencies of crossovers detected as label exchanges in anaphase I chromosomes were about 20% higher than metaphase I chiasma frequencies. Since the synaptonemal complex (SC) is responsible for transmission of the interference, discontinuities in SC may cause that crossover occur in much closer proximity than they normally would with uninterrupted SCs (Sybenga, 1996). Albin and Jones (1990) reported incomplete synapsis in the centromeric region and other irregularities in the SC in the *A. cepa* x *A. fistulosum* hybrids. The failure of synapsis might explain differences in chiasmata frequencies reported by Stevenson et al. (1998). Additionally, Albin and Jones (1990) suggested, that DNA differences between *A. cepa* and *A. fistulosum* chromosomes were localized in the centromeric region, which prevented regular synapsis or progression of synapsis and possible proximal chiasma formation.

The F<sub>1</sub> hybrids between *A. cepa* and *A. fistulosum* can be easily produced, but have low pollen fertility, often not exceeding 10% (H.A. Jones & Mann, 1963; Levan, 1941; Maeda, 1937; Peffley, 1986; van der Valk et al., 1991b). Additionally Emsweller and Jones (1938) reported occurrence of egg sterility of the F<sub>1</sub> hybrids. Successful production of F<sub>2</sub> progenies was reported by Levan (1941). The F<sub>2</sub> plants were exclusively polyploids (tri- and tetraploids). Analysis of meiosis showed frequent disturbances, such as chromatin bridges and micronuclei in dyads and tetrads. Random distribution of chiasmata was dominant.

Cytological analysis of tetraploid forms revealed that they were amphidiploids built up from 2 *cepa* and 2 *fistulosum* genomes. Morphology of the tetraploids was intermediate between the parents, while their pollen fertility varied. One tetraploid was sterile, the other had moderate (50%) pollen fertility. In the triploid form, the frequency of trivalents was high (80-90%). In about 33% of tested cells micronuclei and chromosomal bridges were observed. Pollen fertility was low; not exceeding 10% (Levan, 1936, 1941).

Levan's (1941) attempts to backcross (BC)  $F_1$  hybrid *A. cepa*  $\times$  *A. fistulosum* to *cepa* were unsuccessful. The studies of van der Valk et al. (1991a) showed that difficulties in this type of cross were due to pre-fertilization barrier, as the growth of onion pollen tubes in the style of the hybrid was disturbed. Maeda (1937) backcrossed  $F_1$  to *A. fistulosum* and obtained viable seeds. Emsweller and Jones (1945) obtained several BC progenies, but only when the hybrid was used as the pollen source.

In  $BC_1$ , the most common meiotic configuration were eight bivalents and eight univalents. Both randomized and localized chiasmata were observed (Emsweller & H.A. Jones, 1935b). Multivalents (quadrivalents, pentavalents) were observed in about 40% of the meiocytes. A ring univalent, lagging chromosomes, and chromosomal bridges were also observed (Peffley & Mangum, 1990). Analysis of the structural differences of chromosomes revealed presence of at least three paracentric inversions and one translocation, producing changes in gene order (Ulloa et al., 1994). Emsweller and Jones (1945), using  $F_1$  as a pollen source, backcrossed them to both *A. cepa* and *A. fistulosum*. On average 44% of PMC in population backcrossed to *A. cepa* showed regular chromosome pairing, additionally those plants segregated with regard to male fertility; some individuals after self-pollination yielded in few seeds, and some were complete sterile. The first backcross to *A. fistulosum* possessed both randomized and localized chiasmata, however the second backcross had a high frequency of localized chiasmata (Fig. 1). This increase of localized chiasmata in subsequent backcrosses was correlated with pollen fertility.

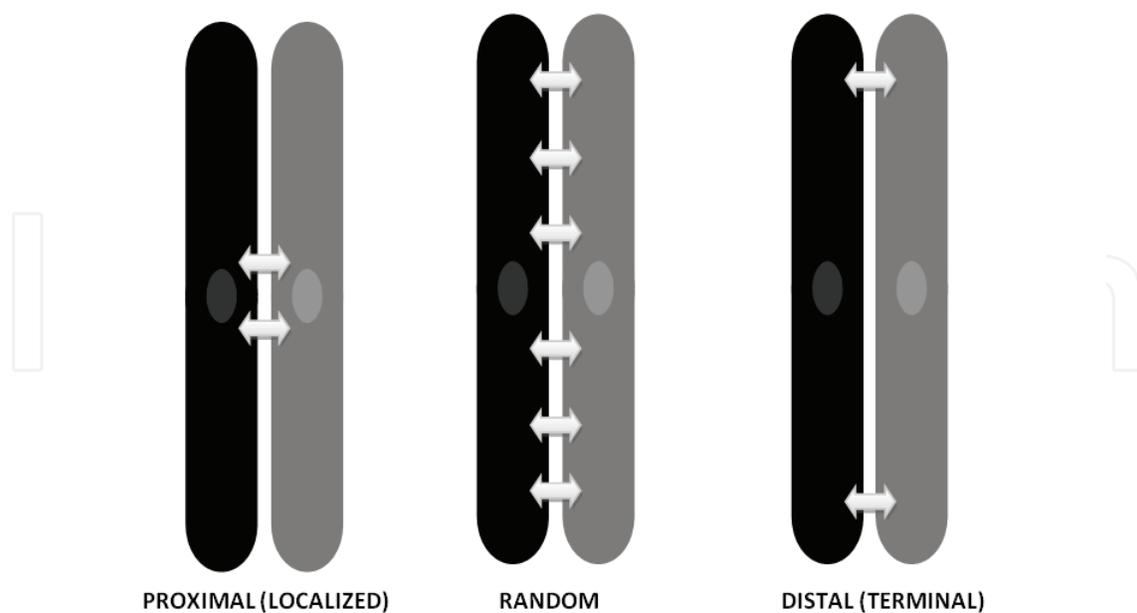


Fig. 1. Diagram showing the types of chiasmata distribution in the interspecific  $F_1$  hybrids within edible alliums.

Arrows indicating possible position of chiasmata between two homologous chromosomes in bivalent.

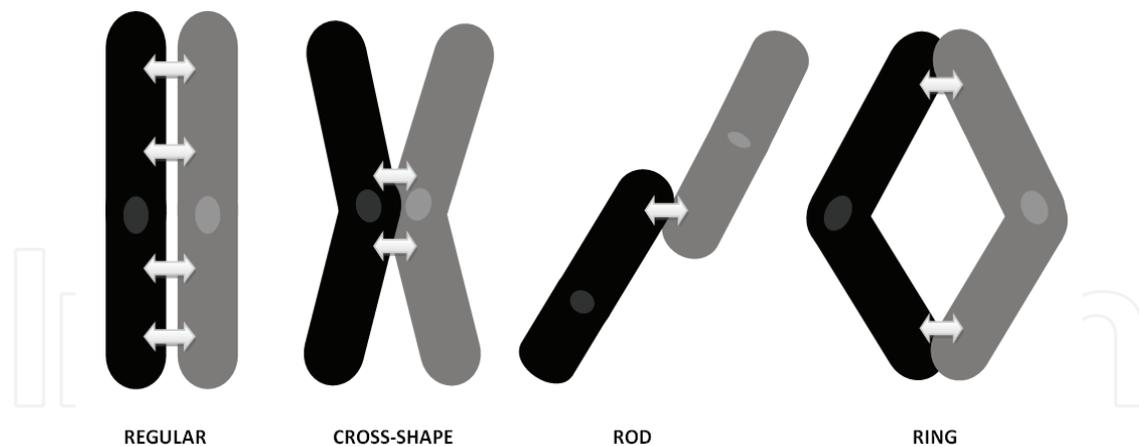


Fig. 2. Diagram showing configurations of bivalents observed in metaphase I of interspecific F1 hybrids within edible alliums.

Arrows indicating position of chiasmata between two homologous chromosomes in bivalent.

The fertile BC<sub>2</sub> plants had localized chiasmata and their morphology was similar to *A. fistulosum*, while sterile plants had mostly randomized chiasmata and morphologically were in the *A. cepa* type. Hou and Peffley (2000) examined 16 BC<sub>3</sub> plants and observed very high pollen fertility (90-92%) of the plants with eight bivalents at metaphase I. Those plants had low percentage of chromosomal aberrations such as bridges, laggards, or micronuclei. One male sterile plant had recombinant chromosomes. Thirteen among sixteen chromosomes in PMCs of the sterile plant gave strong hybridization signals at telomeres when *A. fistulosum* was used as a genomic DNA. Similar GISH patterns were reported by Khrustaleva and Kik (1998), suggesting differences in heterochromatin distribution at the telomeres between two parental species.

Khrustaleva and Kik (1998) introgressed genes from *A. fistulosum* to *A. cepa* using *A. roylei* as a bridge in crossing. Multi-colour GISH was performed to analyze genome organization of the hybrid. Results showed 8 *cepa* chromosomes, 1 metacentric chromosome from *roylei*, and 7 recombinant chromosomes. Recombination between *A. roylei* and *A. fistulosum* took place in distal and interdistal regions of hybrid chromosomes, centromeric regions originated from *roylei*. Meiosis in PMC of the first generation bridge-cross hybrid [*A. cepa* × (*A. fistulosum* × *A. roylei*)] was rather regular, about 53% of tested cells possessed 8 ring bivalents (Fig. 2), however occasional presence of univalents was noted. No multivalents were observed. Some of the bivalents were heteromorphic, indicating homologous pairing and chiasmata formation during prophase I. Pollen viability of the hybrid was about 50-60%. Detailed analysis of meiosis in the second generation hybrid (*A. cepa* × first generation bridge cross) showed that recombination between three genomes was frequent and that chiasmata were randomly distributed (Fig. 1) (Khrustaleva & Kik, 2000). Keeping in mind that chiasmata are located adjacent to the centromere in *A. fistulosum* and randomly distributed in *A. cepa* and *A. roylei* (Emsweller and H.A. Jones, 1935b; Levan, 1933, de Vries et al., 1992) in the bridge-cross hybrid random chiasmata prevailed over the *fistulosum* type. Translocations of *roylei-fistulosum* segment and deficiencies (absence of *roylei* segment) were also reported (Khrustaleva & Kik, 2000). Pollen fertility of the second generation bridge-cross hybrid was variable, what might be caused by the use of CMS onions as the female parent and/or the lack of *roylei* chromosome segments containing male sexual reproduction genes (Khrustaleva & Kik, 2000; Ulloa et al., 1995).

Monosomic addition lines of *fistulosum* – *cepa* (Shigyo et al., 1998) and *cepa* – *fistulosum* (Hang et al., 2004; Peffley et al., 1985) were reported. These lines are valuable to study genome organization in *A. cepa* and *A. fistulosum*.

### 2.3 Hybrids with introgression from *A. ampeloprasum* spp. *porrum*

Leek is a tetraploid species ( $2n=4x=32$ ). Nuclear DNA content is 52,7 pg per 2C (Bennett & Leitch, 2010). Leek belongs to the genus *Allium*, subgenus *Allium*, section *Allium* (Hirschegger et al., 2010).

Meiosis in the leek was first described by Levan in 1940, showing almost complete localization of chiasmata at prophase I. Khazanehdhari et al. (1995) reported frequent formation of quadrivalents at this stage. Further studies showed that those quadrivalents were resolved in to bivalents in metaphase I (G.H. Jones et al., 1996); however, occasional persistence of quadrivalents in this stage was also observed (Koul & Gohil, 1970; Levan, 1940). Formation of bivalents in metaphase I was due to proximal localization of chiasmata in leek (Stack & Roelofs, 1996). Usually, four chromosomes in tetrasome are clustered by chiasmata located immediately adjacent to and on either side of the median or submedian centromere. As pairing partner switches are unlikely to occur between two proximal chiasmata, thus quadrivalent fall apart into two bivalents having a characteristic cross-shape (Fig 2.) (G.H. Jones et al., 1996; Khazanehdhari et al., 1995). Occurrence of univalents in the PMC of the leek was also reported (G.H. Jones et al., 1996; Khazanehdhari & G.H. Jones, 1997).

Interspecific hybrids between *Allium cepa* and *A. ampeloprasum* were generated with the aim of introduction of the S-cytoplasm from onion into leek. Few attempts of sexual hybridization of onion and leek failed, suggesting that this strategy to create F<sub>1</sub> progeny may be difficult (Doležel et al., 1980; Currah, 1986). Peterka et al. (1997) used *in vitro* culture to rescue the F<sub>1</sub> embryos at the early stages of development (7-14 days after pollination); as a result they obtained seven hybrid plants, which were triploids with 24 chromosomes. Authors reported presence of three chromosomes with satellites and two with intercalary pseudosatellites. Onion carries two chromosomes with satellites (Kalkmam, 1984; Taylor, 1925), leek has four, and additionally leek has four chromosomes with intercalary pseudosatellites (Murin, 1964). GISH with onion DNA as a probe, showed hybridization of eight chromosomes of the hybrid plant, the remaining 16 did not hybridized, which enabled identification of onion and leek chromosomes. Further studies of meiosis in the interspecific hybrids showed presence of eight leek bivalents and eight onion univalents in the prophase I (Peterka et al., 2002). The leek bivalents in the hybrids had localized chiasmata (Fig. 1). During late metaphase and early anaphase, in some of the observed cell the onion univalents were arrested at the periphery of the nucleus, while the leek chromatids moved to the poles. The onion chromatids, due to their retarded movement, were frequently excluded from the daughter nuclei in the form of micronuclei observable in the dyad or tetrad stage (Schrader et al., 2000).

Peterka et al. (2002) investigated chromosome composition of the backcross progenies. Their BC<sub>1</sub> plants always possessed eight onion chromosomes and from 30 to 33 leek chromosomes. Only in one tested hybrid a recombinant chromosome was identified. In the BC<sub>2</sub> and BC<sub>3</sub> decreased transmission rate of univalent onion chromosomes were observed, resulting in the production of alloplasmic leek plants in the third backcross.

Buiteveld et al. (1998a, 1998b) reported the symmetric fusion of protoplasts isolated from suspension cultures of *A. ampeloprasum* and leaf mesophyll protoplasts of onion, resulting in somatic hybridization of onion and leek. Analysis of chromosome composition of somatic hybrids was performed using GISH. All obtained hybrids were identified as hexaploids. In eight tested hybrids, chromosome number varied from 41 to 45. Authors found differences among hybrids with regard to the number of parental chromosomes. Some hybrids carried eight onion and less than 32 leek chromosomes, other possessed 12 onion and 30 leek chromosomes. Flow cytometry measurements showed that the suspension culture used for the fusion was of a mixture of aneuploid (hypotetraploid) and normal tetraploid cells of leek. Since aneuploid leek protoplasts were used for the fusion, it is possible that the hybrids resulted from fusions with leek protoplasts with different chromosome numbers, which might explain the differences in the number of leek chromosomes in the hybrids. Loss of the onion chromosomes may be a consequence of spontaneous chromosome elimination after the fusion. Moreover, recombinant chromosomes in cells of leek and onion somatic hybrids were also reported. Two of those chromosomes were of a reciprocal translocation type and one was an interstitial translocation type (Buiteveld, 1998a).

#### 2.4 Hybrids with introgression from *A. sativum*

*A. sativum* L. is a diploid with ( $2n=2x=16$ ) with nuclear DNA content 32,5 pg per 2C (Bennett & Leitch, 2010). The DNA content of garlic is the most similar to onion among the discussed species. Garlic belongs to the genus *Allium*, subgenus *Allium*, section *Allium* (Hirschegger et al., 2006; Keller et al., 1996).

The majority of garlic cultivars are sterile, which preclude to use them as a partner in sexual crossing, however occurrence of fertile garlic plants was also reported (Hong et al., 1997; Kik, 2002). Flowering in some garlic clones is often associated with presence of bulbils formed in the place of aborted flowers. Bulbils are used as a source material for vegetative reproduction (R.N. Jones, 1990; Kik, 2002).

To study meiosis in the garlic, Konvička and Levan (1972) used two fertile clones named OH and LH. The clone OH formed medium size bulbils and normal flowers in the inflorescence. The clone LH had an abundance of flowers together with many small bulbils, moreover this clone formed original chromosome ring at meiosis (amphibivalent) (Levan, 1936). Majority of tested meiocytes in the clone OH formed eight bivalents at meiosis I; however presence of spherical chromatic bodies outside the spindle was observed. Produced pollen grains differ in size. The first meiotic division in the clone LH proceeded regularly, but two out of four bivalents formed an ring consisting of four chromosomes. This structure could be observed from diplotene through diakinesis and metaphase I. In metaphase I authors observed ring configurations in the majority of the cells; only in one of them an open ring was present. The formation of rings caused occurrence of lagging chromosomes observable during the first anaphase. The second division was usually normal, but in few cells chromatin body outside the spindle was present. Two satellite chromosome pairs were noted in cells of both tested clones. The clones had their own characteristic pattern of meiotic abnormalities, what is in contrary to results presented by Koul and Gohil (1970) where in three tested fertile clones meiosis was completely regular. Differences in chromosome length, positions of NOR or arm ratios were variable among garlic clones (R.N. Jones, 1990). Such differences may partially develop after the loss of sexual propagation and changes occurring in the somatic cells of vegetatively propagated garlic.

*Allium cepa* and *A. sativum* for a long time have not been hybridized sexually because of the narrow pool of fertile garlicks and a large genetic distance (Kik, 2002; Keller et al., 1996). The first interspecific hybrids between onion and garlic were reported by Ohsumi et al. in 1993. Authors performed reciprocal crosses of onion and garlic, but embryos were formed only when onion was the female parent. Embryos were rescued in tissue culture. Regenerated hybrids possessed 16 chromosomes in somatic cells, with clearly distinguishable two satellite chromosomes. Since onion cv. 'Sapporoki' used in the study did not possess satellite chromosomes, those chromosomes were inherited from *A. sativum*. Chromosome elimination was not observed in the study. The pollen viability of the obtained hybrid was very low (2%).

Worth mention is work of Yanagino et al. (2003) with aim of increasing fertility in garlic through sexual hybridization with leek. Success of this cross was accelerated, since both leek and garlic belong to the subgenus *Allium*. Leek was used as the female partner. Interspecific hybrids were obtained with the use of the embryo-rescue technique. Hybrids were triploids and possessed 24 chromosomes (16 from onion and 8 from garlic), however meiosis in PMC was not examined. Obtained hybrids were almost completely sterile.

Somatic hybrids of onion and sterile garlic were reported by Yamashita et al. (2002). Onion and garlic have sixteen chromosomes, however obtained hybrids were classified as aneuploids with total number of chromosomes 40 or 41. In the tested somatic cells of the hybrids authors noted presence of two subtelocentric chromosomes and three intercalary satellite chromosomes, inherited from both parents. GISH analysis revealed 17 garlic and 20 or 21 onion chromosomes and three chromosomes consisting of chromosomal regions from both parents. Presence of chimeric chromosomes in the somatic hybrids originated from translocation between chromosomes or chromosome fusions.

### 3. Conclusions and future directions

Pre-fertilization barriers in distant crosses, such as failure in pollen germination, slow pollen tube growth, or foreign pollen tube arrest in the style have been reported in different species (Kielkowska & Adamus, 2006; Manickam & Sarkar, 1999b) including alliums (Gonzalez & Ford-Lloyd, 1987; Ohsumi et al., 1993; van der Valk et al., 1991a). Post-fertilization barriers are related to abnormalities in the development of the zygote, absence or abnormal development of the endosperm which causes embryo starvation and abortion (Zenkeller, 1990). Within the discussed species, the embryos developed regularly in the hybrids with introgression from *A. fistulosum*, or had to be rescued on the early stages of the development in hybrids with the leek and garlic introgression. Cytological studies showed reproductive abnormalities in F<sub>1</sub> hybrids and their progenies. Irregularities of chromosome pairing and occurrence of a range of structural changes in meiotic chromosomes resulted in unbalanced chromosome complements in the gametes, often causing lowered fertility or even sterility of the F<sub>1</sub> hybrids (Khush & Brar, 1992; Peffley, 1986; van der Valk et al., 1991a).

*A. fistulosum* carries resistance genes for fungal, bacterial, and viral diseases (Rabinowitch, 1997). Moreover *fistulosum* has several agronomically important traits such as high dry-matter content, winter-hardiness, high pungency and earlier flowering as compared to onion (van der Meer & van Bennekom, 1978). Hence, hybrids between onion and *A. fistulosum* as well as several backcross progenies were deeply studied, with *A. cepa* as either

the female parent (Emsweller & H.A. Jones, 1935a, 1935b; Levan, 1941; Van der Meer and Van Benekom, 1978) or pollen parent (Peffley, 1986; Peters et al., 1984; van der Valk et al. 1991a). Cytological studies have shown that chromosome pairing is highly variable in the F<sub>1</sub> hybrid depending on the parental combination (Emsweller & H.A. Jones, 1935a, 1953b; Peffley, 1986; Ulloa et al., 1994). Presence of heteromorphic pairing was reported in each of the discussed studies, showing evidence for recombination of genetic material between homologous chromosomes in the F<sub>1</sub> hybrid between *A. cepa* and *A. fistulosum* (Emsweller & H.A. Jones, 1935a, 1935b; Peffley & Mangum, 1990; van der Meer & Van Benekom, 1978), and when the hybrid was backcrossed to *A. cepa* (Hou & Peffley, 2000). Khrustaleva and Kik (1998, 2000) showed that gene exchange is possible even in the three-way (*cepa* x (*fistulosum* x *roylei*)) hybrid, resulting in partially fertile progenies. Nucleo-cytoplasmic incompatibility interactions reported between these two species may also reduce fertility of F<sub>1</sub> hybrids (Ulloa et al., 1994).

Although pollen sterility of hybrids is a major barrier to gene introgression, occurrence of fertile F<sub>1</sub> hybrids able to produce further progenies and introduce them into the breeding process, was also reported. Jones and Clarke (1942) reported obtaining of amphidiploid arose by spontaneous doubling from unreduced gamete of F<sub>1</sub> *A. cepa* x *A. fistulosum* hybrid. At metaphase I of the hybrid, there were 16 bivalents with localized and non-localized chiasmata and meiosis was regular. The obtained plant was fertile, vigorous, and resistant to several diseases. This amphidiploid is known as 'Beltsville Bunching' and was released in the United States in 1950, and sold on the market as green bunching onion (H.A. Jones & Mann, 1963). Many years of research resulted in the release of the several other hybrids grown as vegetatively propagated onions in *fistulosum* type or sexually reproduced bulb onions resistant to pink root (*Phoma terrestris*) (for review see Kik, 2002).

In the leek, the main problem concerning sexual hybridization lies in the high (98%) occurrence of chiasmata localized near the centromere (Levan, 1940). Such localized chiasmata prevent formation of multivalents during meiosis (metaphase I) and prevents recombination on the distal ends of chromosomes (Khazanehdari & G.H. Jones 1997). The localization of chiasmata in this near-centromeric section prevents association of more than two chromosomes during leek meiosis, which may be beneficial for its capacity to form fertile gametes. However, if the pairing behavior in metaphase I is different between sexually hybridized components that may lead to infertility of the hybrids (Brewster, 1994). Peterka et al. (2002) reported complete sterility of onion x leek hybrids.

Morphology and hybrid status of progenies from a cross between *A. cepa* x *A. sativum* were reported (Ohsumi et al., 1993), however, meiotic chromosomes behavior in the hybrids as well as their pollen fertility have not been deeply investigated. Broadening genetic diversity in garlic is very desired. It can be achieved with the use of protoplast cultures, which offers a large spectrum of possibilities with regard to selection of components for the fusion. Sexual hybridization is rather difficult in garlic, due to high seed sterility of the clones. However, utilization of wild relatives and search for novel fertile accessions like the one found in South America (Hirschegger et al., 2006) is very important for increasing available germplasm pool.

During the years of studies researchers attempted to develop techniques helping to overcome barriers between incompatible species for successful production of hybrid seeds.

Worthy mentioning is bridge crossing (Dionne, 1963; McCoy & Echt 1993), use of exogenous plant growth regulators, i.e. gibberelic acid, dichloro-acetic acid (Brock, 1954; Manickam & Sarkar, 1999a), mixed pollen technique (Asano & Myodo, 1977), use of the 'mentor' pollen (Sastri & Shivanna, 1976; Settler, 1968), *in vitro* fertilization (De Verna et al., 1987; Zenkteller et al., 2005), embryo rescue (Sukno et al., 1999; Williams et al., 1982), and somatic cell hybridization (Kirti et al., 1991; Smith, 1976).

Embryo rescue promotes the development of an immature or weak embryo into a viable plant. The most commonly used procedure is careful excision of hybrid embryos and placing directly onto the culture medium. Sometimes when there are difficulties with embryo excision or embryos are very small, whole ovules (ovule culture, *in ovulo*) or ovaries are put to the culture (Bridgen, 1994). Embryo rescue has been widely used for producing hybrid plants in onions. *Alliums* hybrid embryos were usually cultured on a phytohormone-free medium (Amagai et al., 1995; Gonzalez & Ford-Lloyd, 1987; Nomura & Makara, 1993; Umehara et al., 2006). Whole ovary culture supported maturation of viable seeds in hybrids of *A. cepa* x *A. sphaerocephalon* (Bino et al., 1989) or *A. fistulosum* x *A. schoenoprasum* (Umehara et al., 2007). Keller et al. (1996) adopted ovary culture and obtained many hybrids between onion and other distant species. This technique was used in the crosses between onion and *A. fistulosum* (Doležel et al., 1980; van der Valk, 1991a), onion and leek (Peterka et al., 1997), onion and garlic (Ohsumi et al., 1993), rakkyo (*A. chinense*) and *A. fistulosum* L. (Nomura et al., 1994; Nomura & Makara, 1993), Welsh onion and chives (*A. schoenoprasum*) (Umehara et al., 2006) and many others (Gonzalez & Ford-Lloyd, 1987; Nomura et al., 2002; Nomura & Oosawa, 1990; Yanagino et al., 2003). Application of protoplast cultures for obtaining interspecific crosses in edible alliums (Buiteveld et al., 1998a, 1998b; Shimonaka et al., 2002; Yamashita et al., 2002) was also reported. Genomic *in situ* hybridization enabled the identification of genomes in the interspecific and intergeneric hybrids together with direct detection of genetic recombination (Friesen et al., 1997; Schwarzacher et al., 1989; Thomas et al., 1994). It seems that studies on the interspecific crosses in alliums employed a wide range of different biotechnological and cytogenetical tools to facilitate obtainment and characterization of hybrid, however one issue still remains unsolved and problematic. Many authors pointed low pollen fertility of generated hybrids what in consequence significantly decreased the number of obtained seeds and narrowed the pool of accessions for cytogenetic studies (H.A. Jones & Mann, 1963; Peffley, 1986; van der Valk et al., 1991a, 1991b). Most of the hybrids from crosses of *A. cepa* with *A. fistulosum* (Doležel et al., 1980; Emsweller & H.A. Jones 1935a, 1935b; Maeda, 1937), leek (Doležel et al., 1980), garlic (Ohsumi et al., 1993), as well as with *A. galanthum* (Kielkowska & Adamus, 2010), *A. oschaninii* or *A. pskemense* (McCollum, 1971) were reported as sterile.

Possibly, restoration of fertility of interspecific hybrids can be achieved by chromosome doubling (R.N. Jones, 1983). Chromosomes are doubled by treating the plant tissue with antimitotic agents such as colchicine (Blakslee, 1939; Blakslee & Avery, 1937). McCollum (1980) reported fertile amphidiploid of *A. cepa* x *A. galanthum* obtained by colchicine treatment. Autotetraploids in *A. cepa* and *A. fistulosum* were obtained by soaking germinating seeds in aqueous colchicine solution, but the recovery of tetraploids was low (2%) (Toole & Clarke, 1994). Song et al. (1997) treated calli from F<sub>1</sub> hybrids of *A. fistulosum* x *A. cepa* with 0.1 and 0.2% colchicine and regenerated tetraploids. It seems that the potential is promising and the recovery of fertile plants from colchicine-treated F<sub>1</sub> hybrids has been reported in other species (Eigsti & Dustin 1955; Orton & Steidl, 1980). The optimum

concentration and duration of treatment has to be determined empirically as it strongly affects the success in doubling and the survival of the treated plant material (Eikenberry, 1994; Hansen & Andersen 1996; Klima et al., 2008; Wan et al., 1989). In the literature concerning doubled haploids, authors mention use of trifluraline, oryzaline or amiprofos methyl (Hansen and Andersen, 1996; Zhao & Simmonds, 1995) which are considered less toxic and may be beneficial for fertility restoration in onion interspecific hybrids.

The state of knowledge about meiosis in F<sub>1</sub> hybrids and further generations from crossings of onions with *A. fistulosum* was deeply investigated, however meiotic studies of hybrids between onion and garlic and leek is limited. The change of the status is needed, because the understanding of meiotic process is crucial for further research on the reproduction, fertility, genetics and breeding of discussed species.

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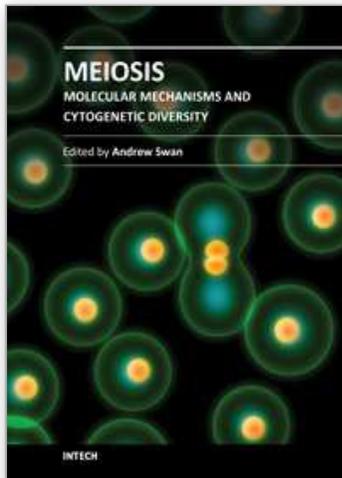
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## **Meiosis - Molecular Mechanisms and Cytogenetic Diversity**

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Unit 405, Office Block, Hotel Equatorial Shanghai  
No.65, Yan An Road (West), Shanghai, 200040, China  
中国上海市延安西路65号上海国际贵都大饭店办公楼405单元  
Phone: +86-21-62489820  
Fax: +86-21-62489821

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