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Meiotic Eccentricities in *A. cepa* × *A. Ampeloprasum* spp. *Porrum* and *A. Cepa* × *A. Sativum*

Solanki Bal
Ph.D. Research Scholar, Department of Vegetable Science, Faculty of Horticulture, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, West Bengal

SUMMARY

Hybridization between species within the genus *Allium* is an important tool in creating genetic variation. Such techniques of sexual hybridization are often accompanied by several difficulties including pre- and post-fertilization barriers. Over the years of studies, researchers tried to develop techniques to overcome hurdles between incompatible species for successful hybrid seed production. Among different *Allium* sp., embryos had to be rescued in very early stages for the development of hybrids with leek and garlic introgression. The purpose of this article is to provide a concise review of meiotic irregularities in *A. cepa* × *ampeloprasum* spp. *porrum* and *A. cepa* × *sativum*.

INTRODUCTION

Within the genus *Allium*, hybridization between species has a long history and is used as an important tool in creating genetic variation (Bal *et al*., 2019; Bal *et al*., 2021; Bal, 2022). Such techniques of sexual hybridization are very often accompanied by several difficulties including pre- and post-fertilization barriers. In distant crosses, pre-fertilization barriers involve a failure in pollen germination, slow pollen tube growth, or foreign pollen tube arrest in the style have been reported in different species including alliums. Whereas, post-fertilization barriers involve abnormalities in the zygote development, abnormal development or absence of zygote development, abnormal development or absence of the endosperm which results in embryo starvation or abortion. Among different *Allium* sp., embryos had to be rescued in very early stages for the development of hybrids with leek and garlic introgression. Cytological studies revealed reproductive abnormalities in F_1 hybrid and their progenies. Such deformities in the pairing of chromosomes and the development of a wide range of changes in the structure of meiotic chromosomes lead ultimately to unbalanced chromosomal complements in the gametes. The purpose of this article is to provide a concise review of meiotic irregularities in *A. cepa* × *ampeloprasum* spp. *porrum* and *A. cepa* × *sativum*.

Meiotic events in *A. ampeloprasum* spp. *porrum*

Leek, botanically which is *A. ampeloprasum* spp. *porrum* is a tetraploid species (2n=4x=32) and its nuclear DNA content was reported to be 52,7 pg per 2C (Bernett & Leitch, 2010). Levan in 1940 first described meiosis, exhibiting complete localization of chiasmata in prophase I with frequent quadrivalent formation at this stage. Studies further also revealed that those quadrivalents formed were resolved into bivalents in metaphase I; nonetheless, occasional endurance of quadrivalents was observed in this stage. In addition, the formation of bivalents in metaphase I was due to the localization of chiasmata in closure proximity in leek. On a usual basis in tetrasome, four chromosomes are clustered by chiasmata situated immediately on either side and adjacent to the median or submedian centromere. As shifting of the pairing partner occurs remotely between two proximal chiasmata, the quadrivalent collapses into two bivalents resulting in a distinguished cross-shape (figure 1). Besides, the occurrence of univalents in pollen mother cells of leek was also reported.

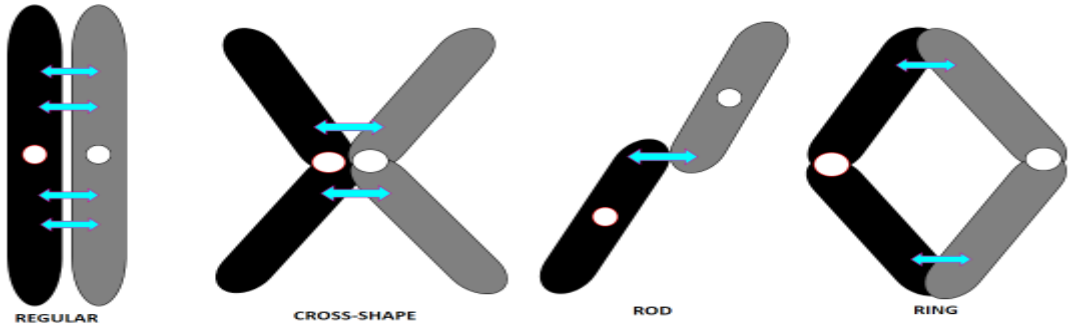

Figure 1: Diagrams revealing configurations of bivalents observed in metaphase I of interspecific F_1 hybrids within alliums.

Meiotic irregularities on hybrids with introgression from *A. ampeloprasum* spp. *porrum*

The aim of interspecific crosses between *Allium cepa* and *Allium ampeloprasum* is to introduce S-cytoplasm from onion to leek. Previously, sexual hybridization between onion and leek had been attempted by several workers but failed to develop F_1 progenies. Peterka *et al.*, (1997) rescued F_1 embryos by using *in vitro* culture technique at an early stage of development i.e., 7-14 days after pollination, as a result of which seven hybrids (triploids with 24 chromosomes) were obtained. They reported the presence of three chromosomes with satellites and two with intercalary pseudo satellites. Leek carries four chromosomes with satellites to that onion with two chromosomes with satellites, but, additionally, leek carries four chromosomes with intercalary pseudo satellites. Using onion DNA as a probe, the GISH study revealed the hybridization of eight chromosomes of the resulting hybrid leaving 16 chromosomes un-hybridized, enabling close identification of onion and leek chromosomes separately. Studies of meiosis in the interspecific hybridization further showed the presence of eight onion univalents and eight leek bivalents in prophase I (Peterka *et al.*, 2002) with localized chiasmata in leek bivalents (figure 2). In some of the observed cells during late metaphase and early anaphase, the onion univalents were arrested at the periphery of the nucleus, whilst chromatids of leek moved towards poles. The chromatids of onion due to their retarded movement were excluded frequently from the daughter nuclei in the form of micronuclei observable in the dyad or tetrad stage.

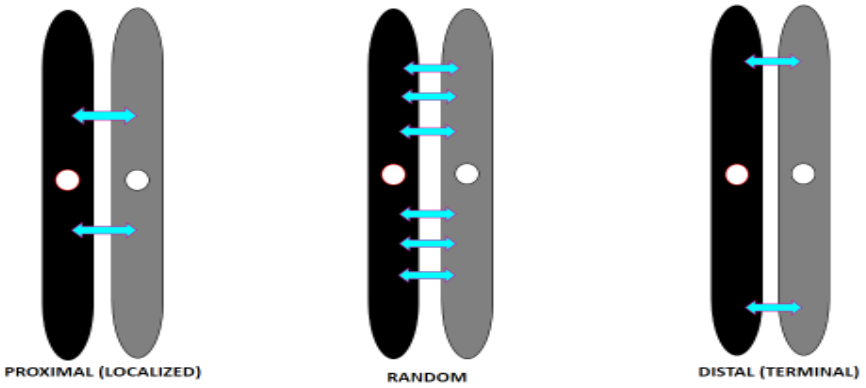

Figure 2: Diagram revealing types of chiasmata distribution in the interspecific F_1 hybrids within alliums.

Buiteveld *et al.*, (1998) observed a symmetric fusion of protoplasts obtained from the suspension cultures of *A. ampeloprasum* and protoplasts in leaf mesophylls of onion, resulting in somatic hybridization of onion and leek. Chromosomal analysis of the composition of somatic hybrids was performed using the GISH technique and all obtained hybrids were recognized as hexaploids. Authors found chromosome numbers to range from 41 to 45 in eight tested hybrids and revealed differences among hybrids with regard to the number of parental chromosomes. Some of the hybrids possessed eight onion and less than 32 leek chromosomes, whereas other hybrids possessed 30 leek and eight onion chromosomes. On flow cytometry, measurements exhibited that the suspension culture used for the fusion was actually a mixture of hypertetraploid and normal tetraploid cells of leek. As aneuploid protoplasts of leek were used for fusion, it was quite possible that such fusions with leek protoplasts resulted in hybrids with different chromosome numbers, explaining differences in the number of leek chromosomes in the hybrids where the loss of onion chromosome might stem out as a consequence of spontaneous elimination of chromosome after the fusion. Nevertheless, recombinant chromosomes in cells of leek and onion somatic hybrids were also reported. In another case, Peterka *et al.*, (2002) investigated the composition of chromosomes of the backcross progenies. Results revealed that BC_1 plants possessed from 30 to 33 leek chromosomes and eight onion chromosomes. Besides, a recombinant chromosome was identified only in one tested hybrid, whereas, in BC_2 and BC_3 progenies low transmission rate of univalent onion chromosomes was observed, leading to the production of alloplasmic leek plants in BC_3.

Meiotic events in *A. sativum*

Garlic, botanically which is *A. sativum* is a diploid (2n=2x=16) having nuclear DNA content of 32,5 pg per 2C (Bennett and Leitch, 2010). Among the different *Allium* species, the DNA content of garlic is most similar to that of onion. Garlic cultivars are majorly sterile which forbids to use it as a partner in sexual hybridization, however, the occurrence of fertile garlic plants was also reported. But flowering in some garlic clones is often

associated with the occurrence of bulbils developed in place of aborted flowers. Two fertile clones named OH and LH were used by researchers to study meiosis in garlic. Clone OH exhibited normal flowers and medium size bulbils in the inflorescence, whereas, the clone LH had an abundance of flowers accompanying many small bulbils. Moreover, this clone LH formed the original chromosome ring at meiosis (amphibivalent). In the clone OH majority of tested meiocytes formed eight bivalents at meiosis I; however, the presence of spherical chromatic bodies outside the spindle was observed. Pollen grains produced varied in size. In the clone LH, the first meiotic division proceeded routinely but two out of four bivalents developed a ring comprising four chromosomes. Such structure could be observed from diplotene via diakinesis and metaphase I. In metaphase I, the researchers observed ring-like configurations in the majority of cells, among which only one of them possessed an open ring. The formation of such rings resulted in the occurrence of lagging chromosomes visible during anaphase. The second division was usually normal and in the cells of both tested clones, two satellite chromosome pairs were observed. The study revealed a characteristic pattern of meiotic abnormalities in the clones.

Meiotic irregularities on hybrids with introgression from *A. sativum*

For a long time, *Allium cepa* and *Allium sativum* have not been sexually hybridized due to the large genetic distance and narrow gene pool of fertile garlic. Ohsumi *et al*. in 1993 reported the first interspecific hybrids between onion and garlic. They performed reciprocal crosses of onion and garlic but embryos were developed only when the onion was used as a female parent and was rescued by tissue culture. The hybrids regenerated possessed 16 chromosomes in somatic cells having two clearly distinguished satellite chromosomes. The researchers used onion cv. 'Sapporoki' in their study which did not possess satellite chromosomes, the obtained chromosomes were actually inherited from *A. sativum*. In addition, the study revealed no chromosomal elimination, and the pollen viability of the hybrid obtained was very low (2%). Yamashita *et al*. (2002) reported somatic hybrids of onion and sterile garlic. Originally onion and garlic has sixteen chromosome numbers, but the obtained hybrids were however classified as aneuploids with 40 or 41 chromosomes. The authors noted three intercalary satellite chromosomes and two subtelocentric chromosomes in tested somatic cells of the hybrids, inherited from both parents. Upon GISH analysis, 20 or 21 onion chromosomes and 17 garlic chromosomes, and three chromosomes comprising chromosomal regions from both parents were revealed. In addition, in the somatic hybrids, the presence of chimeric chromosomes originated from a translocation between chromosomes or chromosomal fusions revealed.

CONCLUSION

Over the years of studies, researchers tried to develop techniques to overcome hurdles between incompatible species for successful hybrid seed production. In leek, the major problem regarding sexual hybridization remains in the high rate of development of chiasmata (98%) located near the centromere. Such localized chiasmata avert the formation of multivalents during the process of meiosis. On the other side, in the case of garlic and its crosses with *A. cepa* had different behavior of meiotic chromosomes of the hybrids, as well as their pollen fertility, have not yet been investigated. In garlic sexual hybridization is rather difficult due to the high seed sterility of clones but utilizing wild relatives and novel fertile accessions is very important in increasing the available gene pool. To date, understanding of meiosis in F_1 hybrids between onion, garlic, and leek is limited so are its advanced generations. Therefore, an understanding of the meiotic process is crucial for further research on genetics and breeding of garlic and leek.

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