Meiosis in the Hybrid Between Beta vulgaris and Beta webbiana

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The three wild species of Beta included in the section Patellares viz. B. webbiana (2n = 18), B. procumbens (2n = 18) and B. patellaris (2n = 36) possess some desirable features in being monogerm, highly resistant to sugarbeet nematode, Cercospora leaf spot and curly top virus (see Oldemeyer 1954), all of which are absent in the sugarbeet. In order to transfer the genes for all or at least some of these characters from the wild species to the sugarbeet, hybrids have been produced between them. However, difficulty arises in raising the F₁ hybrids to maturity since they lack the ability to grow on their own roots. Most of the literature concerning the production of hybrids is described in Filutowicz and Kuzdowicz (1959). Although meiosis has been studied in some hybrids after the diakinesis stage, nothing is known about the pachytene stage so far. The present work comprises a cytological study of meiosis (pachytene to tetrad stage) in the F₁ hybrid between Beta vulgaris and B. webbiana.

Material and methods

Flower buds were obtained from the F₁ hybrid plants grafted on sugarbeet roots and growing in the greenhouse of Max-Planck-Institut, Rosenhof. Some of these hybrids had sugarbeet and others swiss chard for the female parent. The methods used for making the preparations is the same as described earlier for sugarbeet and the wild species (Walia 1968).

Results and discussion

Figures 1–4 represent pachytene stages in PMC’s of the F₁ hybrid. Most of the PMC’s showed clearly thin chromosomes and one or more thicker chromosomes in the same cell (Figs. 1–3). In the pachytene stage shown in Fig. 4 all the chromosomes are observed to be thin. Judging from the thickness alone one is led to speculate whether the thin chromosomes may be designated as univalents and the thicker ones as bivalents or not. Rarely, as seen in Fig. 2 (arrow) the end of a thick chromosome shows the presence of two telomeres. Moreover, a portion of the free lying chromosome in Fig. 3 reveals the presence of two strands suggesting thereby, that it is
Figs. 1-4, 8-12 are from an F₁ hybrid between sugarbeet and *B. webbiana*; Figs. 5-7 from F₁ hybrid between mangold and *B. webbiana*. 1-3, pachytene stages in PMC's showing bivalents and univalents. ×1500. 4, same showing only univalents. ×1500. 5 and 6, diakinesis. ×1500. 7, metaphase I. ×1500. 8, metaphase II. ×1500. 9, ‘tetrad’ with eleven cells. ×1000. Figs. 10-12, ‘dyads’. ×1500.
composed of two chromosomes which are paired with one another. Since
the development of pachytene and diplotene chromosomes in the sugarbeet is
known to take place asynchronously (Walia 1968), it may be surmised that
the thin chromosomes at pachytene stage of this hybrid represent univalents
after complete diplotene separation of the originally paired chromosomes.
Because of the same reason i.e. asynchrony in development, it may appear
that all the thin chromosomes seen in Fig. 4 are in an earlier stage in which
they have not yet begun to pair. However, the size of the cell and the
thickness of the mucilaginous wall suggest that it is more likely to be a
pachytene stage. In any case some amount of pairing does seem to take
place between the chromosomes of *B. vulgaris* and those of *B. webbiana*. Since
Levan (1945) observed pairing of meiotic chromosomes in a haploid
plant of sugarbeet, it could also be possible that each bivalent seen in the
PMC’s of the F₁ hybrids consists of two chromosomes of the same parent
paired with one another. However, because the morphological structure of
the paired chromosomes is not so clear, it is difficult to compare them with
the pachytene chromosomes of the parents described earlier (Walia 1968), so
as to decide whether they belong to one or to different parents.

It may be expected that the paired chromosomes observed in pachytene
should also be seen in diakinesis. Contrarily, 18 univalents could be clearly
counted at early stages of diakinesis. Sometimes two univalents were seen
to lie in a crosswise manner, thus simulating a bivalent with an interstitial
chiasma. But when observed under different foci, the two chromosomes were
seen merely to lie above one another. Similar doubts also arose with other
chromosomes at this stage, where they appeared to lie in some contact with
each other. The possibility exists that a few chromosomes which do pair in
pachytene fall apart completely in diplotene-diakinesis since no chiasmata were
observed between them. Savitsky and Gaskill (1957) describe one to five pairs
of chromosomes in diakinesis in microtome sections of the anthers of the F₁
hybrid. They also mention the presence of one or two terminal or interstitial
chiasmata. In the F₁ hybrid between sugarbeet and *B. procumbens*, Savitsky
(1960) reports a higher degree of chromosome pairing and chiasma frequency
than in the webbiana hybrids. In the squash preparations of the present
study, although some initial pairing is seen at the pachytene stage, the presence
of 18 univalents at diakinesis stage speaks at least for a partial inhomology
between the chromosomes of *B. vulgaris* and *B. webbiana*.

Some of the univalents may undergo fragmentation so that the number
of chromosomes seen at diakinesis increases beyond 18 (Figs. 5, 6). Savitsky
and Gaskill (1957) also recorded fragmentation of univalents at first meiotic
division.

Figure 7 shows the chromosomes at metaphase I. At anaphase I two
groups of chromosomes are seen at the poles and spindle fibers between them.
Lagging chromosomes are also seen at this stage. Figure 8 shows metaphase
II with the univalents scattered in the cytoplasm. At telophase II, the four chromosome groups situated at the poles organize into nuclei. The univalents not included in these nuclei give rise to supernumerary microspores. After wall formation therefore, 5–11 cells of varying sizes are cut off in a ‘tetrad’. The supernumerary microspores later give rise to sterile, empty pollen grains.

Very often meiosis II fails to take place. Cytokinesis occurs after telophase I resulting in the formation of dyads (Figs. 10–12). A dyad may or may not have a supernumerary cell in it. When a supernumerary cell is present, its development is seen to proceed in the following way: before wall formation takes place, one or more univalents become included in a small protrusion of the cytoplasm of the pollen mother cell (Fig. 11). At the time of cytokinesis this protrusion is cut off as a small cell in addition to the two large ones of the dyad (Fig. 12). Even after partitioning of the cytoplasm, persisting spindle fibres are sometimes seen running across the clear space separating the two portions of the cytoplasm (Fig. 10). Due to the formation of supernumerary cells and the uneven distribution of chromosomes on the two poles, it is speculated that each cell of the dyad should contain a variable number of chromosomes. In addition to dyads, Savitsky and Gaskill (1957) also observed the inclusion of all the chromosomes in a single nucleus after meiosis I, giving rise to a restitution nucleus. In the F₁ hybrid between B. vulgaris and B. procumbens, Savitsky (1910) attributes the semifertility of the hybrid to the formation of such restitution nuclei.

**Summary**

1. Paired as well as unpaired chromosomes were observed in pachytene.
2. Eighteen univalents are present at diakinesis; sometimes however, two univalents lying above one another give the impression of a bivalent.
3. Some of the univalents undergo fragmentation at diakinesis.
4. Meiosis II may fail to occur; dyads then form after the first division.
5. Irregularities in meiosis lead to the formation of supernumerary microspores.

**Literature cited**

Savitsky, Helen 1960. Meiosis in an F₁ hybrid between a Turkish wild beet (Beta vulgaris,
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