Ber. Ohara Inst. landw. Biol. Okayama Univ. 19 : 1~10 (1985)

# CYTOMORPHOLOGICAL STUDY OF EU-, HYPO- AND HYPER-TRIPLOIDS IN BARLEY[1]

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## INTRODUCTION

Triploids are useful for genetic research and practical breeding. They are a good source of primary trisomics (Tsuchiya 1960, 1964, Burnham 1962, Gill *et al.* 1970), and have been utilized to produce vigorous, bigger plants or seedless fruits. In barley, triploids have been produced by crossing between auto-tetraploid and diploid plants (Tsuchiya 1952a, b, 1958, 1960b, c, Derenne 1967), from colchicine doubled inter-varietal hybrids (Kerber 1954) and by stripe mosaic virus infection (Sandfaer 1970b, 1973, 1979). However, the frequency of the occurrence of triploids including hypo- and hyper-triploids has always been very low.

We happened to find a large number of triploid plants occurring in a cross between a tetraploid strain of Wase (Early) Golden Melon and a mixoploid strain of the semi-minute type (Prasad *et al.* 1983). The morphological and cytological description of these triploids including hypo- and hyper-triploids are presented in some detail in this paper.

## MATERIALS AND METHODS

A total of 389 viable $F_1$ hybrid seeds were obtained from a cross between a tetraploid strain of Wase (Early) Golden Melon which was produced by colchicine treatment (Ono 1946) and a mixoploid strain SM 5–1B characterized by six-rowed, hooded, semi-dwarf and uzu growth habit. Among them, 330 plants (85% of total) were found to be eu-triploid (3x), and 27 (6.9%) and 15 (3.9%) plants were hypo- and hyper-triploids, respectively. All these triploids, together with their parental strains, were used in this study. However, 14 tetraploids and 3 $F_1$ plants with $3x-2$ and $3x+2$ chromosomes obtained in the same cross were excluded from the materials of this study. From the 389 germinated seeds, 329 triploid plants survived and reached maturity.

Received November 29, 1984

1) Work was done when the senior author stayed at this institute during 1980–81 as a visiting research fellow of the Japan Society for the Promotion of Sciences.

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After collecting root tips for determining their chromosome numbers, these seedlings were grown in pots containing a 2 : 1 soil and vermiculite mixture for about three weeks, and then transplanted into the field. Sporocytes were collected in a 3 : 1 alcohol-acetic solution and preserved in 70% ethanol. Slides were prepared in 2% acetocarmine. Pollen grains were stained in a 2% iodine solution for determining their fertility.

## RESULTS

### 1. *Morphology and Fertility*

At the early growing stage, all the triploid plants were slender with narrow and short leaves. They had fewer seminal roots and much shorter coleoptiles than 4x Wase Golden Melon. This was probably because their original seeds were quite thin and light-weight. At the later stage of growth, however, the eu-triploids (3x) became very vigorous. As shown in Table 1, the plants were about 20% taller and

TABLE 1. Comparison of various characters among the parental forms, 4x Wase Golden Melon and a mixoploid SM 5-1B, and the three types of hybrid plants, eu-, hypo- and hyper-triploids

| Characters | Parents | | Hybrids (selfed) | | |
|---|---|---|---|---|---|
| | Wase Golden 4x | SM 5-1B* | 3x | 3x−1 | 3x+1 |
| No. seminal roots | 6.8±0.4 | 5.0±0.7 | 3.5±0.1 | 3.4±0.3 | 3.0±0.4 |
| Coleoptile length (cm) | 3.9±0.5 | 0.7±0.1 | 2.0±0.5 | 2.0±0.1 | 2.0±0.2 |
| No. fertile tillers | 7.1±0.6 | 6.9±1.1 | 11.5±0.4 | 3.7±0.5 | 4.2±0.7 |
| Stem length (cm) | 80.5±1.6 | 20.8±1.4 | 97.3±0.7 | 63.1±4.2 | 67.9±1.6 |
| Length of uppermost stem-internode (cm) | 40.1±1.2 | 10.4±0.3 | 40.8±0.4 | 26.3±2.5 | 23.0±3.4 |
| Flag leaf length (cm) | 15.8±0.7 | 10.3±0.5 | 18.0±0.3 | 16.4±1.4 | 15.4±2.6 |
| Flag leaf breadth (cm) | 1.6±0.1 | 2.3±0.2 | 1.8±0.3 | 1.5±0.1 | 1.5±0.2 |
| Spike length (cm) | 6.7±0.2 | 5.6±0.2 | 9.0±0.1 | 6.7±0.5 | 6.2±0.5 |
| No. spikelets/ear | 21.4±0.6 | 66.0±1.4 | 28.7±0.3 | 20.6±1.2 | 20.6±1.9 |
| Seed fertility (%) | 89.2 | 83.3 | 9.9 | 7.3 | 6.8 |
| Pollen fertility (%) | 84.1 | 77.5 | 52.3 | 27.8 | 15.9 |

* Mixoploid (dwarf), uzu type with six-rowed spikes.

had 60% more fertile tillers than the 4x Wase Golden Melon. Also, they had larger spikes with more spikelets per spike. Leaves were longer and broader.

Both the hypo-triploids (3x−1) and hyper-triploids (3x+1) were found to be less vigorous than 4x Wase Golden Melon and eu-triploid hybrid plants. The plant height of these aneuploids was about 80% that of 4x

Wase Golden Melon and the number of tillers was only 56%, but the development of spikes in these two types of aneuploids was similar to that of the 4x Wase Golden Melon.

Seed set in the triploid and aneuploid plants was greatly reduced. Eu-triploids produced 3 seeds per spike while hypo- and hyper-triploids bore only 1.5 seeds per spike. Percentage of seemingly good pollen grains was about one half in eu-triploid plants on an average, while those of $3x-1$ and $3x+1$ were 28% and 16%, respectively.

2. *Cytological Observation*

(1) *Metaphase I (MI)*

a) *Chromosome configurations*

Triploid (3x): Number of trivalents ranged from 1 to 7 while bivalents and univalents ranged from 0 to 6 (Table 2). The most pre-

TABLE 2. Frequencies of different types of chromosome configurations at MI in eu-triploid, hypo-triploid and hyper-triploid hybrids

| Eu-triploid | | Hypo-triploid | | Hyper-triploid | |
|---|---|---|---|---|---|
| Chromosome configuration | % | Chromosome configuration | % | Chromosome configuration | % |
| $7^{III}$ | 11.8 | $6^{III}+1^{II}$ | 12.6 | $7^{III}+1^{I}$ | 5.5 |
| $6^{III}+1^{II}+1^{I}$ | 32.4 | $6^{III}+2^{I}$ | 0.1 | $6^{III}+1^{IV}$ | 5.5 |
| $5^{III}+2^{II}+2^{I}$ | 31.8 | $5^{III}+2^{II}+1^{I}$ | 38.1 | $6^{III}+2^{II}$ | 7.0 |
| $4^{III}+3^{II}+3^{I}$ | 17.4 | $5^{III}+1^{II}+3^{I}$ | 1.7 | $6^{III}+1^{II}+2^{I}$ | 9.5 |
| $3^{III}+4^{II}+4^{I}$ | 5.0 | $4^{III}+3^{II}+2^{I}$ | 29.1 | $5^{III}+1^{IV}+1^{II}+1^{I}$ | 9.5 |
| $2^{III}+5^{II}+5^{I}$ | 1.1 | $4^{III}+2^{II}+4^{I}$ | 1.2 | $5^{III}+1^{IV}+3^{I}$ | 0.5 |
| $1^{III}+6^{II}+6^{I}$ | 0.4 | $3^{III}+4^{II}+3^{I}$ | 13.3 | $5^{III}+3^{II}+1^{I}$ | 20.7 |
| $3^{III}+3^{II}+6^{I}$ | 0.1 | $3^{III}+3^{II}+5^{I}$ | 0.4 | $5^{III}+2^{II}+3^{I}$ | 6.8 |
| | | $2^{III}+5^{II}+4^{I}$ | 2.6 | $5^{III}+1^{II}+5^{I}$ | 0.5 |
| | | $1^{III}+6^{II}+5^{I}$ | 0.8 | $4^{III}+1^{IV}+2^{II}+2^{I}$ | 8.2 |
| | | $7^{II}+6^{I}$ | 0.1 | $4^{III}+3^{II}+4^{I}$ | 4.8 |
| | | | | $4^{III}+4^{II}+2^{I}$ | 9.2 |
| | | | | $3^{III}+1^{IV}+3^{II}+3^{I}$ | 2.8 |
| | | | | $3^{III}+5^{II}+3^{I}$ | 3.5 |
| | | | | $*3^{III}+6^{II}+1^{I}$ | 0.7 |
| | | | | $*3^{III}+1^{IV}+4^{II}+1^{I}$ | 0.7 |
| | | | | $2^{III}+1^{IV}+4^{II}+4^{I}$ | 2.3 |
| | | | | $2^{III}+6^{II}+4^{I}$ | 1.0 |
| | | | | $1^{III}+1^{IV}+5^{II}+5^{I}$ | 0.5 |
| | | | | $1^{III}+7^{II}+5^{I}$ | 0.3 |
| | | | | $8^{II}+6^{I}$ | 0.5 |
| Total | 100.0 | | 100.0 | | 100.0 |
| No. of cells observed | 720 | | 730 | | 400 |

* Unexpected configurations resulting from pairing between non-homologous chromosomes.

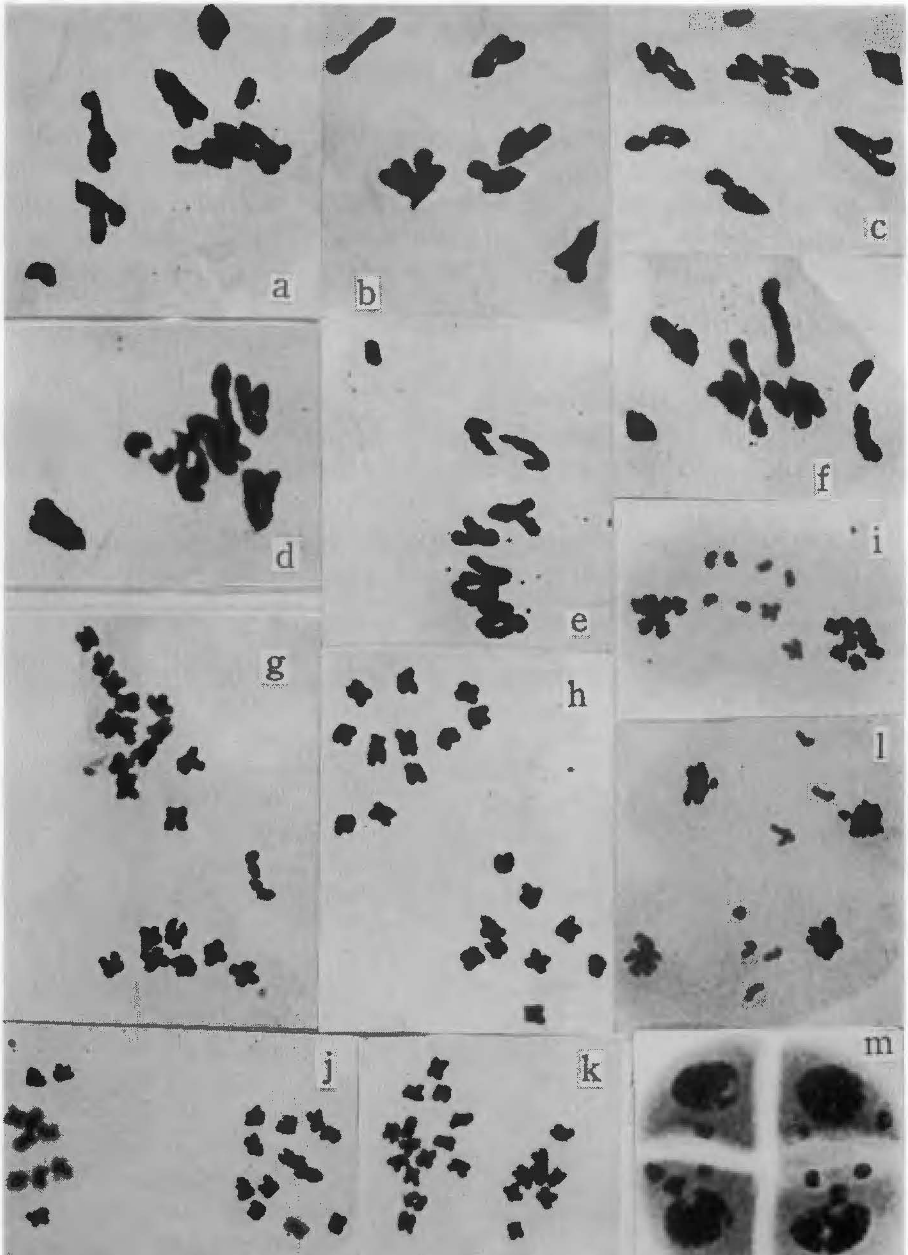


FIG. 1. Meiotic configurations in eu-triploids, hypo-triploids and hyper-triploids.

a. $5^{III}+2^{II}+2^{I}$ at MI in 3x
b. $7^{III}$ at MI in 3x
c. $5^{III}+2^{II}+1^{I}$ at MI in $3x-1$
d. $6^{III}+1^{II}$ at MI in $3x-1$
e. $5^{III}+1^{IV}+1^{II}+1^{I}$ at MI in $3x+1$
f. $6^{III}+2^{II}$ at MI in $3x+1$
g. 13–1–7 separation at AI, precocious centromere division
h. 11–9 separation at AI
i. 8–5–7 separation at AI, precocious centromere division
j. 12–10 separation at AI
k. 14–8 separation at AI
l. laggards at AII
m. micro-nuclei in spores

valent configurations were $6^{III}+1^{II}$ (32.4%) and $5^{III}+2^{II}+2^{I}$ (31.8%, Fig. 1, a). The configuration $7^{III}$ (Fig. 1, b) was observed in 11.8% of cells. The least frequent configuration was $3^{III}+3^{II}+6^{I}$.

Hypo-triploid (3x−1) : Eleven types of chromosome configurations were observed in the hypo-triploid plants (Table 2). Trivalents ranged from 0 to 6 while bivalents and univalents ranged from 0 to 7 and 0 to 6, respectively. The most frequent configuration was $5^{III}+2^{II}+1^{I}$ accounting for 38.1% of the total number (Fig. 1, c), followed by $4^{III}+3^{II}+2^{I}$, $3^{III}+4^{II}+3^{I}$, $6^{III}+1^{II}$ (Fig. 1, d), $2^{III}+5^{II}+4^{I}$, and others (Table 2).

Hyper-triploid (3x+1) : Twenty one different chromosome configurations were recognized at MI of 400 PMC's examined (Table 2). In this plant type, one chromosome was in the tetrasomic condition and thereafter, quadrivalents were observed in 30% of the cells, besides trivalents (0 to 7), bivalents (0 to 8) and univalents (0 to 6). The most frequent configuration was $5^{III}+3^{II}+1^{I}$ which was observed in 20.7% cells. Other prevalent configurations were $5^{III}+1^{IV}+1^{II}+1^{I}$ (Fig. 1, e), $6^{III}+1^{II}+2^{I}$, $4^{III}+4^{II}+2^{I}$, $4^{III}+1^{IV}+2^{II}+2^{I}$, and $6^{III}+2^{II}$ (Fig. 1, f). Two unexpected configurations, namely, $3^{III}+1^{IV}+4^{II}+1^{I}$ and $3^{III}+6^{II}+1^{I}$, were observed at a frequency of 0.7% each (Table 2). Such configurations are possible if pairing occurs between non-homologous chromosomes.

b) *Trivalent types*

Seven types could be distinguished among 2467 trivalents examined at MI of eu-triploid, hypo- and hyper-triploid plants. Table 3 shows the percent frequency of each type. There was an appreciable difference among the three triploid types, but the V-shape is the most frequent, and the Y-shape is the least frequent in all three types.

TABLE 3. Frequencies of different types of trivalent at MI in eu-triploid, hypo-triploid and hyper-triploid hybrids

| Plant | | Trivalent types | | | | | | | Total no. of Trivalents |
|---|---|---|---|---|---|---|---|---|---|
| | | V-shape | Rod-shape | Ring-rod | Frying-pan | J-shape | Y-shape | α-shape | |
| Eu-triploid | No. (%) | 442 (63.8) | 128 (18.5) | 74 (10.7) | 28 (4.0) | 14 (2.0) | 4 (0.6) | 3 (0.4) | 693 (100.0) |
| Hypo-triploid | No. (%) | 526 (70.0) | 109 (14.6) | 60 (8.0) | 30 (4.0) | 17 (2.3) | 8 (1.1) | 0 ( 0 ) | 750 (100.0) |
| Hyper-triploid | No. (%) | 705 (68.8) | 204 (19.9) | 46 (4.5) | 16 (1.6) | 35 (3.4) | 3 (0.3) | 15 (1.5) | 1024 (100.0) |
| Total | No. (%) | 1673 (67.8) | 441 (17.9) | 180 (7.3) | 74 (3.0) | 66 (2.7) | 15 (0.6) | 18 (0.7) | 2467 (100.0) |

(2) *Anaphase I (AI)*

Eu-triploid (3x) : Of various types of chromosome separations at AI, the most frequent was 11–10 (22.3%) (Table 4). Some of the AI cells had 7 chromosomes at one or both poles, such as 14–7, 13–1–7 (Fig. 1, g), 7–7–7. Lagging chromosomes ranging from 1 to 7 were observed in 66.6% of the cells. Some of the laggards showed precocious centromere division (Fig. 1, g).

TABLE 4. Frequencies of different types of chromosome separation at AI in eu-triploid, hypo-triploid and hyper-triploid hybrids

| Eu-triploid | | Hypo-triploid | | Hyper-triploid | |
|---|---|---|---|---|---|
| Chromosome separation | % | Chromosome separation | % | Chromosome separation | % |
| 11–10 | 22.3 | 10–10 | 17.6 | 11–11 | 14.3 |
| 12–9 | 6.3 | 11–9 | 24.1 | 12–10 | 13.2 |
| 13–8 | 4.1 | 12–8 | 7.1 | 13–9 | 4.5 |
| 14–7 | 0.7 | 13–7 | 1.3 | 14–8 | 1.9 |
| 11–1–9 | 14.8 | 10–1–9 | 18.5 | 15–7 | 0.4 |
| 13–1–7 | 1.9 | 11–1–8 | 6.5 | 11–1–10 | 14.7 |
| 10–1–10 | 8.1 | 12–1–7 | 1.1 | 12–1–9 | 6.8 |
| 12–1–8 | 1.1 | 13–1–6 | 0.2 | 13–1–8 | 2.3 |
| 10–2–9 | 14.8 | 9–2–9 | 3.9 | 14–1–7 | 0.8 |
| 11–2–8 | 3.0 | 10–2–8 | 4.9 | 10–2–10 | 6.4 |
| 9–3–9 | 8.1 | 11–2–7 | 1.9 | 11–2–9 | 11.7 |
| 10–3–8 | 3.7 | 9–3–8 | 6.0 | 12–2–8 | 2.3 |
| 11–3–7 | 1.1 | 10–3–7 | 2.2 | 13–2–7 | 1.1 |
| 10–4–7 | 1.5 | 8–4–8 | 1.1 | 10–3–9 | 7.9 |
| 11–4–6 | 0.7 | 9–4–7 | 2.4 | 11–3–8 | 1.1 |
| 9–4–8 | 3.0 | 8–5–7 | 0.8 | 12–3–7 | 0.8 |
| 9–5–7 | 0.7 | 9–5–6 | 0.2 | 9–4–9 | 3.0 |
| 8–6–7 | 3.0 | 10–5–5 | 0.2 | 10–4–8 | 4.1 |
| 7–7–7 | 1.1 | | | 11–4–7 | 0.8 |
| | | | | 9–5–8 | 1.1 |
| | | | | 8–6–8 | 0.4 |
| | | | | 10–6–6 | 0.4 |
| Total | 100.0 | | 100.0 | | 100.0 |
| No. of cell observed | (270) | | (535) | | (265) |

Hypo-triploid (3x−1) : Data shown in Table 4 indicate that there were 18 different types of chromosome separations. The most frequent one was 11–9 (24.1%, Fig. 1, h). AI cells showing 7 chromosomes at one pole, such as 8–5–7 (Fig. 1, i), 9–4–7 and 13–7, accounted for 9.7%. About 50% cells showed laggards ranging from 1 to 5.

Hyper-triploid (3x+1): The most frequent separation was 11-1-10 which was observed in 14.7% cells (Table 4). Other prevalent separations were 12-10 (Fig. 1, j), 11-11, 11-2-9 and 10-3-9. Laggards ranged from 1 to 6 and were observed in 65.6% of the cells.

(3) *Anaphase II (AII)*

Tetrad and spores: At AII, laggards were observed at a considerable frequency of cells (Fig. 1, l). At the tetrad (quartet) stage, pentads and hexads, which formed micropollen were also observed. Triads were also observed in a few cells. Micro-nuclei (Fig. 1, m) ranging from 1 to 3% per spore were observed in most of the spores.

## DISCUSSION

It has been generally recognized that triploids in barley occur rather rarely (Smith 1951, Nilan 1964). Tsuchiya (1960) stated that the production of triploids from the crosses between 4x × 2x was very diffiicult owing to the great difficulty in germination of the hybrid seed. He could obtain only 31 germinated plants from 2721 crossed florets. However, we succeeded in producing as many as 329 triploids including eu-, hypo- and hyper-triploids from 1009 crossed florets. Table 5 compares our data with that of Tsuchiya concerning the fertility and germination of the seeds derived from a 4x × 2x cross of barley. As is apparent in Table 5, the seed germination percentage was only 3.16 in Tsuchiya's experiment whereas it was 65.9 in ours, although the seed fertility itself was not so much different between the two experiments. The cause of the difference is unknown, but it may be attributable to the environmental

TABLE 5. Comparison of our data with Tsuchiya's (1960) regarding the fertility, germination of the seeds and frequency of triploids resulted from a 4x × 2x cross

| Seed size class | Mean 1000 seed wt (g) | Florets crossed | Seeds obtained | Fertility (%) | Germination | | Survival | | Triploids matured | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | No. | (%) | No. | (%) | No. | Per cent of total crossed florets |
| Large | 31.3 | 590 | 21 | | 18 | 85.7 | 17 | 80.9 | 5 | |
| Medium | 7.0 | | 321 | | 310 | 96.6 | 284 | 88.5 | 284 | |
| Small | 2.5 | | 248 | | 61 | 24.6 | 40 | 16.1 | 40 | |
| Tiny | 0.6 | 419 | 0 | | — | — | — | — | — | |
| Ours (subtotal)* | | 1009 | 590 | 58.47 | 389 | 65.9 | 341 | 57.80 | 329 | 32.61 |
| Tsuchiya's** | | 2721 | 980 | 36.02 | 31 | 3.2 | 31 | 3.16 | 31 | 1.14 |

* Prasad *et al.* 1983. Ber. Ohara Inst. landw. Biol. 18(3): 175-182.

** Tsuchiya, T. 1960. Seiken Ziho 11: 29-37.

conditions during seed development, rather than to a genotypic difference in the parental materials.

It is certain that triploid plants were produced by fertilization of diploid egg of 4x Wase Golden Melon with haploid male gamete of mixoploid strain SM 5–1B, while the origin of aneuploids may be attributed to the imbalance of chromosomes in the egg, as the egg can tolerate to some extent the chromosomal imbalance (Burnham 1962). In the study of meiosis in the pollen mother cells of Wase Golden Melon (4x), there occurred 1 to 3 laggards in 20% of AI cells, and unequal separations such as 15–13 and 16–12 were also observed. If these abnormalities occur in megaspore mother cells, eggs with $2x-1$, $2x+1$, $2x-2$ or $2x+2$ may be produced, and they may give rise to various kinds of aneuploids after fertilization with a normal male gamete.

Triploids may be called multiple trisomics. They show different types of chromosome associations such as trivalents, bivalents and univalents as has been observed in the present study and by other workers (Tsuchiya 1952a, Nilan 1964). In case of hyper-triploids, one chromosome is in a tetrasomic condition with a quadrivalent at MI. However, two unexpected configurations ($3^{III}+1^{IV}+4^{II}+1^{I}$ and $3^{III}+6^{II}+1^{I}$) were also observed in the present study. Such configurations occur due to pairing between non-homologous chromosomes. Illegitimate pairing between non-homologous chromosomes has been reported by Tsuchiya (1952a, b) in triploid and hypo-triploid plants. Association of non-homologous chromosomes in barley has been observed by Sadasivaiah and Kasha (1971, 1973) in monoploids (7 chromosomes) in barley and by Kasha *et al.* (1975) in 16-chromosome barley. Non-homologous pairings indicate that there are very few regions of duplications among barley chromosomes (Kasha and Reinbergs 1975). Different chromosome configurations occur by pairing, chiasma formation and orientation of chromosomes at MI. Among the various types of trivalents, the V-shape was the most frequent in this study. Similar results have also been reported by Tsuchiya (1952a, b).

In the present study, 7 chromosomes were found at one or both poles in a considerable number of cells. They were expected to produce fertile spores. Lagging chromosomes at AI and AII produce micro-pollen and micro-nuclei. Tsuchiya (1952a) observed 83% abnormal tetrads including pentads, hexads and triads. Spores with micro-nuclei may be non-functional.

## SUMMARY

A cross between 4x Wase Golden Melon and a mixoploid strain of uzu type SM 5–1B gave 590 seeds out of which 389 seeds germinated.

Three hundred and thirty eu-triploids (3x), 27 hypo-triploids (3x−1) and 15 hyper-triploids (3x+1) were found among them, but a total of 329 triploids or 32.61% of 1009 crossed seeds finally reached maturity.

Seeds of the triploids were thin and light in weight and gave rise to weak and slender seedlings, but eu-triploids became more vigorous than the 4x Wase Golden Melon at later stages of growth. Seed fertility of all the triploids was below 10%. At MI, trivalents, bivalents and univalents were common chromosome configurations. As expected, a quadrivalent configuration was observed in 30% MI cells of hyper-triploids. Two unexpected configurations ($3^{III}+1^{IV}+4^{II}+1^{I}$, $3^{III}+6^{II}+1^{I}$) were also observed indicating pairing between non-homologous chromosomes. The V-shape was the most frequent type of trivalent and the Y-shape was the least frequent. Unequal separation, lagging of chromosomes and precocious centromere division were often observed at AI. At quartet stage, triads, pentads and hexads were also observed in addition to tetrads.

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