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CYTOGENETICS OF INTERGENERIC HYBRIDS BETWEEN DURUM WHEAT (*TRITICUM TURGIDUM* L.) WITH *THINOPYRUM INTERMEDIUM* AND SUB-SPECIES *ACUTUM, GLAUCUM, PULCHERRIMUM, TRICHOPHORUM, VARNENSE*

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Abstract

Towards diversifying the germplasm base available for durum wheat (*Triticum turgidum*) the production and morpho-cytogenetic categorization of F_1 hybrid combinations between durum wheat cultivars and *Thinopyrum intermedium* and its sub-species (*acutum, glaucum, pulcherrimum, trichophorum, varnense*) are reported. All F_1 hybrids were mitotically stable with 2n=5x=35 chromosomes, expressed a co-dominant phenotype and exhibited mean meiotic metaphase I chromosomal associations, that in general, do not support alien genetic introgression into the A and / or B genomes of durum wheat *via* recombinational exchange. This F_1 perennial germplasm has formed the basis to generate backcross derivatives, amphiploids, and shall enable the application of genetic manipulation strategies for transferring useful genes from select combinations for durum wheat improvement. Backcross 1 derivatives (F_1 / durum wheat) were cytologically stable with 2n=7x=49 but exhibited poor self-fertility hampering their maintenance as genetic stocks. Amphiploids however had good stability at the C-0 stage with 2n=10x=70 chromosomes, were self-fertile and set healthy seed progeny. Subsequent generations derived from C-0 seed gave derivatives that were closely true to the C-0 type in composition, as well as combinations that indicated genomic loss where all combinations possessed 56 chromosomal progeny. Aneuploidy, both hyper- and hypo-ploidy, was rampant across both the 56 and 70 chromosome progenies.

Introduction

Sustaining agricultural productivity has been associated with genetic diversity and durability of stress resistances (Mujeeb-Kazi, 1998). For wheat improvement the genetic diversity resides in various species of the primary, secondary and tertiary Triticeae gene pools (Jiang *et al*., 1994). The utilization of this diversity has selective protocols associated with intergeneric or interspecific methodologies. Genes from these species when introgressed and pyramided together can be anticipated to provide crop yield stability by complementing the durability resistance contributed by conventional major and/or minor genes. Numerous wide hybrids have been described during the last decade and a half (Sharma & Gill, 1983; Mujeeb-Kazi & Bernard, 1985; Wang, 1989; Jiang *et al*., 1994. Mujeeb-Kazi & Hettel, 1995; Sharma 1995) essentially due to the circumvention of species crossability barriers coupled with embryo rescue and plantlet regeneration protocols. The hybridization emphasis however, has mainly been with bread wheat x alien species, due to the fact that bread wheat is the major cereal crop across several global mega-environments. Its cultivated hectarage significantly surpasses that of

durum wheat. Though less, durum wheat cultivation does have its special utilization significance, but faces vulnerability to various biotic/abiotic stresses. Some notable stress constraints are lack of, or further need for resistances/tolerances to *Fusarium graminearum, Helminthosporium sativum*, barley yellow dwarf virus, *Septoria nodorum*, drought and salinity tolerance. These constraints can be addressed by exploiting the genetic diversity within the Triticeae gene pools. The first step however, is generation of durum wheat x alien species hybrids, validation and characterization of the germplasm, with ultimate exploitation of the hybrid combinations for agricultural practicality. We describe here the production of intergeneric hybrids of the *Th. intermedium* sub-species group with various durum cultivars, validate them with morphological-cytogenetic documentation and emphasize their potential contribution to practical sustainable crop production outputs exemplified by advancing the F_1 combinations by backcrossing and amphiploid induction.

Materials and Methods

Germplasm: Seeds of the alien Triticeae species used in this hybrid production study were obtained from late Dr. D. R. Dewey, USDA / ARS Logan, Utah and germinated in Jiffy-7 peat pellets. After 6-weeks of juvenile growth, the seedlings were vernalized in a growth chamber under environmental regimes of 8h diffuse light for 8 weeks at 8°C. Following vernalization, the seedlings were transplanted into 20 cm plastic pots filled with a 2:1:1 (soil: sand: peat) steam-sterilized mix and maintained under greenhouse conditions of 16h of natural daylight and 24°C/14°C day/night temperatures. In the same greenhouse, five plantings in pots (four plants/pot) of several *Triticum turgidum* cultivars were made, 15 days apart. The durum cultivar seeds were obtained from CIMMYT's wheat germplasm bank at El Batan, Mexico, the location at which the major part of this study was conducted.

Hybrid production: Spikes of the durum wheat cultivars were emasculated, pollinated by the perennial species pollen 1 to 3 days after emasculation and treated once daily for 3 days with 75ppm gibberellic acid. From the seed set, the embryos were excised 13 to 15 days after pollination and cultured on a special medium for small embryos (Taira & Larter, 1978). These, and subsequent procedures associated with embryo differentiation, plantlet growth, transfer to Jiffy-7 pots, and transplanting to a potted soil mix in the greenhouse, were similar to those reported by Mujeeb-Kazi *et al*., (1987, 1989). The environmental growth regimes were identical to those maintained for the growth of the parental germplasms in this study.

F_1 cloning, somatic/meiotic sampling and colchicine treatment: After assuming vigorous growth, each F_1 hybrid was physically divided into 4 plants, and the clones allowed to grow into vigorous plants. From each clone of each F_1 hybrid, root-tips were collected for somatic cytology and C-banding. The cytological procedures were essentially similar to those described by Mujeeb-Kazi & Miranda, (1985) and Jahan *et al*., (1990).

Spikes for meiotic analyses were collected in early morning hours (8:00-9:00 a.m.), fixed in Carnoy's (6:3:1, absolute alcohol : chloroform : acetic acid) for 48-72h, and stored under refrigeration (4°C) in 70% alcohol until use. Anthers at metaphase 1 were

stained in alcoholic-acid-carmine for several days, and squashed in 45% acetic acid with a drop of 2% aceto-carmine to enhance the coloration. Meiotic chromosome associations were analyzed at metaphase I. Cytological photography was done of quality representative cells on a black and white high contrast film using a special green/yellow filter combination. One clone of each combination was treated with a colchicine (0.05%) and 2.0% di-methyl-sulfoxide (DMSO) solution using the aerated root treatment protocol of Mujeeb-Kazi *et al*., (1987) in order to produce amphiploids.

Spike categorization and backcross-I seed production: Five fully emerged spikes from each F_1 hybrid and its corresponding durum parent were characterized for spike morphology. Between 5 to 10 self-sterile F_1 spikes were further pollinated with *T. turgidum* cultivars to produce the equivalent of a backcross-I (BC_I) progeny.

Results and Discussion

Hybrid production and spike morphology: Crossing between durum cultivars and perennial Triticeae species (Table 1) leading to seed set and putative hybrid embryo excision ranged from 30.0 to 45.5%. All of these high frequency hybrid recovery combinations possessed well-defined embryos, copious endosperm, and produced rapidly growing vigorous regenerants. Percentages of these hybrids were 37.2 (ssp. *acutum*), 44.0 (ssp. *glaucum*), 45.5 (ssp. *intermedium*), 43.8 (ssp. *pulcherrimum*), 30.0 (ssp. *trichophorum*) and 41.9 (ssp. *varnense*). Several cultivars produced hybrids with *Th. intermedium*, its five sub-species. The durum cultivars combined with the above species (Table 1) were high yielding durums, hence desirable alien introgressions may be anticipated to yield practical out-puts in a relatively short time frame.

Table 1. Hybridization details of successful combinations of *Triticum turgidum* L., cultivars with *Thinopyrum intermedium* and its sub-species under greenhouse conditions.

T. turgidum cultivar	Alien species	Florets pollinated	Seeds set	No. of embryos excised	Plants obtained
Cocorit 71	spp. *acutum*	48	33	29	17
Yavaros	spp. *acutum*	52	38	33	18
Arlin	spp. *acutum*	48	31	21	13
Cappelli	spp. *acutum*	51	43	39	26
Chen	spp. *glaucum*	100	74	55	44
Cocorit 71	spp. *intermedium*	128	98	68	56
Yavaros 79	spp. *intermedium*	88	70	59	43
Cappelli	spp. *intermedium*	20	14	10	8
Cocorit 71	spp. *pulcherrimum*	54	32	21	15
Mexicali 75	spp. *pulcherrimum*	96	73	62	40
Yavaros 79	spp. *pulcherrimum*	74	62	55	43
Mexicali 75	spp. *trichophorum*	24	12	7	3
Croc	spp. *trichophorum*	22	14	9	5
Dvergand	spp. *trichophorum*	46	33	26	18
Laru	spp. *trichophorum*	24	18	11	7
Cappelli	spp. *trichophorum*	24	16	12	9
Altar 84	Spp. *varnense*	46	40	32	24
Cappelli	spp. *varnense*	54	38	28	19
Laru	spp. *varnense*	30	22	17	13
Mexicali 75	spp. *varnense*	30	20	15	11

Crossing success could be further enhanced by incorporating procedural manipulations involving early (bud-) and multiple pollinations, pre- and post-pollination hormonal applications (gibberellic acid and 2,4-di-chlorophenoxy-acetic acid), coupled with culture-media formulations (e.g. Taira & Larter, 1978; media for small embryos) where all may as a package significantly modify hybridization outputs.

In bread wheat/alien species hybridization crossability frequencies have received significant mention. Some cultivars like Chinese Spring have been favored since they hybridize readily (Falk & Kasha, 1981) due to the presence of crossability genes *kr1, kr2, kr3* on homoeologous group 5 (Fedak & Jui, 1982; Riley & Chapman 1967) and subsequently the contribution of the *kr4* loci towards improved crossability (Luo *et al*., 1992; Yen *et al*., 1988). Cultivars Asakazekomugi and Fukuhokomugi have better agronomic type than Chinese Spring and are also highly crossable (Jauhar, 1995a, b). In durums, cultivar variability for crossability with rye is present (Immonen *et al*., 1993). Current observations support this durum crossability diversity but for the durum/alien species combinations attempted by us all have been successful. In BW however, some crosses never set seed leading us to infer that crossability control in BW is more stringent than that of durum wheat cultivars.

Phenotype of F_1 hybrids: All hybrids were perennial, possessed a vigorous growth habit and tillered profusely. Each hybrid was self-sterile, but female fertile and set various frequencies of backcross I seed (BC_1) when pollinated by durum cultivars.

A co-dominant wheat/alien species phenotype was a common characteristic (Table 2, Fig. 1) of all hybrids, substantiating alien genetic expressivity in the durum background. The modified F_1 phenotype is advantageous to observe, since this permits the possible selection of beneficial alien characteristics in durum wheats requiring such improvements. The phenotypic parameters generally affected included spike length, spike size, spike width, reduced awn length to even awn absence, lax heads with greater internodal distance and an occasional presence of pubescence (Fig. 1). An intermediate phenotype has been a common observation for several intergeneric hybrids within the Triticeae and has been considered a valid morphological indicator of alien genetic expressivity in a wheat background (Mujeeb-Kazi *et al*., 1995).

Somatic and meiotic cytology: Two satellited chromosomes, (1B and 6B) present as pairs in euploid *T. turgidum* were identified for each F_1 hybrid. Satellites of the alien species were not observed in some hybrid combinations as a consequence of amphiplasty. A mere chromosome count and satellite detail is often enough to initially validate hybridity (Figs. 2a-f). However, when alien species with similar ploidy levels are involved in crosses, additional diagnostics like chromosome banding or *in situ* hybridization become necessary. Unequivocal proof of hybridity however, comes from meiotic analyses that further provide an accurate index of the introgression methodology to be adopted for affecting alien genetic transfers to durum wheats. The meiotic data of Table 3 elucidates the constraints of homoeologous transfers *via* recombination. The *Th. intermedium* species and its sub-species possess two closely related genomes with a distinctly different third genome. Hence, the meiotic associations require careful evaluation before any conclusion is reached to suggest a wheat alien chromosomal union to facilitate a genetic transfer interpretation leading to the crops improvement (Figs. 3a-f).

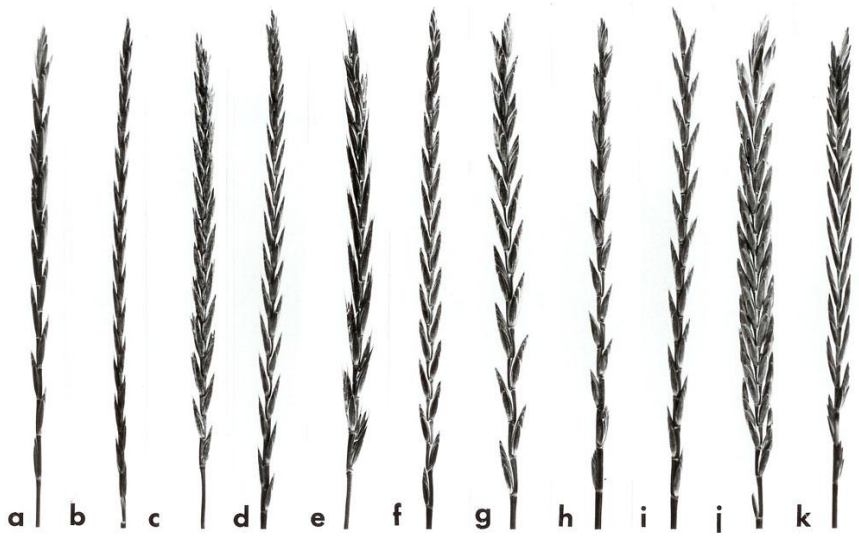

Fig. 1a - **k**. F_1 spikes of intergeneric hybrid combinations involving *Triticum turgidum* cultivars (cv.) and perennial Triticeae sub-species (ssp) of the genus *Thinopyrum* (*Th*) *intermedium* showing in **a.** cv. Arlin / ssp *acutum*, **b**. cv. Cocorit 71 / ssp *acutum*, **c.** cv. Croc / ssp *glaucum*, **d**. cv. Cocorit 71 / *Th. intermedium*, **e.** cv. Yavaros / *Th. intermedium*, **f.** cv. Cappelli / *Th. intermedium*, **g**. cv. Mexicali 75 / ssp *pulcherrimum*, **h.** cv. Dvergand / ssp *trichophorum*, **i**. cv. Laru / ssp *trichophorum*, **j.** cv. Altar 84 / ssp *varnense*, **k.** cv. Cappelli / ssp. *Varnense*.

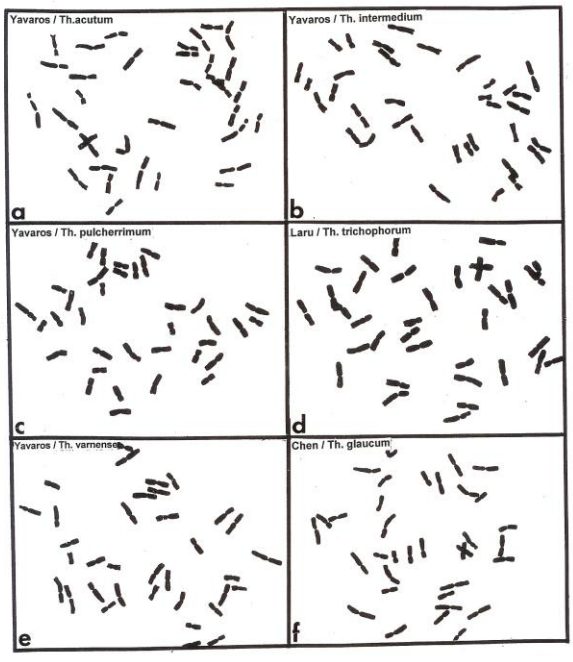

Fig. 2a to **f.** Somatic chromosomes of the hybrid cross combinations between durum and perennial Triticeae sub-species (ssp) of the genus *Thinopyrum* (*Th*) *intermedium* showing in **a**.Yavaros / *Thinopyrum acutum* (2n=5x=35), **b.** Yavaros / *Th. intermedium* (2n=5x=35), **c.** Yavaros / *Th. pulcherrimum* (2n=5x=35), **d.** Laru / *Th. trichophorum* (2n=5x=35), **e.** Yavaros / *Th. varnense* (2n=5x=35), and **f.** Chen / *Th. glaucum* (2n=5x=35).

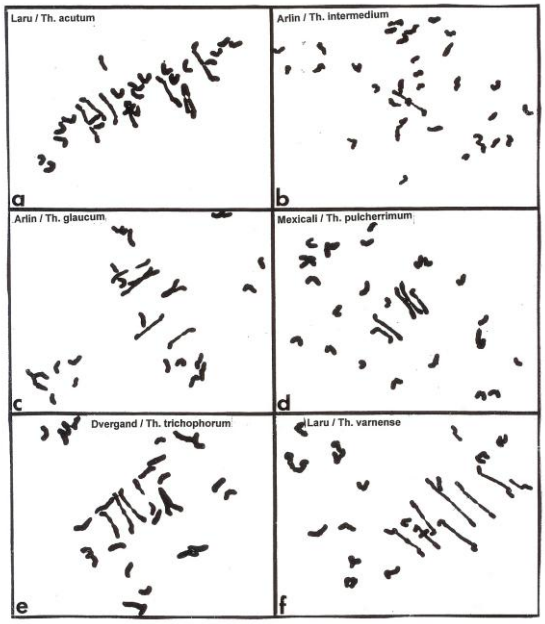

Fig. 3a to **f.** Mean meiotic metaphase I chromosomal relationships in some hybrids amongst durum and perennial Triticeae sub-species (ssp) of the genus *Thinopyrum* (*Th*) *intermedium* showing in **a.** Laru / *Th. acutum* (19_I +5_{II} + 2_{III}), **b.** Arlin / *Th. intermedium* (31_I + 2_{II} rods), **c.** Arlin / *Th. glaucum* (22_I + 5_{II} + 1_{III}), **d.** Arlin / *Th. pulcherrimum* (25_I + 5_{II}), **e.** Dvergand / *Th. trichophorum* (24_I + 4_{II} + 1_{III}), **f.** Laru / *Th. varnense* (19_I + 8_{II})

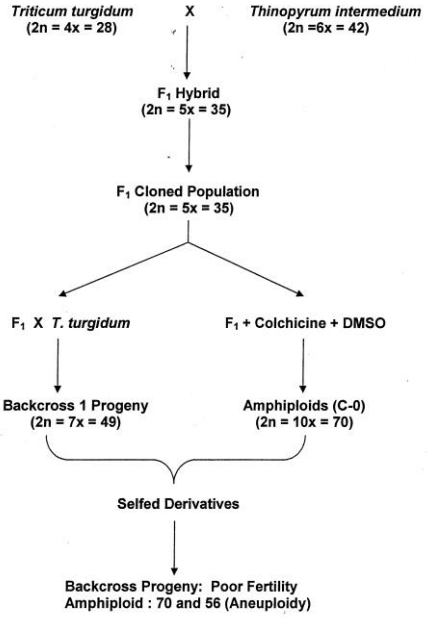

Fig. 4. Schematic elucidating the advance of F1 hybrids to serve maintenance as a clonal population, backcross 1 and amphiploid progeny.

Table 3. Mean and range of meiotic associations at metaphase I in intergeneric hybrids of some *Triticum turgidum* L. (2n=4x=28, AABB) cultivars with *Thinopyrum intermedium* and its sub-species.

Cross combination	Chromosome number	Mean meiotic chromosomal associations					
		I	II	II	Total	III	IV
Cocorit 71 / *Th. acutum*	2n=5x=35	20.3 **(15-26)**	0.6 **(0-2)**	4.9 **(2-8)**	5.5	1.1 **(0-2)**	0.1 **(0-1)**
Yavaros / *Th. acutum*	2n=5x=35	25.0 **(22-27)**	0.4 **(0-2)**	4.0 **(2-5)**	4.4	0.4 **(0-1)**	0 -
Chen / *Th. glaucum*	2n=5x=35	25.0 **(19-31)**	0.1 **(0-1)**	4.0 **(2-7)**	4.1	0.6 **(0-2)**	0 -
Altar 84 / *Th. intermedium*	2n=5x=35	29.9 **(25-35)**	0 -	2.4 **(0-5)**	2.4	0.1 **(0-1)**	0 -
Yavaros / *Th. intermedium*	2n=5x=35	29.3 **(25-33)**	0 -	2.5 **(0-5)**	2.5	0.1 **(0-1)**	0.1 -
Cocorit 71 / *Th. intermedium*	2n=5x=35	32.0 **(31-33)**	0 -	1.2 **(0-2)**	1.2	0.2 **(0-1)**	0 -
Memo / Mexicali // *Th. glaucum*	2n=5x=35	23.1 **(13-30)**	0.3 **(0-1)**	5.1 **(1-8)**	5.4	0.1 **(0-1)**	0.2 **(0-2)**
Cocorit / *Th. pulcherrimum*	2n=5x=35	20.9 **(16-27)**	1.4 **(0-3)**	4.7 **(2-7)**	6.1	0.5 **(0-1)**	0.1 **(0-1)**
Mexical i/ *Th. pulcherrimum*	2n=5x=35	24.7 **(19-29)**	0.5 **(0-1)**	3.9 **(2-6)**	4.4	0.5 **(0-2)**	0 -
Dvergand / *Th. trichophorum*	2n=5x=35	26.1 **(23-33)**	0.6 **(0-2)**	3.2 **(1-6)**	3.8	0.4 **(0-1)**	0 -
Laru / *Th. trichophorum*	2n=5x=35	27.9 **(23-33)**	0.3 **(0-2)**	3.1 **(1-6)**	3.4	0.1 **(0-1)**	0.1 **(0-1)**
Mexicali / *Th. varnense*	2n=5x=35	30.6 **(27-33)**	0 -	2.2 **(1-4)**	2.2	0 -	0 -
Altar / *Th. varnense*	2n=5x=35	31.4 **(29-33)**	0 -	1.8 **(1-3)**	1.8	0 -	0 -

Table 4. Details of amphiploids derived from various F1 hybrids between *Triticum turgidum* X *Thinopyrum intermedium* sub-species and its sub-species.

Cross combination	Expected chromosome number in C–0	Chromosomal range in C-n derivatives
T, turgidum / Th. acutum*	2n=10x=70	55 to 70
T. turgidum / Th. glaucum	2n=10x=70	64 to 71
T. turgidum / Th. intermedium	2n=10x=70	55 to 72
T. turgidum / Th. pulcherrimum	2n=10x=70	58 to 71
T. turgidum / Th. trichophorum	2n=10x=70	65 to 71
T. turgidum / Th. varnense	2n=10x=70	58 to 71

*: *T. turgidum* combinations involve several cultivars (**Table 1**) with each *Th. intermedium* sub-species

Production and maintenance of backcross 1 derivatives and amphiploids. The schematic of Fig. 4 elucidates how from the F_1 hybrid production between durum wheat and *Th. intermedium* its maintenance is done with derivatives serving as a living herbarium. From these F_1s that are male-sterile but female-fertile, BC_1 derivatives are obtained upon crossing with durum cultivars and upon colchicine treatment the F_1s yield amphiploids. Table 4 provides the details of the BC and amphiploid derivative stocks that are available with their brief mitotic characteristics. The expected mitotic counts of all BC_1's expected would be 2n=5x=35 that upon fertilization by the male n=2x=14, AB gamete generate the BC derivative with 49 chromosomes (Fig. 5a). Such derivatives were readily obtained, but contrary to the results seen with similar bread wheat based BC_1's, these durum based BC_1s showed little to no self-fertility. Hence, their best usage would be to immediately advance selected BC_1's by further backcrossing leading to alien chromosomal addition line development, agricultural trait categorization and then enforcing alien gene transfers *via* cytogenetic manipulation procedures.

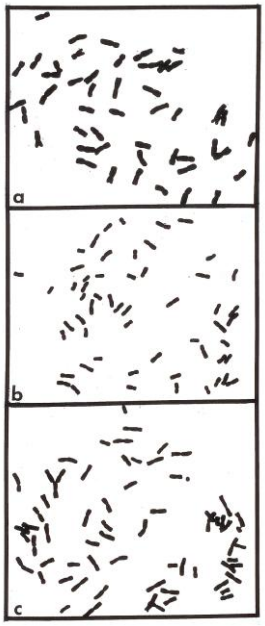

Fig. 5a to **c.** Somatic composition of F1 derived progenies showing in **a.** backcross 1 derivative with 2n=7x=49 chromosomes, **b**. a selfed C-0 derivative with 56 chromosomes indicative of possible genomic elimination, and **c.** a selfed C-0 with the expected near 70 chromosomes (68 with 2 telocentrics)

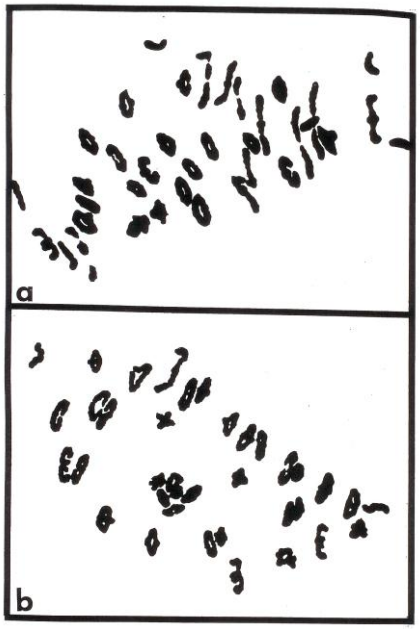

Fig. 6a and **b.** Meiotic association in C-0 selfed derivatives showing in **a.** 4 univalents + 9 rod bivalents + 22 ring bivalents + 1 chain quadrivalent (70 chromosomes), and in **b.** 70 chromosome meiocyte associated as 2 univalents + 3 rod bivalents+32ring bivalents.

All the F_1 hybrids upon colchicine treatment set seed (C-0) that were validated by somatic and meiotic cytology (Figs. 5 and 6). The expected chromosome numbers in the various amphiploids at C-0 generation would be 2n=10x=70 that meiotically associate upto a maximum of 35 bivalents ensuring good fertility and generating healthy seed upon selfing of the various C-0s. This was observed across all amphiploid combinations but aneuploidy was rampant (Fig. 6a, b). More drastic variations from the expected 70 chromosome derivatives were around selfed progeny that had presumably undergone spontaneous genomic loss yielding derivatives with chromosome numbers around 56 (Fig. 5b). These two forms of selfed individuals are classified as complete and partial amphiploids, possess a healthy seed type and are useful genetic stocks for agricultural applications to address biotic and abiotic stress crop production constraints.

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