Genome Analysis of *Aegilops mutica* Boiss. Based on the Chromosome Pairing in Interspecific and Intergeneric Hybrids

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Figure 1. *Aegilops mutica* growing at its natural habitat in the central part of Anatolian Plateau. Photograph was taken at 4.2 km E from Erzincan on the way to Erzurum, Turkey (1,260 m alt.) on August 8, 1982.

CONTENTS

1. INTRODUCTION

Taxonomic treatments of the genera *Aegilops* and *Triticum*

The genus *Aegilops* L. is a wild annual member of the tribe Triticeae Dum. (Hordeae Benth.) of the grass family and it consists of 20 or more species (Table 1). By Zhukovsky (1928) 20 species in the genus were grouped into nine sections while Eig (1929a) grouped 22 species into two subgenera and six sections. Kihara (1954) grouped 21 species including each two cytotypes of *Ae. triaristata* Willd. and *Ae. crassa* Boiss. into six sections based on the results from the genome analysis in the genus. He included *Ae. Kotschyi*, *Ae. Heldreichii*, *Ae. Aucheri* and *Ae. sharonensis* into *Ae. variabilis*, *Ae. comosa*, *Ae. speltoides* and *Ae. longissima*, respectively, because they shared the same genomes. Chennaveeraiah (1960) separated *Ae. vavilovii* as a new hexaploid species from *Ae. crassa* Boiss. by his karyomorphologic study of the genus. Kihara and Tanaka (1970) added *Ae. vavilovii* (Zhuk.) Chenn. as a new hexaploid to the Kihara's classification, and they grouped a total of 22 species into six sections. Recently, Feldman and Kislev (1977) described *Ae. searsii* as a new diploid species in sect. Platystachys Eig. Hammer (1980a, b) treated *Ae. searsii* at a specific rank but put *Ae. vavilovii* in a subspecific rank of *Ae. crassa* Boiss. As a result, he grouped 22 species, many of whose nomenclatures were reconsidered, into three subgenera and four sections.

The genus *Aegilops* is closely related to the genus *Triticum* L. Taxonomic treatments of the species in the latter genus are rather complicated because it includes cultivated wheats. Their diverse

Table 1. A summary of the classifications of the genus *Aegilops* L. described by the previous authors

Zukovsky (1928)	Eig (1929a)	Kihara (1954)	Kihara and Tanaka (1970)	Bowden (1959)	Hammer (1980a, b)
Sect. Polyeides Zhuk.	Subgenus *Amblyopyrym* Jaub. et Sp.	Sect. Polyeides	Sect. Polyeides	Diploid species	Subgenus *Amblyopyrum* Jaub. et Sp
Ae. ovata L.	Sect. Anathera Eig	*Ae. umbellulata* Zhuk.	*Ae. umbellulata* Zhuk.	*T. bicorne* Forsk.	*Ae. mutica* Boiss.
Ae. umbellulata Zhuk.	*Ae. mutica* Boiss.	*Ae. ovata* L.	*Ae. ovata* L.	*T. speltoides* (Tausch) Gren. ex Richter	
Ae. biuncialis Vis.		*Ae. triaristata* Willd. 4*x*	*Ae. triaristata* Willd. 4*x*	*T. comosum* (Sibth. & Sm.) Richter	Subgenus *Sitopsis* Jaub.et Sp
Ae. triaristata Willd.	Subgenus *Eu-Aegilops* Eig	*Ae. triaristata* Willd. 6*x*	*Ae. triaristata* Willd. 6*x*	*T. uniaristatum* (Vis.) Richter	*Ae. speltoides* Tausch
Ae. columnaris Zhuk.	Sect. Platystachys Eig	*Ae. columnaris* Zhuk.	*Ae. columnaris* Zhuk.	*T. longissimum* (Schw. & Musch.) Bowden	*Ae. longissima* Schw. et Musch. em. Eig *s.l*
Sect. Surculosa Zhuk.	*Ae. bicornis* (Forsk.) Jaub. et Sp.	*Ae. biuncialis* Vis.	*Ae. biuncialis* Vis.	*T. umbellulatum* (Zhuk.) Bowden	*Ae. bicornis* (Forsk.) Jaub. et Sp
Ae. triuncialis L.	*Ae. sharonensis* Eig	*Ae. variabilis* Eig (incl. *Ae. Kotschyi* Boiss.)	*Ae. variabilis* Eig (incl. *Ae. kotschyi* Boiss.)	*T. tripsacoides* (Jaub. & Sp.) Bowden	*Ae. searsii* Feld. et Kis ex Hamme
Sect. Cylindropyrum (Jaub. et Sp.) Zhuk.	*Ae. longissima* Schw. et Musch.	*Ae. triuncialis* L. (incl. *Ae. persica* Boiss.)	*Ae. triuncialis* L.	*T. dichasians*(Zhuk.)Bowden	Subgenus *Aegilops*
Ae. cylindrica Host	*Ae. ligustica* Coss.		Sect. Cylindropyrum	*T. aegilops* P.Beauv. ex R.& S.	Sect. Cylindropyrum (Jaub. et Sp.)Zhuk. em. Kihar
	Ae. speltoides Tausch	Sect. Cylindropyrum	*Ae. caudata* L.		*Ae. markgrafii* (Greuter) Hamme
Sect. Vertebrata Zhuk.		*Ae. cylindrica* Host	*Ae. cylindrica* Host	Allopolyploids	
Ae. squarrosa L.	Sect. Pachystachys Eig	*Ae. caudata* L.		*T. ovatum* (L.) Raspail	*Ae. cylindrica* Host
	Ae. squarrosa L.		Sect. Comopyrum	*T. triaristatum* (Willd.) Godr. & Gren.	
Sect. Comopyrum (Jaub. et Sp.) Zhuk.	*Ae. crassa* Boiss.	Sect. Comopyrum	*Ae. comosa* Sibth.et Sm. (incl. *Ae. heldreichii* Holzm.)	*T. kotschyi* (Boiss.)Bowden	Sect. Vertebrata Zhuk. em. Kihar
Ae. caudata L.	*Ae. juvenalis* (Thell.) Eig	*Ae. comosa* Sibth. et Sm. (incl. *Ae. Heldreichii* Holzm.)	*Ae. uniaristata* Vis.	*T. triunciale* (L.) Raspail	*Ae. tauschii* Coss.
Ae. comosa Sibth. et Sm.	*Ae. ventricosa* Tausch			*T. cylindricum* Ces., Pass. & Gib.	*Ae. crassa* Boiss.
Ae. Heldreichii Holzm.		*Ae. uniaristata* Vis.	Sect. Amblyopyrum	*T. macrochaetum* (Shuttl. & Huet.ex Duval-Jouve)Richter	*Ae. ventricosa* Tausch
Ae. uniaristata Vis.	Sect. Monoleptathera Eig		*Ae. mutica* Boiss.	*T. crassum* (Boiss.) Aitch. & Hemsl.	*Ae. turcomanica* Rosh.
	Ae. cylindrica Host	Sect. Amblyopyrum		*T. turcomanicum* (Rosh.) Bowden	*Ae. juvenalis* (Thell.)Ei
Sect. Gastropyrum (Jaub. et Sp.) Zhuk.		*Ae. mutica* Boiss.	Sect. Sitopsis	*T. juvenale* Thell.	
Ae. ventricosa Tausch	Sect. Macrathera Eig		*Ae. speltoides* Tausch (incl. *Ae. aucheri* Boiss.)	*T. ventricosum* Ces., Pass. & Gib.	Sect. Comopyrum (Jaub. et Sp.)Zhuk.em.Sen.-Korch
	Ae. caudata L.	Sect. Sitopsis			*Ae. comosa* Sibth. et Sm.
Sect. Sitopsis (Jaub. et Sp.) Zhuk.	*Ae. comosa* Sibth. et Sm.	*Ae. speltoides* Tausch (incl. *Ae. Aucheri* Boiss.)	*Ae. longissima* Schw. et Musch. (incl. *Ae. sharonensis* Eig)		*Ae. uniaristata* Vis.
Ae. speltoides Tausch	*Ae. uniaristata* Vis.	*Ae. longissima* Schw. et Musch. (incl. *Ae. sharonensis* Eig)	*Ae. bicornis* (Forsk.) Jaub. et Sp.		Sect. Aegilops
Ae. Aucheri Boiss.		*Ae. bicornis* (Forsk.) Jaub. et Sp.			*Ae. umbellulata* Zhuk.
Ae. bicornis (Forsk.) Jaub. et Sp.	Sect. Pleionathera Eig		Sect. Vertebrata		*Ae. peregrina* (Hackel) Maire et Weille
Ae. longissima (Schw. et Musch.) Eig	*Ae. variabilis* Eig	Sect. Vertebrata	*Ae. squarrosa* L.		*Ae. kotschyi* Boiss.
	Ae. Kotschyi Boiss.	*Ae. squarrosa* L.	*Ae. crassa* Boiss. 4*x*		*Ae. triuncialis* L.
Sect. Amblyopyrum (Jaub. et Sp.) Zhuk.	*Ae. triuncialis* L.	*Ae. crassa* Boiss. 4*x*	*Ae. crassa* Boiss. 6*x*		*Ae. lorentii* Hochst.
Ae. mutica Boiss.	*Ae. columnaris* Zhuk.	*Ae. crassa* Boiss. 6*x*	*Ae. vavilovii* (Zhuk.) Chenn.		*Ae. columnaris* Zhuk.
	Ae. biuncialis Vis.	*Ae. juvenalis* (Thell.) Eig	*Ae. ventricosa* Tausch		*Ae. neglecta* Req. ex Bertol
Sect. Polyploides Zhuk.	*Ae. triaristata* Willd.	*Ae. ventricosa* Tausch	*Ae. juvenalis* (Thell.) Eig		*Ae. geniculata* Roth
Ae. crassa Boiss.	*Ae. umbellulata* Zhuk.				
Ae. turcomanica Rosh.	*Ae. ovata* L.				

morphology and economic importance have made their taxonomic treatment more complicated and many non-biological species have been described. Mac Key (1966) rearranged both the wild and cultivated species of the genus into five biological species based on the genetic relationships among them: One was diploid, two were tetraploids and the other two were hexaploids. The members in his five species of genus *Triticum* had the same genome constitutions within each species but had different ones among species. And former species which share the same genome constitution were given the ranks of subspecies or convarieties within the same species. The two genera, *Aegilops* and *Triticum*, biologically comprise a congeneric complex because one of the two genomes of tetraploid wheats, *T. turgidum* (L.) Thell. and *T. timopheevi* Zhuk., and two of the three genomes of bread wheat, *T. aestivum* (L.) Thell., are derived from diploid species of genus *Aegilops*. Bowden (1959) taxonomically treated the two genera as one genus, *Triticum* L. em. Bowden. He renamed 19 *Aegilops* species under this genus (Table 1). In the present study, traditional taxonomic treatment of the genera in which the two genera are regarded as separate ones is conveniently used. Eig's classification (Eig 1929a) with some modifications and Mac Key's classification (Mac Key 1966) are adopted for the genera *Aegilops* and *Triticum*, respectively (Table 2).

The wild species of this congeneric complex are distributed mainly over the Mediterranean region and have their center of distribution at the northeastern corner of the Mediterranean basin (Eig 1929a, 1936). Sakamoto (1973) classified the genera of the tribe Triticeae into two major groups from their geographical distribution: the Mediterranean

Table 2. The classification, distribution of ploidy and genome types in the genera *Aegilops* L.[1] and *Triticum* L.[2]

Section	Species	Ploidy	Genome type
Genus *Aegilops* L.			
Anathera Eig			
	Ae. mutica Boiss.	2*x*	Mt
Platystachys Eig			
	Ae. bicornis (Forsk.) Jaub. et Sp.	2*x*	S^b
	Ae. sharonensis Eig	2*x*	S^l
	Ae. longissima Schw. et Musch.	2*x*	S^l
	Ae. searsii Feld. et Kis.[3]	2*x*	S^s[4]
	Ae. speltoides Tausch (incl. *Ae. ligustica* Coss.)	2*x*	S
Pachystachys Eig			
	Ae. squarrosa L.	2*x*	D
	Ae. crassa Boiss.	4*x*, 6*x*	DM^{cr}, DD^2M^{cr}
	Ae. vavilovii (Zhuk.) Chenn.[5]	6*x*	$DM^{cr}S^c$
	Ae. juvenalis (Thell.) Eig	6*x*	DC^uM^j
	Ae. ventricosa Tausch	4*x*	DM^v
Monoleptathera Eig			
	Ae. cylindrica Host	4*x*	CD
Macrathera Eig			
	Ae. caudata L.	2*x*	C
	Ae. comosa Sibth. et Sm.	2*x*	M
	Ae. uniaristata Vis.	2*x*	M^u
Pleionathera Eig			
	Ae. umbellulata Zhuk.	2*x*	C^u
	Ae. triuncialis L.	4*x*	C^uC
	Ae. columnaris Zhuk.	4*x*	C^uM^c
	Ae. biuncialis Vis.	4*x*	C^uM^b
	Ae. triaristata Willd.	4*x*, 6*x*	C^uM^t, $C^uM^tM^t{}_2$
	Ae. ovata L.	4*x*	C^uM^o
	Ae. variabilis Eig	4*x*	C^uS^v
	Ae. kotschyi Boiss.	4*x*	C^uS^v
Genus *Triticum* L.			
	T. monococcum L.	2*x*	A
	T. timopheevi Zhuk.	4*x*	AG
	T. turgidum (L.) Thell.	4*x*	AB
	T. zhukovskyi Men. et Er.	6*x*	AAG
	T. aestivum (L.) Thell.	6*x*	ABD

1) Summarized and modified from Eig (1929a), Kihara (1947), and Kihara and Tanaka (1970).
2) After Mac Key (1966).
3) Feldman and Kislev (1977).
4) Feldman *et al.* (1979).
5) Chennaveeraiah (1960).

group and the Arctic-temperate group. The former which includes the *Aegilops-Triticum* congeneric complex consists of mostly annual species and the latter largely perennial ones. He concluded that the establishment of the latter group in the Late-Tertiary is earlier than the rapid adaptive differentiation of the former group which took place during the formation of the Mediterranean climate in the Quaternary.

Phylogenetic differentiation of the species in the *Aegilops-Triticum* complex is believed to mainly consist of the three processes: First, differentiation at diploid level; second, polyploidization through interspecific hybridization among diploid species followed by the unreduced gamete formation in the diploid hybrids; and third, differentiation at polyploid level, especially in tetraploid species. In the history of the cytogenetical researches in this plant group, the importance of the second and third processes has often been overestimated and most of the investigations have been concerned with the polyploid species. However, we must remember that about a half of the wild species belonging to this congeneric complex are diploids as shown in Table 2. The differentiation of *Aegilops* species at section level had already occurred in diploids because each section has at least one diploid species. And the morphological and cytogenetical characteristics specific to each section are determined by such diploid species. To know the phylogenetic relationships among the diploid species is, therefore, essential to the understanding of the phylogenetic differentiation of this plant group. Among the diploid species in these genera, *Ae. mutica* Boiss. is especially open to arguments about its relationships with other diploid species both on the

cytogenetical and on the taxonomical viewpoints.

Morphology and geographical distribution of *Aegilops mutica*

Aegilops mutica Boiss. is an annual grass with 70–80 cm height. Its spikes are linear, very long (up to about 30 cm) and not awned (Figure 2). They consist of about 20 or more long spikelets arranged in a row[1]. Each spikelet consists of five to eight (up to 10 or more) florets arranged laxly (Figure 3). All spikelets on a spike are similar both in shape and in size. The relative length of spikelets to the adjacent rachis internodes varies from plant to plant. Spikelets shorter than the adjacent rachis internodes comprise a very lax spike while those slightly longer than the adjacent rachis internodes comprise a less lax spike. Empty glumes cover only less than a half of the spikelets which is resulted from the characteristic of having many laxly arranged florets in the spikelets. They are trapezoids with the upper edge being larger than the base. They do not have any awns, any sharp teeth or any keels. Their upper margin has two very dull teeth with broad bases. An arc, but not an acute notch, divides the dull teeth. A small triangular tooth often exists between the teeth. The empty glumes of some individuals are pubescent (var. *typica*) but those of other individuals are glabrous (var. *loliacea* Eig). Lemmas are not awned. Upper margins of lemmas of the lowest two florets are not pointed but those of upper florets are more or less pointed. Rachis is fragile and each spikelet falls separately with the rachis internode below it (wedge type disarticulation). In addition to this type of disarticulation,

1) in a row: Translation into English from the German term *'einzeilig'* in Eig (1929a).

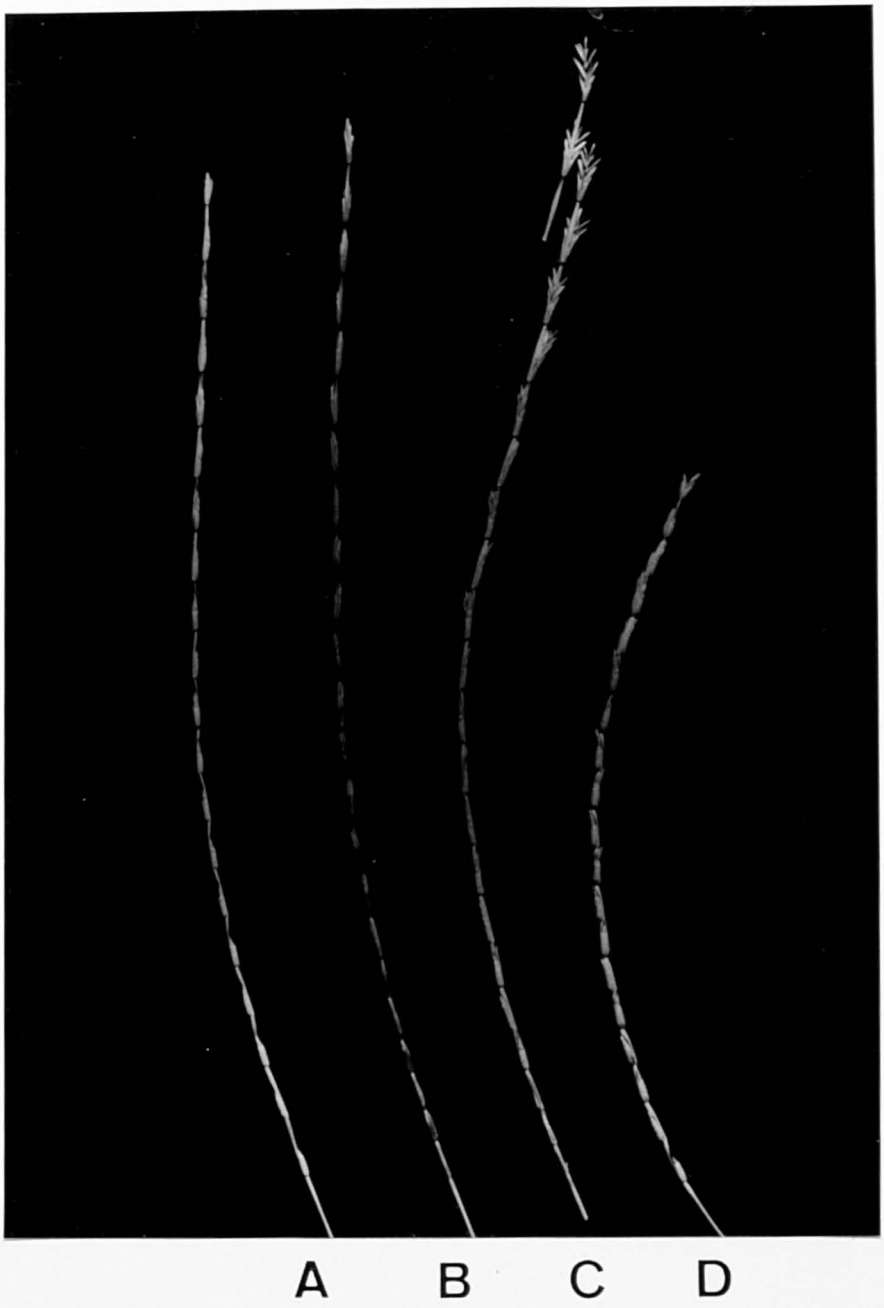


Figure 2. Spike morphology of the *Aegilops mutica* accessions (x 0.5). A: 5641, B: 5641b, C: 5641E, D: 5642c.

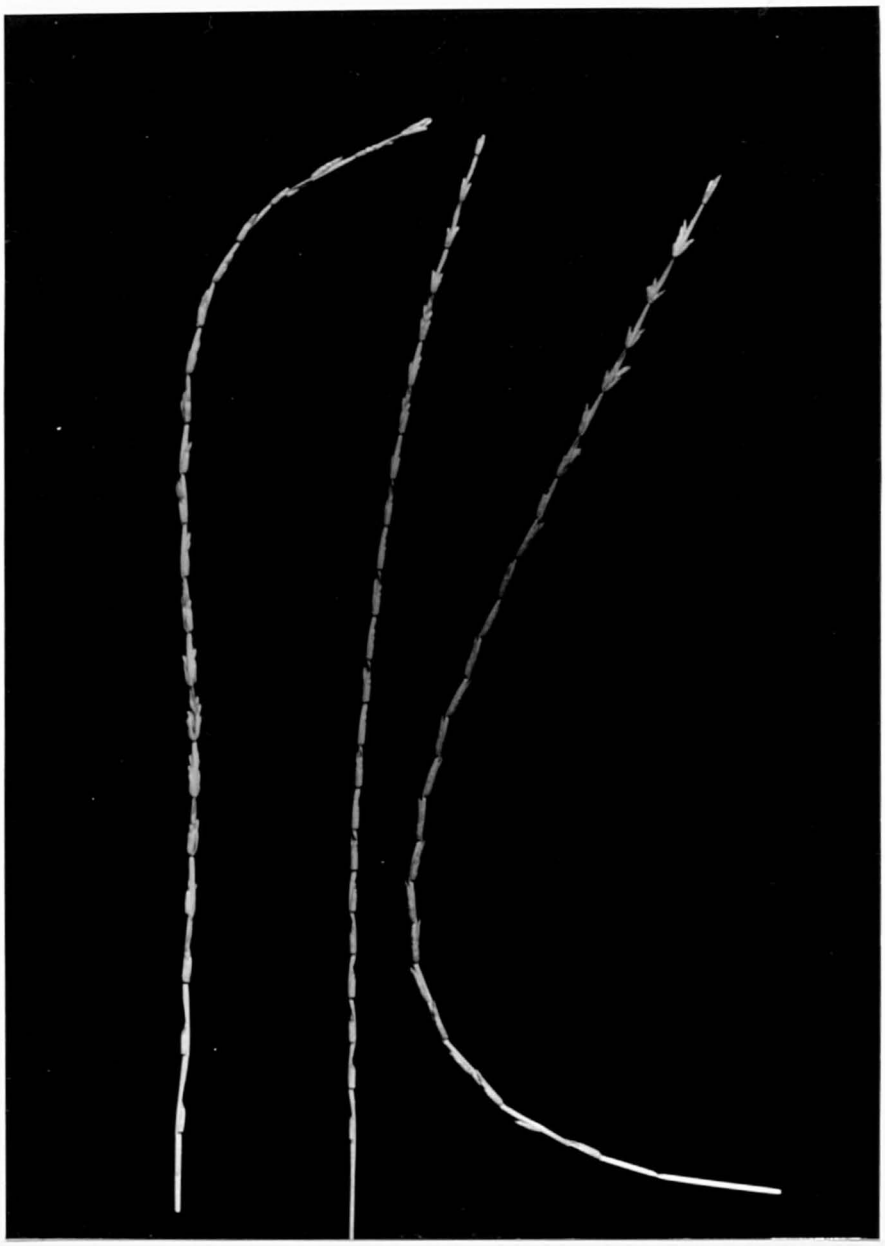


Figure 2. (Continued)
E: 5645, F: 5646B, G: 12004 .

rachillae are also fragile in the upper florets. Florets sit on upper than second one fall separately at maturity (floret type disarticulation) (Figure 3) though the lowest two florets fall together with the empty glumes.

The spike morphology of *Ae. mutica* is much variable, and it varies from plant to plant within a population. For example, Yamashita and Tanaka (1960) reported that plants with lax and dense spikes, with pubescent and glabrous empty glumes, with violet and yellow empty glumes, and with waxy and non-waxy empty glumes were all found in a natural population in Turkey. Furthermore, plants with pubescent or glabrous empty glumes were segregated from the plants with the alternative characteristic. The present author also collected many spikes of *Ae. mutica* at a total of 12 natural populations in Turkey and observed their morphological variation (Table 3). Moreover, the segregation in the characteristic of the pubescence of empty glumes was observed in the experimental populations established from those seed samples (Table 4). And the author obtained the same results as those of Yamashita and Tanaka (1960). Those phenomena are thought to be resulted from the fact that *Ae. mutica* is a cross-fertilizing species. This is reasonably concluded from the experiment using small experimental populations. As shown in Table 5, this species is almost self-incompatible. Among 13 plants pollinated by selfing, only two set seed. The mean percentage seed set by selfing was only 0.4% while that by open-pollination was 60.2%.

Ae. mutica is distributed over the central and western part of Anatolian Plateau, Armenia in Turkey (Eig 1929a, Bor 1970) and Armenia

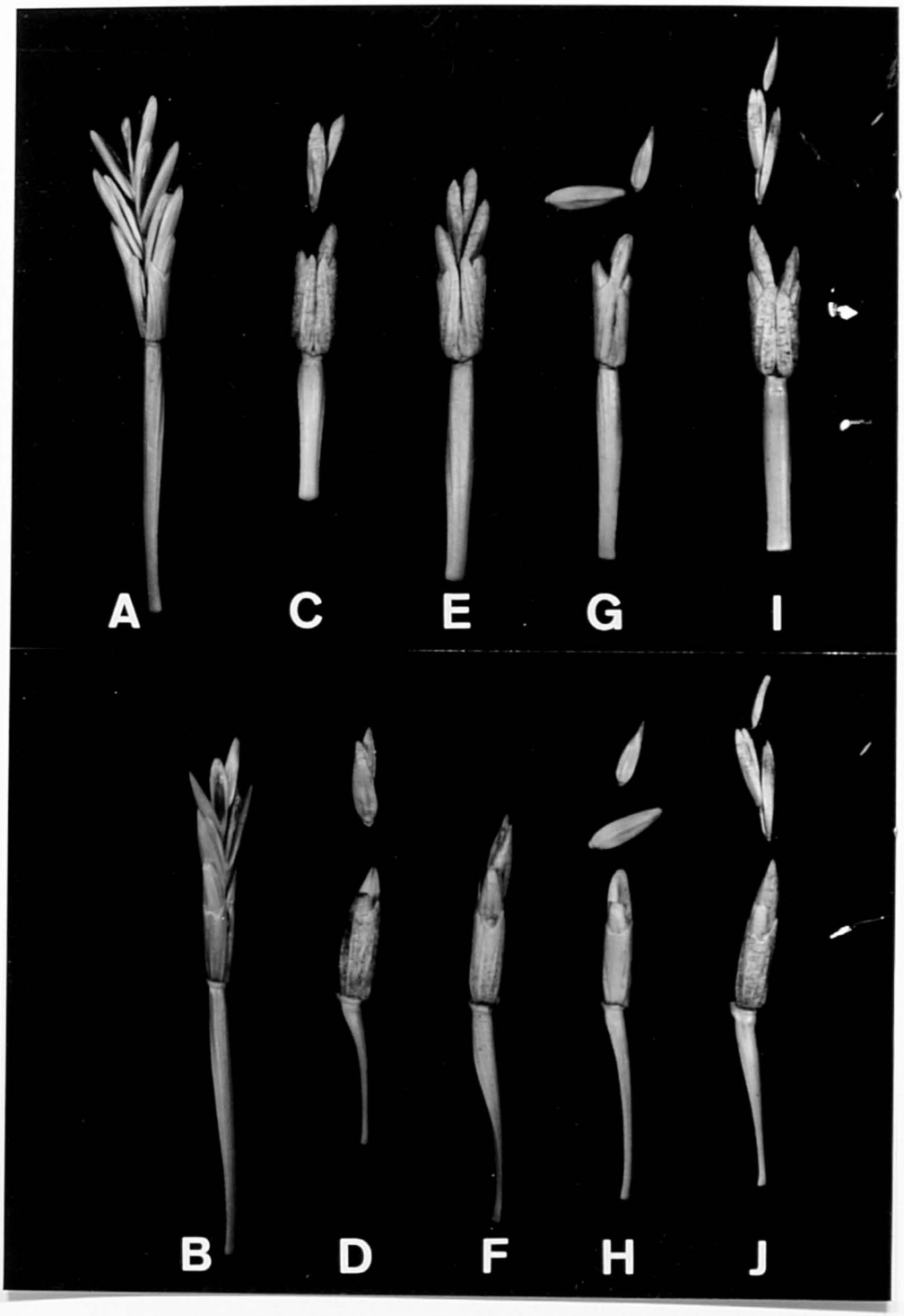


Figure 3. Spikelet morphology of *Aegilops mutica* (x 2.3). A-B: 5641E, C-D: 5642c, E-F: 5645, G-H: 5646B, I-J: 12004.

Table 3. Frequency of the plants with various spike morphology in *Aegilops mutica* collected at the natural populations in Turkey

Collection[1] No. (Population)		No. of plants									
	Glume hair[2] :	pubescent					glabrous				
	Glume color[2] :	yellow		black			yellow		black		
	Rachis color :	y[3]	b[3]	y	b	Total	y	b	y	b	Total	Total
82-7-31-11-4	Obs.[4]	18	17	0	17	52	57	50	0	45	152	204
	Freq.[4]	.09	.08	0	.09	.25	.28	.25	0	.22	.75	1.
82-8-1-4-1	Obs.	36	19	0	4	59	61	8	0	5	74	133
	Freq.	.27	.14	0	.03	.44	.46	.06	0	.04	.56	1.
82-8-1-5-2	Obs.	30	10	0	0	40	33	7	0	2	42	82
	Freq.	.37	.12	0	0	.49	.40	.09	0	.02	.51	1.
82-8-1-7-2	Obs.	10	14	0	2	26	28	20	0	7	55	81
	Freq.	.12	.17	0	.02	.25	.35	.25	0	.09	.68	1.
82-8-7-9-1	Obs.	11	6	0	3	20	191	51	0	92	334	354
	Freq.	.03	.02	0	.01	.06	.54	.14	0	.26	.94	1.
82-8-10-10-7A	Obs.	37	67	0	18	122	96	69	0	6	171	293
	Freq.	.13	.23	0	.06	.42	.33	.24	0	.02	.58	1.
82-8-10-11-1	Obs.	55	9	0	5	69	195	20	0	16	231	300
	Freq.	.18	.03	0	.02	.23	.65	.07	0	.05	.77	1.
82-8-11-2-3	Obs.	33	39	0	21	93	87	81	0	67	235	328
	Freq.	.10	.12	0	.06	.28	.27	.25	0	.20	.72	1.

Table 3. (Continued)

Collection[1] No. (Population)	Glume hair[2] :	No. of plants										
		pubescent					glabrous					
	Glume color[2] :	yellow		black			yellow		black			Total
	Rachis color :	y[3]	b[3]	y	b	Total	y	b	y	b	Total	
82-8-11-3-1	Obs.	32	5	0	4	41	53	12	0	12	77	118
	Freq.	.27	.04	0	.03	.35	.45	.10	0	.10	.65	1.
82-8-11-4-5	Obs.	13	15	0	4	32	53	40	0	17	110	142
	Freq.	.09	.11	0	.03	.23	.37	.28	0	.12	.77	1.
82-8-11-6-2[5]	Obs.					79					160	239
	Freq.					.33					.67	1.
82-8-11-7-3	Obs.	60	22	0	8	90	114	50	0	22	184	274
	Freq.	.22	.08	0	.03	.33	.42	.18	0	.08	.67	1.

1) For detailed collection locality of the each sample, see Sakamoto (1986).
2) Glume hair: Hairiness of empty glumes; Glume color: Color of empty glumes.
3) y: yellow; b: black.
4) Obs.: Number of plants observed; Freq.: Frequency.
5) Color of empty glumes or rachises could not be determined because the spikes were sooted with exhaust gas from automobiles.

Table 4. Segregation in the characteristic of the pubescence of the empty glumes of *Aegilops mutica* plants grown from the original spike samples collected at the natural populations in Turkey

Accession No. (KU)	Pubescence of empty glumes: Original[1] samples	Pubescence of empty glumes: Next generation	No. of plants observed	Accession No. (KU)	Pubescence of empty glumes: Original samples	Pubescence of empty glumes: Next generation	No. of plants observed
12001	pubescent	pubescent	2	12005	pubescent	pubescent	6
		glabrous	6			glabrous	2
	glabrous	pubescent	0		glabrous	pubescent	0
		glabrous	10			glabrous	8
12002	pubescent	pubescent	7	12006	pubescent	pubescent	8
		glabrous	6			glabrous	7
	glabrous	pubescent	2		glabrous	pubescent	0
		glabrous	10			glabrous	10
12003	pubescent	pubescent	7	12007	pubescent	pubescent	8
		glabrous	4			glabrous	6
	glabrous	pubescent	4		glabrous	pubescent	0
		glabrous	11			glabrous	10
12004	pubescent	pubescent	6	12008	pubescent	pubescent	5
		glabrous	1			glabrous	9
	glabrous	pubescent	4		glabrous	pubescent	0
		glabrous	10			glabrous	10

Table 4. (Continued)

Accession No. (KU)	Pubescence of empty glumes: Original[1] samples	Pubescence of empty glumes: Next generation	No. of plants observed
12009	pubescent	pubescent	6
		glabrous	6
	glabrous	pubescent	1
		glabrous	10
12010	pubescent	pubescent	6
		glabrous	7
	glabrous	pubescent	1
		glabrous	10
12011	pubescent	pubescent	11
		glabrous	4
	glabrous	pubescent	3
		glabrous	11
12012	pubescent	pubescent	6
		glabrous	8
	glabrous	pubescent	1
		glabrous	8
Total	pubescent	pubescent	78
		glabrous	66
	glabrous	pubescent	16
		glabrous	118

1) Each original sample consisted of one spike with pubescent or glabrous empty glumes, and the plants in the next generation were grown from the seeds setting on the each original spike samples.

Table 5. Seed fertility by open and self pollination of *Aegilops mutica* plants experimentaly cultivated under a vinyl roof

Accession No. (KU)	Plant No.	Polli-nation	All florets observed			Lowest two florets		
			No.of florets observed	No.of seeds set	Percentage seed set (%)	No.of florets observed	No.of seeds set	Percentage seed set (%)
12001	9	Open	259	77	29.7	126	70	55.6
12001	11	Open	107	53	49.5	47	43	91.5
12002	2	Open	490	73	14.9	134	39	29.1
12002	11	Open	656	126	19.2	208	72	34.6
12002	25	Open	200	6	3.0	101	6	5.9
		Self	115	0	0	36	0	0
12003	2	Open	642	216	33.6	236	187	79.2
12003	7	Open	490	181	36.9	184	123	66.8
12004	1	Open	323	94	29.1	157	88	56.1
12004	7	Open	676	176	26.0	232	156	67.2
12004	8	Open	484	154	31.8	208	131	63.0
12005	3	Open	415	155	37.3	213	134	62.9
12005	8	Open	433	138	31.9	178	124	69.7
12006	7	Open	255	87	34.1	135	57	42.2
		Self	96	0	0	40	0	0
12006	8	Open	679	247	36.4	229	182	79.5
		Self	163	0	0	40	0	0
12006	17	Open	440	185	42.0	194	158	81.4
		Self	126	0	0	40	0	0
12006	23	Open	730	182	24.9	254	86	33.9
		Self	152	0	0	36	0	0
12007	3	Open	694	270	38.9	216	164	75.9
12007	19	Open	515	259	50.3	205	167	81.5
12008	3	Open	440	236	53.6	197	164	83.2
12008	4	Open	473	75	15.9	153	32	20.9
12008	10	Open	715	298	41.7	242	167	69.0
12008	17	Open	472	147	31.1	183	136	74.3

Table 5. (Continued)

Accession No. (KU)	Plant No.	Polli-nation	All florets observed			Lowest two florets		
			No.of florets observed	No.of seeds set	Percentage seed set (%)	No.of florets observed	No.of seeds set	Percentage seed set (%)
12009	4	Open	570	221	38.8	218	148	67.9
		Self	143	0	0	46	0	0
12009	10	Open	390	146	37.4	160	101	63.1
		Self	111	2	1.8	40	2	5.0
12009	11	Open	411	147	35.8	138	113	81.9
12009	18	Open	650	253	38.9	216	155	71.8
		Self	165	0	0	44	0	0
12009	24	Open	428	172	40.2	180	161	89.4
		Self	143	1[1]	0.7	42	0	0
12010	1	Open	648	223	34.4	188	74	39.4
12010	15	Open	446	101	22.6	164	78	47.6
12011	1	Open	610	127	20.8	196	92	46.9
		Self	175	0	0	46	0	0
12011	9	Open	373	85	22.8	94	60	63.8
		Self	208	0	0	44	0	0
12011	25	Open	558	164	29.4	169	96	56.8
		Self	153	0	0	40	0	0
12011	26	Open	585	145	24.8	234	96	41.0
		Self	119	0	0	42	0	0
12012	4	Open	695	328	47.2	210	136	64.8
12012	20	Open	686	124	18.1	212	65	30.7
Total	(35 plants)	Open	17638	5671	32.2	6411	3861	60.2
	(13 plants)	Self	1869	3	0.2	536	2	0.4

1) This seed was set in the sixth floret.

in the USSR (Tsvelev 1983) (Figure 1). Tanaka (1983) suggested that the southeastern limit of its distribution is the northeastern corner of Syria. According to Bor (1968, 1970), this species has not yet been certainly found in Iraq or Iran. But one of the botanical explorations conducted by Kyoto University (BEM) found a small population of *Ae. mutica* at a corner of a wheat field in the northwestern part of Iran. This is probably a recently naturalized population as pointed out by Tanaka (1983). In summary, the center of the distribution of *Ae. mutica* is the central part of Anatolian Plateau. From the center it is naturally distributed over Turkey and Armenia both in Turkey and in the USSR. And it probably grows southward in the northern margin of Syria.

History of the taxonomic treatments and cytogenetical investigations on *Aegilops mutica*

The taxonomic treatments of *Ae. mutica* are summarized in Table 6. It was first described by Boissier (1844) based on the herbarium specimen with the number of Aucher 2977 which was collected by Aucher-Eloy in Cappadocia. Jaubert and Spach (1844-1846) described the species as *Ae. tripsacoides* Jaub. et Sp. based on the specimen collected by Jaubert in Phrygia of Asia Minor and later they also described *Ae. loliacea* Jaub. et Sp. based on the specimen which was collected at the same time as that used by Boissier for the description of *Ae. mutica* and preserved at the Muséum National d'Histoire Naturelle in Paris (Jaubert and Spach 1850-1853). Boissier (1884) treated these species as synonyms of *Ae. mutica* Boiss. and pointed out that *Ae. mutica* is the most similar to *Ae. Aucheri* Boiss., a synonym of *Ae. speltoides* Tausch, in

Table 6. Taxonomic treatments of *Aegilops mutica* Boiss. by the previous workers

Taxonomic treatment	Reference	Notes
Aegilops mutica Boiss.	Boissier (1844)	Holotype: Aucher 2977 (G)
Aegilops tripsacoides Jaub. et Sp.	Jaubert and Spach (1844-1846)	
Aegilops loliacea Jaub. et Sp.	Jaubert and Spach (1850-1853)	Subgenus *Amblyopyrum* Jaub. et Sp. Holotype: Aucher-Eloy 2977 (P)!
Aegilops mutica Boiss.	Boissier (1884)	Morphlogical simality to *Ae. Aucheri*
Aegilops mutica Boiss.	Zhukovsky (1928)	Monotypic section Amblyopyrum (Jaub. et Sp.) Zhuk.
Aegilops mutica Boiss.	Eig (1929a)	Monotypic subgenus *Amblyopyrum* Jaub. et Sp., monotypic section Anathera Eig
Amblyopyrum muticum (Boiss.) Eig	Eig (1929b)	Monotypic genus
Triticum tripsacoides (Jaub. et Sp.) Bowden	Bowden (1959)	*Triticum* (L.) em. Bowden
Amblyopyrum muticum (Boiss.) Eig	Bor (1968, 1970)	Monotypic genus
Aegilops mutica Boiss.	Hammer (1980a, b)	Monotypic subgenus *Amblyopyrum* Jaub. et Sp.
Amblyopyrum muticum (Boiss.) Eig	Tsvelev (1983)	
Amblyopyrum muticum (Boiss.) Eig	Davis (1985)	Monotypic genus

morphology. Zhukovsky (1928) morphologically included this species into a monotypic section Amblyopyrum (Jaub. et Sp.) Zhuk. of genus *Aegilops*. And Eig (1929a) included it into the monotypic subgenus *Amblyopyrum* Jaub. et Sp. which consists of only one monotypic section Anathera Eig. Soon he separated this species from the genus *Aegilops* as the only member of the new genus *Amblyopyrum* Eig and renamed it *Amblyopyrum muticum* (Boiss.) Eig (Eig 1929b), because its morphological characteristics are much different from those of the other species of the genus *Aegilops* and some species of the genus *Agropyrum* have not less morphological characters common with *Ae. mutica* than the other species of the genus *Aegilops* (Eig 1929a, 1929b). Up to now, some taxonomists included this species into the *Aegilops-Triticum* congeneric complex, that is, *Aegilops* L. or *Triticum* L. em. Bowden (Bowden 1959, Hammer 1980) and others included it into the monotypic genus *Amblyopyrum* Eig (Bor 1968, 1970, Tsvelev 1983, Davis 1985).

Cytogenetically, Senjaninova-Korczagina (1932) concluded that the karyotype of *Ae. mutica* is similar to those of *Ae. squarrosa*, *Ae. comosa* and *Ae. Heldreichii*. Kihara and Lilienfeld (1935) observed the mode of seven bivalents and some normal pollen grains in the F_1 hybrid between *Ae. comosa* and *Ae. mutica* (Table 7), then Kihara gave the genome symbol Mt to *Ae. mutica* and grouped it in his cytogenetical M-group together with *Ae. comosa* (incl. *Ae. Heldreichii*), *Ae. uniaristata* and *Ae. squarrosa* (Kihara 1947, Lilienfeld 1951). However, Chennaveeraiah (1960) concluded that the karyotype of *Ae. mutica* is more in line with those of the species of section Sitopsis (= sect. Platystachys Eig). Riley (1966) crossed *T. monococcum*, *T. boeoticum*, *Ae. speltoides*, *Ae.*

Table 7. The frequency and configuration of A-chromosome pairing at MI of meiosis by the previous workers in the F_1 hybrids between *Aegilops mutica* and the other diploid *Aegilops-Triticum* species

Cross combination	No.[1] of Bs	A-chromosome pairing					References
		UNIV.	BIV.	TRIV.	QUADR.	X'ta of As	
Ae. comosa x *Ae. mutica*	0		(3-7)		(0-1)		Kihara and Lilienfeld (1935)
Ae. longissima x *Ae. mutica*	0	3.52 (0-10)	5.06 (2-7)	0.12 (0-1)	-	6.26±0.26	Riley (1966)
	0	1.49 (0-6)	6.26 (4-7)	-	-		Jones and Majisu (1968)
Ae. sharonensis x *Ae. mutica*	0	3.26 (0-8)	5.31 (3-7)	-	0.03 (0-2)		Jones and Majisu (1968)
Ae. speltoides x *Ae. mutica*	0	2.84 (0-10)	5.85 (2-7)	-	-	7.68±0.27	Riley (1966)
	3	13.73 (9-14)	0.63 (0-3)	-	-	0.76±1.00	Vardi and Dover (1972)
	4	11.79 (8-14)	1.00 (0-3)	-	-	1.27±1.20	Vardi and Dover (1972)
	4	13.16 (8-14)	0.43 (0-3)			0.48±0.72	Vardi and Dover (1972)
Ae. caudata x *Ae. mutica*	0	3.53 (1-6)	3.33 (2-6)	1.27 (0-2)	-	6.10±0.26	Riley (1966)
Ae. squarrosa x *Ae. mutica*	0	0.39 (0-2)	6.80 (6-7)	-	-		Jones and Majisu (1968)
T. boeoticum x *Ae. mutica*	0	3.70 (0-8)	4.88 (3-7)	0.10 (0-1)	0.06 (0-1)	6.78±0.24	Riley (1966)
	0	5.63 (2-12)	2.82 (1-6)	0.17 (0-1)	-		Jones and Majisu (1968)
	0	6.11 (2-12)	3.94 (1-6)	-	-		Jones and Majisu (1968)
T. monococcum x *Ae. mutica*	0	2.50 (0-6)	4.96 (3-7)	0.28 (0-1)	0.18 (0-1)	8.26±0.27	Riley (1966)

1) No. of B-chromosomes in the F_1 hybrids.

longissima and *Ae. caudata* with *Ae. mutica* and he observed the chromosome pairing in meiosis of those diploid F_1 hybrids (Table 7). As the result of such an observation, he suggested *Ae. speltoides* and *Ae. mutica* were phylogenetically proximal because of the absence of any translocation difference between them and their similarity in pairing control in addition to the similarity in their karyotypes. Jones and Majisu (1968) suggested *Ae. mutica* has more cytological affinity with *Ae. squarrosa* from their observation of chromosome pairing in the F_1 hybrids between *Ae. squarrosa*, *Ae. longissima* and *T. boeoticum* and *Ae. mutica* (Table 7). Recently, Kimber (1982) concluded the genome of *Triticum tripsacoides* (Jaub. et Sp.) Bowden, a synonym of *Ae. mutica* Boiss., was non-homologous to the A, B, D or U (formerly C^u) genome mainly based on his numerical analysis of the chromosome pairing in meiosis of the F_1 hybrids between five polyploid species and *T. tripsacoides*. Kimber and Tsunewaki (1988) tried to change the two-letter designations of the genome symbols in some *Aegilops* species to single capital letters. And they proposed the genome symbol T for *Ae. mutica* not on the basis of genetical reasons but only on the basis of consistency in the single-lettered genome nomenclature. Thus, the analysis of genome relationships between *Ae. mutica* and the other diploid species is rather sporadically and insufficient. As a result, the treatment of cytogenetical relationship of *Ae. mutica* among the diploid *Aegilops-Triticum* species is rather confused.

The purposes of the present work

One purpose of the present work is to resolve the confused problems

about the taxonomic treatment and the cytogenetical relationship of *Ae. mutica* from the genetical viewpoint based on the chromosome pairing and fertility of the F_1 hybrids between this species and the other diploid species of the *Aegilops-Triticum* complex. Another purpose is to present an opinion on the phylogenetic position of *Ae. mutica* in the complex not only based on the evidence obtained from the present results but also based on the morphological, ecological and cytogenetical evidence by the previous workers. In other words, the present purposes are to answer the following three questions:

1. Is *Ae. mutica* the only member of the monotypic genus *Amblyopyrum* Eig or a member of the *Aegilops-Triticum* congeneric complex ?
2. Which diploid species of the *Aegilops-Triticum* complex is *Ae. mutica* most closely related to ?
3. What phylogenetic position among the diploid species of the *Aegilops-Triticum* complex is *Ae. mutica* located in ?

The present author carried out a series of cytogenetical observations mainly in the F_1 hybrids between *Ae. mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex with or without B-chromosomes of *Ae. mutica* for the purpose of elucidating the phylogenetic relationships between *Ae. mutica* and the diploid species of the genera (Ohta and Tanaka 1982, 1983, Ohta 1988). These cytogenetical observations and some additional observations comprise the present work. Chapter 2 of the present thesis explains the material used in the present work. Chapter 3 deals with the principle of the genome analysis by using B-chromosomes of *Ae. mutica*, detailed methods for crossing and

cytogenetical observations. In Chapters 4 and 5, the results of the present interspecific and intergeneric crosses and of the morphological and cytogenetical observations on the F_1 hybrid plants are described in detail. In Chapters 6 and 7, the genome relationships between *Ae. mutica* and the other diploid species of the *Aegilops-Triticum* complex are discussed based on the present results and the evidence by many previous workers. Based on these results and discussions, a new genome symbol for the genome of *Ae. mutica* is proposed. These chapters deal with the taxonomic position of *Ae. mutica* from the genetical viewpoint, too: Whether this species is a member of the *Aegilops-Triticum* complex or it should be separated from the complex as the member of the monotypic genus *Amblyopyrum* Eig judging from the present results. And the phylogenetic position of *Ae. mutica* in the *Aegilops-Triticum* complex is discussed in Chapter 8 by comparing the morphological, ecological and cytogenetical characteristics of *Ae. mutica* with those of the other diploid *Aegilops-Triticum* species and of the other genera of the tribe Triticeae.

2. MATERIAL

The material used in the present crosses with *Aegilops mutica*

As mentioned in the previous chapter, the present nomenclature and taxonomic treatment of the species in the genera *Aegilops* and *Triticum* are in the manners described by Eig (1929a) with some minor modifications and by Mac Key (1966), respectively. The material, including ten diploid *Aegilops* and one diploid *Triticum* species, used in the present crosses with *Ae. mutica* is listed in Table 8 and shown in Figure 4. The present material consists of one accession of *Ae. bicornis* (Forsk.) Jaub. et Sp. (Figure 4A), two of *Ae. sharonensis* Eig (Figures 4B and C), two of *Ae. longissima* Schw. et Musch. (Figures 4D and E), one of *Ae. searsii* Feld. et Kis. (Figure 4F), 16 of *Ae. speltoides* Tausch including *Ae. ligustica* Coss. (Figures 4G-M), two of *Ae. comosa* Sibth. et Sm. (Figures 4N and O), two of *Ae. uniaristata* Vis. (Figures 4P and Q), two of *Ae. caudata* L. (Figures 4R and S), two of *Ae. umbellulata* Zhuk. (Figures 4T and U), three of *Ae. squarrosa* L. (Figure 4V) and three of the wild subspecies of *T. monococcum* L. (Figures 4W-Y). All the accessions are maintained by self-pollination using paraffin paper bags at the Plant Germ-plasm Institute, Kyoto University. Some of them are maintained as the standard experiment lines of the Institute but others were collected more recently by the botanical explorations conducted by Kyoto University: KUSE (1955), BMUK (1959), BEM (1970) and KUET (1976); for the abbreviations, see Table 8. Especially all of the 16 accessions of *Ae. speltoides* used were collected by three of these four explorations. For *Ae. squarrosa* an artificially synthesized

Table 8. Material used in the present crosses with *Aegilops mutica*

Species	Accession No. (KU)	Collection locality	Donor; Year of primary storage	Donor No.
Genus *Aegilops* L.				
Aegilops bicornis (Forsk.) Jaub. et Sp.				
	3-1	unknown	Miczynski; 1934	
Aegilops sharonensis Eig				
	5-1	unknown	Sears; 1948	
	5-3	near Màagan Micheal, ISRAEL	Jenkins; 1960	
Aegilops longissima Schw. et Musch.				
	4-1	Herzlia, ISRAEL	Eig; 1934	1932-7
	4-4	unknown	Jenkins; 1960	
Aegilops searsii Feld. et Kis.				
	4-6	13 km N of Hebron (Hebron - Jerusalem), JORDAN	BMUK[1]	1959-5-13-5a
Aegilops speltoides Tausch				
	2201B	Suburbs of Harran (Urfa - Harran), TURKEY	KUET[2]	1976-7-25-3A
	2213D	Suburbs of Malabadi (Diyarbakir - Malabadi), TURKEY	KUET	1976-7-27-1A
	2214D	Suburbs of Malabadi (Diyarbakir - Malabadi), TURKEY	KUET	1976-7-27-1B
	2241A	96 km N of Maras (Kayseri - Maras), TURKEY	KUET	1976-8-13-8P
	2263	Tunceli, TURKEY (Collection of Ankara University)	KUET	1976-A13a
	2273	Maras, TURKEY (Collection of Ankara University)	KUET	1976-A146
	2282	53 km SW of Maras (Maras - Adana), TURKEY	KUET	1976-8-14-4A
	5725B	12 km NE of Ankara, TURKEY	BMUK	1959-7-5-2a
	7719	near Sarchinar Hotel, Sulaymaniyah, IRAQ	BEM[3]	1970-5-27-Ext.-1
	7761	32.6 km SSW from Taq-Taq to Kirkuk, IRAQ	BEM	1970-6-5-1-A-2
	7799B	7.1 km NE from Shaqlawa to Rowanduz, IRAQ	BEM	1970-6-11-1-1-E-3
	7930	34.6 km N from Elazig to Hozat, TURKEY	BEM	1970-6-30-8-1-B
	7943	40.1 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-5-1-D-5
	7972	62.2 km E from Elazig to Bingöl, TURKEY	BEM	1970-7-2-2-3-C-6
	7974	63.3 km W from Bingöl to Elazig, TURKEY	BEM	1970-7-2-3-2-1
	7976	29.1 km S from Bingöl to Lice, TURKEY	BEM	1970-7-2-8-C-1

Table 8. (Continued)

Species	Accession No. (KU)	Collection locality	Donor; Year of primary storage	Donor No.
Aegilops squarrosa L.				
ssp. *eusquarrosa* Eig				
	20-5	unknown	Matsumura; 1958	
	20-10	9 km NW of Ramsar (Chalus - Rasht), IRAN	KUSE[4)]	1955-K7-21-2
ssp. *strangulata* Eig				
	20-9	5 km W of Behshahr (Sari - Behshahr), IRAN	KUSE	1955-K7-19-5
Aegilops caudata L.				
	6-1	unknown	Kappert; 1934	
	6-2	11 km S of Ma'aret el Nu'man (Aleppo - Hama), SYRIA	BMUK	1959-5-17-7g
Aegilops comosa Sibth. et Sm.				
ssp. *eu-comosa* Eig				
	17-1	GREECE	Vavilov; 1930	9805
ssp. *heldreichii* (Holz.) Eig				
	17-2	TURKEY	Kappert; 1934	
Aegilops uniaristata Vis.				
	19-2	unknown	Kappert; 1934	
	19-3	In the ruins of Olympia, GREECE	BMUK	1959-6-6-1e
Aegilops umbellulata Zhuk.				
	8-1	Suburbs of Bozanti, TURKEY	Eig; 1934	1932-240
	8-2	Suburbs of Bozanti, TURKEY	Eig; 1934	1932-238
Artificially synthesized autotetraploid of the genus *Aegilops* L.				
Aegilops squarrosa (4x)				
	29	Colchicine treatment of *Ae. squarrosa* ssp. *eusquarrosa* (KU 20-2)	N. Kondo; 1949	

Table 8. (Continued)

Species	Accession No. (KU)	Collection locality	Donor; Year of primary storage	Donor No.
Genus *Triticum* L.				
Triticum monococcum L.				
ssp. *boeoticum* (Bioss.) Mac Key				
	101-1[5]	(Collection of College of Agr., Hokkaido Univ., Japan)		
	103[5]	IRAN (Collection of Agr. Exp. Station, Tehran)	KUSE	
	199-8[6]	Baal Bek, LEBANON	Johnson; 1977	G3155

1) BMUK: Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries (in 1959).
2) KUET: Kyoto University Scientific Exploration to the Eastern Turkey (in 1976).
3) BEM: Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia (in 1970).
4) KUSE: Kyoto University Scientific Expedition to Karakoram and Hindukush (in 1955).
5) *Triticum boeoticum* Boiss.
6) *Triticum urartu* Thum.

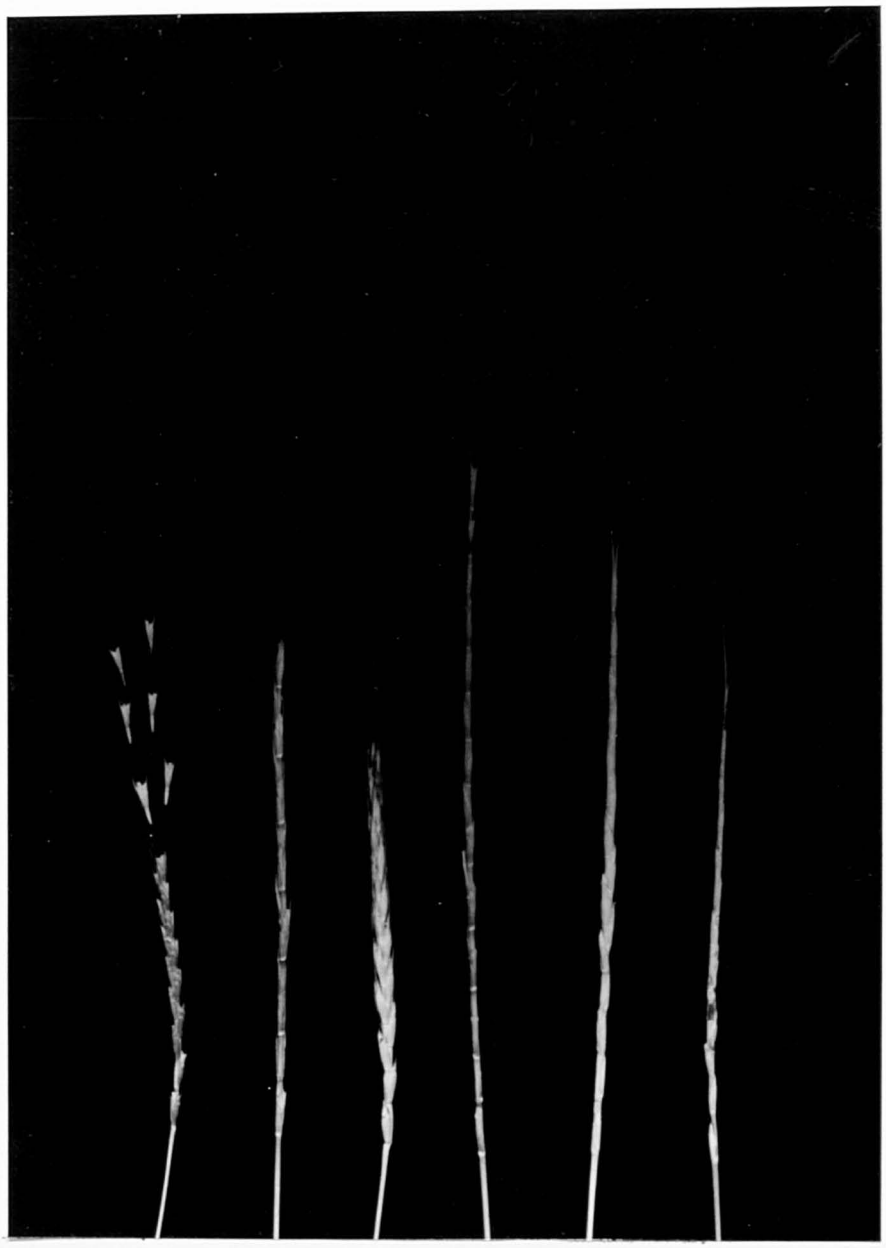


Figure 4. Spike morphology of the accessions of the diploid species of the congeneric *Aegilops-Triticum* complex used in the present crosses (x 0.5). A: *Ae. bicornis* (KU 3-1), B-C: *Ae. sharonensis* (B: KU 5-1, C: KU 5-3), D-E: *Ae. longissima* (D: KU 4-1, E: KU 4-4), F: *Ae. searsii* (KU 4-6).

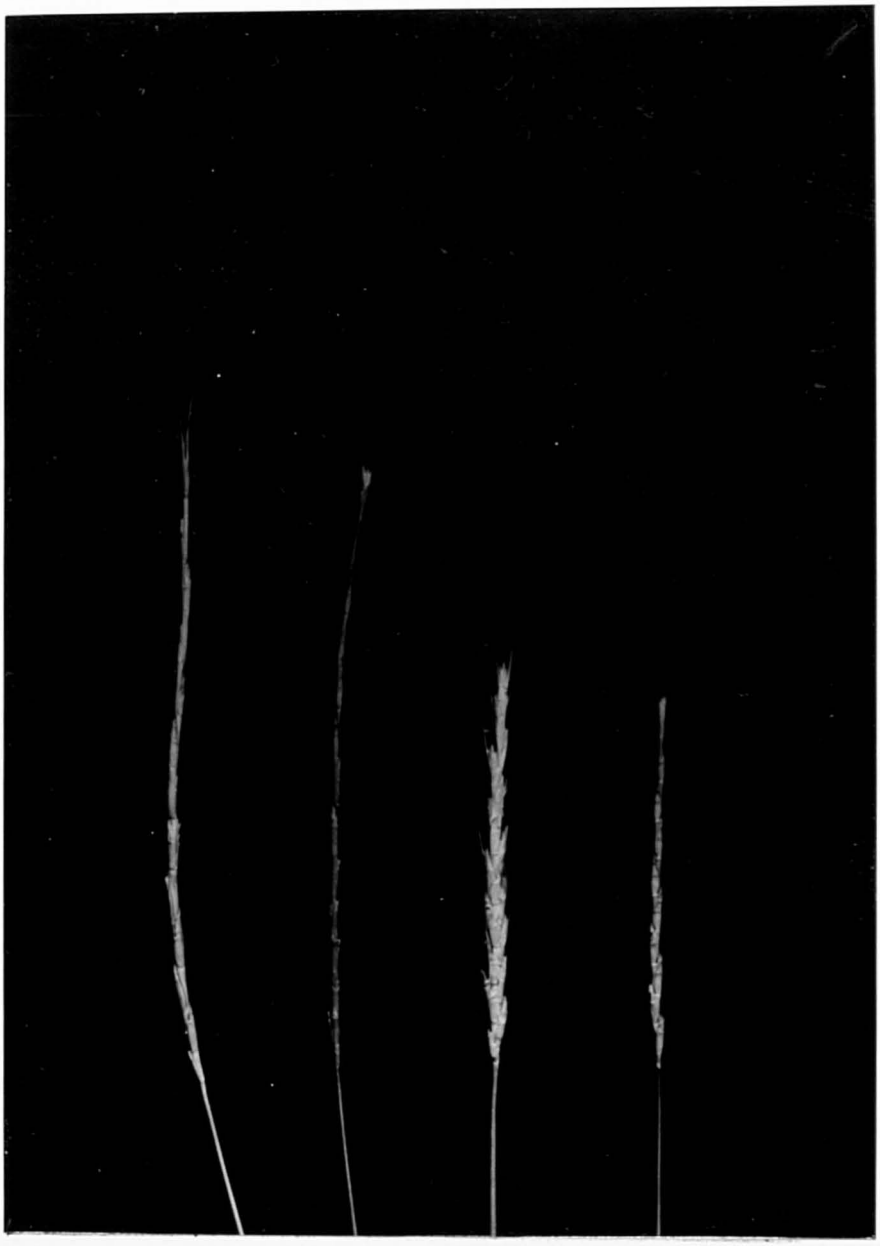


Figure 4. (Continued)

G-J: *Ae. speltoides* (G: KU 2201B, H: KU 2213D, I: KU 2263, J: KU 2282.

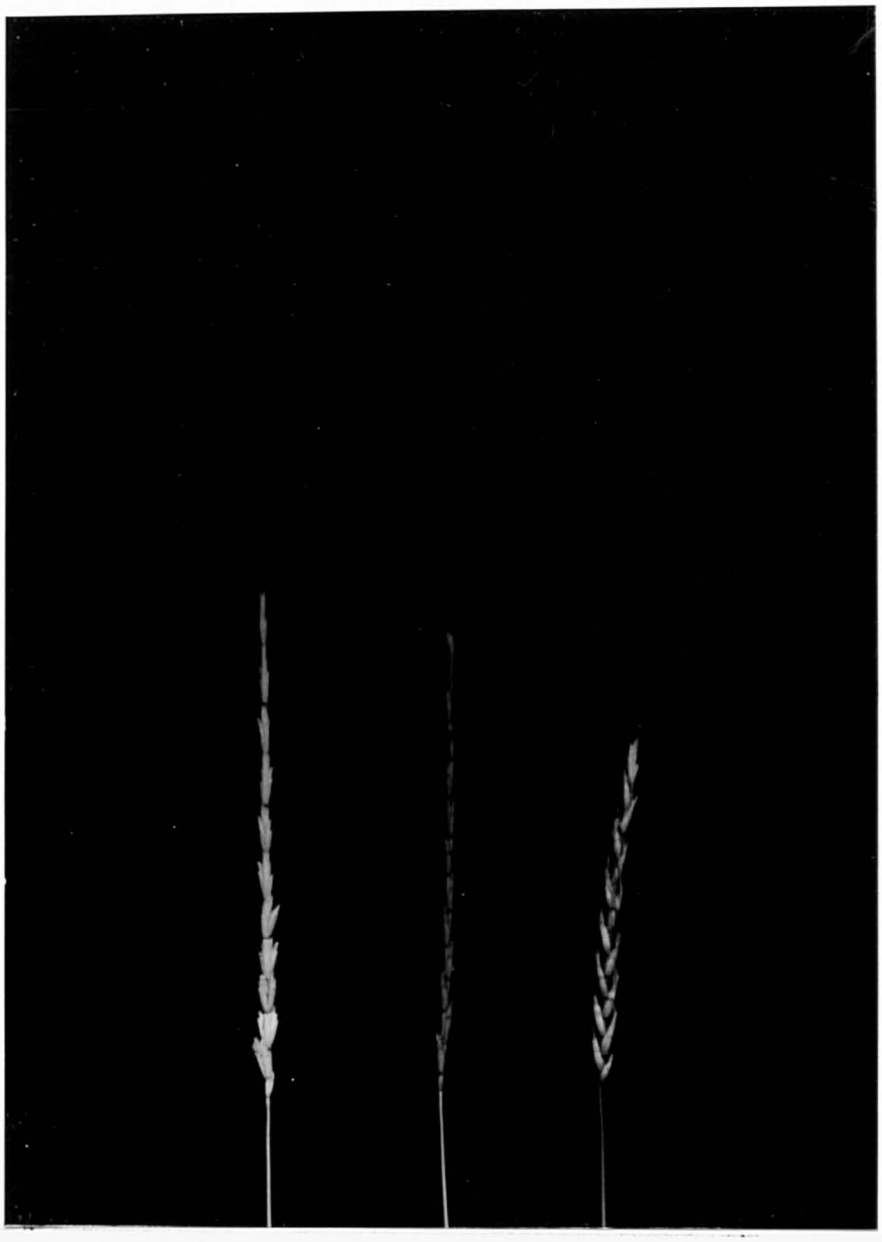


Figure 4. (Continued)

K-M: *Ae. speltoides* (K: KU 7761, L: KU 7943, M: KU 7972).

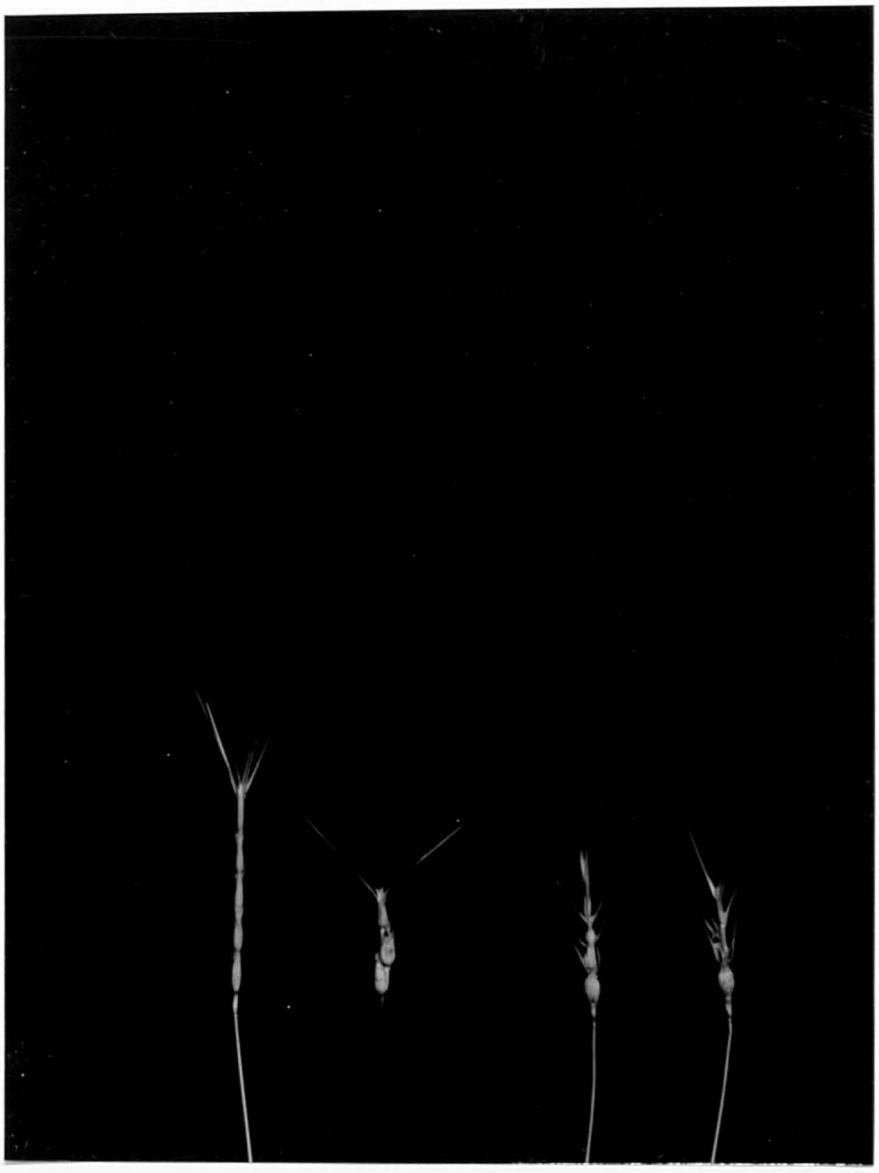


Figure 4. (Continued)

N-O: *Ae. comosa* (N: ssp. *eu-comosa* KU 17-1, O: ssp. *heldreichii* KU 17-2), P-Q: *Ae. uniaristata* (P: KU 19-2, Q: KU 19-3).

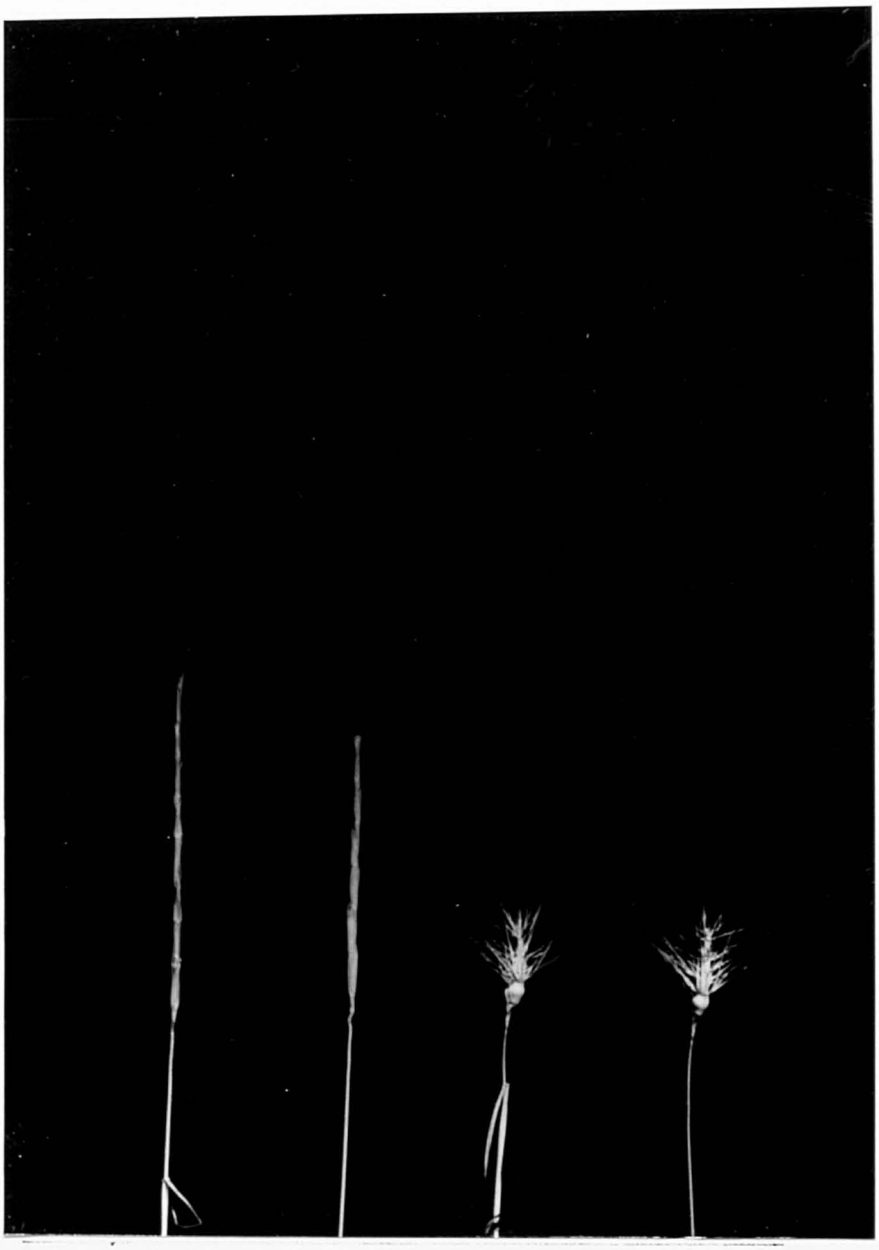


Figure 4. (Continued)

R-S: *Ae. caudata* (R: var. *polyathera* KU 6-1, S: var. *typica* KU 6-2), T-U: *Ae. umbellulata* (T: KU 8-1, U: KU 8-2).

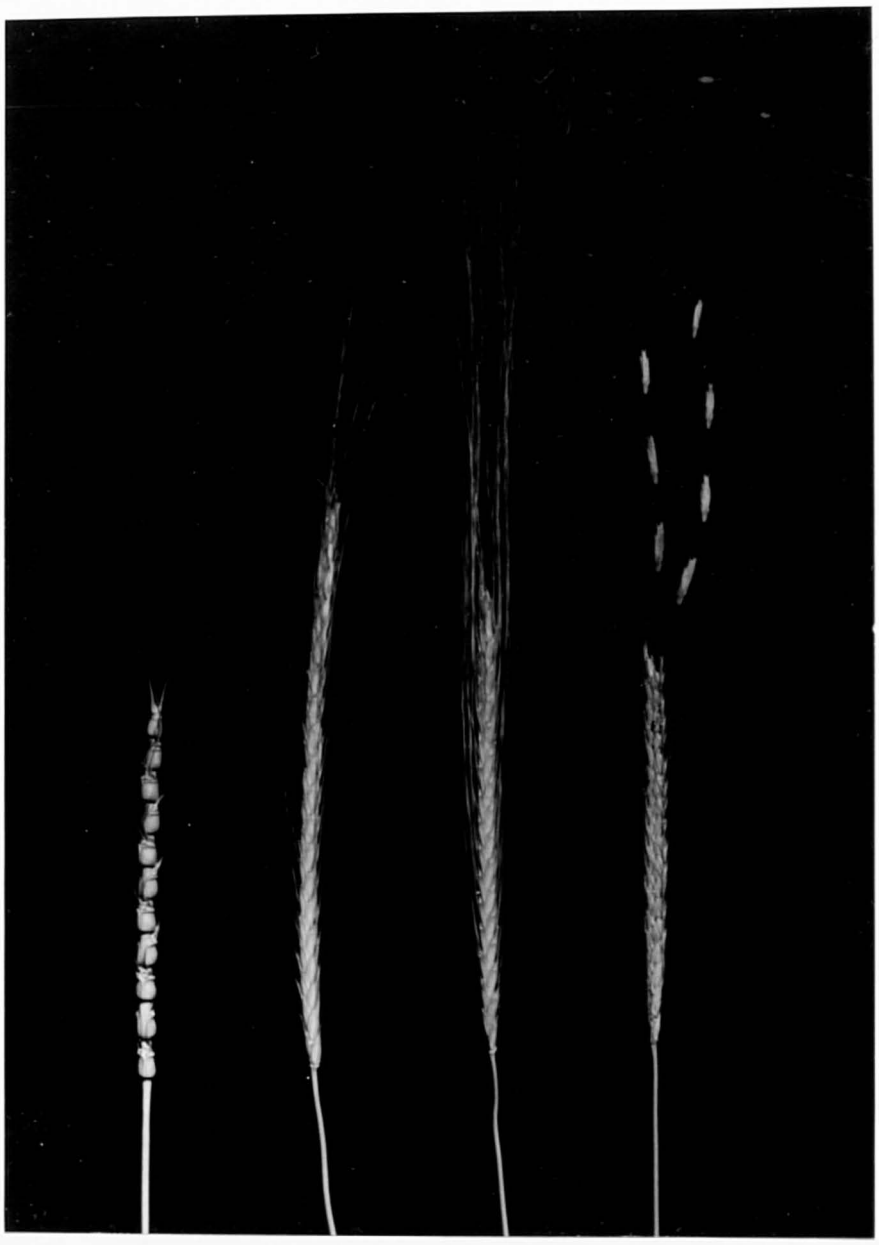


Figure 4. (Continued)

V: *Ae. squarrosa* (KU 20-9), W-Y: *T. monococcum* ssp. *boeoticum* (W: KU 101-1, X: KU 103, Y: KU 199-8; W and X belong to former species *T. boeoticum* and Y belongs to *T. urartu*).

autotetraploid was used in addition to the diploid accessions, because the F_1 hybrid plants could not obtained from the cross of *Ae. squarrosa* (2*x*) x *Ae. mutica* though many F_1 seeds set from that cross combination. *T. monococcum* ssp. *boeoticum* (Boiss.) Mac Key used in the present crosses contains two former species. Accession Nos. KU 101-1 and KU 103 are included in former species *T. boeoticum* Boiss. and the accession KU 199-8 is in *T. urartu* Thum., respectively.

The material of *Aegilops mutica* used in the present crosses

Forty seven individuals from 14 accessions of *Ae. mutica* were used in the present crosses (Table 9). They were all collected from their native populations in Turkey by the three botanical explorations conducted by Kyoto University: BEM (1970), KUET (1976) and KUSWE (1982); for the abbreviations, see Table 9. And they are maintained at the Plant Germ-plasm Institute, Kyoto University. This species is almost self-incompatible and we can obtain few seeds by self-pollination (Table 5). Small experiment populations of *Ae. mutica* each of which comprise about ten or more individuals were isolated spatially and the seeds were obtained by the open-pollination among the individuals within each population. Some of the individuals used in the present crosses arose from the original seed samples collected from the natural populations but others, and the majority, arose from the multiplied seed samples. Thirteen of the individuals used in the crosses did not have any B-chromosomes (Bs) but the rest carried various number of B-chromosomes in addition to the usual chromosome complements of 14 A-chromosomes (As). Sixteen individuals had one B-chromosome, 10 had two, six had three and

Table 9. Material of *Aegilops mutica* Boiss. used in the present interspecific crosses

Accession No. (KU)	Culture No.	No. of Bs	Collection locality	Donor[1)]	Donor No.
5598	81-5598-3	2	38.3 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-4-2-C-17 " -3-C-7
5606	81-5606-1	1	38.3 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-4-2-C-25 " -3-C-11
5610	83-5610A-16	0	40.1 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-5-E-3
5613	81-5613-8	0	40.1 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-5-E-6
5616	81-5616-2	2	40.1 km SW from Malatya to Maras, TURKEY	BEM	1970-7-1-5-E-9
5641	77-5641-4[2)]	1	near bus terminal in Ankara, TURKEY	KUET	1976-7-16-2A
5641	78-5641b-10	2	"	"	"
5641	78-5641e-6	1	"	"	"
5641	79-5641A-3	0	"	"	"
5641	80-5641A1-2	2	"	"	"
5641	80-5641A1-6	2	"	"	"
5641	80-5641E-1	1	"	"	"
5641	80-5641E-2	1	"	"	"
5641	80-5641E-9	1	"	"	"
5641	83-5641-6	1	"	"	"
5641	83-5641-8	2	"	"	"
5641	85-5641A-10	2	"	"	"
5641	85-5641B-6	2	"	"	"
5642	77-5642-2[2)]	3	near bus terminal in Ankara, TURKEY	KUET	1976-7-16-2B
5642	77-5642-4[2)]	3	"	"	"
5642	78-5642c-4	1	"	"	"
5642	79-5642A-2	1	"	"	"
5642	79-5642B-10	3	"	"	"
5643	77-5643-4[2)]	3	near bus terminal in Ankara, TURKEY	KUET	1976-7-17-4A
5643	78-5643d-2	2	"	"	"
5643	78-5643d-4	1	"	"	"
5643	79-5643A-3	0	"	"	"

Table 9. (Continued)

Accession No. (KU)	Culture No.	No. of Bs	Collection locality	Donor[1]	Donor No.
5645	77-5645-4[2]	2	West side of Lake Mugan (Ankara - Çakal), TURKEY	KUET	1976-7-18-1A
5645	78-5645b-3	1	"	"	"
5645	78-5645b-8	1	"	"	"
5645	79-5645A-3	3	"	"	"
5645	79-5645B-4	3	"	"	"
5645	80-5645C-1	1	"	"	"
5645	80-5645C-7	1	"	"	"
5645	80-5645C-10	1	"	"	"
5645	81-5645B-8	1	"	"	"
5646	78-5646-1	0	West side of Lake Mugan (Ankara - Çakal), TURKEY	KUET	1976-7-18-1B
5646	78-5646-6	0	"	"	"
5646	83-5646-2	0	"	"	"
5646	83-5646-3	0	"	"	"
5646	83-5646-4	0	"	"	"
5649	77-5649-3[2]	0	Suburbs of Konya (Konya - Sille), TURKEY	KUET	1976-7-21-3D
5652	77-5652-4[2]	0	89 km NE of Kayseri (Sivas - Kayseri), TURKEY	KUET	1976-8-12-8C
5653	78-5653-10	0	N of Konya (Konya - Ankara), TURKEY	KUET	1976-8-16-3A
5653	81-5653-5	0	"	"	"
12004	85-12004-5	4	5.1 km N from Kalecik to Çankiri, TURKEY	KUSWE82	1982-8-1-7-2
12004	85-12004-9	4	"	"	"

1) Abbreviations of donors:
BEM: Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia (in 1970).
KUET: Kyoto University Scientific Exploration to the Eastern Turkey (in 1976).
KUSWE82: Kyoto University Scientific Expedition to Southwestern Eurasia (in 1982).
2) Plants arising from the original seed samples.

the other two had four Bs. As possible as many *mutica* plants with one B-chromosome were used as male parents in the crosses to obtain F_1 hybrid plants both with two Bs and without Bs from the same cross combinations. A univalent of B-chromosome at meiosis is eliminated in some degree at the anaphase or telophase of the first division and B-chromosomes still existing in the young pollen grains undergo non-disjunction of their sister chromatids at the anaphase of the first division of pollen grain mitosis and the two chromatids are preferentially contain in the generative nucleus at the following telophase. As a result, both 0B and 2B hybrids are obtained from the crosses using *mutica* plants with one B-chromosome as male parents (Ohta 1986). This is important to obtain the F_1 siblings similar to one another in their genotypes. However, the individuals with two B-chromosomes were also used especially in the cross combinations showing low crossability such as *Ae. umbellulata* x *Ae. mutica* and *Ae. caudata* x *Ae. mutica*. When *Ae. mutica* was used as female parents in the crosses with *Ae. squarrosa*, individuals of *Ae. mutica* with higher number of B-chromosomes, three or four Bs, were also used to obtain their F_1 hybrids with two Bs. Because the B-chromosomes do not undergo non-disjunction or preferential distribution at any process during embryo sac cell divisions after meiosis. Indeed, F_1 hybrids only with one B-chromosome were obtained from the present cross of *Ae. mutica* with 2Bs x *Ae. squarrosa* though a 2B hybrid plant was obtained from the cross of *Ae. mutica* with 4Bs x *Ae. squarrosa*.

3. METHODS

The chromosome pairing and the fertility in F_1 hybrids as the most effective measures of the phylogenetic relationships

Chromosome pairing in F_1 hybrids has been an effective measure for the estimation of phylogenetic relationships among related plant species. Kihara and his collaborators utilized the analyser-method to genome analysis in polyploid wheats and their relatives (Kihara and Nishiyama 1930) and they elucidated the genome constitutions of those species mainly based on the chromosome pairing in the F_1 hybrids between them and the diploid species used as the analyzers (Kihara 1954, 1963, Kihara and Tanaka 1970). However, in the *Aegilops-Triticum* complex, many genic systems have proved to control the frequency of chromosome pairing in meiosis such as *Ph1* locus located on chromosome 5B of hexaploid wheat (Okamoto 1957, Riley and Chapman 1958, Riley 1966, Wall, Riley and Chapman 1971, Wall, Riley and Gale 1971, Sears 1976, 1982). Among the diploid *Aegilops* species, five are found to have certain genotypes which affect the frequency of chromosome pairing at meiosis in interspecific F_1 hybrids. Upadhya (1966) reported that *Ae. caudata* promotes to a certain degree the association of chromosomes in the F_1 hybrids with *T. aestivum*. A certain line of *Ae. longissima* showed a higher level of chromosome pairing in the F_1 hybrids with *T. aestivum* than the other lines (Mello-Sampayo 1971). *Ae. squarrosa* was reported to have weak suppressor of homoeologous chromosome pairing (Ekingen *et al.* 1977, Attia *et al.* 1979). The effects on the frequency of chromosome pairing shown in these three diploid species are not so

drastic as *Ph1* locus of *T. aestivum* but rather minute. In contrast with these species, *Ae. speltoides* and *Ae. mutica* have some genes which drastically suppress the activity of the *Ph1* locus of *T. aestivum* (Riley *et al.* 1961, Riley 1966, Dover and Riley 1972a). Sears (1941) already found that one of the *Ae. speltoides* lines used in his crosses among diploid species showed apparently lower frequency of chromosome pairing than another *Ae. speltoides* line. Since such effective genes as *Ph1* of wheat are not found in diploid species so far, this variation in chromosome pairing found by Sears is thought to be due to other genic systems than above-mentioned genes which suppress the activity of *Ph1* gene. Chen and Dvořák (1984) also suggested the presence of minor genic systems in *Ae. speltoides* affecting the chromosome pairing in addition to major genic systems suppressing *Ph1* activity.

The estimation of genome relationships among related species from chromosome pairing in their F_1 hybrids is sometimes confused by such genic variations in the frequency of chromosome pairing. One possible resolution is to use a lot of material in an interspecific cross combination and to carefully observe chromosome pairing in the parental lines of the F_1 hybrids too (Bothmer *et al.* 1986). If many F_1 hybrid plants are observed, genic variants in the frequency of chromosome pairing can be detectable as few exceptional individuals showing much different frequency and configuration of chromosome pairing from those of the majority. By observing chromosome pairing in the parental lines, the effects of asynaptic or desynaptic genes on chromosome pairing in F_1 hybrids can be detected, when they affect homologous chromosome pairing as well as homoeologous chromosome pairing. When we carry out the

analysis of chromosome pairing carefully it is still the most effective measure of the phylogenetic relationships among related species, because many genes and many chromosomal segments along the whole chromosome length are involved as pointed out by Kimber (1983).

In addition to chromosome pairing in F_1 hybrids, their fertility is also a good measure for the estimation of genome relationships and phylogenetic relationships between their parental species. Interspecific hybrids often show various degree of sterility and such sterility is one of the main reproductive isolation barriers genetically separating closely related plant species. Clausen *et al.* (1939) defined the concept of species based on experiments. They also regarded the hybrid sterility as an important internal barrier separating species and used it as one of their criteria for the systematic units comparable to taxonomic species or species complexes. In the congeneric *Aegilops-Triticum* complex, most interspecific diploid hybrids are completely sterile (Sears 1941) except for those among the species within subsection Emarginata of section Platystachys (Tanaka 1955a, Feldman *et al.* 1979). If at least some fertility is observed in addition to almost normal chromosome pairing at the first metaphase (MI) of meiosis in interspecific hybrids, it is good evidence for a very close genetic relationship between the parental species.

Genome analysis using B-chromosomes of *Aegilops mutica*

One of the other difficulties in estimating genome relationships among diploid species by meiotic chromosome pairing in their F_1 hybrids is that non-homologous but partially homologous or homoeologous

chromosomes from the both parents pair with their counterparts because of the lack of preferential pairing as in polyploid hybrids and because of no effective genes which suppress the pairing between homoeologous chromosomes. When parental diploid species are closely related to each other as in the *Aegilops-Triticum* complex, this homoeologous chromosome pairing makes the estimation more difficult.

In the present cross experiment, the author utilized B-chromosomes of *Ae. mutica* as a useful tool for suppressing such homoeologous chromosome pairing in the F_1 hybrids between diploid *Aegilops-Triticum* species and *Ae. mutica*. Mochizuki (1957) was the first that found B-chromosomes of *Ae. mutica*. Later he cytologically observed the young leaf meristems of a total of 573 plants of *Ae. mutica* collected from four natural populations in central Turkey by the members of one of the botanical explorations of Kyoto University (BMUK). He found the plants with various number of B-chromosomes in all the populations observed (Mochizuki 1960). Some cytological characteristics specific to B-chromosomes of *Ae. mutica* can be summarized as follows: First, they are smaller than A-chromosomes and have median centromeres; second, they do not pair with A-chromosomes in meiosis; third, non-disjunction of their sister chromatids takes place at anaphase of the first division of pollen grain mitosis and both the sister chromatids preferentially contain in the generative nucleus at the following telophase; fourth, they are absent from root systems though they are present stably in the germ line cells (Mochizuki 1957, Ohta 1986). In addition to these characteristics, a remarkable cytological effect of the B-chromosomes on the homoeologous chromosome pairing was reported. Mochizuki (1964)

found that the B-chromosomes of *Ae. mutica* are similar to the chromosome 5B of hexaploid wheat in its effect on the pairing between homoeologous chromosomes and that they drastically reduce the frequency of homoeologous chromosome pairing in wheat-*mutica* hybrids nullisomic for the chromosome 5B of wheat. Furthermore, Dover and Riley (1972b) reported that B-chromosomes of *Ae. mutica* effectively suppress homoeologous chromosome pairing in the F_1 hybrids between *T. aestivum* monosomic for chromosome 5B and *Ae. mutica* when the F_1 hybrids do not have chromosome 5B of *T. aestivum*. In contrast with this drastic effect of B-chromosomes of *Ae. mutica* on the homoeologous chromosome pairing, they do not affect the pairing between fully homologous ones. Vardi and Dover (1972) reported no effect of B-chromosomes on homologous chromosome pairing from their observation on the chiasma frequency of *Ae. mutica* both without and with various number of B-chromosomes as well as on the chromosome pairing in the pentaploid plants with duplicated genomes of *T. dicoccoides* and one of *Ae. mutica* obtained from a backcross of *T. dicoccoides* to the F_1 hybrid between *T. dicoccoides* and *Ae. mutica* with B-chromosomes. The present author also confirmed the no effect of B-chromosomes of *Ae. mutica* on fully homologous chromosome pairing in the triploid plants with two B-chromosomes in addition to two *longissima* and one *mutica* genomes (genome constitution S^lS^lMt + 2Bs) (Ohta and Tanaka 1982). A total of 150 PMCs of the three triploid plants were observed and all of them showed seven tightly associated bivalents of 14 *longissima* chromosomes and seven univalents of *mutica* chromosomes in addition to a small ring-shaped bivalent of B-chromosomes (Table 21 and Figure 18 in Chapter 5). The result clearly indicates

that B-chromosomes of *Ae. mutica* do not suppress the association of fully homologous chromosomes of *Ae. longissima*.

In the present work on the genome analysis of *Ae. mutica*, a new method for estimating the genome relationships between *Ae. mutica* and the other diploid *Aegilops-Triticum* species was schemed by utilizing the above-mentioned cytological characteristic of B-chromosomes of *Ae. mutica*. The simplified principle of the new method using B-chromosomes of *Ae. mutica* is shown in Figure 5. Based on the chromosome pairing at MI of meiosis in the F_1 hybrids both with and without B-chromosomes between diploid species and *Ae. mutica*, the genomes of the diploid species are classified into the following three classes according to the degree of their homology or homoeology with the genome of *Ae. mutica* (designated as Mt in Figure 5): (a) The genome (designated as X) is **homologous** with the genome of *Ae. mutica* when the F_1 hybrids both without B-chromosomes (0B hybrids) and with two B-chromosomes (2B hybrids) show a very high frequency and a regular configuration of A-chromosome pairing such as seven bivalents; (b) the genome Y is **homoeologous** or **partially homologous** with that of *Ae. mutica* when the 0B hybrids show a very high frequency and an almost regular configuration of chromosome pairing such as seven bivalents while the 2B hybrids show drastically low frequency of chromosome pairing and characteristically form 14 univalents of A-chromosomes at MI in their PMCs, because B-chromosomes effectively suppress homoeologous chromosome pairing; and (c) the genome Z is **non-homologous** with that of *Ae. mutica* when the A-chromosomes come from the two parents do not pair at all and only 14 univalents are observed in both the 0B and 2B hybrids. This scheme is

	(a)		(b)		(c)	
Genome constitution of parental species and cross combination :	XX x MtMt		YY x MtMt		ZZ x MtMt	
Genome constitution of the F_1 hybrids :	XMt		YMt		ZMt	
No. of B-chromosomes in the F_1 hybrids :	0B	2Bs	0B	2Bs	0B	2Bs
Configuration of chromosome pairing at MI in the F_1 hybrids :	7_{II}	7_{II}	7_{II}	14_{I}	14_{I}	14_{I}
Relationship between the parental genomes :	Homologous		Homoeologous or Partially homologous		Non-homologous	

Figure 5. The principle of the present new method for estimating genome relationships between diploid species of the *Aegilops-Triticum* complex and *Ae. mutica* from the chromosome pairing in their F_1 hybrids with and without B-chromosomes.

of course much simplified and the intermediate classes of chromosome pairing among the three classes were often observed in the present interspecific hybrids.

The methods for cultivation, crossing and cytogenetical observations in the present study

Ten diploid *Aegilops* and a diploid *Triticum* species in addition to an artificially synthesized autotetraploid of *Ae. squarrosa* were crossed with *Ae. mutica* in the present work. These diploid species and the autotetraploid species were grown in the experiment field of the Plant Germ-plasm Institute, Kyoto University and *Ae. mutica* was planted in pots with a diameter of about 10 inches under a vinyl roof. Generally speaking, *Ae. mutica* flowers rather late compared with early flowering *Aegilops* species such as *Ae. bicornis*. Some individuals of *Ae. mutica* were put in the growth chamber and grown under long day condition after they produced enough tillers in order to make the flowering earlier. The chromosome number of each individual of *Ae. mutica* was counted to check the number of B-chromosomes it carried. One of the three anthers in its floret was smeared in aceto-carmine and the number of B-chromosomes was determined from the PMCs at MI of meiosis. And the other two anthers in the same floret were fixed in acetic alcohol (ethyl alcohol 3 : acetic acid 1) and stored in a refrigerator conditioned at about 5°C for further cytogenetical observations. The anthers containing PMCs at MI of meiosis of the other *Aegilops* and *Triticum* species used in the present work were also fixed in acetic alcohol and stored.

The above-mentioned 11 diploid *Aegilops-Triticum* species and an artificially synthesized autotetraploid of *Ae. squarrosa* were used as female parents and *Ae. mutica* was used as male parents in most cross combinations. Because *Ae. mutica*, which is an out-breeding species, has quite many florets on its spikes and its anthers shed abundant pollen grains at anthesis. The lowest two florets in each spikelet of the female parents were used in the crosses. They were emasculated two to four days before anthesis and their emasculated spikes were bagged by paraffin paper bags. They were pollinated with abundant and fresh pollen grains of *Ae. mutica* when they flowered and the spikes were again bagged until harvest. *Ae. mutica* usually flowers almost simultaneously just before sunrise on clear days. Its spikes were lighted with a small lamp at one to four o'clock in the midnight and emerging anthers before anthesis were used for pollination. By that method abundant and fresh pollen grains of *Ae. mutica* could be obtained during pollination for several hours. In some interspecific and intergeneric cross combinations, successfully obtained F_1 hybrid seeds from the crosses using *Ae. mutica* as male parents did not germinate at all. In the combination between *Ae. squarrosa* and *Ae. mutica* among those combinations, *Ae. mutica* was used not only as a male parent but also as a female parent. Its lowest two florets in each spikelet were emasculated before anthesis and pollinated with fresh pollen grains of *Ae. squarrosa*. The lowest floret of the uppermost spikelet flowers more than a week earlier than the second floret of the lowest spikelet. The emasculated spikes of *Ae. mutica* were pollinated repeatedly from the upper part to the lower part. In addition to the cross combination

involving *Ae. squarrosa*, *Ae. speltoides* was crossed with *Ae. mutica* reciprocally by the same method as *Ae. squarrosa*.

Successfully obtained F_1 hybrid seeds were sown in the sterilized soil of seedling boxes in autumn. Seedlings obtained from the seeds were transplanted to the experiment field of the Plant Germ-plasm Institute or to pots under a vinyl roof about a month after the seeds were sown. Most of those F_1 hybrid plants grew under the natural day length and the natural temperature in Kyoto. Their anthers containing PMCs at MI and/or at other stages of meiosis desirable for cytological observations were fixed in acetic alcohol for further cytogenetical observations after confirmation of their meiotic stages by smearing one of the three anthers of a floret in aceto-carmine. Some of the F_1 hybrids between *Ae. speltoides* and *Ae. mutica* and between *Ae. squarrosa* and *Ae. mutica* were put in a growth chamber conditioned at 20°C and continuous light condition when they produced enough tillers. They moved into an unheated greenhouse after their anthers containing PMCs at MI or the first anaphase (AI) of meiosis were fixed in acetic alcohol. All the anthers fixed in acetic alcohol were stored in a refrigerator at about 5°C. For detailed cytogenetical observations, those fixed anthers of the F_1 hybrids as well as of their parental lines were mordanted in 2% iron alum aqueous solution, stained with aceto-carmine, and squashed in 45% acetic acid on a slide. Then the frequency and the configuration of chromosome pairing at MI of meiosis or the segregation of associated chromosomes at AI of meiosis were observed. The number of chiasmata formed on associated chromosomes was counted in the manner described by Darlington (1937).

The pollen grains of the F_1 hybrids and some of their parental lines were collected from anthers in the lowest florets of one or two spikelets in the middle part of their spikes. They were stained and mounted in dilute aceto-carmine solution containing glycerin as a mounting medium. The well stained pollen grains with three nuclei were regarded as normal. Pollen fertility was represented by the proportion of the normal pollen grains among a total of five hundreds to four thousands observed pollen grains. The diameters of normal pollen grains found in some F_1 hybrids between *Ae. speltoides* and *Ae. mutica* were measured on the same slides as used for the estimation of their pollen fertility. They were measured under a microscope with a scale on an eyepiece and they were represented by the mean lengths of major and minor axes of pollen grains.

The chromosome numbers in root tips were counted in the three plants of the second generation of the hybrids between *Ae. speltoides* and *Ae. mutica*. Their root tips were cut from seedlings and fixed in acetic alcohol after pre-treatment in water at 0°C for 24 hours. They were stained in aceto-carmine with a thin unplated iron wire as a mordant. Then they were squashed in 45% acetic acid on a slide and their chromosome numbers were counted in several well spread cells at metaphase of mitosis.

4. CHROMOSOME PAIRING AND POLLEN FERTILITY IN THE PARENTAL INDIVIDUALS USED IN THE PRESENT CROSSES

Chromosome pairing and pollen fertility in the parental lines used in the present crosses with *Aegilops mutica*

As shown in Table 10 and Figure 6, chromosome pairing of the parental lines used in the present crosses with *Ae. mutica* was observed at MI of meiosis in their PMCs. All the observed lines showed a normal frequency and a regular configuration of chromosome pairing. They formed a very high frequency of chiasmata and most bivalents observed in their PMCs were ring-shaped. And a few univalents were found in some lines but none in others. In *Ae. caudata*, *Ae. uniaristata* and *Ae. umbellulata*, the number of paired arms was fewer and the frequency of rod-shaped bivalents was higher than those in the other species. This may be due to the association between subtelocentric chromosomes in their chromosome complements (for their karyotypes, see Chennaveeraiah 1960).

The anthers of all the lines normally dehisced at anthesis and shed abundant pollen grains. Pollen fertility estimated in some lines was quite normal.

Chromosome pairing and pollen fertility in the individuals of *Aegilops mutica* used in the present crosses

Among a total of 29 plants from 12 accessions of *Ae. mutica*, 28 from 11 accessions contributed to the F_1 hybrids with the other diploid species of the congeneric *Aegilops-Triticum* complex. As shown in Table

Table 10. The mean configuration and frequency of chromosome pairing and their ranges at MI of meiosis of the parental lines of the F_1 hybrids successfully obtained from the present crosses involving *Ae. mutica*

Accession No. (KU)	No.of cells observed	Chromosome pairing at MI[1] UNIV.	BIV. Total	BIV. Rod Ring	No.of[2] arms paired	No.of chiasmata per cell
Aegilops bicornis						
3-1	50	-	7.00 (7)	0.80 6.20 (0-4)(3-7)	13.20 (10-14)	13.78 (11-17)
Aegilops sharonensis						
5-1	50	0.04 (0-2)	6.98 (6-7)	0.10 6.88 (0-1)(6-7)	13.86 (12-14)	13.86 (12-14)
5-3	50	-	7.00 (7)	0.48 6.52 (0-2)(5-7)	13.52 (12-14)	13.68 (12-15)
Aegilops longissima						
4-1	50	-	7.00 (7)	0.38 6.62 (0-2)(5-7)	13.62 (12-14)	13.80 (12-16)
4-4	30	-	7.00 (7)	0.33 6.67 (0-2)(5-7)	13.67 (12-14)	13.70 (12-15)
Aegilops speltoides						
2201B	50	0.36 (0-4)	6.82 (5-7)	0.72 6.10 (0-2)(4-7)	12.92 (9-14)	12.96 (9-15)
2213D	not obs.					
2263	not obs.					
2282	50	-	7.00 (7)	0.18 6.82 (0-1)(6-7)	13.82 (13-14)	13.82 (13-14)
5725B	35	0.28 (0-4)	6.86 (5-7)	0.34 6.51 (0-2)(5-7)	13.37 (10-14)	13.37 (10-14)
7761	50	0.04 (0-2)	6.98 (6-7)	0.38 6.60 (0-3)(4-7)	13.58 (11-14)	13.58 (11-14)
7943	50	0.12 (0-2)	6.94 (6-7)	0.60 6.34 (0-3)(4-7)	13.28 (11-14)	13.38 (11-14)
7972	50	-	7.00 (7)	0.36 6.64 (0-2)(5-7)	13.64 (12-14)	13.64 (12-14)
Aegilops squarrosa						
20-9	50	0.12 (0-2)	6.94 (6-7)	0.16 6.78 (0-2)(5-7)	13.72 (12-14)	14.10 (12-16)

Table 10. (Continued)

Accession No. (KU)	No.of cells observed	Chromosome pairing at MI[1]					
		UNIV.	BIV.			No.of[2] arms paired	No.of chiasmata per cell
			Total	Rod	Ring		
Aegilops caudata							
6-1	50	0.04 (0-2)	6.98 (6-7)	1.98 (0-4)	5.00 (3-7)	11.98 (10-14)	12.66 (10-16)
6-2	50	0.08 (0-2)	6.96 (6-7)	1.44 (0-3)	5.52 (4-6)	12.48 (11-13)	13.40 (12-17)
Aegilops comosa							
17-1	50	0.04 (0-2)	6.98 (6-7)	0.66 (0-3)	6.32 (4-7)	13.30 (11-12)	13.30 (11-14)
17-2	50	0.12 (0-2)	6.94 (6-7)	1.18 (0-4)	5.76 (3-7)	12.70 (10-14)	12.70 (10-14)
Aegilops uniaristata							
19-3	5	0.40 (0-2)	6.80 (6-7)	1.60 (0-3)	5.20 (3-7)	12.00 (9-14)	12.20 (9-14)
Aegilops umbellulata							
8-2	5	-	7.00 (7)	3.00 (3)	4.00 (4)	11.00 (11)	11.40 (11-13)
Triticum monococcum							
101-1	50	-	7.00 (7)	0.14 (0-1)	6.86 (6-7)	13.86 (13-14)	14.04 (13-16)
103	50	-	7.00 (7)	0.14 (0-2)	6.86 (5-7)	13.86 (12-14)	14.26 (12-16)

1) Figures in the parentheses represent the ranges observed.
2) Figures represent the half numbers of paired arms.

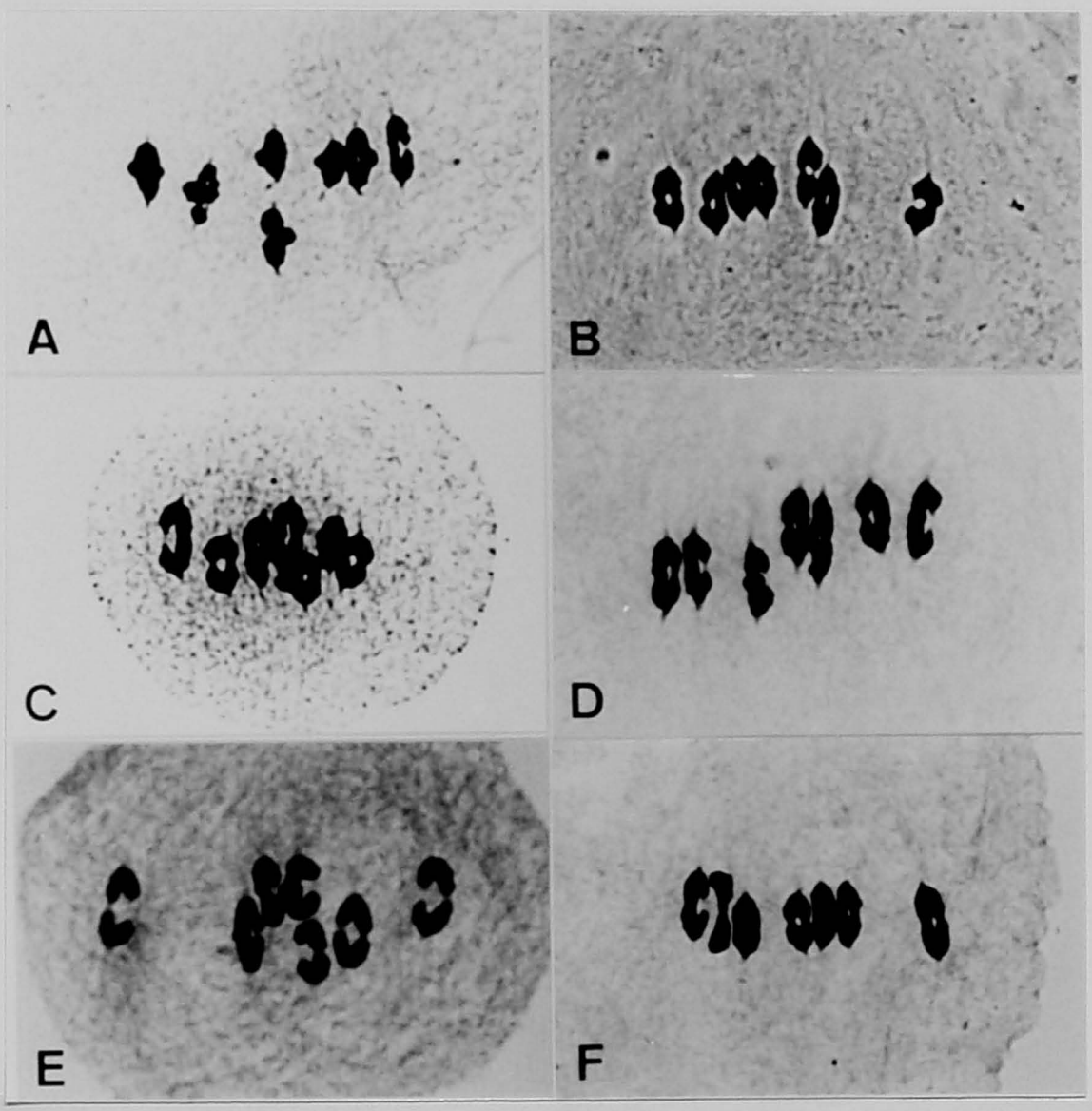


Figure 6. The configuration of chromosome pairing at MI of meiosis in the parental species of the F_1 hybrids successfully obtained from the crosses with *Ae. mutica* (x 1,100). A: *Ae. bicornis* (KU 3-1), B-C: *Ae. sharonensis* (B: KU 5-1, C: KU 5-3), D-E: *Ae. longissima* (D: KU 4-1, E: KU 4-4), F: *Ae. speltoides* (KU 2201B).

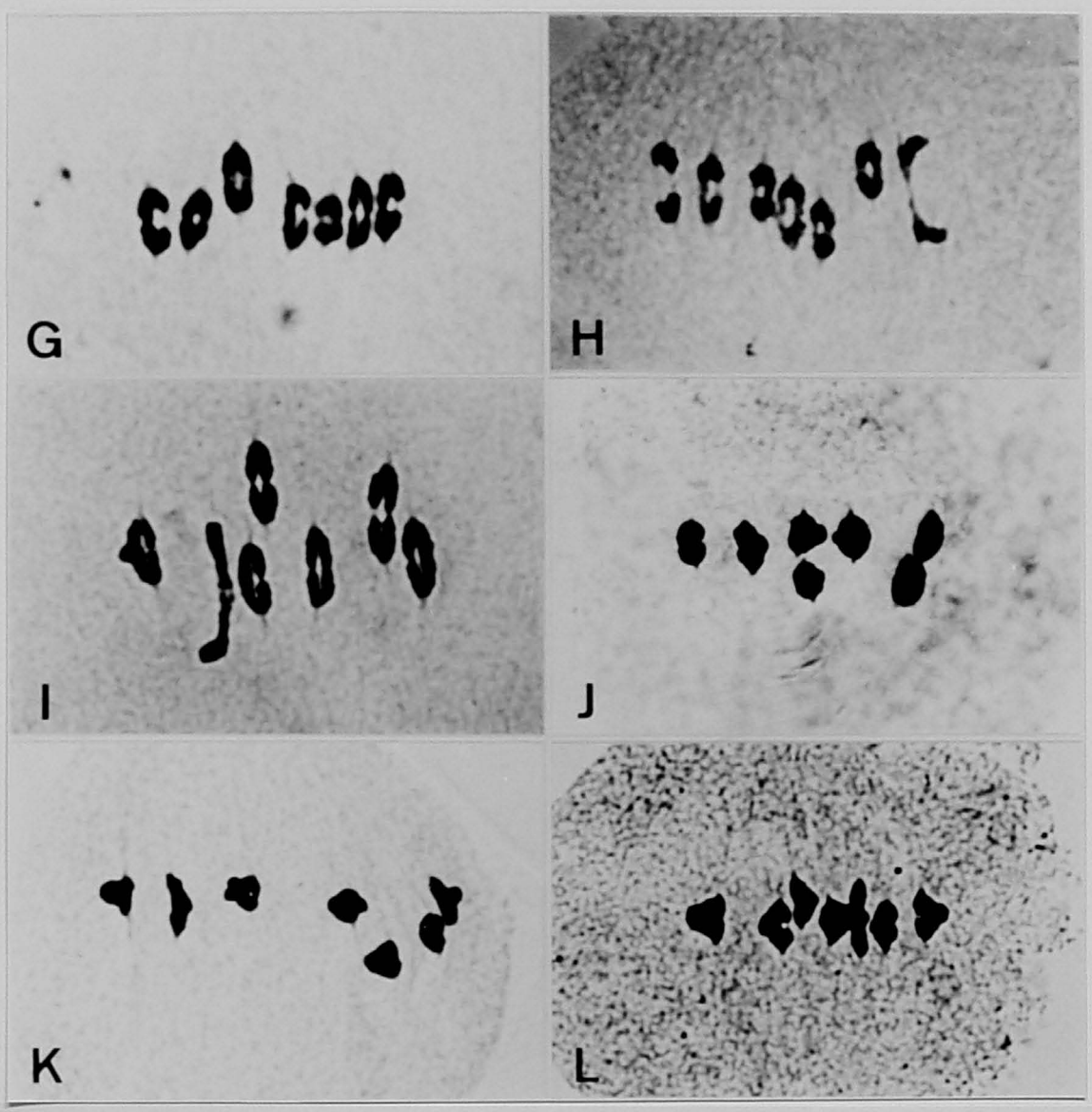


Figure 6. (Continued)

G-I: *Ae. speltoides* (G: KU 2282, H: KU 7761, I: KU 7943), J: *Ae. squarrosa* (KU 20-9), K-L: *Ae. caudata* (K: KU 6-1, L: KU 6-2)

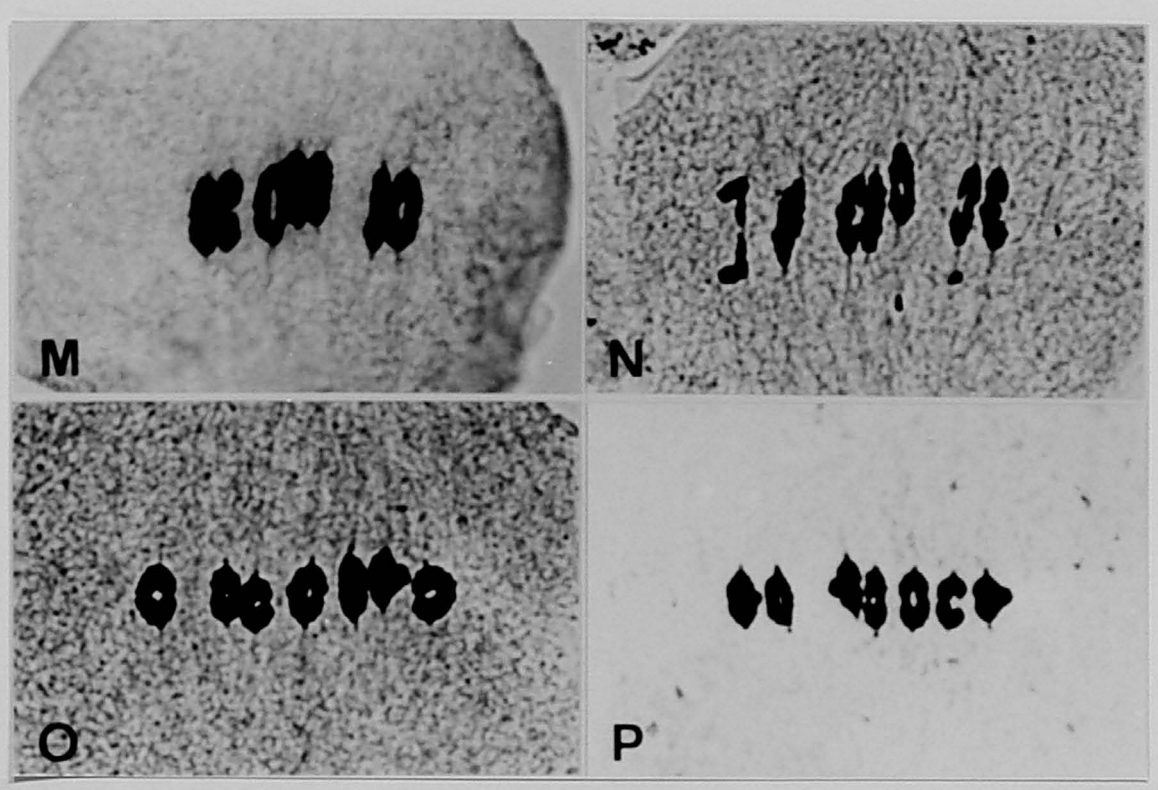


Figure 6. (Continued)

M-N: *Ae. comosa* (M: KU 17-1, N: KU 17-2), O-P: *T. monococcum* (O: KU 101-1, P: KU 103).

11 and Figure 7, all the observed individuals showed quite normal configuration and frequency of chromosome pairing except for only one plant (Culture No. 83-5610A-16). They showed a very high frequency of chiasmata and ring-shaped bivalents but no or few univalents in their PMCs. One plant from the accession KU5610, 83-5610A-16, showed a high frequency but an irregular configuration of chromosome pairing: A quadrivalent was observed at a high frequency in its PMCs (Figure 7A).

Among a total of 28 plants of *Ae. mutica* contributing to the F_1 hybrids, ten plants had one B-chromosome, five had two, three had three and one had four B-chromosomes in addition to their normal chromosome complements of 14 A-chromosomes, while the other nine had no B-chromosome. In the plants with only one B-chromosome, it always behaved as a univalent at MI of meiosis in their PMCs (Figures 7B, H and J). When plants carried two B-chromosomes, they formed a small but tightly associated ring-shaped bivalent in most of their PMCs (Figure 7C), and a rod-shaped bivalent (Figure 7D) or two univalents of Bs (Figures 7E and I) were found in a few cells. Three B-chromosomes at MI of meiosis of 3B plants showed more complicated configuration of association. They often formed a frying pan shaped trivalent (Figure 7F) or a ring-shaped bivalent with a univalent (Figure 7G). However, three univalents of B-chromosomes were not observed in any PMCs. In a plant with four B-chromosomes, they formed a small quadrivalent with complicated associations in many PMCs such as an 8-shaped, an O-shaped, a chain-shaped quadrivalent, and so on. And in some cells two bivalents of B-chromosomes were found.

As shown in Table 11, the frequency of pairing between A-

Table 11. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in *Aegilops mutica* used as the parental lines of successfully obtained F_1 hybrid plants

Accession No. (KU)	Culture No.	No. of Bs	No. of cells observed	A-Chromosome pairing at MI[1]									
				UNIV.	BIV.			TRIV.	QUADRIV.			No. of[2] arms paired	No. of chiasmata per cell
					Total	Rod	Ring		Total	Chain	Ring		
5598	81-5598-3	2	50	0.04 (0-2)	6.98 (6-7)	0.66 (0-2)	6.32 (5-7)	-	-	-	-	13.30 (12-14)	13.62 (12-17)
5610	83-5610A-16	0	50	0.08 (0-2)	5.50 (4-7)	0.70 (0-3)	4.80 (3-6)	0.04 (0-1)	0.70 (0-1)	0.44 (0-1)	0.26 (0-1)	12.74 (11-14)	12.80 (11-15)
5613	81-5613-8	0	not obs.[3]										
5641	77-5641-4	1	29	0.48 (0-2)	6.76 (6-7)	1.48 (0-3)	5.28 (4-6)	-	-	-	-	12.03 (10-13)	12.24 (10-14)
5641	78-5641e-6	1	30	-	7.00 (7)	1.83 (0-4)	5.17 (3-7)	-	-	-	-	12.17 (10-14)	not obs.
5641	80-5641A1-6	2	50	-	7.00 (7)	0.64 (0-2)	6.36 (5-7)	-	-	-	-	13.36 (12-14)	13.54 (12-15)
5641	80-5641E-1	1	50	0.04 (0-2)	6.98 (6-7)	1.20 (0-4)	5.78 (3-7)	-	-	-	-	12.76 (10-14)	12.90 (10-15)
5641	80-5641E-9	1	50	0.04 (0-2)	6.98 (6-7)	0.36 (0-2)	6.62 (5-7)	-	-	-	-	13.60 (12-14)	13.76 (12-15)
5641	83-5641-6	1	50	0.04 (0-2)	6.98 (6-7)	1.02 (0-4)	5.96 (3-7)	-	-	-	-	12.94 (10-14)	13.02 (10-16)
5641	83-5641-8	2	50	0.04 (0-2)	6.98 (6-7)	0.72 (0-3)	6.26 (4-7)	-	-	-	-	13.24 (11-14)	13.26 (11-15)
5641	85-5641B-6	2	24	0.08 (0-2)	6.96 (6-7)	1.50 (0-3)	5.46 (4-7)	-	-	-	-	12.42 (11-14)	12.46 (11-15)
5642	77-5642-2	3	not obs.										
5642	78-5642c-4	1	30	-	7.00 (7)	0.17 (0-1)	6.83 (6-7)	-	-	-	-	13.83 (13-14)	not obs.
5642	79-5642B-10	3	50	0.08 (0-4)	6.96 (5-7)	0.68 (0-1)	6.28 (5-7)	-	-	-	-	13.24 (6-14)	not obs.

Table 11. (Continued)

Accession No. (KU)	Culture No.	No. of Bs	No.of cells observed	A-Chromosome pairing at MI[1]								No.of[2] arms paired	No.of chiasmata per cell
				UNIV.	BIV.			TRIV.	QUADRIV.				
					Total	Rod	Ring		Total	Chain	Ring		
5643	77-5643-4	3	not obs.										
5643	78-5643d-4	1	30	-	7.00 (7)	0.90 (0-3)	6.10 (4-7)	-	-	-	-	13.10 (11-14)	13.20 (11-14)
5645	77-5645-4	2	19	0.11 (0-2)	6.95 (6-7)	1.53 (0-3)	5.42 (4-7)	-	-	-	-	12.37 (11-14)	not obs.
5645	78-5645b-3	1	30	0.07 (0-2)	6.97 (6-7)	1.07 (0-3)	5.90 (4-7)	-	-	-	-	12.87 (11-14)	not obs.
5645	78-5645b-8	1	50	0.04 (0-2)	6.98 (6-7)	0.92 (0-3)	6.06 (4-7)	-	-	-	-	13.04 (11-14)	13.24 (11-15)
5645	80-5645C-10	1	not obs.										
5646	78-5646-1	0	20	-	7.00 (7)	0.50 (0-3)	6.50 (4-7)	-	-	-	-	13.50 (11-14)	not obs.
5646	78-5646-6	0	30	0.07 (0-2)	6.97 (6-7)	0.37 (0-2)	6.60 (5-7)	-	-	-	-	13.57 (12-14)	not obs.
5646	83-5646-2	0	50	-	7.00 (7)	0.60 (0-2)	6.40 (5-7)	-	-	-	-	13.40 (12-14)	13.58 (12-15)
5646	83-5646-3	0	50	-	7.00 (7)	0.90 (0-3)	6.10 (4-7)	-	-	-	-	13.10 (11-14)	13.20 (11-15)
5649	77-5649-3	0	50	0.04 (0-2)	6.98 (6-7)	0.36 (0-2)	6.62 (5-7)	-	-	-	-	13.60 (12-14)	14.32 (12-16)
5653	78-5653-10	0	not obs.										
5653	81-5653-5	0	50	-	7.00 (7)	0.26 (0-2)	6.74 (5-7)	-	-	-	-	13.74 (12-14)	13.94 (12-15)
12004	85-12004-5	4	23	-	7.00 (7)	1.35 (0-4)	5.65 (3-7)	-	-	-	-	12.65 (10-14)	13.17 (11-15)

1) Figures in the parentheses represent the ranges observed.
2) Figures represent the half numbers of paired arms.
3) not obs.: not observed.

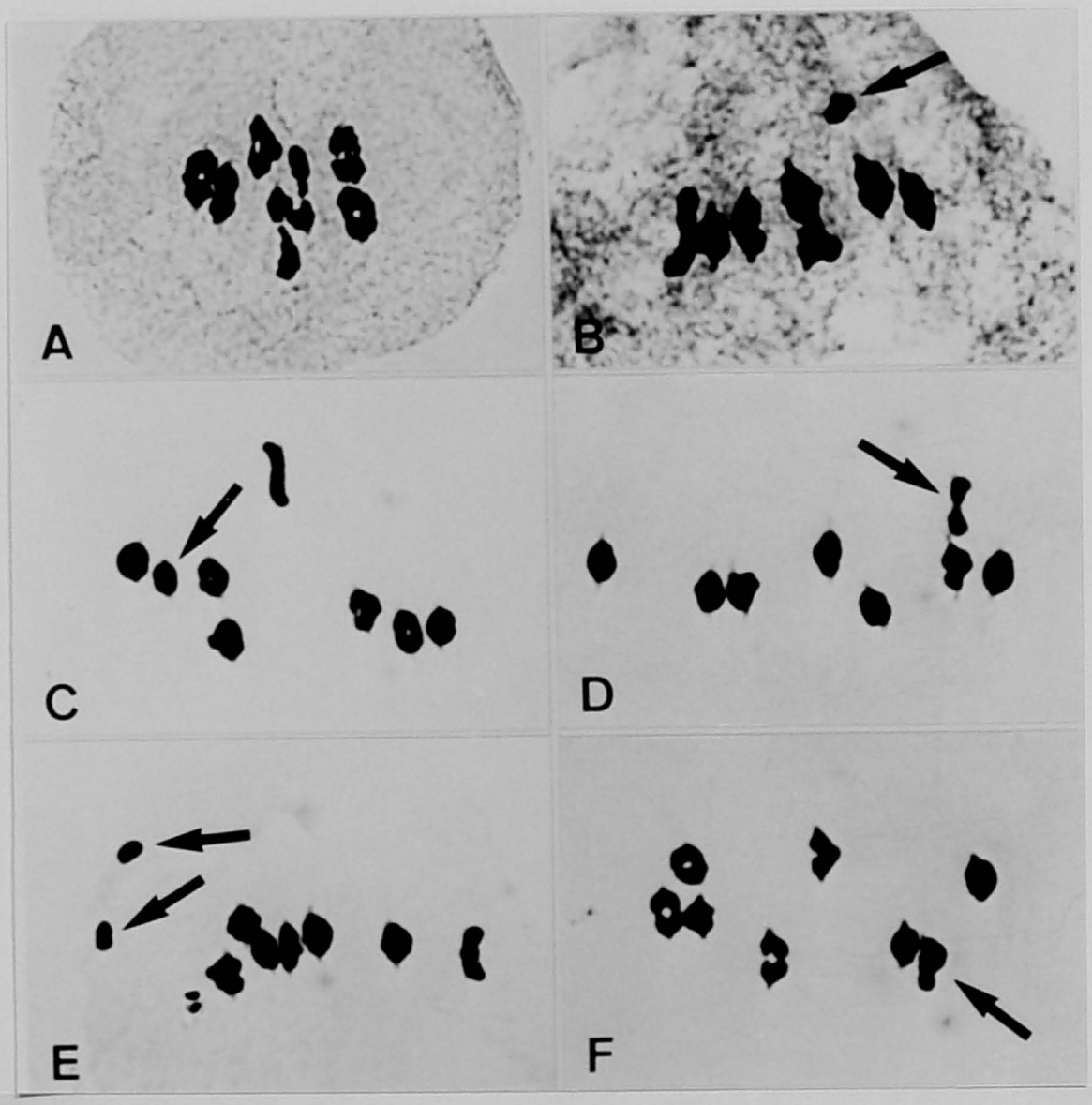


Figure 7. The configuration of chromosome pairing at MI of meiosis in *Aegilops mutica* without or with various numbers of B-chromosomes used as the parents of the F_1 hybrids successfully obtained from the present crosses (x 1,100). B-chromosomes are indicated with arrows. A: 83-5610A-16 without Bs, $5_{II}+1_{IU}$; B: 78-5641e-6 with 1B, 7_{II} of As + 1_I of B; C-E: 80-5641A1-6 with 2Bs, C: 7_{II} of As + $1ring_{II}$ of Bs, D: 7_{II} of As + $1rod_{II}$ of Bs, E: 7_{II} of As + 2_I of Bs; F-G: 79-5642B-10 with 3Bs, F: 7_{II} of As + 1_{III}(frying pan) of Bs.

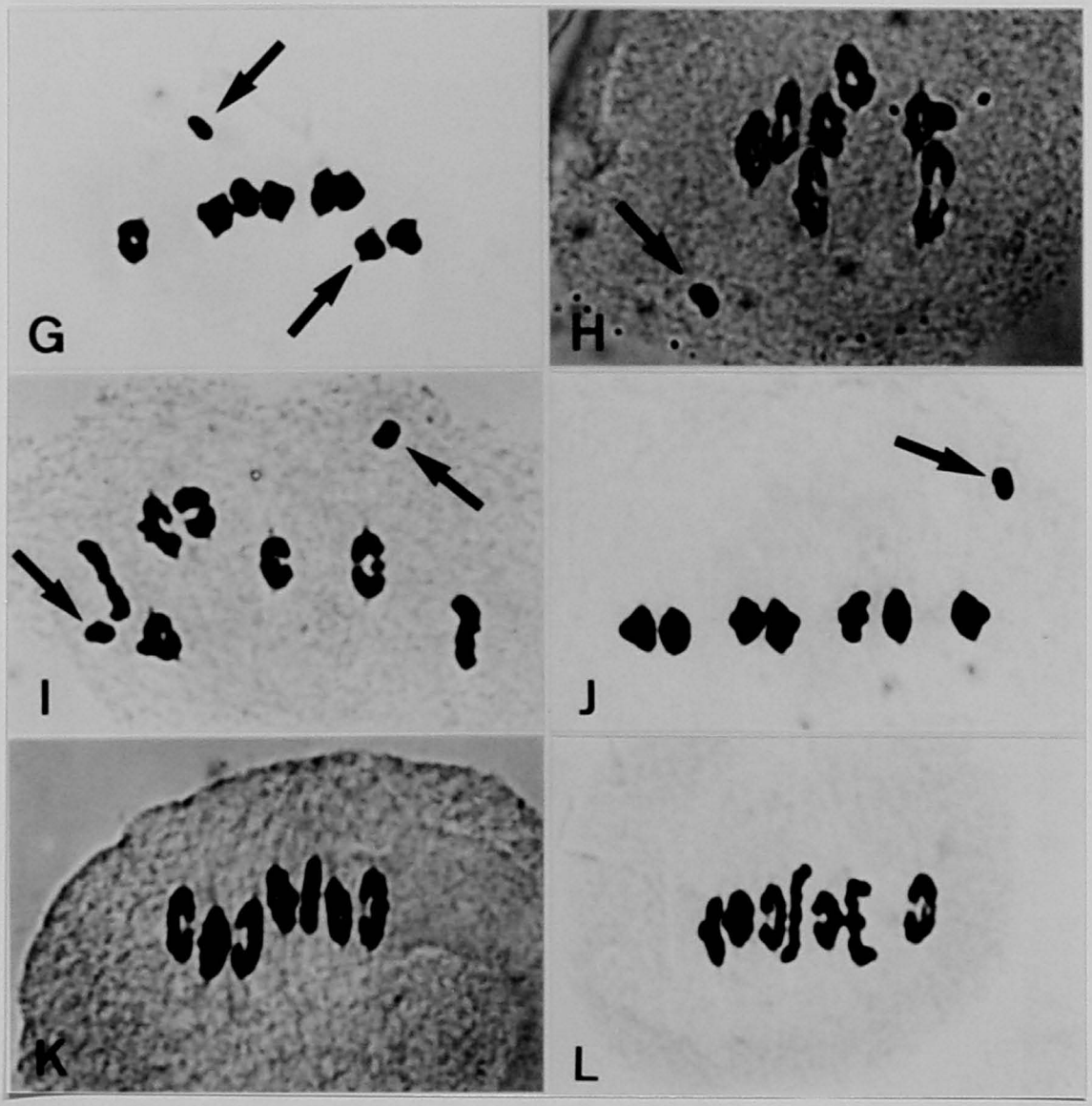


Figure 7. (Continued)

G: 79-5642B-10 (Continued), 7_{II} of As + 1_{I}+1ring$_{II}$ of Bs; H: 83-5641-6 with 1B, 7_{II} of As + 1_{I} of B; I: 83-5641-8 with 2Bs, 7_{II} of As + 2_{I} of Bs; J: 78-5645b-8 with 1B, 7_{II} of As + 1_{I} of B; K: 83-5646-2 without Bs, 7_{II}; L: 83-5646-3 without Bs, 7_{II}.

chromosomes in plants of *Ae. mutica* with various number of B-chromosomes was quite normal and it was not different at all from that in the plants without B-chromosomes. This indicates that B-chromosomes do not affect the frequency of homologous chromosome pairing as shown in the previous works (Vardi and Dover 1972, Ohta and Tanaka 1982).

The anthers of all the lines used in the present crosses normally dehisced at anthesis. Pollen fertility observed in some individuals was quite normal and their pollen fertility was more than 80% or 90%.

5. MORPHOLOGICAL AND CYTOGENETICAL CHARACTERISTICS OF THE PRESENT INTERSPECIFIC AND INTERGENERIC F_1 HYBRIDS

(1) *Aegilops bicornis* x *Ae. mutica*

Result of the crosses

An accession of *Aegilops bicornis* and two of *Ae. mutica* were used in the present crosses (Table 12). From the two cross combinations 44 seeds were obtained and the mean seed set was 61%. Seven of them germinated and six F_1 hybrid plants grew vigorously. The mean germination rate was 16%. Two of the F_1 hybrid plants were obtained from the cross combination of 3-1 x 80-5641E-1. One of them had two B-chromosomes derived from the *mutica* plant with a B-chromosome used as the male parent but another had no B-chromosome. The other four F_1 hybrids were obtained from the cross combination of 3-1 x 78-5653-10 and none of them had B-chromosomes.

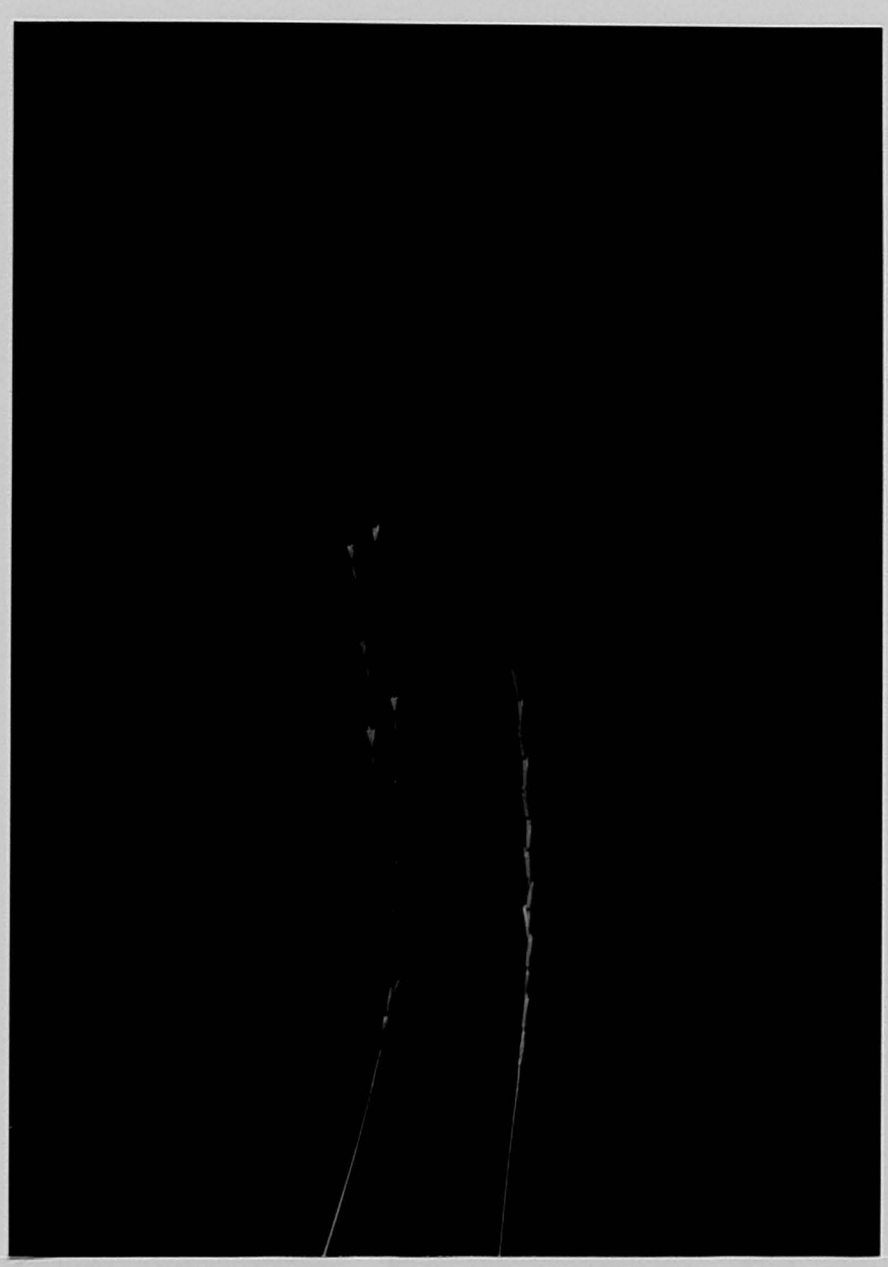
Morphology of *Aegilops bicornis* and the F_1 hybrids between *Ae. bicornis* and *Ae. mutica*

Ae. bicornis (Figures 8A, 9A and C) has linear compressed spikes consisting of about 15 or more spikelets arranged in two rows[1]. Its spike has no rudimentary or sterile spikelet in any parts. The spikelet consists of three florets. All the lateral spikelets are similar both in shape and in size along the whole spike length. They are more than three times as long as the adjacent rachis internodes in the middle part

1) in two rows: Translation into English from the German term *'zweizeilig'* in Eig (1929a).

Table 12. Result of the crosses between *Aegilops bicornis* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops bicornis x *Ae. mutica*						
3-1 x 80-5641E-1	45	30	67	30	3	10
3-1 x 78-5653-10	26	14	54	14	4	29
Total	71	44	61	44	7	16



A B

Figure 8. Spike morphology of *Ae. bicornis* and the F_1 hybrids between *Ae. bicornis* and *Ae. mutica* (x 0.5). A: *Ae. bicornis* (KU 3-1), B: F_1 hybrid between *Ae. bicornis* and *Ae. mutica* (79934-P1), the upper half of the spike of the F_1 hybrid already fell down.

A B C D

Figure 9. Spikelet morphology of *Ae. bicornis* and the F_1 hybrids between *Ae. bicornis* and *Ae. mutica* (x 2.4). A and C: *Ae. bicornis* (KU 3-1), B and D: F_1 hybrid between *Ae. bicornis* and *Ae. mutica* (79934-P1).

of the spikes. In the upper and lower parts of the spikes they are slightly longer than the adjacent rachis internodes. Empty glumes cover about a half to two thirds of the each spikelet. There are two teeth divided with a shallow dull notch on their upper margins. One of the teeth is a tip of a keel and sharp while another is dull. Neither of them tapers into an awn. Tips of the lemmas of the lowest two florets taper into thin awns. The awns become shorter in the lower part of a spike and become teeth in the lowest part of a spike. Rachis is very fragile and easy to break at maturity or even before maturity when the spike specimen are dried up. Each rachis node breaks at maturity and each spikelet falls separately with the rachis internode below it (wedge type disarticulation). Rachillae are tough.

The F_1 hybrids between *Ae. bicornis* and *Ae. mutica* (Figures 8B, 9B and D) had long linear spikes on which spikelets were arranged almost in a row. And they did not have any rudimentary spikelets or any awns on their spikes. These characteristics of the F_1 hybrids gave the impression that they were much similar to *Ae. mutica* in their spike morphology. However, the detailed observations about their morphology revealed that they had intermediate characteristics between *Ae. bicornis* and *Ae. mutica* in morphology of many of their parts. The spikelets of the F_1 hybrids were much shorter than those of *Ae. mutica* which was resulted from fewer florets in the F_1 hybrids than *Ae. mutica*. Each spikelet of the F_1 hybrids had four or five florets while that of *Ae. mutica* and *Ae. bicornis* usually had five to eight and three florets, respectively. The length of their empty glumes was similar to that of *Ae. mutica*, and as a result, their length relative to spikelets was much

longer than that of *Ae. mutica* and they covered about two thirds of the each spikelet. The empty glumes of the F_1 hybrids had a weak keel on the same position as those of *Ae. bicornis*. There was no sharp tooth or no sharp notch between teeth on the upper margin of the empty glumes. Lemmas had no awns. The rachises of the F_1 hybrids were fragile and each rachis node disarticulated at maturity (wedge type disarticulation) but their rachillae were tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

The frequency and configuration of A-chromosome pairing at MI of the obtained F_1 hybrids are shown in Table 13 and Figure 10. Four F_1 hybrids without B-chromosomes obtained from the cross combination, 3-1 x 78-5653-10 (Culture No. 79934) showed a very high frequency of A-chromosome pairing at MI of meiosis in their PMCs. Their mean chiasma frequency ranged from 12.43 to 10.57 per cell. They could be divided into two groups according to the mean number of their arm paired. One consisted of the two plants showing the higher frequency of chromosome pairing, 79934-P2 and -P4. Their mean chiasma frequency was 12.27 per cell and the mean configuration of A-chromosome pairing was 0.24_{I} + $(1.60\text{rod} + 5.28\text{ring})_{II}$ per cell. Another consisted of the other two plants, 79934-P1 and -P3. Their mean chiasma frequency and mean configuration of A-chromosome pairing were 10.77 and 0.67_{I} + $(2.65\text{rod} + 4.02\text{ring})_{II}$ per cell, respectively. The former group showed slightly but significantly ($\chi^2 > 24.49$) higher frequency of chromosome pairing than the latter. The 0B hybrid plant from the other cross combination (Culture No. 81725) also showed a very high frequency of A-chromosome

Table 13. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops bicornis* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
3-1 x 78-5653-10													
79934-P2	0	30	0.20 (0-2)	6.90 (6-7)	1.50 (0-4)	5.40 (3-7)	-	-	-	-	-	12.30 (9-14)	12.43 (9-15)
-P4	0	30	0.27 (0-2)	6.87 (6-7)	1.70 (0-4)	5.17 (2-7)	-	-	-	-	-	12.03 (8-14)	12.10 (8-15)
-P3	0	30	0.53 (0-6)	6.73 (4-7)	2.57 (0-7)	4.17 (0-7)	-	-	-	-	-	10.90 (7-14)	10.96 (7-14)
-P1	0	30	0.80 (0-4)	6.60 (5-7)	2.73 (0-5)	3.87 (2-7)	-	-	-	-	-	10.47 (7-14)	10.57 (7-14)
3-1 x 80-5641E-1													
81725-P2	0	50	0.40 (0-6)	6.80 (4-7)	2.80 (0-6)	4.00 (1-7)	-	-	-	-	-	10.80 (7-14)	10.80 (7-14)
-P1	2	50	13.92 (12-14)	0.04 (0-1)	0.04 (0-1)	-	-	-	-	-	-	0.04 (0-1)	0.04 (0-1)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

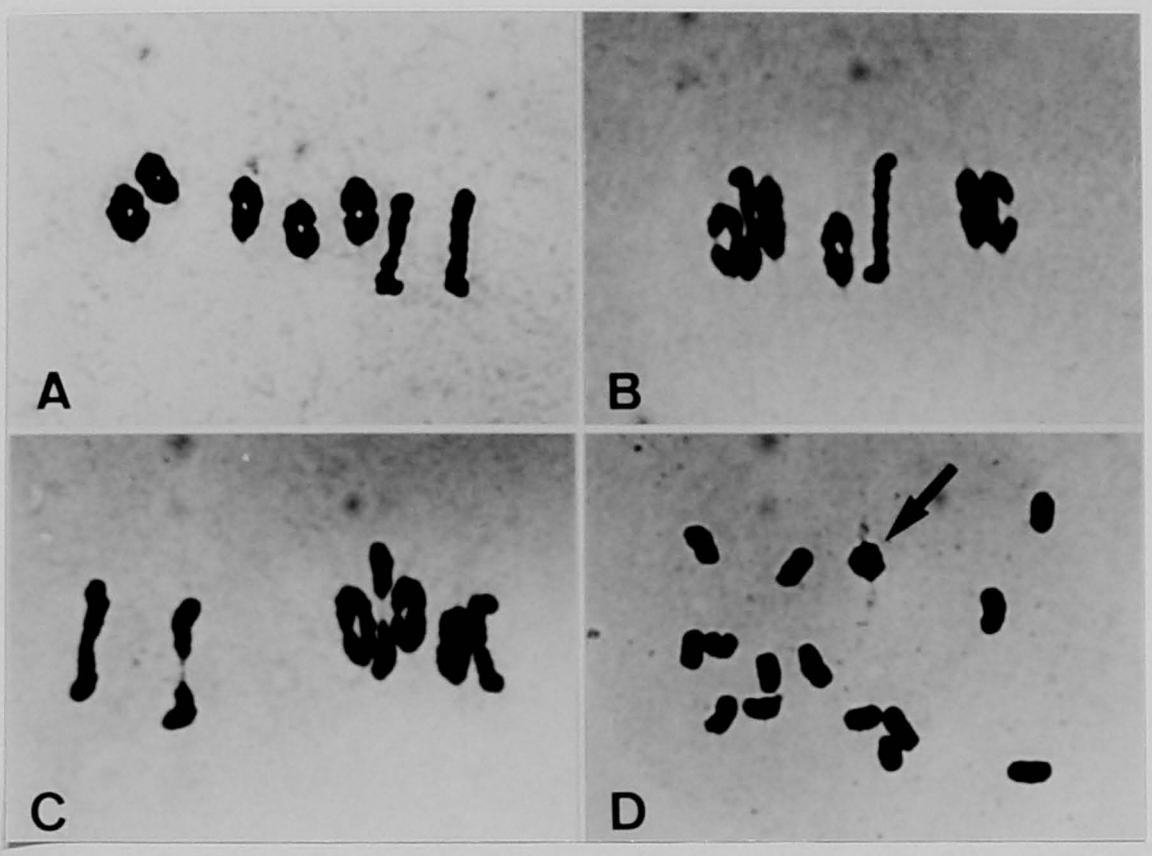


Figure 10. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with or without B-chromosomes (Bs) between *Aegilops bicornis* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with an arrow. A: 79934-P2 without Bs, 7_{II}; B-C: 81725-P2 without Bs, 7_{II}; D: 81725-P1 with 2Bs, 14_I of As + $1ring_{II}$ of Bs.

pairing. Its mean chiasma frequency and mean configuration of A-chromosome pairing were 10.80 per cell and 0.40_{I} + (2.80rod + 4.00ring)$_{II}$, respectively. This plant could be included in the latter group according to the number of paired arms. In spite of the slight difference in the frequency of chromosome pairing, all the 0B hybrids obtained from the two cross combinations showed a very regular configuration of chromosome pairing (Figures 10A-C). Among a total of 170 cells observed in the five 0B hybrids from the two cross combinations, 139 (82%) formed seven bivalents, of which 14 formed seven ring-shaped bivalents. And about two thirds of bivalents observed in those plants were ring-shaped ones. However, no cell formed multivalents and the frequency of univalents was very low.

On the contrary to these 0B hybrids, the F_1 hybrid plant with two B-chromosomes (Culture No. 81725-P1) showed a drastically low frequency of A-chromosome pairing at MI. The mean chiasma frequency and the mean configuration of A-chromosome pairing were 0.04 and 13.92_{I} + $0.04rod_{II}$ per cell, respectively. Forty eight (96%) of the total observed PMCs formed 14 univalents of A-chromosomes with a tightly associated small ring-shaped bivalent of B-chromosomes (Figure 10D). Only two cells formed a rod-shaped bivalent of A-chromosomes.

Fertility of the F_1 hybrids

None of the F_1 hybrids obtained from the above mentioned two cross combinations dehisced their anthers. The pollen fertility was examined in three of them after staining their pollen grains with dilute aceto-carmine solution (Table 14). Most of their pollen grains were round but

Table 14. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops bicornis* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
3-1 x 78-5653-10			
79934-P1	0	0	-
-P2	0	0.4	-
-P3	0	0	-

1) No. of B-chromosomes in the F_1 hybrids
2) +: dehiscent, ±: partially dehiscent,
-: indehiscent.

empty. Two of them had no normal pollen grains and they were completely sterile. The other showed only 0.4% of normal pollen grains.

(2) *Aegilops sharonensis* x *Ae. mutica*

Result of crosses

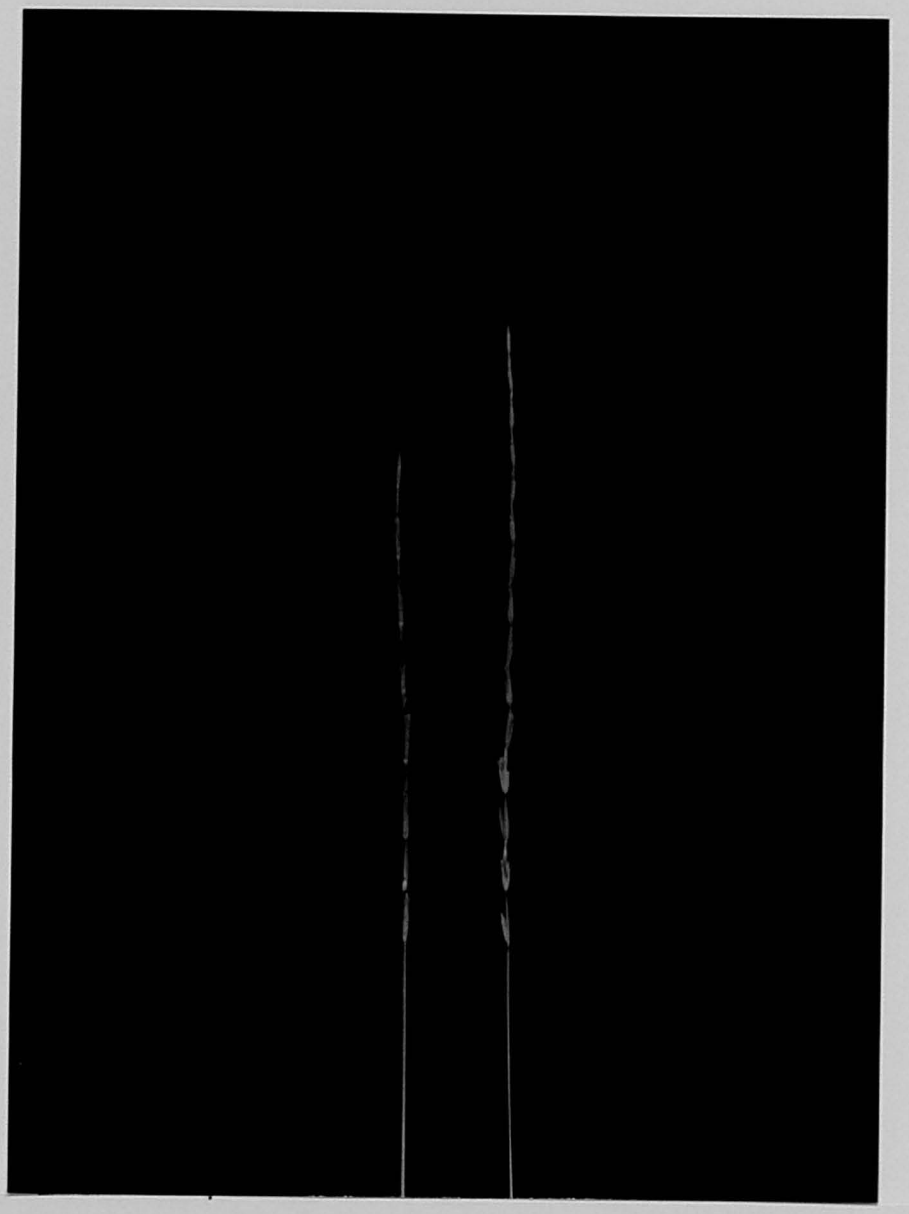
Two accessions of *Aegilops sharonensis* and three accessions of *Ae. mutica* were used in the present crosses (Table 15). The crossability between these two species was so high. A total of 100 florets of *Ae. sharonensis* were pollinated with the pollen grains of *Ae. mutica* and 32 seeds were successfully obtained. The mean seed set was 32%, but one cross combination, 5-1 x 81-5653-5, gave a percentage seed set as higher as 78%. The lower seed set observed in the other cross combinations, 5-3 x 81-5613-8 and 5-3 x 81-5616-2, is thought to be caused by the failure of pollination, because spikes of the accession KU 5-3 of *Ae. sharonensis* emerged much later than those of the accessions of *Ae. mutica*. Thirteen seedlings were obtained from the 14 seeds sown, and the mean germination rate was 93 %.

Morphology of *Aegilops sharonensis* and the F_1 hybrids between *Ae. sharonensis* and *Ae. mutica*

Ae. sharonensis has linear and compressed spikes usually consisting of 13 to 15 spikelets arranged in two rows (Figures 11A, 12A and C). Each spikelet consists of three to five florets. All spikelets are similar both in shape and in size. They are much longer than the adjacent rachis internodes. Empty glumes cover about two thirds or three fourths of the each spikelet. They are not awned but have two

Table 15. Result of the crosses between *Aegilops sharonensis* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops sharonensis x *Ae. mutica*						
5-1 x 81-5653-5	36	28	78	10	9	90
5-3 x 81-5613-8	32	3	9	3	3	100
5-3 x 81-5616-2	32	1	3	1	1	100
Total	100	32	32	14	13	93



A B

Figure 11. Spike morphology of *Aegilops shronensis* and the F_1 hybrids between *Ae. sharonensis* and *Ae. mutica* (x 0.5). A: *Ae. sharonensis* (KU 5-1), B: F_1 hybrid between *Ae. sharonensis* and *Ae. mutica* (82233-P1).

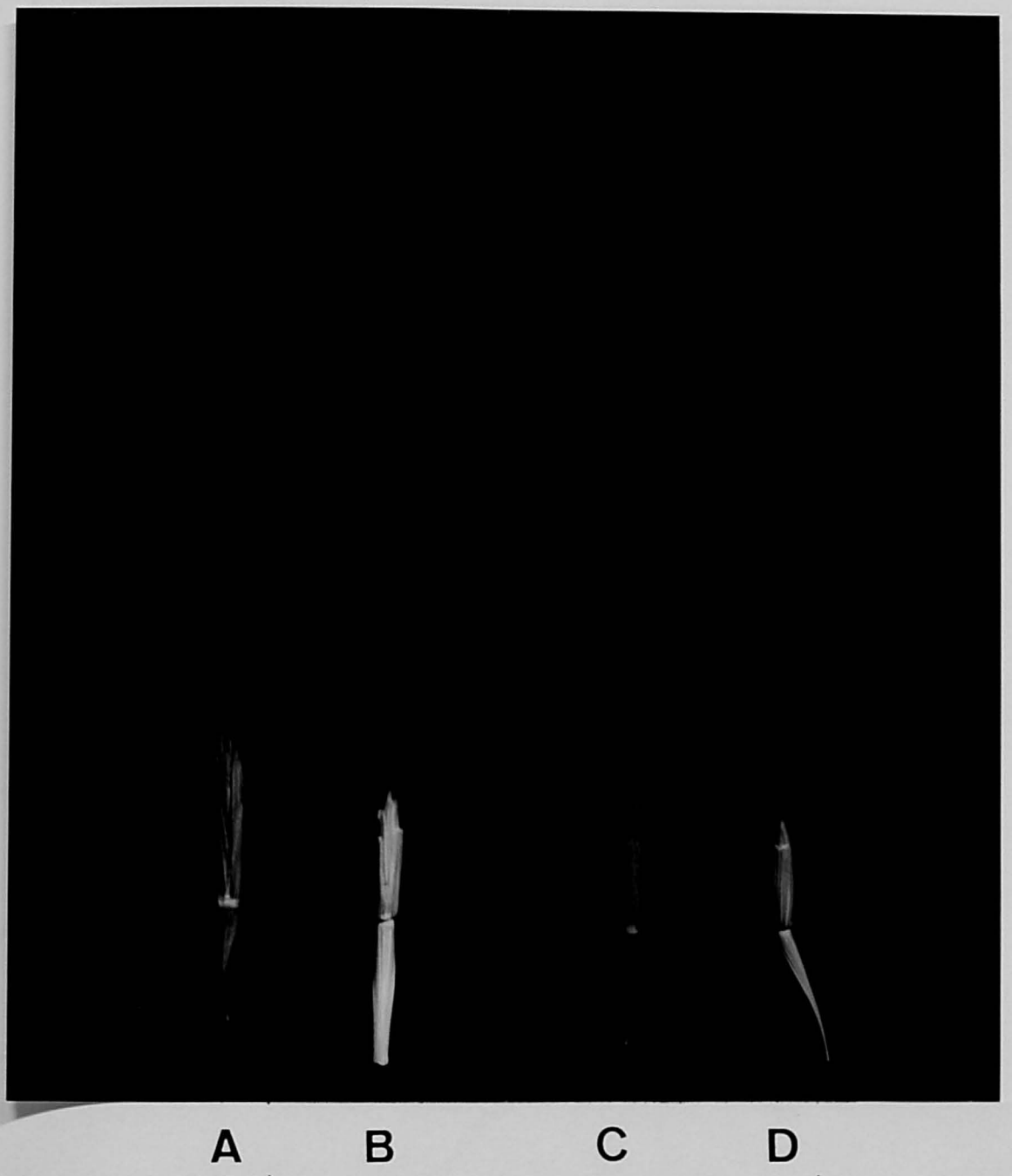


Figure 12. Spikelet morphology of *Aegilops sharonensis* and the F_1 hybrids between *Ae. sharonensis* and *Ae. mutica* (x 2.0). A and C: *Ae. sharonensis* (KU 5-1), B and D: F_1 hybrid between *Ae. sharonensis* and *Ae. mutica* (82233-P1).

small teeth on their upper margin. The teeth are divided by a shallow notch with a membranous edge. Lemmas of the lowest two florets of the each spikelet have an awn and at the base of the awn they have two broad lateral teeth. Sometimes lemma of the third floret has a short awn. Rachis is fragile. Each rachis node breaks at maturity and each spikelet falls together with the rachis internode below it (wedge type disarticulation). Rachilla is tough.

The F_1 hybrids between *Ae. sharonensis* and *Ae. mutica* had long linear spikes without awns (Figures 11B, 12B and C). Each rachis internode was almost as long as the adjacent spikelet in the middle part of a spike and it was longer than the spikelet in the upper and lower parts of a spike. As a result, their spikelets arranged in a row on a spike. The spikes consisted of 15 or more spikelets. Each spikelet usually had four or five florets and its empty glumes covered about lower two thirds of the each spikelet. Empty glumes had two dull teeth and a shallow, dull notch between them. Furthermore, one of the veins on the empty glumes was a weak keel. Their lemmas also had a weak keel on the same position as the empty glumes but their tips were dull and did not taper into awns. Rachis was fragile. Their spikes showed the wedge type disarticulation and broke into each spikelet with the rachis internode below it at maturity. Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

Five F_1 hybrid plants from the two cross combinations were cytologically observed in their PMCs at MI of meiosis (Table 16 and Figure 13). They were all 0B plants and showed very high frequency of chromosome pairing with the mean chiasma frequency ranging from 9.48 to

Table 16. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops sharonensis* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
5-1 x 81-5653-5													
82233-P1	0	50	0.96 (0-6)	6.52 (4-7)	2.04 (0-6)	4.48 (0-7)	-	-	-	-	-	11.00 (4-14)	11.00 (4-14)
-P4	0	50	1.24 (0-8)	6.34 (3-7)	2.90 (1-6)	3.44 (1-6)	-	0.02 (0-1)	0.02 (0-1)	-	-	9.84 (4-13)	9.84 (4-13)
-P5	0	50	1.18 (0-4)	6.38 (5-7)	3.28 (1-6)	3.10 (1-6)	0.02 (0-1)	-	-	-	-	9.52 (6-13)	9.54 (6-13)
-P3	0	50	1.42 (0-8)	6.22 (3-7)	3.06 (0-6)	3.16 (0-7)	0.02 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	9.48 (4-14)	9.48 (4-14)
5-3 x 81-5613-8													
82234-P2	0	100	0.91 (0-6)	6.51 (4-7)	3.14 (0-6)	3.37 (0-6)	0.01 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	9.93 (4-13)	9.93 (4-13)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

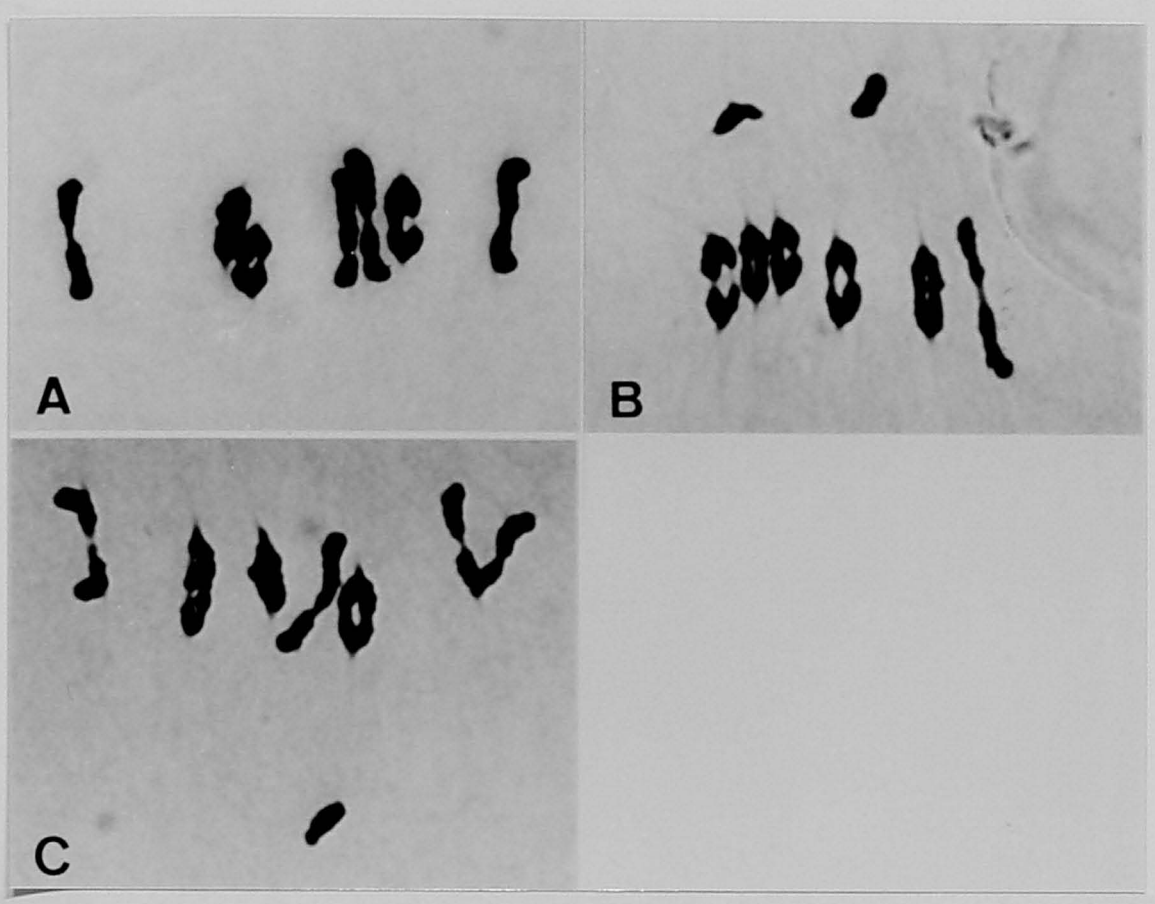


Figure 13. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrid (Culture No. 82234-P2) between *Aegilops sharonensis* and *Ae. mutica* (x 1,100). A: 7_{II}, B: 2_I+6_{II}, C: $1_I+5_{II}+1_{III}$.

11.00 per cell. Their configurations of chromosome pairing at MI were almost regular and many ring-shaped bivalents were observed. Only few multivalents were observed. Among a total of 300 cells observed in the five hybrid plants, 179 (60%) formed seven bivalents (Figure 13A), of which seven formed seven ring-shaped bivalents. However, a quadrivalent or a trivalent was observed only in six (2%) cells (Figure 13C). The mean configuration of A-chromosome pairing and the mean chiasma frequency of the five plants from the two cross combinations were 1.10_{I} + $(2.93rod + 3.49ring)_{II}$ + 0.01_{III} + 0.01_{IV} and 9.95 per cell, respectively.

Fertility of the F_1 hybrids

Pollen fertility was not examined in the F_1 hybrid plants. However, they were highly sterile and their anthers did not dehisce at all.

(3) *Aegilops longissima* x *Ae. mutica*

Result of the crosses

Two accessions of *Aegilops longissima* and eight plants from six accessions of *Ae. mutica* were used in the present crosses. The crossability in this interspecific cross combination was high as shown in Table 17. A total of 258 emasculated florets of *Ae. longissima* were pollinated with the fresh pollen grains of *Ae. mutica*. Among a total of 145 seeds obtained 105 germinated, the mean percentage seed set and the mean germination rate being 56% and 72%, respectively. The highest percentage seed set was 90% which was obtained from the cross

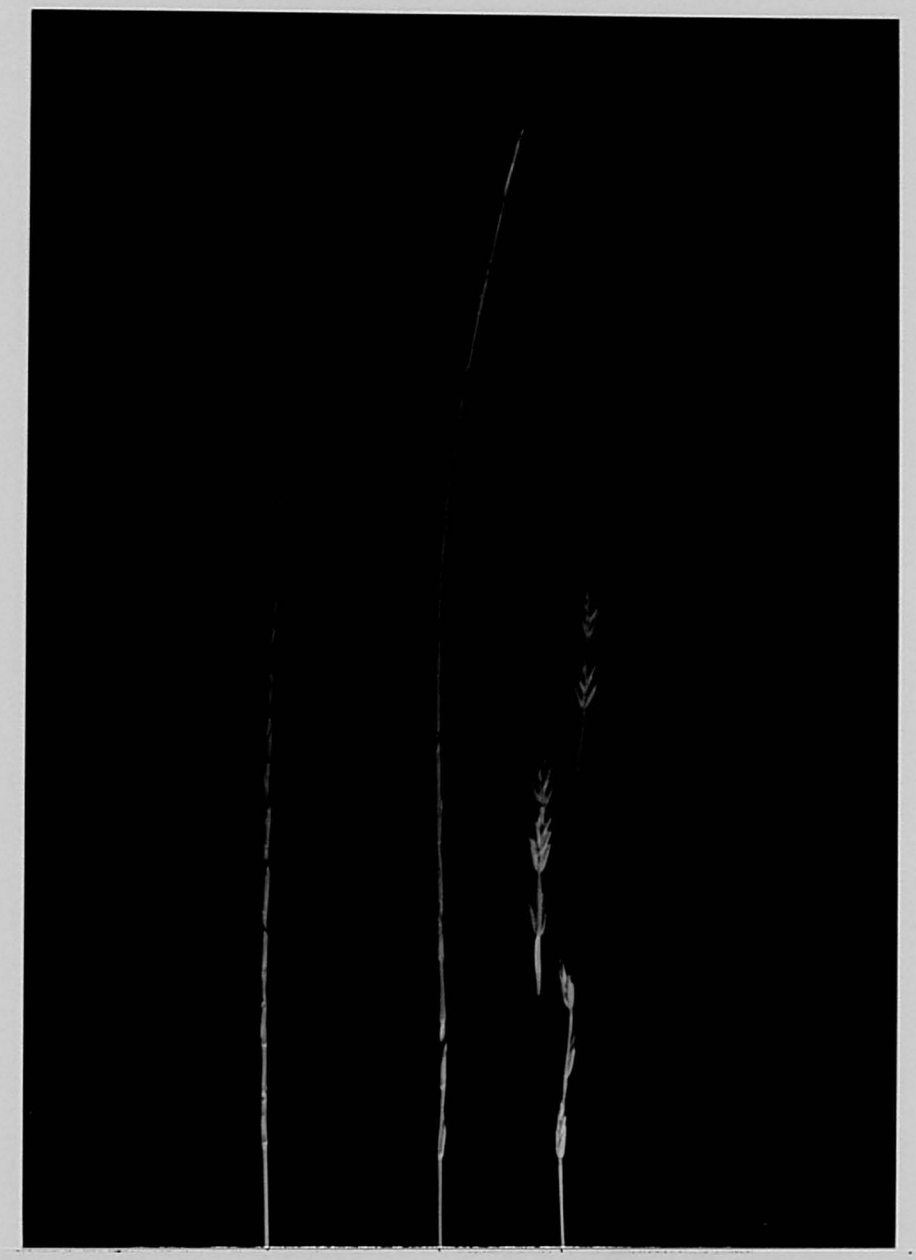
Table 17. Result of the crosses between *Aegilops longissima* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops longissima x *Ae. mutica*						
4-1 x 78-5645b-8	28	12	43	12	8	67
4-1 x 78-5646-6	34	15	44	15	8	53
4-4 x 81-5598-3	86	57	66	57	51	89
4-4 x 80-5641A1-6	20	1	5	1	0	0
4-4 x 78-5641e-6	30	25	83	25	24	96
4-4 x 78-5642c-4	16	2	13	2	0	0
4-4 x 78-5643d-4	30	27	90	27	10	37
4-4 x 78-5646-1	14	6	43	6	4	67
Total	258	145	56	145	105	72

combination of 4-4 x 78-5643d-4, being followed by 83% from the cross combination of 4-4 x 78-5641e-6. The highest germination rate was obtained from the cross combination of 4-4 x 78-5641e-6 and it was 96%.

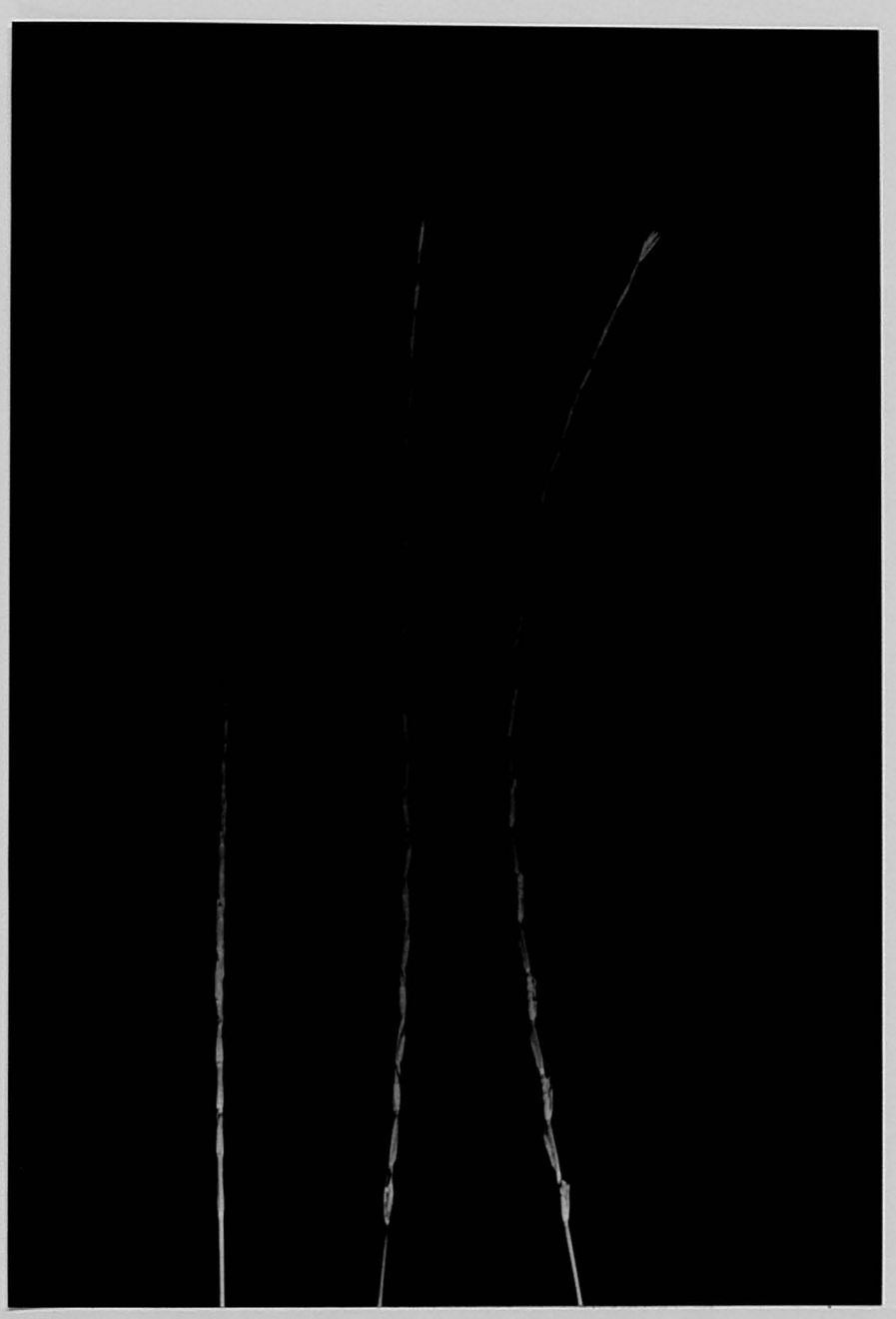
Morphology of *Aegilops longissima* and the F_1 hybrids between *Ae. longissima* and *Ae. mutica*

Ae. longissima has long linear spikes usually with 13 to 15 spikelets arranged in a row in most parts of a spike (Figures 14A, D, 15A and C). Below the middle part of a spike, its spikelets are arranged in two rows. Spikes do not have any rudimentary or sterile spikelets. Each spikelet consists of three to five florets. All spikelets are similar but become slightly smaller to the top of the spike. They are almost as long as the adjacent rachis internodes but below the middle part of a spike they are much longer than the adjacent rachis internodes. Empty glumes of the lateral spikelets cover a half or two thirds of the each spikelet. They are bidentate and the teeth divided by a notch with a membranous edge do not taper into awns. One of the teeth is a tip of weak keel on the empty glume. Lemmas have a keel and their upper margins are pointed. Only in the uppermost spikelet, lemmas of the lowest two florets taper into a long awn. Rachis is fragile only below the middle part of a spike where rachis internodes are much shorter than the adjacent spikelets and spikelets are arranged in two rows. In that part of a spike, rachis nodes break at maturity and the spikelets upper than the broken rachis node fall together. Three or four spikelets below the middle part of a spike fall separately with the rachis internodes below them (wedge type



A B C

Figure 14. Spike morphology of *Aegilops longissima* and the F_1 hybrids between *Ae. longissima* and *Ae. mutica* (x 0.5). A: *Ae. longissima* (KU 4-1), B-C: F_1 hybrids between *Ae. longissima* (KU 4-1) and *Ae. mutica* (B: 79935-P4, C: 79936-P3).



D E F

Figure 14. (Continued)

D: *Ae. longissima* (KU 4-4), E-F: F_1 hybrids between *Ae. longissima* (KU 4-4) and *Ae. mutica* (E: 79938-P21, F: 79940-P5).

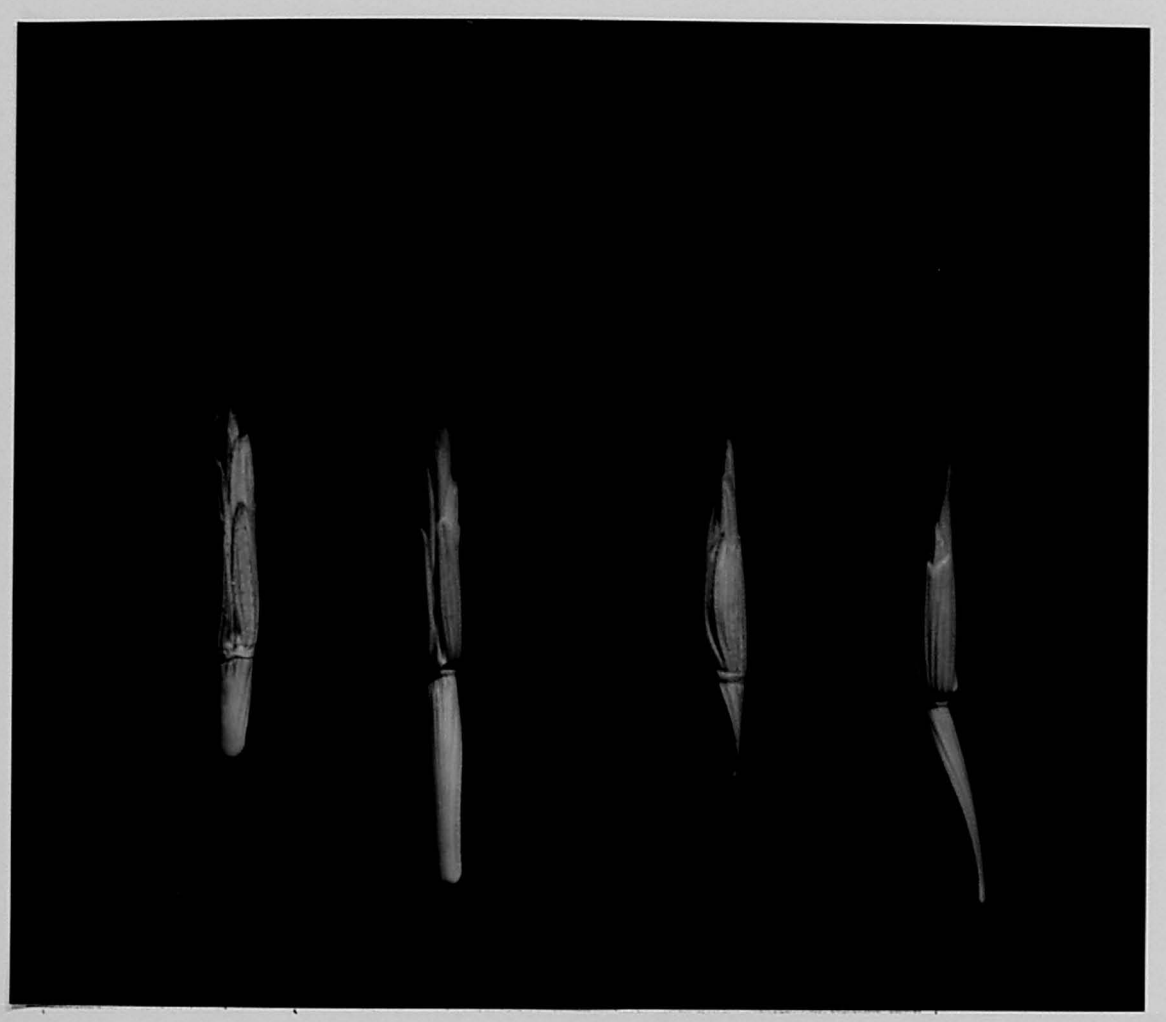


Figure 15. Spikelet morphology of *Aegilops longissima* and the F_1 hybrid between *Ae. longissima* and *Ae. mutica* (x 2.5). A and C: Spikelet in the middle part of a spike of *Ae. longissima* (KU 4-4), B and D: F_1 hybrid between *Ae. longissima* and *Ae. mutica* (79940-P5).

disarticulation). Rachilla is tough.

Linear spikes of the F_1 hybrids between *Ae. longissima* and *Ae. mutica* were as long as those of *Ae. mutica* and they consisted of more than 20 spikelets arranged in a row like as those of *Ae. mutica* (Figures 14B, C, E and F). They had no awn in any parts of them though those of *Ae. longissima* had a long awn on the lemmas of their uppermost spikelets. Each spikelet of the F_1 hybrids usually consisted of four to six florets and about three thirds of it was covered with empty glumes (Figures 15B and D). The empty glumes had two teeth and a shallow, dull notch between them. And they also had a keel on the same position as those of *Ae. longissima* but the keel of the F_1 hybrids was much weaker than that of *Ae. longissima*. The lemmas of the F_1 hybrids also had a weaker keel but their tips were dull as those of *Ae. mutica*. The rachis of the F_1 hybrid was fragile and each rachis node disarticulated at maturity (wedge type disarticulation) but their rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

Pollen mother cells at MI of meiosis in a total of 38 F_1 hybrid plants obtained from the five cross combinations were observed to examine their chromosome pairing (Table 18, Figures 16 and 17). Among them four plants had two B-chromosomes, two had one B-chromosome and the other 32 did not have any B-chromosomes. The F_1 hybrid plants without B-chromosomes showed a very high frequency of A-chromosome pairing in their PMCs with the chiasma frequency from 7.80 to 11.07 per cell. A chain-shaped quadrivalent or a trivalent was characteristically observed in those 0B hybrids (Figure 16). Among a total of 960 cells observed in

Table 18. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops longissima* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
4-1 x 78-5646-6													
79935-P4	0	30	1.57 (0-5)	5.07 (3-7)	3.33 (2-7)	1.73 (0-3)	0.37 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	8.43 (6-10)	8.47 (6-10)
-P1	0	30	1.83 (0-5)	5.26 (3-7)	3.96 (1-7)	1.30 (0-3)	0.40 (0-1)	0.07 (0-1)	0.03 (0-1)	0.03 (0-1)	0.03_U (0-1)	7.73 (5-10)	7.80 (5-10)
4-1 x 78-5645b-8													
79936-P3	0	30	1.70 (0-5)	5.00 (3-7)	3.33 (1-6)	1.67 (0-4)	0.37 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	8.30 (6-10)	8.37 (6-11)
4-4 x 78-5646-1													
79937-P1	0	30	0.67 (0-2)	5.43 (4-7)	1.77 (0-4)	3.67 (2-6)	0.33 (0-1)	0.37 (0-1)	0.37 (0-1)	-	-	10.87 (8-13)	10.90 (8-14)
-P4	0	30	0.83 (0-3)	5.13 (4-7)	2.07 (0-4)	3.07 (1-5)	0.37 (0-1)	0.40 (0-1)	0.40 (0-1)	-	0.03_{U1} (0-1)	10.30 (7-13)	10.43 (7-13)
-P3	0	30	0.90 (0-3)	5.17 (4-7)	2.20 (0-5)	2.97 (1-4)	0.57 (0-1)	0.27 (0-1)	0.27 (0-1)	-	-	10.07 (8-12)	10.10 (8-12)
-P2	0	30	1.07 (0-3)	5.13 (4-7)	2.20 (0-4)	2.93 (1-4)	0.53 (0-1)	0.27 (0-1)	0.27 (0-1)	-	-	9.93 (8-12)	9.97 (8-12)
4-4 x 78-5641e-6													
79938-P19	0	30	0.76 (0-4)	5.30 (4-7)	1.83 (0-4)	3.46 (2-6)	0.30 (0-1)	0.43 (0-1)	0.43 (0-1)	-	-	10.67 (7-13)	11.07 (7-13)
-P20	0	30	0.63 (0-2)	5.40 (5-7)	2.03 (0-4)	3.37 (2-5)	0.37 (0-1)	0.37 (0-1)	0.37 (0-1)	-	-	10.60 (8-13)	10.60 (8-13)
-P18	0	30	0.70 (0-4)	5.07 (4-7)	2.07 (0-4)	3.00 (2-5)	0.43 (0-1)	0.47 (0-1)	0.47 (0-1)	-	-	10.33 (8-13)	10.63 (8-13)
-P 3	0	30	0.93 (0-4)	5.33 (4-7)	2.17 (1-6)	3.17 (1-5)	0.27 (0-1)	0.40 (0-1)	0.40 (0-1)	-	-	10.23 (8-13)	10.53 (8-13)
-P 6	0	30	0.70 (0-3)	5.37 (4-7)	2.37 (0-7)	3.00 (0-5)	0.50 (0-1)	0.27 (0-1)	0.27 (0-1)	-	-	10.17 (7-12)	10.50 (7-13)
-P23	0	30	0.77 (0-2)	5.03 (4-6)	2.13 (0-4)	2.90 (0-5)	0.57 (0-2)	0.37 (0-1)	0.37 (0-1)	-	-	10.17 (8-12)	10.27 (8-12)

Table 18. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
79938-P 1	0	30	0.70 (0-4)	5.17 (3-7)	2.43 (1-4)	2.73 (2-5)	0.37 (0-2)	0.47 (0-1)	0.47 (0-1)	-	-	10.03 (8-12)	10.13 (8-12)
-P 7	0	30	1.10 (0-4)	5.07 (4-7)	2.13 (0-6)	2.93 (0-6)	0.57 (0-2)	0.27 (0-1)	0.27 (0-1)	-	-	9.93 (5-13)	10.00 (5-13)
-P 2	0	30	0.70 (0-4)	5.77 (4-7)	2.93 (1-5)	2.83 (2-5)	0.23 (0-1)	0.27 (0-1)	0.27 (0-1)	-	-	9.87 (8-12)	10.07 (8-12)
-P14	0	30	1.27 (0-4)	5.37 (4-7)	2.40 (1-5)	2.97 (0-5)	0.27 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	9.77 (5-12)	10.03 (5-13)
-P 4	0	30	1.06 (0-4)	5.17 (4-7)	2.40 (0-6)	2.77 (0-5)	0.47 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	9.77 (6-12)	9.93 (6-13)
-P24	0	30	1.03 (0-4)	5.30 (4-7)	2.53 (1-5)	2.77 (1-4)	0.30 (0-1)	0.37 (0-1)	0.37 (0-1)	-	-	9.77 (6-12)	9.93 (6-13)
-P10	0	30	1.13 (0-4)	5.16 (4-7)	2.47 (0-4)	2.70 (1-5)	0.53 (0-1)	0.23 (0-1)	0.23 (0-1)	-	-	9.63 (6-12)	9.90 (6-12)
-P11	0	30	1.06 (0-6)	5.33 (4-7)	2.60 (0-6)	2.73 (0-5)	0.53 (0-2)	0.17 (0-1)	0.17 (0-1)	-	-	9.63 (4-13)	9.73 (4-13)
-P 9	0	30	1.40 (0-4)	5.37 (4-7)	2.43 (0-5)	2.93 (0-5)	0.40 (0-1)	0.17 (0-1)	0.17 (0-1)	-	-	9.60 (5-12)	9.63 (5-12)
-P16	0	30	1.50 (0-6)	5.16 (3-7)	2.57 (0-5)	2.60 (1-5)	0.50 (0-2)	0.17 (0-1)	0.17 (0-1)	-	-	9.27 (5-12)	9.26 (5-12)
-P13	0	30	2.10 (0-10)	4.87 (2-6)	2.50 (0-5)	2.37 (0-4)	0.50 (0-1)	0.17 (0-1)	0.17 (0-1)	-	-	8.73 (4-11)	8.80 (4-11)
-P12	0	30	2.03 (0-6)	5.07 (3-7)	2.73 (0-5)	2.33 (0-4)	0.43 (0-1)	0.13 (0-1)	0.13 (0-1)	-	-	8.67 (5-11)	8.70 (5-11)
-P 5	0	30	2.03 (0-6)	4.93 (3-7)	2.63 (0-6)	2.30 (0-5)	0.57 (0-1)	0.10 (0-1)	0.10 (0-1)	-	-	8.67 (7-12)	8.67 (4-12)
-P21	1	30	11.07 (4-14)	1.46 (0-5)	1.43 (0-5)	0.03 (0-1)	-	-	-	-	-	1.50 (0-5)	1.50 (0-5)
-P17	2	30	13.20 (8-14)	0.40 (0-3)	0.40 (0-3)	-	-	-	-	-	-	0.40 (0-3)	0.40 (0-3)

Table 18. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
4-4 x 78-5643d-4													
79940-P 2	0	30	0.80 (0-3)	5.03 (4-6)	1.93 (0-4)	3.10 (1-5)	0.47 (0-1)	0.43 (0-1)	0.43 (0-1)	-	-	10.37 (7-13)	10.47 (7-13)
-P 5	0	30	0.93 (0-3)	5.23 (4-7)	1.90 (0-4)	3.33 (1-5)	0.47 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	10.40 (7-13)	10.40 (7-13)
-P 9	0	30	1.33 (0-4)	5.17 (4-7)	1.77 (0-4)	3.40 (1-5)	0.47 (0-1)	0.23 (0-1)	0.23 (0-1)	-	-	10.20 (6-13)	10.20 (6-13)
-P 6	0	30	1.33 (0-4)	5.03 (4-7)	1.83 (0-5)	3.20 (1-5)	0.60 (0-1)	0.20 (0-1)	0.20 (0-1)	-	-	10.03 (7-12)	10.03 (7-12)
-P10	0	30	1.17 (0-4)	5.27 (4-7)	2.20 (0-5)	3.07 (0-5)	0.50 (0-1)	0.20 (0-1)	0.20 (0-1)	-	-	9.93 (7-12)	9.93 (7-12)
-P 8	0	30	1.46 (0-4)	5.07 (4-7)	2.47 (0-5)	2.60 (0-5)	0.40 (0-1)	0.30 (0-1)	0.30 (0-1)	-	-	9.37 (5-13)	9.43 (5-13)
-P 1	1	30	8.00 (4-14)	3.00 (0-5)	2.60 (0-5)	0.40 (0-2)	-	-	-	-	-	3.40 (0-7)	3.40 (0-7)
-P 3	2	30	11.07 (8-14)	1.47 (0-3)	1.47 (0-3)	-	-	-	-	-	-	1.47 (0-3)	1.47 (0-3)
-P 7	2	30	12.13 (8-14)	0.93 (0-3)	0.80 (0-2)	0.13 (0-1)	-	-	-	-	-	1.07 (0-4)	1.07 (0-4)
-P 4	2	30	13.07 (10-14)	0.47 (0-2)	0.47 (0-2)	-	-	-	-	-	-	0.47 (0-2)	0.47 (0-2)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

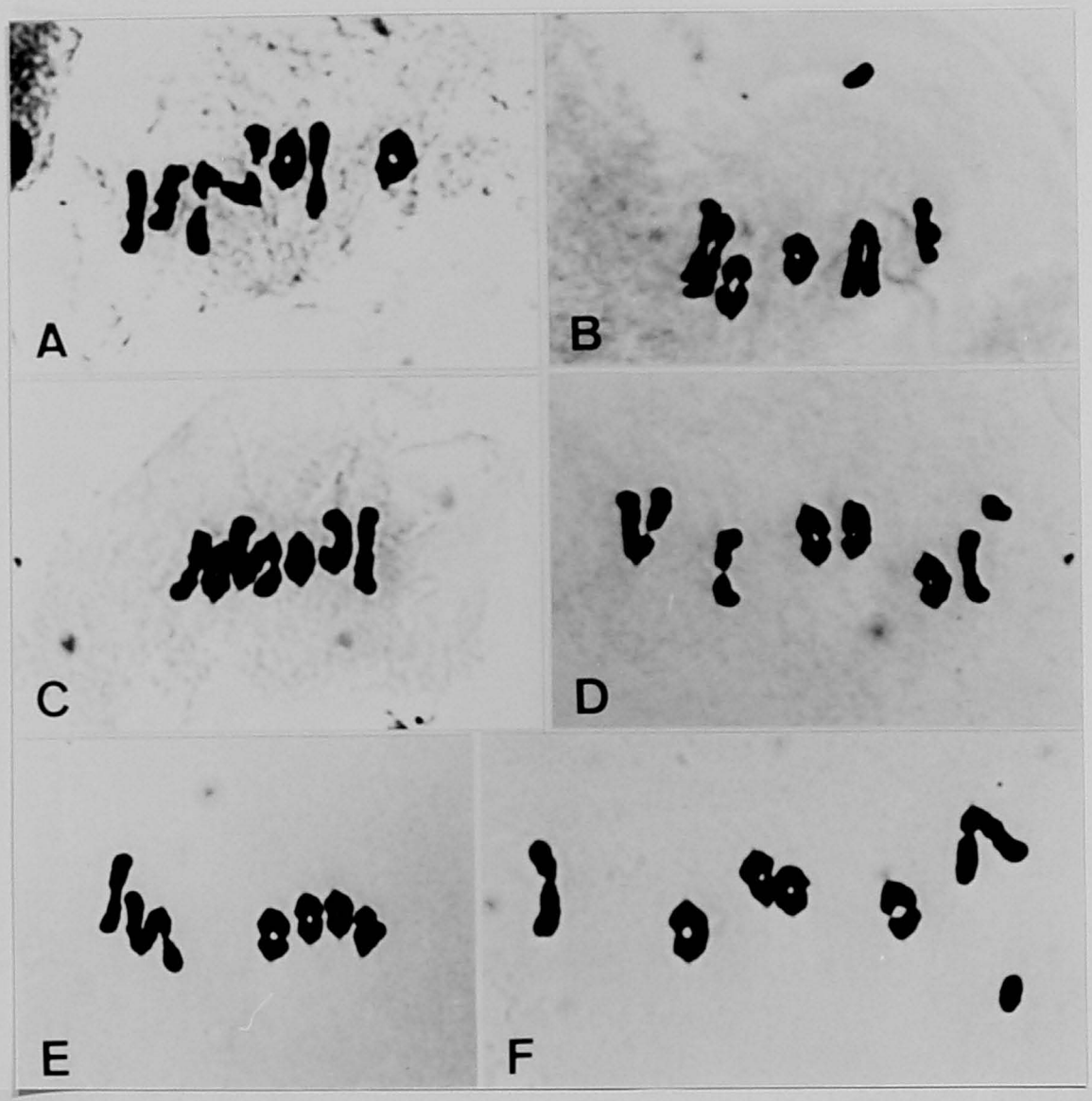


Figure 16. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids without B-chromosomes (Bs) between *Aegilops longissima* and *Ae. mutica* (x 1,100). A: 79938-P1, $5_{II}+1_{IV}$; B: 79938-P4, $1_I+5_{II}+1_{III}$; C: 79938-P7, $5_{II}+1_{IV}$; D: 79938-P11, $1_I+5_{II}+1_{III}$; E: 79938-P13, $5_{II}+1_{IV}$; F: 79940-P5, $1_I+5_{II}+1_{III}$.

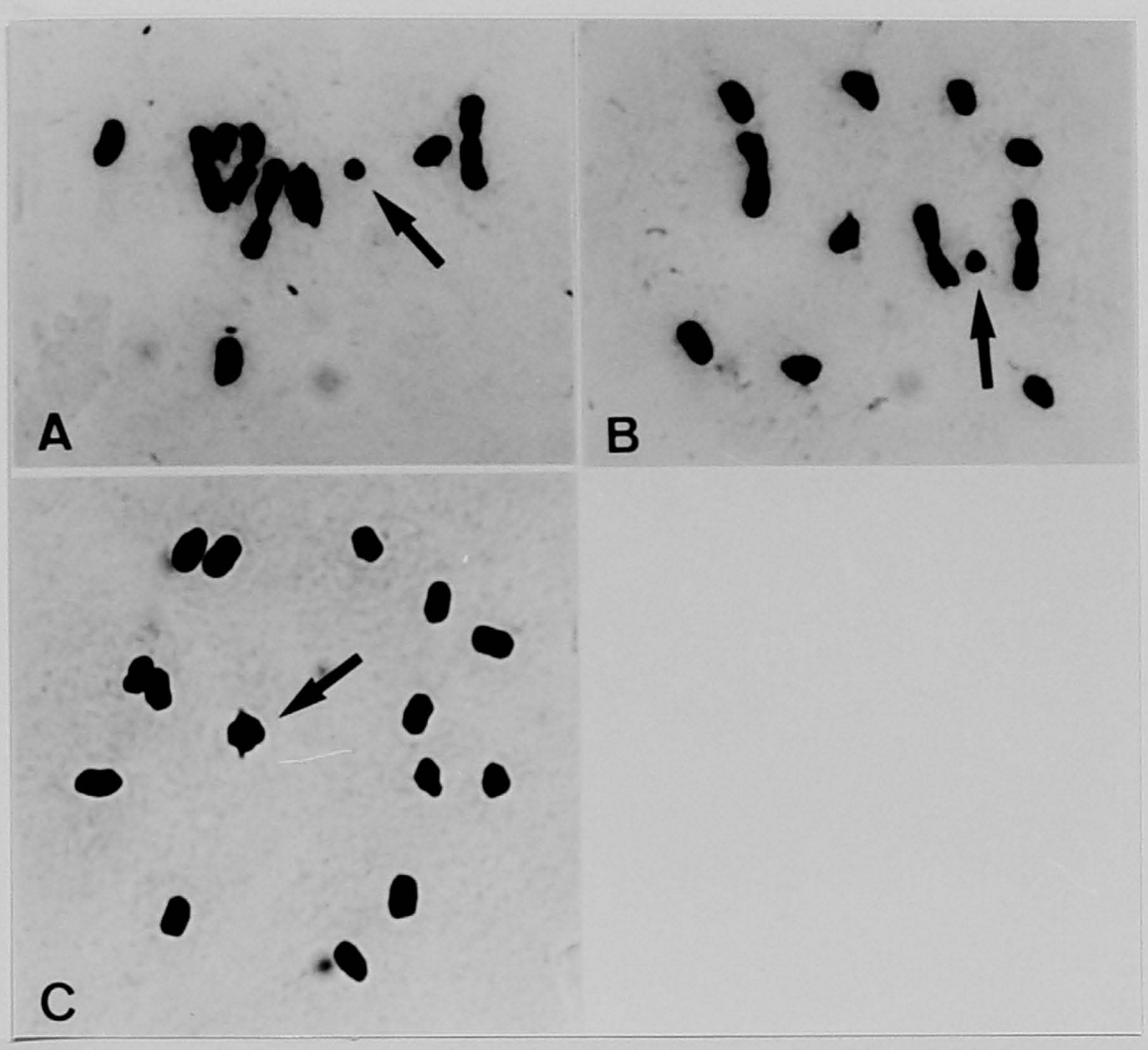


Figure 17. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with B-chromosomes (Bs) between *Aegilops longissima* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A-B: 79940-P1 with a minute telocentric B (A: 4_I+5_{II} of As + 1_I of B, B: 8_I+3_{II} of As + 1_I of B); C: 79940-P4 with 2Bs, 14_I of As + $1ring_{II}$ of Bs.

the 32 hybrids without B-chromosomes from the five cross combinations, 408 (43%) formed a trivalent and 270 (28%) formed a chain-shaped quadrivalent. In addition to such configurations of chromosome pairing, a sexivalent, a quinquevalent and a ring-shaped quadrivalent were found in one cell each. Furthermore, two trivalents were found in five cells. The other 274 (29%) cells contained no multivalent; 96 of them formed seven bivalents, 128 formed six bivalents with two univalents, 43 formed five bivalents with four univalents, six formed four bivalents with six univalents and one formed two bivalents with 10 univalents.

The frequency of chromosome pairing in those 0B hybrids could be classified into two groups depending on the accessions of *Ae. longissima*. When the accession KU 4-1 of *Ae. longissima* was used as the female parent, the F_1 hybrids showed slightly but significantly lower frequency of chromosome pairing than those obtained from another accession KU 4-4 (χ^2=20.97). The chiasma frequency in the former ranged from 7.80 to 8.47 per cell, but that in the latter ranged from 8.67 to 11.07 per cell. Because the *mutica* accession KU 5646 was used in common in the crosses with those two *longissima* accessions, it is suggested that the difference in the frequency and configuration of chromosome pairing observed in those hybrid plants might be caused by small differences in the chromosomal structure or in the genotypes affecting homoeologous chromosome pairing between the two accessions of *Ae. longissima*.

Four F_1 hybrid plants with two B-chromosomes were obtained from two cross combinations involving one *longissima* accession and two *mutica* accessions. In contrast with the above-mentioned 0B hybrids, those 2B

hybrids showed drastically low frequency of A-chromosome pairing. Fourteen univalents of A-chromosomes in addition to a small ring-shaped bivalent of B-chromosomes were characteristically observed at MI of meiosis in their PMCs (Figure 17C). Among a total of 120 cells observed in those 2B hybrids, 57 (47%) contained only 14 univalents of A-chromosomes, 36 (30%) formed a bivalent with 12 univalents, 19 (16%) formed two bivalents with 10 univalents and the other eight (7%) formed three bivalents with eight univalents of A-chromosomes. Most of the bivalents of A-chromosomes observed were rod-shaped and a ring-shaped bivalent was observed only in nine cells in one of the 2B hybrids (Culture No. 79940-P7). The mean configuration of A-chromosome pairing and mean chiasma frequency of those 2B hybrids were 13.20_{I} + $0.40rod_{II}$ and 0.40 per cell for the cross combination 4-4 x 78-5641e-6 (Culture No. 79938), and 12.09_{I} + $(0.91rod + 0.04ring)_{II}$ and 1.00 per cell for the three plants from the cross combination of 4-4 x 78-5643d-4 (Culture No. 79940).

In addition to above 0B and 2B hybrids, F_1 hybrid plants with a B-chromosome were obtained from the two cross combinations. The B-chromosomes contained in the both 1B hybrids were telocentric and much smaller than those found in the parental plants of *Ae. mutica*. They did not pair with A-chromosomes at all and they were formed a small univalent in all the PMCs observed. The configuration and frequency of A-chromosome pairing in those 1B plants were intermediate between above 0B and 2B hybrids (Figures 17A and B). Among a total of 60 cells observed in those two 1B hybrids, only five (8%) cells contained 14 univalents of A-chromosomes, 17 (28%) formed a bivalent, 13 (22%) formed

two bivalents, 13 (22%) formed three bivalents, eight (13%) formed four bivalents and the other four (7%) formed five bivalents of A-chromosomes. However, no cell formed multivalents. Their mean pairing configuration and mean chiasma frequency were 11.07_{I} + (1.43rod + 0.03ring)$_{II}$ and 1.50 chiasmata per cell for the F_1 hybrid obtained from the cross of 4-4 x 78-5641e-6 (Culture No. 79938-P21), and 8.00_{I} + (2.60rod + 0.40ring)$_{II}$ and 3.40 chiasmata per cell for the cross of 4-4 x 78-5643d-4 (Culture No. 79940-P1).

Fertility of the F_1 hybrids and chromosome pairing in the BC_1F_1 plants

All the F_1 hybrid plants, except two plants from the cross combination of 4-4 x 78-5641e-6, were highly or completely sterile and the anthers in none of them dehisced at anthesis. Their pollen fertility ranged from 0 to 0.9%. Anthers of the exceptional two plants, 79938-P8 and 79938-P22, normally dehisced and they shed abundant pollen grains at anthesis (Table 19). Their pollen fertility was 63.0% and 66.2%, respectively. By backcrossing to one of them, 79938-P22, with the parental line of *Ae. longissima*, 17 seeds were obtained as shown in Table 20, 12 of which were developed well but five were slightly shrivelled. Five BC_1F_1 plants successfully grew from those seeds, and the germination rate was 29%. They all proved to have two B-chromosomes in addition to 21 A-chromosomes in their PMCs. Three of them were cytologically examined at MI in their PMCs (Table 21 and Figure 18). All the PMCs examined formed seven tightly associated bivalents and seven univalents of A-chromosomes with a small ring-shaped bivalent of B-chromosomes. Their mean pairing configuration was 7.00_{I} + (0.31rod +

Table 19. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops longissima* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
4-4 x 78-5641e-6			
79938-P 1	0	0	-
-P 3	0	0.5	-
-P 4	0	0.2	-
-P10	0	0	-
-P11	0	0.9	-
-P 8	2	63.0	+[3]
-P22	2	66.2	+[3]
4-4 x 78-5643d-4			
79940-P 5	0	0	-
-P 6	0	0	-
-P 4	2	0	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent, -: indehiscent.
3) Good fertility was due to the formation of unreduced gametes.

Table 20. Result of the backcross of *Aegilops longissima* to the F_1 hybrid plant between *Ae. longissima* x *Ae. mutica* which formed unreduced gametes

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
(*Aegilops longissima* x *Ae. mutica*) x *Ae. longissima* (4-4 x 78-5641e-6) x 4-4	100	17	17	17	5	29

Table 21. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the first backcross generation (BC_1F_1) from the cross of *Aegilops longissima* to the F_1 hybrids between *Ae. longissima* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
(*Aegilops longissima* x *Ae. mutica*) x *Ae. longissima* (4-4 x 78-5641e-6) x 4-4													
80791-P1	2	50	7.00 (7)	7.00 (7)	0.20 (0-2)	6.80 (5-7)	-	-	-	-	-	13.80 (12-14)	14.22 (12-16)
-P3	2	50	7.00 (7)	7.00 (7)	0.28 (0-2)	6.72 (5-7)	-	-	-	-	-	13.72 (12-14)	13.98 (12-15)
-P4	2	50	7.00 (7)	7.00 (7)	0.44 (0-3)	6.56 (4-7)	-	-	-	-	-	13.56 (11-14)	14.06 (11-16)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

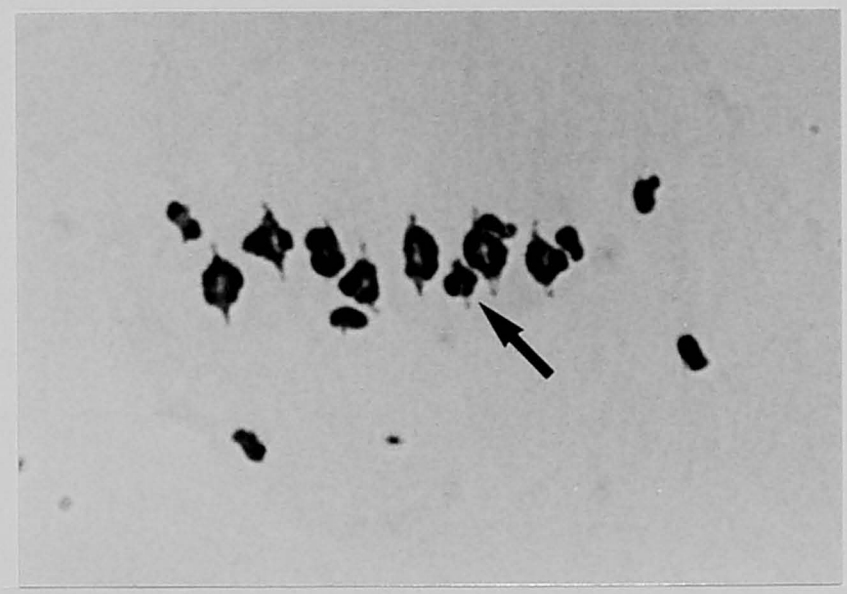


Figure 18. The configuration of chromosome pairing at MI of meiosis in the triploid BC_1F_1 plant with two B-chromosomes between *Aegilops longissima* and *Ae. mutica* (Culture No. 80791-P1). $7_I+7ring_{II}$ of As + $1ring_{II}$ of Bs (x 1,100). B-chromosomes are indicated with an arrow.

6.69ring)$_{11}$, and the mean chiasma frequency was 14.09 per cell. The bivalent configuration and the chiasma frequency were quite similar to those of the parental line of *Ae. longissima* shown in Table 10. Judging from the pairing configuration it is concluded that those BC_1F_1 plants contained two *longissima* genomes and one *mutica* genome in addition to two B-chromosomes derived from the *mutica* parent. And the good fertility observed in the two F_1 hybrids, 79938-P8 and 79938-P22, is reasonably concluded to be due to the formation of unreduced gametes during the process of gamete formation in the F_1 hybrids.

(4) ***Aegilops searsii* x *Ae. mutica***

One accession of *Aegilops searsii* and two of *Ae. mutica* were used in the present crosses (Table 22). One of the parental plants of *Ae. mutica* (Culture No. 81-5613-8) had no B-chromosomes and another (Culture No. 81-5616-2) had two B-chromosomes. Both the two cross combinations showed a quite similar result to each other. Though the number of florets pollinated was not so many, hybrid seeds were easily obtained from the both combinations. Their percentage seed set was 50% and 58%, respectively, and the mean percentage seed set was 54%. In contrast with that constancy of seed set, the hybrid seeds sown did not germinate at all. Consequently, any F_1 hybrid plants between these two species could not been obtained from the present crosses.

Table 22. Result of the crosses between *Aegilops searsii* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops searsii x *Ae. mutica*						
4-6 x 81-5613-8	14	7	50	7	0	0
4-6 x 81-5616-2	12	7	58	7	0	0
Total	26	14	54	14	0	0

(5) *Aegilops speltoides* x *Ae. mutica*

Result of crosses

Aegilops speltoides and *Ae. mutica* were crossed intensively because the analysis in chromosome pairing in the F_1 hybrids from this interspecific cross combination was much important for the present work (Table 23). Sixteen accessions of *Ae. speltoides* were crossed by 16 plants from the six accessions of *Ae. mutica* with or without B-chromosomes. A total of 2,212 emasculated florets of *Ae. speltoides* were pollinated with the pollen grains of *Ae. mutica*. Crossability was not so high compared with most of the above-mentioned interspecific combinations involving the other species in sect. Platystachys. The hybrid seeds were successfully obtained from 28 cross combinations among a total of 32 combinations. The percentage seed set ranged from 0 to 58% and the mean seed set was 15%. The highest percentage seed set was observed in the cross combination of 2263 x 80-5641A1-6. In that combination 35 seeds were obtained but they did not germinate at all. The germination rate ranged from 0 to 67% and the mean germination rate was 10%. Among 28 combinations from which the hybrid seeds were obtained, most combinations gave the germination rate below 25% and 13 combinations gave no seedlings at all. Thirty four seedlings were successfully obtained from 15 cross combinations. Generally speaking, they grew slower than the other interspecific hybrid seedlings. Ae. mutica was used as the female parent in a cross combination and 12 seeds were obtained. The percentage seed set was 40%. But they did not germinate at all.

Table 23. Result of the reciprocal crosses between *Aegilops speltoides* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops speltoides x *Ae. mutica*						
2201B x 81-5653-5	20	4	20	4	1	25
2213D x 79-5641A-3	30	2	7	2	1	50
2213D x 79-5642B-10	40	4	10	4	1	25
2213D x 79-5643A-3	20	3	15	3	2	67
2213D x 79-5645B-4	18	4	22	4	0	0
2214D x 79-5641A-3	40	11	28	11	1	9
2214D x 79-5645B-4	40	13	33	13	0	0
2241A x 78-5641b-10	83	11	13	11	1	9
2263 x 77-5641-4	38	3	8	3	0	0
2263 x 80-5641A1-6	60	35	58	35	0	0
2263 x 77-5642-2	20	4	20	4	1	25
2263 x 79-5642A-2	56	16	29	16	0	0
2263 x 79-5645A-3	40	20	50	20	0	0
2263 x 79-5645B-4	40	19	48	19	0	0
2273 x 79-5641A-3	20	7	35	7	1	14
2273 x 79-5645B-4	40	13	33	13	0	0
2282 x 83-5646-3	88	29	33	29	1	3

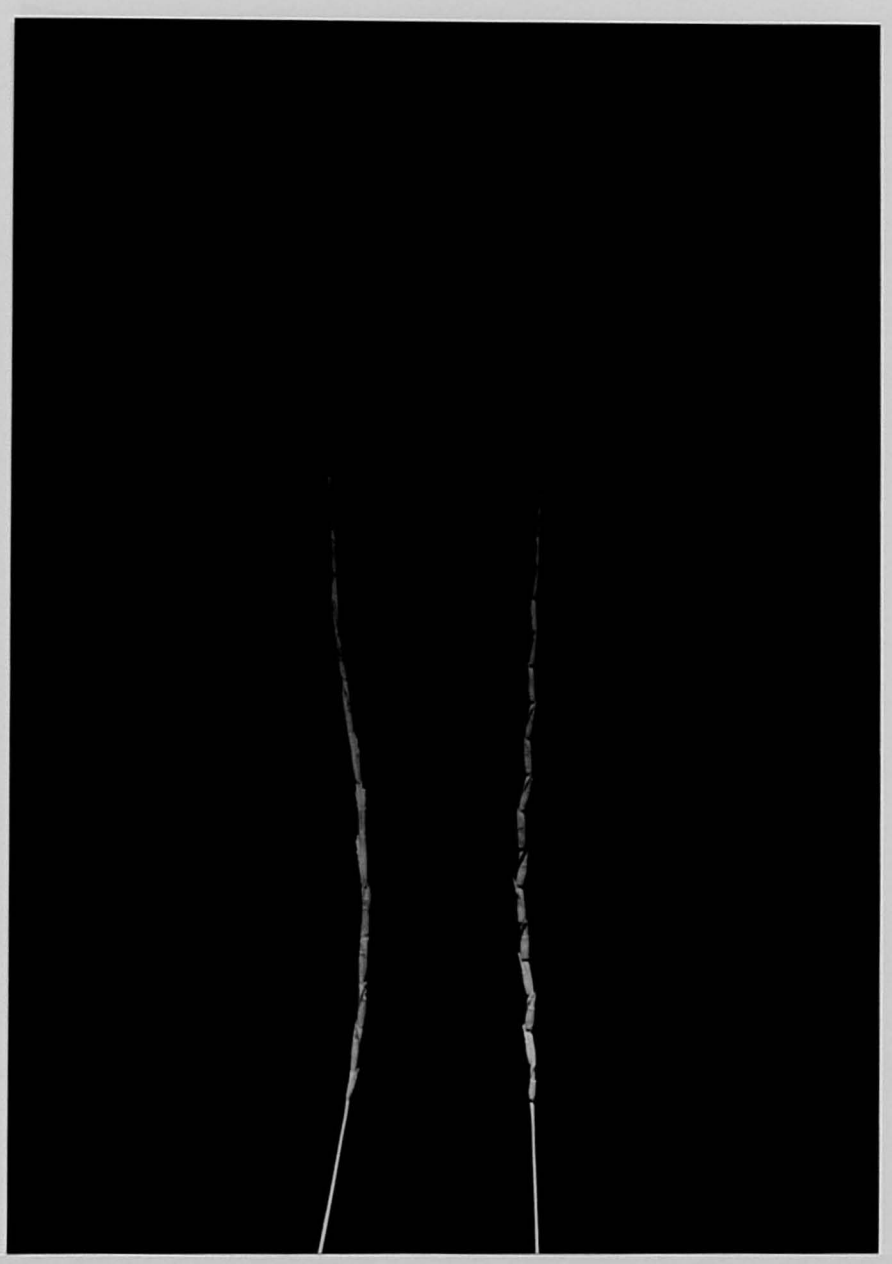
Table 23. (Continued)

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops speltoides x *Ae. mutica*						
5725B x 83-5646-2	120	39	33	39	2	5
7719 x 79-5643A-3	42	1	2	1	0	0
7761 x 83-5646-3	96	10	10	10	6	60
7799 x 83-5642-2	14	0	0	-	-	-
7799B x 80-5641A1-6	62	0	0	-	-	-
7799B x 80-5645C-1	199	2	1	2	0	0
7799B x 80-5645C-7	44	3	7	3	0	0
7930 x 83-5641-8	98	0	0	-	-	-
7930 x 83-5646-2	96	2	2	2	0	0
7943 x 83-5641-8	92	33	36	33	5	15
7943 x 83-5646-2	104	39	38	39	8	21
7972 x 83-5641-6	126	6	5	6	2	33
7974 x 83-5641-6	370	3	1	3	1	33
7976 x 83-5641-8	28	0	0	-	-	-
7976 x 83-5646-2	28	1	4	1	0	0
Total	2212	337	15	337	34	10
Aegilops mutica x *Ae. speltoides*						
83-5646-4 x 7930	30	12	40	12	0	0

Morphology of *Aegilops speltoides* and the F_1 hybrids between *Ae. speltoides* and *Ae. mutica*

Two spike morphology types of *Ae. speltoides* were used in the present crosses. One of them belongs to former species *Ae. ligustica* Coss. and the other belongs to *Ae. speltoides* Tausch *sensu strict* (Tausch 1837). *Ae. ligustica* Coss. has linear and compressed spikes consisting of seven to 15 spikelets arranged in two rows (Figures 19E, O, 20A and C). All spikelets except the lowest one are similar to one another both in shape and in size. They are more or less longer than the adjacent rachis internodes. Especially, in the middle part of a spike, they are much longer than the adjacent rachis internodes. The lowest spikelet is much smaller than the other ones and sometimes becomes rudimentary. Each spikelet consists of four to five florets. Empty glumes are truncate and cover only less than a lower half of the each spikelet. Their upper margin is horizontal and has a tooth on the inner end. The tooth is a tip of a keel on the empty glume. Lemmas also have a keel on the same position as empty glumes and the tip of the keel tapers into an awn. The awns of spikelets in the lower part of spikes usually become shorter and sometimes rudimentary. Rachis is fragile. Each rachis node disarticulates at maturity and each spikelet falls separately with the rachis internode below it (wedge type disarticulation). Rachilla is tough.

On the other hand, *Ae. speltoides* Tausch *sensu strict* (Tausch 1837) has long linear spikes consisting of six to 15 (usually seven to 10) spikelets arranged in a row (Figures 19A, C, G, I and K). Spikelets are narrow-lanceolate or linear. They all, except the lowest one or two,



A B

Figure 19. Spike morphology of *Aegilops speltoides*, the F_1 hybrids between *Ae. speltoides* and *Ae. mutica*, and the plant obtained by open-pollination among the F_1 hybrid plants (x 0.5). A: *Ae. speltoides* (KU 2201B), B: F_1 hybrid involving *Ae. speltoides* KU 2201B (82236-P1).

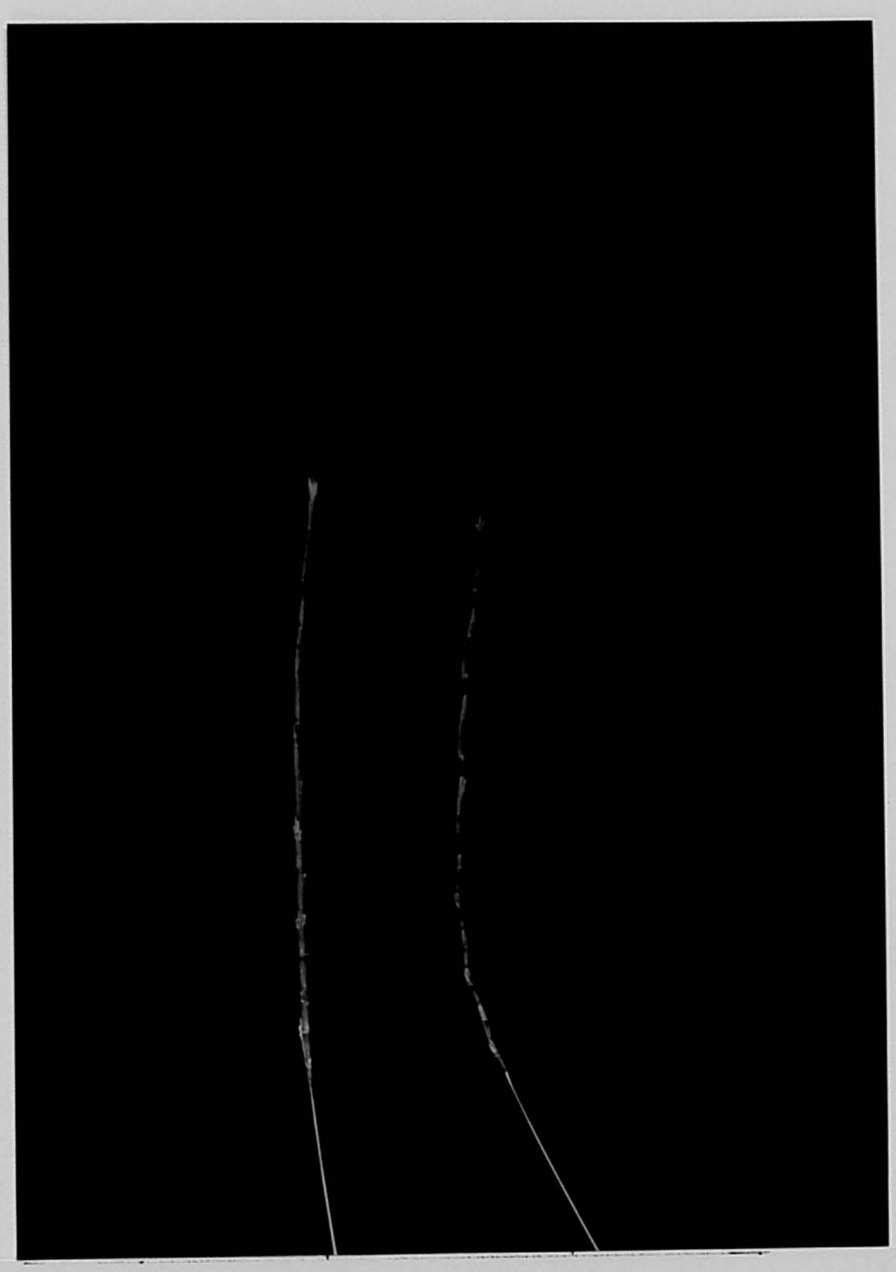


Figure 19. (Continued)
C: *Ae. speltoides* (KU 2213D), D: F_1 hybrid involving *Ae. speltoides* KU 2213D (80775-P1).

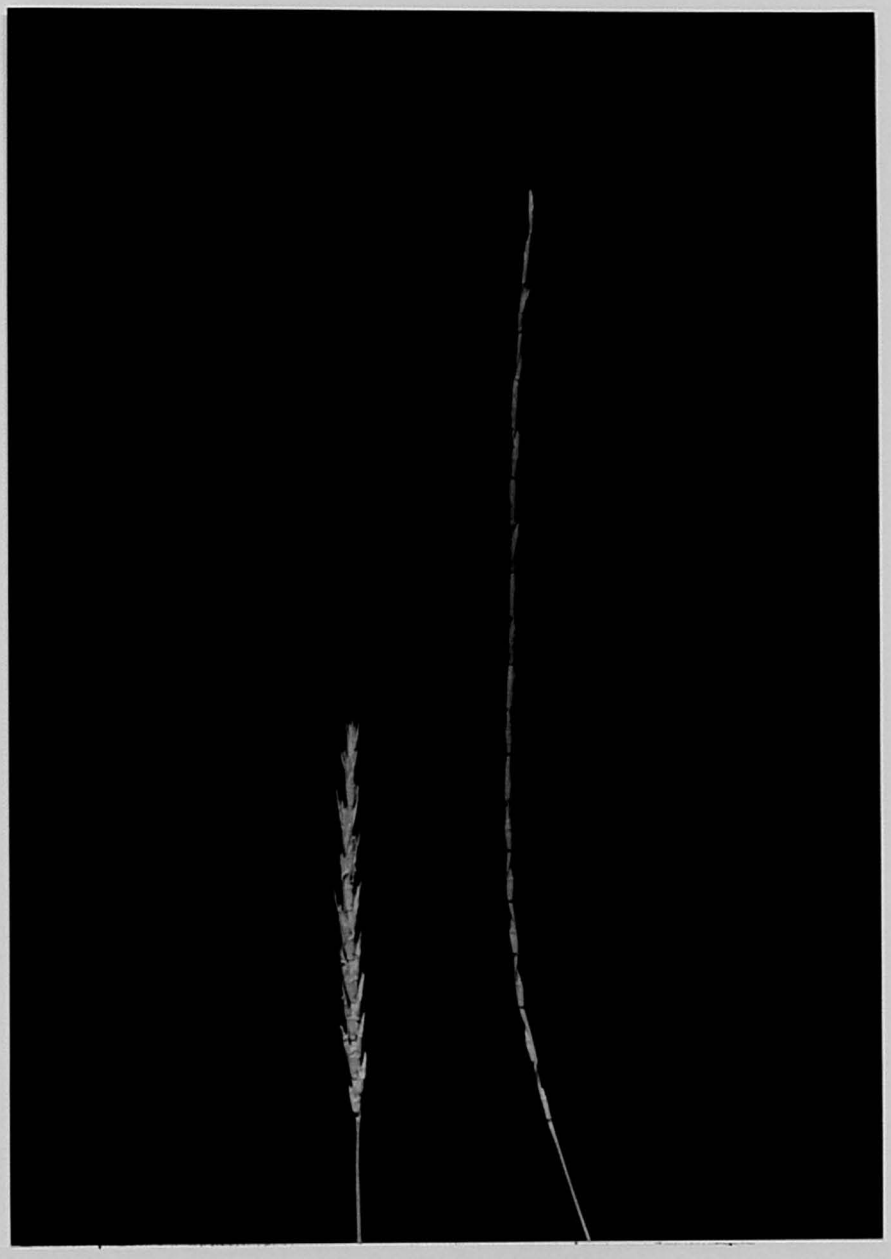
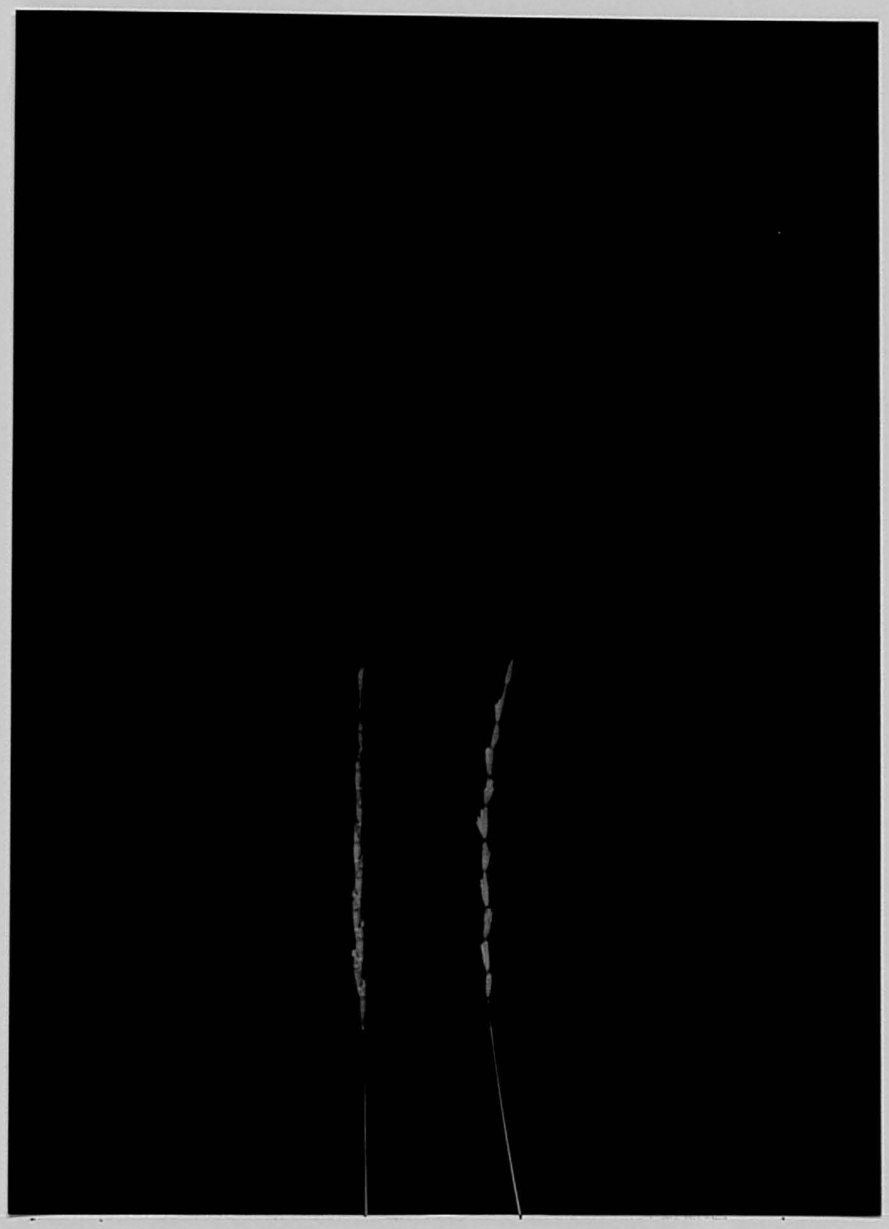


Figure 19. (Continued)
E: *Ae. speltoides* (KU 2263), F: F_1 hybrid involving *Ae. speltoides* KU 2263 (78418-P1).



G H

Figure 19. (Continued)

G: *Ae. speltoides* (KU 2282), H: F_1 hybrid involving *Ae. speltoides* KU 2282 (84001-P1).

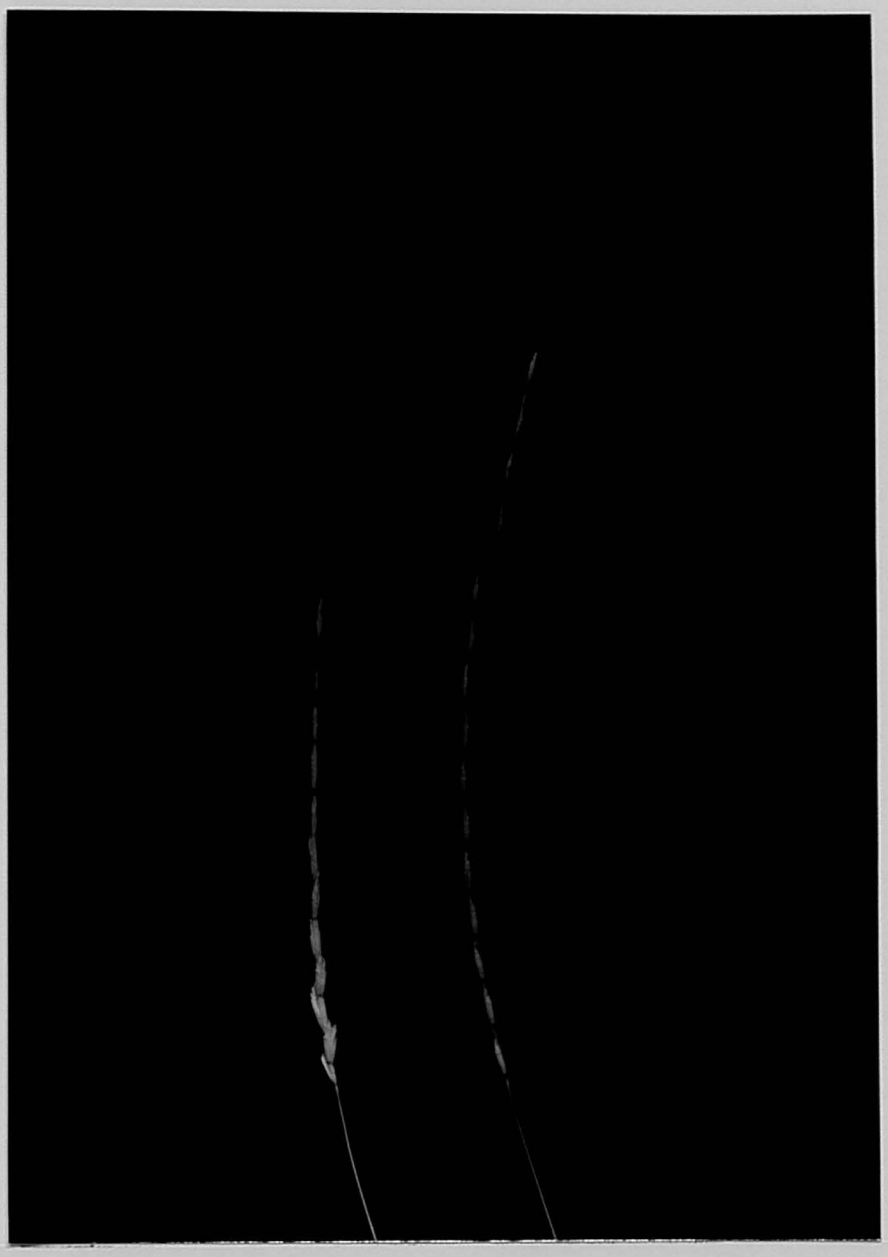


Figure 19. (Continued)
I: *Ae. speltoides* (KU 7761), J: F_1 hybrid involving *Ae. speltoides* KU 7761 (84003-P4).

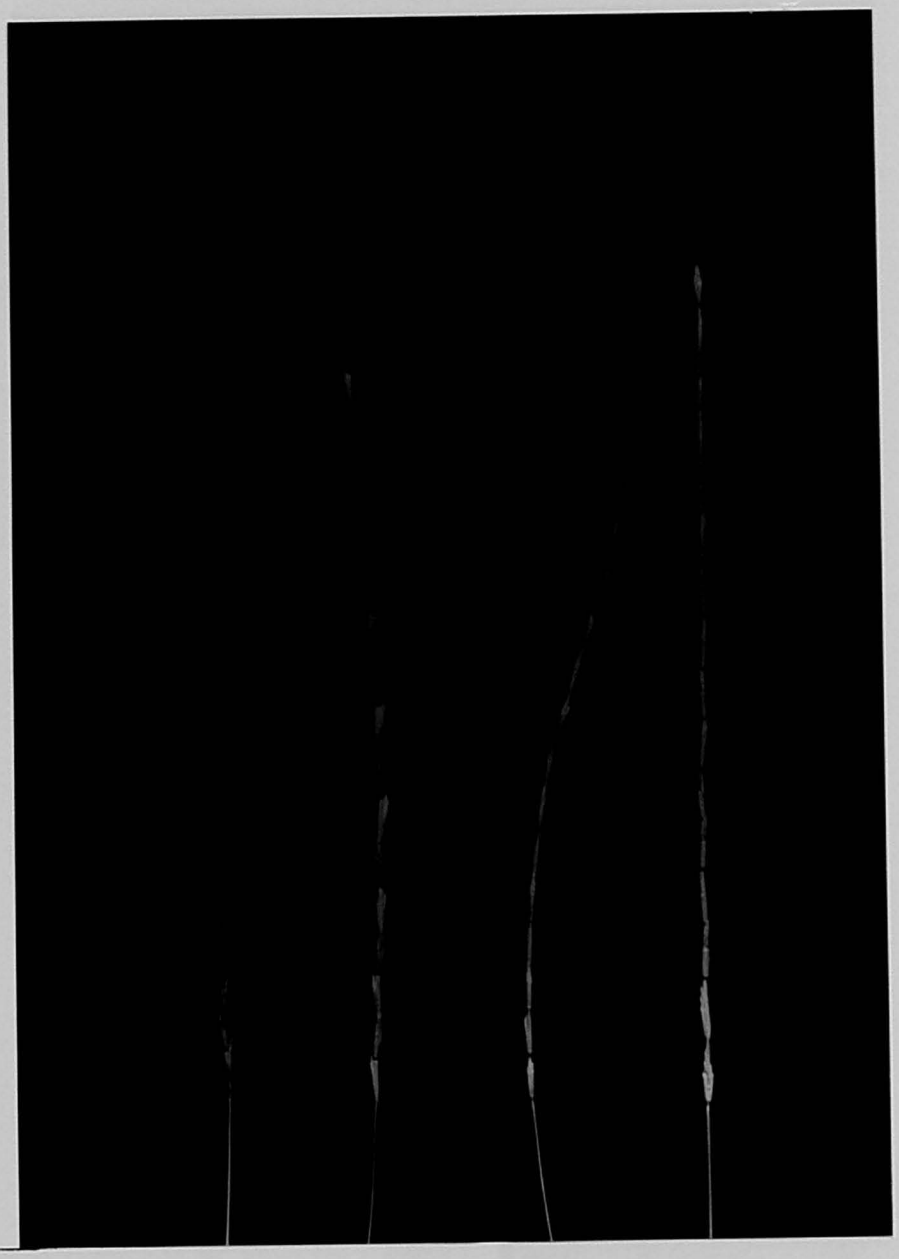


Figure 19. (Continued)
K: *Ae. speltoides* (KU 7943), L-M: F_1 hybrids involving *Ae. speltoides* KU 7943 (L: 84006-P3, M: 84007-P4), N: Plant obtained by the open-pollination of the F_1 hybrid 84007-P1 (86307-P2).

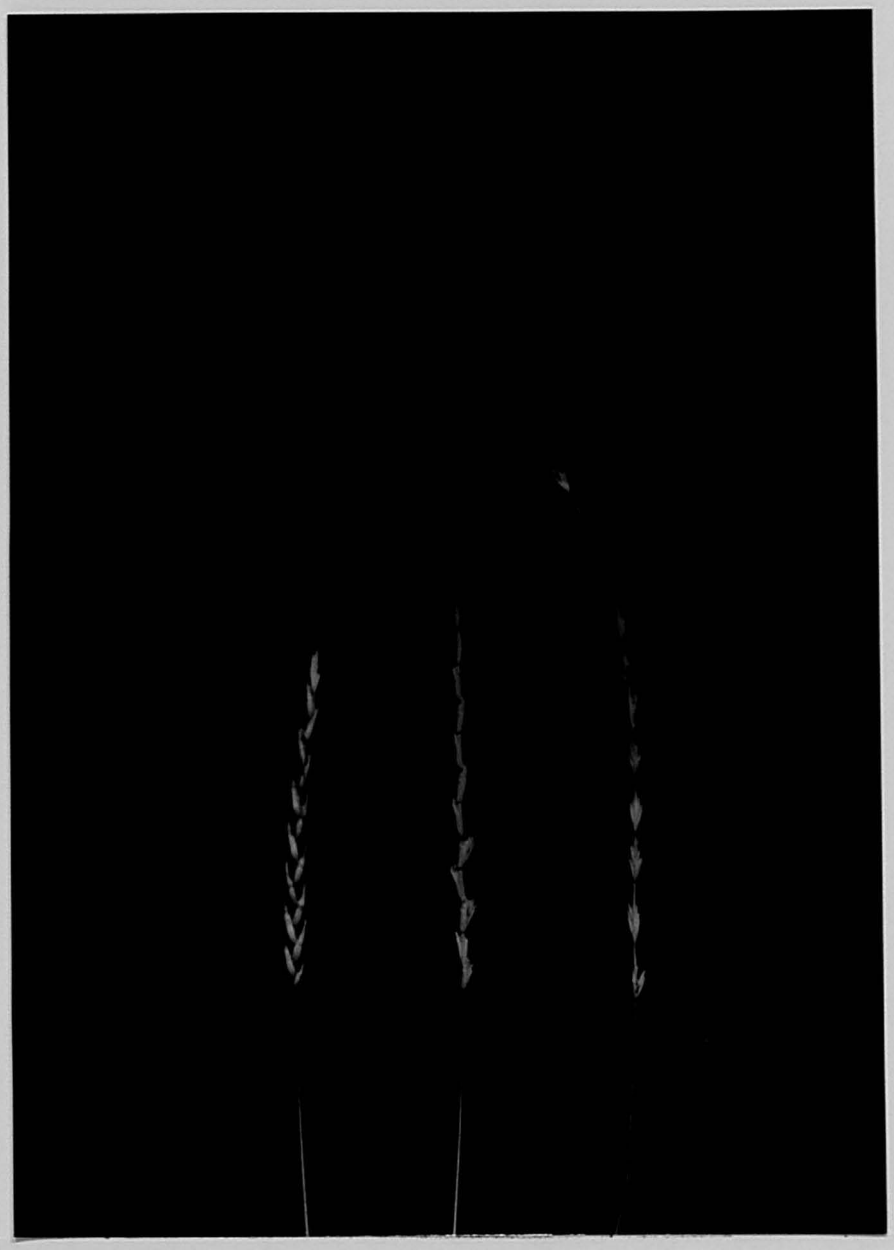


Figure 19. (Continued)

O: *Ae. speltoides* (KU 7972), P-Q: F_1 hybrids involving *Ae. speltoides* KU 7972 (P: 84008-P1, Q: 84008-P2).

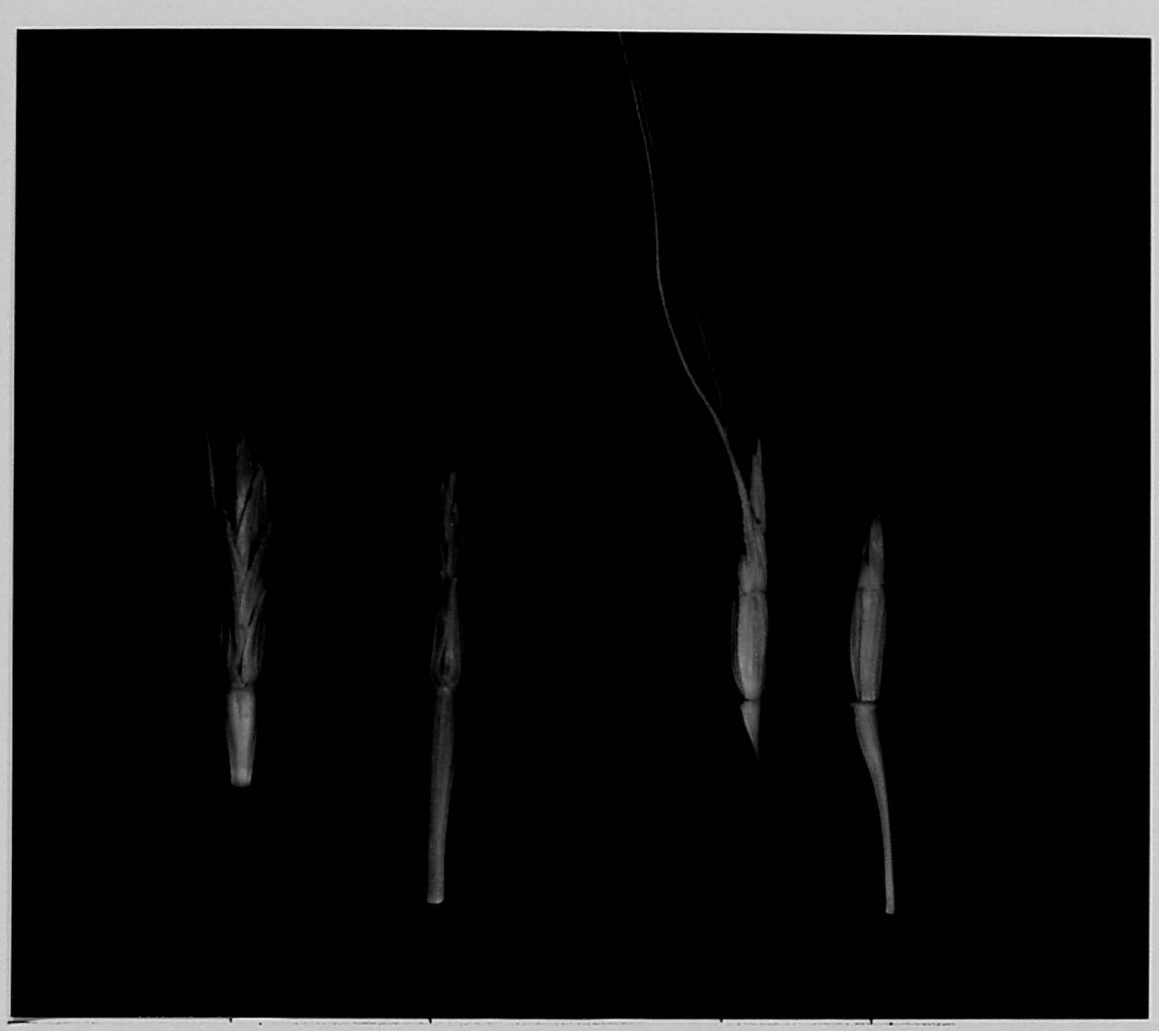


Figure 20. Spikelet morphology of *Aegilops speltoides* and the F_1 hybrid between *Ae. speltoides* and *Ae. mutica* (x 2.3). A and C: *Ae. speltoides* (KU 2263), B and D: F_1 hybrid between *Ae. speltoides* KU 2263 and *Ae. mutica* (78418-P1).

are almost similar in shape along the whole spike length but become slightly smaller to the top of a spike. They are as long as the adjacent rachis internodes. The lowest one or two spikelets at the base of a spike are much smaller than the others, especially the lowest spikelet is very small and rudimentary. The shape and size of empty glumes are similar to those of *Ae. ligustica*. However, lemmas of the lateral spikelets of *Ae. speltoides sensu strict* usually have no awns. Lemmas of the lowest two florets only in the uppermost spikelet taper into a long awn. Lemma of the third floret of the uppermost spikelet sometimes has a short awn. The rachis node only at the base of a spike is fragile. Entire spike except the lowest rudimentary spikelet falls together at maturity (umbrella type disarticulation). Rachilla is tough.

The morphology of the F_1 hybrids between both the spike types of *Ae. speltoides* and *Ae. mutica* was similar to each other with only small difference in their awnedness (Figures 19B, D, F, H, J, L, M, P, Q, 20B and D). The spikes of the F_1 hybrids between both types of *Ae. speltoides* and *Ae. mutica* were long and linear and they consisted of intermediate number of spikelets between their parents. For example, *Ae. speltoides* KU7943 and *Ae. mutica* KU5646 had about 12 and 25 spikelets on their spikes, respectively, and their F_1 hybrids (Culture No. 84007) usually had 15 or 16 spikelets arranged in a row. Most spikelets of the F_1 hybrids between *Ae. speltoides* and *Ae. mutica* were as long as the rachis internodes adjacent to them. In some hybrid combinations their spikelets in the middle part of a spike were slightly longer than the adjacent rachis internodes, and in other combinations

those in the upper or lower parts of their spikes were slightly shorter than the adjacent rachis internodes. The spikes had no rudimentary spikelet at their base. The spikelets consisted of five to six florets arranged laxly. Any spikelets of the F_1 hybrids were not awned, but the lemmas of the lowest florets in the uppermost two or three spikelets on some spikes in the F_1 hybrids between *ligustica*-type *Ae. speltoides* and *Ae. mutica* had a weak awn. The expression of this characteristic was unstable and the awnedness varied among spikes within the same individuals. The lower halves of the spikelets were covered with empty glumes. This characteristic was common with the both *Ae. speltoides* and *Ae. mutica*. The empty glumes of the F_1 hybrids showed the intermediate shape between those of two parents. Their upper margins were almost horizontal with a very small tooth at their ends. This tooth was a tip of the very weak keel on the empty glumes. The lemmas of the F_1 hybrids also had a weak keel on the same position as the empty glumes. The rachises of the spikes were fragile and each rachis node broke at maturity (wedge type disarticulation). The rachillae of the upper part of the spikelets was sometimes easy to be broken by some pressure.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

A total of 21 F_1 hybrids obtained from nine cross combinations were cytologically observed in their PMCs at MI of meiosis (Table 24). Fifteen hybrid plants had no B-chromosomes, five had two B-chromosomes and one had a B-chromosome. All the hybrid plants without B-chromosomes showed a very high frequency and an almost regular configuration of chromosome pairing (Figure 21). Their mean chiasma frequency ranged

Table 24. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops speltoides* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
2201B x 81-5653-5													
82236-P1	0	100	2.13 (0-10)	5.81 (2-7)	2.75 (0-6)	3.06 (0-6)	0.03 (0-1)	0.04 (0-1)	0.04 (0-1)	-	-	9.05 (2-13)	9.10 (2-13)
2213D x 79-5642B-10													
80775-P1	2	100	5.98 (0-14)	3.90 (0-7)	3.05 (0-6)	0.85 (0-4)	0.06 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	4.90 (0-9)	4.95 (0-9)
2263 x 77-5642-2													
78418-P1	1	50	1.00 (0-6)	6.36 (2-7)	2.68 (1-5)	3.68 (1-7)	0.04 (0-1)	0.04 (0-1)	0.04 (0-1)	-	-	10.24 (6-14)	10.91 (7-15)
2282 x 83-5646-3													
84001-P1[4]	0	280	1.99 (0-8)	5.91 (2-7)	3.27 (1-7)	2.64 (0-3)	0.04 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	8.68 (3-14)	8.70 (3-14)
5725B x 83-5646-2													
84002-P2	0	198	0.35 (0-4)	6.82 (5-7)	1.94 (0-7)	4.88 (0-7)	0.005 (0-1)	-	-	-	-	11.71 (6-14)	11.72 (6-14)
-P1[4]	0	338	1.12 (0-6)	6.43 (3-7)	2.99 (0-6)	3.43 (1-7)	0.003 (0-1)	0.003 (0-1)	0.003 (0-1)	-	-	9.88 (6-14)	9.96 (6-14)
7761 x 83-5646-3													
84003-P1[4]	0	153	0.71 (0-6)	6.58 (4-7)	2.20 (0-6)	4.39 (0-7)	0.03 (0-2)	0.01 (0-1)	0.01 (0-1)	-	-	11.06 (6-14)	11.12 (6-15)
-P2[4]	0	230	1.39 (0-8)	6.21 (2-7)	2.70 (0-6)	3.51 (0-7)	0.04 (0-2)	0.01 (0-1)	0.01 (0-1)	-	-	9.85 (4-14)	9.87 (4-14)
-P5	0	671	1.43 (0-10)	6.25 (2-7)	2.73 (0-7)	3.52 (0-7)	0.01 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	9.82 (3-14)	9.84 (3-15)
-P3	0	364	1.36 (0-8)	6.25 (3-7)	2.80 (0-6)	3.45 (0-7)	0.02 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	9.79 (4-14)	9.80 (4-14)
-P4	0	191	1.93 (0-10)	5.97 (2-7)	2.90 (0-6)	3.07 (0-6)	0.03 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	9.13 (2-13)	9.14 (2-14)

Table 24. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
7943 x 83-5641-8													
84006-P2[4]	2	256	1.60 (0-6)	6.15 (4-7)	3.09 (0-6)	3.06 (0-6)	0.02 (0-1)	0.01 (0-1)	0.01 (0-1)			9.28 (4-13)	9.52 (4-14)
-P3	2	69	3.77 (0-8)	5.12 (3-7)	3.78 (1-7)	1.33 (0-3)	-	-	-	-	-	6.45 (3-9)	6.52 (3-9)
-P1[4]	2	90	5.38 (0-14)	4.29 (0-7)	3.42 (0-7)	0.87 (0-4)	-	0.01 (0-1)	0.01 (0-1)	-	-	5.19 (0-10)	5.27 (0-11)
7943 x 83-5646-2													
84007-P2[4]	0	407	0.99 (0-6)	6.47 (4-7)	2.73 (0-6)	3.73 (0-7)	0.01 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	10.26 (4-14)	10.27 (4-14)
-P4	0	417	1.27 (0-8)	6.29 (2-7)	3.07 (0-6)	3.23 (0-6)	0.02 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	9.63 (3-13)	9.64 (3-13)
-P1[4]	0	281	1.62 (0-12)	6.14 (1-7)	3.32 (0-7)	2.82 (0-6)	0.01 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	9.04 (1-13)	9.04 (1-14)
-P3	0	1,056	1.88 (0-10)	5.90 (1-7)	3.26 (0-7)	2.64 (0-7)	0.05 (0-2)	0.04 (0-1)	0.04 (0-1)	-	-	8.77 (2-14)	8.80 (2-14)
-P7	0	276	2.21 (0-10)	5.74 (1-7)	3.39 (0-7)	2.35 (0-6)	0.06 (0-2)	0.03 (0-1)	0.03 (0-1)	-	-	8.30 (2-13)	8.30 (2-13)
7972 x 83-5641-6													
84008-P1[4]	0	100	2.15 (0-8)	5.85 (2-7)	2.77 (0-6)	3.08 (0-6)	0.05 (0-1)	-	-	-	-	9.03 (5-13)	9.03 (5-13)
-P2[4]	2	113	3.35 (0-10)	5.27 (2-7)	2.24 (0-6)	3.02 (0-6)	0.01 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	8.37 (3-13)	8.44 (3-13)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.
4) Plants grown under the condition controlled at 20°C and continuous light.

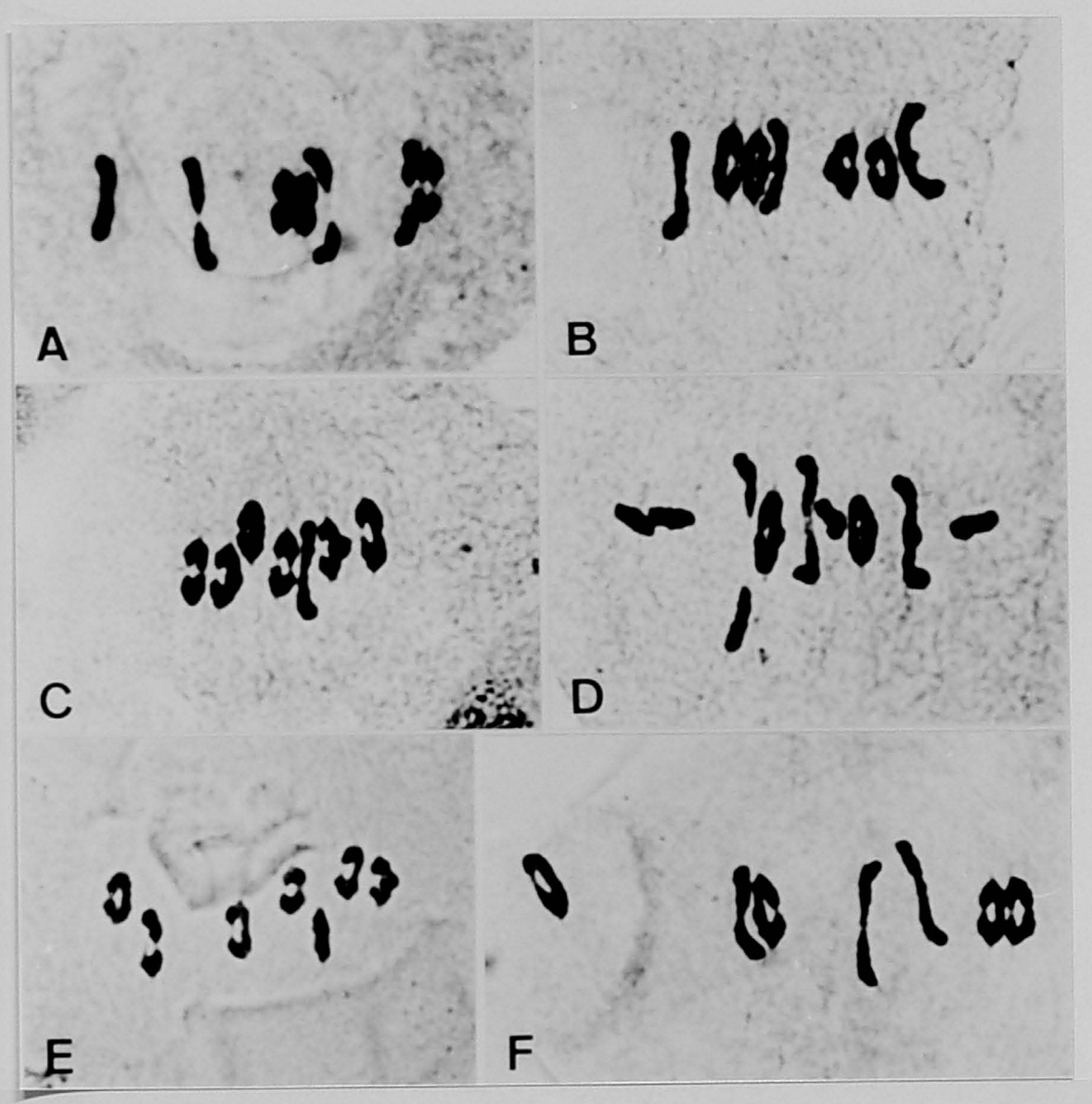


Figure 21. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids without B-chromosomes (Bs) between *Aegilops speltoides* and *Ae. mutica* (x 1,100). A: 82236-P1, 7_{II}; B: 84002-P2, 7_{II}; C-D: 84003-P2 (C: 7_{II}, D: 4_I+5_{II}); E: 84003-P5, $7ring_{II}$; F: 84007-P2, 7_{II}.

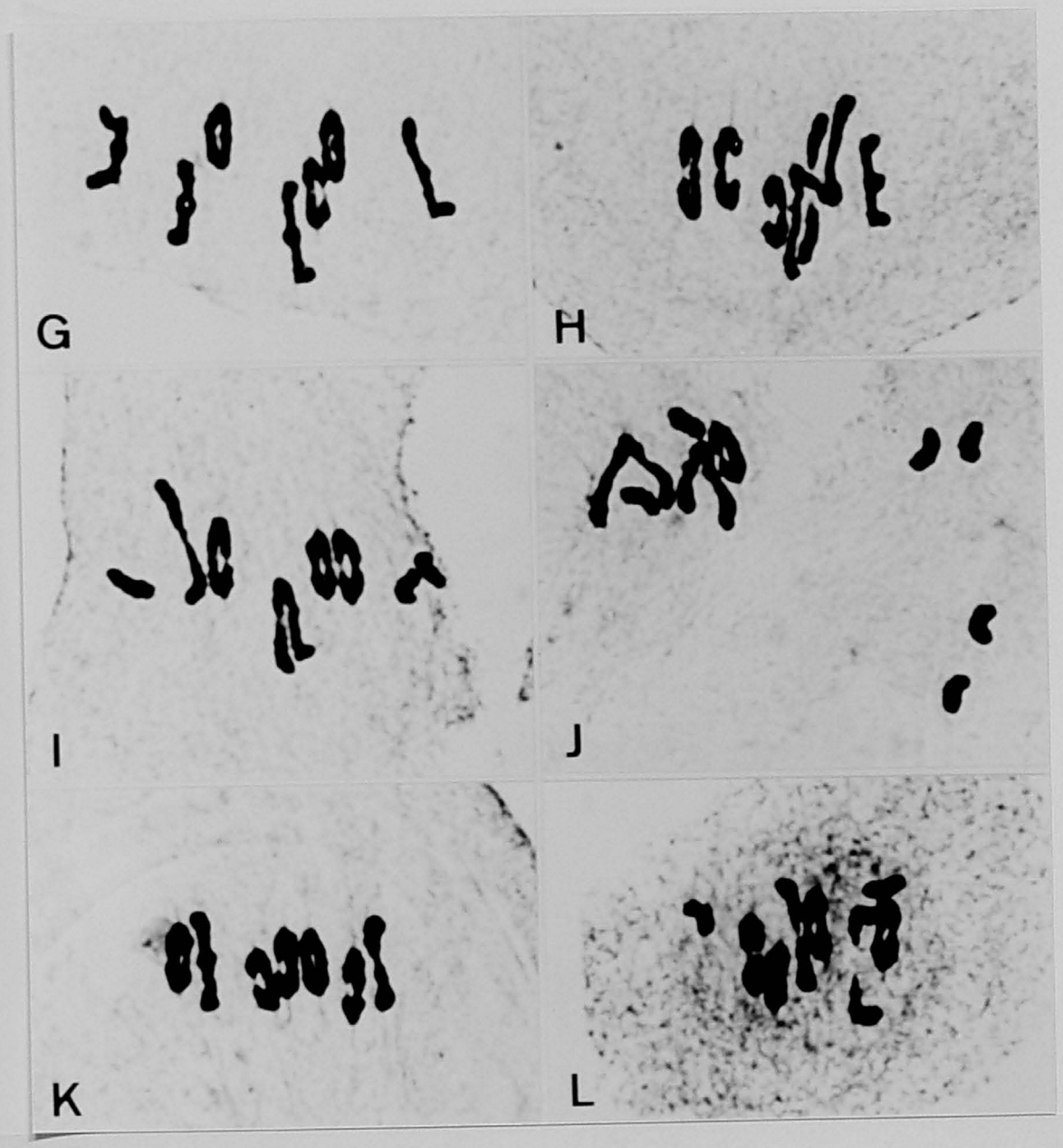


Figure 21. (Continued)
G-J: 84007-P3 (G: 7_{II}, H: $5_{II}+1_{IU}$, I: $3_{I}+4_{II}+1_{III}$, J: $6_{I}+1_{II}+2_{III}$); K: 84007-P7, 7_{II}; L: 84008-P1, $2_{I}+6_{II}$.

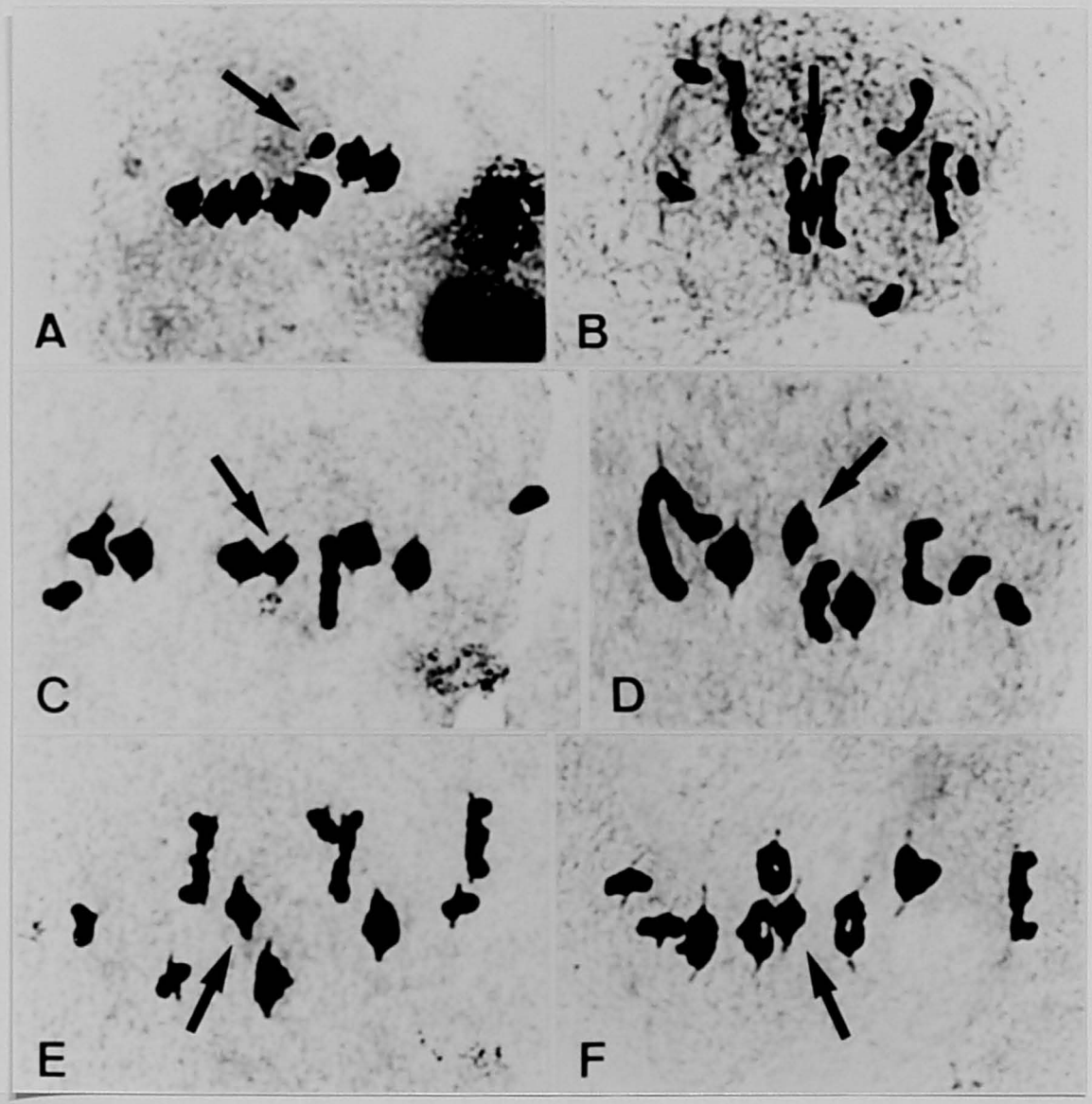


Figure 22. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with B-chromosomes (Bs) between *Aegilops speltoides* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A: 78418-P1 with 1B, 7_{II} of As + 1_I of B; B: 80775-P1 with 2Bs, 5_{II} of As + $1ring_{II}$ of Bs; C-D: 84006-P2 with 2Bs, C: 2_I+6_{II} of As + $1ring_{II}$ of Bs; D: $2_I+4_{II}+1_{IV}$ of As + $1ring_{II}$ of Bs; E: 84006-P3, 4_I+5_{II} of As + $1ring_{II}$ of Bs; F: 84008-P2, 2_I+6_{II} of As + $1ring_{II}$ of Bs.

from 8.30 to 11.72 per cell. The highest chiasma frequency was observed in one of the hybrid plants obtained from the cross combination of 5725B x 83-5646-2 (Culture No. 84002-P2) and its pairing configuration was almost regular with only few multivalents and univalents. Its mean configuration of chromosome pairing was 0.35_{I} + $(1.94rod + 4.88ring)_{II}$ + 0.005_{III}. Seventy two per cent of bivalents observed in this plant were ring-shaped. Twenty three (12%) among a total of 198 cells observed formed seven ring-shaped bivalents, 36 (18%) formed six ring-shaped and one rod-shaped bivalents, and 57 (29%) formed five ring-shaped and two rod-shaped bivalents. Only one cell contained a frying pan shaped trivalent with a univalent. But univalents were observed only in 31 cells (12%). Another plant from the same cross combination (Culture No. 84002-P1) also showed a high frequency of chromosome pairing, and its mean chiasma frequency and mean configuration of chromosome pairing were 9.96 per cell and 1.12_{I} + $(2.99rod + 3.43ring)_{II}$ + 0.003_{III} + $0.003chain_{IV}$, respectively. Hybrid plants without Bs obtained from the other cross combinations between *Ae. speltoides* and *Ae. mutica* showed a similar pairing configuration to that of these two plants.

The F_1 hybrid plant with a B-chromosome was obtained from the cross combination of 2263 x 77-5642-2. That hybrid plant (Culture No. 78418-P1) showed a very high frequency of A-chromosome pairing with the mean chiasma frequency as high as 10.91 per cell (Figure 22A). Its configuration of A-chromosome pairing was 1.00_{I} + $(2.68rod + 3.68ring)_{II}$ + 0.04_{III} + 0.04_{IV}. The frequency and configuration of A-chromosome pairing were quite similar to those of 0B hybrid plants. Its B-chromosome with the normal size was metacentric and always observed as a

univalent at MI of meiosis.

Five F_1 hybrid plants with two B-chromosomes were obtained from three cross combinations. Their B-chromosomes formed a tightly associated small ring-shaped bivalent in most PMCs. In contrast to the 2B hybrid plants obtained from the other interspecific cross combinations, they showed variable but much higher frequency of A-chromosome pairing (Figures 22B-F). Their mean chiasma frequency ranged from 4.95 to 9.52 per cell. The mean chiasma frequency in the two plants showing the highest mean chiasma frequency among the obtained 2B hybrids (Culture Nos. 84006-P2 and 84008-P2) was within the variation of the mean chiasma frequency in the above-mentioned 0B and 1B plants. In one of them (84006-P2), 112 (42%) among a total of 265 observed cells formed seven bivalents of A-chromosomes. Six univalents were observed in 11 cells (4%) but no cell showed 14 univalents of A-chromosomes. Its mean configuration of A-chromosome pairing was 1.60_{I} + $(3.09\text{rod} + 3.06\text{ring})_{II}$ + 0.02_{III} + 0.01chain_{IV} (Figures 22C and D). Even the lowest mean chiasma frequency, 4.95 chiasmata per cell, observed in one of the 2B hybrids (Culture No. 80775-P1) was significantly higher than those observed in the 2B plants of the other interspecific cross combinations. In that plant, up to six rod-shaped bivalents were observed in 99 among a total of 100 observed cells and up to four ring-shaped bivalents were found in 55 cells (Figure 22B). Even seven bivalents, consisting of five rod-shaped and two ring-shaped bivalents, were formed in a single cell but 14 univalents of A-chromosomes were observed only in one cell. Its mean configuration of A-chromosome pairing was 5.98_{I} + $(3.05\text{rod} + 0.85\text{ring})_{II}$ + 0.06_{III} + 0.01chain_{IV}. It was quite contrasted to the

drastically low frequency of A-chromosome pairing observed in the 2B hybrids from the other interspecific combinations. From the cross combination 7972 x 83-5641-6, both 0B and 2B hybrid plants were obtained. These two plants showed similar frequency and configuration of A-chromosome pairing. The 0B hybrid showed the configuration of 2.15_{I} + (2.77rod + 3.08ring)$_{II}$ + 0.05_{III} and 9.03 chiasmata per cell, and the 2B hybrid showed 3.35_{I} + (2.24rod + 3.02ring)$_{II}$ + 0.01_{III} + 0.02_{IV} and 8.44 chiasmata per cell (Figures 21L and 22F).

Formation of chromatid bridges and acentric fragments at AI of meiosis in the F_1 hybrids

Pollen mother cells at AI were observed in one of the F_1 hybrid plants obtained from the cross of 7761 x 83-5646-3 (Culture No. 84003-P2) (Table 25 and Figure 23). In seven (11%) among a total of 66 observed PMCs, chromatid bridges and acentric chromatid fragments were found. One of these PMCs contained two chromatid bridges and two acentric fragments, and the other six formed one bridge and one fragment.

Pollen fertility in the F_1 hybrids

Pollen fertility in thirteen F_1 hybrid plants obtained from eight cross combinations was examined (Table 26). Eight of them had no B-chromosomes, four had two B-chromosomes and another had one B-chromosome. Their pollen fertility was variable and ranged from 0 to 62.1%. Four plants showed the pollen fertility more than 5%. The 1B hybrid plant obtained from the cross combination of 2263 x 77-5642-2 (Culture No. 78418-P1) showed the highest pollen fertility as high as

Table 25. The mode of chromosome segregation to the opposite poles of PMCs and the frequency of chromatid bridges with acentric chromatid fragments observed at the first anaphase (AI) of meiosis in the F_1 hybrid between *Aegilops speltoides* and *Ae. mutica* (Culture No. 84003-P2)

Mode of chromosome segregation	No. of PMCs observed				
	No. of bridges	0	1	1	2
	No. of fragments	0	0	1	2	Total (%)
7[0] - 7[0][1]		35	1	2		38 (57.6)
6[2] - 6[2]		14		2		16 (24.3)
5[4] - 5[4]		7		2		9 (13.6)
8[0] - 6[0]		1				1 (1.5)
7[1] - 6[1]					1	1 (1.5)
2[10]- 2[10]		1				1 (1.5)
Total (%)		58(87.9)	1(1.5)	6(9.1)	1(1.5)	66(100.0)

1) Figures in the square brackets represent the number of sister chromatids derived from the equational division of univalents at AI.

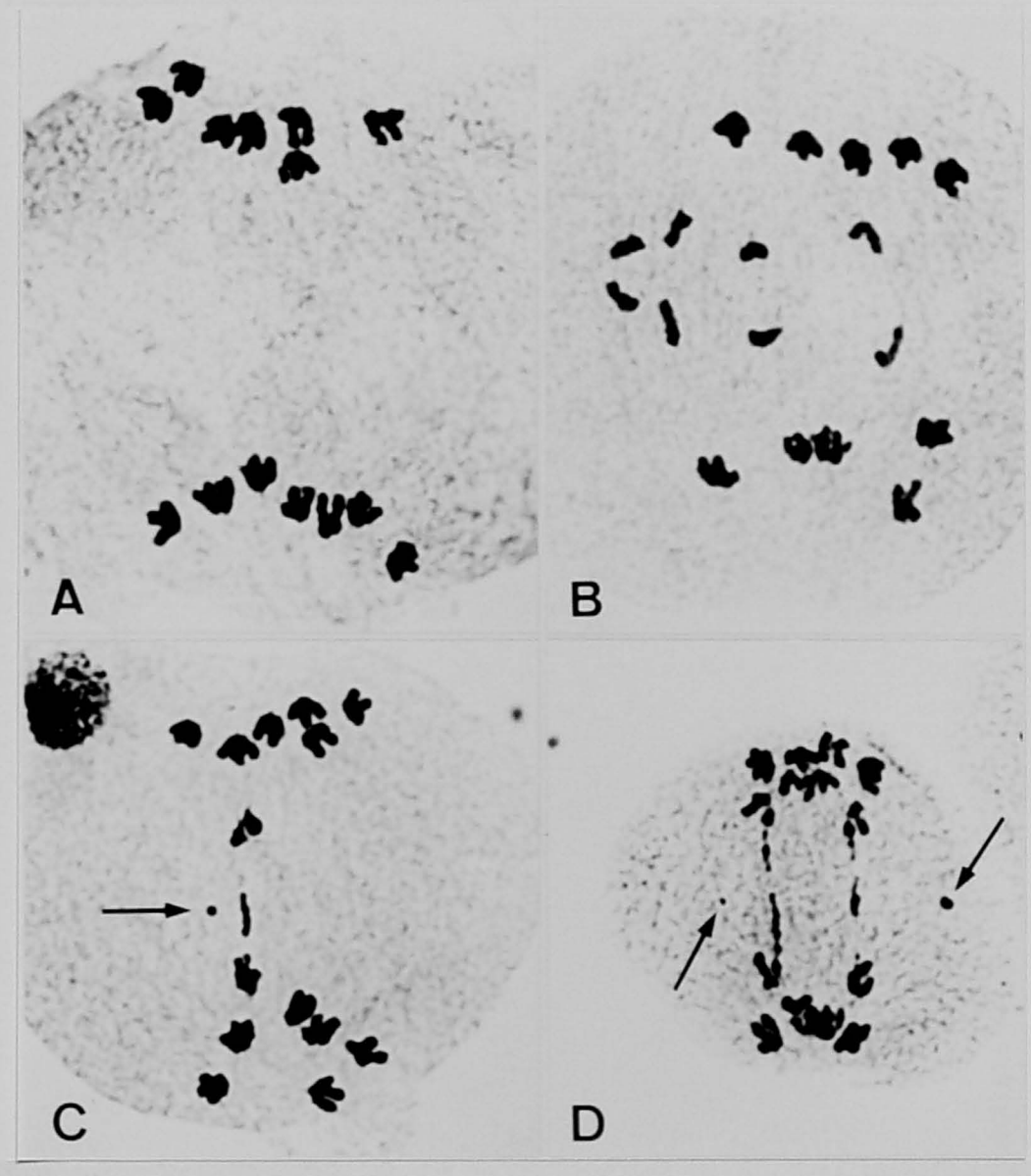


Figure 23. Segregation of chromosomes to the opposite poles at AI of meiosis in one of the F_1 hybrids (Culture No. 84003-P2) between *Aegilops speltoides* and *Ae. mutica* (x 1,100). A: All the chromosomes segregate normally to the opposite poles (7 : 7), B: Ten chromosomes segregate normally to the opposite poles (5 : 5) but the sister chromatids of the other four chromosomes (which were probably derived from univalents at MI) are equationally divided, C: A chromatid bridge and a chromatid fragment are formed, D: Two chromatid bridges and two chromatid fragments are formed. Chromatid fragments are indicated with arrows.

Table 26. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops speltoides* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
2213D x 79-5642B-10			
80775-P1	2	1.9	-
2263 x 77-5642-2			
78418-P1	1	62.1	+[3]
2282 x 83-5646-3			
84001-P1	0	0.4	-
5725B x 83-5646-2			
84002-P1	0	16.7	±
-P2	0	9.0	±
7761 x 83-5646-3			
84003-P1	0	0.2	-
-P2	0	1.7	-
7943 x 83-5641-8			
84006-P1	2	0	±
-P2	2	0	-
7943 x 83-5646-2			
84007-P1[4]	0	5.9	-
-P2	0	3.2	-
7972 x 83-5641-6			
84008-P1	0	3.7	-
-P2	2	2.7	-[3]

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent, -: indehiscent.
3) Good fertility was due to the formation of unreduced gametes.
4) Six plump seeds were born on this individual by the open-pollination among the F_1 hybrid plants between *Ae. speltoides* and *Ae. mutica*.

62.1% among all the F_1 hybrids between *Ae. speltoides* and *Ae. mutica*. Most of its anthers normally dehisced and shed abundant pollen grains at anthesis. In that plant large pollen grains with 14 A-chromosomes were observed at metaphase of the first division of pollen grain mitosis (Figure 24). The observation indicates that the good pollen fertility was caused by the formation of unreduced gametes. The similar result was observed in one of the 2B hybrids which obtained from the cross of 7972 x 83-5641-6 (Culture No. 84008-P2). Its anthers partially dehisced and its pollen fertility was 2.7%. The diameter of its normal pollen grains showed a bimodal distribution (Figures 25E and 26E). One of the modes (4.0 to 4.5 x 10^{-2} mm) was similar to that of the parental species (Figures 25A, B, 26A and B) while another mode (7.0 to 7.5 x 10^{-2} mm) was much larger than that of those pollen grains. The distribution of the diameter of these larger pollen grains was similar to that of the F_1 hybrid between *Ae. longissima* and *Ae. mutica* which formed unreduced gametes and whose anthers dehisced (Figures 25F and 26F). The lowest fertility was found in the two 2B hybrids obtained from the cross of 7943 x 83-5641-8 (Culture Nos. 84006-P1 and -P2). Though most of their pollen grains observed were empty and no normal pollen grains were found, anthers partially dehisced in one of them. A possible explanation for the dihiscence of its anthers is also the formation of unreduced gametes. Such unreduced gametes are thought to be formed at a high frequency in its dehiscent anthers but not in the indehiscent anthers.

All the 0B hybrids formed at least some normal pollen grains and their pollen fertility ranged from 0.2% to 16.7%. The highest pollen

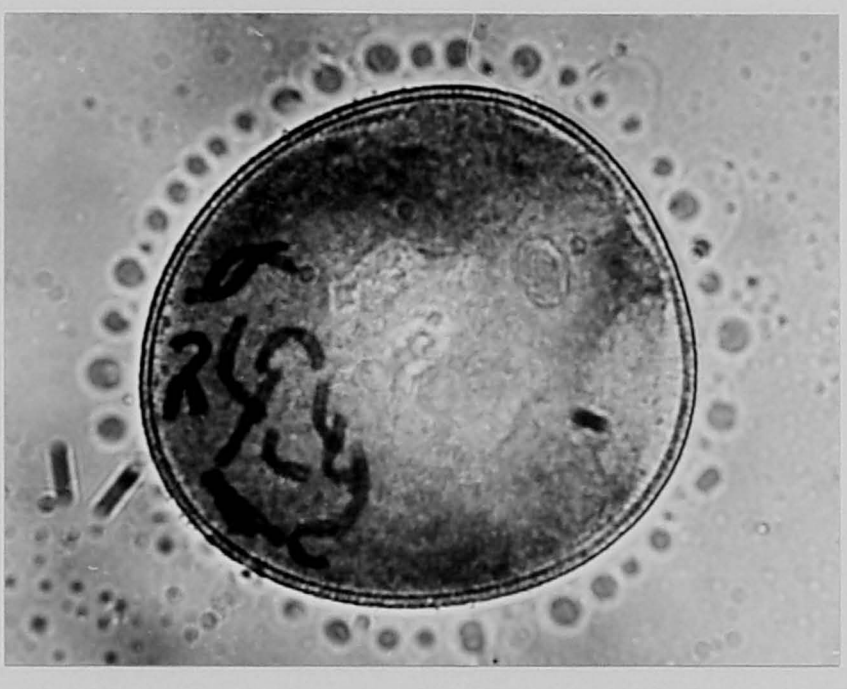


Figure 24. Chromosomes at metaphase of the first division of pollen grain mitosis in the young pollen grain having the unreduced number (n = 14) of chromosomes observed in the 1B hybrid plant (Culture No. 78418-P1) between *Aegilops speltoides* and *Ae. mutica* (x 1,330).

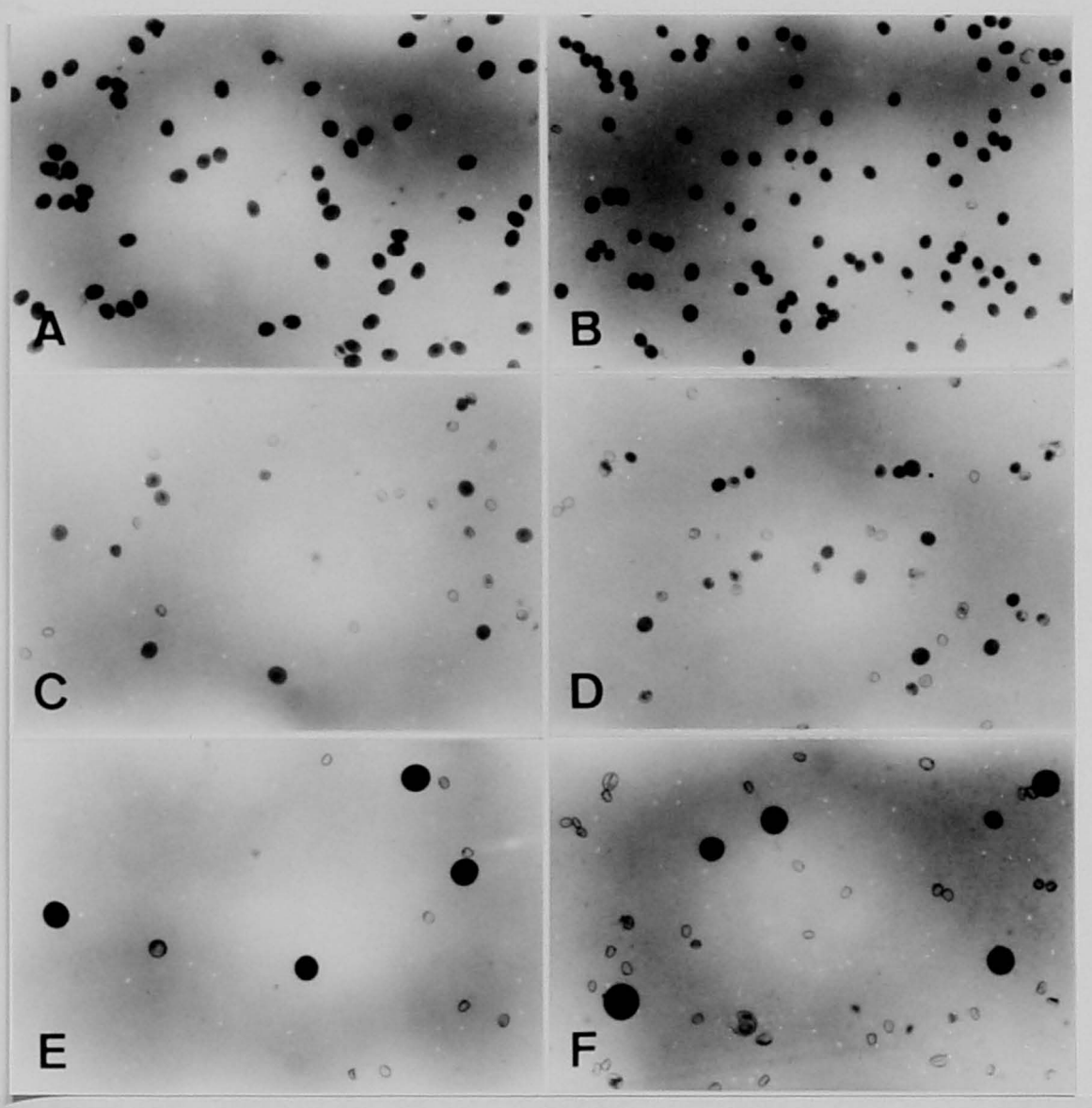


Figure 25. Pollen grains of *Aegilops speltoides*, *Ae. mutica*, their F_1 hybrids, and the F_1 hybrid between *Ae. longissima* and *Ae. mutica* which formed unreduced gametes. All the plates are in the same magnification (x 47). A: *Ae. speltoides* (KU 7943), B: *Ae. mutica* (KU 5646), C and D: 0B hybrids between *Ae. speltoides* and *Ae. mutica* (C: 84002-P1, D: 84007-P1), E: 2B hybrid between *Ae. speltoides* and *Ae. mutica* (84008-P1), F: F_1 hybrid between *Ae. longissima* and *Ae. mutica* which formed unreduced gametes and whose anthers dehisced at anthesis.

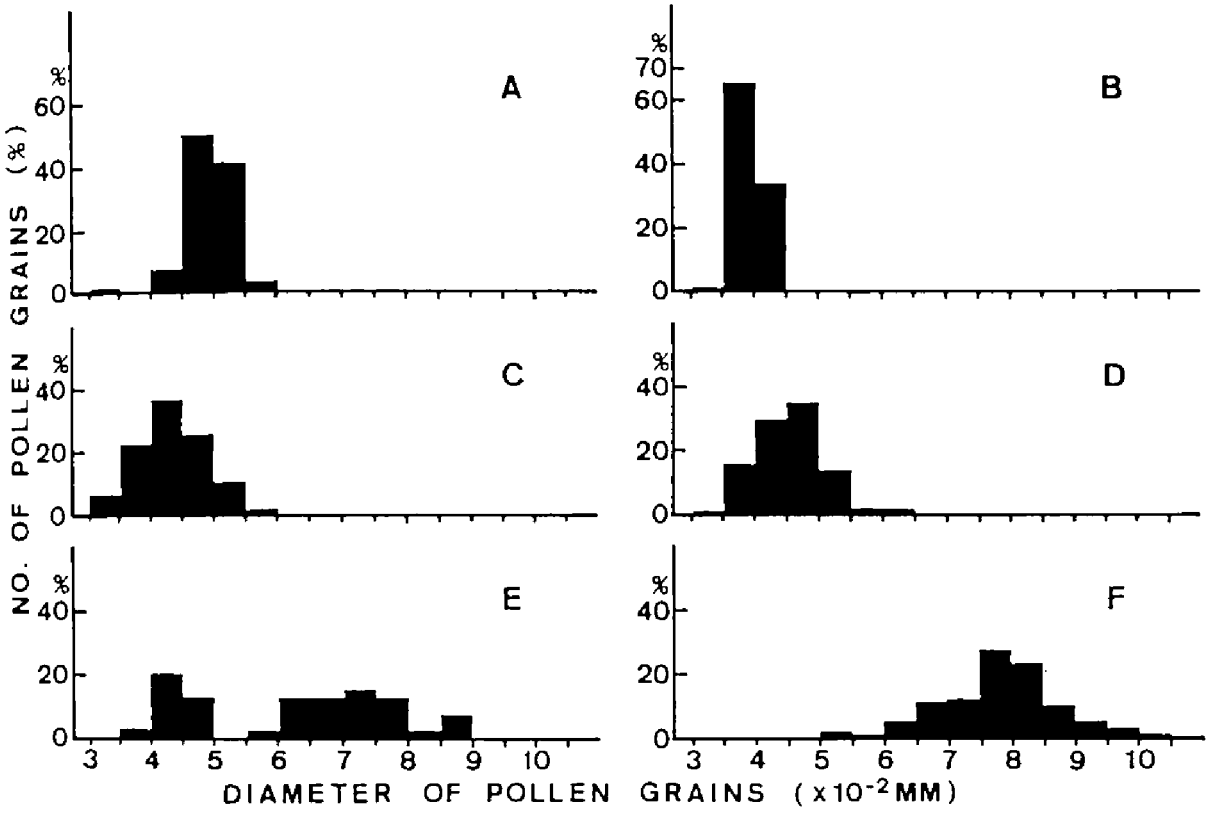


Figure 26. Frequency distribution of the diameter of the normal pollen grains in the F_1 hybrids between *Aegilops speltoides* and *Ae. mutica* and their parental species. A: *Ae. speltoides* (KU 7943), B: *Ae. mutica* (KU 5646), C and D: 0B hybrids between *Ae. speltoides* and *Ae. mutica* (C: 84002-P1, D: 84007-P2), E: 2B hybrid between *Ae. speltoides* and *Ae. mutica* (84008-P2), F: F_1 hybrid between *Ae. longissima* and *Ae. mutica* which formed unreduced gametes and whose anthers dehisced at anthesis.

fertility was found in the two hybrid plants obtained from the cross of 5725B x 83-5646-2 (Culture No. 84002-P1 and -P2). Their pollen fertility was 16.7% and 9.0%. About a half of their anthers dehisced and shed pollen grains at anthesis (Figure 27). In contrast with above-mentioned 2B hybrids, they had the normal pollen grains with a diameter only similar to that of the parental species, *Ae. speltoides* and *Ae. mutica*. The mode of the pollen diameter in one of them was 4.0 to 4.5 x 10^{-2} mm (Figures 25C and 26C). Normal pollen grains observed in another 0B hybrid with the pollen fertility of 5.9% obtained from the cross of 7943 x 83-5646-2 (Culture No. 84007-P1) also showed similar distribution in their diameter to that of its parental species and the above-mentioned 0B hybrids. Its mode was 4.5 to 5.0 x 10^{-2} mm (Figures 25D and 26D). The other 0B hybrids also had normal pollen grains with the similar diameter to these 0B hybrids and their parental species.

Seed fertility of the F_1 hybrids and the chromosome number of the seedlings in the second generation

The seed set by the open-pollination among the present F_1 hybrids was examined in one of the F_1 hybrid plants obtained from the cross of 7943 x 83-5646-2 (Culture No. 84007-P1). Plump seeds set on six of 298 examined florets of this plant and the percentage seed set was 2.0%. These seeds were sown in sterilized soil and three of them germinated. They normally grew till mature stage (Figure 19N). The chromosome numbers in their root tips determined by the aceto-carmine squash technique proved all three to be diploids: Two of them had 14 chromosomes and one had 15 chromosomes (Figure 28).

Figure 27. Herbarium specimen of the F_1 hybrid without B-chromosomes (84002-P1) between *Aegilops speltoides* and *Ae. mutica* which showed the highest pollen fertility and whose anthers dehisced at anthesis (x 0.35). Dehiscent anthers can be seen in its spikes and in the vinyl bag on the sheet.

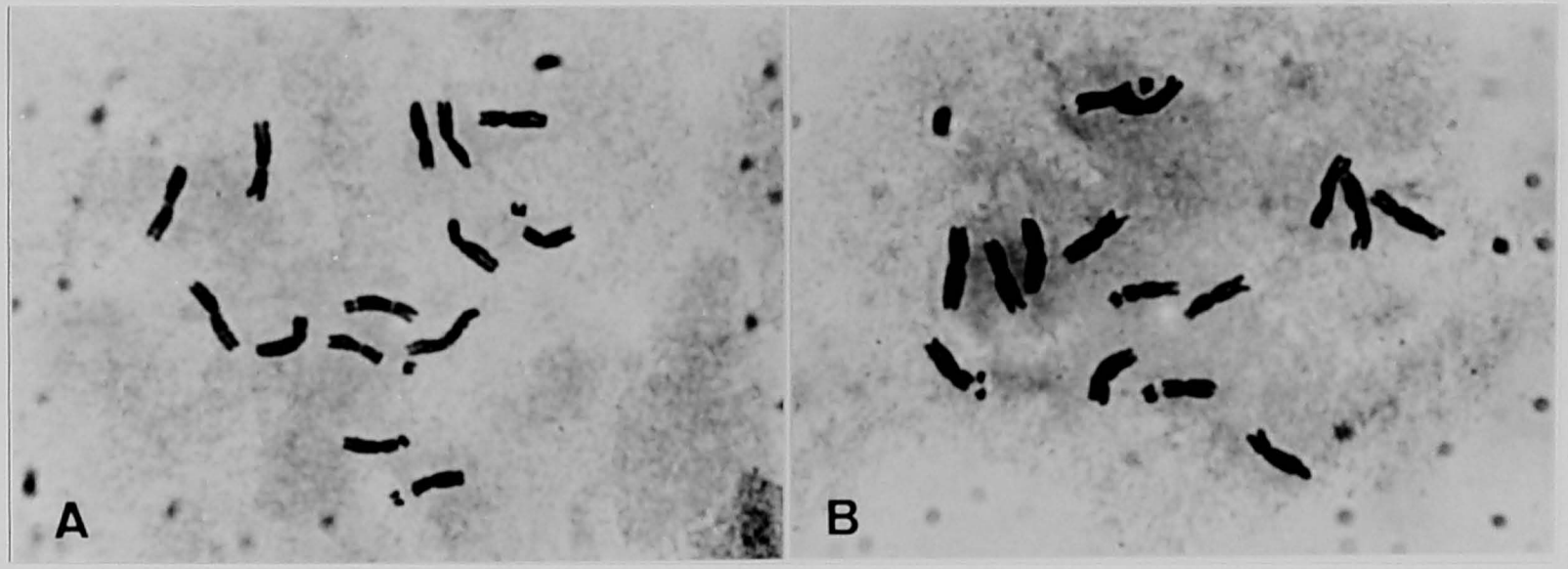


Figure 28. Chromosomes at metaphase of somatic division in the root tips of the plants obtained from the F_1 hybrid between *Aegilops speltoides* and *Ae. mutica* (Culture No. 84007-P1) by open pollination among the F_1 hybrids (x 1,500). A: 86307-P2, $2n = 14$, B: 86307-P1, $2n = 15$.

(6a) *Aegilops mutica* x *Ae. squarrosa*

Result of crosses

Three accessions of *Aegilops squarrosa* and 12 plants from eight accessions of *Ae. mutica* were used in the reciprocal crosses (Table 27). When the plants of *Ae. squarrosa* were used as female parents in the crosses, obtained hybrid seeds did not germinate and no F_1 seedlings were obtained. A total of 174 emasculated florets of three accessions of *Ae. squarrosa* were pollinated with the pollen grains of *Ae. mutica*. Ninety eight large but slightly shrivelled seeds were easily obtained and the mean percentage seed set was 56%. One of the cross combinations, 20-9 x 78-5646-6, gave the highest percentage seed set of 96%. In spite of that high percentage seed set, those seeds obtained from the crosses using *Ae. squarrosa* as female parents did not germinate at all.

In contrast to these crosses, the hybrid seeds obtained from the crosses using *Ae. squarrosa* as male parents could germinate with a high germination rate. Only the lowest two florets in each spikelet of *Ae. mutica* were emasculated and used in the crosses. A total of 189 emasculated florets of *Ae. mutica* were pollinated with the pollen grains of *Ae. squarrosa*. These emasculated florets of *Ae. mutica* were repeatedly pollinated with the pollen grains of *Ae. squarrosa* because the florets in the uppermost spikelets on the long spikes of *Ae. mutica* flower about a week earlier than those in the lowest ones. As a result of such an intensive pollination, 54 hybrid seeds were obtained and the mean percentage seed set was 29%. Those 54 seeds were sown in the

Table 27. Result of the crosses between *Aegilops squarrosa* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops squarrosa x *Ae. mutica*						
20-5 x 81-5653-3	42	14	33	14	0	0
20-5 x 81-5653-5	28	11	39	11	0	0
20-9 x 81-5606-1	24	21	88	21	0	0
20-9 x 78-5643d-2	16	5	31	5	0	0
20-9 x 78-5646-6	24	23	96	23	0	0
20-9 x 78-5653-10	20	12	60	12	0	0
20-10 x 81-5606-1	20	12	60	12	0	0
Total	174	98	56	98	0	0
Aegilops mutica x *Ae. squarrosa*						
83-5610A-16 x 20-9	28	8	29	8	5	63
85-5641B-6 x 20-9	81	44	54	44	31	70
80-5641E-2 x 20-10	26	1	4	1	0	0
85-12004-5 x 20-9	34	1	3	1	1	100
85-12004-9 x 20-9	20	0	0	-	-	-
Total	189	54	29	54	37	69
Artificially synthesized autotetraploid of *Aegilops squarrosa* x *Ae. mutica*						
29 x 81-5645B-8	23	0	0	-	-	-
29 x 81-5653-5	12	3	25	3	2	67
Total	35	3	9	3	2	67

sterilized soil and they gave 37 seedlings. The mean germination rate was 69%.

Morphology of *Aegilops squarrosa* and the F_1 hybrids between *Ae. mutica* and *Ae. squarrosa*

Ae. squarrosa ssp. *strangulata* used in the present crosses has cylindrical spikes without rudimentary spikelets (Figures 29A and 30A). The accession used in the present cross (KU 20-9) had black spikes. Its spikes consist of about ten square spikelets arranged in a row. All spikelets are similar to one another both in shape and in size along the whole spike length. Each spikelet usually has four florets and it is as long as the adjacent rachis internode. Thick empty glumes cover about three fourths of the each spikelet. The empty glume is a square shape and its upper margin without awns or teeth is truncate. Upper margin of its lemma is also truncate but it has a tooth or a short awn, especially in the upper part of the spikes a tooth becomes a short awn. Rachis is fragile. Each rachis node breaks at maturity and each spikelet falls separately with its adjacent rachis internode (barrel type disarticulation). Rachilla is tough.

The black spikes of the F_1 hybrids between *Ae. mutica* and *Ae. squarrosa* ssp. *strangulata* were linear and slenderer than those of *Ae. squarrosa* (Figures 29B, C and 30B). They consisted of about 15 cylindrical spikelets arranged in a row and well developed spikes did not have any rudimentary spikelets. Each spikelet had about five or six florets and was as long as the adjacent rachis internode. Empty glumes covered about a half of the each spikelet. The empty glumes were thick and not awned. Their upper margins were almost truncate sometimes with

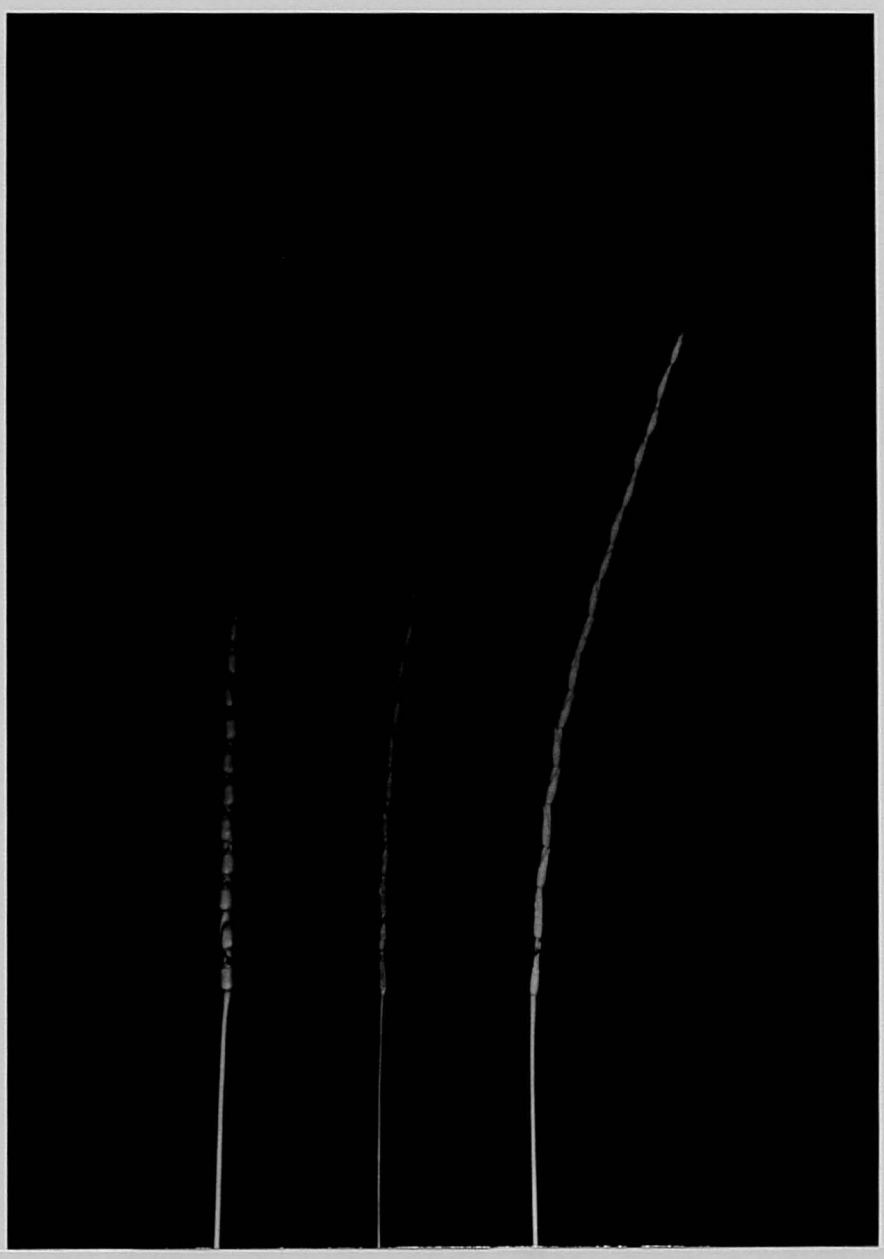
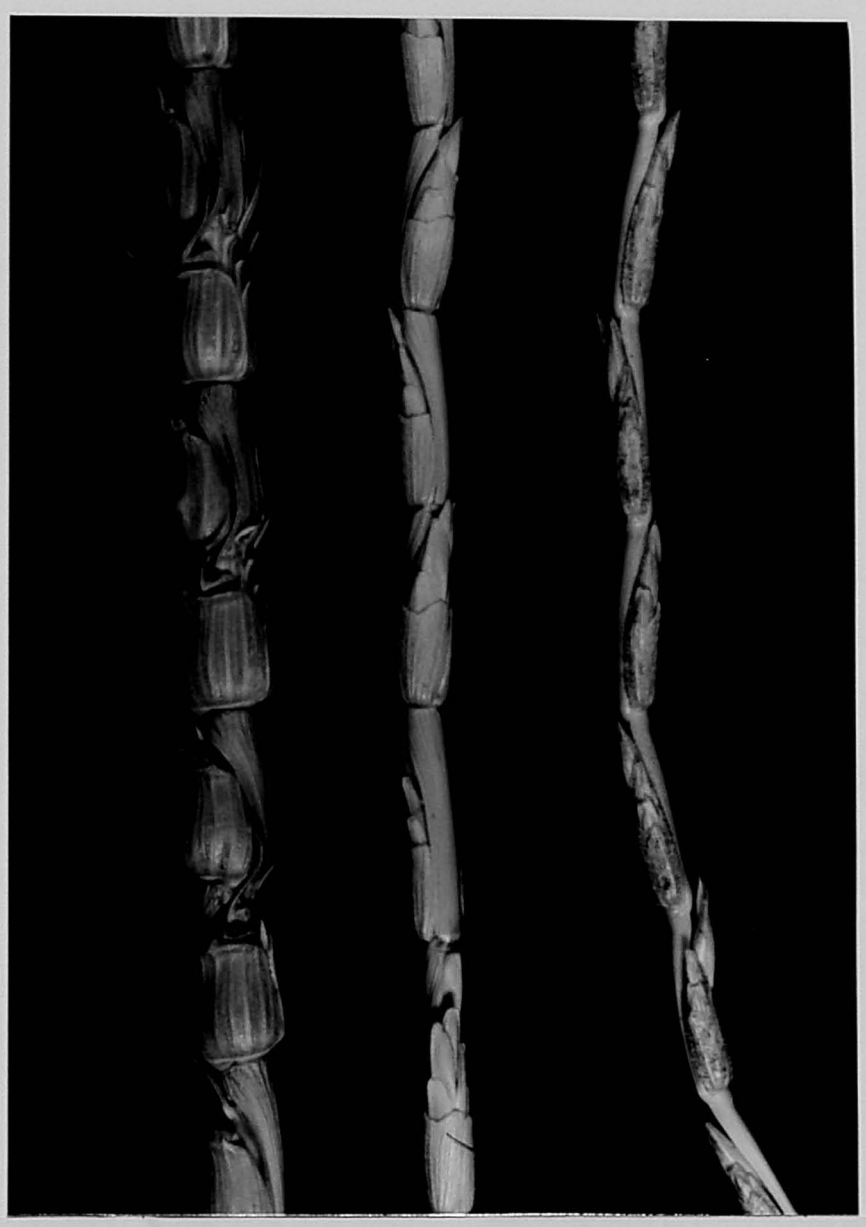


Figure 29. Spike morphology of *Aegilops squarrosa* and the F_1 hybrids between *Ae. mutica* and *Ae. squarrosa* (x 0.5). A: *Ae. squarrosa* (KU 20-9), B-C: F_1 hybrid between *Ae. mutica* and *Ae. squarrosa* KU 20-9 (B: 84011-P1, C: 86303-P1).



A B C

Figure 30. Spikelet morphology of *Aegilops squarrosa*, *Ae. mutica* and their F_1 hybrid (x 2.3). A: *Ae. squarrosa* (KU 20-9), B: F_1 hybrid between *Ae. mutica* and *Ae. squarrosa* KU 20-9 (86303-P1), C: *Ae. mutica* (KU 12004).

a shallow dull notch. Those of their lemmas were not pointed and they did not have any awns or teeth. The rachis was fragile while the rachilla was tough at maturity. Each rachis node broke at maturity and each spikelet fell separately with the rachis internode below it (wedge type disarticulation).

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

The PMCs of the five F_1 hybrid plants were cytologically observed (Table 28 and Figure 31). Three of the F_1 hybrids had no B-chromosomes, one had a B-chromosome and another carried two Bs. Three 0B hybrids showed a very high frequency of chromosome pairing with the mean chiasma frequency ranging from 11.70 to 10.07 per cell and two of them formed up to seven ring-shaped bivalents in their PMCs. These three 0B hybrids could be classified into two groups based on the configuration of chromosome pairing. One of them showed almost regular configuration of chromosome pairing with only few multivalents (Culture No. 84011-P1) (Figure 31B) and the other two formed a high frequency of quadrivalents (Culture Nos. 84011-P2 and -P4) (Figure 31A). In the former, 56 among a total of 100 observed PMCs contained seven bivalents; 17 of which formed four ring-shaped and three rod-shaped bivalents, 17 formed five ring-shaped and two rod-shaped bivalents, six formed six ring-shaped and one rod-shaped bivalents, and the other one formed seven ring-shaped bivalents. However, a chain-shaped quadrivalent was found only in two cells. In contrast with this plant, the latter showed the pairing configuration with a high frequency of quadrivalents. A chain-shaped quadrivalent was found in 41 among a total of 100 PMCs observed in one

Table 28. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops mutica* and *Ae. squarrosa*

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
Aegilops mutica x *Ae. squarrosa*													
83-5610A-16 x 20-9													
84011-P4	0	100	0.16 (0-2)	5.89 (4-7)	1.78 (0-5)	4.11 (2-7)	0.02 (0-1)	0.50 (0-1)	0.41 (0-1)	0.09 (0-1)	-	11.63 (9-14)	11.70 (9-15)
-P1[4]	0	100	1.09 (0-6)	6.40 (4-7)	2.62 (0-6)	3.78 (0-7)	0.01 (0-1)	0.02 (0-1)	0.02 (0-1)	-	-	10.26 (4-14)	10.27 (4-14)
-P2[4]	0	46	0.69 (0-6)	6.11 (2-7)	3.07 (1-6)	3.04 (0-6)	0.04 (0-1)	0.24 (0-1)	0.22 (0-1)	0.02 (0-1)	-	9.98 (6-13)	10.07 (6-13)
85-5641B-6 x 20-9													
86302-P21	1	238	1.47 (0-8)	6.26 (3-7)	2.86 (0-6)	3.40 (0-6)	-	-	-	-	-	9.67 (4-13)	9.71 (4-13)
85-12004-5 x 20-9													
86303-P1	2	100	4.62 (0-10)	4.61 (2-7)	3.08 (0-6)	1.53 (0-4)	0.04 (0-1)	0.01 (0-1)	0.01 (0-1)	-	-	6.25 (2-11)	6.25 (2-11)
Mean A-chromosome pairing in the PMCs with the doubled chromosome number[5] observed in the 2B hybrids from the cross of 85-12004-5 x 20-9													
86303-P1	4	12	-	14.00 (14)	0.50 (0-1)	13.50 (11-14)	-	-	-	-	-	27.50 (25-28)	not obs.[6]

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.
4) Plants grown under the condition controlled at 20°C and continuous light.
5) These PMCs had 28 A-chromosomes in addition to four B-chromosomes, and the mean configuration of B-chromosome pairing in them was $0.17_{I} + (0.08\text{rod}+0.83\text{ring})_{II} + 0.50_{IV}$.
6) not obs.: not observed.

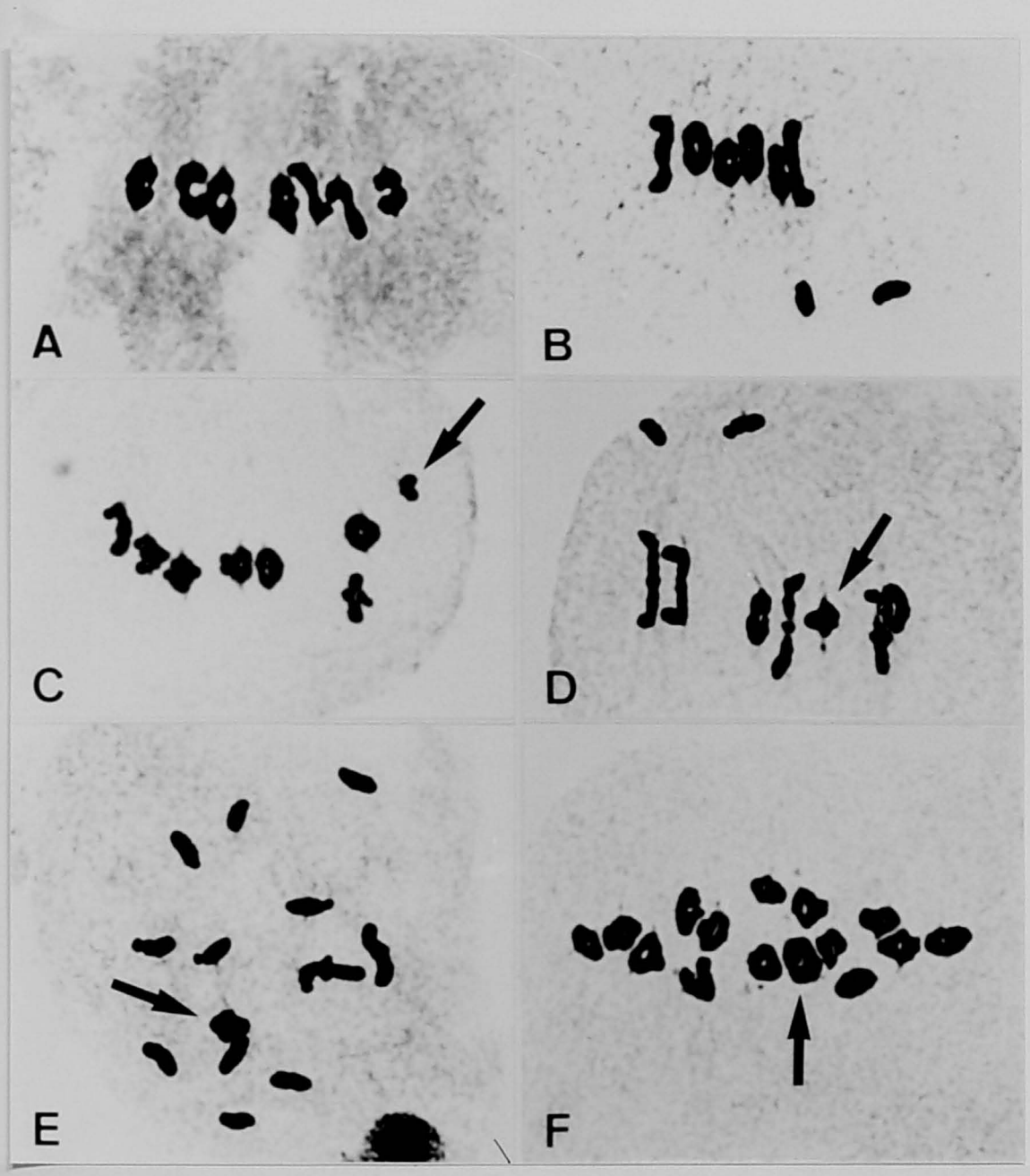


Figure 31. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with or without B-chromosomes (Bs) between *Aegilops mutica* and *Ae. squarrosa* (x 1,100). B-chromosomes are indicated with arrows. A: 84011-P4 without Bs, $5_{II}+1_{IU}$; B: 84011-P1 without Bs, 2_I+6_{II}; C: 86302-P21 with 1B, 7_{II} of As + 1_I of B; D-E: 86303-P1 with 2Bs (D: 2_I+6_{II} of As + $1ring_{II}$ of Bs, E: 10_I+2_{II} of As + $1ring_{II}$ of Bs); F: a $4n$ cell observed in the F_1 hybrid 86303-P1, 14_{II} of As + $1ring_{IU}$ of Bs.

of the two plants of this group (Culture No. 84011-P4) and a ring-shaped quadrivalent was found in nine cells. In the other plant (No. 84011-P2), 11 (24%) among a total of 46 observed PMCs contained a quadrivalent including a ring-shaped one. In addition, these three 0B hybrids could be divided into two groups based on their frequency of chromosome pairing. One of them showing the highest pairing frequency (No. 84011-P4) was slightly but significantly (χ^2=50.18) different from the other two in the frequency of chromosome pairing.

Only one F_1 hybrid plant with two B-chromosomes was obtained (Culture No. 86303-P1) and its PMCs at MI of meiosis were cytologically observed (Figures 31D-F). The frequency of A-chromosome pairing in this 2B plant was not drastically reduced but it was clearly lower than that in the above 0B hybrid plants ($\chi^2 \geq 273.50$) (Figures 31D and E). Compared with the 0B hybrids, ring-shaped bivalents were reduced but up to seven bivalents were formed in the PMCs of this 2B hybrid. No univalents of A-chromosomes were found in 10 among a total of 100 PMCs observed in this 2B hybrid. Seven bivalents were found in nine of them and five bivalents with a quadrivalent were found in one cell. Two to ten univalents were observed in the other 90 cells. However, PMCs with 14 univalents of A-chromosomes, which were characteristic to most interspecific 2B hybrids involving *Ae. mutica*, were not found in this 2B hybrid between *Ae. squarrosa* and *Ae. mutica*. Its mean configuration of A-chromosome pairing and mean chiasma frequency were 4.62_{I} + $(3.08\text{rod} + 1.53\text{ring})_{II}$ + 0.04_{III} + 0.01chain_{IV} per cell and 6.25 per cell, respectively.

The PMCs with the doubled number of chromosomes were observed in

this 2B hybrid plants in addition to the above-mentioned normal cells with 14 A-chromosomes and two B-chromosomes. All of them formed 14 bivalents of A-chromosomes with two small bivalents or a small quadrivalent of B-chromosomes (Table 28 and Figure 31F). Most of the bivalents observed in those cells with the doubled chromosome number were ring-shaped. The mean configuration of A-chromosome pairing of 12 cells observed was $(0.50rod + 13.50ring)_{II}$.

In addition to the 0B and 2B hybrids, an F_1 hybrid with one B-chromosome was cytologically observed (Culture No. 86302-P21). Its B-chromosome was normal in its size and metacentric in its morphology. The configuration of A-chromosome pairing in this 1B plant was similar to that of the 0B hybrid with few multivalents (Figure 31C). But its pairing frequency was slightly lower than that of the 0B hybrids belonging to the lower pairing group (χ^2=7.68). And it was clearly higher than that of the 2B hybrid (χ^2=247.96). Its mean chiasma frequency of A-chromosomes and its mean configuration of A-chromosome pairing were 9.71 per cell and $1.47_I + (2.86rod + 3.40ring)_{II}$ per cell, respectively.

Fertility of the F_1 hybrids

All the F_1 hybrids both with and without B-chromosomes were highly sterile and their anthers did not dehisce at all. Pollen fertility was estimated in two of the 0B hybrids (Table 29). Their pollen fertility was very low: 0.7% and 2.9%, respectively.

Table 29. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops mutica* and *Ae. squarrosa*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
83-5641A-16 x 20-9			
84011-P1	0	0.7	-
-P2	0	2.9	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent,
-: indehiscent.

(6b) The artificially synthesized autotetraploid of *Aegilops squarrosa* x *Ae. mutica*

In addition to the above crosses between the diploid *Ae. squarrosa* and *Ae. mutica*, an artificially synthesized autotetraploid of *Ae. squarrosa* (KU 29) was crossed with *Ae. mutica* (Table 27). A total of 35 emasculated florets of a tetraploid line of *Ae. squarrosa* were pollinated with pollen grains of *Ae. mutica*. Three seeds were successfully obtained from such a cross and two of them germinated. The mean percentage seed set and the mean germination rate were 9% and 67%, respectively. This was quite contrasted with the cross combination of the diploid lines of *Ae. squarrosa* x *Ae. mutica* mentioned above. When the diploid lines of *Ae. squarrosa* were used as the female parents in the cross, the obtained hybrid seeds did not germinate at all. However, triploid hybrid seeds obtained from the cross using the tetraploid line of *Ae. squarrosa* as the female parent could germinate with a high germination rate.

The PMCs of one of these two triploid hybrid plants (Culture No. 82242-P1) were cytogenetically observed (Table 30 and Figure 32). That triploid F_1 hybrid plant carried no B-chromosome and it had two genomes of *Ae. squarrosa* and one of *Ae. mutica*. Up to four trivalents were observed in 31 (62%) cells among a total of 50 PMCs observed in that plant. A trivalent was found in 15 (30%) cells, one of which formed a quinquevalent in addition to a trivalent, two trivalents were found in 10 (20%) cells, three trivalents were found in five (10%) cells, and four trivalents were found in one cell. Most of the observed trivalents

Table 30. Mean configuration and frequency of chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between the artificially synthesized autotetraploid of *Aegilops squarrosa* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	Chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.[3] Total	TRIV. V	TRIV. Y	TRIV. FP	QUAD.	OTHERS	No.of[4] arms paired	No.of chiasmata per cell
Artificially synthesized autotetraploid of *Aegilops squarrosa* x *Ae. mutica*														
29 x 81-5653-5 82242-P1	0	50	6.32 (3-11)	5.54 (2-8)	3.28 (1-7)	2.26 (0-6)	1.08 (0-4)	0.92 (0-4)	0.08 (0-1)	0.08 (0-1)	0.04 (0-1)	0.04_0 (0-1)	10.32 (6-14)	10.50 (7-14)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) V, Y and FP represent V-shaped, Y-shaped and frying pan shaped trivalents, respectively.
4) Figures represent the half numbers of paired arms.

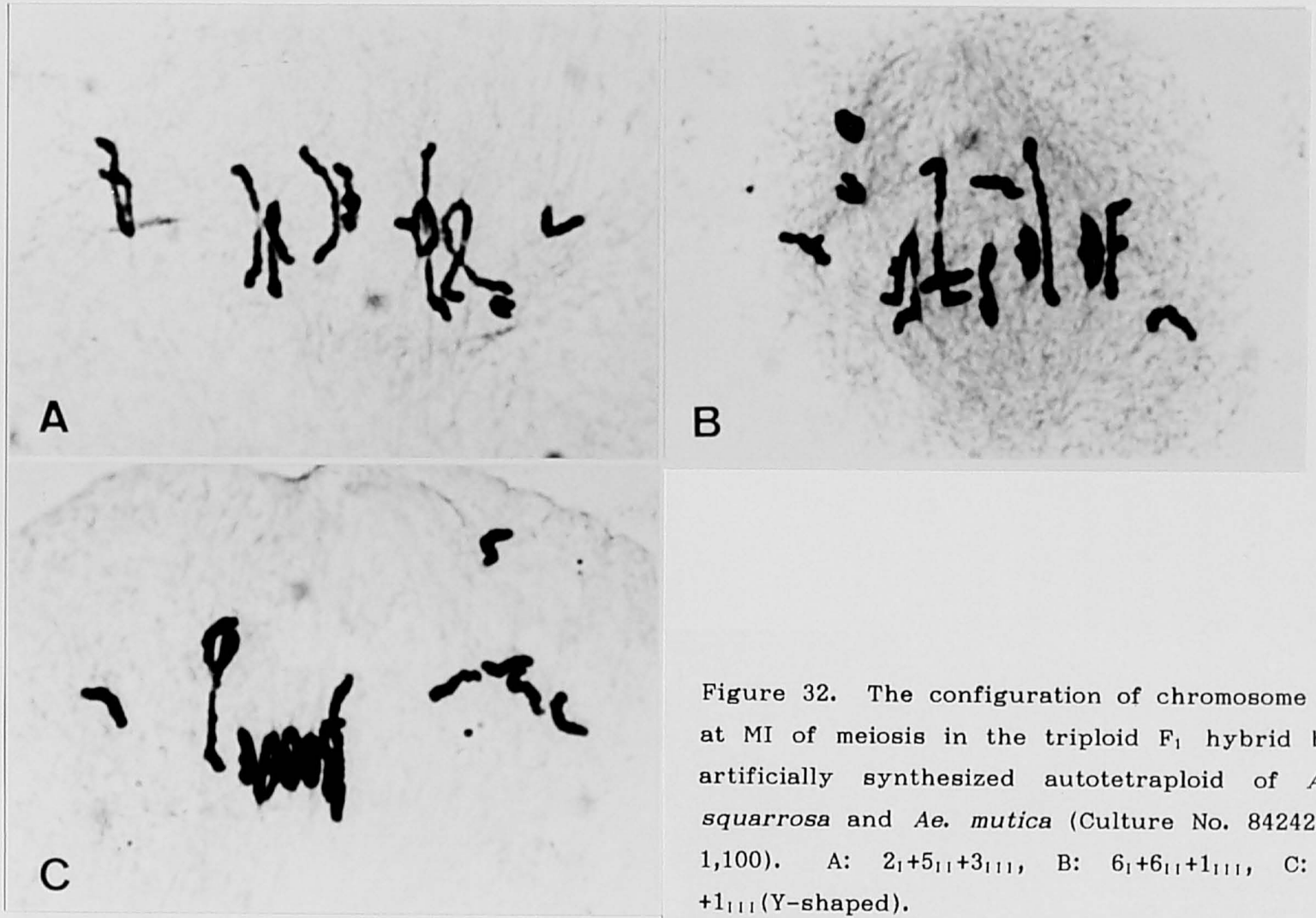


Figure 32. The configuration of chromosome pairing at MI of meiosis in the triploid F_1 hybrid between artificially synthesized autotetraploid of *Aegilops squarrosa* and *Ae. mutica* (Culture No. 84242-P1) (x 1,100). A: $2_I+5_{II}+3_{III}$, B: $6_I+6_{II}+1_{III}$, C: $6_I+6_{II}+1_{III}$(Y-shaped).

were V-shaped. 46 (85%) among a total of observed 54 trivalents were V-shaped and a Y- or frying pan shaped trivalent was found only in four cells each. No trivalent was formed in 19 (38%) cells but a quinquevalent and a chain-shaped quadrivalent were formed in one and in two cells, respectively. Three to 11 univalents were contained in every cell observed and the mean frequency of univalents per cell was 6.32. The mean configuration of chromosome pairing and the mean chiasma frequency in that 0B triploid hybrid were 6.32_{I} + $(3.28rod + 2.26ring)_{II}$ + 1.08_{III} + $0.04chain_{IV}$ + 0.04_{V} and 10.50 per cell, respectively.

(7) *Aegilops caudata* x *Ae. mutica*

Result of crosses

Two accessions of *Aegilops caudata* and six plants from five accessions of *Ae. mutica* were used in the present crosses (Table 31). Their percentage seed set was low and only 10 seeds were obtained from a total of 170 pollinated florets of *Ae. caudata*. Their mean percentage seed set was only 6%. However, the germination rate was not low. Five seedlings were obtained from the 10 seeds and the mean germination rate was 50%.

Morphology of *Aegilops caudata* and the F_1 hybrids between *Ae. caudata* and *Ae. mutica*

The morphology of spikes and spikelets of *Ae. caudata* and the F_1 hybrids between it and *Ae. mutica* is shown in Figures 33 and 34. *Ae. caudata* has linear spikes usually with five to eight spikelets arranged in a row. Its spikes have one to three rudimentary spikelets at the

Table 31. Result of the crosses between *Aegilops caudata* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops caudata x *Ae. mutica*						
6-1 x 78-5645b-3	18	3	17	3	2	67
6-2 x 77-5641-4	28	0	0	-	-	-
6-2 x 77-5643-4	30	2	7	2	1	50
6-2 x 77-5645-4	30	3	10	3	1	33
6-2 x 78-5646-1	24	2	8	2	1	50
6-2 x 77-5649-3	40	0	0	-	-	-
Total	170	10	6	10	5	50

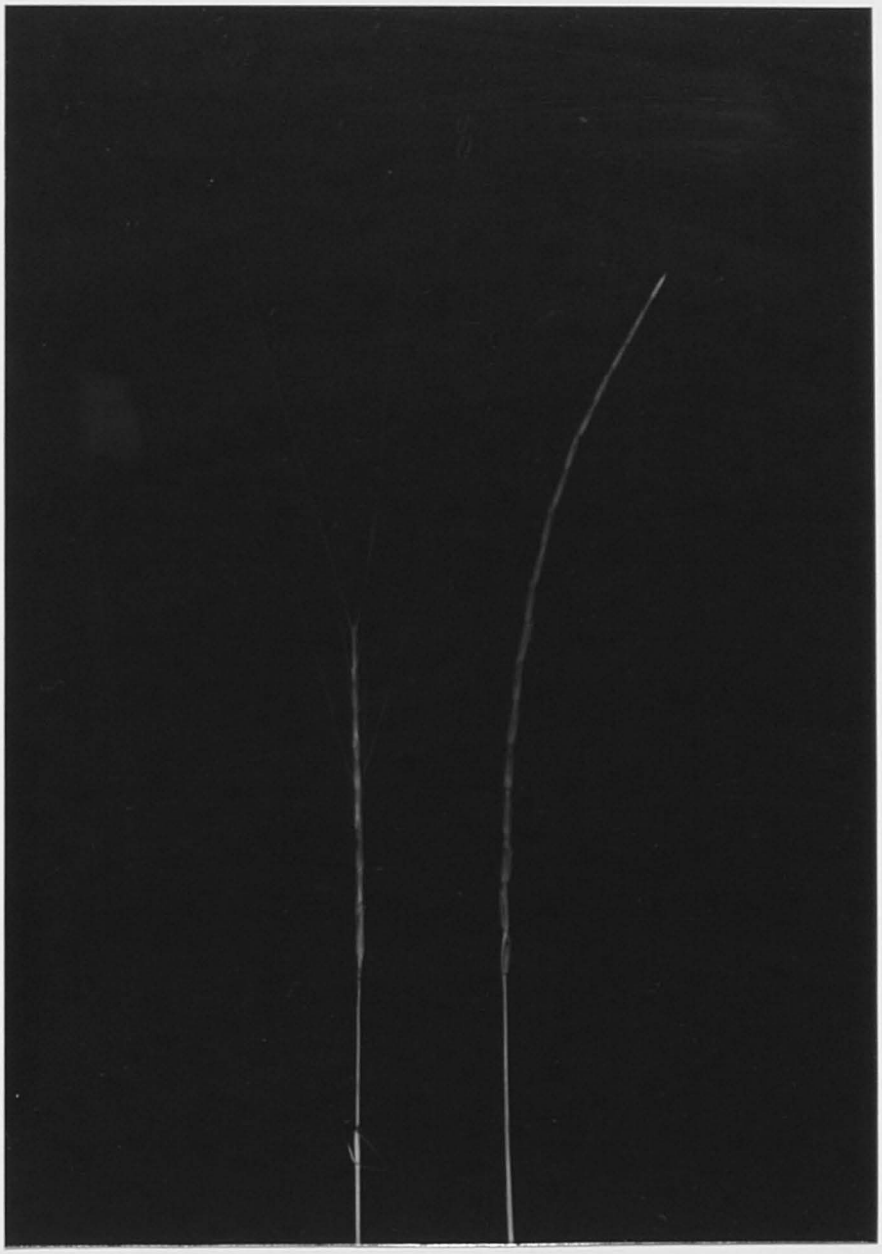


Figure 33. Spike morphology of *Aegilops caudata* and the F_1 hybrids between *Ae. caudata* and *Ae. mutica* (x 0.5). A: *Ae. caudata* (KU 6-1), B: F_1 hybrid involving *Ae. caudata* KU 6-1 (79941-P1).

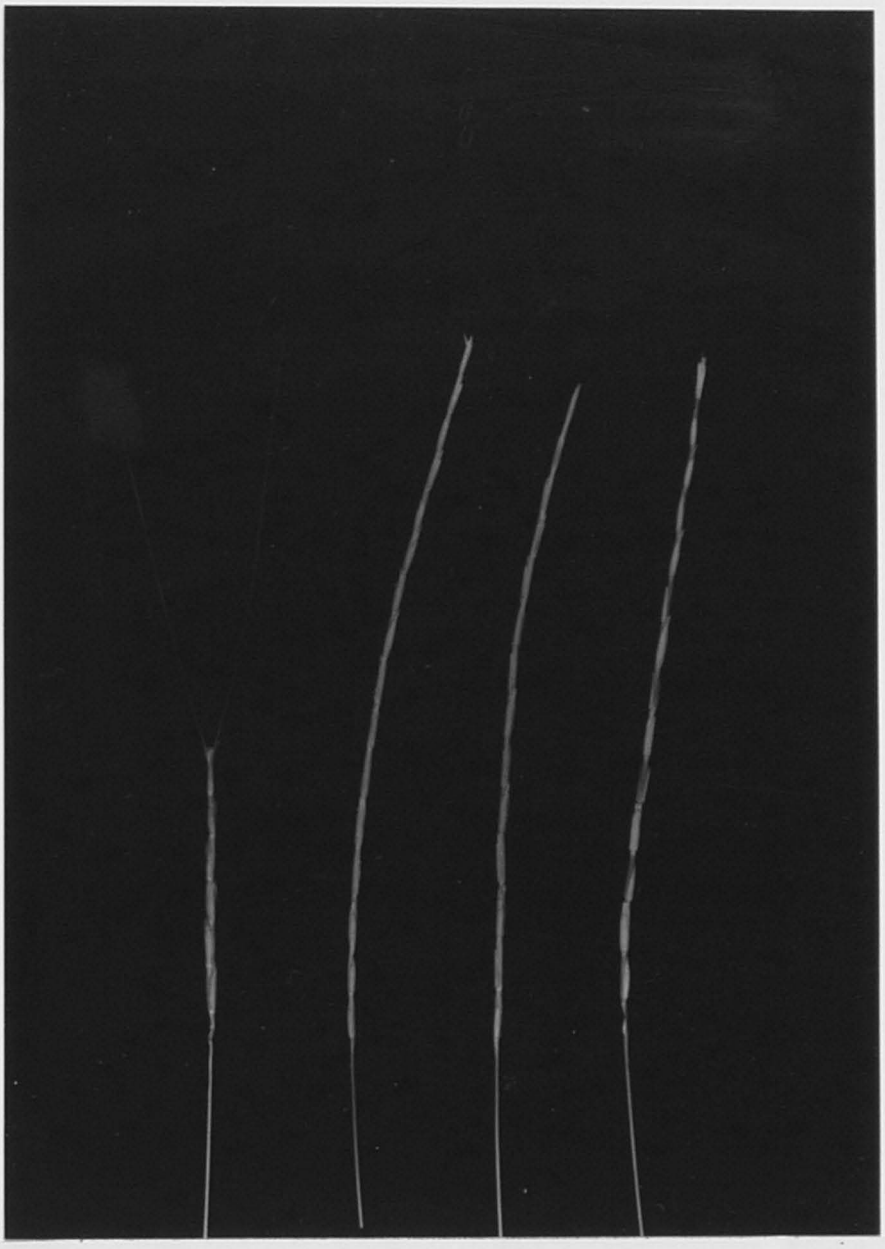


Figure 33. (Continued)

C: *Ae. caudata* (KU 6-2), D-F: F_1 hybrids involving *Ae. caudata* KU 6-2 (D: 78403-P1, E: 78404-P1, F: 79942-P1).

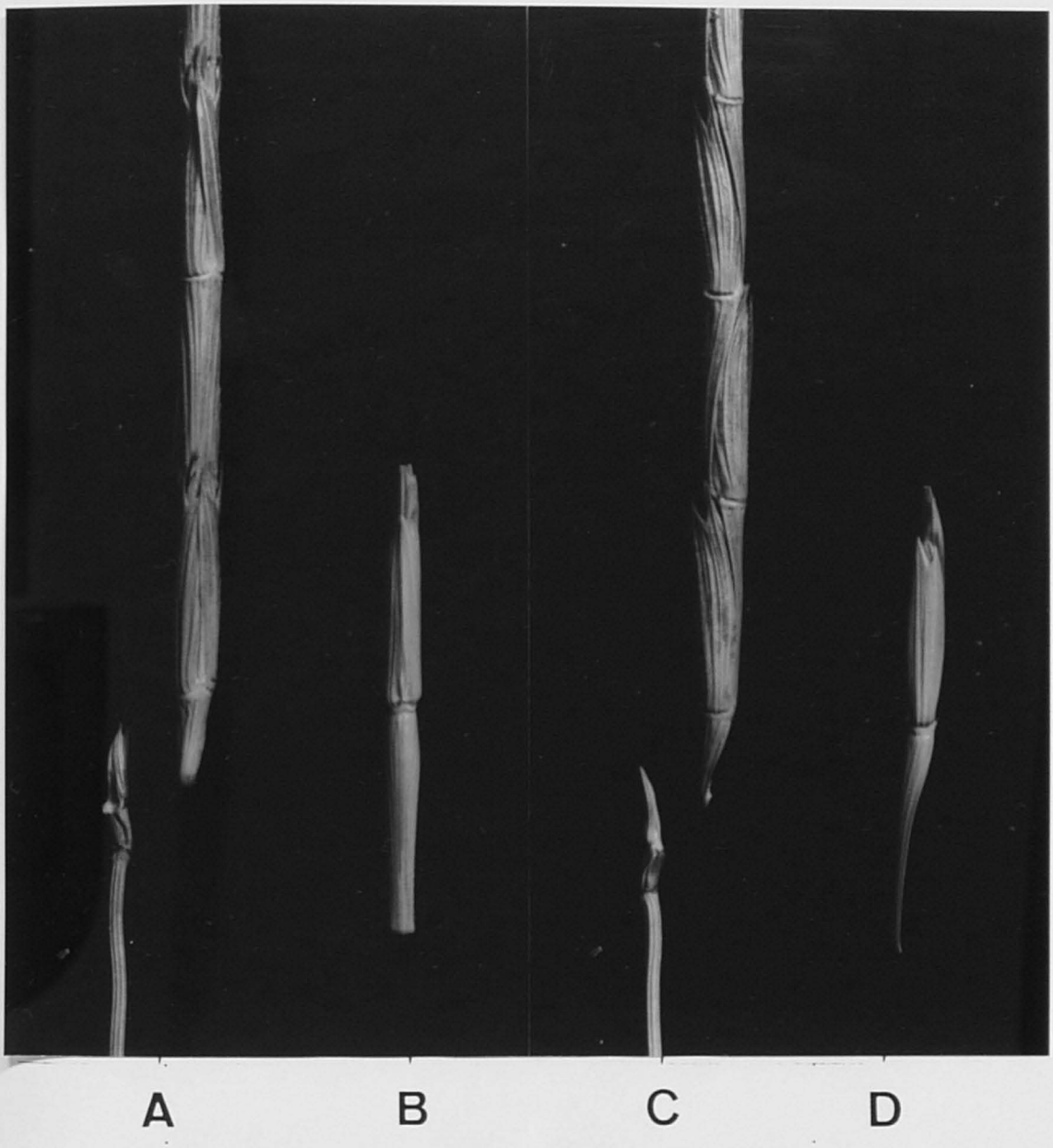


Figure 34. Spikelet morphology of *Aegilops caudata* and the F_1 hybrid between *Ae. caudata* and *Ae. mutica* (x 2.5). A-B: *Ae. caudata* (KU 6-2); C-D: F_1 hybrid between *Ae. caudata* KU 6-2 and *Ae. mutica* (78404-P1).

base. The spikelets are lanceolate and each spikelet consists of about four florets. All spikelets except the rudimentary ones are similar to one another in shape but they become slightly smaller to the top of a spike. They are covered with empty glumes almost entirely. The empty glumes of its lateral spikelets are bidentate in var. *typica* (KU 6-2) (Figure 33C) but one of the teeth forms a narrow awn in var. *polyathera* Eig (KU 6-1) (Figure 33A). Empty glumes of the uppermost spikelets of the both varieties taper into a long awn. Only the rachis nodes adjacent to the rudimentary spikelets at the base of the spike disarticulate. They break at maturity and the whole spike falls together (umbrella type disarticulation). Rachilla is tough.

Spikes of the F_1 hybrids between *Ae. caudata* and *Ae. mutica* were linear and about twice as long as those of *Ae. caudata*. They did not have any rudimentary spikelets and consisted of 14 or 15 spikelets arranged in a row. Each spikelet had five to six florets and was as long as its adjacent rachis internode. All the spikelets along the whole spike length were similar to one another both in shape and in size. Empty glumes covered about four fifths of the entire length of each spikelet. Empty glumes of the lateral spikelets were not awned but bidentate even when var. *polyathera* of *Ae. caudata* was used as female parents and they were similar to those of *Ae. caudata* var. *typica* (Figure 34). The empty glumes of the uppermost spikelets had three teeth but had no awn. Each rachis node broke at maturity and each spikelet fell separately with the rachis internode below it (wedge type disarticulation). Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

The chromosome pairing at MI of meiosis was observed in the four F_1 hybrids obtained from four cross combinations (Table 32 and Figure 35). One of them did not have any B-chromosomes and the other three had two B-chromosomes. The hybrid plant without B-chromosomes showed a complicated configuration of chromosome pairing. One or two trivalents were found in 28 (93%) among a total of 30 PMCs observed (Figure 35A). Two trivalents were found in 11 (37%) cells and a trivalent was formed in 17 (57%) cells. The mean frequency of trivalents was 1.30 per cell. Only up to two ring-shaped bivalents were observed in 19 (63%) cells. The mean configuration and mean frequency of chromosome pairing in that 0B plant were 3.03_{I} + $(2.83rod + 0.70ring)_{II}$ + 1.30_{III} and 7.70 chiasmata per cell.

In contrast with that 0B hybrid plant, three F_1 hybrids with two B-chromosomes showed drastically low frequency of A-chromosome pairing (Figures 38B-D). Their chiasma frequency ranged from 1.20 to 0.70 but they could not be significantly classified into any groups. Fourteen univalents or twelve univalents with a rod-shaped bivalent of A-chromosomes were characteristically observed in most PMCs and most of bivalents observed were rod-shaped. None of the A-chromosomes paired with one another (14 univalents) in 42 (32%) among a total of 130 observed PMCs, and 12 univalents with a rod-shaped bivalent of A-chromosomes were found in 54 cells (42%). A ring-shaped bivalent was found only in two cells in one of the 2B hybrids (Culture No. 78403-P1). A trivalent was found in three cells in two of the 2B hybrids.

Table 32. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops caudata* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
6-1 x 78-5645b-3													
79941-P1	2	30	12.60 (8-14)	0.70 (0-3)	0.70 (0-3)	-	-	-	-	-	-	0.70 (0-3)	0.70 (0-3)
6-2 x 78-5646-1													
79942-P1	0	30	3.03 (1-5)	3.53 (2-5)	2.83 (1-5)	0.70 (0-2)	1.30 (0-2)	-	-	-	-	6.83 (5-9)	7.70 (6-10)
6-2 x 77-5645-4													
78403-P1	2	50	11.68 (8-14)	1.16 (0-3)	1.12 (0-3)	0.04 (0-1)	0.04 (0-1)	-	-	-	-	1.20 (0-4)	1.20 (0-4)
6-2 x 77-5643-4													
78404-P1	2	50	12.02 (8-14)	0.96 (0-3)	0.96 (0-3)	-	0.02 (0-1)	-	-	-	-	1.00 (0-3)	not observed

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

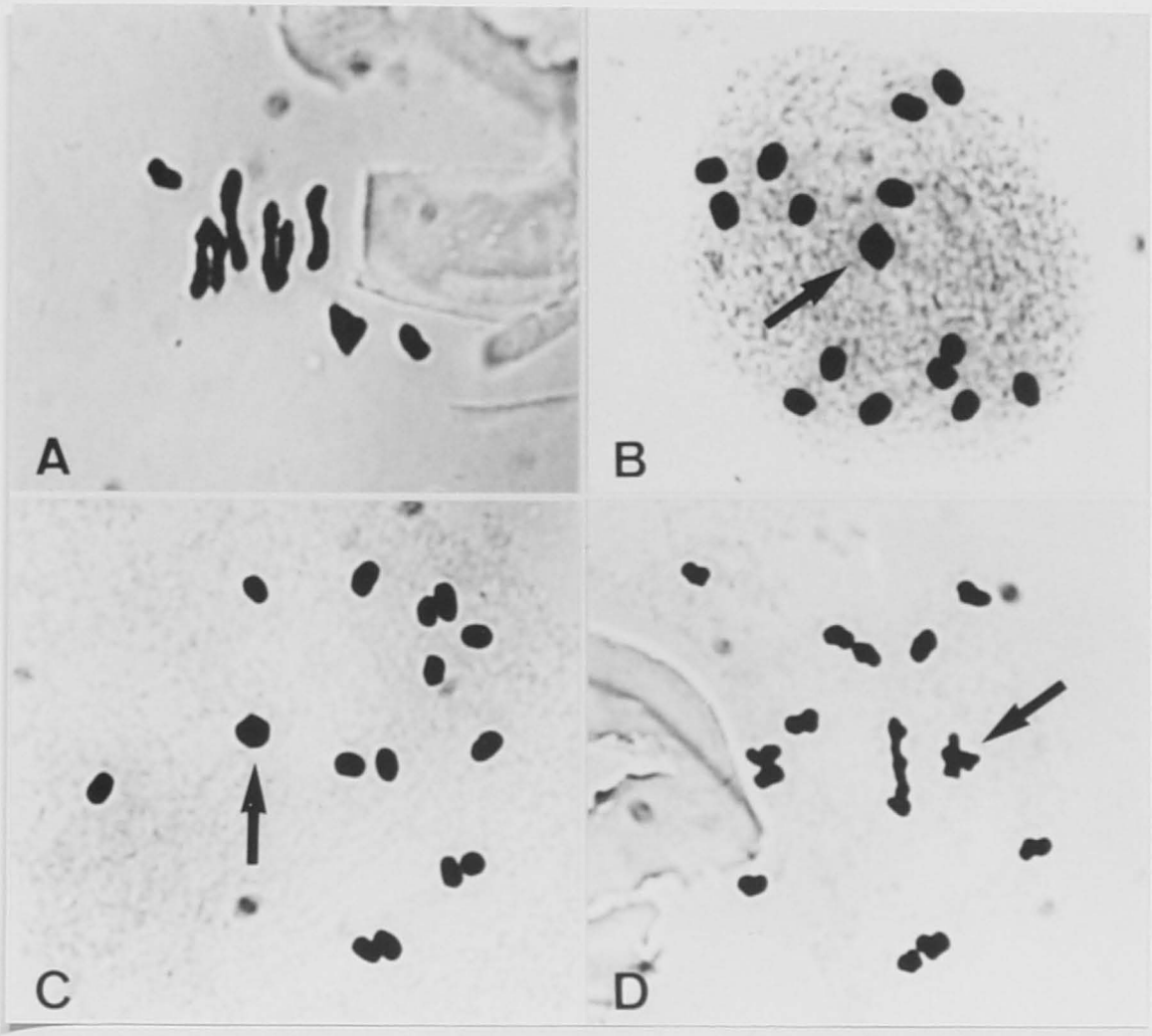


Figure 35. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with or without B-chromosomes (Bs) between *Aegilops caudata* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A: 79942-P1 without Bs, $2_I+3_{II}+2_{III}$; B: 79941-P1 with 2Bs, 14_I of As + $1ring_{II}$ of Bs; C: 78403-P1 with 2Bs, 14_I of As + $1ring_{II}$ of Bs; D: 78404-P1 with 2Bs, 12_I+1_{II} of As + 1_{II} of Bs.

Table 33. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops caudata* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
6-1 x 78-5645b-3 79941-P1	2	0	-
6-2 x 78-5646-1 79942-P1	0	0	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent, -: indehiscent.

Fertility of the F_1 hybrids

All the F_1 plants were completely sterile and any of their anthers did not dehisce normally. Pollen fertility was estimated in two of them but normal pollen grains were not found at all (Table 33).

(8) *Aegilops comosa* x *Ae. mutica*

Result of crosses

Two accessions of *Aegilops comosa* were crossed with five plants from four accessions of *Ae. mutica* (Table 34). The accession KU 17-1 of *Ae.* comosa belongs to subspecies *eu-comosa* Eig and the other, KU 17-2, belongs to subspecies *heldreichii* (Holzm.) Eig. Fifty seeds were obtained from a total of 90 florets pollinated with pollen grains of *Ae. mutica*. The mean percentage seed set was 56%. The highest seed set was found in the cross combination of 17-2 x 77-5642-4 and it was 70% though none of the seeds obtained from that cross combination germinated. No difference was found in the seed set between two subspecies of *Ae. comosa* used as female parents. Eighteen seedlings were obtained from those 50 seeds sown in the sterilized soil. The mean germination rate was 36% and the highest rate was found in the cross combination of 17-1 x 78-5646-1. In that cross, all the sown seeds germinated.

Morphology of *Aegilops comosa* and the F_1 hybrids between *Ae. comosa* and *Ae. mutica*

Two subspecies of *Ae. comosa* were used in the present crosses. The morphology of spikes and spikelets of those subspecies and the F_1 hybrids between them and *Ae. mutica* is shown in Figures 36 and 37. Ssp.

Table 34. Result of the crosses between *Aegilops comosa* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops comosa x *Ae. mutica*						
17-1 x 78-5642c-4	14	8	57	8	7	88
17-1 x 78-5646-1	6	4	67	4	4	100
17-2 x 77-5641-4	20	11	55	11	2	18
17-2 x 77-5642-4	20	14	70	14	0	0
17-2 x 78-5642c-4	22	13	59	13	5	38
17-2 x 77-5652-4	8	0	0	-	-	-
Total	90	50	56	50	18	36

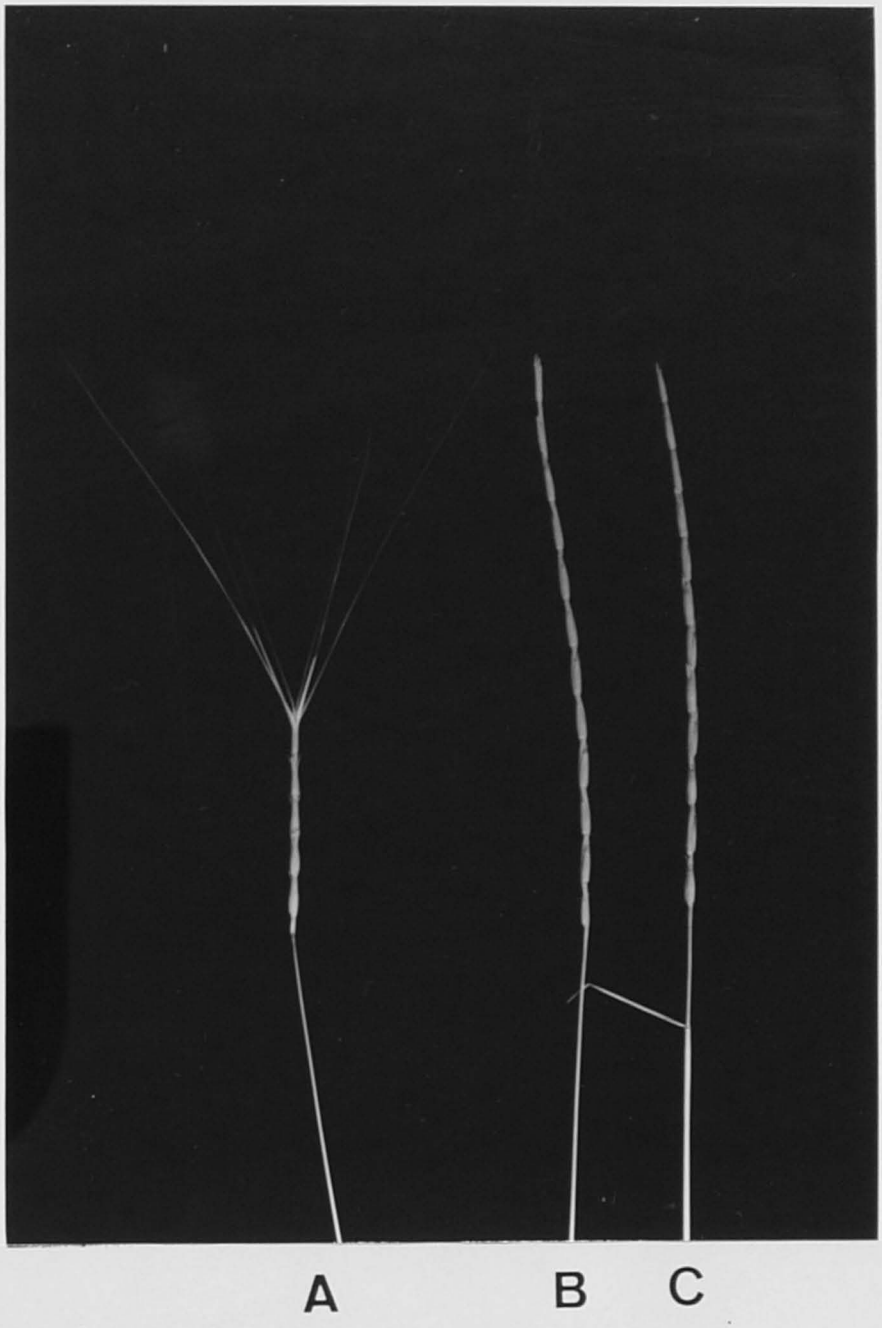
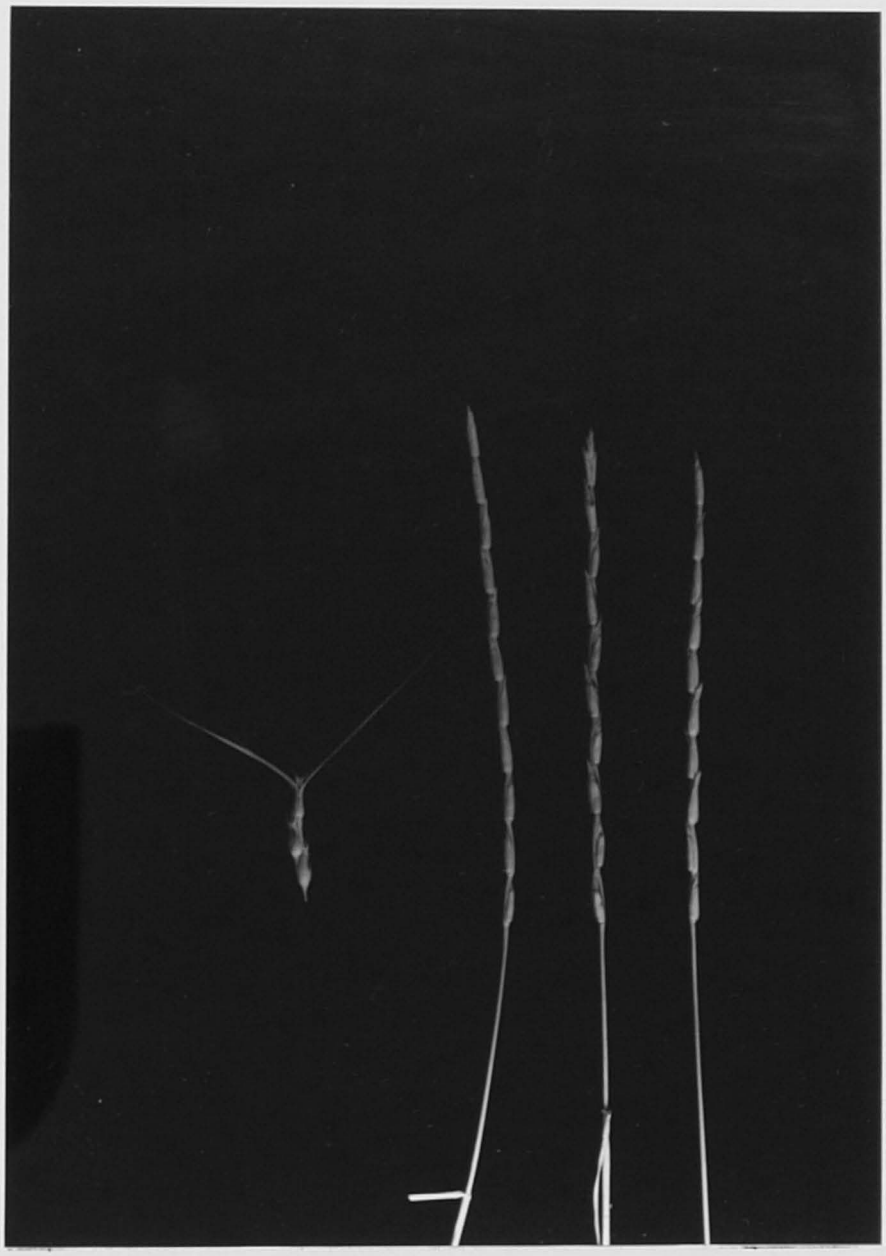


Figure 36. Spike morphology of *Aegilops comosa* and the F_1 hybrids between *Ae. comosa* and *Ae. mutica* (x 0.5). A: *Ae. comosa* ssp. *eu-comosa* (KU 17-1), B-C: F_1 hybrids involving *Ae. comosa* ssp. *eu-comosa* KU 17-1 (B: 79947-P1, C: 79948-P4).



D E F G

Figure 36. (Continued)

D: *Ae. comosa* ssp. *heldreichii* (KU17-2), E-G: F_1 hybrids involving *Ae. comosa* ssp. *heldreichii* KU 17-2 (E: 78409-P2, F: 78410-F3, G: 79949-P4).

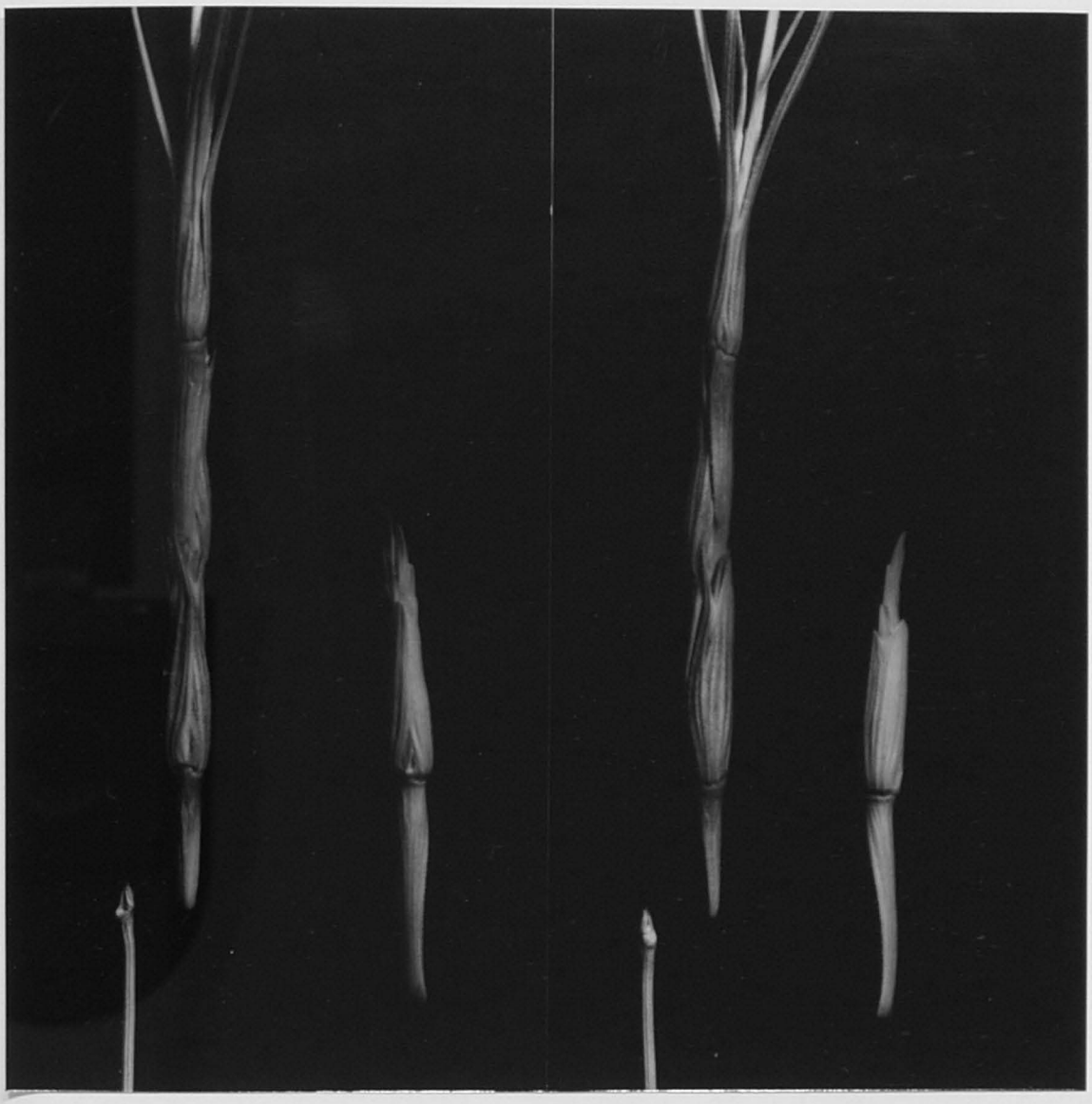


Figure 37. Spikelet morphology of *Aegilops comosa* and the F_1 hybrids between *Ae. comosa* and *Ae. mutica* (x 2.5). A and C: *Ae. comosa* ssp. *eu-comosa* (KU 17-1), B and D: F_1 hybrid involving *Ae. comosa* ssp. *eu-comosa* KU 17-1 (79947-P2).

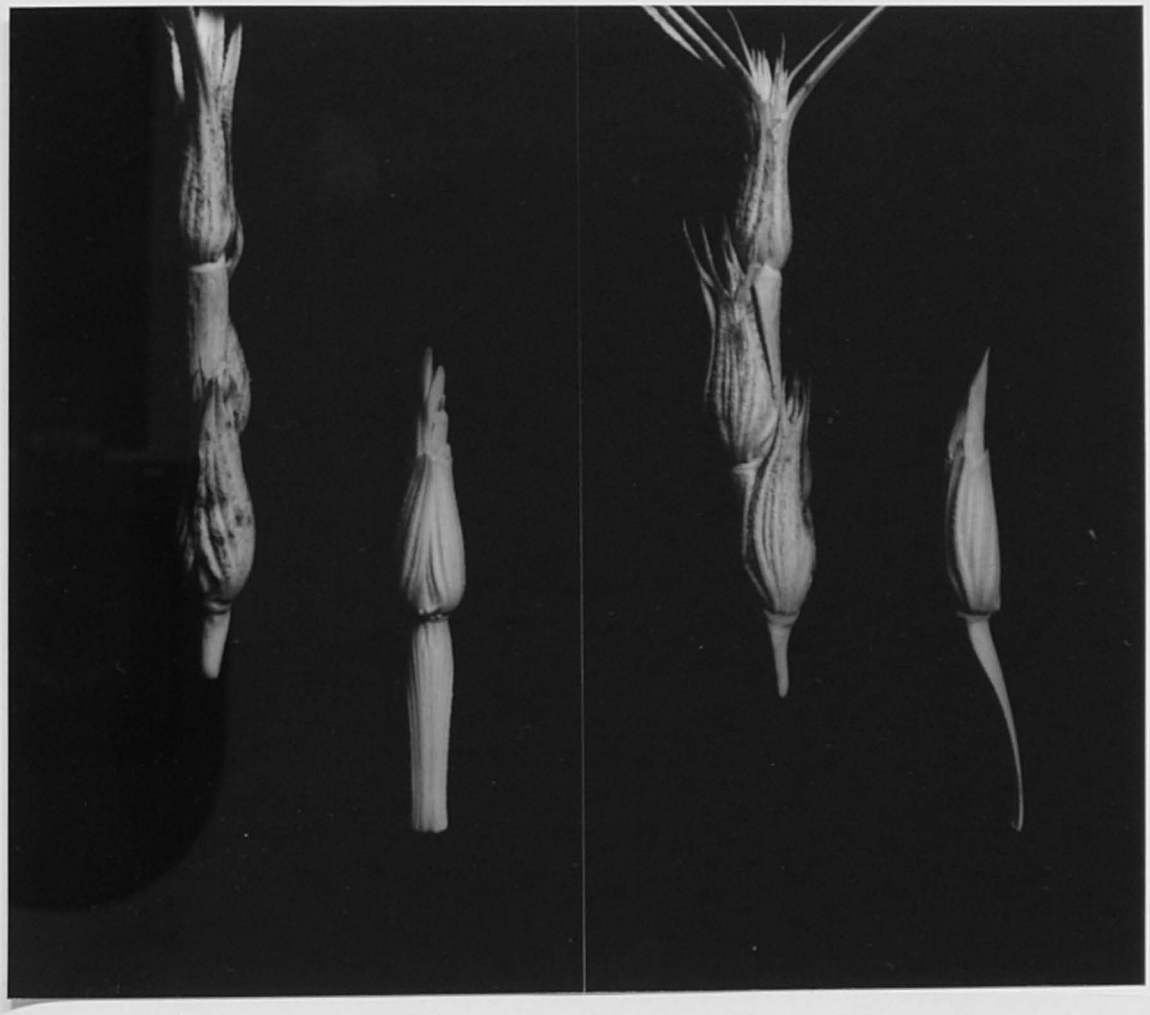


Figure 37. (Continued)

E and G: *Ae. comosa* ssp. *heldreichii* (KU 17-2); F and H: F_1 hybrid involving *Ae. comosa* ssp. *heldreichii* KU 17-2 (79949-P5).

eu-comosa Eig (Figures 36A, 37A and C) has lanceolate spikes consisting of four or five lanceolate fertile spikelets arranged in a row. All the lateral spikelets except the lowest one are almost similar both in shape and in size along the whole spike length. They consist of three or four florets and are almost as long as the adjacent rachis internodes. Ssp. *heldreichii* (Holzm.) Eig has narrow conical spikes usually with three ovate fertile spikelets consisting of three or four florets (Figures 36D, 37E and G). The uppermost spikelet is somewhat smaller than the lateral ones. The lateral spikelets except the rudimentary one at the base of a spike are more or less longer than the adjacent rachis internodes, especially the lowest fertile spikelet being clearly longer than the adjacent rachis internode. Both subspecies, ssp. *eu-comosa* and ssp. *heldreichii*, have a rudimentary spikelet at the base of their spikes. Their lateral spikelets are entirely covered with empty glumes with two long teeth divided by a sharp deep notch. The empty glumes of their uppermost spikelets taper into one or three long awns. Subspecies *eu-comosa* usually has three awns in both the upper and lower empty glumes while ssp. *heldreichii* usually has a one-awned lower glume and a three-awned upper glume in the uppermost spikelet. In both subspecies, lemmas of lateral spikelets do not have any awns and those of the uppermost spikelet are tridentate, the middle one being longer than the lateral ones and sometimes becoming an awn, and the accession KU 17-1 used in the present crosses had a long awn on the lemmas of the uppermost spikelet. Rachis node only at the base of their spikes is fragile. Entire spike without the lowest rudimentary spikelet falls together at maturity (umbrella type disarticulation). Rachilla is

tough.

The F_1 hybrids between the two subspecies of *Ae. comosa* and *Ae. mutica* had long and linear spikes usually without awns or rudimentary spikelets. Spikelets were arranged in a row on a spike and all of them were similar both in shape and in size. They were almost as long as the adjacent rachis internodes. Lemmas of the uppermost spikelets of some hybrid individuals from the cross of ssp. *eu-comosa* x *Ae. mutica* had a very short awn but their empty glumes were not awned. The number of spikelets on their spikes was intermediate between that of their parents and, therefore, the spike length of the F_1 hybrids was intermediate between their parents. The F_1 hybrids had 12 or 13 spikelets on their spikes while the spikes of *Ae. mutica* had more than 20 spikelets. The shape of the lateral spikelets of the F_1 hybrids derived from the two subspecies of *Ae. comosa* slightly differed from each other. The F_1 hybrids involving ssp. eu-comosa had lanceolate spikelets but those involving ssp. *heldreichii* had ovate-oblong spikelets (Figure 37). Each spikelet of the hybrids from the both combinations consisted of four to six florets arranged laxly. Only two thirds of the total length of a spikelet was covered with empty glumes having two dull teeth divided by a shallow notch. Rachis is fragile. Each rachis node broke at maturity and each spikelet fell separately with the rachis internode below it (wedge type disarticulation). Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

Nineteen plants obtained from five cross combinations were cytogenetically observed in their PMCs at MI of meiosis (Table 35 and

Figure 38). Nine of them were without B-chromosomes, three had a B-chromosome and the other seven had two Bs. The F_1 hybrid plants without B-chromosomes showed a very high frequency of chromosome pairing. Their mean chiasma frequency ranged from 8.77 to 11.50 per cell, and especially it was high in the 0B hybrids from the cross combination of 17-1 x 78-5646-1 (Culture No. 79947). They showed mean chiasma frequency as high as 11.50 to 10.00 per cell. The frequency of chromosome pairing of the F_1 hybrids from this cross combination was slightly but significantly higher than that of the 0B hybrids from the other cross combinations. And their configuration of chromosome pairing was almost regular. Seven bivalents were formed in 91 (76%) among a total of 120 observed PMCs of these four hybrid plants. Even seven ring-shaped bivalents were observed in four (3%) cells. But no multivalent was observed in this cross combination.

However, the configuration of chromosome pairing at MI in the 0B hybrids significantly varied depending on the accessions of *Ae. comosa* used as female parents. When the accession KU 17-1 was used in crosses, the F_1 hybrids showed almost regular configuration of chromosome pairing as mentioned above. They formed seven bivalents including many ring-shaped ones but formed no or only few multivalents in their PMCs. 0B hybrids from one of the combinations (Culture No. 79947) showed most regular pairing configuration with few univalents and no multivalent (Figure 38A) while those from another combination (Culture No. 79948) showed a slightly complicated pairing configuration with some higher frequency of univalents and a few multivalents. On the contrary, when the accession KU 17-2 of *Ae. comosa* was used as female parents in the

Table 35. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops comosa* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
17-1 x 78-5646-1													
79947-P2	0	30	0.53 (0-2)	6.73 (6-7)	2.23 (0-5)	4.50 (2-7)	-	-	-	-	-	11.23 (8-14)	11.50 (9-14)
-P4	0	30	0.53 (0-2)	6.73 (6-7)	2.73 (1-4)	4.00 (2-5)	-	-	-	-	-	10.73 (8-12)	10.97 (8-13)
-P1	0	30	0.33 (0-2)	6.83 (6-7)	2.87 (0-5)	3.97 (2-7)	-	-	-	-	-	10.80 (8-14)	10.90 (8-14)
-P3	0	30	0.87 (0-6)	6.57 (4-7)	3.33 (1-7)	3.23 (0-6)	-	-	-	-	-	9.80 (7-13)	10.00 (7-13)
17-1 x 78-5642c-4													
79948-P5	0	30	1.60 (0-8)	6.13 (3-7)	3.27 (1-6)	2.87 (0-5)	-	0.03 (0-1)	0.03 (0-1)	-	-	9.10 (4-12)	9.23 (4-12)
-P7	0	30	1.93 (0-6)	6.03 (4-7)	3.37 (0-5)	2.67 (0-6)	-	-	-	-	-	8.70 (5-12)	8.77 (5-12)
-P1	1	30	4.47 (0-10)	4.60 (2-7)	3.27 (1-7)	1.33 (0-4)	0.07 (0-1)	0.03 (0-1)	0.03 (0-1)	-	-	6.20 (2-11)	6.23 (2-11)
-P2	2	30	13.00 (10-14)	0.50 (0-2)	0.50 (0-2)	-	-	-	-	-	-	0.50 (0-2)	0.50 (0-2)
17-2 x 77-5641-4													
78409-P1	1	50	1.40 (0-4)	5.10 (4-7)	2.96 (1-5)	2.14 (0-4)	0.72 (0-1)	0.06 (0-1)	0.06 (0-1)	-	-	8.86 (7-11)	9.48 (7-12)
-P2	1	50	5.86 (0-12)	3.74 (1-7)	3.24 (1-6)	0.50 (0-2)	0.22 (0-1)	-	-	-	-	4.68 (1-8)	4.68 (1-8)

Table 35. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
17-2 x 78-5642c-4													
79949-P1	0	30	1.07 (0-4)	4.93 (3-7)	2.33 (0-5)	2.60 (0-4)	0.40 (0-1)	0.47 (0-1)	0.47 (0-1)	-	-	9.73 (8-12)	9.83 (8-13)
-P5	0	30	1.17 (0-4)	4.93 (4-7)	2.33 (0-5)	2.60 (1-4)	0.37 (0-1)	0.47 (0-1)	0.47 (0-1)	-	-	9.67 (6-12)	9.83 (6-12)
-P3	0	30	1.23 (0-5)	4.80 (3-7)	3.03 (0-7)	1.77 (0-3)	0.37 (0-1)	0.47 (0-1)	0.47 (0-1)	-	0.03VI (0-1)	8.86 (6-11)	8.93 (6-11)
-P2	2	30	13.47 (10-14)	0.27 (0-2)	0.27 (0-2)	-	-	-	-	-	-	0.27 (0-2)	0.27 (0-2)
17-2 x 77-5645-4													
78410-P2	2	50	8.10 (2-14)	2.74 (0-6)	2.34 (0-6)	0.40 (0-3)	0.14 (0-1)	-	-	-	-	3.42 (0-8)	3.56 (0-8)
-F3	2	50	8.90 (6-14)	2.40 (0-4)	2.20 (0-4)	0.20 (0-1)	0.10 (0-1)	-	-	-	-	2.80 (0-5)	2.90 (0-7)
-F2	2	50	11.52 (6-14)	1.24 (0-4)	1.14 (0-4)	0.10 (0-1)	-	-	-	-	-	1.34 (0-5)	1.34 (0-5)
-P3	2	50	12.88 (8-14)	0.56 (0-3)	0.56 (0-3)	-	-	-	-	-	-	0.56 (0-3)	0.56 (0-3)
-P1	2	50	13.68 (12-14)	0.16 (0-1)	0.16 (0-1)	-	-	-	-	-	-	0.16 (0-1)	0.16 (0-1)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

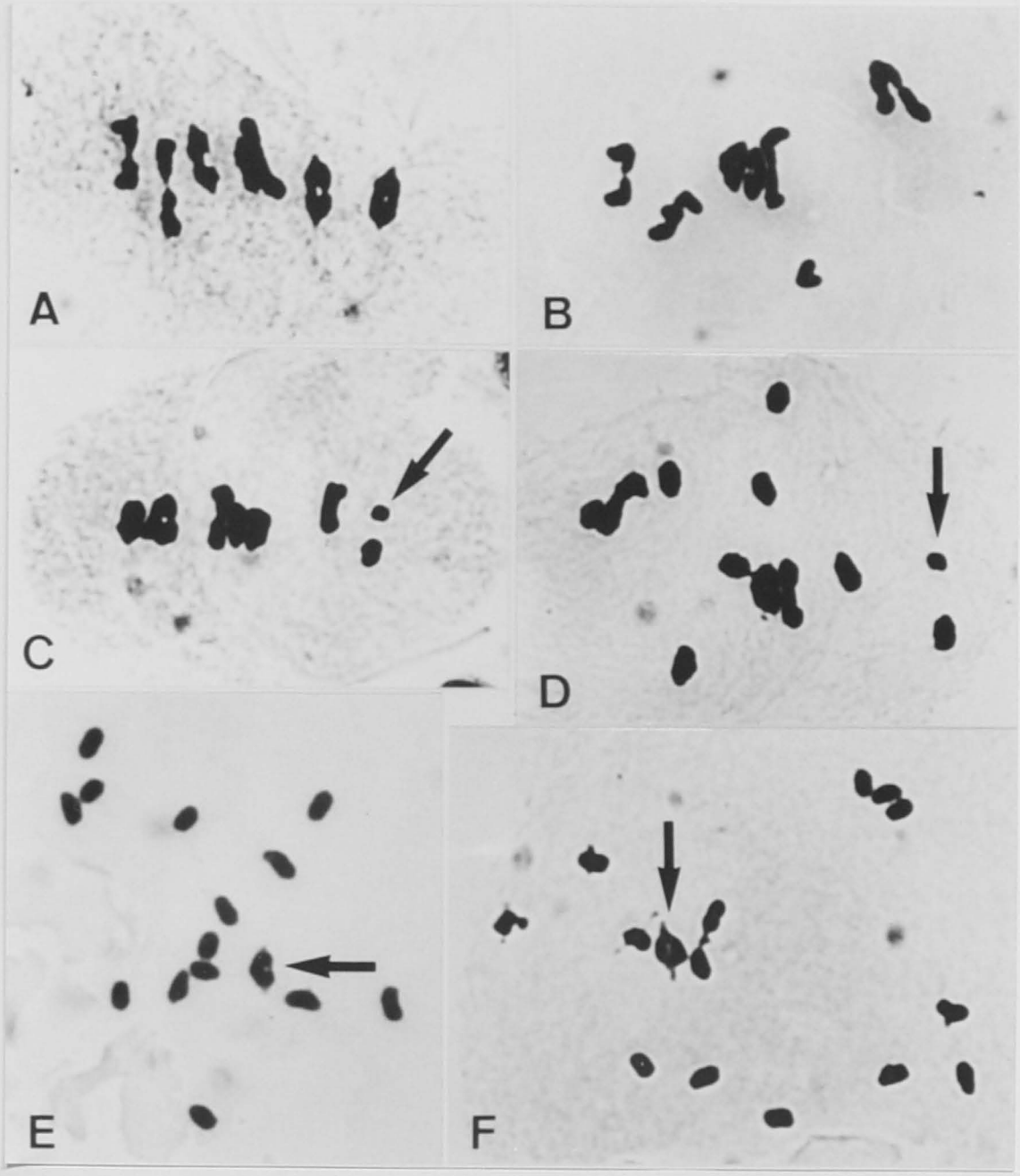


Figure 38. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with or without B-chromosomes (Bs) between *Aegilops comosa* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A: 79947-P1 without Bs, 7_{II}; B: 79949-P5 without Bs, $1_I+5_{II}+1_{III}$; C: 78409-P1 with a minute telocentric B, $1_I+5_{II}+1_{III}$ of As + 1_I of B; D: 78409-P2 with a minute telocentric B, 8_I+3_{II} of As + 1_I of B; E: 79948-P2 with 2Bs, 14_I of As + $1ring_{II}$ of Bs; F: 79949-P2, 12_I+1_{II} of As + $1ring_{II}$ of Bs.

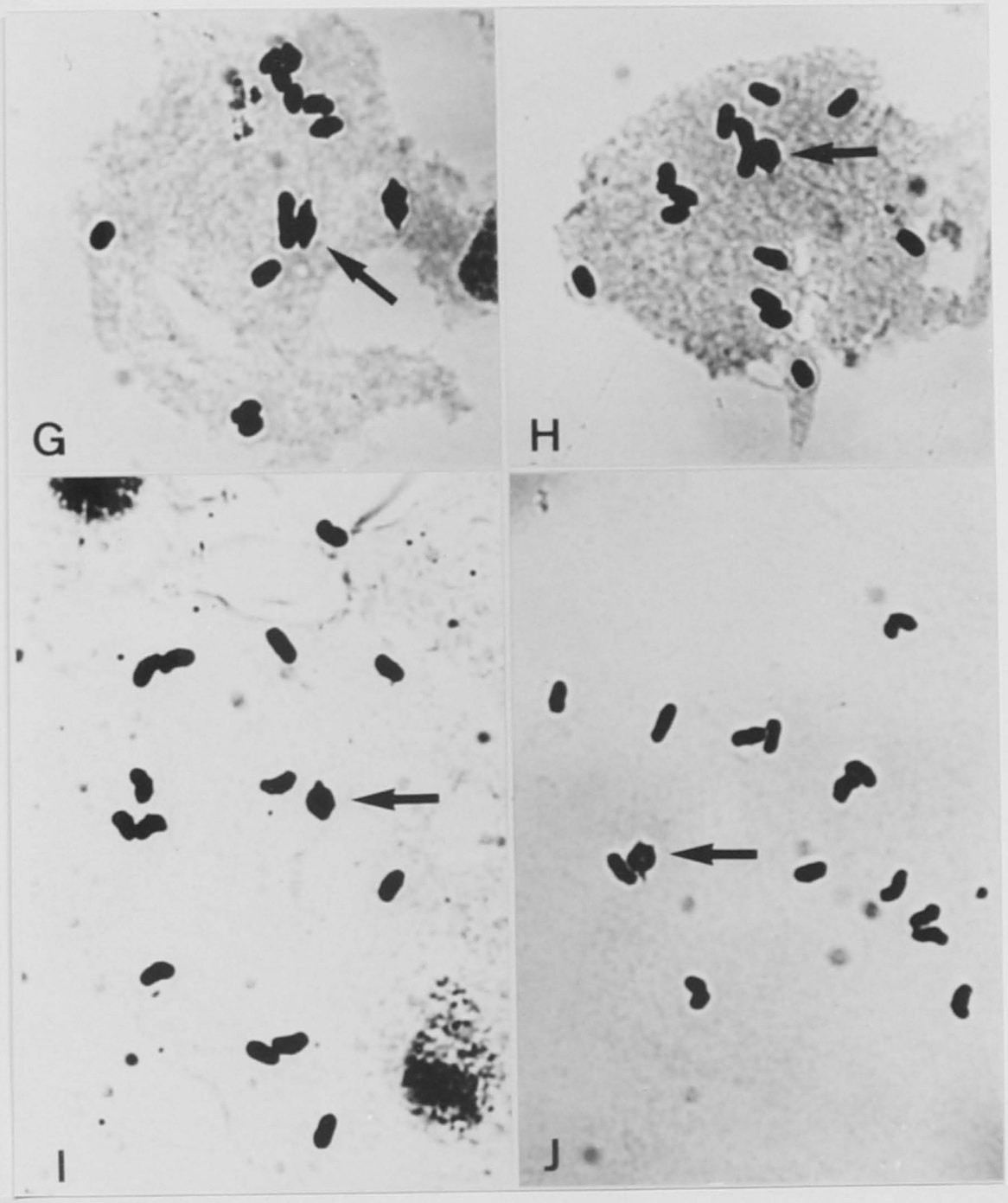


Figure 38. (Continued)
G: 78410-F3 with 2Bs, $10_{I}+2_{II}$ of As + $1ring_{II}$ of Bs; H: 78410-F2 with 2Bs, $12_{I}+1_{II}$ of As + $1ring_{II}$ of Bs; I: 78410-P3 with 2Bs, 14_{I} of As + $1ring_{II}$ of Bs; J: 78410-P1 with 2Bs, 14_{I} of As + $1ring_{II}$ of Bs.

crosses, the obtained F_1 hybrids showed more complicated configuration of chromosome pairing at MI of meiosis. In the three 0B hybrid plants obtained from the cross combination of 17-2 x 78-5642c-4 (Culture Nos. 79949-P1, -P3 and -P5), 77 (86%) of a total of 90 observed PMCs formed a multivalent (Figure 38B): 42 (47%) formed a quadrivalent, 34 (38%) formed a trivalent and the other (1%) formed a sexivalent. Only in five (6%) cells, seven bivalents were found. The same parental plant of *Ae. mutica* (Culture No. 78-5642c-4) was crossed in common as the male parent to the both accessions, 17-1 and 17-2, of *Ae. comosa*. And pairing configuration in the obtained 0B hybrids (Culture Nos. 79948 and 79949) remarkably differed between two cross combinations. In spite of such difference in pairing configuration depending on the accessions of *Ae. comosa*, their pairing frequency did not significantly differ from each other. The two 0B hybrid plants of No. 79948 and three of No. 79949 showed the similar pairing frequency as shown in Table 35.

On the contrary to those 0B hybrids showing a very high frequency of chromosome pairing, the hybrid plants with two B-chromosomes showed drastically low frequency of chromosome pairing (Figures 38E-J). The mean chiasma frequency of seven 2B hybrids obtained from three cross combinations ranged from 0.16 to 3.56 per cell. Fourteen univalents of A-chromosomes with a tightly associated small bivalent of B-chromosomes were characteristically observed in the 2B hybrid plants from the crosses of 17-1 x 78-5642c-4 and 17-2 x 78-5642c-4 as well as the two plants from the cross of 17-2 x 77-5645-4 (Culture Nos. 79948-P2, 79949-P2, 78410-P1 and -P3). In those four 2B hybrids, 114 (71%) among a total of 160 observed PMCs contained 14 univalents of A-chromosomes with

a small bivalent of B-chromosomes (Figures 38E, I and J). Up to three rod-shaped bivalents of A-chromosomes were observed only in 46 (29%) cells, 35 of which formed only one bivalent in addition to a bivalent of B-chromosomes (Figure 38F). Their mean chiasma frequency and the number of paired arms of A-chromosomes per cell varied from 0.16 to 0.56, but it did not significantly differ from one another. Other two 2B plants from the cross of 17-2 x 77-5645-4 (Culture Nos. 78410-P2 and -F3) showed slightly higher frequency of chromosome pairing than the above four 2B hybrids. Their mean chiasma frequency was 2.90 and 3.56 per cell, and a few ring-shaped bivalents and a trivalent of A-chromosomes were observed in addition to rod-shaped bivalents (Figure 38G). However, the frequency of univalents was so high and varied from 8.10 to 8.90 per cell. More than seven univalents of A-chromosomes were observed in 64 (64%) among a total of 100 observed PMCs in those two plants, and 14 univalents of A-chromosomes were observed in four cells. However, no cell formed seven bivalents of A-chromosomes. Another 2B hybrid plant (Culture No. 78410-F2) showed intermediate frequency of A-chromosome pairing between the above-mentioned two groups of 2B hybrids (Figure 38H). Its mean chiasma frequency was 1.34 per cell, and one ring-shaped bivalent of A-chromosomes was found in five cells. Thus, seven 2B hybrids obtained in the present work classified into three groups according to their frequency of chromosome pairing. The difference among them was statistically significant ($\chi^2<159.2$) but much smaller compared with the difference between 0B and 2B hybrids ($\chi^2>546.5$).

In addition to those 0B and 2B hybrids, three hybrid plants with a

B-chromosome were obtained from two cross combinations. One of them was obtained from the cross of 17-1 x 78-5642c-4 (Culture No. 79948-P1) and the other two was from the cross of 17-2 x 77-5641-4 (Culture Nos. 78409-P1 and -P2) (Figures 38C and D). B-chromosomes found in PMCs of those 1B hybrid plants were all minute and telocentric. And they were observed as a small univalent at MI of meiosis. The 1B hybrid plant from the cross of 17-1 x 78-5642c-4 showed the intermediate frequency of A-chromosome pairing between the 0B and 2B hybrid plants obtained from the same cross combination. Its mean chiasma frequency and mean configuration of A-chromosome pairing were 6.23 and 4.47_{I} + (3.27rod + 1.33ring)$_{II}$ + 0.07_{III} + 0.03chain$_{IV}$ per cell, respectively. The other two 1B hybrid plants were obtained from the one cross combination but their frequency of A-chromosome pairing significantly differed from each other. One of them (78409-P2) showed intermediate frequency of chromosome pairing between the above-mentioned 0B and 2B hybrids and its mean chiasma frequency was 4.68 per cell (Figure 38D). However, the other plant (78409-P1) formed many bivalents including ring-shaped ones and trivalents but it showed low frequency of univalents (Figure 38C). Its mean chiasma frequency was 9.48 per cell and its mean configuration of A-chromosome pairing was 1.40_{I} + (2.96rod + 2.14ring)$_{II}$ + 0.72_{III} + 0.06_{IV}, which were compared to those of 0B hybrid plants obtained from the cross of 17-2 x 78-5642c-4 except that the frequency of trivalents was higher and the frequency of quadrivalents was lower in the former than in the latter. Indeed, the frequency of A-chromosome pairing of this plant did not significantly differ from the 0B hybrids of Culture

Table 36. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops comosa* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
17-1 x 78-5646-1			
79947-P1	0	0	-
-P2	0	0	-
-P3	0	0	-
-P4	0	0	-
17-1 x 78-5642c-4			
79948-P6	0	0.3	-
-P7	0	0	-
17-2 x 78-5642c-4			
79949-P1	0	0.2	-
-P3	0	0.2	-
-P4	0	0.1	-
-P2	2	0	-
17-2 x 77-5645-4			
78410-P1	2	0.8	-
-P2	2	2.2	-
-F3	2	0.5	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent,
-: indehiscent.

Nos. 79948 and 79949.

Fertility of the F_1 hybrids

In any hybrid plants including 0B, 1B and 2B plants, their anthers did not dehisce at all. Pollen fertility was estimated in the thirteen hybrid plants obtained from four cross combinations (Table 36). All of them showed a very low pollen fertility less than 3%. Six of them formed no normal pollen grains, six showed the fertility below 1% and the other showed 2.2%.

(9) *Aegilops uniaristata* x *Ae. mutica*

Result of crosses

Two accessions of *Aegilops uniaristata* and nine plants from six accessions of *Ae. mutica* were used in the crosses (Table 37). The crossability was low. From a total of 341 pollinated florets of *Ae. uniaristata*, 46 seeds were obtained from the seven cross combinations. Their percentage seed set ranged from 0 to 50% and the mean percentage seed set was 13%. In addition to that low percentage seed set, the germination rate of those hybrid seeds was low. Only three seedlings were obtained from one cross combination, 19-3 x 77-5649-3, and the mean germination rate was only 7%. All the obtained seedlings grew vigorously till mature stage. None of them had B-chromosomes.

Morphology of *Aegilops uniaristata* and the F_1 hybrids between *Ae. uniaristata* and *Ae. mutica*.

The morphology of spikes and spikelets of *Ae. uniaristata* and the

Table 37. Result of the crosses between *Aegilops uniaristata* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops uniaristata x *Ae. mutica*						
19-2 x 77-5641-4	58	7	12	7	0	0
19-2 x 80-5641A1-2	12	0	0	-	-	-
19-2 x 80-5641A1-6	20	0	0	-	-	-
19-2 x 78-5643d-4	12	1	8	1	0	0
19-2 x 83-5646-3	59	0	0	-	-	-
19-3 x 77-5641-4	20	1	5	1	0	0
19-3 x 85-5641A-10	92	8	9	8	0	0
19-3 x 77-5642-4	10	3	30	3	0	0
19-3 x 77-5645-4	26	10	38	10	0	0
19-3 x 77-5649-3	32	16	50	16	3	19
Total	341	46	13	46	3	7

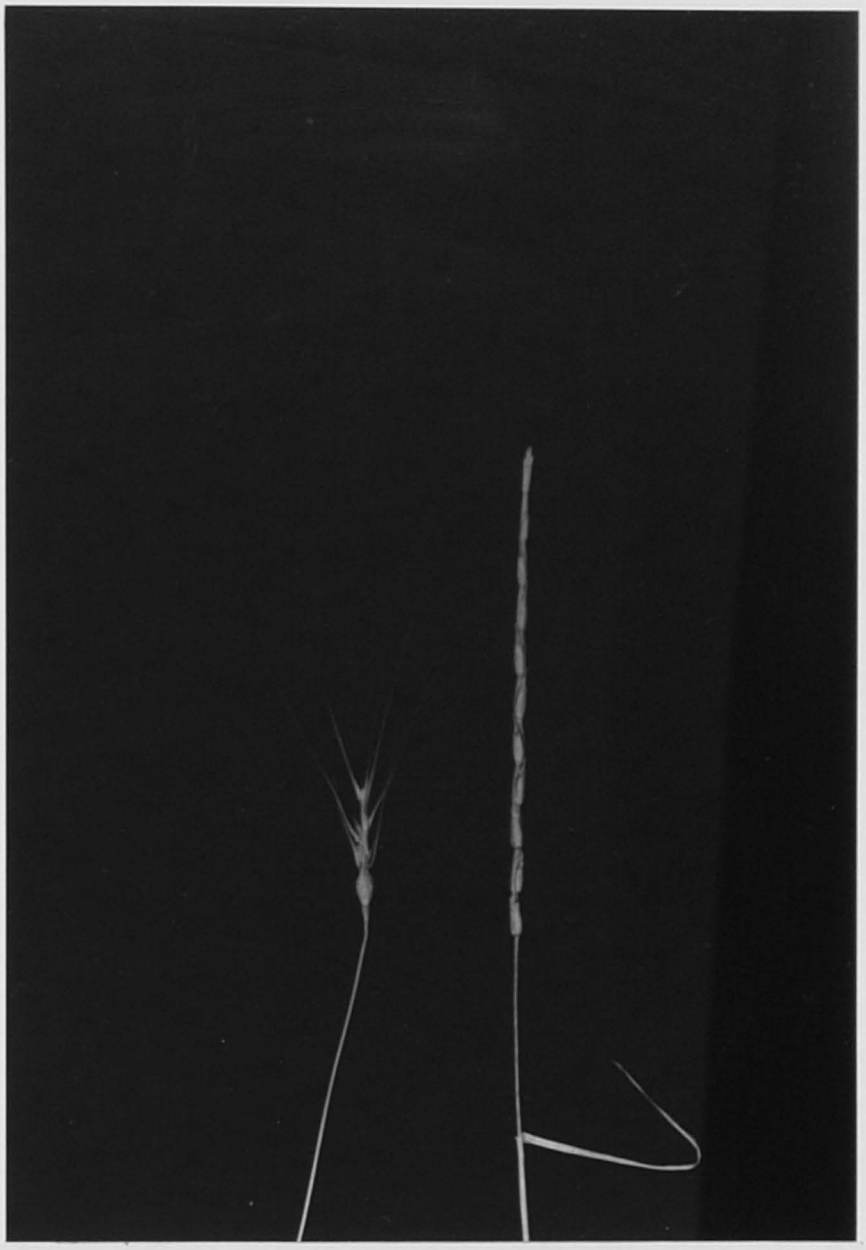


Figure 39. Spike morphology of *Aegilops uniaristata* and the F_1 hybrid between *Ae. uniaristata* and *Ae. mutica* (x 0.5). A: *Ae. uniaristata* (KU 19-3), B: F_1 hybrid between *Ae. uniaristata* and *Ae. mutica* (78412-P1).

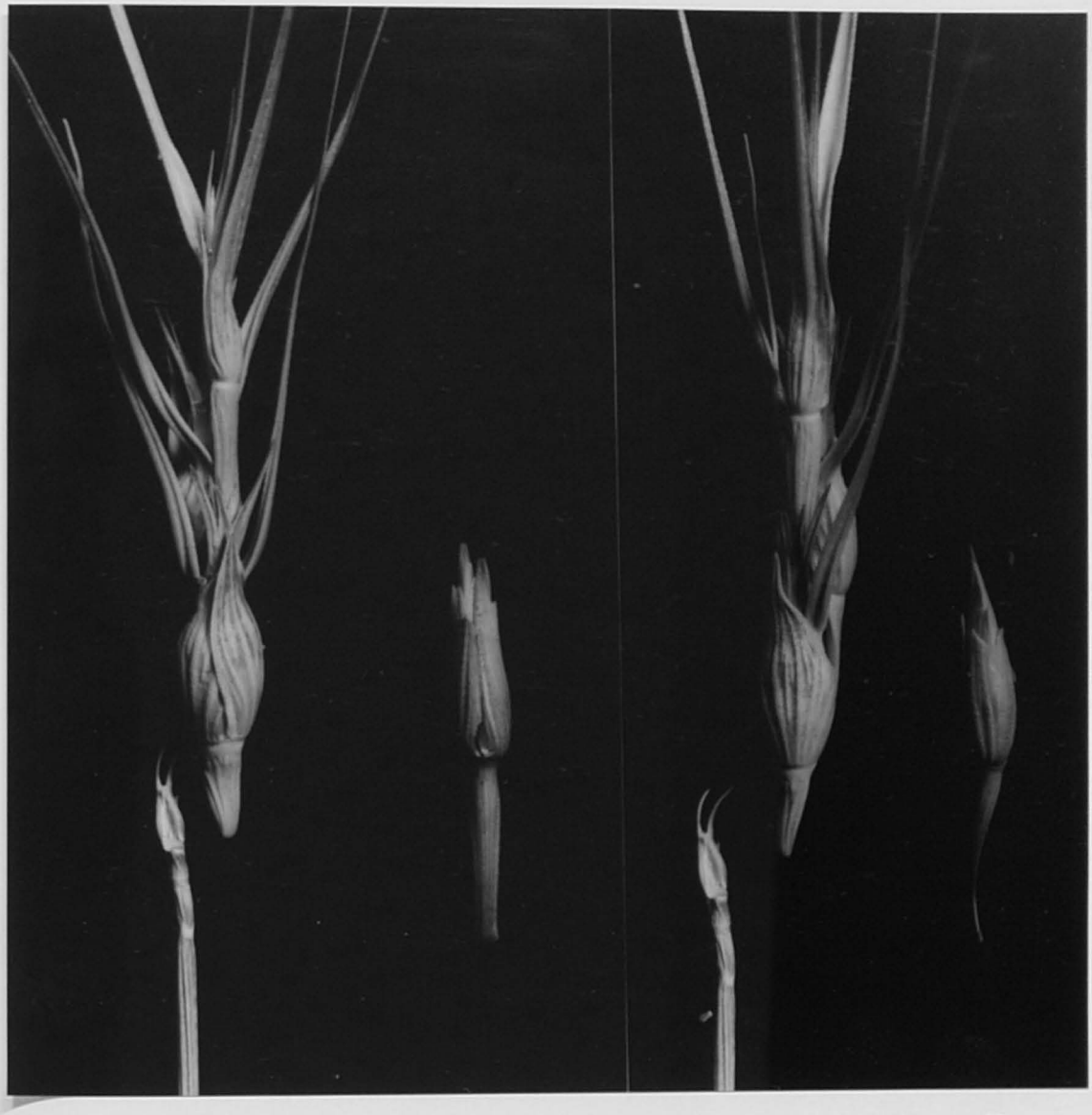


Figure 40. Spikelet morphology of *Aegilops uniaristata* and the F_1 hybrid between *Ae. uniaristata* and *Ae. mutica* (x 2.5). A and C: *Ae. uniaristata* (KU 19-3), B and D: F_1 hybrid between *Ae. uniaristata* and *Ae. mutica* (78412-P1).

F_1 hybrid between it and *Ae. mutica* is shown in Figures 39 and 40. *Ae. uniaristata* has narrow conical spikes with three to five fertile spikelets in addition to three or four rudimentary spikelets at the base. Fertile spikelets are ovate and gradually reduce their size from the base to the top of a spike. Each of them consists of four florets and is somewhat longer than the adjacent rachis internode. The almost whole spikelet is covered with empty glumes. Empty glumes of its lateral spikelets have a triangular broad tooth and an awn, and those of the uppermost ones taper into a broad awn. The upper margin of lemmas in lateral spikelets is bidentate but has no awn. Lemmas in the uppermost spikelet taper into a short awn. Only the rachis nodes adjacent to the rudimentary spikelets at the base of the spike are fragile and the whole spike falls together at maturity (umbrella type disarticulation). Rachilla is tough.

The F_1 hybrids between *Ae. uniaristata* and *Ae. mutica* had long linear spikes without any rudimentary spikelets. Their spikes consisted of 11 or 12 ovate-oblong spikelets arranged in a row. Each spikelet consists of five to six laxly arranged florets. Spikelets were almost as long as their adjacent rachis internodes along the whole spike length. A half or two thirds of the whole length of the spikelet was covered with empty glumes. The upper margins of the empty glumes of lateral spikelets had two teeth. The base of one tooth was broader than the other. Those of the uppermost spikelets had three teeth which were similar to one another in length and in shape. There were not awns either on empty glumes or on lemmas. Rachis was fragile. Each rachis node disarticulated at maturity and each spikelet fell separately with

the rachis internode below it (wedge type disarticulation). Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

Only three 0B hybrids were obtained in this cross combination. The chromosome pairing at MI of meiosis was observed in two F_1 hybrid plants (Table 38 and Figure 41). Those hybrids showed a similar but rather low frequency of chromosome pairing. Their mean chiasma frequency was 5.98 and 5.45 per cell, respectively. A ring-shaped bivalent was found only in 21 (26%) among a total of 81 observed PMCs in the two plants and most of bivalents observed were rod-shaped. One to ten univalents were observed in 80 cells (99%) and the mean frequency of univalents per cell in each plant was 4.44 and 4.48, respectively. The F_1 hybrids formed a trivalent in many PMCs, and one or two trivalents were observed in 38 cells (47%) of the two plants. Especially in one of them (Culture No. 78412-P1), three cells contained two trivalents, two of which formed two V-shaped trivalents and another formed one V-shaped and one Y-shaped trivalents. The mean frequency of trivalents in each plant was 0.60 and 0.35 per cell, respectively. No quadrivalents were observed in those hybrid plants between *Ae. uniaristata* and *Ae. mutica*.

Fertility of the F_1 hybrids

In none of the hybrid plants, their anthers dehisced. Pollen fertility was estimated in one of them and no normal pollen grains were found (Table 39).

Table 38. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops uniaristata* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No.of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.[4] Total	TRIV. V	TRIV. Y	OTHERS	No.of[3] arms paired	No.of chiasmata per cell
19-3 x 77-5649-3												
78412-P1	0	50	4.44 (0-10)	3.88 (1-6)	3.54 (1-6)	0.34 (0-1)	0.60 (0-2)	0.56 (0-2)	0.04 (0-1)	-	5.42 (2-8)	5.98 (2-9)
-F1	0	31	4.48 (1-10)	4.23 (2-6)	4.10 (2-6)	0.13 (0-1)	0.35 (0-1)	0.35 (0-1)	-	-	5.06 (2-7)	5.45 (2-9)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.
4) V and Y represent V-shaped and Y-shaped trivalents, respectively.

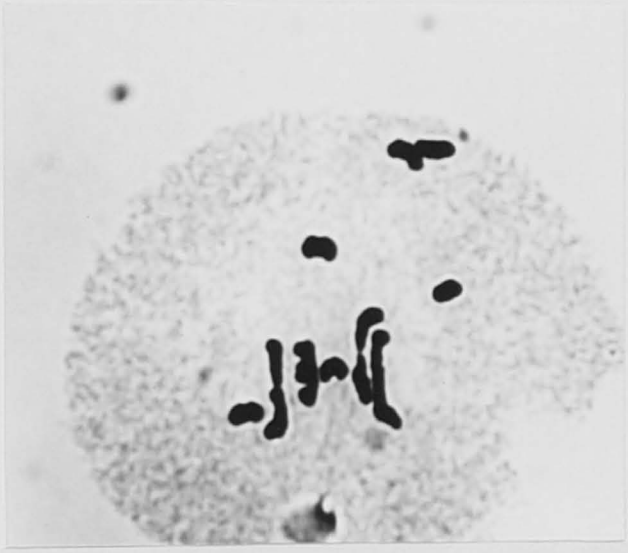


Figure 41. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrid (Culture No. 78412-F1) between *Aegilops uniaristata* and *Ae. mutica*, 6_I+4rod_{II} (x 1,100).

Table 39. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops uniaristata* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
19-3 x 77-5649-3 78412-P1	0	0	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent, -: indehiscent

(10) *Aegilops umbellulata* x *Ae. mutica*

Result of crosses

Two accessions of *Aegilops umbellulata* and 12 individuals from eight accessions of *Ae. mutica* were used in the present crosses (Table 40). A total of 284 emasculated florets of *Ae. umbellulata* were pollinated with the fresh pollen grains of *Ae. mutica*. Among the 12 cross combinations, 11 gave a total of 108 hybrid seeds and the mean percentage seed set was 38%. However, the seeds obtained from only three cross combinations germinated and the mean germination rate was 20%. Those three cross combinations involved one accession of *Ae. umbellulata*, KU 8-2, and three of *Ae. mutica*, KU 5598, KU 5646 and KU 5649. From the two cross combinations F_1 hybrid plants only without B-chromosomes were obtained (Culture Nos. 78405 and 79943) and from the other combination those with two B-chromosomes were obtained (Culture No. 82237).

Morphology of *Aegilops umbellulata* and the F_1 hybrids between *Ae. umbellulata* and *Ae. mutica*

The morphology of spikes and spikelets of *Ae. umbellulata* and the F_1 hybrids between it and *Ae. mutica* is shown in Figures 42 and 43. *Ae. umbellulata* has short and conical spikes consisting of two or three large fertile spikelets, two or three rudimentary spikelets at the base and one to three small sterile spikelets at the top. The spike becomes narrow suddenly in its upper part. Its fertile large spikelets are obovate. They have an abrupt inflation above the middle part and have a thin neck just above the inflation. Each fertile spikelet consists of

Table 40. Result of the crosses between *Aegilops umbellulata* and *Ae. mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Aegilops umbellulata x *Ae. mutica*						
8-1 x 80-5641A1-6	62	20	32	20	0	0
8-1 x 80-5645C-10	36	2	6	2	0	0
8-2 x 81-5598-3	42	18	43	18	12	67
8-2 x 77-5641-4	20	3	15	3	0	0
8-2 x 78-5641b-10	12	9	75	9	0	0
8-2 x 77-5642-4	12	3	25	3	0	0
8-2 x 78-5643d-4	12	2	17	2	0	0
8-2 x 77-5645-4	12	9	75	9	0	0
8-2 x 78-5645b-3	10	4	40	4	0	0
8-2 x 78-5646-1	22	17	77	17	4	24
8-2 x 77-5649-3	36	21	58	21	10	48
8-2 x 77-5652-4	8	0	0	-	-	-
Total	284	108	38	108	22	20

Figure 42. Spike morphology of *Aegilops umbellulata* and the F_1 hybrids between *Ae. umbellulata* and *Ae. mutica* (x 0.5). A: *Ae. umbellulata* (KU 8-2), B-D: F_1 hybrids between *Ae. umbellulata* and *Ae. mutica* (B: 78405-P1, C: 79943-P3, D: 82237-P1).

Figure 43. Spikelet morphology of *Aegilops umbellulata* and the F_1 hybrid between *Ae. umbellulata* and *Ae. mutica* (x 2.4). A: *Ae. umbellulata* (KU 8-2); B-E: F_1 hybrid between *Ae. umbellulata* and *Ae. mutica* (79943-P2), B and D: spikelet in the middle part of a spike of the F_1 hybrid, C and E: spikelet in the upper part of a spike of the F_1 hybrid.

four florets. The rachis internodes of the lower part of the spikes are much shorter than the adjacent fertile spikelets. Empty glumes cover about a lower half of the each fertile spikelet. They are also suddenly inflated above the middle part, just above which they become a thin neck. The number of awns on the empty glumes of the fertile spikelets is four or five. They are all similar to one another both in shape and in length, and they spread almost horizontally forming an umbrella-like shape. Lemmas have two or three awns similar to those of empty glumes. Rachis nodes only adjacent to basal rudimentary spikelets disarticulate and the whole spikes fall together at maturity (umbrella type disarticulation). Rachilla is tough.

The spikes of the F_1 hybrids between *Ae. umbellulata* and *Ae. mutica* were linear and they consisted of about 15 spikelets arranged in a row. They usually had one or two rudimentary spikelets at the base but no sterile spikelets at the top. All the spikelets along the whole spike length except rudimentary ones were similar to one another in size. They were almost as long as the adjacent rachis internodes. Each spikelet consisted of five or six florets. Two thirds or three fourths of the each spikelet was covered with empty glumes. Empty glumes were tridentate. The middle tooth was small triangular and shorter than the lateral ones (Figures 43B and D). The lateral teeth on the empty glumes often became short thin awns especially in the upper part of the spikes (Figures 43C and E). Tips of lemmas also often became short awns. Rachis was fragile. Each rachis node broke when matured and each spikelet fell separately with the rachis internode below it (wedge type

disarticulation). Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

The PMCs at MI of meiosis in seven 0B hybrid plants from two cross combinations and in two 2B hybrids from a cross combination were cytologically observed (Table 41 and Figure 44). Seven 0B hybrids between *Ae. umbellulata* and *Ae. mutica* obtained in the present crosses showed a similar configuration and frequency of chromosome pairing to one another. These 0B hybrid plants showed the most complicated configuration of A-chromosome pairing among all the diploid interspecific F_1 hybrids observed in the present study (Figures 44A and B). Their PMCs frequently contained multivalents up to an octavalent. All the 0B hybrids formed up to three trivalents or a quinquevalent in some cells. Fifty six (21%) among a total of 270 PMCs observed in these seven 0B hybrids formed three trivalents, 15 (6%) formed two trivalents with a quinquevalent or with a quadrivalent, and 83 (31%) formed two trivalents (Figure 44B). Eighty five cells (31%) formed a trivalent; one of them contained a octavalent, one contained a quadrivalent, eight contained an quinquevalent (Figure 44A) and the other two contained a quadrivalent in addition to a trivalent. Furthermore, four (1%) cells formed a quinquevalent and three (1%) formed a quadrivalent. As a result, only 24 cells (9%) of the total observed cells had no multivalent. In nine cells as many as 11 chromosomes participated in forming multivalents. Their pairing configuration was 1_I + $1rod_{II}$ + 2_{III} + 1_U in seven cells, 3_I + 2_{III} + 1_U in one cell and 1_I + $1rod_{II}$ + 1_{III} + $1_{U\,III}$ in one cells. And in seven cells 10 chromosomes took part

Table 41. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Aegilops umbellulata* and *Ae. mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
8-2 x 77-5649-3													
78405-P1	0	50	2.60 (0-7)	2.22 (0-5)	2.16 (0-5)	0.06 (0-1)	2.02 (0-4)	0.04 (0-1)	0.04 (0-1)	-	$0.10_{II}+0.04_{III}$ (0-1) (0-1)	7.04 (4-9)	7.04 (4-9)
-F2	0	50	3.64 (0-12)	2.58 (0-4)	2.56 (0-4)	0.02 (0-1)	1.60 (0-3)	-	-	-	0.08_{II} (0-1)	6.12 (1-9)	6.12 (1-9)
-F1	0	50	4.00 (0-10)	2.60 (1-5)	2.52 (1-5)	0.08 (0-1)	1.54 (0-3)	0.02 (0-1)	0.02 (0-1)	-	0.02_{II} (0-1)	5.90 (2-8)	5.90 (2-8)
8-2 x 78-5646-1													
79943-P4	0	30	2.17 (0-5)	2.80 (1-6)	2.63 (1-5)	0.17 (0-1)	1.80 (0-3)	0.17 (0-1)	0.17 (0-1)	-	0.03_{II} (0-1)	7.20 (5-9)	7.33 (5-10)
-P2	0	30	2.47 (1-5)	2.40 (1-6)	2.37 (1-6)	0.03 (0-1)	1.83 (0-3)	0.03 (0-1)	0.03 (0-1)	-	$0.17_{II}+0.03_{III}$ (0-1) (0-1)	7.10 (5-10)	7.10 (5-10)
-P1	0	30	2.80 (0-6)	2.83 (1-5)	2.70 (0-5)	0.13 (0-1)	1.63 (0-3)	0.03 (0-1)	0.03 (0-1)	-	0.10_{II} (0-1)	6.73 (5-9)	6.77 (5-9)
-P3	0	30	4.23 (0-10)	2.83 (0-5)	2.50 (0-5)	0.33 (0-1)	1.17 (0-3)	0.07 (0-1)	0.07 (0-1)	-	0.07_{II} (0-1)	5.97 (3-9)	6.03 (3-9)
8-2 x 81-5598-3													
82237-P8	2	100	7.23 (1-14)	2.45 (0-5)	2.42 (0-5)	0.03 (0-1)	0.61 (0-2)	0.01 (0-1)	0.01 (0-1)	-	-	3.73 (0-8)	3.73 (0-8)
-P1	2	100	9.67 (4-14)	1.85 (0-5)	1.83 (0-5)	0.02 (0-1)	0.21 (0-1)	-	-	-	-	2.29 (0-5)	2.31 (0-5)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

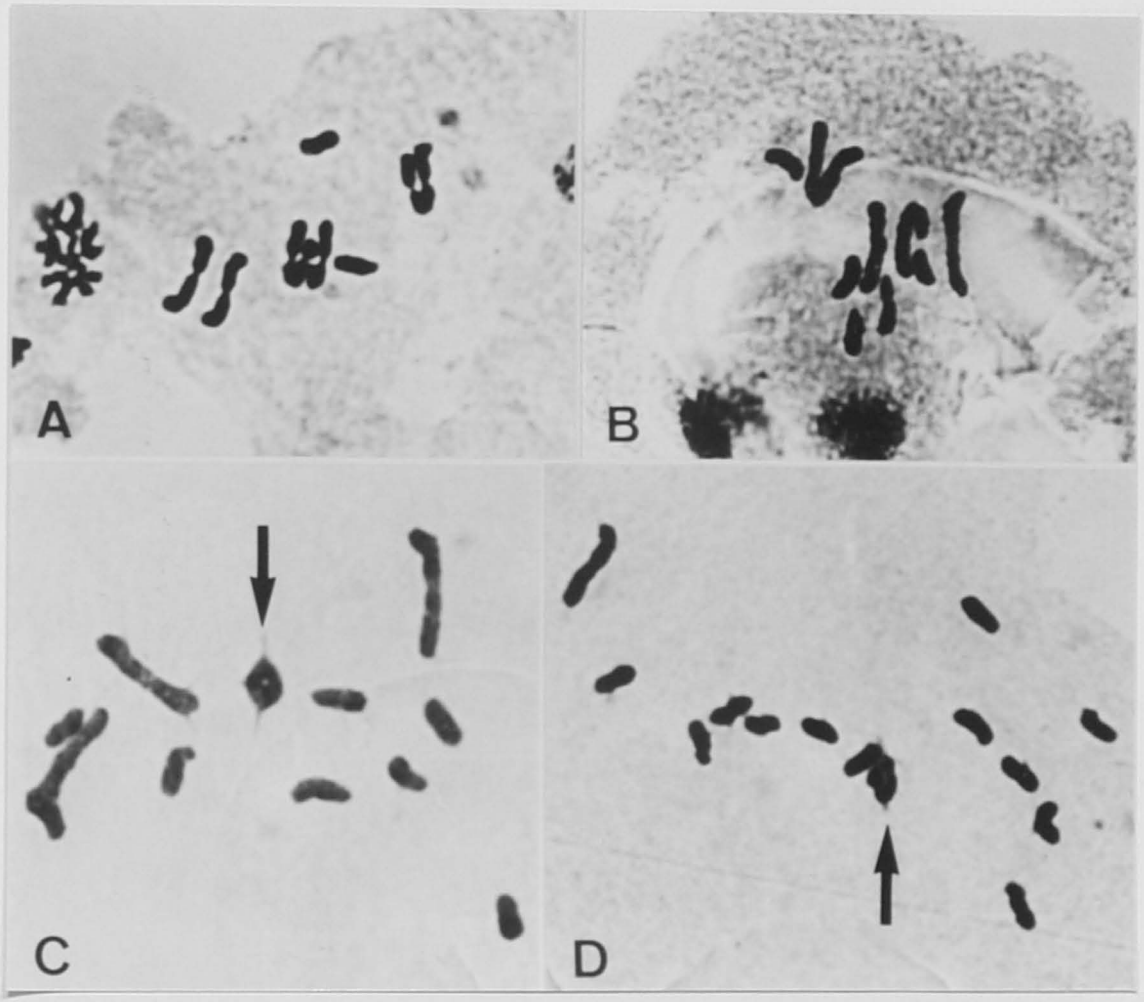


Figure 44. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with or without B-chromosomes (Bs) between *Aegilops umbellulata* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A: 78405-F2 without Bs, $2_I+2_{II}+1_{III}+1_U$; B: 79943-P1 without Bs, $4_I+2_{II}+2_{III}$; C: 82237-P8 with 2Bs, 8_I+3_{II} of As + $1ring_{II}$ of Bs; D: 82237-P1 with 2Bs, 12_I+1_{II} of As + $1ring_{II}$ of Bs.

in forming multivalents: $2rod_{II}$ + 2_{III} + 1_{IV} in one cell and 2_{I} + $1rod_{II}$ + 2_{III} + 1_{IV} in six cells. In those 0B hybrids a ring-shaped bivalent was found only in 28 cells (10%) and most of their bivalents were rod-shaped. The mean pairing configuration of these 0B hybrids was 3.41_{I} + $(2.41rod + 0.05ring)_{II}$ + 1.72_{III} + 0.02_{IV} + 0.07_{V} + $0.01_{V\,I}$ in Culture No. 78405 and 2.92_{I} + $(2.55rod + 0.17ring)_{II}$ + 1.61_{III} + 0.08_{IV} + 0.09_{V} + $0.01_{V\,III}$ in Culture No. 79943, respectively.

Such complicated association of chromosomes observed in the 0B plants was drastically reduced by two B-chromosomes derived from *Ae. mutica* (Figures 44C and D). Two F_1 hybrid plants with two B-chromosomes showed a very low frequency of A-chromosome pairing with the mean chiasma frequency of 3.73 and 2.31 per cell, respectively. One of them (Culture No. 82237-P8) showed a slightly but significantly higher frequency of A-chromosome pairing than the other (No. 82237-P1). In the former 2B hybrid (82237-P8) up to five bivalents were observed. Five rod-shaped bivalents were found in two cells, and a trivalent and a ring-shaped bivalent were also formed in addition to four rod-shaped bivalents in one cell. Three or four bivalents were found in 46 cells (Figure 44C), two of which formed two trivalents and 16 formed a trivalent in addition to rod-shaped bivalents. However, a ring-shaped bivalent of A-chromosomes was found only in two cells among those 46 cells. Two cells contained 14 univalents of A-chromosomes and seven cells contained 12 univalents with a rod-shaped bivalent of A-chromosomes. The mean configuration of A-chromosome pairing in this 2B plant was 7.23_{I} + $(2.42rod + 0.03ring)_{II}$ + 0.61_{III} + $0.01chain_{IV}$. In the other 2B hybrid (Culture No. 82237-P1), 24 among a total of 100 PMCs

Table 42. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Aegilops umbellulata* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
8-2 x 77-5649-3 78405-P1	0	0	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent, -: indehiscent.

observed formed 12 univalents with a rod-shaped bivalent of A-chromosomes (Figure 44D), 10 formed 14 univalents of A-chromosomes and 21 formed a trivalent with 0 to three bivalents. Its mean configuration per cell was 9.67_{I} + $(1.83rod + 0.02ring)_{II}$ + 0.21_{III}. These two 2B hybrids were significantly different from each other in their pairing frequency (χ^2=43.27) but the difference between 2B and 0B hybrids was much more drastic ($\chi^2 \geq 124.54$).

Fertility of the F_1 hybrids

The anthers of the obtained F_1 hybrid plants both with and without B-chromosomes did not dehisce at all. Pollen fertility was observed in one of the F_1 hybrids without B-chromosomes but that plant was completely sterile (Table 42).

(11) *Triticum monococcum* x *Aegilops mutica*

Result of crosses

Three accessions of wild forms of *Triticum monococcum* were crossed with five individuals from three accessions of *Ae. mutica* (Table 43). Two accessions of the wild forms of *T. monococcum* (KU 101-1 and KU 103) formerly belong to *T. boeoticum* Boiss. and another (KU 199-8) belongs to *T. urartu* Thum., respectively. Crossability in those cross combinations differed from one another depending on the accessions of genus *Triticum* used as female parents. When two accessions from former species *T. boeoticum* (KU 101-1 and KU 103) were crossed with *Ae. mutica*, the percentage seed set and the germination rate were so high. A total of 204 emasculated florets of *T. boeoticum* were pollinated with the fresh

Table 43. Result of the crosses between *Triticum monococcum* ssp. *boeoticum* and *Aegilops mutica*

Cross combination	No. of florets pollinated	No. of seeds obtained	Seed set (%)	No. of seeds sown	No. of seeds germinated	Germination rate (%)
Triticum monococcum ssp. *boeoticum* (*T. boeoticum* Boiss.) x *Ae. mutica*						
101-1 x 80-5641A1-6	26	25	96	25	7	28
101-1 x 80-5641E-9	22	9	41	9	2	22
101-1 x 80-5645C-10	64	18	28	18	8	44
101-1 x 78-5646-1	34	24	71	24	15	63
103 x 78-5646-6	58	27	47	27	20	74
Total	204	103	50	103	52	50
Triticum monococcum ssp. *boeoticum* (*T. urartu* Thum.) x *Ae. mutica*						
199-8 x 78-5646-1	40	13	33	13	0	0

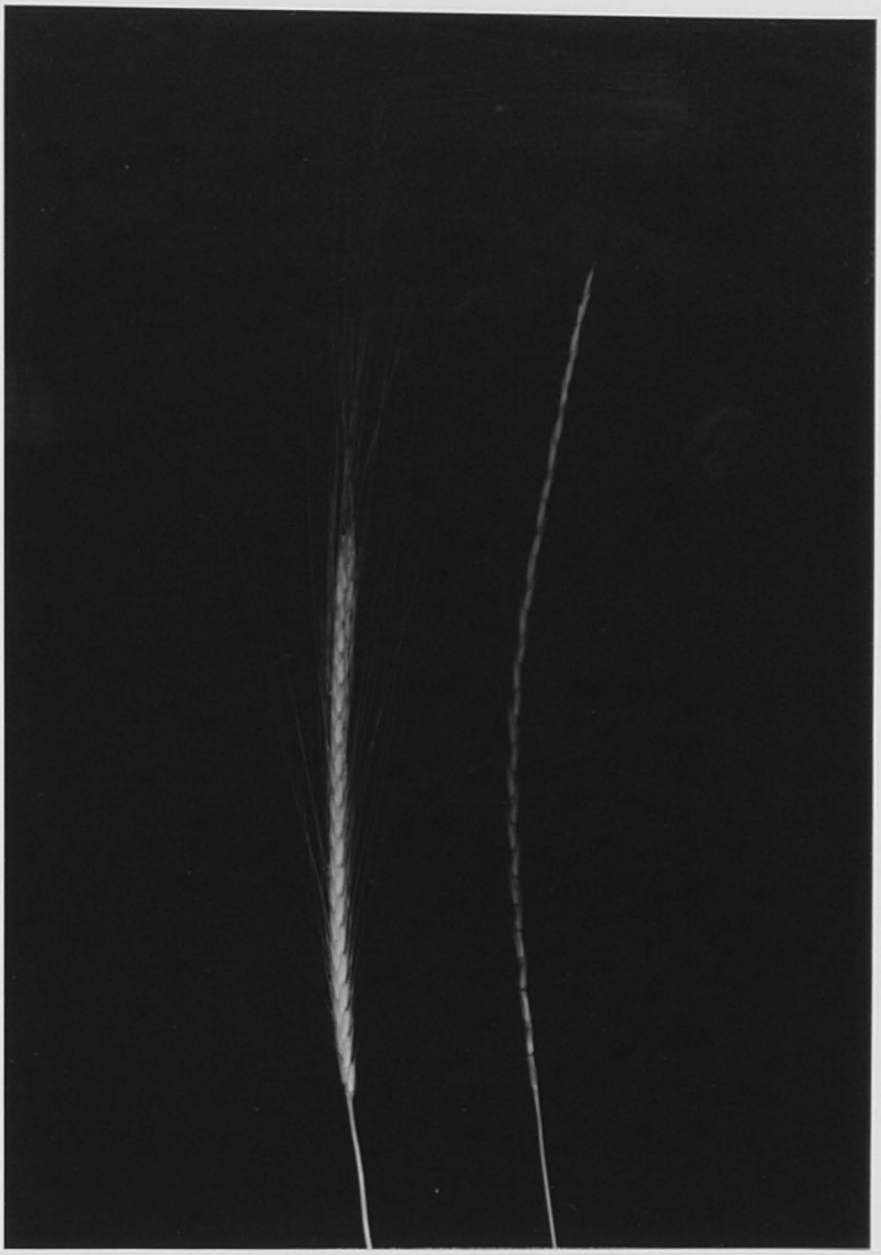
pollen grains of *Ae. mutica*. Hybrid seeds were born in 103 florets among them. The mean percentage seed set was 50%, and that of each cross combination ranged from 28% to 96%. Fifty two seedlings were successfully obtained from these 103 seeds sown. The mean germination rate was 50% and that of each cross combination ranged from 22% to 74%.

On the other hand, no hybrid seedling was obtained when the accession of former species *T. urartu* (KU 199-8) was used as a female parent. Hybrid seeds were born in 13 florets among a total of 40 emasculated florets of *T. urartu* which were pollinated with *Ae. mutica*. The mean percentage seed set was 33% and it was not so lower than that in the crosses between *T. boeoticum* and *Ae. mutica* mentioned above. However, those seeds did not germinate at all. Consequently, F_1 hybrid plants between *T. urartu* and *Ae. mutica* could not be obtained in the present work.

Morphology of *Triticum monococcum* ssp. *boeoticum* and the F_1 hybrids between *T. monococcum* ssp. *boeoticum* and *Ae. mutica*

The morphology of spikes and spikelets of *T. monococcum* ssp. *boeoticum* and the F_1 hybrids between it and *Ae. mutica* is shown in Figures 45 and 46. *T. monococcum* ssp. *boeoticum* has linear and compressed spikes consisting of about 30 spikelets arranged in two rows. Its spike has usually two or three rudimentary spikelets at the base but they sometimes develop well into fertile ones. All the spikelets except these rudimentary ones are similar both in shape and in size. Each spikelet is compressed and consists of two or three florets. It is much longer than the adjacent rachis internode densely covered with long soft

Figure 45. Spike morphology of *Triticum monococcum* ssp. *boeoticum* and the F_1 hybrids between *T. monococcum* ssp. *boeoticum* and *Ae. mutica* (x 0.5). A: *T. monococcum* ssp. *boeoticum* (KU 101-1), B: F_1 hybrid involving *T. monococcum* KU 101-1 (79981-P4).



A B

Figure 45. Spike morphology of *Triticum monococcum* ssp. *boeoticum* and the F_1 hybrids between *T. monococcum* ssp. *boeoticum* and *Ae. mutica* (x 0.5). A: *T. monococcum* ssp. *boeoticum* (KU 101-1), B: F_1 hybrid involving *T. monococcum* KU 101-1 (79981-P4).

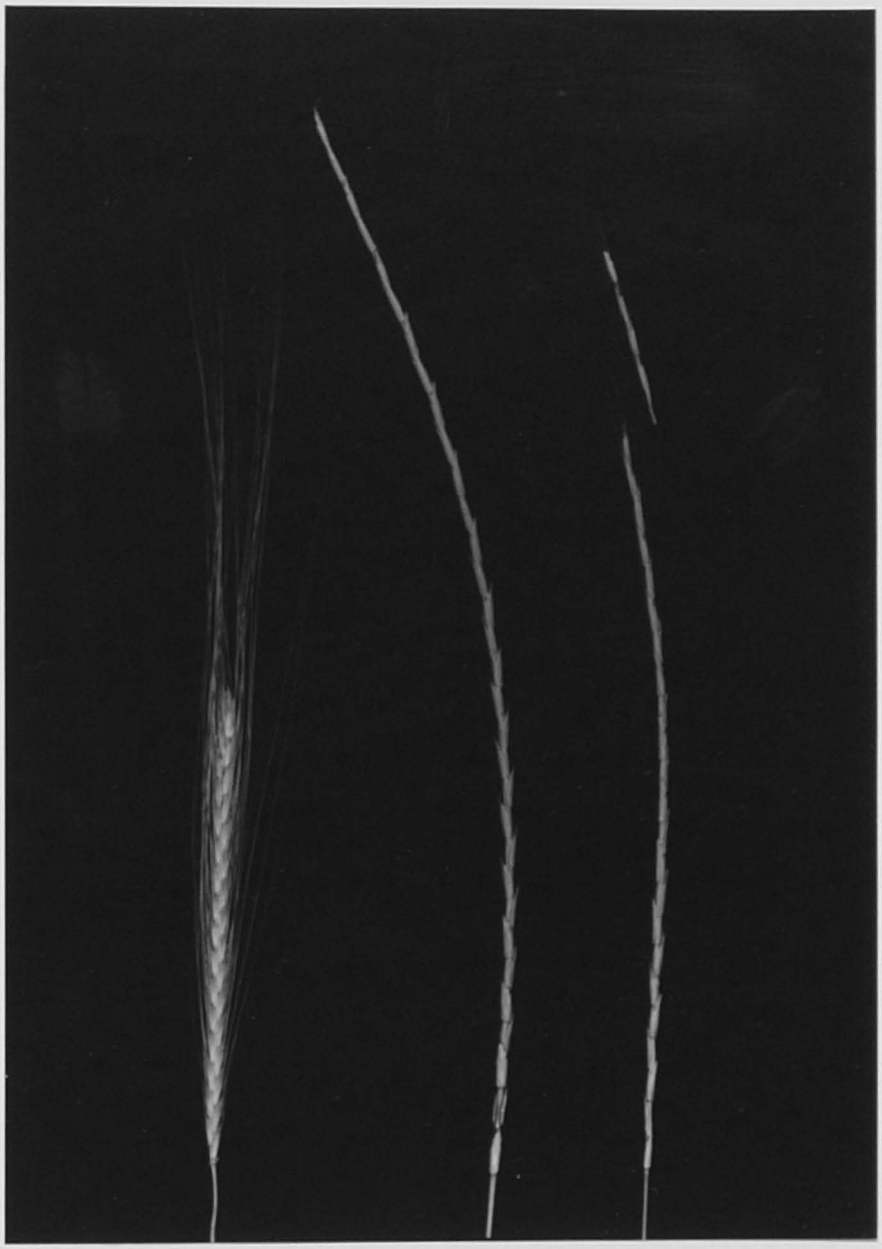


Figure 45. (Continued)

C: *T. monococcum* ssp. *boeoticum* (KU 103), D-E: F_1 hybrids involving *T. monococcum* KU 103 (D: 79982-P9, E: 79982-P12).

hairs. Empty glumes have two prominent keels and the tips of the keels become sharp teeth, one of which is larger than the other. Tips of lemmas of the lowest two florets become a long thin awn in the accession KU 103 (Figure 45C) but awns of the second florets do not develop well in the accession KU 101-1 (Figure 45A). Rachis is fragile. Each rachis node breaks and each spikelet falls separately with the rachis internode below it when matured (wedge type disarticulation). Rachilla is tough.

The spikes of the F_1 hybrids between *T. monococcum* ssp. *boeoticum* and *Ae. mutica* were long and linear. They consisted of 25 to 30 spikelets arranged in a row. They did not have any rudimentary spikelets at the base. All spikelets were similar to one another in shape but the spikelets of upper spike part were slightly smaller than those of middle and lower parts of the spikes. Each spikelet consisted of four florets and it was somewhat longer than the adjacent rachis internode. Only its lower half was covered with empty glumes. Rachis internodes were usually glabrous but a few very short hairs sometimes existed on the rachis nodes. Empty glumes were more similar to those of *T. monococcum* used as the female parent than those of *Ae. mutica*. They had two keels which were weaker than those of *T. monococcum*. Their tips became two small teeth similar to each other. Lemmas were usually not awned but their tips occasionally tapered into a short thin awns. In two individuals obtained from the cross of 103 x 78-5646-6 (Culture Nos. 79982-P5 and -P12) lemmas of all the spikelets from the uppermost to lowest ones had a short awn (Figures 45E, 46C and F) but these individuals were quite exceptional. Rachis was fragile. Each rachis node broke at maturity and spikes broke into each spikelet with the

rachis internode below it (wedge type disarticulation). Rachilla was tough.

Chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids

A total of 36 F_1 hybrid plants were cytologically observed (Table 44 and Figures 47 and 48). Thirty one of them did not have any B-chromosomes, one had a B-chromosome and the other four had two B-chromosomes in addition to 14 A-chromosomes. All the 0B hybrid plants obtained from the three cross combinations showed a very high frequency of chromosome pairing with few univalents at MI of meiosis in their PMCs (Figure 47). Their chiasma frequency per cell varied from 10.98 to 9.68 in the four plants from the cross combination of 101-1 x 80-5645C-10 (Culture No. 81737), from 10.27 to 8.67 in the 11 plants from 101-1 x 78-5646-1 (Culture No. 79981), and from 11.00 to 8.27 in the 16 plants from 103 x 78-5646-6 (Culture No. 79982). These 0B hybrids could not be significantly divided into any groups within the each cross combination according to their frequency of chromosome pairing, because their pairing frequency varied continuously. 485 (48%) cells among a total of 1,010 PMCs observed in the 31 hybrid plants without Bs contained no multivalent. A quadrivalent was characteristically found in their PMCs and the mean frequency of quadrivalents ranged from 0.70 to 0.20 per cell. A chain-shaped quadrivalent was found in 295 (29%) cells and a ring-shaped one was found in 112 (11%) cells. A quinquevalent or a sexivalent was also found in three cells of the three plants (Culture Nos. 79982-P6, -P13 and -P18). The mean configuration of chromosome pairing in the each cross combination was 1.33_{I} + $(2.69rod + 2.58ring)_{II}$

Table 44. Mean configuration and frequency of A-chromosome pairing and their ranges at MI of meiosis in the F_1 hybrids between *Triticum monococcum* ssp. *boeoticum* and *Aegilops mutica*

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
101-1 x 80-5645C-10													
81737-P3	0	50	1.04 (0-6)	5.20 (4-7)	1.60 (0-5)	3.60 (1-6)	0.16 (0-1)	0.52 (0-1)	0.30 (0-1)	0.22 (0-1)	-	10.90 (5-14)	10.98 (6-14)
-F2	0	50	0.90 (0-6)	4.94 (4-7)	1.70 (0-4)	3.24 (1-5)	0.14 (0-1)	0.70 (0-1)	0.40 (0-1)	0.30 (0-1)	-	10.86 (6-13)	10.88 (6-13)
-P1	0	50	0.78 (0-4)	5.38 (4-7)	2.58 (0-7)	2.80 (1-6)	0.34 (0-1)	0.36 (0-1)	0.20 (0-1)	0.16 (0-1)	-	10.10 (6-13)	10.12 (6-13)
-P2	0	50	1.20 (0-8)	5.06 (3-7)	2.58 (0-7)	2.48 (0-5)	0.28 (0-1)	0.46 (0-1)	0.32 (0-1)	0.14 (0-1)	-	9.64 (5-14)	9.68 (5-14)
101-1 x 78-5646-1													
79981-P15	0	30	0.63 (0-4)	5.53 (4-7)	2.70 (0-6)	2.83 (1-5)	0.10 (0-1)	0.50 (0-1)	0.37 (0-1)	0.13 (0-1)	-	10.20 (7-13)	10.27 (7-13)
-P12	0	30	1.13 (0-6)	5.33 (4-7)	2.20 (0-5)	3.13 (2-5)	0.20 (0-1)	0.40 (0-1)	0.30 (0-1)	0.10 (0-1)	-	10.17 (6-14)	10.23 (6-14)
-P3	0	30	1.23 (0-6)	5.16 (3-7)	2.06 (0-4)	3.10 (1-6)	0.23 (0-1)	0.43 (0-1)	0.27 (0-1)	0.17 (0-1)	-	10.20 (5-13)	10.20 (5-13)
-P2	0	30	0.90 (0-4)	5.80 (5-7)	3.23 (0-7)	2.57 (1-6)	0.23 (0-1)	0.20 (0-1)	0.10 (0-1)	0.10 (0-1)	-	9.53 (7-14)	9.67 (7-14)
-P11	0	30	1.06 (0-4)	5.60 (4-7)	2.93 (1-5)	2.67 (1-6)	0.27 (0-1)	0.23 (0-1)	0.23 (0-1)	-	-	9.50 (7-13)	9.57 (7-14)
-P10	0	30	1.43 (0-6)	5.10 (4-7)	2.63 (1-5)	2.47 (1-5)	0.17 (0-1)	0.47 (0-1)	0.37 (0-1)	0.10 (0-1)	-	9.40 (5-13)	9.47 (5-13)
-P4	0	30	1.13 (0-7)	4.93 (2-7)	2.77 (1-5)	2.17 (0-4)	0.33 (0-1)	0.50 (0-1)	0.43 (0-1)	0.07 (0-1)	-	9.33 (5-12)	9.40 (5-12)
-P13	0	30	1.67 (0-8)	5.23 (3-7)	2.57 (0-6)	2.67 (1-4)	0.27 (0-1)	0.27 (0-1)	0.20 (0-1)	0.07 (0-1)	-	9.30 (4-13)	9.30 (4-13)
-P8	0	30	1.77 (0-6)	5.33 (4-7)	2.73 (0-6)	2.60 (0-6)	0.17 (0-1)	0.27 (0-1)	0.17 (0-1)	0.10 (0-1)	-	9.17 (4-13)	9.23 (4-13)
-P9	0	30	1.63 (0-6)	4.97 (3-7)	3.00 (1-7)	1.97 (0-6)	0.37 (0-1)	0.33 (0-1)	0.30 (0-1)	0.03 (0-1)	-	8.70 (6-13)	8.73 (6-13)
-P14	0	30	2.03 (0-6)	5.03 (3-7)	2.80 (1-5)	2.23 (0-5)	0.23 (0-1)	0.30 (0-1)	0.27 (0-1)	0.03 (0-1)	-	8.67 (4-12)	8.67 (4-12)

Table 44. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
101-1 x 80-5641E-9													
81736-P1	1	50	12.52 (8-14)	0.74 (0-3)	0.74 (0-3)	-	-	-	-	-	-	0.74 (0-3)	0.74 (0-3)
101-1 x 80-5641A1-6													
81735-P3	2	100	9.44 (4-14)	2.22 (0-5)	1.98 (0-5)	0.24 (0-2)	0.04 (0-1)	-	-	-	-	2.54 (0-6)	2.56 (0-6)
-P2	2	50	13.52 (12-14)	0.24 (0-1)	0.24 (0-1)	-	-	-	-	-	-	0.24 (0-1)	0.24 (0-1)
-F2	2	50	13.88 (12-14)	0.06 (0-1)	0.06 (0-1)	-	-	-	-	-	-	0.06 (0-1)	0.06 (0-1)
-F1	2	50	13.92 (12-14)	0.04 (0-1)	0.04 (0-1)	-	-	-	-	-	-	0.04 (0-1)	0.04 (0-1)
103 x 78-5646-6													
79982-P5	0	30	0.50 (0-4)	5.67 (5-7)	2.17 (0-4)	3.50 (2-5)	0.10 (0-1)	0.47 (0-1)	0.30 (0-1)	0.17 (0-1)	-	10.93 (9-14)	11.00 (9-14)
-P3	0	30	0.47 (0-2)	5.67 (5-7)	2.57 (1-5)	3.10 (1-6)	0.20 (0-1)	0.40 (0-1)	0.30 (0-1)	0.10 (0-1)	-	10.47 (8-13)	10.73 (8-13)
-P11	0	30	0.70 (0-3)	5.37 (4-7)	2.33 (1-6)	3.03 (1-6)	0.23 (0-1)	0.47 (0-1)	0.33 (0-1)	0.13 (0-1)	-	10.40 (7-13)	10.40 (7-13)
-P13	0	30	0.97 (0-4)	5.60 (3-7)	2.23 (0-5)	3.37 (2-5)	0.23 (0-1)	0.23 (0-1)	0.20 (0-1)	0.03 (0-1)	0.03 (0-1)	10.33 (8-13)	10.33 (8-13)
-P6	0	30	1.00 (0-5)	5.17 (3-7)	2.13 (0-5)	3.03 (1-5)	0.17 (0-1)	0.50 (0-1)	0.40 (0-1)	0.10 (0-1)	0.03 (0-1)	10.27 (6-13)	10.27 (6-13)
-P4	0	30	0.90 (0-4)	5.20 (4-7)	2.37 (1-6)	2.83 (1-4)	0.23 (0-1)	0.50 (0-1)	0.37 (0-1)	0.13 (0-1)	-	10.13 (8-13)	10.13 (8-13)
-P1	0	30	0.67 (0-2)	5.57 (4-7)	2.97 (0-6)	2.60 (0-5)	0.20 (0-1)	0.40 (0-1)	0.30 (0-1)	0.10 (0-1)	-	9.87 (7-13)	10.07 (7-14)
-P9	0	30	0.97 (0-4)	5.30 (4-7)	2.40 (0-5)	2.90 (0-5)	0.23 (0-1)	0.43 (0-1)	0.37 (0-1)	0.07 (0-1)	-	10.03 (6-13)	10.07 (6-13)

Table 44. (Continued)

Cross combination and Culture No.	No.[1] of Bs	No. of cells observed	A-chromosome pairing[2] UNIV.	BIV. Total	BIV. Rod	BIV. Ring	TRIV.	QUADRIV. Total	QUADRIV. Chain	QUADRIV. Ring	OTHERS	No. of[3] arms paired	No. of chiasmata per cell
79982-P18	0	30	1.33 (0-6)	5.10 (4-6)	2.17 (0-5)	2.93 (1-5)	0.13 (0-1)	0.47 (0-1)	0.40 (0-1)	0.07 (0-1)	0.03 (0-1)	9.93 (5-13)	9.97 (5-13)
-P15	0	30	1.20 (0-4)	5.10 (3-7)	2.33 (0-4)	2.77 (1-5)	0.20 (0-1)	0.50 (0-1)	0.33 (0-1)	0.17 (0-1)	-	9.93 (6-12)	9.93 (6-12)
-P17	0	30	1.30 (0-4)	5.03 (4-7)	2.23 (0-6)	2.80 (1-5)	0.43 (0-2)	0.33 (0-1)	0.23 (0-1)	0.10 (0-1)	-	9.80 (8-13)	9.80 (8-13)
-P19	0	30	1.57 (0-4)	5.13 (3-7)	2.23 (1-4)	2.90 (0-5)	0.23 (0-1)	0.37 (0-1)	0.30 (0-1)	0.07 (0-1)	-	9.67 (6-13)	9.67 (6-13)
-P12	0	30	1.67 (0-6)	5.13 (3-7)	2.53 (1-5)	2.60 (0-4)	0.33 (0-1)	0.27 (0-1)	0.20 (0-1)	0.07 (0-1)	-	9.27 (4-12)	9.50 (5-13)
-P14	0	30	1.33 (0-6)	5.30 (4-7)	2.73 (1-5)	2.57 (1-5)	0.20 (0-1)	0.37 (0-1)	0.23 (0-1)	0.13 (0-1)	-	9.50 (5-13)	9.50 (5-13)
-P2	0	30	1.60 (0-8)	5.17 (3-7)	2.73 (0-7)	2.43 (0-5)	0.20 (0-1)	0.37 (0-1)	0.33 (0-1)	0.03 (0-1)	-	9.13 (3-13)	9.17 (3-13)
-P16	0	30	2.27 (0-8)	5.07 (3-7)	3.00 (1-6)	2.07 (0-4)	0.27 (0-1)	0.20 (0-1)	0.20 (0-1)	-	-	8.27 (5-12)	8.27 (5-12)

1) No. of B-chromosomes in the F_1 hybrids.
2) Figures in the parentheses represent the ranges observed.
3) Figures represent the half numbers of paired arms.

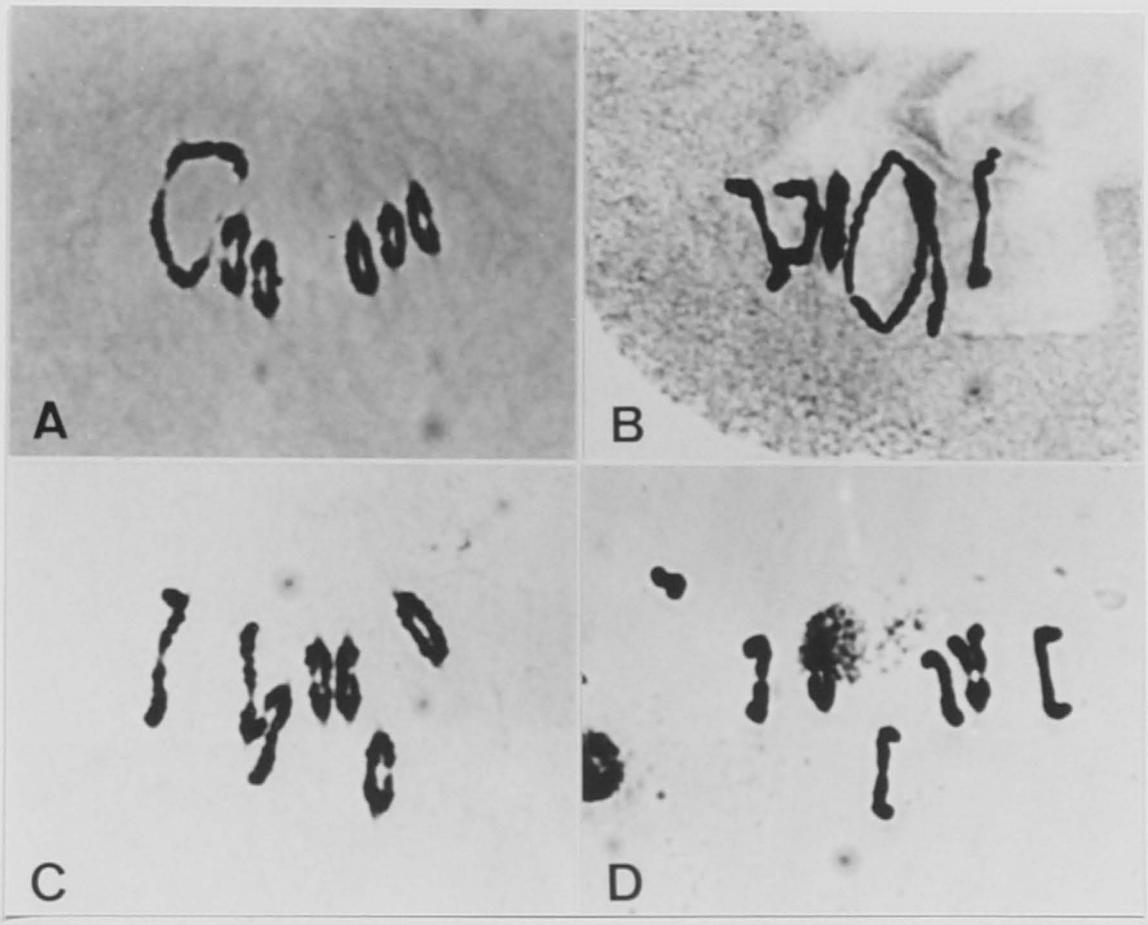


Figure 47. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids without B-chromosomes (Bs) between *Triticum monococcum* ssp. *boeoticum* and *Ae. mutica* (x 1,100). A: 81737-P2, 5_{II}+1ring$_{IV}$; B: 79981-P9, 5_{II}+1ring$_{IV}$; C: 79981-P13, 5_{II}+1chain$_{IV}$; D: 79981-P15, 1_I+5_{II}+1_{III}.

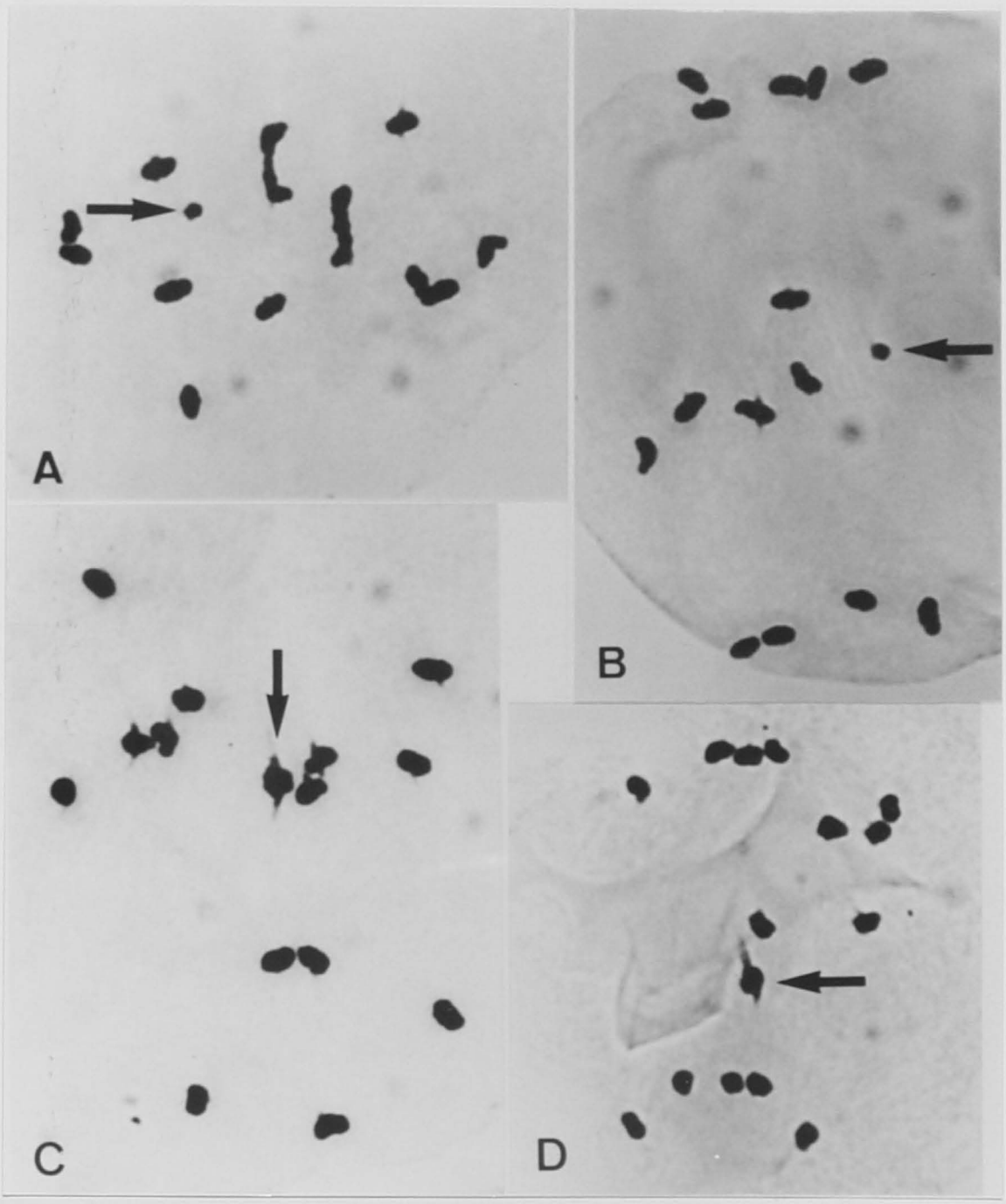


Figure 48. The configuration of chromosome pairing at MI of meiosis in the F_1 hybrids with B-chromosomes (Bs) between *Triticum monococcum* ssp. *boeoticum* and *Ae. mutica* (x 1,100). B-chromosomes are indicated with arrows. A-B: 81736-P1 with a minute telocentric B (A: 10_I+2_{II} of As + 1_I of B, B: 14_I of As + 1_I of B); C: 81735-P3 with 2Bs, 14_I of As + $1ring_{II}$ of Bs; D: 81735-P2 with 2Bs, 14_I of As + $1ring_{II}$ of Bs.

+ 0.23_{III} + (0.28chain + 0.08ring)$_{IV}$ for Culture No. 79981, 0.98_{I} + (2.12rod + 3.03ring)$_{II}$ + 0.23_{III} + (0.30chain + 0.21ring)$_{IV}$ for No.81737, and 1.15_{I} + (2.45rod + 2.84ring)$_{II}$ + 0.23_{III} + (0.30chain + 0.09ring)$_{IV}$ + 0.00_{V} + 0.00_{VI} for No. 79982, respectively.

In contrast with those 0B hybrid plants showing a high frequency of chromosome pairing, four hybrid plants with two B-chromosomes obtained from the cross combination of 101-1 x 80-5641A1-6 showed a drastically low frequency of A-chromosome pairing (Figures 48C and D). The pairing of A-chromosomes in three of those 2B hybrids (Culture Nos. 81735-P2, -F1 and -F2) was almost completely suppressed by their B-chromosomes. Only 14 univalents of A-chromosomes with a small bivalent of B-chromosomes were observed in 133 (89%) cells among a total of 150 PMCs observed. A rod-shaped bivalent with 12 univalents of A-chromosomes was observed in 17 (11%) cells but ring-shaped bivalents of A-chromosomes were not observed at all. The other 2B hybrid (Culture No. 81735-P3) showed slightly higher frequency of chromosome pairing than the above three 2B hybrids. In this plant, 14 univalents of A-chromosomes were observed only in 6 (6%) cells among a total of 100 observed cells but up to five bivalents including ring-shaped ones were often observed.

In addition to those 0B and 2B hybrids, an F_1 hybrid with a B-chromosome was obtained (Culture No. 81736-P1). Its B-chromosome was telocentric and minute. The frequency of A-chromosome pairing in this 1B hybrid was slightly higher than that of the above three 2B hybrids showing a drastically low pairing frequency (χ^2=53.27) though it was slightly lower than another 2B hybrid (Figures 48A and B). However, it

Table 45. Pollen fertility and the dehiscence of anthers in the F_1 hybrids between *Triticum monococcum* ssp. *boeoticum* and *Ae. mutica*

Cross combination and Culture No.	No.of[1] Bs	Pollen fertility (%)	Dehiscence[2] of anthers
103 x 78-5646-6			
79982-P2	0	0	-
-P3	0	0	-
-P4	0	0	-
-P5	0	0	-
-P6	0	0	-
-P9	0	0	-
-P14	0	0	-
-P15	0	0	-
-P16	0	0	-
-P17	0	0	-
-P18	0	0	-
-P19	0	0	-

1) No. of B-chromosomes in the F_1 hybrids.
2) +: dehiscent, ±: partially dehiscent,
-: indehiscent.

was quite significantly lower than that of 0B hybrids ($\chi^2 \geq 977.76$).

Fertility of the F_1 hybrids

The F_1 hybrids between *T. monococcum* ssp. *boeoticum* and *Ae. mutica* both with and without B-chromosomes were all completely sterile and none of their anthers dehisced at anthesis. Pollen fertility was estimated in 12 hybrid plants without B-chromosomes obtained from a cross combination, 103 x 78-5646-6 (Table 45). However, no normal pollen grain was found in those plants.

6. DISCUSSION

As mentioned in Chapter 3, chromosome pairing and fertility of the F_1 hybrid plants give us valuable and indispensable informations about the genetic relationships and, therefore, phylogenetic relationships between their parental species. In addition to the informations from meiosis and fertility, those from crossability between the parental species and various abnormalities found at the vegetative growth stage of the F_1 hybrids are also valuable for estimating the genetic relationships between the parental species. Because these informations are all attributed to the internal reproductive isolation barriers between the species used as parents. To what degree and how these internal barriers serve to reproductively isolate certain taxa are much important for experimentally delimiting biological species. Furthermore, morphological comparisons between the obtained F_1 hybrid plants and their parental species suggest whether the genetic systems controlling the morphological characteristics in which the parental species differ from each other are complex or simple. This information from their morphology is also important for estimating their genetic relationships, because we can distinguish a certain taxon from others mainly based on the difference in their morphology. Especially, when we have to examine herbarium specimens and identify them, we can realize it only based on the morphology of the plants on sheets.

In the present study, 10 diploid *Aegilops* and a diploid *Triticum* species were crossed with *Ae. mutica* with or without B-chromosomes to estimate the cytogenetical relationships between those diploid species

and *Ae. mutica*. And the F_1 hybrids were successfully obtained from 10 interspecific and intergeneric cross combinations except *Ae. searsii* x *Ae. mutica*. Here, I discuss from the above-mentioned viewpoint about the crossability between *Ae. mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex, the abnormalities at the vegetative growth stage of their F_1 hybrids, the morphology of the F_1 hybrids and their parental species, chromosome pairing at MI of meiosis in their PMCs, and their fertility.

Crossability between *Aegilops mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex

Ae. mutica was used as male parents in most of the present crosses. In the crosses between species of sect. Platystachys (= sect. Sitopsis) and *Ae. mutica*, F_1 hybrid seeds were more easily obtained from the crosses involving three of the four species of subsect. Emarginata, *Ae. bicornis*, *Ae. longissima* and *Ae. sharonensis*, than that involving the species of subsect. Truncata, *Ae. speltoides*. The mean percentage seed set of the former cross combinations were 61%, 58% and 32%, respectively. However, the latter cross combination, *Ae. speltoides* x *Ae. mutica*, gave the mean percentage seed set of only 15% in spite of such intensive crosses that a total of 2,212 florets of *Ae. speltoides* were pollinated with pollen grains of *Ae. mutica*. The mean germination rate of this cross combination was also lower than the cross combinations involving the species of subsect. Emarginata. The crosses between *Ae. speltoides* and *Ae. mutica* gave only 10% of germination rate of F_1 hybrid seeds while the above three combinations involving subsect.

Emarginata gave 16 to 93% of germination rates. As a result of the low percentage seed set and the low germination rate, only 1.5% of the pollinated florets contributed to making the F_1 seedlings in the cross between *Ae. speltoides* and *Ae. mutica*. In the cross combination involving another species of subsect. Emarginata, *Ae. searsii* x *Ae. mutica*, F_1 hybrids seeds were easily obtained but they did not germinate at all and no F_1 hybrid plant was obtained. Feldman *et al.* (1979) reported a similar result in the reciprocal crosses between *Ae. searsii* and *Ae. longissima* which are very closely related to each other and placed in the same subsection of section Platystachys. The cross combination of *Ae. longissima* x *Ae. searsii* successfully gave the F_1 hybrid plants growing vigorously while the cross of *Ae. searsii* x *Ae. longissima* resulted in the failure in germination of the F_1 hybrid seeds.

Section Pachystachys (= sect. Vertebrata) has a diploid species, *Ae. squarrosa*. In the reciprocal cross combinations between *Ae. squarrosa* and *Ae. mutica*, a similar result to that involving *Ae. searsii* was obtained. When *Ae. squarrosa* was used as a female parent, large but slightly shrivelled F_1 hybrid seeds were easily obtained and the mean percentage seed set was 56%. In spite of that high percentage seed set, any seeds did not germinate at all and no F_1 seedling could be obtained. In contrast, the F_1 hybrid seeds obtained from the cross combinations having *Ae. squarrosa* as a male parent successfully germinated and gave F_1 hybrid plants. The mean percentage seed set and the mean germination rate were 29% and 69%, respectively.

Jones and Majisu (1968) reported a similar result to the present

one that the crosses between *Ae. squarrosa* and *Ae. mutica* having *Ae. squarrosa* as a female parent gave the many shrivelled seeds which did not germinate. They successfully obtained their F_1 hybrid plants when immature hybrid embryos were cultured. In the present crosses, F_1 hybrid plants were obtained from the crosses having *Ae. squarrosa* as a male parent. In addition, the present cross of an artificially synthesized tetraploid of *Ae. squarrosa* x *Ae. mutica* successfully gave the viable triploid hybrid seeds. These seeds normally germinated and the obtained seedlings vigorously grew till mature stage. This result indicates that the difference in germination between the reciprocal crosses involving *Ae. squarrosa* and *Ae. mutica* was not attributed to the cytoplasmic difference between the parental species.

Among the crosses involving the three species of sect. Macrathera (= sect. Comopyrum and sect. Cylindropyrum), *Ae. comosa* (including *Ae. heldreichii*), *Ae. uniaristata* and *Ae. caudata*, the interspecific cross combination of *Ae. comosa* x *Ae. mutica* gave as high as 56% of seed set. In this combination 36% of the obtained F_1 seeds germinated. However, *Ae. uniaristata* showed very low crossability to *Ae. mutica*. The mean percentage seed set of the crosses, *Ae. uniaristata* x *Ae. mutica*, was 13% and the mean germination rate was 7%. Consequently, only 0.9% of pollinated florets of *Ae. uniaristata* contributed to making the F_1 seedlings. *Ae. caudata* also showed very low seed set when it was crossed with *Ae. mutica* but the germination rate of the F_1 hybrid seeds was as high as 50%. Among a total of 170 pollinated florets of *Ae. caudata*, only five (2.9%) successfully gave the F_1 seedlings.

Section Pleionathera (= sect. Polyeides) has only one diploid

species, *Ae. umbellulata*. The mean percentage seed set and the mean germination rate in the cross of *Ae. umbellulata* x *Ae. mutica* were 38% and 20% respectively.

For the genus *Triticum*, three accessions of the wild subspecies of *T. monococcum* were crossed with *Ae. mutica*, two of which belong to former species *T. boeoticum* Boiss. and the other to former species *T. urartu* Thum. Many F_1 seeds were obtained from the cross having former species *T. urartu* as a female parent, they did not germinate at all. However, in the cross combination involving the other former species, *T. boeoticum*, as a female parent, many F_1 hybrid plants were obtained from the easily obtained F_1 seeds. The mean percentage seed set and the mean germination rate of the F_1 seeds in the cross combination, *T. boeoticum* x *Ae. mutica*, were so high as 50%. And among a total of 204 pollinated florets of *T. boeoticum*, 52 (25%) contributed to F_1 seedlings. A similar result was reported in the crosses between *T. urartu* and *T. boeoticum* by Johnson and Dhaliwal (1976), Yamagishi and Tanaka (1978, 1983) and Yamagishi (1987). Johnson and Dhaliwal (1976) found that the F_1 hybrid seeds resulted from the cross of *T. urartu* x *T. boeoticum* did not germinate while those from the cross of *T. boeoticum* x *T. urartu* could germinate and gave the F_1 seedlings. And they suggested that the cytoplasm of *T. urartu* in combination with the genome of *T. boeoticum* inhibited the development of viable F_1 hybrid seeds. Soon after it, Dhaliwal (1977) suggested that the difference in germination between reciprocal crosses may not always be attributed to cytoplasmic difference between the parental species and he concluded that the difference between the reciprocal crosses was attributable to different

genomic ratios between *boeoticum* and *urartu* in the triploid endosperm.

Crossability is affected by many factors other than the genetic relationships between the parental species, such as physiological condition of the plants, technical levels of the researchers and climatic condition during and after pollination, and so on. However, generally speaking, the crossability between *Ae. mutica* and the other diploid species of the *Aegilops-Triticum* complex was enough high and it was compared to that of the other interspecific cross combinations among diploid *Aegilops-Triticum* species.

Reproductive isolation barriers at the vegetative growth stage

No reproductive isolation barriers after germination at the vegetative growth stage such as necrosis, chlorosis, dwarfness or other hybrid weakness were not observed in the present F_1 hybrids between the 10 diploid *Aegilops-Triticum* species and *Ae. mutica*. Most of the F_1 seedlings obtained from the present interspecific and intergeneric crosses involving *Ae. mutica* grew normally and vigorously. Most of them had normal three anthers in the each floret and flowered normally even when they were highly sterile.

Morphology of the F_1 hybrid plants

All the F_1 hybrids between the diploid species of the *Aegilops-Triticum* complex and *Ae. mutica* had linear spikes on which spikelets were arranged in a row. And the length of their spikes was intermediate between those of the two parental species. These characteristics of the F_1 hybrids are resulted from the facts that the length of rachis

internodes in the F_1 hybrids was similar to that of *Ae. mutica* and that the number of the spikelets comprising the spikes of the F_1 hybrids was intermediate between the two parental species used in the crosses. The other prominent characteristic common to the present F_1 hybrids was the awnlessness of their spikes without rudimentary spikelets. Except for the F_1 hybrids involving *Ae. umbellulata*, those from all the interspecific and intergeneric cross combinations had spikes without awns though every diploid species of the *Aegilops-Triticum* complex had awns on their empty glumes and/or lemmas. Spikes of some F_1 hybrids between *Ae. speltoides* or *T. monococcum* and *Ae. mutica* had very short awns on their lemmas but the majority of the F_1 hybrids obtained from those cross combinations did not have any awns. This indicates that the awnless empty glumes and lemmas of *Ae. mutica* is genetically epistatic or dominant over the awned empty glumes and lemmas of the other species. Furthermore, the spikes of the present F_1 hybrids involving the diploid *Aegilops-Triticum* species except *Ae. umbellulata* did not have any rudimentary or sterile spikelets at their any parts. This indicates that the spikes without any rudimentary spikelets of *Ae. mutica* are also genetically epistatic or dominant over those with rudimentary spikelets of the other diploid species.

From these reasons, the long and linear spikes of the F_1 hybrids between the species with many spikelets of sect. Platystachys, *Ae. squarrosa* or *T. monococcum* and *Ae. mutica* looked like those of *Ae. mutica* at a glance. The present F_1 hybrids involving *Ae. caudata*, *Ae. comosa* or *Ae. uniaristata* had awnless spikes like *Ae. mutica* but their spike length was much shorter than that of *Ae. mutica*. Among the

diploid species of the *Aegilops-Triticum* complex, *Ae. umbellulata* is morphologically the most different from *Ae. mutica*. Their F_1 hybrids showed the intermediate morphology between their parental species even in some of the above characteristics in which the other F_1 hybrids were much similar to *Ae. mutica*. They had one or two basal rudimentary spikelets on the spikes. And both their empty glumes and lemmas had short awns. These results indicate that the difference in spike morphology between *Ae. mutica* and *Ae. umbellulata* is controlled with many genes gradually differentiated during a long geological time.

In addition to those characteristics, the wedge type disarticulation in *Ae. mutica* was also genetically epistatic or dominant over the other disarticulation types such as the barrel type in *Ae. squarrosa* and the umbrella type of *Ae. speltoides* (*sensu strict*), *Ae. caudata*, *Ae. comosa*, *Ae. uniaristata* and *Ae. umbellulata*. However, another type of disarticulation, floret type, of *Ae. mutica* was not found in the F_1 hybrids though the hybrids between *Ae. speltoides* and *Ae. mutica* had somewhat fragile rachillae. Both *Ae. mutica* and *Ae. speltoides* have spikelets with more florets than the other diploid species of the *Aegilops-Triticum* complex. And their florets are more or less laxly arranged. Their F_1 hybrids also had these characteristics common to their parents. From these results, it is suggested that the many florets and their lax arrangement in the spikelets may genetically associate with fragile rachillae.

Many of the other morphological characteristics in the F_1 hybrids were intermediate between the two parental species. The number of spikelets, the number of florets in a spikelet, the number and the shape

of teeth on empty glumes, the prominence of keel on empty glumes and the shape of empty glumes and lemmas of the F_1 hybrids were all, roughly speaking, intermediate between *Ae. mutica* and the other diploid species. These characteristics, therefore, may be controlled by many genes or many polygenic systems much different between the parental species.

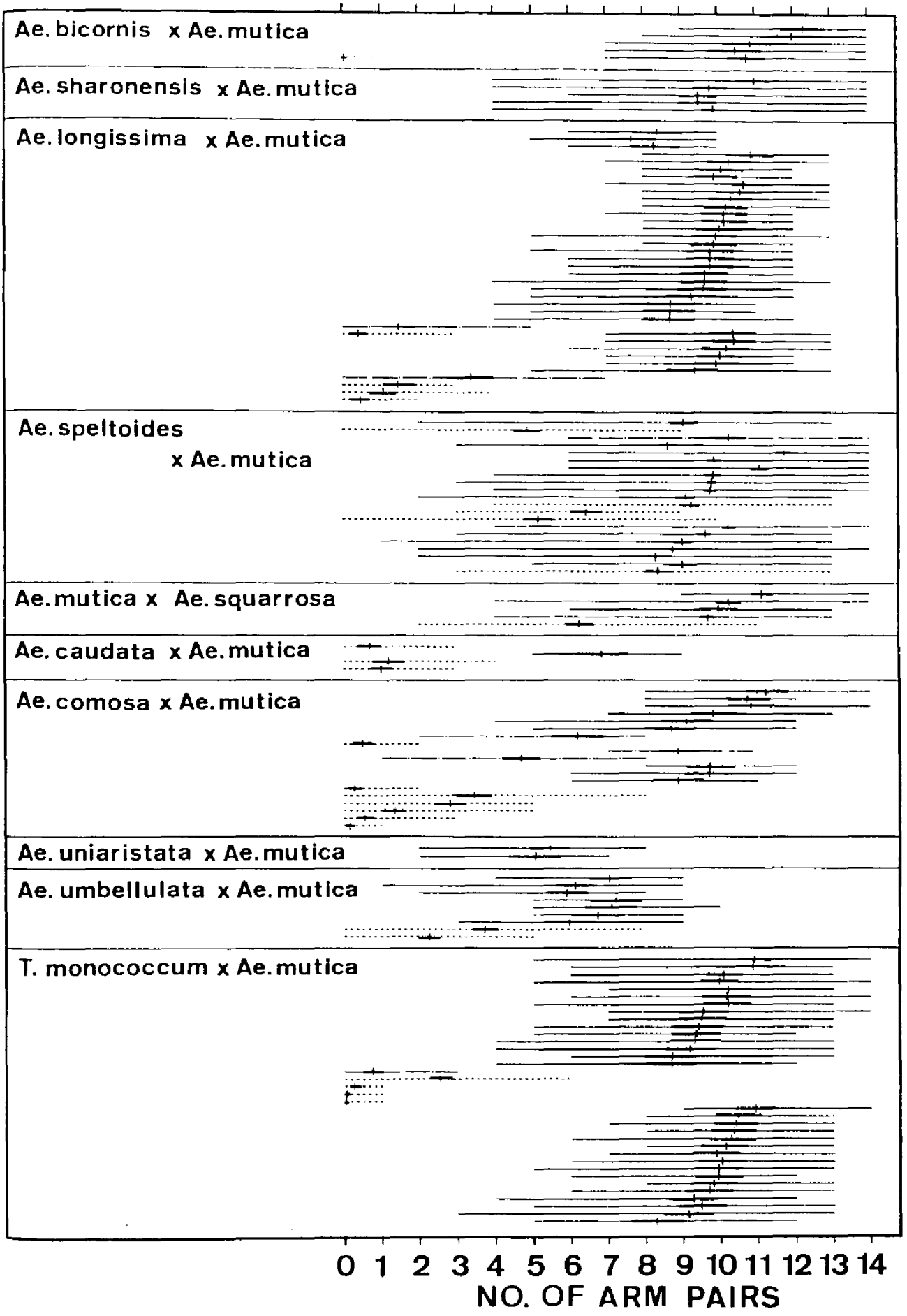
Considering all the morphological characteristics observed in the present F_1 hybrids, it can be concluded that among all the obtained interspecific and intergeneric F_1 hybrids, those between the species of sect. Platystachys and *Ae. mutica* were the most similar to *Ae. mutica*. Especially, the F_1 hybrids between the accessions having many florets of *Ae. speltoides* and *Ae. mutica* were much similar to *Ae. mutica*. They had long linear spikes consisting of many spikelets with many florets laxly arranged in the spikelets. Their empty glumes covered only a lower half of their spikelet. Furthermore, their rachillae were partly fragile in addition to the wedge type disarticulation of their rachis. These resemblances in spike morphology between the F_1 hybrids and *Ae. mutica* are thought to be resulted from the following two reasons: First, their parental species, *Ae. speltoides* and *Ae. mutica*, have many morphological characteristics in common; second, many of the morphological characteristics different between the two parental species are controlled by rather simple genic systems than complex polygenic systems. From these consideration, I conclude that *Ae. mutica* is the most similar to *Ae. speltoides* in the spike morphology among the diploid species of the congeneric *Aegilops-Triticum* complex. Boissier (1884) already pointed out that *Ae. mutica* most resembles *Ae. Aucheri* Boiss., a synonym of *Ae. speltoides* Tausch, in morphology. In the present work on

the F_1 hybrids among the diploid *Aegilops-Triticum* species, I reached the same conclusion as Boissier's one.

Chromosome pairing at MI of meiosis in the F_1 hybrid plants between *Aegilops mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex

In the present work, 10 diploid *Aegilops* and one diploid *Triticum* species were crossed with *Ae. mutica* with or without B-chromosomes. F_1 hybrids were successfully obtained from the 10 interspecific and intergeneric cross combinations involving nine *Aegilops* and one *Triticum* species: *Ae. bicornis* x *Ae. mutica*, *Ae. sharonensis* x *Ae. mutica*, *Ae. longissima* x *Ae. mutica*, *Ae. speltoides* x *Ae. mutica*, *Ae. mutica* x *Ae. squarrosa*, *Ae. caudata* x *Ae. mutica*, *Ae. comosa* x *Ae. mutica*, *Ae. uniaristata* x *Ae. mutica*, *Ae. umbellulata* x *Ae. mutica*, and *T. monococcum* ssp. *boeoticum* x *Ae. mutica*. And chromosome pairing at MI of meiosis in their PMCs was analyzed in detail using B-chromosomes of *Ae. mutica* for effectively suppressing the pairing between homoeologous or partially homologous chromosomes. The mean and range of the numbers of arm pairs per PMC in the every present F_1 hybrid with or without B-chromosomes are summarized in Figure 49. The principle of the present genome analysis using B-chromosomes was shown in Figure 5 and explained in Chapter 3. In this section, the relationships between the genome of

Figure 49. Mean and range of the numbers of arm pairs per PMC in the every F_1 hybrid plant obtained in the present crosses between *Aegilops mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex. Solid, broken and dotted horizontal lines represent the ranges of the numbers of arm pairs per PMC in the hybrid plants with 0B, 1B and 2Bs, respectively. Short vertical lines and thick horizontal lines indicate the mean numbers of arm pairs and their 95% confidence limits, respectively.


Ae. bicornis x Ae. mutica
Ae. sharonensis x Ae. mutica
Ae. longissima x Ae. mutica
Ae. speltoides
x Ae. mutica
Ae. mutica x Ae. squarrosa
Ae. caudata x Ae. mutica
Ae. comosa x Ae. mutica
Ae. uniaristata x Ae. mutica
Ae. umbellulata x Ae. mutica
T. monococcum x Ae. mutica
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
NO. OF ARM PAIRS

Ae. mutica and those of the other diploid species in the congeneric *Aegilops-Triticum* complex are discussed based on that principle of the present genome analysis.

1) Chromosome pairing in the F_1 hybrids without B-chromosomes

The F_1 hybrids without B-chromosomes between *Ae. mutica* and the following seven species, *Ae. bicornis*, *Ae. sharonensis*, *Ae. longissima*, *Ae. speltoides*, *Ae. squarrosa*, *Ae. comosa* and *T. monococcum*, showed a very high frequency of chromosome pairing though the F_1 hybrid plants from some cross combinations showed a high frequency of chain- or ring-shaped quadrivalents. In the crosses between *Ae. comosa* and *Ae. mutica*, the frequency of multivalents greatly differed between the F_1 hybrids obtained from the two subspecies of *Ae. comosa* involved. The hybrids having ssp. *eu-comosa* Eig (KU 17-1) as female parents showed few or no quadrivalents while those having ssp. *heldreichii* (Holzm.) Eig (KU 17-2) as female parents frequently formed a quadrivalent or a trivalent, even when the same individual of *Ae. mutica*, 78-5642c-4, was used as the male parents. Kihara (1937) reported that a quadrivalent was observed in the F_1 hybrids between *Ae. comosa* Sibth. et Sm. (= *Ae. comosa* ssp. *eu-comosa* Eig) and *Ae. Heldreichii* Holzm. (= *Ae. comosa* ssp. *heldreichii* (Holzm.) Eig). Yamada and Suzuki (1941) also found a quadrivalent in the F_1 hybrids from the same cross combination. The difference in the frequency of multivalents observed in the present F_1 hybrids involving these two subspecies of *Ae. comosa* can be explained by these findings: Chromosomal structures of these two subspecies of *Ae. comosa* differ from each other by an interchange of their segments. Furthermore, the F_1

hybrids obtained from the same cross combination between *Ae. mutica* and *Ae. squarrosa* showed the quite different frequency of quadrivalent formation (Culture No. 84011). The parental individual of *Ae. mutica* used in that cross combination (83-5610A-16) formed a quadrivalent in its PMCs at MI of meiosis and proved to be a heterozygote for an interchange of its chromosomes (Table 11 and Figure 7A). Therefore, the difference in the frequency of multivalents between the 0B hybrids was resulted from that heterozygosity of the chromosomal structure in the parental *mutica* plant. In spite of those differences in the frequency of multivalent formation, all the 0B hybrids obtained from the crosses of the two subspecies of *Ae. comosa* x *Ae. mutica* and *Ae. mutica* x *Ae. squarrosa* showed a very high frequency of chromosome pairing.

However, the 0B hybrid plants obtained from the crosses of *Ae. caudata*, *Ae. uniaristata* and *Ae. umbellulata* x *Ae. mutica* showed a lower frequency of A-chromosome pairing than those from the above cross combinations. And a more complicated configuration of A-chromosome pairing was observed especially in the two cross combinations, *Ae. caudata* and *Ae. umbellulata* x *Ae. mutica*, compared with the 0B hybrids obtained from the above-mentioned seven cross combinations. These results indicate that the chromosomes of *Ae. mutica* much differ by many structural arrangements from those of *Ae. caudata*, *Ae. uniaristata* and *Ae. umbellulata*, and that the genome of *Ae. mutica* is distantly related to those of these three species.

2) Chromosome pairing in the F_1 hybrids with two B-chromosomes

The F_1 hybrid plants with two B-chromosomes obtained from the

crosses of *Ae. bicornis*, *Ae. longissima*, *Ae. caudata*, *Ae. comosa*, *Ae. umbellulata* and *T. monococcum* x *Ae. mutica* showed a very low frequency of A-chromosome pairing. In those F_1 hybrids, 14 univalents or 12 univalents with a rod-shaped bivalent of A-chromosomes were characteristically found in addition to a tightly associated small ring-shaped bivalent of B-chromosomes at MI of meiosis in their PMCs.

In contrast with those 2B hybrid plants, those obtained from the crosses of *Ae. speltoides* x *Ae. mutica* and *Ae. mutica* x *Ae. squarrosa* showed a remarkably higher frequency of A-chromosome pairing with many ring-shaped bivalents. The frequency of A-chromosome pairing in the 2B hybrids between *Ae. speltoides* and *Ae. mutica* varied widely. The plant showing the highest pairing frequency formed 9.52 chiasmata per cell but that showing the lowest frequency formed 4.95 chiasmata per cell. The pairing frequency observed in two of the 2B hybrids (Culture Nos. 84006-P2 and 84008-P2) between *Ae. speltoides* and *Ae. mutica* did not differ significantly from the frequency observed in the 0B hybrids. Even the lowest pairing frequency among those observed in all the 2B hybrids between *Ae. speltoides* and *Ae. mutica* (Culture No. 80775-P1) was significantly higher than those in the 2B F_1 hybrids obtained from the other interspecific cross combinations. From the cross combination, 7972 x 83-5641-6, two F_1 hybrids were obtained, one of which had no B-chromosomes but the other had two Bs. In those F_1 hybrids, the frequency and configuration of A-chromosome pairing were almost similar to each other. In the cross combination of *Ae. mutica* x *Ae. squarrosa*, only one 2B hybrid was obtained and it showed the similar configuration and frequency of A-chromosome pairing to the above-mentioned 2B hybrids

between *Ae. speltoides* and *Ae. mutica*.

It is well known that B-chromosomes of *Ae. mutica* effectively suppress the pairing between homoeologous or partially homologous chromosome but they do not affect the pairing between fully homologous ones (Mochizuki 1964, Dover and Riley 1972b, Vardi and Dover 1972, Ohta and Tanaka 1982). This fact and the present result obtained from the chromosome pairing in the F_1 hybrids with two B-chromosomes clearly indicate that the genome of *Ae. mutica* is almost homologous with those of *Ae. speltoides* and *Ae. squarrosa*. Furthermore, they indicate that it is only homoeologous with those of *Ae. bicornis*, *Ae. longissima*, *Ae. comosa*, *T. monococcum* though the F_1 hybrids without B-chromosomes between these four species and *Ae. mutica* showed almost regular and high frequency of chromosome pairing.

However, the genome of *Ae. mutica* is not fully homologous with even those of *Ae. speltoides* and *Ae. squarrosa*, because the A-chromosome pairing in the F_1 hybrids between these species and *Ae. mutica* was reduced by the two B-chromosomes carried by those 2B hybrids. In addition, the mean frequency of univalents and trivalents in the present triploid hybrid with two genomes of *Ae. squarrosa* and one of *Ae. mutica* were 6.32 and 1.08 per cell, respectively. Moreover, all the PMCs with the doubled number of chromosomes found in the present 2B hybrid (Culture No. 86303-P1) between *Ae. mutica* and *Ae. squarrosa* formed 14 tightly associated bivalents of A-chromosomes besides their four B-chromosomes. Those present observations suggest that the genome of *Ae. mutica* is so different from the genome of *Ae. squarrosa* that two genomes of *Ae. squarrosa* preferentially pair with each other in the triploid

hybrid, and that only homologous chromosomes transmitted from the each parental species can pair in the 4*n* cells with four B-chromosomes in the plant of No. 86303-P1. Vardi and Dover (1972) reported a very low frequency of chromosome pairing in the F_1 hybrids with three or four B-chromosomes between *Ae. speltoides* and *Ae. mutica*. Because the B-chromosomes in their F_1 hybrids were derived from both *Ae. speltoides* and *Ae. mutica*, it is impossible to directly compare the present results with their result. However, their result suggests that three or more B-chromosomes derived from *Ae. mutica* may be able to suppress the association between the A-chromosomes of *Ae. speltoides* and *Ae. mutica*, judging from the fact that B-chromosomes of *Ae. speltoides* have a similar effect on chromosome pairing to those of *Ae. mutica* (Dover and Riley 1972b). This also supports that the genomes of *Ae. mutica* and *Ae. speltoides* are almost but not fully homologous.

3) Chromosome pairing in the F_1 hybrids with a B-chromosome and a dosage effect of B-chromosomes

In addition to 0B and 2B hybrid plants, F_1 hybrids with one B-chromosome were obtained from the crosses involving *Ae. longissima*, *Ae. speltoides*, *Ae. comosa*, *Ae. squarrosa* and *T. monococcum*. The B-chromosomes found in the 1B hybrids obtained from the crosses of *Ae. longissima* x *Ae. mutica*, *Ae. comosa* x *Ae. mutica* and *T. monococcum* x *Ae. mutica* were minute and telocentric. The morphology of the normal B-chromosome of *Ae. mutica* is two thirds of the shortest A-chromosome in size and metacentric in shape, and all the B-chromosomes observed in the parental lines of *Ae. mutica* had the normal morphology. Those minute telocentric B-chromosomes found in the F_1 hybrids were probably derived

from the normal ones through the misdivision of their centromeres during the meiotic process in the parental lines when the normal B-chromosome behaved as a univalent in their PMCs. The frequency and configuration of A-chromosome pairing in those 1B hybrids were, roughly speaking, intermediate between 0B and 2B hybrids. In the combination of *Ae. longissima* x *Ae. mutica*, two 1B plants showed slightly higher frequency of A-chromosome pairing than the 2B hybrids obtained from the same cross combinations. In the combination of *Ae. comosa* x *Ae. mutica* hybrids, the result was more complicated than the combination involving *Ae. longissima*. One of the three 1B hybrids (Culture No. 79948-P1) showed the intermediate frequency of chromosome pairing between the 0B and 2B hybrids from the same cross combination, 17-1 x 78-5642c-4. The other two 1B hybrids were obtained from the cross combination of 17-2 x 77-5641-4 but their frequency of A-chromosome pairing significantly differed from each other. One of them (Culture No. 78409-P1) showed the similar frequency and configuration of A-chromosome pairing to the 0B hybrids obtained from the cross combination having the same accession of *Ae. comosa* as a female parent. In contrast with that plant, another (Culture No. 78409-P2) showed the intermediate frequency of A-chromosome pairing between the 0B and 2B hybrids. The most plausible explanation for this difference in the pairing frequency is that the minute telocentric B-chromosomes found in those 1B plants were derived from the different arms of the B-chromosome carried by the parental 1B plant (77-5641-4) and, at the same time, the genetic factor(s) effective to the frequency of A-chromosome pairing locates on only one of two morphologically similar arms of the normal metacentric B-chromosome.

One of the plants (Culture No. 78409-P1) contained the telocentric B-chromosome derived from the arm which did not have genetic factors effective to A-chromosome pairing but another (Culture No. 78409-P2) had that derived from the B-chromosome arm effective to A-chromosome pairing. From the present result that most 1B hybrids showed the intermediate frequency of chromosome pairing between 0B and 2B hybrid plants, B-chromosomes of *Ae. mutica* are concluded to have a dosage effect on association between partially homologous chromosomes.

In contrast with the minute telocentric B-chromosomes found in the F_1 hybrids involving *Ae. longissima*, *Ae. comosa* and *T. monococcum*, those found in the 1B hybrids obtained from the other two interspecific cross combinations, *Ae. speltoides* x *Ae. mutica* and *Ae. mutica* x *Ae. squarrosa* were the normal metacentric ones. In spite of the entirety of their B-chromosomes, the frequency and configuration of A-chromosome pairing in those 1B hybrids were quite similar to those of the 0B hybrid plants showing a very high frequency and almost regular configuration of A-chromosome pairing. This result suggests that the genome of *Ae. mutica* is so homologous with those of *Ae. speltoides* and *Ae. squarrosa* that the pairing between their A-chromosomes can not be effectively reduced in the 1B hybrids. And this supports the present conclusion that the genome of *Ae. mutica* is almost homologous with those of *Ae. speltoides* and *Ae. squarrosa*.

4) Relationships between the genomes of ten diploid species of the congeneric *Aegilops-Triticum* complex and the genome of *Ae. mutica* based on the present new method for the genome analysis using B-chromosomes

In the light of the principle of the present new method for the genome analysis using B-chromosomes of *Ae. mutica* (Figure 5), the genomes of ten diploid species of the *Aegilops-Triticum* complex used in the present study were classified into the following three groups based on their relationships to the genome of *Ae. mutica* (Table 46): First, the genomes of *Ae. bicornis*, *Ae. longissima*, *Ae. comosa* and *T. monococcum* ssp. *boeoticum* are classified into the Class (b) in Figure 5 and they are only homoeologous with that of *Ae. mutica*. For *Ae. sharonensis*, only 0B hybrids were obtained but it is reasonably concluded that chromosome pairing observed in those 0B hybrids are between homoeologous ones. Because *Ae. longissima* and *Ae. sharonensis* are cytogenetically very closely related to each other and share the same genome (Kihara 1954, Tanaka 1955a). For these reasons, the genome of *Ae. sharonensis* should be placed in this group together with those of the other species belonging to subsection Emarginata of sect. Platystachys. Second, the genomes of *Ae. caudata* and *Ae. umbellulata* are more distantly related to that of *Ae. mutica* than those of the above five species and they are classified into the intermediate class between the Classes (b) and (c) in Figure 5. Any 2B hybrids were not obtained from the cross combination of *Ae. uniaristata* x *Ae. mutica*. However, judging from the low crossability and the low pairing frequency in the 0B hybrids between this species and *Ae. mutica*, its genome can be concluded to be distantly related to that of *Ae. mutica* and it should be

Table 46. Relationships between the genome of ten diploid species in the genera *Aegilops* and *Triticum* and the genome of *Ae. mutica*, by the principle of the present new method for the genome analysis shown in Figure 5.

Relationships with the genome of *Ae. mutica*	Class shown in Figure 5	Species
Homologous	(a)	None
Homologous - Homoeologous	Intermediate between (a) and (b)	*Ae. speltoides*, *Ae. squarrosa*
Homoeologous	(b)	*Ae. bicornis*, *Ae. sharonensis*, *Ae. longissima*, *Ae. comosa*, *T. monococcum*
Homoeologous - Non-homologous	Intermediate between (b) and (c)	*Ae. caudata*, *Ae. uniaristata*, *Ae. umbellulata*
Non-homologous	(c)	None

placed in this group together with *Ae. caudata* and *Ae. umbellulata*.

And third, in contrast with the above eight species, even 2B hybrids between *Ae. speltoides* or *Ae. squarrosa* and *Ae. mutica* showed a high frequency of A-chromosome pairing as well as their 0B hybrids did. The genomes of these two species are very closely related to that of *Ae. mutica* and they are almost homologous with that of *Ae. mutica*. As a result, they are classified into the intermediate class between the Classes (a) and (b) in Figure 5.

Fertility of the F_1 hybrids

1) Close genetic relationship between *Aegilops speltoides* and *Ae. mutica*

The F_1 hybrids obtained from most interspecific and intergeneric cross combinations in the present work were completely sterile and their anthers did not dehisce at all except the individuals which formed unreduced gametes. All the F_1 hybrids obtained from the present crosses involving the eight diploid species, *Ae. bicornis*, *Ae. sharonensis*, *Ae. squarrosa*, *Ae. caudata*, *Ae. comosa*, *Ae. uniaristata*, *Ae. umbellulata* and *T. monococcum* showed complete or almost complete pollen sterility and most of their pollen grains were empty whether they had B-chromosomes or not. Most of the F_1 hybrid plants between *Ae. longissima* and *Ae. mutica* were also completely sterile but two 2B hybrids (Culture No. 79938-P8 and -P22) showed a good pollen fertility and their anthers normally dehisced. The BC_1F_1 plants (Culture No. 79791) obtained from the backcross of the parental accession of *Ae. longissima* to one of them had

21 A-chromosomes in addition to two B-chromosomes. Judging from their configuration and frequency of A-chromosome pairing at MI, they proved to contain two genomes of *Ae. longissima* and one of *Ae. mutica*. And from the genome constitution of the BC_1F_1 plants, it can be reasonably concluded that the good fertility observed in those two 2B hybrid plants between *Ae. longissima* and *Ae. mutica* is not due to their close genetic relationship but to the formation of unreduced gametes in the F_1 hybrids.

In contrast with the complete or almost complete sterility in the F_1 hybrids from the above-mentioned nine cross combinations, partially fertile 0B hybrids were obtained from the crosses between *Ae. speltoides* and *Ae. mutica*. None of the 0B hybrids between *Ae. speltoides* and *Ae. mutica* showed complete male sterility. Their lowest pollen fertility was 0.2%. And the highest fertility was obtained from the two hybrid plants from the cross combination of 5725B x 83-5646-2. Their pollen fertility was 16.7% and 9.0%, and about a half of their anthers dehisced at anthesis. Their normal pollen grains had normally reduced number of chromosomes judging from their size. Furthermore, one of the 0B hybrids (Culture No. 84007-P1) set six well developed seeds in its florets by the open-pollination among the F_1 hybrid plants between *Ae. speltoides* and *Ae. mutica* which grew together. Three of them germinated and grew to mature plants. The chromosome numbers in root tips in two of them were 14 and in another 15. They were, therefore, resulted from the fertilization between normally reduced male and female gametes with basically seven chromosomes. The present observations at MI and AI of meiosis in the 0B hybrids between *Ae. speltoides* and *Ae. mutica* show

that a high frequency of genetic recombination or exchange of chromatid segments occurred during meiosis between the two different genomes derived from the parental species. Because chiasmata observed at MI or diakinesis is the cytological evidence of genetic recombinations or crossing-overs between sister chromatids of the two parental chromosomes, and because chromatid bridges with chromatid fragments at AI are also resulted from the crossing-overs among sister chromatids during pachytene in the heterozygotes for paracentric inversions. The fact that viable and functional male and female gametes with seven chromosomes could be produced in spite of a high frequency of gene exchanges between the parental genomes through crossing-overs clearly indicates that the two parental species, *Ae. speltoides* and *Ae. mutica*, are genetically very closely related to each other.

Sears (1941) crossed a total of nine diploid *Aegilops* and *Triticum* species with one another. And he successfully obtained the F_1 hybrids from 32 cross combinations among them. He reported that those F_1 hybrids were highly sterile and their pollen fertility was lower than 5% except for the F_1 hybrids between *Ae. speltoides* and *Ae. sharonensis* whose pollen fertility was 12%, and that no hybrid set seeds. *Ae. speltoides* and *Ae. sharonensis* are closely related to each other. They are morphologically placed in the same section of *Aegilops*, sect. Platystachys (Eig 1929a), and cytogenetically have the same basic genome 'S' (Kihara 1954, Kihara and Tanaka 1970). Kihara (1937) summarized the chromosome pairing and seed fertility of the F_1 hybrids from 15 interspecific cross combinations among diploid species of the genera *Aegilops* and *Triticum*. And those hybrids were completely sterile except

for those forming unreduced gametes. In the present F_1 hybrids between *Ae. speltoides* and *Ae. mutica*, the highest pollen fertility was about 17% and three of the eight 0B hybrids formed more than 5% of normal pollen grains in their anthers. Judging from these facts and the present result from the fertility of the F_1 hybrids, I reasonably conclude that *Ae. speltoides* and *Ae. mutica* are genetically very closely related to each other and they have the same basic genome. And I propose that the genome of *Ae. mutica* should be renamed to 'S^m' from 'Mt' in order to represent its close genetic relationship with the genome 'S' of *Ae. speltoides*.

2) Unreduced gamete formation in the F_1 hybrids with B-chromosomes

Among the F_1 hybrid plants resulted from one of the crosses between *Ae. longissima* and *Ae. mutica*, two F_1 hybrids with two B-chromosomes showed a good pollen fertility due to the formation of unreduced gametes, and their anthers normally dehisced at anthesis. However, the other F_1 hybrids between *Ae. longissima* and *Ae. mutica* were completely sterile or showed drastically low pollen fertility up to 0.9%. And their anthers did not dehisce at all. Another plant with a high frequency of normal pollen grains due to the unreduced gametes formation was found in the cross combination of *Ae. speltoides* x *Ae. mutica* (Culture No. 78418-P1). Its pollen fertility was 62.1% and its anthers normally dehisced at anthesis. That plant had a B-chromosome and that B was normal in morphology. In addition to those three F_1 hybrid plants which formed unreduced gametes in a high frequency, two F_1 plants with two B-chromosomes obtained from the cross combination of *Ae. speltoides*

x *Ae. mutica* proved to have formed unreduced gametes. In one of them (Culture No. 84006-P1) its anthers partially dehisced while in the other (Culture No. 84008-P2) did not. In contrast with those F_1 hybrid plants with B-chromosomes, none of the 0B hybrids showed the formation of unreduced gametes. Even when much more 0B hybrids than 2B hybrids were obtained from the same cross combination between *Ae. longissima* and *Ae. mutica* (4-4 x 78-5641e-6), those 0B plants did not form any unreduced gametes at all while two 2B hybrids formed unreduced gametes in a high frequency. The present result suggests that B-chromosomes of *Ae. mutica* are responsible to the unreduced gametes formation in those F_1 hybrids.

Vardi and Dover (1972) found that many pollen mother cells had double the expected number of chromosomes in most F_1 hybrid between *T. aestivum* or *Ae. speltoides* and *Ae. mutica* containing B-chromosomes derived from *Ae. mutica*. And they suggested that it is a result of the failure of the pre-meiotic mitotic spindles in the presence of the B-chromosomes of *Ae. mutica*. The present finding of $4n$ pollen mother cells with the doubled chromosome number (28 A-chromosomes and four B-chromosomes) in the 2B F_1 hybrid plants between *Ae. mutica* and *Ae. squarrosa* coincides with their observation and supports their suggestion. However, this 2B hybrid plant was highly sterile. The above three 1B and 2B hybrid plants showing a high pollen fertility by the unreduced gamete formation did not have PMCs with the doubled chromosome number but had normal ones with 14 A-chromosomes with B-chromosome(s). The present observations suggest that the chromosome doubling which leaded to the formation of unreduced gametes in those three hybrid plants occurred not at pre-meiotic stage but during meiotic

divisions. Considering from these observations and the fact, it is suggested that B-chromosomes of *Ae. mutica* can cooperate with certain genotype(s) located on A-chromosomes of some *Aegilops-Triticum* species to inhibit the formation of spindle fibers during pre-meiotic or meiotic divisions, and that a high fertility by the unreduced gamete formation in the present hybrids was caused mainly by such an inhibition during meiotic divisions.

Mechanisms of the sterility in the interspecific F_1 hybrids between diploid species of the congeneric *Aegilops-Triticum* complex and *Ae. mutica*

Interspecific hybrids between closely related species often show complete sterility or semi-sterility though their chromosome pairing in meiosis is nearly normal (Stebbins 1945, 1950). Stebbins (1945) explained that cryptic structural hybridity caused such sterility in those interspecific hybrids. He defined cryptic structural hybridity as chromosomal sterility due to heterozygosity for structural differences so small as not materially influence chromosome pairing at meiosis.

The present diploid F_1 hybrids without B-chromosomes from many cross combinations involving *Ae. mutica* showed complete sterility or semi-sterility though they showed a very high frequency and almost regular configuration of chromosome pairing at MI of meiosis. It can not be strictly decided whether the sterility observed in the present F_1 hybrids is chromosomal sterility or genic sterility, because the decision can be made only after allopolyploids induced from the F_1 hybrids by chromosome doubling are obtained. Such artificial

allopolyploids were not induced in the present study. However, in the present work, an F_1 hybrid with a B-chromosome between *Ae. speltoides* and *Ae. mutica* which formed unreduced gametes showed more than 60% of pollen fertility. Furthermore, two F_1 hybrids with two B-chromosomes between *Ae. longissima* and *Ae. mutica* also showed a good pollen fertility. These facts indicate that pollen grains containing unreduced chromosome complements can restore their fertility and this suggests that the sterility of the F_1 hybrids is not genic but chromosomal.

Most of the 0B hybrids between *Ae. speltoides* and *Ae. mutica* obtained from the present crosses formed a low frequency of trivalents and quadrivalents. In addition, one of them formed chromatid bridges and acentric chromatid fragments at AI of meiosis showing to be heterozygous for paracentric inversions. These observations indicate that the parental two genomes differ from each other by small interchanges and inversions of their chromosomes and they suggest that the semi-sterility in the F_1 hybrids is resulted from the heterozygosity for small structural differences of their chromosomes, *i.e.* the cryptic structural hybridity.

Sears (1941) obtained amphidiploids from the 20 cross combinations among nine diploid *Aegilops* and *Triticum* species by the colchicine treatment to their F_1 hybrids. Those amphidiploids restored their fertility and showed normal or almost normal pollen fertility while the F_1 hybrids from which the amphidiploids derived were highly sterile. Kondo (1941) produced an amphidiploid between *Ae. caudata* and *Ae. umbellulata* by colchicine treatment to their F_1 hybrid. The amphidiploid showed a normal seed fertility as high as 64% though the F_1

hybrid was completely sterile. Tanaka (1955b) subjected the F_1 hybrids between *Ae. sharonensis* and *Ae. umbellulata* to colchicine treatment and successfully obtained their amphidiploid. It also showed an almost normal pollen and seed fertility. These facts indicate that the chromosomal sterility is more common as one of the most effective reproductive isolation mechanisms acting among the species of the *Aegilops-Triticum* complex than the genic one. This also supports the present conclusion that the sterility observed in the present F_1 hybrids involving *Ae. mutica* is a chromosomal sterility mainly caused by the cryptic structural hybridity defined by Stebbins (1945).

7. CONCLUSION OF THE PRESENT CROSSING EXPERIMENT

As discussed above, *Ae. mutica* showed a good crossability to many diploid species in the congeneric *Aegilops-Triticum* complex. The F_1 hybrids between those species and *Ae. mutica* grew vigorously and many of them showed a high frequency of chromosome pairing when they did not contain B-chromosomes derived from *Ae. mutica*. Furthermore, the F_1 hybrids between *Ae. speltoides* and *Ae. mutica* showed partial fertility. To conclude from these results, *Ae. mutica* belongs to congeneric *Aegilops-Triticum* complex and should not be divided into the independent genus *Amblyopyrum* as Eig (1929b) proposed.

Among the diploid species of the *Aegilops-Triticum* complex, *Ae. mutica* is most closely related to *Ae. speltoides*. Because the F_1 hybrids between these two species showed a very high and a regular configuration of chromosome pairing when they did not contain B-chromosomes of *Ae. mutica* and such a high frequency of chromosome pairing was not drastically reduced even when two B-chromosomes were contained in the F_1 hybrids. Moreover, their F_1 hybrids formed viable male and female gametes with normally reduced seven chromosomes though their two parental genomes frequently exchanged their genes during the meiotic process in the F_1 plants. The seedlings in the next generation developed from the seeds obtained through the fertilization between those viable gametes normally grew into mature plants. These facts also clearly show that *Ae. mutica* and *Ae. speltoides* are genetically very closely related to each other. In addition, *Ae. mutica* is very closely related to *Ae. squarrosa* because the frequency of A-chromosome pairing

in their F_1 hybrids with two B-chromosomes was not drastically low. However, their F_1 hybrids were highly sterile in contrast with those between *Ae. speltoides* and *Ae. mutica*. To conclude from these facts, I propose that the genome symbol of *Ae. mutica* should be renamed into 'S^m' from 'Mt' as a very closely related genome to 'S' of *Ae. speltoides*.

The conclusion obtained from the present results on morphology, chromosome pairing and fertility in the F_1 hybrids almost coincides with two previous karyomorphological studies, one is by Senjaninova-Korczagina (1932) and another by Chennaveeraiah (1960). Senjaninova-Korczagina concluded that the karyotype of *Ae. mutica* is similar to those of *Ae. squarrosa*, *Ae. comosa* and *Ae. heldreichii* but it is very different from those of *Ae. caudata* and *Ae. umbellulata*. Chennaveeraiah concluded that the karyotype of *Ae. mutica* is different from those of *Ae. comosa* including *Ae. heldreichii* and *Ae. squarrosa* but that it is more in line with those of the Sitopsis (= sect. Platystachys) species, especially with that of *Ae. speltoides* including *Ae. aucheri*. Moreover, Riley (1966) suggested that *Ae. speltoides* and *Ae. mutica* are phylogenetically proximal because of the absence of any translocation difference between them and because of their similarities in karyotype and pairing control. He could not obtain a reasonably high frequency of chromosome pairing in the F_1 hybrid between *Ae. mutica* and *Ae. speltoides*. However, in the present study, a high frequency of A-chromosome pairing was observed even in the 1B and 2B hybrids between them as well as their 0B hybrids. My present conclusion that the genome of *Ae. mutica* is very closely related, especially, to that of *Ae. speltoides* coincides with the Riley's suggestion.

In the *Aegilops-Triticum* complex, various genetic mechanisms for the reproductive isolation are operating among the diploid species. Among them the most effective barrier is complete sterility or semi-sterility in the interspecific F_1 hybrids. That hybrid sterility is the chromosomal sterility resulted from the cryptic structural hybridity. The semi-sterility observed in the F_1 hybrids between *Ae. speltoides* and *Ae. mutica* is also due to the cryptic structural hybridity. In the natural habitats, these two species sometimes grow sympatrically in Anatolian Plateau in Turkey. However, no natural hybrids between these two species were reported though they are out-breeding species (Yamashita and Tanaka 1960, Zohary and Imber 1963). The present author also saw their sympatric stand in Anatolian Plateau in 1982 (Sakamoto 1986) but could not find their natural hybrids at all. The low percentage seed set and low rate of germination of the hybrid seeds observed in the present study may function as one of effective reproductive isolation barriers between *Ae. speltoides* and *Ae. mutica* at their natural habitats in addition to the hybrid semi-sterility.

8. PHYLOGENETIC POSITION OF *AEGILOPS MUTICA* AMONG THE DIPLOID SPECIES OF THE CONGENERIC *AEGILOPS-TRITICUM* COMPLEX

Each section of genus *Aegilops* except sect. Monoleptathera contains at least one diploid species, and genus *Triticum* also has a wild diploid taxon *T. monococcum* ssp. *boeoticum*. The section Monoleptathera is monotypic and is consisted of a tetraploid species, *Ae. cylindrica*. This species proved to have originated from the hybridization between two diploid species, *Ae. caudata* and *Ae. squarrosa* (Kihara 1937, Kihara and Matsumura 1941, McFadden and Sears 1946), and it was grouped in the sect. Cylindropyrum together with a diploid species *Ae. caudata* by Kihara (1949). These facts show that the differentiation among sections in the *Aegilops-Triticum* complex already occurred at diploid level, and that the morphological and cytogenetical characteristics specific to the each section are determined by such diploid species. Therefore, it is essential for understanding phylogenetic differentiation in this plant group to elucidate the phylogenetic relationships among diploid species of the *Aegilops-Triticum* complex. The importance of the the diploid species for differentiation of this plant group is indicated also by the fact that about a half of the wild species belonging to these genera are diploids. In this chapter the phylogenetic position of *Ae. mutica* among the diploid species of the congeneric *Aegilops-Triticum* complex will be discussed.

Morphological characteristics

Eig (1929a) characterized genus *Aegilops* in the tribe Hordeae mainly by the following four morphological characteristics which are shared by many of *Aegilops* species: a) spikes with many awns, b) ovate spikelets, c) ovoid spikes, and d) spikes falling as entire when riped. He found these four characteristics in sect. Pleionathera in the highest degree and he concluded this section is most distantly differentiated from the 'Ur-*Aegilops*-Typ' which once differentiated from the prototype of the tribe. In contrast with that section, these four characteristics are seen in sect. Platystachys in the lowest degree. And this section has many morphological characteristics common to the other genera in tribe Hordeae. From this fact, Eig concluded the species of sect. Platystachys are the most similar to the old *Aegilops* form among those of genus *Aegilops*.

However, he discussed about the phylogenetic differentiation of genus *Aegilops* only within subgenus *Eu-Aegilops* of the genus. He excluded monotypic subgenus *Amblyopyrum*, to which only one species *Ae. mutica* belongs, from his discussions about the evolutionary process of genus *Aegilops*. Because *Ae. mutica* has such an extraordinary morphology in the genus *Aegilops* that later he separated it from the genus as an independent genus *Amblyopyrum* Eig (Eig 1929b). In the present work, it was proved that *Ae. mutica* is genetically closely related to many diploid species of the *Aegilops-Triticum* complex, and that it is especially very closely related to *Ae. speltoides* of sect. Platystachys. From this result, it was concluded that *Ae. mutica* should not be separated from the genus *Aegilops* as the independent genus but it should be included in the genus *Aegilops*, therefore, in the congeneric

Aegilops-Triticum complex. Here, I discuss about the phylogenetic position of *Ae. mutica* in the congeneric complex based on this conclusion.

The morphology of *Ae. mutica* is characterized mainly by the long linear awnless spikes with many spikelets and by the many florets in each spikelet. Its rachis is fragile and each spikelet falls separately with the rachis internode below it (wedge type disarticulation). And its rachilla is also fragile and each floret falls separately especially in the upper part of each spikelet (floret type disarticulation). Tanaka (1958) compared 13 morphological characters of spikes in nine diploid *Aegilops* species. *Ae. mutica* and *Ae. speltoides* had six among those 13 characteristics in common and they were similar to each other in additional three characteristics. They were clearly different from each other only in the two characters of their empty glumes: the presence of keels and the shape of their upper margins. As a result of his comparison, it is able to be concluded that *Ae. mutica* is morphologically most similar to *Ae. speltoides* among the nine diploid *Aegilops* species. This means that *Ae. mutica* is one of the candidates for the species most similar to the old *Aegilops* form or to 'Ur-*Aegilops*-Typ' in the sense of Eig (1929a). Indeed, it has none of the four morphological characteristics listed by Eig (1929a) which separate the typical species of genus *Aegilops* from the other genera of tribe Hordeae.

Table 47 shows the comparison of some morphological characters among the diploid species within the *Aegilops-Triticum* complex and among the genera in tribe Triticeae (= tribe Hordeae). The characteristics of

Table 47. Morphological charasteristics in the genera of tribe Triticeae and the wild diploid species of the genera *Aegilops* and *Triticum* (summerized from Percival 1921, Eig 1929a, Tanaka 1958, Sakamoto 1973, Tsvelev 1983, Melderis 1985a-l and Tan 1985a, b)

Genus and species[1]	No. of florets in each spikelet	Patterns of seed dispersal		Classification by Sakamoto (1973)
		rachis	rachilla	
Aegilops L.		fragile of partly fragile	tough or partly fragile	Mediterranean group
Ae. mutica	5 - 8	fragile; wedge	partly fragile; lowest two florets fall with spikelet	
Ae. bicornis	3	fragile; wedge	tough	
Ae. sharonensis	3 - 5	fragile; wedge	tough	
Ae. longissima	3 - 5	partly fragile; wedge	tough	
Ae. ligustica	4 - 5(6)	fragile; wedge	tough	
Ae. speltoides	4 - 6(8)	partly fragile; umbrella	tough	
Ae. squarrosa	(3-)4(-5)	fragile; barrel	tough	
Ae. caudata	3 -(4)	partly fragile; umbrella	tough	
Ae. comosa	3 - 4	partly fragile; umbrella	tough	
Ae. uniaristata	4	partly fragile; umbrella	tough	
Ae. umbellulata	4	partly fragile; umbrella	tough	

Table 47. (Continued)

Genus and species[1]	No. of florets in each spikelet	Patterns of seed dispersal: rachis	Patterns of seed dispersal: rachilla	Classification by Sakamoto (1973)
Triticum L.		fragile	tough	Mediterranean group
T. boeoticum Boiss.	2	fragile; wedge	tough	
T. dicoccoides (Koern.) Koern.	3	fragile; wedge	tough	
Eremopyrum (Ledeb.) Jaub. & Spach	2 - several	fragile; wedge		Mediterranean group
Heteranthelium Hochst.	1 - 2	partly fragile		Mediterranean group
Crithopsis Jaub. & Spach	2	fragile; wedge	fragile; disarticulating below florets	Mediterranean group
Dasypyrum (Coss. & Dur.) Cand.	2 - 4	fragile; wedge		Meditarranean group
Secale L.	2 -(3)	fragile; wedge		Mediterranean group
Psathyrostachys Nevski	1 - 3	fragile; wedge	tough	Mediterranean group
Taeniatherum Nevski	2	tough	fragile; disarticulating above glumes	Mediterranean group

Table 47. (Continued)

Genus and species[1]	No. of florets in each spikelet	Patterns of seed dispersal: rachis	Patterns of seed dispersal: rachilla	Classification by Sakamoto (1973)
Henrardia C.E.Hubbard	1 - 2	fragile; barrel		Mediterranean group
Agropyron Gaertner	3 -10	tough or fragile	fragile; disarticulating below florets	Arctic-temperate group
Hystrix Moench	2 - 3(5)	tough	fragile	Arctic-temperate group
Elymus L.	4 - 7	tough or fragile	tough or fragile	Arctic-temperate group
Hordeum L.	1 -(2)	fragile; wedge	tough	Arctic-temperate group
Leymus Hochst.	2 - 5	tough	fragile; disarticulating beneath each floret	Arctic-temperate group

1) The taxonomic treatment and nomenclature by Melderis (1985a-l) and Tan (1985a, b) in *Flora of Turkey and the East Aegean Islands* (Davis, P. H. ed.) are adopted for the genera except *Aegilops* L. and *Hystrix* Moench. Their morphological characteristics are based on Percival (1921), Sakamoto (1973), Melderis (1985a-l) and Tan (1985a, b). The taxonomic treatment, nomenclature and morphological characteristics of genus *Hystrix* Moench are after Tsvelev (1983) and those of genus *Aegilops* L. are based on Eig (1929a) and Tanaka (1958).

Ae. mutica, many florets in each spikelet and fragile rachillae (floret type disarticulation), are common especially to the genera *Agropyron*, *Elymus* and *Leymus*. These genera belong to the Arctic-temperate group according to the classification by Sakamoto (1973), and the Mediterranean group in which the congeneric *Aegilops-Triticum* complex are included is thought to be radically differentiated from the Arctic-temperate group after the establishment of the Mediterranean climate in the Mediterranean region (Sakamoto 1973). The morphological characteristics of *Ae. mutica*, such as long linear spikes with many spikelets, many florets in each spikelet, and floret type disarticulation in addition to wedge type one, are common to the older Arctic-temperate group. This fact indicates that *Ae. mutica* has more characteristics similar to the putative common ancestor of the congeneric *Aegilops-Triticum* complex than the other species belonging to this plant group.

Cytogenetical characteristics

The karyotypes of the species in genus *Aegilops* were investigated in detail by Senjaninova-Korczagina (1932) and by Chennaveeraiah (1960). The conclusion obtained from the present work almost coincides with the two previous works. According to Senjaninova-Korczagina, the karyotype of *Ae. mutica* consists of four types of chromosomes all with submedian centromeres one of which has a satellite on its short arm. And she concluded that it is similar to those of *Ae. squarrosa*, *Ae. comosa* and *Ae. heldreichii* but is very different from those of *Ae. caudata* and *Ae.*

umbellulata. *Ae. umbellulata* has four pairs of chromosomes with subterminal centromeres and one pair of chromosomes with almost terminal centromeres. *Ae. caudata* has no chromosomes with median or submedian centromeres and it has three pairs of chromosomes with almost terminal centromeres. Chennaveeraiah concluded that *Ae. mutica* has two chromosome pairs with fairly large satellites on their short arms and they do not differ much in size and the rest of the chromosome pairs have submedian centromeres. He suggested based on his result that the karyotype of *Ae. mutica* is different from those of *Ae. comosa* (incl. *Ae. heldreichii*) and *Ae. squarrosa*, but that it is more in line with those of the species of sect. Sitopsis (= sect. Platystachys), especially with that of *Ae. speltoides*. He concluded *Ae. caudata* and *Ae. umbellulata* have the most diverged chromosome morphology in the genus *Aegilops* as mentioned by Senjaninova-Korczagina.

The karyotypes of the diploid species of the other genera in tribe Triticeae have been investigated by some previous workers. Recently, Hsiao *et al.* (1986) observed in detail the karyotypes of 22 diploid species in the tribe. Those species belonged to the following eight genera: *Agropyron*, *Thinopyrum*, *Pseudoroegneria*, *Psathyrostachys* (including one species from former genus *Elymus*), *Australopyrum*, *Critesion* (formerly included in genus *Hordeum*), *Hordeum* and *Secale*. They represented many of the genomes shared by the perennial species in the tribe. Most of the chromosome pairs of their karyotypes had median or submedian centromeres. All the genera except *Secale* are included in the Arctic-temperate group in the sense of Sakamoto (1973). Their result and this fact indicate that 'Ur-*Aegilops*-Typ' had the karyotype

composed only of chromosome pairs with median or submedian centromeres. From this point of view, *Ae. mutica* is also one of the candidates for 'Ur-*Aegilops*-Typ' besides the species of sect. Platystachys, *Ae. comosa* and *Ae. squarrosa*.

In the present study, chromosome pairing in the F_1 hybrids between *Ae. mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex was analyzed. The F_1 hybrids involving the species of sect. Platystachys, *Ae. comosa*, *Ae. squarrosa* and *T. monococcum* showed a very high frequency and almost regular configuration of chromosome pairing at MI of meiosis when they had no B-chromosome. Kihara and Lilienfeld (1935) reported chromosome pairing in the F_1 hybrids between *T. aegilopoides* (= *T. monococcum* ssp. *boeoticum*) and *Ae. squarrosa* and between *Ae. comosa* and *Ae. squarrosa*. The mean frequency of chromosome pairing in the former F_1 hybrid was equivalent to 2.4 bivalents per cell and in the latter to 5.9 bivalents per cell, respectively. And the frequency is lower than that obtained from the present F_1 hybrids between *Ae. mutica* and *Ae. squarrosa*, between *Ae. comosa* and *Ae. mutica*, and between *T. monococcum* and *Ae. mutica*. Sears (1941) crossed nine diploid *Aegilops* and *Triticum* species with one another and successfully obtained their F_1 hybrid plants from the 33 cross combinations. His F_1 hybrids between *Ae. speltoides* and *T. monococcum* and between *Ae. speltoides* and *Ae. comosa* show a similar amount of chromosome pairing to the present F_1 hybrids between *T. monococcum* and *Ae. mutica*, between *Ae. comosa* and *Ae. mutica*, and between *Ae. speltoides* and *Ae. mutica*. However, the F_1 hybrids between *T. monococcum* and *Ae. comosa*, and between *T. monococcum* and *Ae. squarrosa* show significantly lower

frequency of chromosome pairing than the present hybrids between *Ae. mutica* and these three species. These results can be interpreted by that *T. monococcum*, *Ae. squarrosa* and *Ae. comosa* were cytogenetically differentiated separately from the common center of evolution consisted of *Ae. mutica* and *Ae. speltoides* which were very closely related to each other. In other words, genus *Triticum*, sect. Pachystachys and sect. Macrathera of genus *Aegilops* were evolved through different evolutionary ways from the common center consisted of the closely related two species *Ae. mutica* and *Ae. speltoides*. Indeed, the diploid species of genus *Triticum* and of these sections of genus *Aegilops* are quite different from each other in their ecology as well as their morphology. The other section of genus *Aegilops*, sect. Pleionathera, was differentiated so distantly that it has no longer direct cytogenetical relationship with the common center of evolution of the congeneric *Aegilops-Triticum* complex.

Ecological characteristics

All the species of the *Aegilops-Triticum* complex except *Ae. mutica* and *Ae. speltoides* have self-fertilized breeding system. Only two species, *Ae. mutica* and *Ae. speltoides*, have cross-fertilized breeding system (Yamashita and Tanaka 1960, Zohary and Imber 1963). *Ae. mutica* is almost completely self-incompatible though *Ae. speltoides* is self-compatible. Stebbins (1957) concluded that plants which are regularly self fertilized are most probably derived from cross fertilizing ancestors. He listed the four reasons which point to this conclusion

based on the evidence obtained from many plant species: First, the self-fertilizing species appear to be more specialized in morphological characteristics than many of their cross-fertilizing relatives; second, many self-fertilizing species possess structures which could have a high selective value only in connection with cross-fertilization; third, self-fertilizing species or populations have originated in historical times from cross-fertilizing species in some plant groups; and fourth, different genera of the same family or in closely related families which contain self-incompatible species usually have a similar genetic basis for the self-incompatibility, and based on genetic works the origin of self-incompatibility systems requires the accumulation of a series of rarely occurring genetic events while self-compatibility can arise relatively easily from self-incompatibility through mutations suppressing the activity of the self-incompatibility alleles. If we accept his conclusion, we reach the conclusion that the self-compatible diploid species of the congeneric *Aegilops-Triticum* complex were also derived from the self-incompatible or out-breeding species, *Ae. mutica* and *Ae. speltoides*, and that *Ae. mutica* which is almost self-incompatible is thought to be the most probable 'Urtyp' species of this plant group. Indeed, these two species, especially *Ae. mutica*, have many morphological and cytogenetical characteristics common to the other genera of tribe Triticeae, in other words, they are not specialized in morphological and cytogenetical characteristics.

Conclusion

The four evidences were obtained from the comparison in morphological, cytogenetical and ecological characteristics between *Ae. mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex as well as between the diploid species of the complex and the other genera of tribe Triticeae. They are as follows: First, *Ae. mutica* is the least specialized in the morphological characteristics from the other genera of tribe Triticeae, especially from the old genera of the tribe, *i.e.* the Arctic-temperate group. *Ae. mutica* has long linear spikes with many spikelets but without any rudimentary spikelets. And the spikes show floret type disarticulation as well as wedge type disarticulation. And each spikelet has many florets. Second, the karyotype of this species consists of only the chromosome pairs with median or submedian centromeres. And such a karyotype is much common to the diploid species of the Arctic-temperate group of tribe Triticeae. Third, the F_1 hybrids without B-chromosomes between *Ae. mutica* and many of the other diploid species in the congeneric *Aegilops-Triticum* complex show a very high frequency and an almost regular configuration of chromosome pairing at meiosis, while some of the F_1 hybrids among these diploid species which show a nearly normal pairing in the hybrids with *Ae. mutica* show a lower frequency of chromosome pairing at MI. It may be acceptable by the explanation that *Ae. mutica* and *Ae. speltoides* are in the center of cytogenetical divergence of this plant group and the other species evolved toward different directions from the center. Fourth, most of the species in the *Aegilops-Triticum* complex are self-compatible and *Ae. mutica* is the only almost self-incompatible species

in this plant group. According to Stebbins (1957), the self-compatible species are most probably derived from self-incompatible species by the evidences from many plant groups. Judging from these four evidences, I can reasonably conclude that *Ae. mutica* is the most similar to the putative common ancestor, or 'Urtyp', of the congeneric *Aegilops-Triticum* complex among the living diploid species of this plant group.

9. SUMMARY

Aegilops mutica Boiss. is one of the diploid species of the congeneric *Aegilops-Triticum* complex. It has long, linear spikes consisting of many spikelets with up to 10 florets. And its spikes do not have any awns dissimilar to the other species of the congeneric complex. Based on these extraordinary morphology, some taxonomists have separated this species from the genus *Aegilops* or the *Aegilops-Triticum* complex and have regarded it as the member of monotypic genus *Amblyopyrum*. Cytogenetically, *Ae. mutica* has been crossed only sporadically with the other diploid and polyploid species, and the genetic relationships between *Ae. mutica* and the other diploid species of the *Aegilops-Triticum* complex have been still open to arguments.

In the present study, *Ae. mutica* with and without B-chromosomes was crossed with 11 diploid species belonging to the congeneric *Aegilops-Triticum* complex. The crossability was enough high to regard *Ae. mutica* as a member of the complex and the F_1 hybrids were successfully obtained from the 10 interspecific cross combinations involving nine *Aegilops* and one *Triticum* species: *Ae. bicornis* x *Ae. mutica*, *Ae. sharonensis* x *Ae. mutica*, *Ae. longissima* x *Ae. mutica*, *Ae. speltoides* x *Ae. mutica*, *Ae. mutica* x *Ae. squarrosa*, *Ae. caudata* x *Ae. mutica*, *Ae. comosa* x *Ae. mutica*, *Ae. uniaristata* x *Ae. mutica*, *Ae. umbellulata* x *Ae. mutica* and *T. monococcum* x *Ae. mutica*.

The genetic relationships between *Ae. mutica* and the 10 diploid species were estimated mainly from the frequency and configuration of chromosome pairing at MI of meiosis in the PMCs of the F_1 hybrids and

from their fertility. The new method of genome analysis was schemed for estimating the genetic relationships based on the frequency of chromosome pairing in their F_1 hybrids as shown in Figure 5. In the present scheme of genome analysis, B-chromosomes of *Ae. mutica* were used in order to effectively suppress the pairing among the homoeologous chromosomes in the F_1 hybrids. As a result of the analysis, the genomes of the 10 diploid species of the *Aegilops-Triticum* complex were classified into the following three groups based on their relationships to the genome of *Ae. mutica* (Table 46): First, the genomes of *Ae. bicornis*, *Ae. sharonensis*, *Ae. longissima*, *Ae. comosa* and *T. monococcum* ssp. *boeoticum* are only homoeologous with that of *Ae. mutica*. Second, the genomes of *Ae. caudata*, *Ae. uniaristata* and *Ae. umbellulata* are more distantly related to that of *Ae. mutica* than those of the above five species. And third, the genomes of *Ae. speltoides* and *Ae. squarrosa* are very closely related to that of *Ae. mutica*. They are not fully but almost homologous to that of Ae. mutica. Moreover, the F_1 hybrids between *Ae. speltoides* and *Ae. mutica* were not completely sterile but only semi-sterile. That observation confirmed the above conclusion that *Ae. mutica* is cytogenetically very closely related to *Ae. speltoides*. In addition to those cytogenetical evidences, the comparison in some morphological characteristics of the obtained F_1 hybrids and their parental species also supported the close genetic relationship between *Ae. mutica* and *Ae. speltoides*.

Based on those evidences, I reasonably concluded as follows: *Ae. mutica* is a member of the congeneric *Aegilops-Triticum* complex and should not be divided into the independent genus *Amblyopyrum*. Second,

Ae. mutica is genetically most closely related to *Ae. speltoides* among the diploid species of the congeneric complex, and the genomes of those two species are almost homologous. And I proposed that the genome symbol of *Ae. mutica* should be renamed into 'S^m' from 'Mt' as a very closely related genome to 'S' of *Ae. speltoides*.

The phylogenetic position of *Ae. mutica* in the *Aegilops-Triticum* complex was discussed by comparing the morphological, cytogenetical and ecological characteristics of *Ae. mutica* with those of the other diploid *Aegilops-Triticum* species and with the other genera of tribe Triticeae as well as by the evidences obtained from the present cytogenetical work. Based on those comparisons, I concluded that *Ae. mutica* is the most similar to the putative common ancestor of the congeneric *Aegilops-Triticum* complex among the living diploid species of this plant group.

I answer, finally, the three questions given in the last section of Chapter 1 as the summary of the present work and this volume:

Q1. Is *Ae. mutica* the only member of the monotypic genus *Amblyopyrum* Eig or a member of the congeneric *Aegilops-Triticum* complex ?

Answer: **_Ae. mutica_ is a member of the congeneric _Aegilops-Triticum_ complex.**

Q2. Which diploid species of the *Aegilops-Triticum* complex is *Ae. mutica* most closely related to ?

Answer: **_Ae. mutica_ is genetically most closely related to _Ae. speltoides_ among the diploid species of the congeneric**

complex.

Q3. What phylogenetic position among the diploid species of the *Aegilops-Triticum* complex is *Ae. mutica* located in ?

Answer: ***Ae. mutica* is the most similar to the putative common ancestor of the congeneric *Aegilops-Triticum* complex among the living diploid species of this plant group.**

10. ACKNOWLEDGEMENTS

This volume is the outcome of my work for thirteen years. My research project on the cytogenetical relationships between *Aegilops mutica* and the other diploid species of the congeneric *Aegilops-Triticum* complex started in April, 1977. Professor Dr. Masatake Tanaka, Kihara Memorial Yokohama Foundation for the Advancement of Life Science, who was former director of the Plant Germ-plasm Institute, Kyoto University and is not only an cytogeneticist but also an expert in taxonomy of the genera *Aegilops* and *Triticum*, gave me the research project as a theme for my postgraduate course. It was the first time that I saw *Aegilops* and wild *Triticum* species, and of course *Ae. mutica*. I would like to say the greatest and hearty thanks to him for his continuous and patient guidance not only when he was at the position of the Institute but also after he retired from the Institute in March of 1984. I was not always a hard worker even in these short research period of mine. Sometimes or often, I was suddenly absent from the Institute and the soil in the pots dried up just as that of the native habitat of some *Aegilops* species during dry season. However, Professor Tanaka did not scold this lost sheep who forgot to feed on goat grass but always encouraged and guided him just as the good shepherd.

And I would like to heartily thank Professor Dr. Sadao Sakamoto, the present director of the Plant Germ-plasm Institute, for giving me the chance of my field research in Greece and Turkey in 1982 and for opening my field of view from a small country of *Aegilops* into the large world of tribe Triticeae and other plant groups. If I did not see him

at the Institute when I was a postgraduate, Chapter 8 of this thesis could be achieved neither in this volume nor in my mind. This volume was performed from discussions and by direct or indirect assistance of many other people such as my present and previous colleagues, our graduate students and technical staffs. Among them I would like to thank Mr. Jun'ichi Sano, Faculty of Education, Miyazaki University, who gave me a lot of suggestion on cytogenetics, especially on B-chromosomes, and Dr. Makoto Kawase, National Institute of Agrobiological Resources, Ministry of Agriculture, Forestry and Fisheries, with whom I discussed about our life as well as about many topics on biology. Mr. Masaaki Mizuguchi, Mrs. Etsuko Hasegawa and Mrs. Yasuko Jo helped me with my work as efficient technical staffs. And I heartily thank my wife Natsuko for her indirect but indispensable assistance to this volume.

Finally, I shall say my hearty thanks to the late Dr. Yasuo Nakai for his fruitful, suggestive and exciting discussions about the phylogeny of genera *Aegilops* and *Triticum*.

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