Genetic differentiation and post-glacial establishment of the geographical distribution in *Aegilops caudata* L.

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Aegilops caudata L. is a diploid wild relative of wheat distributed over the north-eastern Mediterranean from Greece to northern Iraq. To elucidate the geographical differentiation pattern, 35 accessions derived from the entire distribution area were crossed with four Tester strains. Pollen fertility in the F_1 hybrids varied from 0 to 96.3% among cross combinations, closely correlating with the geographical regions where the parental accessions were collected. Based on the intraspecific hybrid sterility, the present distribution area of *Ae. caudata* was divided into two geographical regions effectively isolated by the mountainous region lying between West Anatolia and Central Anatolia. The western region is composed of Greece and West Anatolia, while the eastern region consists of Central Anatolia, South Anatolia, East Anatolia and northern Iraq. The present results and the facts from recent palaeopalynological works suggest that during the maximum glacial period from 18000 BP to 16000 BP, *Ae. caudata* occurred in the two isolated regions, i.e., the region surrounding the Aegean Sea and the western Levant or some sheltered habitats in the East Taurus / Zagros mountains arc, and that it migrated into Central and East Anatolia from the latter regions as the climate became warmer. Furthermore, it is also suggested that the Levant populations now occur in the eastern region of the distribution, while those occurring in the Aegean Sea region during the last glacial period now occupy the western region of the distribution.

INTRODUCTION

Aegilops caudata L. (syn. *Ae. markgrafii* (Greuter) Hammer, $2n = 2x = 14$) is an annual, wild relative of wheat distributed over the northeastern Mediterranean basin from Greece to the northern part of Iraq (Eig, 1929; Bor, 1968, 1970). Two varieties are described in this species based on spike morphology, var. *typica* and var. *polyathera* Boiss. (Eig, 1929), or *Ae. markgrafii* var. *markgrafii* and var. *polyathera* (Boiss.) Hammer (Hammer, 1980). They often occur sympatrically in the Aegean islands (Rechinger, 1943; Ohta, 1992). Tanaka et al. (1967) was the first to find remarked sterility in inter-varietal F_1 hybrids (F_1 's) of *Ae. caudata*. Recently, however, the F_1 's between the two varieties collected from the sympatric stands on the Aegean islands were found to be fully fertile (Ohta, 1992). The author furthermore crossed nine Aegean and one Iraqi accessions with the four Tester strains collected from different geographical areas, concluded that intraspecific hybrid sterility is not specific to the varieties but correlated with the geographical areas,

and suggested that the distribution area of *Ae. caudata* can be divided into the western and the eastern regions based on the hybrid sterility. The former is composed of the Greek mainland and Aegean islands, and the latter of the Anatolian Plateau, Syria and Iraq (Ohta, 1992). The aim of the present study is to reveal the geographical differentiation pattern in *Ae. caudata* over its entire distribution area. Accessions collected from the entire distribution area were crossed with the four Tester strains. Based on pollen and seed fertility and chromosome pairing at the first metaphase (MI) of meiosis in the F_1 's and the parental lines, I discuss the geographical differentiation pattern and the post-glacial establishment of the geographical distribution in *Ae. caudata*.

MATERIALS AND METHODS

Plant materials. Collection sites and morphological varieties of the 35 accessions of *Ae. caudata* and the four Testers are shown in Fig. 1 and Tables 1, 2 and 3. They were collected from the entire distribution area of the species. Nine of them were collected from the Aegean islands (Sites 1 to 9), 23 from Turkey (Sites 10 to 32) and the other three from northern Iraq (Sites 33 to 35). They

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Fig. 1. Collection sites of the four Testers (A, B, C and D) and 35 accessions of *Ae. caudata* used in the present study. Mountainous regions higher than 1500 m above sea level are shadowed with dots. A broken line indicates the border between the two geographical regions defined from intraspecific hybrid sterility.

are all maintained at the Plant Germ-plasm Institute, Kyoto University and at Fukui Prefectural University. For the detailed localities of the collection sites, refer to Tanaka (1983) and Sakamoto (1986). The Turkish sites were grouped into four geographical divisions after Davis (1965). Three sites (Sites 10 to 12) were located in West Anatolia, eight (Sites 13 to 20) in Central Anatolia, three (Sites 21 to 23) in South Anatolia and nine (Sites 24 to 32) in East Anatolia. The four Tester strains were collected from peripheral localities of the distribution area (Fig. 1), and the F_1 's among them were highly sterile (Tanaka et al., 1967; Ohta, 1992).

Crossing, cultivation and cytology. The 35 accessions were hand-pollinated with the four Testers after emasculation. Parental lines and F_1 's were grown under a vinyl roof under natural day-length and temperature conditions, and they all grew vigorously to maturity. Chromosome pairing at MI in the pollen mother cells (PMCs) was examined by the aceto-carmin smear technique. To sample the pollen grains, three anthers were picked from each floret on a slide just before anthesis. Pollen grains were stained in a dilute aceto-carmin solution and at least 2000 pollen grains from each slide were counted. They were classified into following five classes according to the degree of development: Empty pollen grains with no nucleus (PE), pollen grains with a nucleus (P1), with two nuclei (P2), with three nuclei but with poor starch development (P3), and normal pollen grains with three nuclei and normal starch development (PN). Two estimates were calculated for the degree of

pollen normality. One was the percentage of PN to the total number of pollen grains observed (PPN). The other was the pollen development index (PDI) calculated as $100 \times (0 \times PE + 0.25 \times P1 + 0.5 \times P2 + 0.75 \times P3 + 1 \times PN)$ / the total number of pollen grains observed. A value for each class was applied arbitrarily so that the PDI ranges from 0 (all pollen grains empty) to 100 (all pollen grains normal). The PDI was adopted because the proportions of the aborted pollen grains at various developmental stages varied among the F_1 's showing a similar PPN value. The percentage of dehiscent anthers to all of the anthers examined (PDA) was also examined using the same anther samples as pollen normality. The PDA ranges from 0 (no anther dehiscent) to 100 (all anthers dehiscent). Anthers were sampled from each plant at least twice at an interval of three to seven days and the averages were calculated for the above three estimates. For the estimate of embryo-sac normality, seed set after open-pollination was examined based on the seed set on the lowest two florets of at least 10 spikes from each parent and F_1 hybrid. It was given as the percentage of the florets bearing plump seeds to the total number of florets examined. Voucher specimens are preserved at Fukui Prefectural University, the National Science Museum, Japan, and the Royal Botanic Gardens, Kew, U. K.

RESULTS

Chromosome pairing. Chromosome pairing at MI in all of the parental accessions and F_1 's was normal and seven tightly associated bivalents were formed in most

Table 1. The estimates of pollen and seed fertility in the F₁ hybrids between the four Testers and the 12 accessions of *Ae. caudata* from the Aegean islands and West Anatolia. PPN: percentage normal pollen grains, PDI: pollen development index, PDA: percentage dehiscent anthers, and PSS: percentage seed set

Site No.	Accession ^{a)} No.	Var. ^{b)}	Esti- mates	Testers			
				A KU6-1 T	B KU5852 P	C KU5864 T	D KU5871 T
Aegean Islands							
1	KU12044B	P	PPN	0	0	0	25.0
			PDI	0	0.9	16.6	34.2
			PDA	0	0	0	16.7
			PSS	0	22.5	31.5	74.1
2	KU12055B	P	PPN	0	0	14.5	83.5
			PDI	8.0	8.6	50.0	85.6
			PDA	0	0	73.3	90.4
			PSS	10.0	38.9	37.1	75.9
3	KU12155B	P	PPN	0	0	0	69.1
			PDI	5.1	12.9	0.3	77.9
			PDA	0	0	0	100.0
			PSS	14.1	21.4	27.3	78.6
4	KU12162A	T	PPN	0	0	0	72.2
			PDI	11.4	5.9	11.3	74.2
			PDA	0	0	0	76.2
			PSS	13.0	23.5	50.7	82.4
5	KU12163A	T	PPN	0.1	0	0.8	96.3
			PDI	3.5	2.0	20.1	96.5
			PDA	0	0	0	95.2
			PSS	8.6	14.8	n.o. ^{c)}	80.6
6	KU12073A	T	PPN	0	0.1	0	0
			PDI	1.2	4.3	15.7	5.0
			PDA	0	0	0	0
			PSS	22.7	42.9	40.0	43.8
7	KU12100B	P	PPN	0	15.1	42.6	86.3
			PDI	10.1	35.4	58.7	91.3
			PDA	0	55.6	71.4	66.7
			PSS	31.8	62.9	63.2	89.6
8	KU12117B	P	PPN	0	0.1	8.9	56.0
			PDI	0.5	0.3	21.2	69.5
			PDA	0	0	28.6	100.0
			PSS	5.3	7.1	52.8	77.5
9	KU12121A	T	PPN	0	0.3	0.2	0.1
			PDI	0.1	0.4	16.4	1.1
			PDA	0	0	0	0
			PSS	0	1.8	21.5	2.0
West Anatolia							
10	KU11401	T	PPN	0	0	13.7	68.8
			PDI	4.2	10.8	59.5	83.2
			PDA	0	0	80.0	100.0
			PSS	19.2	16.9	48.2	91.5
11	KU11403	T	PPN	0	n.o.	22.7	8.9
			PDI	6.2	n.o.	53.4	38.0
			PDA	0	n.o.	88.9	0
			PSS	7.7	n.o.	11.0	8.0
12	KU12169	T	PPN	0.8	0.2	20.3	36.9
			PDI	26.0	38.2	63.3	62.0
			PDA	0	0	54.2	92.6
			PSS	26.3	19.6	30.5	51.5

^{a)} KU: Accession numbers assigned by Kyoto University.

^{b)} Variety: P and T indicate var. *polyathera* and var. *typica*, respectively.

^{c)} n.o.: no observation.

Table 2. The estimates of pollen and seed fertility in the F_1 hybrids between the four Testers and the eight accessions of *Ae. caudata* from Central Anatolia. For the abbreviations of estimates and varieties, see Table 1

Site No.	Accession No.	Var.	Estimates	Testers			
				A	B	C	D
13	KU5853	P	PPN	0	17.8	0	n.o.
			PDI	19.6	54.9	1.1	n.o.
			PDA	0	23.3	0	n.o.
			PSS	12.5	29.2	0.6	n.o.
14	KU5854	P	PPN	n.o.	51.8	0	0
			PDI	n.o.	80.3	5.7	23.7
			PDA	n.o.	41.7	0	0
			PSS	n.o.	63.3	3.6	12.5
15	KU5859	P	PPN	n.o.	65.4	0	0
			PDI	n.o.	81.5	0.9	8.5
			PDA	n.o.	100.0	0	0
			PSS	n.o.	31.7	3.3	9.3
16	KU5860	P	PPN	13.1	0	0	0
			PDI	49.3	37.9	1.8	2.4
			PDA	8.3	0	0	0
			PSS	14.1	11.4	1.6	n.o.
17	KU5863	P	PPN	0.1	31.3	0	0
			PDI	33.6	70.5	10.3	0.6
			PDA	0	88.7	0	0
			PSS	12.3	43.4	0.7	7.1
18	KU5888	P	PPN	0.2	95.5	0	0
			PDI	32.1	97.2	1.1	27.2
			PDA	0	88.9	0	0
			PSS	31.7	64.4	10.7	19.8
19	KU5896	P	PPN	n.o.	66.9	0	0
			PDI	n.o.	82.5	7.6	2.2
			PDA	n.o.	100.0	0	0
			PSS	n.o.	48.3	2.2	3.4
20	KU12165	P	PPN	10.3	1.5	0	0
			PDI	55.0	40.7	2.6	25.7
			PDA	6.7	0	0	0
			PSS	19.1	31.3	3.2	16.5

PMCs observed.

Pollen fertility. Anthers of all of the parental accessions and the four Testers were normally dehiscid at anthesis. The PPN was very high, ranging from 71.8 to 98.7. Three estimates representing pollen fertility studied in the F_1 's are shown in Tables 1, 2 and 3. They varied widely among cross combinations. The PPN, PDI and PDA ranged from 0 to 96.3, 0 to 97.2 and 0 to 100, respectively, and they correlated significantly with one another (Table 4). Furthermore, distinct correlation was observed, as mentioned below, between the pollen fertility of the F_1 's and the geographical regions where the parental accessions were collected.

(a) The Aegean islands. The F_1 's between all of the nine accessions from the Aegean islands and Tester A showed drastically low pollen fertility (Table 1). The

PPN ranged from 0 to 0.1 and the anthers never dehiscid (PDA = 0). All the F_1 's between Tester B and the Aegean accessions except one from Site 7 showed almost complete sterility. The F_1 involving the accession from Site 7 showed slightly higher pollen fertility (PPN = 15.1). The F_1 between this accession and Tester C showed a PPN as high as 42.6 and the PDA was 71.4. In addition, the F_1 's between Tester C and the accessions from Sites 2 and 8 were partially fertile, PPN's being 14.5 and 8.9, respectively. However, the F_1 's between the other six accessions and Tester C showed almost complete sterility. In contrast to these hybrids, the F_1 's between six of the nine Aegean accessions and Tester D showed a high pollen fertility, with the PPN ranging from 56.0 to 96.3 and the PDA ranging from 66.7 to 100. The F_1 involving the accession from Site 1 was partially fertile (PPN = 25.0). The F_1 's between all of the four Testers and the accessions from Sites 6 and 9 were highly sterile.

Table 3. The estimates of pollen and seed fertility in the F₁ hybrids between the four Testers and the 15 accessions of *Ae. caudata* from South Anatolia, East Anatolia and northern Iraq. For the abbreviations of estimates and varieties, see Table 1

Site No.	Accession No.	Var.	Estimates	Testers			
				A	B	C	D
South Anatolia							
21	KU5867	P	PPN	14.1	28.9	0	0
			PDI	52.4	60.9	6.8	11.4
			PDA	10.0	61.1	0	0
			PSS	52.3	51.8	8.7	8.1
22	KU5897	P	PPN	62.5	0	n.o.	n.o.
			PDI	86.3	42.1	n.o.	n.o.
			PDA	100.0	0	n.o.	n.o.
			PSS	65.1	28.4	n.o.	n.o.
23	KU5899	P	PPN	93.3	0.5	0	3.5
			PDI	96.9	47.6	4.5	26.6
			PDA	100.0	10.0	0	3.3
			PSS	80.0	58.9	5.1	18.5
East Anatolia							
24	KU5484	P	PPN	24.2	0	0	0
			PDI	56.9	23.2	5.4	23.6
			PDA	36.7	0	0	0
			PSS	50.0	39.7	1.4	13.8
25	KU5485	T	PPN	0	61.0	0	0
			PDI	33.1	86.7	7.5	19.5
			PDA	0	100.0	0	0
			PSS	41.0	43.1	4.1	32.1
26	KU5489	T	PPN	27.0	19.3	0	0
			PDI	67.9	62.6	3.1	15.4
			PDA	96.7	66.7	0	0
			PSS	55.6	39.3	3.8	18.7
27	KU5490	P	PPN	69.7	9.4	0	0
			PDI	90.2	41.3	10.2	9.7
			PDA	87.5	5.6	0	0
			PSS	61.2	59.8	6.2	2.8
28	KU5491	P	PPN	95.3	17.2	0	0
			PDI	96.9	58.6	4.7	12.5
			PDA	100.0	33.3	0	0
			PSS	82.9	50.2	6.3	6.3
29	KU5492	P	PPN	75.4	19.1	0	0
			PDI	91.4	59.4	4.8	12.1
			PDA	100.0	66.7	0	0
			PSS	54.9	74.2	0.7	8.3
30	KU5885	T	PPN	65.9	11.9	0	0
			PDI	83.3	62.7	7.5	8.9
			PDA	96.7	33.3	0	0
			PSS	83.6	43.3	n.o.	5.6
31	KU5889	P	PPN	81.3	0.4	0	0
			PDI	90.1	38.7	n.o.	17.5
			PDA	96.7	0	0	0
			PSS	70.7	53.7	n.o.	17.6
32	KU5891	T	PPN	7.5	54.3	0	0
			PDI	62.4	85.2	16.4	17.9
			PDA	16.7	100.0	0	0
			PSS	39.0	54.6	2.6	17.8
Northern Iraq							
33	KU5475	P	PPN	72.8	43.0	0	0
			PDI	91.3	75.4	12.9	14.7
			PDA ^{a)}	+	+	—	—
			PSS	70.0	50.0	3.1	21.2
34	KU5472	T	PPN	66.2	6.0	0	0.2
			PDI	86.5	48.6	7.2	28.2
			PDA	91.7	4.2	0	0
			PSS	65.7	35.0	7.3	n.o.
35	KU5482	P	PPN	34.0	4.1	0	0
			PDI	76.4	49.4	8.7	30.0
			PDA	100.0	25.0	0	0
			PSS	70.2	46.6	5.6	12.0

^{a)} +: anther normally dehiscent, —: anther indehiscent.

Table 4. Correlation coefficients among the estimates of pollen and seed fertility

Estimates	PPN	PDI	PDA
PDI	0.884		
PDA	0.895	0.888	
PSS	0.786	0.825	0.766

(b) West Anatolia. All the F_1 's involving Testers A and B were almost completely sterile (Table 1). For the two accessions from Sites 10 and 12, the F_1 's involving Tester D showed the highest fertility and those involving Tester C followed them. For the accession from Site 11, the F_1 involving Tester C showed the highest fertility and that with Tester D gave the second highest.

(c) Central Anatolia. In contrast to the Aegean and the West Anatolian accessions, the F_1 's between all of the eight Central Anatolian accessions and Testers C and D were completely sterile (Table 2). For Tester B, the F_1 's involving the accessions from three sites (Sites 15, 18 and 19) showed a high pollen fertility, the PPN ranging from 65.4 to 95.5. The F_1 's involving the three accessions from Sites 13, 14 and 17 showed partial pollen fertility whose PPN ranged from 17.8 to 51.8. The other two accessions from Sites 16 and 20 produced almost completely sterile F_1 's when crossed with Tester B, the PPN being 0 and 1.5, respectively. For Tester A, three accessions from Sites 13, 17 and 18 produced almost completely sterile F_1 's whose PPN was 0 to 0.2 and the PDA was 0. The other two accessions from Sites 16 and 20 produced partially fertile F_1 's, the PPN being 13.1 and 10.3, respectively.

(d) South Anatolia, East Anatolia and northern Iraq. The accessions from South Anatolia, East Anatolia and northern Iraq showed similar results in the fertility of the F_1 's (Table 3). The F_1 's from the crosses of all of the accessions, except one from Site 23, with Testers C and D were completely or almost completely sterile, the PPN being 0 or 0.2 and the PDA being 0. The F_1 between the accession from Site 23 and Tester D showed slightly higher fertility but its PPN was as low as 3.5. For Tester A, the F_1 's involving nine accessions (Sites 22, 23, 27 to 31, 33 and 34) showed normal or almost normal anther dehiscence and high PPN values ranging from 62.5 to 95.3. The F_1 's between Tester A and the accessions from Sites 26 and 35 also showed normal or almost normal anther dehiscence in spite of a PPN as low as 27.0 and 34.0, respectively. The PDI values of those hybrids were 67.9 and 76.4, indicating that abnormal pollen grains developed in almost normal stages. The F_1 's between Tester B and three (Sites 22, 23 and 31) of the above 11 accessions were completely or almost completely sterile. Those between the other eight accessions and Tester B were partially fertile, whose PPN ranged from 4.1 to 43.0

and the PDA was 0 or 10.0. The accession from Site 21 produced partially fertile F_1 's when crossed with Testers A and B. For the accession from Site 24, the F_1 involving Tester A was partially fertile while that involving Tester B was completely sterile. The F_1 's between the accessions from Sites 25 and 32 and Tester B showed high pollen fertility and normal anther dehiscence. When crossed with Tester A, the former produced a sterile F_1 while the latter produced a partially fertile F_1 .

Seed set after open-pollination. The percentage seed set after open-pollination (PSS) in the parental lines including the four Testers ranged from 52.0 to 97.9. The PSS in the F_1 's ranged from 0 to 91.5 (Tables 1, 2 and 3). It significantly correlated with the three estimates for pollen fertility ($p < 0.01$), especially with the PDI (Table 4).

DISCUSSION

Correlation among the estimates for pollen and seed fertility. Three estimates were adopted for pollen fertility in the present study, and they closely correlated with one another. High correlation between pollen normality (PPN or PDI) and anther dehiscence (PDA) suggests that the anther indehiscence observed in the sterile F_1 's might be due to pollen abnormality, i. e., the low percentage of normal pollen grains in the anthers. Close correlation between seed set (PSS) and pollen fertility suggests that the degree of embryo-sac abortion was similar to that in the pollen grains. Among the three estimates of pollen fertility, the PDI correlated most closely with the PSS. This suggests the possibility that moderately aborted embryo-sacs maintained the ability to be fertilized and to develop plump endosperms. An anatomical study of the embryo-sac of the F_1 's is necessary for precisely elucidating the development of the female gametophytes in the F_1 's.

Geographical differentiation in *Ae. caudata*. Tanaka et al. (1967) was the first to find the intraspecific hybrid sterility in *Ae. caudata* and they concluded that the sterility is characteristic to intervarietal hybrids. The two varieties that they used were collected from different geographical regions. Ohta (1992) found that F_1 hybrids between the two varieties originating in sympatric stands on the Aegean islands are fully fertile. Furthermore, he crossed 10 accessions from the Aegean islands and Iraq with the four Testers and concluded that intraspecific hybrid sterility in *Ae. caudata* does not correlate with the taxonomic variety but with the geographical area where the parental lines were collected. In the present study, 25 additional accessions collected from Anatolia and northern Iraq were crossed with the four Tester strains. The results confirmed the previous conclusion as discussed

below.

(a) No relation between taxonomic varieties and hybrid sterility. Two varieties were taxonomically described in *Ae. caudata* based on the spike morphology (Eig, 1929). One is var. *typica* with an awn on the empty glumes of only the apical spikelet, and the other is var. *polyathera* with an awn on the empty glumes of both apical and lateral spikelets. Among the four Testers, only Tester B belonged to var. *polyathera* and the others to var. *typica* (Table 1). The three West Anatolian accessions belonged to var. *typica*. All of the F_1 's between them and Tester A were sterile while those involving Testers C and D were at least partially fertile. Variety *polyathera* occurs exclusively in Central Anatolia, and the F_1 's between Central Anatolian accessions and Tester A or B were fertile. The three South Anatolian accessions also belonged to var. *polyathera*. However, two of them produced fertile F_1 's when crossed with Tester A belonging to var. *typica*. The 12 accessions from East Anatolia and northern Iraq produced fertile F_1 's when crossed with Tester A and/or B irrespective of the variety. These results clearly indicate that the fertility of the F_1 's is not correlated with the taxonomic variety of the parental lines.

(b) Correlation between geography and hybrid sterility. Many accessions from the Aegean islands and West Anatolia produced at least partially fertile F_1 's when crossed with Testers C and D, while they produced highly sterile F_1 's when crossed with Testers A and B (Table 1). On the contrary, many of the Central, South and East Anatolian and Iraqi accessions produced fertile F_1 's when crossed with Testers A and B, but no accession produced fertile hybrids involving Testers C and D (Tables 2 and 3). The accession from Site 7 was the only exception in producing fertile F_1 's when crossed with the three Testers B, C and D. These results confirm the previous conclusion (Ohta, 1992) that the fertility of the F_1 's correlates with geographical area where the parental accessions occurred, and that the present distribution area of *Ae. caudata* is divided into two geographical regions based on intraspecific hybrid sterility. Furthermore, based on the results from the present Tester crosses using the 25 additional accessions from Anatolia and Iraq, the two geographical regions were more precisely determined. Davis (1965) divided Turkey into six geographical divisions based on topography. The two geographical regions defined from the hybrid sterility coincide with Davis' divisions. The western region is composed of Greece and West Anatolia, and the eastern region consists of Central Anatolia, South Anatolia, East Anatolia and northern Iraq. The boundary between the two geographical regions is the mountainous region lying between West Anatolia and Central Anatolia (Fig. 1). The border region

consisting of mountains higher than 1000 m may be an effective geographical barrier preventing gene flow between the western and the eastern regions, because *Ae. caudata* is predominantly a lowland species occurring below 1000 m above sea level (Hodgkin et al., 1992; Slageren, 1994). In addition to this major division into the two geographical regions, some minor genetic differentiation can be recognized within each geographical region. Within the western region, most of the accessions derived from the southern Aegean islands (Sites 1 to 5) produced sterile F_1 's when crossed with Tester C, while those from West Anatolia and the northwestern Aegean islands adjacent to West Anatolia (Sites 7 to 12) produced partially fertile F_1 's. In addition, two accessions (Sites 6 and 9) produced only sterile F_1 's when crossed with all of the Tester strains. These results suggest that the western region of the distribution can be further subdivided into at least two additional regions. In the eastern region, many Central Anatolian accessions produced F_1 's that showed the highest fertility when crossed with Tester B, while most of the South Anatolian, the East Anatolian and the northern Iraqi accessions produced the F_1 's with the highest fertility when crossed with Tester A. This also suggests that the eastern region of the distribution can be subdivided into Central Anatolia and the more southern regions.

Post-glacial establishment of the geographical distribution in *Ae. caudata*. Sakamoto (1973) grouped the 16 genera of the tribe Triticeae Dum. into the Arctic-temperate group and the Mediterranean group, based on the geographical distribution and ecological characteristics. The latter consists mainly of annual genera and the former of perennial genera. The latter group, to which the genus *Aegilops* belongs, was thought to be differentiated from the former group as the Mediterranean climate became established in the Quaternary (Sakamoto, 1973). The Quaternary is characterized by having several glacial periods. The geographical distribution of *Aegilops* and wild *Triticum* species was greatly affected by climatic changes during the glacial and interglacial periods. For elucidating not only the specific and intraspecific differentiation but also the establishment of the present geographical distribution of the genus *Aegilops*, it is important to take into consideration the shift in geographical distribution during the last glacial period. Recent palaeopalynological studies in the Near East allow us to reconstruct the shift in the geographical distribution of plant species in the late Quaternary. Van Zeist and Bottema (1991) presented a visual overview of the geographical shift in vegetation in the late Pleistocene and Holocene. In the period from 18000 BP to 16000 BP, the temperature dropped to a minimum, and steppe and desert-steppe with *Artemisia* and *Chenopodiaceae* covered the greater part of the Near East, which is now the pri-

mary diversity center of the wild *Triticum* and *Aegilops* species. As the climate became warmer, the woodland and forest-steppe zone, the habitats of wild wheat, expanded considerably. In the early Holocene, 8000 BP, the woodland and forest-steppe zone gradually spread into the inland areas of the Anatolian Plateau from the western Levant or the sheltered habitats in the East Taurus / Zagros mountains arc such as the Ruwandiz area in northern Iraq (van Zeist and Bottema, 1991). Hillman (1996) reconstructed the spread of wild einkorn across the northern Fertile Crescent based on the vegetation maps by van Zeist and Bottema (1991), and suggested that wild einkorn penetrated into the central Anatolian Plateau from the northeastern corner of the Mediterranean basin after the last glacial period.

The present study on intraspecific hybrid sterility revealed that the present geographical distribution of *Ae. caudata* is clearly divided into the two geographical regions. The establishment of the geographical distribution of *Ae. caudata* can be reconstructed based on the present results and the vegetation maps by van Zeist and Bottema (1991). In the maximum glacial period from 18000 BP to 16000 BP, *Ae. caudata* did not occur in Central and East Anatolia, and its distribution area was geographically divided into the two isolated regions. One was the region surrounding the Aegean Sea where the climate was affected by the sea and was not excessively cold or dry, and the other was the western Levant or some sheltered habitats in the East Taurus / Zagros mountains arc. As the climate became warmer, *Ae. caudata* migrated into Central and East Anatolia with the spread of oak woodland from the latter region, and now occupies the eastern region of the distribution. On the other hand, the western region of the present distribution was established by populations that occurred in the Aegean Sea region during the last glacial period.

Ohta (1995) suggested that intraspecific hybrid sterility in *Ae. caudata* is caused by cryptic structural hybridity defined as a chromosomal sterility due to heterozygosity for structural differences so small as not to materially influence chromosome pairing at MI (Stebbins, 1945). This mechanism causing hybrid sterility between the western and the eastern regions may have evolved during the last glacial period at the latest, and geographical isolation promoted intraspecific genetic differentiation. In the process of migration after the last glacial period, the chromosome structure of *Ae. caudata* continues to change, resulting in subdivision within each distribution region. Thus, *Ae. caudata* is thought currently to be in the process of speciation. Further studies of intraspecific differentia-

tion in *Ae. caudata* will give us a key to elucidating how the speciation occurred, and continues to occur, in the diploid wheat group.

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