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H. Kihara and M. Tanaka:

Morphological and physiological variation among *Aegilops squarrosa* strains collected in Pakistan, Afghanistan and Iran[1])

In honour of the 85th anniversary of Professor Bohumil Němec

Since *Aegilops squarrosa* L. was found to be one of the ancestors of common wheat (McFadden and Sears, 1944, 1946, Kihara, 1944, Kihara and Lilienfeld, 1949), it became our great concern to investigate this species from various points of view. Accordingly a collection of different varieties and strains of this species was urgently needed.

In 1955 the senior author went to Pakistan, Afghanistan and Iran as the leader of the Kyoto University Scientific Expedition to the Karakoram and Hindukush. The party consisted of 4 botanists, 3 anthropologists, 2 archaeologists and 2 geologists. One of the most important tasks of the botanists was to collect wheat and *Aegilops*. Two members of the botany team, Dr. Y. Yamashita and the senior author, have assumed this task. The collecting tour of 3 botanists (Kitamura, Yamashita and Kihara) started from Quetta (Pakistan) at the end of May and they traveled together to Kabul, the capital of Afghanistan. There the party split. Dr. Kitamura, a taxonomist, went to Nuristan mainly for the collection of wild plants. Dr. Yamashita traveled in the north region of Afghanistan. He collected wheat and *Aegilops*, driving along the „Silkroad", via Pulikhumri, Mezarisharif, Maimana and Herat. Then he proceeded to Teheran (Iran) and joined Kihara, who arrived earlier at this capital directly from Kabul by air.

A great many ears and seeds have been collected of *Triticum*, *Aegilops* and other cultivated plants along the coast of the Caspian Sea and in Azerbaijan. The collecting tour ended on the 30th of July at Tabriz, since at that time the wheat season was over. Fig. 1 shows the whole route of our collecting tour. According to geological as well as ecological considerations, the whole area has been divided into 9 regions: namely Quetta, Kabul, Pulikhumri, Maimana, Teheran, Isfahan, Gorgan, Pahlavi and Tabriz.

Except for Isfahan, where not a single species of *Aegilops* was found, everywhere both *Triticum* and *Aegilops* species have been obtained. During this expedition 8 *Aegilops* species have been found, namely *Ae. squarrosa*, *Ae. crassa* (4*x* and 6*x*), *Ae. cylindrica*, *Ae. triuncialis*, *Ae. triaristata*, (4*x*), *Ae. columnaris*, *Ae. juvenalis* and *Ae. umbellulata*. Only the last 2 species were not collected by ourselves. These were given to us by the courtesy of Mr. M. Mojitahedi, Department of Agriculture, Teheran.

Along the distance of over 6,000 km, ears and sometimes whole plants of *Aegilops squarrosa* were collected in 105 different habitats. According to

[1]) Contributions from the National Institute of Genetics, Japan, No. 227.
Contributions from the Laboratory of Genetics, Biological Institute, Kyoto University, No. 276.

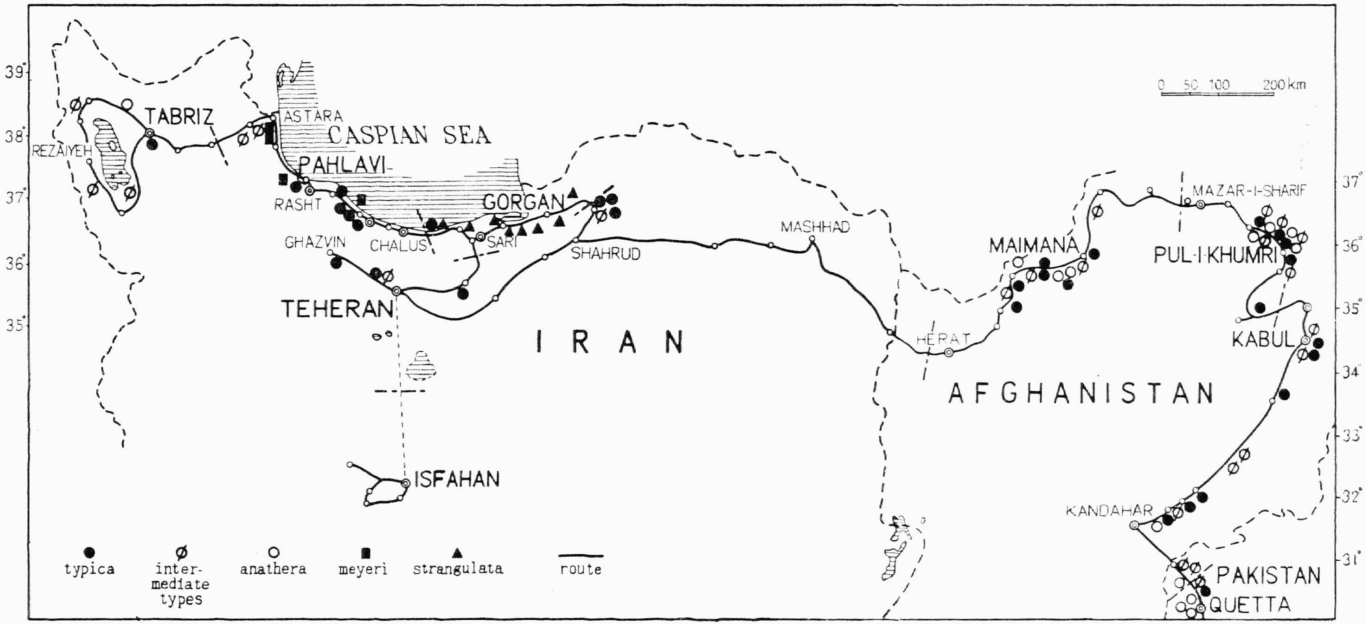


Fig. 1. Map showing the route of Kyoto University Scientific Expedition to Pakistan, Afghanistan and Iran and localities, where various varieties of *Ae. squarrosa* were found.

the differences in their habitats and morphological characteristics they were divided in 176 strains.[2]) This paper deals with a study of the morphological and physiological variation of these strains under cultivation in the experimental fields in Misima and Kyoto. Fertility and chromosome conjugation in F_1 hybrids among the strains obtained from different regions are also reported.

I. Morphological characters

Ae. squarrosa, a diploid species, differs from other diploid species of *Aegilops* by its barrel-type articulation and truncate sterile glumes. After Eig (1929) this species is divided into two subspecies, namely ssp. *squarrosa* and ssp. *strangulata*. Ssp. *squarrosa* has 3 varieties (*typica*, *meyeri* and *anathera*). After Eig they are described as follows:

Var. *typica*. This variety has the largest distribution. Ears are thick and the number of spikelets is numerous (9—11 or more). Spikelets are thick and provided with long awns.

Var. *meyeri*. Ear is very slender and short. Number of spikelets is 4—8. Awned except the 2 lowest spikelets.

Var. *anathera*. All spikelets except the 2 apical ones are awnless.

Though it seems that awnlessness (*anathera*) is associated with thin and short ears, and awnedness with thick and long ears, there are many exceptions, e. g. *anathera*-type which has thick and short ears. Pl. XIII. a—g shows different types of ears found within ssp. *squarrosa*.

Ssp. *strangulata* is characterized by its short and bead-like ears. The width of sterile glume usually exceeds the length. Grains are round. Morphologically there is no apparent variation in this group. Pl. XIII. h shows an ear of *strangulata*.

In two monographs of *Aegilops* written by Zhukovsky (1928) and Eig (1929), *Ae. squarrosa* is described from herbarium materials. However, we used mainly living plants under cultivation for morphological studies. Therefore some characters are strikingly different from those of the original habitats. For instance the plants under cultivation grow much taller than the plants grown wild. However the relative size of different strains did not change at all under the influence of cultivation.

1) Distribution of different varieties

As mentioned above, there are three known varieties within ssp. *squarrosa*. Two of them (*typica* and *anathera*) and their intermediate types can be found in the whole area.

It seems that there are at least 3 sets of allelomorphic pairs among ssp. *squarrosa*, namely: long vs. short ears, thick vs. thin spikelets, and awned vs. awnless (or short awned) outer glumes. The first alternatives, i. e. long ears, thick spikelets and awned glumes characterize var. *typica*, while the second alternatives belong to var. *anathera*. If so, it is very easy to explain why there are many recombinants, e. g. and awned type with thin and short spikes like var. *meyeri*.

The *meyeri*-type and also monotypic ssp. *strangulata*, are localized in Pahlavi and Gorgan respectively. Fig. 1. shows the distribution along our expedition routes of three varieties of var. *typica* together with the intermediate forms and var. *strangulata*.

[2]) Wheat Information Service, No. 3,1956.

Symbols given along the route indicate the habitats of the respective varieties or types. Since 176 strains could not be given consideration because of lack of space, the number of symbols in each region was reduced in proportion to the number of the various types.

Ae. squarrosa is usually found in or along the borders of wheat fields whereas it was found only in one of 38 barley fields. This exceptional barley field was located near a wheat field, where wheat and *squarrosa* grew mixed together.

Of course *Ae. squarrosa* grows wild in many places. But even so, its populations are usually found in gardens surrounded by high walls where they are protected from greedy grazing of sheep and goats. However Yamashita could find wild colonies of *squarrosa* stretching as far as the eye can reach north-west of Pulikhumri.

Tab. 1 shows the number of *squarrosa* strains collected in 6 regions (Pulikhumri, and Maimana are not taken into consideration). They are divided into two groups according to the places of collection, wheat fields or otherwise. Notwithstanding we were traveling usually along the roads by cars, the figures of Tab. 1 indicate a strong connection between *squarrosa* and wheats. This close relationship remembers us of that found between *Oryza* and *Echinochloa*. In Tabriz Yamashita bought a small quantity of wheat grains sold for chicken feed. It contained among other weeds many seeds of *squarrosa*. Similar seeds were sent to us by Mr. H. K a k i z a k i, who got them from a village near Chalus. This sample also contained seeds of many weeds, especially *Ae. squarrosa* (Tab. 2).

2) Height and procumbent character of culms

In our present investigations, the plants were divided into 4 classes according to their height: less than 50 cm., 50—65 cm., 65—80 cm. and over 80 cm. From the degree of procumbent habitus we have divided this character into 4 categories; procumbent, semi-procumbent, semi-standing and standing. The distribution of these characters is shown in Tab. 3.

It is noteworthy that many tall plants were found in Gorgan. All of them belong to var. *strangulata*. To show how tall *strangulata* is, two plants from natural habitats, *anathera* (Quetta) and *strangulata* (Gorgan), are shown side by side in Pl. XIV. *Typica*-strains having standing tillers were found in Teheran. They are tall at the same time. Procumbent and short types are found only in Pahlavi. They belong to var. *meyeri*.

3) Waxy leaves and green seedlings

Almost all *Aegilops* species have green leaves, stems and ears. In *Ae. triuncialis*, there are waxy and non-waxy (green) strains. So far we had no waxy strains in our old collection of *Ae. squarrosa*. However waxy strains were found in Iran. 8 out of 17 strains collected in Teheran were waxy. Waxy plants were found also in three neighboring regions, Teheran, Pahlavi and Tabriz, but none in other regions.

Purple seedlings are of common occurrence in *Ae. squarrosa*. Strains with green seedlings were found among strains obtained in 2 isolated regions, Tabriz and Maimana.

4) Other characters

Ears of *Ae. squarrosa* are usually cylindrical. Zigzag spikes were found in some strains. Variations in the color of ears (black, purple, yellow) and also of stems (purple, yellow) were observed.

II. Physiological characters

Differentiation in physiological characters was also observed among strains collected in Pakistan, Afghanistan and Iran. The distribution of these characters is rather restricted.

1) Resistance to rusts

So far we have established by infection experiments conducted by Dr.

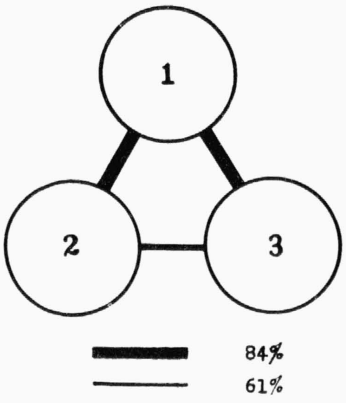


Fig. 2. Seed fertility relationships among 3 *squarrosa* strains (Nos. 1—3) after Kihara, 1954.

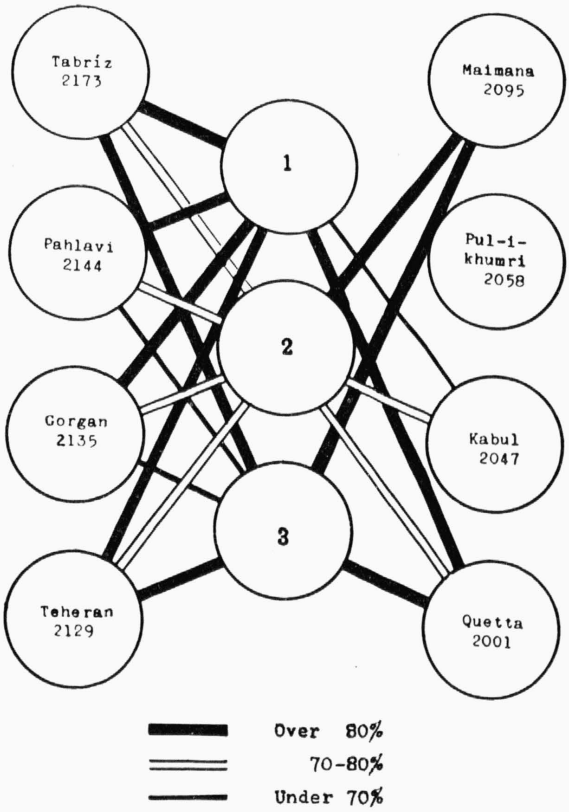


Fig. 3. Seed fertility relationships in the hybrids between strains Nos. 1—3 on one hand and 8 strains representing 8 regions on the other.

Hiratsuka (unpublished) that all of the strains of *Ae. squarrosa* var. *typica*, var. *anathera* and their intermediate types are susceptible to *Puccinia triticina* and *P. graminis* f. sp. *tritici*, while among strains of var. *meyeri* and var. *strangulata* there are such which differ in their reaction to the above rust strains. The results of infection experiments with seedlings of various *Ae. squarrosa* strains are shown in Tab. 4.

2) Earliness as shown by shooting date

Early, intermediate and late shooting strains were found. There was

a marked tendency to late flowering in the regions of higher latitudes, while early flowering types were found more often among plants of lower latitudes (Tab. 5).

3) Growing habit

Winter-growing habit prevails in diploid species of *Triticum* and *Aegilops*. Therefore it may be assumed that this is an ancestral type. Among *Ae. squarrosa* used for our examination, spring-type and intermediate type strains were found in 4 regions of Afghanistan and Pakistan. In all other regions in Iran only wintertype strains were found (Tab. 6).

III. Fertility and chromosome conjugation in F_1 hybrids between strains from different regions

The strains used in the crosses are listed in Tab. 7.

24 different hybrids out of 56 possible interregional cross combinations were made. Meiosis of PMCs in the parental strains as well as the hybrids was observed. There are 7 bivalents. Throughout meiotic divisions, the behavior of chromosomes is normal. Pollen fertility was examined in all hybrids. Pollen fertility of F_1 was usually slightly lower than that of the parents, appr. 80 to 97%, in one case 72%. Seed fertility was high. It amounted to more than 80% in most cases. However there are hybrids whose fertility is as low as 50%.

At first we had expected that some differentiation of the D-genome of *squarrosa* could be found among varieties or strains obtained from distant places. Low fertility was definitely observed in some interregional combinations. But they do not represent the whole situation. For instance a hybrid, *strangulata* × *meyeri* showed high fertility (95%) in one combination (2144 × 2135 and rec.), while the same combination, using other strains (2155 × 2115), gave low fertility (62%). So far it seems that sterility is dependent on minor differences in the genotypes of the parents and also on environmental conditions. That the last factors can play sometimes an important role, can be seen from the seed fertility of the parental strains (Tab. 7).

For further investigation of hybrid sterilities, we have used our 3 old strains, which were preserved in Kyoto for many years.[1]) The sterility relationships among them can be seen from Fig. 2. The fertility is calculated from reciprocal hybrids of the respective combinations. There was no significant difference in the fertility of reciprocal hybrids (K i h a r a, 1954).

Using the 3 old strains on one hand and 8 strains representing 8 regions on the other, we have obtained 19 out of 24 possible cross combinations. The results are shown in Fig. 3.

No. 2 gives rise to many sterile hybrids, while hybrids of No. 1 are highly fertile. It is as difficult to draw general conclusions from these results as from the crosses among interregional strains.

This of course could have been expected, as we can not draw any distinct lines between two regions and introgressive hybridization may have taken place fairly often between different strains. Indeed the senior author found a wheat field near the border of Gorgan and Pahlavi, where *strangulata, typica* and their intermediate types grew mixed together.

Differentiation in the karyotype of *Ae. squarrosa* strains was clearly observ-

1) See Wheat Information Service, No. 1, 1954.

ed. The difference lies in the morphology of a Sat-chromosome. This investigation is still under way.

Considerations

Throughout the whole route of our expedition which extended from Quetta to Tabriz (Isfahan excepted), *Ae. squarrosa* was found almost continuously. Only along the route between Mashhad and Teheran, we could not find a single specimen. This area seems to be rarely inhabited by the species at least along our route, which runs partly along the border of the Elburz Mountains and the Kavir desert. However Kuckuck (1954), who was staying 3 years in Teheran as a FAO expert, collected *Ae. squarrosa* in the province of Khorasan, near Mashhad, Chuchan, Bojnurd and Sabzeber. There he obtained also three other species (*Ae. triuncialis, cylindrica* and *crassa*). Therefore this area, especially in the mountainous districts, is also inhabited by the genus *Aegilops*.

In the mountainous districts (Damaneh and Shahr-Kord) of Isfahan, no *Aegilops* species was found. Neither could Kuckuck during his two collecting tours succeed in finding *Aegilops*. The conditions in the spelt region (altitude 2000—2380 meters) probably are, as he states, unfavorable to *Aegilops*.

In Azerbaijan, Kuckuck failed to collect *Ae. squarrosa*, though he has found many other *Aegilops* species. However we were fortunate in finding *Ae. squarrosa* in many places along the route around Lake Rezaiyeh, as shown in Fig. 1.

Ae. squarrosa is rich in variation. In short we can say that within this wild species there is a series of parallel variations, similar to those which occur among cultivated cereals like wheat and rye. Such characters as spring growing habit, early flowering, erect culms and large grains are usually found in crops which man has cultivated for many centuries.

Such characters might have arisen as spontaneous mutations and been subjected to selection for many years, since they were growing in wheat fields.

We will assume a *squarrosa* strain, which grows among a spring wheat population is harvested together with the wheat and sown together in a different place. If this process were repeated for many generations, this *squarrosa* strain would never survive unless it acquired the spring-growing habit. For earliness, a similar selection would take place. Of course if *squarrosa* strains with ancestral characters grew very often near or in wheat fields, this process of selection would not be simple. In fact we found that often plants belonging to the *anathera*-type—presumably an ancestral type—grow in wheat fields.

Varietal difference within the collective *squarrosa* species lie in the morphology of the ear, namely size, shape and number of spikelets with or without awns. Two varieties, *typica* and *anathera*, can be found almost everywhere. Two varieties, *meyeri* and *strangulata*, occupy narrow places along the Caspian Sea. Var. *meyeri* is distributed along the west coast (Pahlavi), while *strangulata* is found along the south-eastern coast, near Gorgan. Both of them showed resistance to certain rust strains. This character might be advantageous to them as these regions are very humid as compared with other arid regions. In general we might be allowed to say that physiological mutants grow in their respective habitats owing to their adaptation. Among morphological characteristics, height seems to be also subjected to natural selection. In

Gorgan weeds are luxuriant and tall, and var. *strangulata*, only one representative of this species in this area, is very tall.

A wealth of various forms of *Ae. squarrosa* was encountered in Iran, especially the districts around the Elburz Mountains. Here almost all of the variations were concentrated. Among them occurred types which distinguish cultivated plants from their wild ancestral forms, namely erect habit, large grains and height. Waxy leaves may be also counted as such. Their occurrence indicates existence of long duration under cultivated conditions.

S u m m a r y

1) 176 strains of *Ae. squarrosa* were collected along a route of over 6000 km in Pakistan, Afghanistan and Iran. The whole area, where *Triticum* and *Aegilops* were collected, is divided into 8 regions from geological as well as ecological considerations: Quetta, Kabul, Pulikhumri, Maimana, Teheran, Gorgan, Pahlavi and Tabriz (Fig. 1).

2) Morphological studies of these strains were undertaken mainly with plants cultivated in the experimental fields in Kyoto and Misima. Physiological investigations were made with a part of strains representing 8 regions.

3) *Ae. squarrosa* is a polymorphic species. Two subspecies, ssp. *squarrosa*, and ssp. *strangulata*, are clearly distinguished.

4) Among ssp. *squarrosa*, there are known three varieties: *typica*, *anathera* and *meyeri* (Pl. XIII.). There are many intermediate types between the first two, which are found almost in the whole area. *Meyeri*, which is morphologically an intermediate type between the two, is found solely on the west coast of the Caspian Sea.

5) Ssp. *strangulata* is localized along a narrow stretch of the south east coast of the Caspian Sea (Gorgan). Its occurrence along the route was estimated to cover 320 kilometers.

6) *Ae. squarrosa* was found very often in wheat fields. Therefore it is no wonder that we could find abundant spikelets of *Ae. squarrosa* in wheat grains sold as chicken feed.

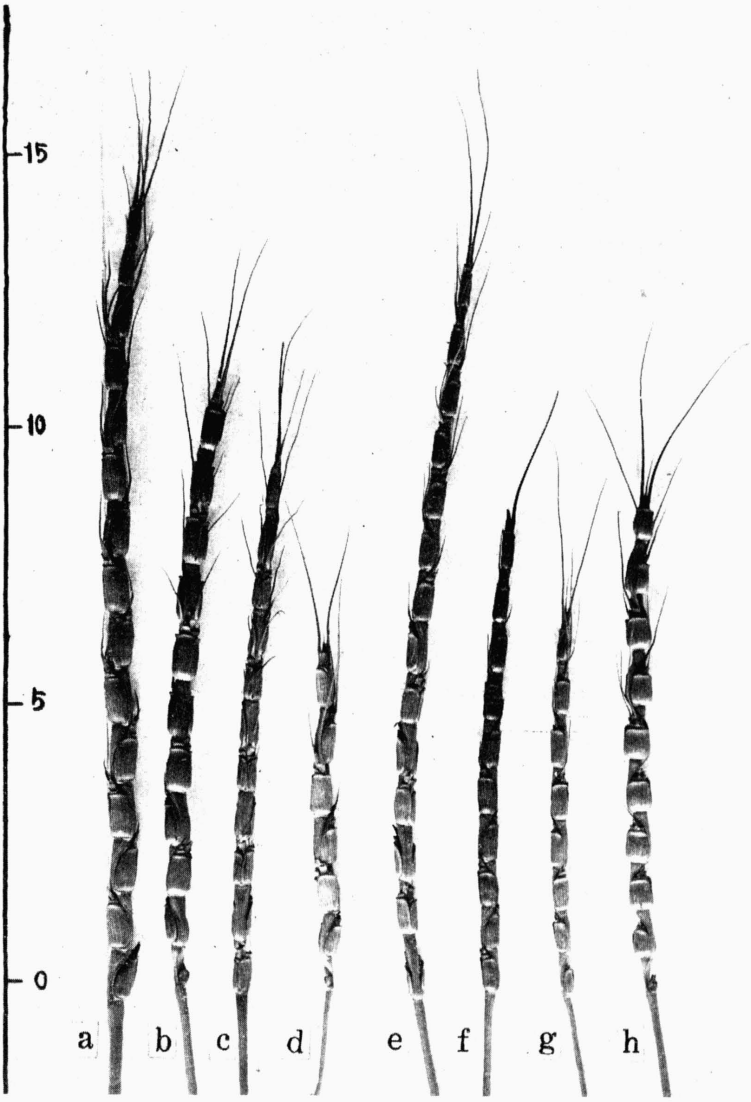
7) Such characters as erect culms and large grains, which can be found among cultivated wheats, are found only among *Ae. squarrosa* strains collected in wheat fields.

8) Many morphological variations were discovered. They are related to plant height, growth habit (procumbent or erect), waxy (non-waxy) leaves and colour of seedlings (red or green) etc.

9) Variations in physiological characters were also found. They are related to resistance to some rust strains, earliness and habit, namely winter, intermediate and spring growth. As to these characters some local varieties seem to have adapted themselves to their habitats. For instance vars. *meyeri* and *strangulata*, which are resistant to certain rust strains, grow in very humid places, along the coast of the Caspian Sea. All other regions are extremely arid.

10) Hybrids between strains from 8 regions and also hybrids between three old strains (Nos. 1—3) on one hand and 8 strains from 8 regions on the other were produced. All F_1 hybrids have shown 7 bivalents. Meiosis is normal.

Fertility is normal in most cases. However some combinations show lower fertility. Hybrids of strains No. 2 give very often rise to higher sterility (Fig. 3).



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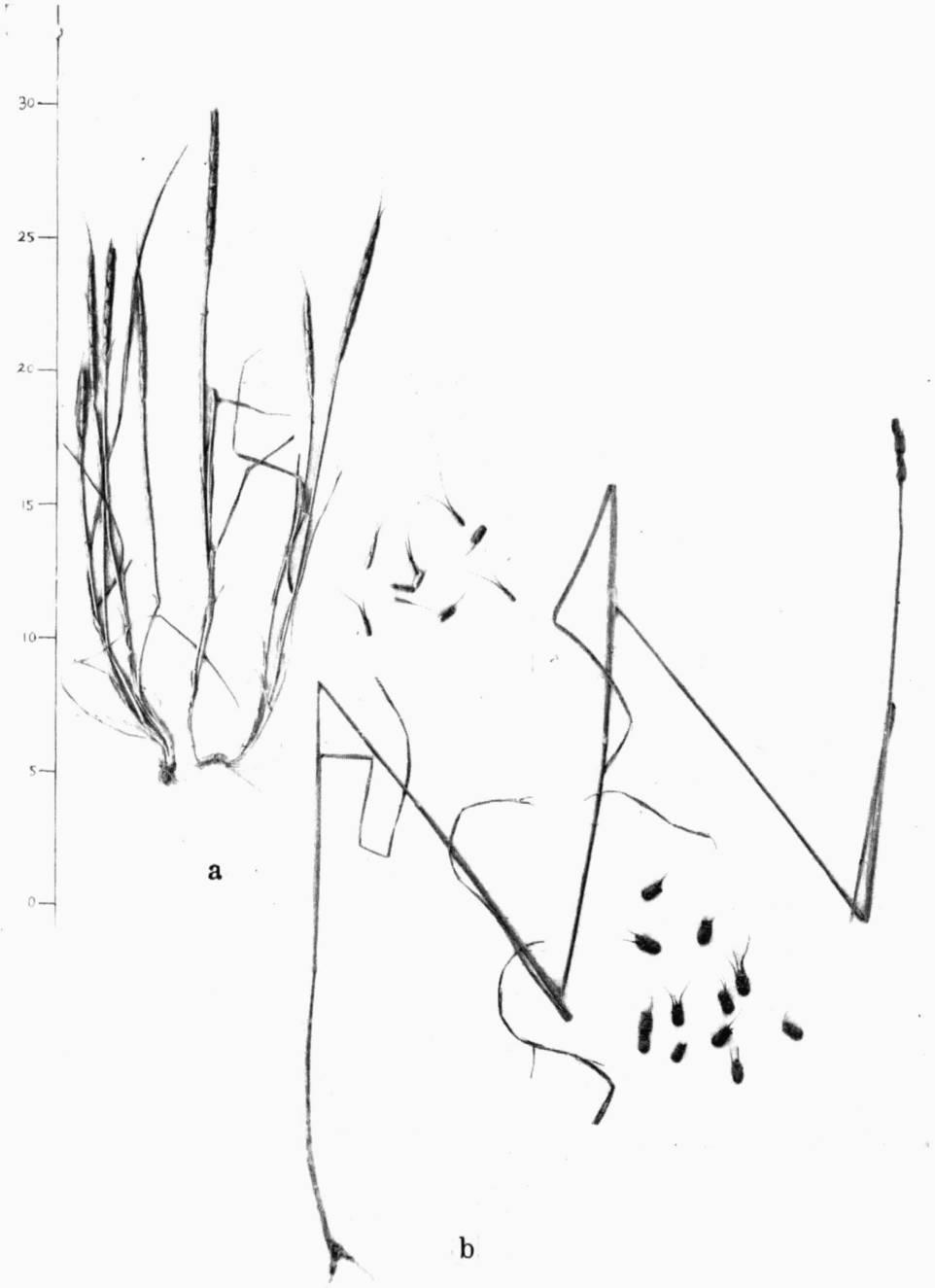

Kihara H. and Tanaka M.: Morphological and physiological variations among *Aegilops squarrosa* strains collected in Pakistan, Afganistan and Iran.

11) Sterility of the intra-species crosses seems to depend on the genotypes of the parents and partly on environmental conditions.

12) Most probably Iran is the center of diversity of *Ae. squarrosa*.

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Tab. 1. Number of *Aegilops squarrosa* strains collected in wheat fields and other places

Varieties of *Ae. squarrosa*	*Typica*	Intermediates	*Anathera*	*Meyeri*	*Strangulata*	Str. +* typ.	Total
Main crops:							
T. vulgare	16	11	4	0	13	3	47
T. durum	0	0	0	0	1	0	1
	16	11	4	0	14	3	48 (59%)
Places other than wheat fields:	9	13	3	7	1	0	33 (41%)
Total	25	24	7	7	15	3	81 (100%)

*) Mixed population of *strangulata* and *typica*.

Tab. 2. Number of seeds of wheat and *Ae. squarrosa* found in chicken feed

Origin	Wheat (grains)	*Ae. squarrosa* (spikelets)	Other seeds
Tabriz	8441[1])	31	*Ae. cylindrica*, *Ae. crassa*, *Ae. triuncialis*, barley etc.
Chalus	2998	870	Barley, wild oats, *Galium* sp., *Lolium* sp.

[1]) Among these grains probably 51 are rye.

Tab. 3. Variation in plant height and procumbency of tillers

Regions	Height (cm)				Habit			
	—50	50—65	65—80	80—	Procumbent	Semi-procumbent	Semi-standing	Standing
Quetta	4	4	1	0	0	0	9	0
Kabul	3	11	18	0	0	1	31	0
Pulikhumri	4	27	1	0	0	7	25	0
Maimana	4	14	5	0	0	3	20	0
Teheran	1	8	3	3	0	4	7	4
Gorgan	0	0	10	10	0	3	17	0
Pahlavi	8	14	0	0	13	9	0	0
Tabriz	2	4	6	0	0	4	8	0
Total	26	82	44	13	13	31	117	4

Tab. 4. Susceptibility/resistance of *squarrosa* seedlings to 4 rust strains (*Puccinia triticina*, *P. graminis* f. sp. *tritici* and *P. hordei*)[1])

No. of strains	Varieties (Habitats)	*P. triticina* 1 A	*P. triticina* 21 B	*P. graminis* f. sp. *tritici*	*P. hordei*
2003	*Aegilops squarrosa* v. *anathera* (Quetta)	S	S	S	R
2026	*Ae. squarrosa* v. *typica* (Kandahar)	S	S	S	R
2046	*Ae. squarrosa* v. *typica* (Kabul)	S	S	S	R
2058	*Ae. squarrosa* v. *anathera* (Pulikhumri)	S	S	S	R
2095	*Ae. squarrosa* v. *anathera* (Maimana)	S	S	S	R
2107a	*Ae. squarrosa* v. *typica* (Teheran)	S	S	S	R
2129	*Ae. squarrosa* v. *typica* (Khoshyailagh)	S	S	S	R
2112	*Ae. squarrosa* v. *strangulata* (Behshahr)	MR	MR	MR	R
2118	*Ae. squarrosa* v. *strangulata* (Gorgan)	R	MR	S	R
2144	*Ae. squarrosa* v. *meyeri* (Ramsar)	R	R	R-MR	R
2150	*Ae. squarrosa* v. *typica* (Pahlavi)	S	S	S	R
2163	*Ae. squarrosa* v. *typica* (Ardabil)	S	S	S	R
2173	*Ae. squarrosa* v. *anathera* (Tabriz)	S	S	S	R

R = resistant, MR = moderately resistant, S = susceptible. (Hiratsuka 1956.)
[1]) The rust strains used for this inoculation are the most common strains in Japan.

Tab. 5. Frequency of early and late shooting strains obtained from 8 regions

Regions	Date of shooting (5 day interval)								
	–5/V	–10/V	–15/V	–20/V	–25/V	–31/V	–5/VI	–10/VI	–15/VI
Quetta		5	3	1					
Kabul	1	5	8	7	7	2	1		
Pulikhumri		7	19	3	1	1			
Maimana		5	13	4	1				
Teheran				1	7	3	1	0	1
Gorgan						12	6	2	
Pahlavi					5	7	7	3	
Tabriz					3	1	3		

Kyoto, 1956

Tab. 6. Distribution of winter, intermediate and spring-types in *Ae. squarrosa*

Region	Winter	Intermediate	Spring	Total
Quetta	0	1	4	5
Kabul	3	3	1	7
Pulikhumri	1	0	2	3
Maimana	0	3	0	3
Teheran	4	0	0	4
Gorgan	2	0	0	2
Pahlavi	4	0	0	4
Tabriz	3	0	0	3
Total	17	7	7	31

Tab. 7. Seed fertility of strains from 8 regions used in crosses and 3 strains (Nos. 1—3) from the old collection of Kyoto University used in test crosses

No. of strains	Region (Habitat)	Varieties	Descriptions	Seed fertility (1956)
2001	Quetta	*typica*		86.1
2047	Kabul	*typica*		73.0
2058	Pulikhumri (Haibak)	*anathera*	short awns	92.7
2095	Maimana	*anathera*	yellow ears	92.7
2129	Teheran (Khoshyailagh)	*typica*	zigzag ears, tall	81.2
2135	Gorgan (Sari-Behshahr)	*strangulata*		92.0
2144	Pahlavi (Ramsar)	*meyeri*		81.9
2173	Tabriz (Khoy-Tabriz)	*anathera*	thick ears	93.1
1	(Derbent)	*typica*	zigzag ears	82.3
2	—	*typica*		91.4
3	(Tashkent)	*typica*		86.1

Explanation of Plates XIII and XIV

Plate XIII. Ear types of *Ae. squarrosa*.—a—g, ssp. *squarrosa*, c—f, intermediate forms between b and f. h, ssp. *strangulata*. a, var. *typica* (a giant form), b, var. *typica* (normal). c, var. *typica* (thin). d, var. *typica* (short). e, var. *anathera* (long). f, var. *anathera*. g, var. *meyeri*. h, var. *strangulata*.

Plate XIV. Plant height of *Ae. squarrosa* var. *anathera* (a) (Quetta) and var. *strangulata* (b) (Gorgan).