Origin and Dispersal of Common Millet and Foxtail Millet*

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In Eurasia, both winter and summer cereal crops have been cultivated over a wide range of environmental conditions. Winter cereals, such as wheat and barley, were domesticated in the Middle East about 10,000 years ago. Rice is a representative of summer cereals originating in southern Asia, and it has been grown widely in Asian countries. In addition to rice, several kinds of millets have been domesticated in Eurasia, some in east or central Asia and others in the Indian subcontinent. Among them, common millet (*Panicum miliaceum* L.) and foxtail millet (*Setaria italica* (L.) P. Beauv.) are thought to be the most anciently domesticated cereals in Eurasia. In the present paper, a new theory on the origin and dispersal of those two millets based on the results of recent field research on the two millets in southwestern Eurasia and those of the experimental works on landraces of the millets collected from the vast areas of Eurasia is discussed.

Botanical origin of common millet and foxtail millet

The botanical origin of common millet is still unknown. The probable progenitor of this millet in the genus *Panicum* based on the genetical studies has not been found yet. On the other hand, green foxtail (*S. viridis* (L.) P. Beauv.) is presumed a wild ancestor of foxtail millet, *S. italica*. The two species are diploids with the same chromosome number (2n=18). The F_1 hybrid between them is fertile and chromosome pairing in F_1 is normal with nine bivalents at the MI of the PMCs[4]. This indicates that these two species are biologically the same species and *S. viridis* is the probable ancestor of domesticated foxtail millet. However, because of wide occurrence of *S. viridis* in Eurasia, it is almost impossible to localize the place of domestication of foxtail millet mainly on the geographical distribution of wild ancestral species.

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Current theories on the geographical origin of common millet and foxtail millet

Vavilov[14] assumed that common millet and foxtail millet originated in East Asia based on the following two lines of botanical evidence: (1) sharp increase in diversity in common millet toward East Asia and an exceptional diversity of biological characters of this millet in Mongolia and Manchuria, an area of Chinese civilization, and (2) the principle center of the diversity of foxtail millet is eastern Asia including China and Japan, where it is cultivated as a cereal crop for food. Vavilov's theory has been supported by the findings of archaeological remains of these two millets from the Neolithic Yan-shao villages of China, which were established about 4,000 BC.

Quite interestingly, the earliest palaeoethnobotanical finds of common millet in the West came from the Neolithic sites of central Europe. Foxtail millet has also been found in some Neolithic sites in Europe, and this millet was chiefly cultivated in the Bronze Age in alpine Europe[7]. Carbonized grains of common millet have also been reported from the aceramic levels at Argissa-Maghilla in Greece (5,000–6,000 BC) and from the Jemdet Nasr

period in Mesopotamia dating around 3,000 BC[9]. The palaeoethnobotanical data obtained so far evidently indicate that common millet and foxtail millet have been the staple food for the people since a very early period of agricultural development in Eurasia. Therefore, recently, Harlan[2] suggested the possibility of independent domestication of these two millets at least in China and Europe. He discussed three different possibilities on the domestication and dispersal of these two crops considering the archaeological findings from Neolithic sites in China and Europe; (1) common millet and foxtail millet were domesticated in China and dispersed to Europe before 4,000 BC, (2) they were domesticated in the West and dispersed to China before Yang-shao times, and (3) there was more than one domestication. He believed that the independent domestication was the most likely answer because no other known crop has such a distribution in that time range. He mentioned further that in our present ignorance to these two millets, independent domestication appears to be the most likely but new information would easily lead to other conclusions.

Our recent research results

In 1978, 1979, 1980 and 1982, we made four botanical expeditions to Afghanistan, Turkey, Greece, Romania, France and Spain. During these field research works, we collected many samples of common millet and foxtail millet together with information on traditional cultivation methods and utilization for food. At the same time, during these years, we collected many different landraces of these two millets from the vast areas of Eurasia. Using these materials we carried out an analysis of genetic variations and their geographical distribution.

1) Finding of a weed form of common millet

During our field research in 1980, we collected a weed form of common millet along the road located in the western suburbs of Iasi, Moldavia Province of Romania[11]. This form occurred abundantly forming a dense belt between the road and the maize field and partly invaded into the cultivation fields. The morphological characteristics of this form are very similar to the cultivated common millet except for the shorter stature, more sparsely opened panicles, fewer spikelets per panicle, smaller floral glumes and brittle spikelets. The average heading date of this weed grown in a glasshouse was 39 days, which was very similar to those of cultivated Romanian forms.

Based on the resemblance of this form to the cultivated one, it was classified as *P. miliaceum* subspecies *ruderale* (Kitag.) Tzelev[13], which was found in Manchuria and originally named as *P. miliaceum* var. *ruderale* Kitagawa[5]. Popova[8] reported a very similar readily shattering form of common millet from the Central-Boharian Oasis. This form is distributed not only in Manchuria but also in Siberia and Central Asia[13]. A similar plant is described in the European weed flora.

The origin of common millet is still unknown. A more detailed study of this weed form in Romania may provide some ideas on the botanical origin of this crop, although it is often difficult to distinguish the wild form from the weedy race which sometimes might possibly be derived from an escaped cultivated form. However, judging from the wide occurrence of this weed form, from Manchuria to East Europe through Central Asia, detailed genetic analysis of this form with the cultivated form is expected to provide some positive ideas on the botanical origin of common millet that has been completely ignored and unexplored.

2) Traditional utilization methods

If common millet and foxtail millet have been cultivated extensively in wide areas of Eurasia since ancient times, there must be the traditional way of utilization for those two millets. During our field research work, we gathered information on this subject from local people in each region. Table 1 gives a summary of the results. The information on China and Caucasia was obtained from the literature.

Generally speaking, the utilization methods of cereal grains are divided into two groups, one for foods and the other for drinks. The former is further divided into three categories, grain, meal and flour, and the latter non-alcoholic and alcoholic drinks. For preparation of food from the grains of common millet and foxtail millet, seven

Table 1. Foods and drinks made from the grains of common millet and foxtail millet in Eurasia

Region		Type of cooking								
		Grain			Meal	Flour			Drink	
		Boiled grain	Gruel	*Mochi*	Porridge	Dumpling (*dango*)	Flour porridge	Bread	Non-alcoholic	Alcoholic
Japan	non-waxy	+	+							
	waxy	+		+		+				+
Korea	non-waxy	+								
	waxy	+		+						+
China	non-waxy	+	+					+		+
	waxy			+				+		+
Taiwan	non-waxy	+								
	waxy	+		+		+				+
Batan Islands					+					
Halmahera Islands					+					
India		+			+		+	+		
Afghanistan					+			+		
Caucasia					+				+	
Turkey					+					
Bulgaria					+			+	+	
Romania					+				+	
Italy					+					
France					+					

subcategories have been recorded, namely boiled grain, gruel, *mochi* (cake made from waxy starch), porridge and dumplings (*dango*), flour porridge and bread. It is interesting to note, as seen in Table 1, that in East Asia preparation of boiled grain, gruel, *mochi* and alcoholic drinks is popular, while in the area from Southeast Asia and India to Europe, porridge, flour porridge, bread and non-alcoholic drinks are prevailing.

3) *Morphological variation and its distribution*

No comparative studies of the characteristics of these two millets covering all of Eurasia have been made so far. There is only the taxonomic study on common millet from European parts of USSR, Caucasia, Central Asia, Siberia, Mongolia and Manchuria made by Lyssov[6]. He lists 78 varieties classified into five subspecies. Thirteen varieties of foxtail millet were reported in Georgia, western Transcaucasia[1]. The collections of millets in Hindukush made by the German Hindukush Expedition in 1937 and 1938 were studied by Scheibe[12]. He classified 103 collections of foxtail millet into 15 varieties belonging to two subspecies. He also classified 118 samples of common millet into seven varieties.

To shed light on this problem, comparative studies of common millet using 43 samples from Afghanistan (15 samples), Romania (8), Turkey (2), Greece (2), Bulgaria (1), Czekoslovakia (2), Central Asia (7) and Japan (6), and 70 samples of foxtail millet from Afghanistan (25), Europe (8), Central Asia (7), India (4), Taiwan (2), Korea (6) and Japan (18), were carried out in Kyoto in 1981[10].

All European and Central Asiatic strains of common millet were very early varieties, while the Afghan strains include both intermediate and late varieties. The Afghan strains showed a wide variation in plant height, the number of tillers and the length of panicle in addition to the number of days from sowing to heading and the number of leaves. Romanian strains were intermediate between Central Asiatic and other European strains.

Field observation of foxtail millet in Afghanistan indicated that they are characterized by early heading and short plant height. According to our experiment, the Afghan strains were clearly characterized by very early heading as were those of European and Central Asiatic strains, which were quite different from the East Asiatic ones used for comparison. Another remarkable characteristic of the Afghan strains was the large number of tillers from 7 to 41. These characteristics are very sim-

ilar with those observed in *S. viridis*, a probable ancestor of this millet. This indicates that the Afghan foxtail millet has conserved rather primitive features. Furthermore, the present comparative studies suggest that there is a distinct difference between the strains of the West and those of the East, Afghanistan and its vicinity being a distributional boundary.

4) *Geographical distribution of landrace groups of foxtail millet classified by hybrid pollen sterility*

Through the dispersal process of a given crop from the place of its domestication, genetic differentiation adapted to various ecological conditions and agricultural practices occurs, and this process produces specific landraces of the crop. A well-known example is Japonica, Indica and Javanica type differentiation in cultivated Asian rice. Similar genetic differentiation might be expected in common millet and foxtail millet but there have been no experimental studies.

To clarify the genetic differentiation among local landraces of foxtail millet, we produced 223 combinations of intraspecific hybrids using 83 strains collected from various parts of Eurasia. These strains were crossed with three tester strains, one (tester A) from Japan, one (B) from Taiwan and one (C) from Europe[3]. Among the 83 strains of foxtail millet used in this experiment, 62 strains successfully produced F_1 hybrids with these testers. They could be classified into types A, B, C, AC, BC and X by means of intraspecific hybrid partial pollen sterility. Namely, the strains of type A, B, C were those which produced F_1 hybrids having normal pollen fertility when crossed with tester A, B, and C, respectively. When both F_1 hybrids from the crosses with two testers, A and C, or B and C, showed normal pollen fertility, the strain was classified as type AC or BC. The strains whose F_1 hybrids always showed pollen fertility of less than 75% in all three cross combinations were designated as type X.

Most strains of type A are distributed in Japan, Korea and China. The strains of *S. italica* in these regions are thought to be closely related with one another and are clustered as a single landrace group. Another phylogenetic group might be distributed in south China because the strains from Hunan and Yunnan Provinces were not type A. The strains of type B are narrowly distributed in the mountainous areas of Taiwan and in the southwestern part of the Nansei Islands (Okinawa Prefecture) of Japan in the neighborhood of Taiwan. This strongly suggests that the strains of the southwestern part of the Nansei Islands were introduced from Taiwan. Type C is found especially in most European strains. This indicates that the European strains also form a distinct landrace group. Type AC strains are distributed in Afghanistan and type BC in India. These types are thought to be less specialized genetically than type A, B or C. Type X might include more than one type, because different kinds of pollen fertility

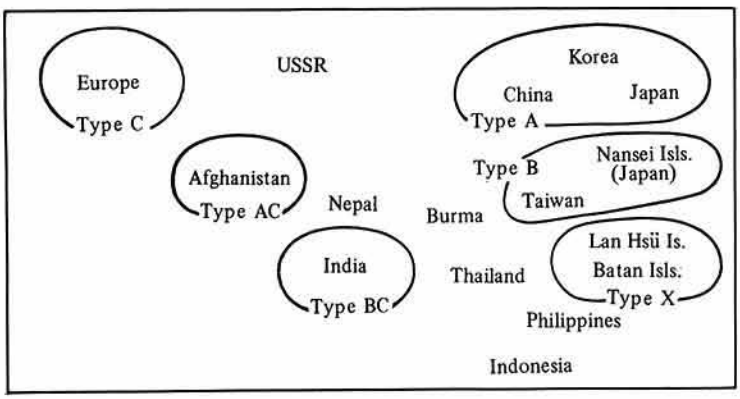

Fig. 1. Geographical distribution of six landrace groups of foxtail millet
Data based on Kawase & Sakamoto[3].

arrays in the three cross combinations are recognized among the strains classified as type X. The type X strains from Lan Hsü Island of Taiwan and the Batan Islands of the Philippines might belong to a single landrace group, because these islands are located in a close vicinity. Some strains of type X might have been originated in different ways, since they are sporadically distributed in different regions. To elucidate these problems, further cross experiments are needed.

Partial hybrid pollen sterility occurs as the result of genetic differentiation between strains. Therefore, these types are thought to reflect the phylogenetically differentiated landrace groups. Each of these landrace groups showed a rather limited geographical distribution, and was often found endemic to small areas as shown in Fig. 1. The indigenousness of these six landrace groups differentiating with one another implies a long history of cultivation of foxtail millet in each region. The differentiation of a landrace group in foxtail millet is thought to have occurred along with the dispersal from the place of domestication as is the case for Asian rice.

A new theory on the geographical origin of common millet and foxtail millet

The foregoing discussion is summarized as follows:

(1) Archaeological remains of common millet and foxtail millet were found in Neolithic sites not only in East Asia and Europe but also in the central part of Asia and Middle East. This indicates that these two millets are the most anciently domesticated cereals in Eurasia, and that they have been cultivated throughout most of Eurasia.

(2) Traditional utilization of those two millets can still be found in various parts of Eurasia.

(3) The diversity of botanical characters is observed not only in East Asia but also in Central Asia and its vicinities.

(4) The wide distribution of a weed form closely related to cultivated common millet from North China to East Europe through Central Asia was evident. Therefore, this form is assumed to be the progenitor of common millet.

(5) Foxtail millet collected from Afghanistan was characterized by short plant height with quite a few tillers and consequently with many small panicles as observed in green foxtail, *S. viridis*, a probable ancestor of this millet. This indicates that Afghan foxtail millet has conserved rather primitive features.

(6) From the analysis of partial pollen sterility observed in intraspecific hybrids of foxtail millet, genetically less specialized landraces, i. e. type AC and type BC, were found in those from Afghanistan and India.

Based on these findings, a new theory on the geographical origin of common millet and foxtail millet is proposed: Common millet and foxtail millet were first domesticated within the area ranging from Central Asia and Afghanistan to India, and from there they were dispersed both westward to Europe and eastward to East Asia being gradually differentiated genetically. They have expanded their cultivation southeastward to continental parts of Southeast Asia and finally to the Pacific islands of Southeast Asia through the Indian subcontinent. The archaeological evidence of the Neolithic occurrence of those two millets both in North China and Europe is in good agreement with this theory.

As mentioned before, the possibility of Chinese origin of those two millets has been supported by the archaeological remains from Neolithic Yanshao sites. The comparative studies made under experimental conditions in the present investigation also demonstrated a large diversity in East Asian strains of both millets concerning some quantitative as well as qualitative characters. Some authors have pointed out that the center of diversity is not necessarily the center of origin. The large morphological diversity in East Asia as observed by Vavilov[14] could have resulted merely from the intensive cultivation of the landraces of both millets for a long time. Therefore, East Asia might be a secondary center of diversity but not the place of domestication.

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