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## 巻頭言——多様な生活文化の中の雑穀（特集）

このくにはユーラシア大陸の極東に位置し、海洋に囲まれながら、多数の巨大都市や工業地帯を構築した今日でさえ、ありがたいことに領域の約64%が山林に被われている。島ぐにであると同時に山ぐにであるという特異な自然環境に立地している。台風や地震などの自然災害は多いが、このことを忘れずに、禍福転じて暮らせば、平常時にはとても穏やかで豊かな自然環境にある。

大陸から直接東漸して、あるいは花綵列島を伝って間接的に南下あるいは北上して、次々と多様な民族がそれぞれの生活文化をもってやってきて、定住した。島々の先は太平洋だから、この先には行けなかった。豊かな自然は行く必要も感じさせなかったのだろう。約1万年前に農耕文化が獲得された後には、栽培植物を含む農耕文化複合も伴って移住してきた。

この見方からすれば、このくには、ヤマト族だけではなく、アイヌ、オロッコ、ギリヤーク、朝鮮族などの混合民族によって構成され、山住の縄文文化の系譜をうけた畑作農耕から、平住（低地）の弥生文化の系譜による水田稲作農耕へと歴史的に進展してきたと考えられる。農耕が始まる以前の無土器文化であれ、その後の農耕文化であれ、このくには生活文化は途切れることの無い時を経ながら重層的に蓄積されてきたはずだ。

ところが、第二次世界大戦後、何故か、柳田国男による日本の単一民族論、平住（低地）の弥生文化の系譜のみを重視する水田稲作農耕が優勢になった。これが今日の日本の農業や農耕のあり方を著しく歪め、父祖以来の食糧自給の努力を捨て去り、食糧輸入に依存する体制に導いた思想の一つであるとする。江戸時代の米石高制に加えて、明治維新の殖産興業、戦時中の米配給制度、アメリカに敗戦した後の小麦・脱脂粉乳などの食糧援助が、この国の人々をし

て、独立心を喪失した「米悲願単一民族」に仕立て上げた。柳田の思想の一部、微瑕が拡大解釈されて、この政策に与したのだろう。

人間も生き物であるから、食料の安全・安心確保は第一の欲求である。ところが、この国の政策は食糧安全保障を放棄したのである。水田稲作のみに集中した結果の米の過剰生産を減反の強制によって対応した。生産を放棄することに対して補助金を出したのである。稲の多収よりも安全・安定生産、畑作の麦・雑穀の生産も維持すべきであった。世界的な人口激増や環境変動のもとで、不安定な食糧生産と需要の拡大によって、海外からの食糧輸入に全面的な依存はできない。この国が農業生産を軽視し、食料安全保障を怠っているのも、多様な食料の安全・安心は家族で、地域社会で確保せねばならない。

私の第2の人生は、ユーラシア大陸各地および日本各地への旅に多くの年月を費やした。インド（バンガロール、農科大学）とイギリス（カンタベリー、ケント大学）の地方都市にはサバティカルで、タイ（バンコック、ラジャバト・プラナコン大学）には大学院の集中講義などで、しばらく暮らす機会を得た。このため、とりわけインド農村の暮らし、西欧の農村景観から大きな心象を受けた。第3の人生では、旅で観たこと、考えたこと、旅の後の調査研究の成果をアーカイヴすることにした。

この第9号はユーラシアの旅行でたくさんの農家から分譲を受けた栽培植物の種子・標本を用いた実験研究の成果をまとめた。研究の一部は東京学芸大学民族植物学研究室のインド雑穀研究チームの成果である。彼らの卒業論文や修士論文の成果は各自のものであり、いずれ彼らが公表することを願いながら、ここでは概要を未発表として記録しておく。

木俣美樹男（2015-9-24）





# Agricultural complex of millets in the Indian subcontinent

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The Indian subcontinent is a wonderland for studying the domestication process of grain crops. Several species of millet are domesticated in this region. Cooking of cereals forms an important part of the agricultural complex. The agricultural complex is composed of their vernacular names, religious function, archaeological evidence, etc. The first author had participated six times in expeditions for millet research and collected numerous accessions of millets and their relative species, with information on their agricultural complex, from hundreds of farmers in their villages and fields. Ancient farmers had originally domesticated six species of millet from the relative weed species in India. Indian millet species were domesticated in the process of diffusion from humid paddy fields in Eastern India to dry upland rice fields in the Deccan Plateau, Southern India.

Key words: agricultural complex, domestication, Indian subcontinent, millet, tertiary crop

## Introduction

The Indian subcontinent is a wonderland for studying the domestication process of grain crops. Several species of millet are domesticated in this region. The grain crops cultivated in this subcontinent are classified into the following four groups on the basis of geographical origin: (I) African, *Eleusine coracana* (L.) Gaertn., *Pennisetum glaucum* (L.) R. Br., and *Sorghum bicolor* Moench; (II) Mediterranean, *Hordeum vulgare* L. and *Triticum spp.*; (III) Asian, including four subgroups, (a) *Panicum miliaceum* L. and *Setaria italica* (L.) P. Beauv., (b) *Coix lacryma-jobi* L. var. *ma-yuen* (Roman.)

Stapf. and *Oryza sativa* L., (c) *Echinochloa frumentacea* (Roxb.) Link, *Panicum sumatrense* Poth., *Paspalum scrobiculatum* L., *Digitaria cruciata* (Nees) A. Camus., *Setaria pumila* (Poir.) Roem. & Schult, and *Brachiaria ramosa* (L.) Stapf.; and (d) Southwestern China, *Fagopyrum esculentum* Moench, *Fagopyrum tataricum* (L.) Gaertn.; and (IV) New World, *Zea mays* L., including *Amaranthus hypocondriacus* L., *Amaranthus caudatus* L., and *Chenopodium quinoa* Willd. These four cereal and pseudocereal groups accompanied by agricultural complexes have been introduced several times during prehistoric and historic ages from many regions into the subcontinent.

Indian food culture has been a reflection of the people's heritage. It represents India's historical development, religious beliefs, cultural practices, and above all, geographical attributes (Sahni 1986). In the Indian subcontinent, staple foods made using grain crops are served with various types of spicy curries and legume *dal* stews. Many unique cooking styles can be found for each cereal in any part of the subcontinent (Aziz 1983, Sahni 1986). Cooking of cereals forms an important part of the agricultural complex (Maeshwari 1987, Sakamoto 1988). Indian cooking consists of a unique combination of special cooking styles developed for each grain crop (Kimata et al. 2000). Moreover, the agricultural complex is composed of their vernacular names, religious function, archaeological evidence, etc.

This special issue is composed of studies on the agricultural complex, domestication process, and dispersal of millets, especially *Setaria pumila* (syn. *Setaria glauca*) and *Panicum miliaceum* and not major crops such as rice, wheat, barely, and maize, in the

Table 1. Grain crops grown in the Indian subcontinent

Geographical origin Scientific name	Japanese name	Indian name	Chromosome number	Growth habit	Botanical origin
<b>Africa</b>					
<i>Sorghum bicolor</i>	m orokoshi	ḡwar	2n=20 (2x)	annual	<i>S. bicolor</i> var. <i>verticilliflorum</i>
<i>Pennisetum americanum</i>	to u jinn-bie	bajra	2n=14 (2x)	annual	<i>P. violaceum</i>
<i>Eleusine coracana</i>	sh koku-bie	ragi	2n=36 (4x)	annual	<i>E. coracana</i> var. <i>africana</i>
<b>Asia</b>					
<b>1. India</b>					
<i>Panicum sumatrense</i>		sam ai	2n=36 (4x)	annual	<i>P. sumatrense</i> ssp. <i>osilopodium</i>
<i>Paspalum scrobiculatum</i>		kodo	2n=40 (4x)	perennial	wild
<i>Echinochloa flumentacea</i>	indo-bie	ḡngora	2n=54 (6x)	annual	<i>E. colona</i>
<i>Brachiaria ramosa</i>		kome		annual	wild
<i>Setaria pumila</i>	kn-enokoro	ko lati		annual	wild
<i>Digitaria cruciata</i>		raishan		annual	wild
<b>2. South-eastern Asia</b>					
<i>Coix lacryma-jobi</i> var. <i>ma-yuen</i>	hatom ugi		2n=20 (2x)	perennial	<i>C. lacryma-jobi</i> var. <i>lacryma-jobi</i>
<b>3. Central Asia</b>					
<i>Setaria italica</i>	awa	thenai	2n=18 (2x)	annual	<i>S. italica</i> ssp. <i>viridis</i>
<i>Panicum miliaceum</i>	kbi	cheena	2n=36 (4x)	annual	<i>P. miliaceum</i> ssp. <i>ruderales</i>
<b>4. South-western Asia</b>					
<i>Fagopyrum esculentum</i>	soba		2n=16 (2x)	annual	<i>Fagopyrum esculentum</i> ssp. <i>ancestralis</i>
<i>Fagopyrum tartaricum</i>	dattan-soba		2n=16 (2x)	annual	<i>Fagopyrum tartaricum</i> ssp. <i>notanini</i>
<b>New world</b>					
<i>Amaranthus hypocondriacus</i>	sen-ninkoku		2n=32, 34 (2x)	annual	<i>A. cruentus</i> ( <i>A. hybridus</i> )
<i>Amaranthus caudatus</i>	hin oge itou		2n=32, 34 (2x)	annual	<i>A. cruentus</i> ( <i>A. hybridus</i> )
<i>Chenopodium quinoa</i>	khoa		2n=36 (4x)	annual	<i>C. quinoa</i> ssp. <i>millenium</i>

Indian subcontinent. *Setaria pumila* has been dispersed in only a very limited area of the Deccan Plateau (Kimata 2015a, 2015b), while *Panicum miliaceum* has been dispersed throughout Eurasia (Kimata 2015d), including the Indian subcontinent, and recently North America and Australia. It is very fascinating from an environmental perspective of history and geography that the distribution patterns of *Setaria pumila* and *Panicum miliaceum* are remarkably different.

#### Many species of millet cultivated in the Indian subcontinent

Many species of millet are still grown by numerous farmers in the Indian subcontinent. These species are divided into three groups on the basis of place of origin: (1) Asia, including the indigenous Indian subcontinent, Central Asia, Southeast Asia, and Tibet; (2) Africa; and (3) the New World (Table 1). The following seven species of Asian millet were introduced from Central Asia, Southeast Asia, and Tibet: *Panicum miliaceum*, *Setaria italica*, *Coix lacryma-jobi* var. *ma-yuen*, *Fagopyrum esculentum*, and *Fagopyrum tartaricum*. The African millet species are *Eleusine coracana*, *Sorghum bicolor*,

and *Pennisetum glaucum*. These species were introduced via the Arabian peninsula in about 2000 BC (Sakamoto 1987, Ohnishi 1998). The New World pseudocereals are *Amaranthus caudatus*, *Amaranthus hypocondriacus*, and *Chenopodium quinoa*, and they were introduced in 19th century (Sauer 1976).

Indigenous millet species have been domesticated in the Indian subcontinent for about 3500 years (Fuller 2002). These millet species are *Echinochloa furumentacea*, *Panicum sumatrense*, *Paspalum scrobiculatum*, *Brachiaria ramosa*, *Setaria pumila*, *Digitaria cruciata*, and *Digitaria sanguinalis*. The former three species seemed to be secondary in origin through mimic and/or companion weeds with rain-fed paddy and upland rice in Eastern India. The next two species, *Brachiaria ramosa* and *Setaria pumila*, were domesticated as a secondary crop associated with the other millet species via their mimic/companion weed types in Southern India. *Digitaria cruciata* was domesticated in the late 19th century by Kashi natives in Meghalaya, and it is cultivated in the Kashi Hills (Singh and Arora 1972). Unfortunately, *Digitaria sanguinalis* has disappeared, and its origin is unclear.

Table 2. Expeditions of millet research in the Indian subcontinent between 1983 and 2001.

Year (month)	Locality	Research Team
1983.9- 11	Nepal India (Haryana)	The Japanese Scientific Expedition for Nepalese Agricultural Research
1985.9- 11	Pakistan (Northwest province), India (Karnataka, Andhra Pradesh, and Tamil Nadu)	Kyoto University Scientific Expedition to the Indian Subcontinent
1987.9- 11	India (Jammu and Kashmir, West Bengal, Orissa, and Assam), Pakistan (India)	Kyoto University Scientific Expedition to the Indian Subcontinent
1989.9- 10	Pakistan (Azad Kashmir), India (Karnataka, Madhya Pradesh, and Maharashtra)	Kyoto University Scientific Expedition to the Indian Subcontinent
1996.9~97.6	India (Karnataka, Andhra Pradesh, Tamil Nadu, Orissa, Himachal Pradesh, and Uttar Pradesh)	Research abroad supported by Japanese Government, University of Agricultural Sciences at Bangalore
2001.9- 10	India (Karnataka and Orissa)	Tokyo Gakugei University Scientific Expedition to the Indian Subcontinent

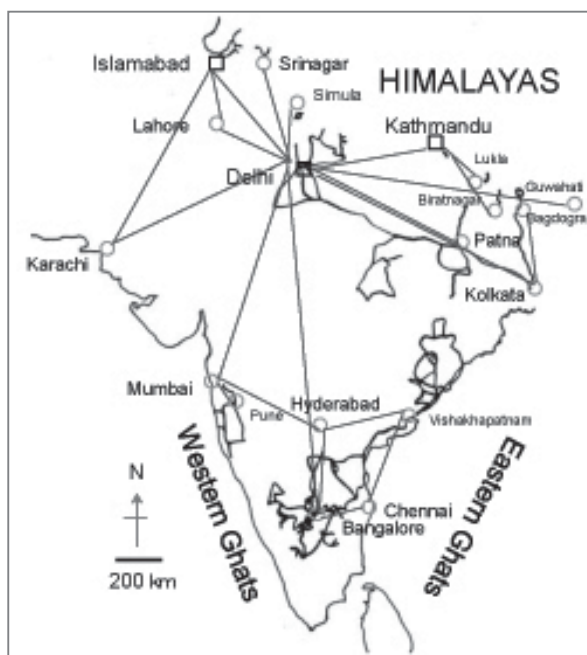


Fig. 1. Expedition routes in the Himalayas, Western Ghats and Eastern Ghats between 1983 and 2001.

A domesticated plant is always accompanied by the basic agricultural complex, which includes cultivation practices, processing, cookery, religious use, vernacular names, and other aspects.

A domestication centre for millet covers the Eastern Ghats and Southern Deccan Plateau on the basis of field observation, experimental results, linguistic sources, and archaeological data. Although this process is quite complicated among millet and its relatives, it is very effective for understanding domestication by a secondary origin via an insurance crop, a mimic companion weed, and weed types. The domestication process indicates the importance of the weed-crop complex and basic agricultural complexes as a plant-man symbiosis.

Moreover, it is obvious that several words of the old Indo-Aryan and Dravidian languages are related to the vernacular names of millets. Consequently, *Brachiaria ramosa* and *Setaria pumila* are called 'tertiary crops', which means they are double secondary crops for other millet species and upland rice. The order of first occurrence for millet species in historical sites generally supports this evolutionary process.

#### Field trips in the Indian subcontinent

The first author had participated six times in expeditions for millet research and collected numerous accessions of millets and their relative species, with information on their agricultural complex, from hundreds of farmers in their villages and fields (Table 2). He mainly visited the southern foot of the Himalayas and Western and Eastern Ghats in and around the Indian subcontinent between 1983 and 2001. The research team used many means of transportation, such as car, train, airplane, and their feet, for frequent field trips (Fig. 1). Particularly, the trips extended widely over Karnataka, Andhra Pradesh, Tamil Nadu, Maharashtra, Telangana, Maharashtra, Madhya Pradesh, Orissa, Chhattisgarh, Jharkhand, West Bengal, Bihar, Uttar Pradesh, Uttarakhand, Himachal Pradesh, and Jammu and Kashmir in India and the North-West Frontier in Pakistan and Eastern Nepal.

#### Millets domesticated in the Indian subcontinent

Ancient farmers had originally domesticated six species of millet from the relative weed species in India



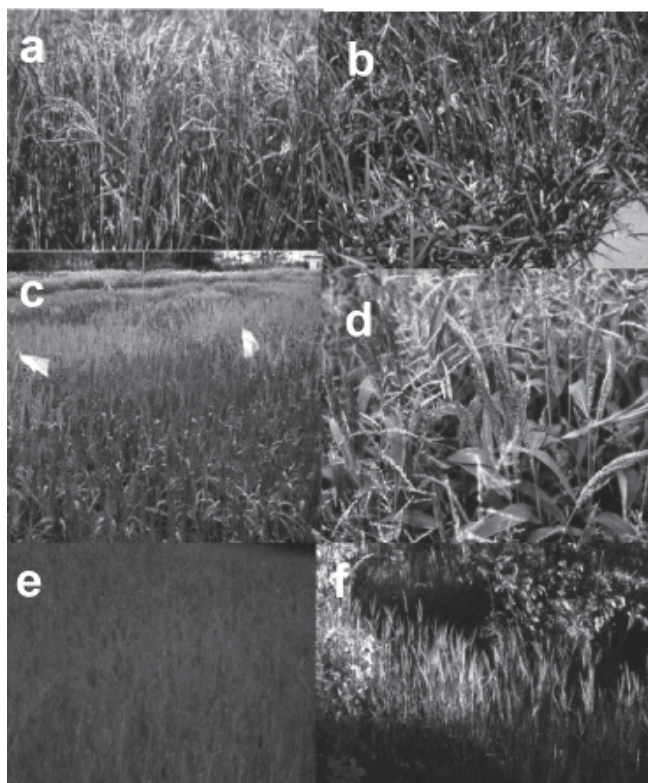


Fig. 2. Five species of millet domesticated in the Indian subcontinent and wild rice: a, *Panicum sumatrense*; b, *Paspalum scrobiculatum*; c, *Echinochloa frumentacea*; d, *Brachiaria ramosa*; e, *Setaria pumila*; and f, *Oryza rufipogon* in the irrigation canal.

(Table 1). Then, these plants were distributed over the Indian subcontinent and neighbouring areas.

*Panicum sumatrense* (*samai*) is an annual plant ( $2n = 36$ , tetraploid) derived from *Panicum sumatrense* ssp. *psilopodium* (Fig. 2a). *Paspalum scrobiculatum* (*kodo*) is a perennial plant ( $2n = 40$ , tetraploid, Fig. 2b). *Echinochloa frumentacea* (*jangora*) is an annual plant ( $2n = 54$ , hexaploid, Fig. 2c) derived from the relative weed *Echinochloa colona*. *Brachiaria ramosa* (*korne*) and *Setaria pumila* (*kolati*) are annual plants (Fig. 2d and 2e). These plants are secondary crops domesticated from their relative weeds in paddy fields. This will be discussed in detail below. *Digitaria cruciata* (*raishan*) is an annual plant derived from the relative weed grown in maize or vegetable fields (Singh and Arora 1972). In addition, *Oryza rufipogon* Griff. (wild rice) is used as an offering for gods and goddesses during festivals. It grows in ponds and irrigation canals near paddy fields (Fig. 2f).

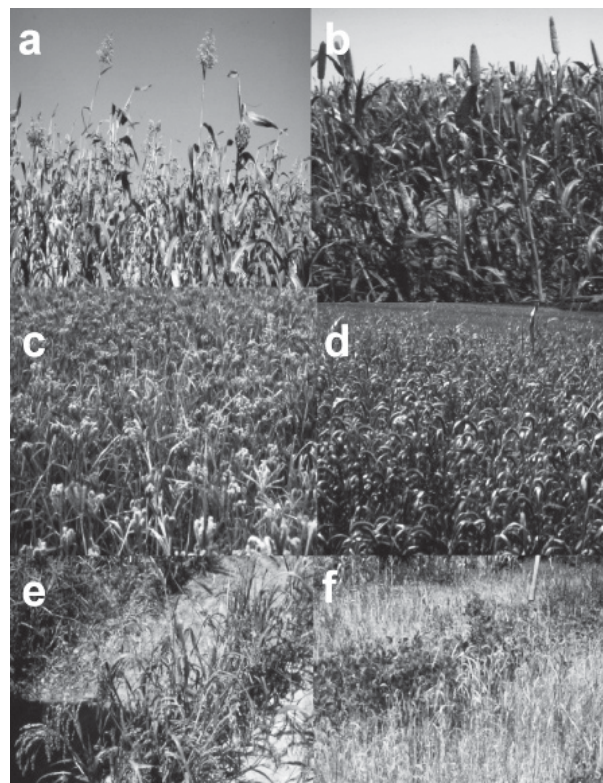


Fig. 3. Five species of millet introduced into the Indian subcontinent and a field of inter-cropping with *Setaria italica* and *Glycine max*: a, *Sorghum bicolor*; b, *Pennisetum glaucum*; c, *Eleusine coracana*; d, *Setaria italica*; e, *Panicum miliaceum*; and f, an inter-cropping field.

#### Other millet species grown in the Indian subcontinent

Indian farmers introduced six species of millet (Table 1) from Africa via the Arabian Peninsula, Central Asia through the Himalayas, and South-Eastern Asia via Assam in the Indian subcontinent during the Indus Civilization Age or before the dawn of history.

*Sorghum bicolor* (*jowar*) is an annual plant ( $2n = 20$ , diploid, Fig. 3a) derived from *Sorghum bicolor* var. *verticilliflorum* in Eastern Africa. *Pennisetum glaucum* (*bajra*) is an annual plant ( $2n = 14$ , diploid, Fig. 3b) domesticated from *Pennisetum violaceum* in Africa. *Eleusine coracana* (*ragi*) is an annual plant ( $2n = 36$ , tetraploid, Fig. 3c) domesticated from *Eleusine coracana* var. *africana* in Eastern Africa.

*Setaria italica* (*thenai*) is an annual plant ( $2n = 18$ , diploid, Fig. 3d) derived from *Setaria viridis*, a cosmopolitan weed in Central Asia. *Panicum miliaceum* (*cheena*) is an annual plant ( $2n = 36$ , tetraploid, Fig. 3e)



Table 3. Millets and their food in the Indian subcontinent

Species name	Food									
	Indian name	bhat	upma	roti	vada	dosa	idoli	mudde	ganji	mave
	Japanese name	meshi		pan	age pan		mushipan	oneri	konagayu	shitogi
<i>Sorghum bicolor</i>		○	○	◎	○	△	○	○	○	
<i>Pennisetum americanum</i>		○	○	◎				○	○	
<i>Eleusine coracana</i>		△	○	○	○	○	○	◎	○	
<i>Setaria italica</i>		◎	△	△	○	○		○	○	○
<i>Panicum miliaceum</i>		◎	△	○	△			○	○	
<i>Panicum sumatrense</i>		◎	○	△	○	○		○	○	
<i>Paspalum scrobiculatum</i>		◎		○				○	○	
<i>Echinochloa flumentacea</i>		◎	△		○			○	○	
<i>Brachiaria ramosa</i>		◎		○	○			○	○	
<i>Setaria pumila</i>		◎		△				△	△	
<i>Digitaria crusiata</i>		◎		○						

◎, main ingredient used; ○, generally; △, rarely or supplement mixed.

domesticated from *Panicum miliaceum* ssp. *ruderales* in Central Asia. *Coix lacryma-jobi* var. *ma-yuen* is a perennial plant ( $2n = 20$ , diploid) domesticated from *Coix lacryma-jobi* var. *lacryma-jobi* in South-Eastern Asia. These millet species are mostly grown by mixed cropping or intercropping, for example, *Setaria italica* is grown and mixed with *Glycine max* (Leguminosae), as shown in Fig. 3f.

Moreover, five species of pseudocereals are grown in the Indian subcontinent. *Fagopyrum esculentum* and *Fagopyrum tartaricum* (both annual,  $2n = 16$ , diploid) were introduced from Tibet. Recently, *Amaranthus caudatus*, *Amaranthus hypocondriacus* (both annual,  $2n = 32$  or  $34$ , diploid), and *Chenopodium quinoa* (annual,  $2n = 36$ , tetraploid) were dispersed from the New World.

### Foods made using millets

People have cooked many types of food using millets and cereals. Mainly *bhat* (*meshi* in Japanese), *roti* (*pan*), and *mudde* (*oneri*) are cooked because they are frequently made using most of the cereals listed in Table 3 (Kimata 1987). *Bhat* is the most popular food, a boiled grain food made using all the ingredients shown in Fig. 4a, 4d right, and 5a (2nd from upper right). *Bhat* originated in ancient China and was brought to the Indian subcontinent via Eastern India. *Roti* is also a popular food made from cereal flour and originated from the cooking of wheat bread in the Fertile Crescent and was brought to the subcontinent via Western India

(Fig. 5a, 1st, 2nd, and 3rd from lower left). *Mudde* is a popular food made from cereal flour and originated from the cooking of *ugari* brought from Eastern Africa via the Arabian Peninsula (Fig. 4d and Fig. 5b). Figure 4 shows cooking methods for cereals in the Indian subcontinent: (a) a traditional boiled rice with *papad* (crispy salted wafer made from *dal*, vegetables, and cereals); (b) *upma* and *kesari bhat*; (c) *dosa*; (d) *mudde* and boiled grain made using *Brachiaria ramosa*; (e) *puli*; and (f) *idli*.

*Sorghum bicolor* and *Pennisetum glaucum* are mainly used for making *roti*, while *Eleusine coracana* is mostly used for making *mudde* (Fig. 5b) and fermented alcoholic drink *chan* (Fig. 6a, b, and c). Other millet species are mainly used for *bhat*. A special food, *mavu*, is made from the raw flour of *Setaria italica* and *Oryza sativa* as offering for gods and goddesses during festivals. Nine foods are made using *Brachiaria ramosa* (Fig. 5a), *mudde* is made using *Eleusine coracana* (Fig. 5b), and *chapati* is made using wheat, *Triticum aestivum* (Fig. 5c and Fig. 6d, upper). With respect to fermented foods, a starter is made from *Hordeum vulgare* (Fig. 6a, starter; 6b, a jar for fermentation; 6c, alcohol drink, *chan*, made from *Eleusine coracana*; and 6d, yogurt, *dahi*).

Other cookeries are shown in Table 3, Fig. 4, and Fig. 5. *Upma* is a coarse-ground grain food (Fig. 4b, right). *Dosa* is a thin leavened pancake stuffed with potato curry (Fig. 4c). *Idli* is a leavened pound cake made using the same ingredients as *dosa* (Fig. 4f). *Vada* is a cake made from freshly ground *dal* or millet flour. *Ganji* is a

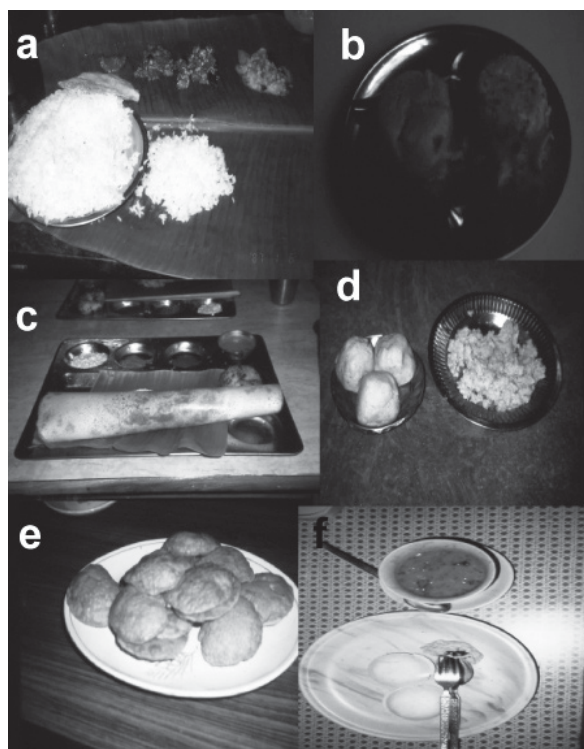


Fig. 4. Cookeries of cereal in the Indian subcontinent: a, a traditional boiled rice (*bhat*) with *papad*; b, *upuma* and *khesari bhat*; c, *dosa*; d, *mudde* and boiled grain made from *Brachiaria ramosa*; e, *puli*; f, *idoli*.

very thin starch-paste made from the same ingredients as *mudde*.

#### Dispersal routes of millets in the Indian subcontinent

Our team studied the domestication process and dispersal routes of Indian millets. An outline of the research results is given below.

*Kodora*, *Paspalum scrobiculatum*, was domesticated since about 2000 BC in India. This species is cultivated throughout the Indian subcontinent, but mainly in Madhya Pradesh. Ecological and morphological characteristics were compared using 32 accessions (including weed forms) of *Paspalum scrobiculatum*. In addition, the relationship between plant pigmentation and mimicry of rice was observed in 16 accessions, including six accessions collected from upland rice fields. Domestication process of the secondary crop to upland rice was discussed (Ishikawa unpublished). This species shifted from perennial to annual and obtained crop-like traits by accessions with rice cultivation. Both amplified fragment length polymorphism (AFLP) analysis and



Fig. 5. Cookeries of nine foods made from *Brachiaria ramosa* (a), *chapati* from wheat (b) and *mudde* from *Eleusine coracana* (c).

nucleotide sequence variation of the chloroplast trnK/matK region divided cultivated accessions into two groups, northern and southern groups. The northern cultivated accessions were genetically related to weed accessions collected from upland rice fields in Orissa. However, southern cultivated accessions showed close relationships to both accessions of upland rice fields in Orissa and the weed type in southern states. Furthermore, two alternate hypotheses for the origin of *Paspalum scrobiculatum* were summarized: (1) kodo millet was domesticated once in Orissa and then diffused to inland and southern states and (2) kodo millet was domesticated in Orissa and somewhere in the southern states of India, independently (Ishikawa 2007).

*Jangora*, *Echinochloa furumentacea*, is cultivated for food, fodder, and as an emergency crop in India, Nepal, and Pakistan. Its ancestor is a weed, *Echinochloa colona*, found in paddy fields. Morphological characteristics and AFLP analysis results of seven accessions of *Echinochloa colona* and 42 accessions of *Echinochloa furumentacea* were compared. On the basis of the results, the place of origin was assumed to be around Bihar, and then it was distributed to Tamil Nadu via Karnataka (Kagami unpublished).

*Samai*, *Panicum sumatrense*, is cultivated for food



Fig. 6. Fermented foods: a, starter made from *Hordeum vulgare*; b, a jar for fermentation, c, alcohol drink (*chan*) made from *Eleusine coracana* and d, yogurt, *dahi*.

and fodder in India, Nepal, Sri Lanka, and Myanmar. Its ancestor is a weed, *Panicum sumatrense* subsp. *psilopodium*, found in paddy fields. Morphological characteristics and AFLP analysis results of 38 accessions and 281 herbarium specimens of *Panicum sumatrense* were compared. On the basis of the results, the place of origin was assumed to be Eastern India, and it was then distributed in Southern India (Otsuka unpublished).

*Korne*, *Brachiaria ramosa*, is grown by very extensive farming for food in only India. Its ancestor is a weed found in paddy fields. Morphological characteristics and AFLP analysis results of 70 accessions of *Brachiaria ramosa*, including both weed and domesticated types, collected from Pakistan and India were compared. On the basis of the results, the place of origin was assumed to be the southern part of Orissa, and it was then distributed in the Deccan Plateau via Tamil Nadu (Otsuka unpublished).

*Korati*, *Setaria pumila*, is a cosmopolitan weed, but

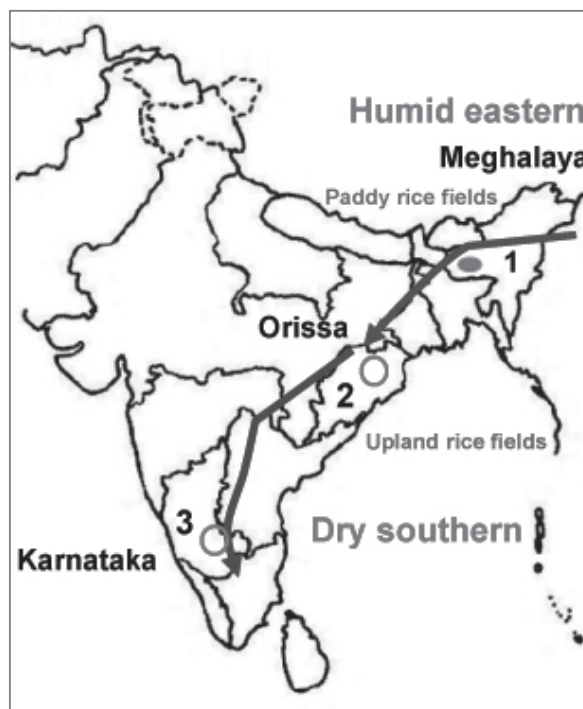


Fig. 7. Main dispersal route of Indian millets.

its domesticated type is mostly grown by mixed cropping with *Paspalum scrobiculatum* or *Panicum sumatrense* in only India (Kimata et al. 2000). This domestication process is discussed in detail below.

#### Dispersal route of Indian millets in the Indian subcontinent

The integrating hypothesis for the dispersal route of Indian millets is illustrated in Fig. 7 on the basis of the results. *Echinochloa furumentacea*, *Panicum sumatrense*, and *Paspalum scrobiculatum* were secondary crops to upland rice. First, their ancestral plants were companion weeds derived from the relative weeds that invaded paddy fields in humid regions of Eastern India. Second, the companion weeds became insurance crops in upland rice fields, and they spread to a dry region in the Deccan Plateau (Kobayashi 1987, 1989). *Brachiaria ramosa* and *Setaria pumila* were so called 'tertiary crops' because they were secondary crops to other millet species domesticated from their relative weeds in upland fields. On the other hand, *Digitaria cruciata* has been recently derived from the relative weed grown in maize or vegetable fields, Kashi Hill, Meghalaya, and is limited to the same area (Singh and Arora 1972).



Tentatively, Indian millet species were domesticated in the process of diffusion from humid paddy fields in Eastern India to dry upland rice fields in the Deccan Plateau, Southern India.

### Acknowledgements

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# Domestication process and linguistic differentiation of millets in the Indian subcontinent

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Plants and People Museum

The vernacular names of millets were gathered through field surveys in the Indian subcontinent since 1983. Farmers have an appropriate awareness of the status of millets and their relative weeds in the domestication process. This symbiotic process between millets and farmers was reconstructed by integrating field observations, botanical experiments, archaeological data, and linguistic sources. There were various vernacular names in the Eastern Ghats and Southern Deccan Plateau, where Indian millets were widely cultivated with their relative species today. It is obvious that the several names in the old Indo-Aryan and Dravidian languages are related to the vernacular names of millets. *Brachiaria ramosa* and *Setaria pumila* have been domesticated from the weeds that grew around upland rice fields via a mimic companion weed type that was mainly related to *Panicum sumatrense* and other grain crops. *Brachiaria ramosa* has become an independent crop in pure stands, while *Setaria pumila* grows as a mixed crop with *Panicum sumatrense* and other millets. Consequently, *Brachiaria ramosa* and *Setaria pumila* are so-called “tertiary crops,” meaning, they are a double secondary crop for the other millets and upland rice. The order of first occurrence of millets from historical sites generally supports this evolutionary process. This domestication center of millets covered the Eastern Ghats and Southern Deccan Plateau.

Key words: dispersal, domestication, linguistic differentiation, millets, mimic companion weeds

## Introduction

The indigenous millets of the Indian subcontinent

have been domesticated across their ranges of present-day cultivation for some 3500 years (de Wet et al. 1983a; Fuller 2002; Pokharia 2008). These millets include *Paspalum scrobiculatum* L. (kodo millet), *Echinochloa frumentacea* Link (Indian barnyard millet), *Panicum sumatrense* Roth. (little millet), *Brachiaria ramosa* (L.) Stapf. (*korne*), *Setaria pumila* (Poir.) Roem. & Schult. (*korati*; syn. *Setaria glauca* (L.) P. Beauv.), *Digitaria cruciata* (Nees) A. Camus (*raishan*), and *Digitaria sanguinalis* (L.) Scop. (Chandra and Koppa 1990; de Wet et al. 1983a, b, c). The former three species seem to be secondary in origin, through the mimic and/or companion weeds of the rain-fed paddy and then upland rice in Eastern India. The next two species, *Brachiaria ramosa* and *Setaria pumila*, were domesticated as secondary crops that were associated with the other millets via their mimic companion weed types in South India (Kimata et al. 2000; Kimata 2015a, 2015b, Kobayashi 1987, 1989). *Digitaria cruciata* was domesticated in the late nineteenth century by Kashi natives in Meghalaya and is cultivated only in the Kashi Hills (Singh and Arara 1972). Unfortunately, *Digitaria sanguinalis* has disappeared, and its origin is not clear.

In contrast to other millets, which were probably domesticated in humid Eastern India, *Brachiaria ramosa* and *Setaria pumila* have adapted to the dry climate of the semi-arid tropics. *Brachiaria ramosa* was cultivated in the hot, arid red soil region of Southern India, whereas *Setaria pumila* was cultivated in the hot sub-humid ecoregion in red and lateritic soils of Orissa, as well as in the hot semi-arid ecoregion on red loamy soils of Southern India (Sehgal et al. 1992). *Brachiaria ramosa* tolerates drought better than *Setaria pumila*, it

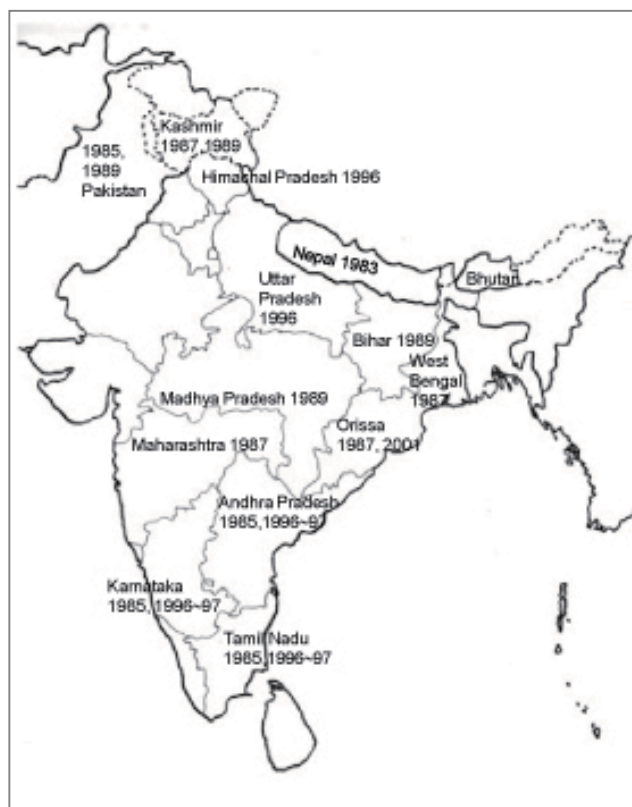


Fig. 1. Field surveys in the Indian subcontinent.

has undergone a specializing adaptation to arid regions, and it has nearly attained the tertiary domesticated phase (Kimata et al. 2000). On the other hand, the local varieties of *Setaria pumila* have adapted to drier fields in Southern India than in Orissa. *Setaria pumila* was normally grown with *Panicum sumatrense*, but it seemed to grow singly when the latter failed to grow in severe droughts, which was observed in our 1987 survey. This possibly suggests that *Setaria pumila* could become an independent crop. *Brachiaria ramosa* is an underutilized millet that is restricted in cultivation today to dry areas in the two border districts of Tumkur and Anantapur in the states of Karnataka and Andhra Pradesh, respectively. *Brachiaria ramosa* is cultivated in pure stands as a sole tertiary crop, while *Setaria pumila* is still cultivated by mixed cropping with *Panicum sumatrense* and other grain crops as a minor domesticated plant. A tertiary crop is a type of double secondary crop of *Panicum sumatrense* and others and a secondary crop of upland rice.

The methodological concept of the “basic

agricultural complex,” the so-called “from seeds to stomach” idea, was proposed by Nakao (1967) while studying the origin of agriculture. A domesticated plant always is accompanied by a cultural complex, which includes cultivation practices, processing, cookery, religious use, vernacular names, and other aspects (Kimata and Sakamoto 1992). Bellwood and Renfrew (2002) recently proposed and examined their “farming/language dispersal hypothesis” cooperative across the disciplines of archaeology, linguistics, and genetics from a broad comparative perspective. These millets and their relative weeds also have many vernacular names in each locality and language. This report is concerned with the reconstruction of their domestication process, particularly *Brachiaria ramosa* and *Setaria pumila*, from the point of view of their vernacular names with reference to linguistic archaeology, because good linguistic data have not yet been sufficient for the indigenous millets (Fuller 2002; Southworth 2005).

#### Field surveys and methods

Extensive field surveys were conducted in Karnataka, Andhra Pradesh, and Tamil Nadu in 1985, 1996, 1997, and 2001; Maharashtra in 1987; Orissa in 1987 and 2001; Madhya Pradesh and Bihar in 1989; and Himachal Pradesh and Uttar Pradesh in 1996. Furthermore, the surveys were added in Nepal in 1983 and Pakistan in 1985 and 1989 (edited by Sakamoto 1987, 1989, 1991). The observations that concentrated on *Brachiaria ramosa* and *Setaria pumila* were made in the local fields, particularly in 1996 to 1997 and 2001 (Fig. 1). The vernacular names of cereals and their wild/weed relatives were gathered from local farmers in each locality and language, used to construct a database, and were also extracted from the literature about Indian agriculture. The vernacular names from farmers were given an expression that was written in English by local farmers and regional researchers from agriculture extension stations. Moreover, the vernacular names of food items were collected from the English menu of local restaurants and cookbooks from each state.



Table 1. Vernacular names of *Brachiaria ramosa*, summer annual in India

State	Language	Status	Vernacular names
Orissa	Oriya	Weed with <i>Pas. scrobiculatum</i>	gusara pata, chusara mata
		Weed/Domesticated?	ghusara pata, lota, ghada langi
Maharashtra	Marathi	Domesticated	chama pothaval <sup>3)</sup>
Andhra Pradesh	Telugu	Weed	akki hullu, votlu kosavu
		Domesticated	andakora, anda korra, <i>pedda sama</i> <sup>1)</sup> , disakalu, edurigaddi
Karnataka	Kannada	Domesticated	kornne, korale, korne, korneki, kornike, bennakki hullu <sup>3)</sup>
Tamil Nadu	Tamil	Mimic companion weed with <i>P. sumatrense</i>	koothi same, sakkalati same, <i>sama melatti</i> <sup>5)</sup> , pil sama, pani varagu
		Domesticated	kam pampul, palapul <sup>3)</sup>
Kelara	Malayalam	Domesticated	chama pothaval <sup>3)</sup>

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 3) Ambasta 1986.

## Results

*Brachiaria ramosa* was cultivated mainly in a few states of South India. This semi-arid area is subject to a savanna climate in Deccan Plateau. *Brachiaria ramosa* and its relatives are summer annuals and have many vernacular names in each locality and language as shown in Table 1. The following tables contain some vernacular names that are cited for the convenience of discussion, but the results of surveys are from the author's own data. This domesticated type has been known by various vernacular names in Maharashtra and South India (cf. Chandra and Koppa 1990; Kawase 1987; Kimata et al. 2000; Kobayashi 1987, 1989). The domesticated type was called similar names: *hama pothaval* in Maharashtra, *chama pothaval* in Kelara, and *kama pampul* and *palapul* in Tamil Nadu. On the other hand, it was called different names in the border area between Andhra Pradesh and Karnataka, mainly *korne*, *korneki*, and *andakora*, and sometimes *pedda sama* and *disakalu*. The mimic companion weed type was known as *koothi same*, *sakalati same*, and *pil same* in Tamil Nadu. The weed type was known as *gusara pata* and *chusara mata* in Orissa, and *akki hullu* and *votlu kosavu* in Andhra Pradesh.

*Setaria pumila* was cultivated at a few hill sites that were mainly in Orissa and South India. This semi-arid area is also subject to a savanna climate in Deccan Plateau. *Setaria pumila* and its relatives are summer annuals and have many vernacular names in

each locality and language as shown in Table 2. The domesticated type was known by a great variety of vernacular names in Orissa and in the border area between Andhra Pradesh and Karnataka (cf. Chandra and Koppa 1990; Kawase 1987; Kimata et al. 2000; Kobayashi 1987, 1989). These names were usually shortened to a single word, such as *nehari* in Orissa, *lingudi* in Maharashtra, *korati* in Andhra Pradesh, *korlu* in Tamil Nadu, and *korin* in Karnataka, and the names were sometimes composed of two words, including *kuku lange* and *kukur lange* in Orissa, *kora samuru* in Andhra Pradesh, and *samuru korra* in Karnataka. The mimic companion weed type was known by many vernacular names, too. Further, these names were usually a single word, such as *nauri* in Bihar, *lingri* in Orissa, *nauri* in Madhya Pradesh, *korale* in Andhra Pradesh, and *erikorra* in Karnataka. They sometimes have adjectives that indicate the associated plants, for example, in Andhra Pradesh, *varagu korali* and *varagu sakkalathi* indicate a companion weed of *kodo* millet, while *samalu korali* and *arasama* indicate a companion weed of little millet. The weed type was often called *navari* in Madhya Pradesh, *ghas* in Orissa, and unique names such as *ghoda langi*, meaning horse tail, in Orissa and *sana korulu*, meaning little foxtail millet.

The vernacular names of other indigenous millets and rice in the Indian subcontinent are shown in Table 3. The domesticated type of *Panicum sumatrense*, a summer annual, was usually called *samai*, *sama*, *sama*,

**Table 2. Vernacular names of *Setaria pumila*, summer annual in India**

State	Language	Status	Vernacular names
Bihar	Hindi	Mimic companion weed with <i>Pas. scrobiculatum</i>	nauri navri nebri neuri nevri nbri harri tutuam
Orissa	Oriya	Weed	ghoda langi kuku lange, brai lange and gaso (Kondha), ghas: <i>bilai lance</i> and <i>lota</i> <sup>2)</sup>
		Mimic companion weed with <i>E. coracana</i> , <i>Pas. scrobiculatum</i> , <i>P. sumatrense</i> and <i>Oryza sativa</i>	lingri ghas lingudi kukuru lange: <i>ghas lingri</i> <sup>2)</sup>
		Domesticated type with <i>Pas. scrobiculatum</i> and <i>P. sumatrense</i>	nehari kuku lange, kukur lange (Konda Dora), kukuru range: <i>kukuru lange</i> <sup>5)</sup> , kuku lange, lingudi lengudi kukukangdi
Madhya Pradesh		Weed	navari navri naviri (Variga)
		Mimic companion weed with <i>Pas. scrobiculatum</i>	harri, nauri, navri, neuri, nibri, tutuam, nebri and nevri <sup>2)</sup>
Maharashtra	Marathi	Weed	ghas lingudi
		Domesticated type	lingudi lengudi
Andhra Pradesh	Telugu	Weed	sana korulu
		Mimic companion weed with <i>Pas. scrobiculatum</i> and <i>P. sumatrense</i>	korale, kurala, kurala kaddi korinlu, samuru korali, arasama, varagu korali, varagu sakka lathi
		Domesticated type	korati korindlu, korinlu, korali kora samuru, same korulu, same lu, sama, arasama, china sama, tela samuru, nerige, nerigali, <i>samuru korra</i> <sup>2)</sup>
Tamil Nadu	Tamil	Domesticated type	korlu, korati
Karnataka	Kannada	Mimic companion weed with <i>E. coracana</i> , <i>Pas. scrobiculatum</i> , <i>P. sumatrense</i> and <i>Oryza sativa</i>	erkorra, korindlu, arasama, nerigali, neriya
		Domesticated type with <i>P. sumatrense</i>	korin, korra, korulu, samuru korra
Others	Hindi	Domesticated type	<i>bandhra</i> <sup>1)</sup>

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991.

Austin 2006: *korai* [*kora*, *korali*] (Bengali, Deccan, Hindi, India and Bangladesh), *bandra* (Hindi, India), *varagu korali* (*varagu*, firewood, *korali*, ear or corn, Tamil)

and similar names in South India, while it was called *vari* and *wari* in Maharashtra, *gurji* and *koeri* in Orissa, and *gondula* in West Bengal. Further, indigenous people called it various names, including *kutki* (Vaiga) and *mejheri* (Gobdi) in Madhya Pradesh; *gundli* (Munda) in Bihar; *ghantia* (Kunda Tading), *gurgi* (Kunda Dora), and *suau* (Paraja) in Orissa; and *batta* (Kotha) in Tamil Nadu. The mimic companion weed type was identified and called *akki marri bullu*, meaning weed-like rice, *kadu same*, meaning weed little millet, and *kosu samalu* only in Karnataka, while the weed type was sometimes called *kadu* and *fodo* in Karnataka, *gabai* in Maharashtra, and *erigola* and *arasama* in Andhra Pradesh.

The domesticated type of *Paspalum scrobiculatum*, a perennial, was mainly called *kodo*, *kodora*, and similar names, but it had different names such as *harik* in Maharashtra; *arika* in Andhra Pradesh; *arka*, *alka*, and

*varagu* in Karnataka; and *varagu* in Tamil Nadu. The mimic companion weed grew in upland rice fields. It was called *kodo* and *kodaira* in Madhya Pradesh, *kodo war* in Bihar, and *kodoghas* (Paraja) in Orissa. The wild/weed type was called *kotocha* in Maharashtra, *khar sami* and *kodo wani* in Bihar, and *kodo ghas* in Orissa.

The domesticated type of *Echinochloa frumentacea*, a summer annual, was known as *jangora* in Uttar Pradesh; *sawan* and similar names in Madhya Pradesh and Bihar; *sankari wari* in Maharashtra; *jhari*, *dhabela*, and *gruji suau* (Paraja) in Orissa; *ooda* in Andhra Pradesh; *kudurai vali* in Tamil Nadu; and *wadalu* in Karnataka. The ancestral weed species, *Echinochloa colona* was called *chichivi* in Maharashtra, *dhela* in Orissa, and probably *sain* in Bihar. *Digitaria cruciata* was a summer annual called *raishan* only in Kashi Hills. The domesticated type of *Coix lacryma-jobi* was a perennial called *re-si* in Nagaland (Church 1886), while the other weed species

Table 3. Vernacular names of other indigenous millets and rice in Indian Subcontinent

Country State	Language	Status	Vernacular names (Indigenous people)					
			<i>Panicum sumatrense</i> summer annual	<i>Paspalum scrobiculatum</i> perennial	<i>Echinochloa frumentacea</i> summer annual	<i>Digitaria curuciata</i> summer annual	<i>Coix lacryma-jobi</i> perennial	<i>Oryza sativa</i> perennial
Growth habit								
Pakistan								
NWFP								chaw l
Gilgit								
Balistan								
Punjab								
Baluchistan						sarou <sup>4)</sup> , swank and sawank <sup>6)</sup> savara <sup>6)</sup>		
India								
Jammu & Kashmir		domest				karin <sup>4)</sup>		
Himachal Pradesh		domest		katai				
Uttar Pradesh		domest		koda				dhan
(Uttaranchal)		domest				jangora, jangora, madira		dhan
Punjab		domest	kutki <sup>4)</sup>	kodra <sup>4)</sup>				
Haryana								
Rajasthan								
Gujarat		domest		menva <sup>4)</sup>				
Madhya Pradesh		weed comp. weed						
				kodo, kodaira, kodaila and marenda <sup>2)</sup>	chichvi = E. colona chichvi nauri <sup>2)</sup>	gulu = C. acantia	pasahi = O. rufipoda	
		domest	kutki (Vaga), meheri (Gondi Kaland Vaga)	marenda kodo	sawan, savan, sawai			dhan, chawal lehi = upland rice
Maharashtra	Marathi	wild weed domest	gabat varig, wari nagri sam a, varag, kodra, warai <sup>2)</sup>	kotcha kodo, kodora, hark	sankariwari wari			deobath = O. rufipoda  tandu l
Bihar (Jharkhand)	Hindi	wild		khar sam i = Pas. indicum, kodo wani; matwani and kharasani (Pas. sp.) <sup>2)</sup> kodo war, marenda <sup>2)</sup>	sañ			
		comp. weed						
		domest	gundli (Munda)	kodo (Munda)	sawan, swan, sam a			chawal dhan, gora- dhan = upland rice
Orissa (Chattisgarh) Oriya		weed comp. weed		kodo-ghas, goddo  kodoghas (Paraj), mandia and kodo <sup>2)</sup>	dhe la = E. colona	korankhar = C. acantia, gorigodo	balunga	
		domest	gurji, koeri, suan	kodo, koddo, koda	jari dhate la			dhan, gadeba dhan = upland rice
			ghantia (Kunda Tading), gurgi (Kunda Dora), suau (Paraj), naisuan, kusuda, kosula (Others)		gruji suau (Paraj)			
	Others	domest						
Andhra Pradesh	Telugu	weed domest	ara sam a, erigola sam e, sam a, sam uru, nella <sup>4)</sup> shama <sup>4)</sup>	arka, allu <sup>4)</sup>	ooda, oodalli bouth-shama <sup>4)</sup>			paddy, biyyam
Tamil Nadu	Tamil	domest	saw a, sam a, sam uru, sam ai cha'mai and shama <sup>6)</sup> , batta (Kotha)	varagu, waragu <sup>2)</sup> , kodra and hanik <sup>2)</sup>	kudura-vali korali	kassabiya <sup>4)</sup>		paddy
Karnataka	Kannada	weed comp. weed	kadu, fodo akkim arri hullu, akki hullu, kavadadara hullu, kaddu same, kosu samalu and verri arasamulu <sup>2)</sup>					
		domest	sam e, sawan, sam i he janve, pani varagu and samulu <sup>2)</sup>	varagu, arka, aka, kodo	wadalu			gouri
Kerala								
West Bengal	Bengali	weed/ domest			shama = E. colona <sup>4)</sup>		garema = C. gigantia	
		domest	condula <sup>4)</sup>	koda <sup>4)</sup>	sama and kheri <sup>4)</sup>		aururu and kunch <sup>4)</sup>	
Megaraya	Khasi	domest				raishan		
Nagaland		domest						
Others	Hindi	domest	shavan <sup>1)</sup> , kutki and gundi <sup>4)</sup>	kodu and kodhra <sup>1)</sup> , kodaka <sup>4)</sup>	sa'nwa, sa'muka and sawa <sup>4)</sup> , shama, sanwa and sawank <sup>1)</sup>	re-si' <sup>4)</sup> gurli, girai and garahedua <sup>1)</sup> , kauch- gurgur, saukru <sup>1)</sup> and lechusa <sup>4)</sup>	chahau vrihi <sup>1)</sup>	
	Sanskrit	domest		kora'susha and kodrava <sup>4)</sup>				
	NW Province	domest		kodon and marsi <sup>4)</sup>	sarwak and shamak = E. colonum <sup>4)</sup>			
	Deccan	domest			kathli <sup>4)</sup>			
	unknown	domest						
Nepal	Nepalese	weed			sam a and ketu (Newar) = E. oryzicola			
		domest		kodra				dhan, paddy
Bhutan	Bhutanese	domest						
Bangladesh		domest						
Sri Lanka	Sinhalese	domest	meneri <sup>4)</sup>	wel-amu <sup>4)</sup>	wel-manukka <sup>4)</sup>	ki'kir-rindi <sup>4)</sup>		

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 4) Church 1886, 6) Kawase 1991, ...

that often invaded rice paddy fields was called *gulru* in Madhya Pradesh, *gurya*, meaning small, in Bihar, *korankhar* in Orissa, and *garemara* in West Bengal.

*Oryza sativa* L., a perennial, was usually called *chawal* or *dhan*, but the upland rice was called *lehi* in Madhya Pradesh, *gora dhan* in Bihar, *gadeba dhan* in

**Table 4. Vernacular names of Asian and African millets in Indian Subcontinent**

Country State	Language	Status	Vernacular names (Indigenous people)				
			<i>Panicum miliaceum</i> summer annual	<i>Setaria italica</i> summer annual	<i>Eleusine coracana</i> summer annual	<i>Sorghum bicolor</i> summer annual	<i>Pennisetum glaucum</i> summer annual
Growth habit							
Pakistan							
NWFP			olean <sup>6)</sup>	ghgh, ghok, gokhton, gokhtan, grashik, grach, aras and arass <sup>6)</sup>			ba jra, bajera
Gilgit			olean, chiena, cheena, bau and onu <sup>6)</sup>	gras, cha, cheng and cheena <sup>6)</sup>			
Balistan			tetze <sup>6)</sup>	cha <sup>6)</sup>			
Punjab				kangani, kangni and konooni <sup>6)</sup>	mandoh <sup>6)</sup>	pw ar, jowari <sup>6)</sup>	ba ja,
Baluchistan							
India							
Jammu & Kashmir	Kashmiri			kauni			
Himachal Pradesh							
Uttar Pradesh	Hindi	weed	charai		khadua = hybrid by <i>E. indica</i> <sup>2)</sup>		
		comp. weed			jhadua = hybrid by Indaf <sup>2)</sup>		
		dom est	china, sawan	kangani kangooni	m andua, ragi	pw ar, jwar, jara	ba ja
(Uttaranchal)		dom est	cheena, chin	kauni kouni korin, konin	m andua, m anduwa, marwa, koda		
Punjab	Punjabi						
Haryana							
Rajasthan							
Gujarat	Gujarati						
Madhya Pradesh		wild/weed					
		dom est		kang, kakun	ragimadia	pw ar	ba jra
Maharashtra	Marathi	wild/weed			nachuni = <i>E. indica</i>		
		dom est	wari tane	rala, rai	nachani nachuni nachana, ragi	pw ar, pwari, pwary	ba jri, bajri
Bihar (Jharkhand)	Hindi Bihari	weed			marwani, malwa = <i>E. indica</i> <sup>2)</sup>		
		dom est	cheena	kauni	marwa, maruwa, malwa	pw ar	ba jra
Orissa (Chattisgarh)	Orya	wild/weed			jngali-suau (Paraj) = <i>E. indica</i>		
		dom est	pani-varagu, cheena	kangu, gangu	ragimanaj-suau (Paraj), mandia (Kondho), pahado-mandia (KondDora)	pnna, jna, pwary, pw ar	kayna
	Others	dom est		kangul (Paraj)			
Andhra Pradesh	Telugu	dom est	variga	korra, kora, koralu, navane	ragitamada	pnna, pwer	ba jra, saja, gentilu <sup>4)</sup>
TamilNadu	Tamil	dom est	panivaragu, varagu and katacuni <sup>4)</sup>	thenai korra, thennai <sup>1)</sup> , tinai <sup>4)</sup>	ragikapai	pw ar, jra, pra, cho lam	ba jra, cum ba, cum bu, cumbu <sup>4)</sup> , kambu <sup>6)</sup>
Karnataka	Kannada	weed			kadu ragi, ragi kaddi, = <i>E. indica</i> <sup>2)</sup> ; hullu = hybrid by Indaf <sup>2)</sup>		
		dom est	baragu	navane, nawane	raginachha	pw ar	ba ja
Kerala							
West Bengal	Bengali	dom est	cheena <sup>5)</sup>	ka'kun <sup>4)</sup>	kodo	pw ar, jiner o	
Others	Hindi	dom est	chin, morha and anu <sup>1)</sup> , chena and ch'ina <sup>4)</sup> , cheena <sup>5)</sup>	kangni, kangu and kakun <sup>1)</sup> , ka'ngni, ta'ngan, kavuni and rawla <sup>4)</sup>	ragi <sup>4)</sup>		ba jra, ba jri and lahra <sup>4)</sup>
	Sanskrit	dom est	vrihitheda <sup>4)</sup> , u'nu <sup>^</sup> and vrelib-heda <sup>5)</sup>	ka'ngu and priyangu <sup>4)</sup> , kunau <sup>^</sup> and privunau <sup>^</sup> <sup>5)</sup>			
	unknown	dom est	sa'wan-jethwa, kuri, phikar, rali and bausi <sup>4)</sup> , worra (Telinga) <sup>5)</sup>			joar <sup>4)</sup>	
Nepal	Nepalese	dom est	china	kauni kaoni-tangure	kodo	jiner o-makai	ba ja
Bhutan	Bhutaneese			kaaun			
Bangladesh				tana-ha' <sup>4)</sup>			
Sri Lanka	Sinhalese						

Italics cited from 1) Fuller 2002, 2) Kobayashi 1991, 4) Church 1886, 5) de Candolle 1989, 6) Kawase 1991.

Orissa, and probably *gouri* in Karnataka. The wild relative *O. rufipogon* Griff. was used specially for a festival food and called *pasahi* in Madhya Pradesh, *deobath* in Maharashtra and probably *balunga* in Orissa.

The vernacular names of Asian and African millets in the Indian subcontinent are shown for comparison

with those of Indian millets in Table 4. These species are all summer annuals. *Panicum miliaceum* L. was widely called *cheena* and similar names, while it was known as *wari* and *tane* in Maharashtra and *varagu* and similar names in Orissa, Andhra Pradesh, Tamil Nadu, and Karnataka. *Setaria italica* (L.) P. Beauv. was



**Table 5. Vernacular names of other cereals in the Indian subcontinent**

Country State	Language	Status	Vernacular names (Indigenous people)			
			<i>Triticum aestivum</i> winter annual	<i>Hordeum vulgare</i> winter annual	<i>Avena sp.</i> winter annual	<i>Zea mays</i> summer annual
<b>Growth habit</b>						
<b>Pakistan</b>			ghandam, suji			makai
<b>India</b>						
Jammu & Kashmir						
Himachal Pradesh						makka
Uttar Pradesh	Hindi	domestic				makai, makka, maki
(Uttaranchal)		domestic	gehun			makka
Punjab						
Haryana						
Rajasthan						
Gujarat						
Madhya Pradesh		wild/weed				
		domestic	gahun	jao		makai
Maharashtra	Marathi	wild/weed				
		domestic				makka
Bihar (Jharkhand)	Hindi	domestic				makai, jenera =
Orissa (Chattisgarh)	Oriya	wild/weed				teosinte
		domestic	ghaun, gahom o			makka
Andhra Pradesh	Telugu	domestic				
Tamil Nadu	Tamil	domestic	godil gangil = <i>T. diccoccum</i> ;	gangi		
			<i>godome, kothirai and kothi</i> <sup>4)</sup>			
Karnataka	Kannada	domestic	<i>aḷa</i> = <i>T. diccoccum</i>			makai
Kerala						
West Bengal	Bengali	domestic				
Meghalaya						
Nagaland						
Others	Hindi	domestic				
	unknown	domestic				
<b>Nepal</b>	Nepalese	domestic	gaun, tro	jau, ne, uwa (Sherpa)		makai
<b>Bhutan</b>	Bhutanese					
<b>Bangladesh</b>						
<b>Sri Lanka</b>	Sinhalese					

also widely called *kangani*, *kauni*, and similar names in Sanskrit, while it was called *rala* and *rai* in Maharashtra, *korra* and *navane* in Andhra Pradesh, *korra* and *thenai* in Tamil Nadu, and *navane* in Karnataka. *Eleusine coracana* Gaertn. was usually called *ragi* in Madhya Pradesh, Orissa, and South India, while it was called *mandua*, *marwa*, and similar names in Uttar Pradesh and Bihar, *natuni* and similar names in Maharashtra and Karnataka, *tamada* in Andhra Pradesh, *kapai* in Tamil Nadu, and *kodo* and similar names in Uttar Pradesh, West Bengal, and Nepal. Further, indigenous people called it various names, such as *manje suau* (Paraja), *mandia* (Kondho), and *pahado mandia* (Kond Dora) in Orissa. *Sorghum bicolor* Moench was generally called *jowar* and similar names, but it was called *cholam*

in Tamil Nadu, *junero* in West Bengal, and *junero makai* in Nepal. *Pennisetum glaucum* (L.) R. Br. was also generally called *bajra* and similar names, but it was sometimes called *kayna* in Orissa, *sajja* in Andhra Pradesh, and *cumba* and similar names in Tamil Nadu.

The vernacular names of the other cereals are shown in Table 5. *Triticum aestivum* L. was called *gehun*, *godil*, and similar names. *Triticum diccoccum* Schübler, Char. et Descr. was *gangil* in Tamil Nadu and *aḷa* in Karnataka. *Hordeum vulgare* L. was called *jao* and similar names. Those two species are winter annuals. *Avena sativa* L. was not cultivated in South India. *Zea mays* L., a summer annual, was widely called *makai* and similar names, while the relative teosinte was introduced for fodder and was called *jenera* in Bihar.

The vernacular names of Indian cookery-used cereals are shown in Table 6. The various millets were cultivated and used for a lot of cookery, particularly in South India. Each cookery had slight differences in the vernacular name. However, there were a few exceptions of cookery-used millets and rice. For example, the boiled grain was widely called *chawal* or *bhat*, but it was also known as *annam* in Andhra Pradesh, *sadam* and *soru* in Tamil Nadu, and *anna* in Karnataka. Further, the thick porridge was called *onda* in Orisa, *samkati* in Andhra Pradesh, *kali* in Tamil Nadu, *mude* and similar names in Karnataka, and *dhido* and *senne* (Sherpa) in Nepal. The thin porridge was called *bari* in Uttar Pradesh, *peja* in Madhya Pradesh, *ambal* in Maharashtra, *jau* in Orissa, *ganji* in Andhra Pradesh and Karnataka, and *kulu* in Tamil Nadu. *Mave* was a raw flour food that was offered to gods and made only from foxtail millet and rice in Tamil Nadu.

## Discussion

The wild types, which were ancestral species of Indian millets, grew in wet places or habitats such as around pond peripheries and river sides. They also invaded rice paddy fields. In Pakistan, Nepal and India, many grass species, Poaceae, grow in paddy fields and on levees. Eventually, these weeds grew together in rice paddy and/or upland fields as a sympatric habitat and then became companion weeds. Some companion weeds mimicked the morphological and ecological traits of rice and became mimic companion weeds. The relationship between these plants and farmers gradually changed from subconscious and antagonistic to friendly. Farmers began to use them for fodder and insurance crops under a semi-domesticated status through the symbiotic situation. Finally, these plants were independently cultivated for food grains under a domesticated status. Therefore, this evolutionary process established a symbiotic relationship among plants and farmers (Kimata 2015a, 2015b). There are two types of mimicry in this process. One type is inter-specific to different species under the status of companion weed type, while the other is intra-specific

Table 6. Vernacular names of Indian foods made from cereals

Country State	Grain			Meal grain			Flour/baked breads			/fried			/roasted			/steamed /boiled			thin porridge			sweet			Raw flour			Alcoholic drink
	chawal	/boiled	chawal	chawal	upma	chapati	roti	paratha	nani	fermented	nani	purī	samosa	vada	murukku	dosa	tsuama	idli	mude	cani	kheer	bari	peja	ambal	peja	ambal	peja	ambal
Pakistan																												
NWFP																												
Gilgit																												
Baluchistan																												
Punjab																												
Baluchistan																												
India																												
Jammu & Kashmir																												
Himachal Pradesh																												
Uttar Pradesh																												
Uttaranchal																												
Punjab																												
Haryana																												
Rajasthan																												
Gujarat																												
Madhya Pradesh																												
Maharashtra																												
Bihar (Jharkhand)																												
Orissa (Chhattisgarh)																												
Andhra Pradesh																												
Tamil Nadu																												
Karnataka																												
Kerala																												
Nepal																												
Bhutan																												
Bangladesh																												
Sri Lanka																												

Italics cited from 6) Kawase (1991).

Table 7. Summary on linguistic archaeological names of millets and other cereals

Species name	English name	Old Indo-Aryan	Dravidian	Others
<i>Brachiaria ramosa</i>	browntop millet	?	see Table 1	
<i>Setaria verticillata</i>	bristly foxtail	?	?	
<i>Setaria pumila</i>	yellow foxtail	?	see Table 2	
<i>Panicum sumatrense</i>	little millet	?	see Table 3	
<i>Paspalum scrobiculatum</i>	kodo millet	<i>kodrava</i>	*ar- V- k-, *var- ak-	*var- ak- (Tam il, Malayalam, Kannada), *ar- V- k- (Kannada, Telugu)
<i>Echinochloa frumentacea</i>	Sawamillet	<i>syamaka</i>	see Table 3	
<i>Digitaria cruciata</i>	Khasimillet	nil	nil	see Table 3
<i>Coix lacryma-jobi</i>	Job's tear	nil	?	
<i>Oryza sativa</i>	rice	<i>vrihi</i>	*var- inc	see Table 3
<i>Oryza rufipogon</i>	wild rice	<i>nivara</i>	<i>navarai/ nivari</i>	see Table 3
<i>Panicum miliaceum</i>	common millet	<i>cina(ka)</i>	*var- ak-	*a- ria (Proto-Munda), *var- ak- (Telugu)
<i>Setaria italica</i>	foxtailmillet	<i>kanku(ni)</i> , * <i>kangu(ni)</i> , <i>tanuini. (rahala)</i>	*kot-, * <i>tinai</i> , * <i>tin- ay</i> , * <i>nuv- an- av</i>	* <i>kam- pu</i> (Tam il, Malayalam), * <i>ar- V- k-</i> (Kannada, Gondi/Gorum, Kuw il), <i>derav</i> (Kherwarian Munda), * <i>anaŋ- )aav</i> (Proto-Munda)
<i>Eleusine coracana</i>	finger millet	<i>madaka</i>	* <i>arak/ *arak-</i>	* <i>kam- pu</i> (Kannada, Telugu)
<i>Sorghum bicolor</i>	sorghum	<i>yavanala, yavakara</i>	* <i>conn- al</i>	<i>oodi</i> (Kannada), <i>kaj</i> (Kota/Konkan il), <i>koj</i> (Toda), <i>gajja</i> (Prakrit)
<i>Pennisetum glaucum</i>	pearlmillet	* <i>bajara</i>	* <i>kampu</i>	
<i>Triticum aestivum</i>	wheat	<i>godhuma</i>	* <i>kul- i</i>	
<i>Hordeum vulgare</i>	barley	<i>yava</i>	* <i>koc- / *kac-</i>	
<i>Avena sativa</i>	oat	?	?	see Table 5
<i>Zea mays</i>	maize	nil	nil	see Table 5

Modified and based on F.C. Southworth (2005)

Reconstructed forms are conventionally preceded by asterisks to denote non-attestation (Southworth 2005)

to the same species as a result of hybridization between the domesticated type and the closely related weed type.

The domestication process is supported by the linguistic recognition of various types by farmers, such as the weed, companion weed, mimic companion weed, semi-domesticated, and domesticated types of *Brachiaria ramosa* and *Setaria pumila*, in their vernacular names (Tables 1 and 2). The linguistic differentiation shows a close relationship to the domestication process, for instance, in Jalaripalli Village, Andhra Pradesh, where *Setaria pumila* that is mixed with little millet is called *kora samuru*, meaning foxtail millet-like little millet, and *tela samuru*, meaning the grains mixed with little millet, which is sold at a local market. This linguistic recognition suggests clearly the agro-ecological status of *Setaria pumila* as a secondary origin (Kimata et al. 2000).

The vernacular names of *Panicum sumatrense* and *Paspalum scrobiculatum* distinguish three types in their domestication process. The names of the mimic companion weed type are called, for example, *akki bullu* (little millet), meaning a rice-like weed, and *kodoghas*, meaning a kodo millet-like weed in upland rice fields (Kobayashi 1991). The linguistic differentiation indicates that both species were also a secondary crop

via a mimic companion weed in upland rice fields. This thoroughly conforms to the observations that were made in the fields. The vernacular name of *Echinochloa frumentacea* is clearly distinguished from that of *Echinochloa colona*, which is one of the ancestral species (Yabuno 1962). For instance, the former is called *jhari* and the latter is *dhela* in Orissa (Table 3). Sometimes, the same names were used by farmers to name *Panicum sumatrense* and *Echinochloa frumentacea*, *same* and *sawan*, but the names were not used in the same place and time. In the same way, the vernacular name of *Eleusine coracana* is distinguished from a relative weed, *Eleusine indica*, and the hybrids. However, the weeds associated with other millets and cereals have no names (Tables 4 and 5). Interestingly, *Panicum miliaceum* and *Setaria italica* have various names in North-West Frontier Province and Gilgit, Pakistan (Kawase 1991). The vernacular names of Indian cookery-used millets are unique, particularly in South India, because rice (eastward) and wheat (westward) are staple foods today in the other states (Table 6) (Kimata 1991).

The linguistic archaeological names of millets and other cereals are summarized in Table 7. The old Indo-Aryan names for *Brachiaria ramosa*, *Setaria verticillata*, *Setaria pumila*, and *Panicum sumatrense* are not found

Table 8. Summary on the first occurrence of grain crops in South Asian

Species	Period	Early	Mature	Late	(South India)		-0 A.D.	1500 A.D.	1900 A.D.
		4500 B.C.-	-2600 B.C.	-2000 B.C.	2300-1800 B.C.	1800-1200 B.C.			
<i>Paspalum scrobiculatum</i>						trace			
<i>Panicum sumatrense</i>					trace	a few			
<i>Echinochloa cf. colona</i>						many			
<i>Brachiaria ramosa</i>				wild?	many	many			
<i>Setaria verticillata</i>				wild?	many	many			
<i>Setaria pumila</i>				wild?	trace	trace			
<i>Setaria sp.</i>				a great many					
<i>Digitaria cruciata</i>									domesticated
<i>Digitaria sanguinalis</i>								(unknown, disappeared)	
<i>Panicum miliaceum</i>			a few						
<i>Panicum sp.</i>				a few					
<i>Setaria italica</i>				possible					
<i>Eleusine coracana</i>				?	possible				
<i>Sorghum bicolor</i>				many					
<i>Pennisetum glaucum</i>				trace	trace	trace			
<i>Coix lacryma-jobi</i>							possible		
<i>Oriza sativa</i>			many		trace	trace			
<i>Hordeum vulgare</i>	a great many				many	many			
<i>Triticum dicoccum</i>					trace	trace			
<i>Triticum durum/aestivum</i>					many	trace			
<i>Triticum sp.</i>	a great many				many	many			
<i>Avena sativa</i>	a few								
<i>Zea mays</i>									introduced

Modified and Based on Fuller et al 2001, Fuller and Madella 2001, and Fuller (personal communication).

in the ancient literature (cf. Southworth 2005). This might indicate that these millets were domesticated in India relatively recently. In contrast, because *Paspalum scrobiculatum* is named *kodorava*, this word is considered to be the origin of *kodo* and *kodora*. The word *syamaka* for *Echinochloa frumentacea* is considered a derivation of *shama* and *sama*. The word *cina(ka)* of *Panicum miliaceum* is also considered to be the origin of *cheena*, and the words *kanku(ni)* and *rahala* for *Setaria italica* are the origin of *kangani*, which was widely used, and *rala*, which was used in Maharashtra. The word *madaka* for *Eleusine coracana* is considered to be the origin of *mandua* in Uttar Pradesh and the word *\*bajjara* is the origin of *bajra* (\*, reconstructed forms by Southworth 2005). The Dravidian name *\*var-ak-* for *Paspalum scrobiculatum* and *Panicum miliaceum* is considered to be the origin of *varagu*, and the names *\*tinai* and *\*nuv-an-ay* for *Setaria italica* are the origin of *thenai* in Tamil Nadu and *navane* in Andhra Pradesh and Karnataka. Because these species have old Indo-Aryan or Dravidian names, they might have been introduced from the Western areas or domesticated within India a relatively long time ago, according to the archaeological evidence (Weber 1992).

The first occurrence of grain crops in South Asia is summarized in Table 8, which is based on Fuller et al.

(2001) but modified with additional information (Fuller and Madella 2001; Fuller, personal communication). *H. vulgare*, *Triticum* species (great many), and *Avena sativa* (a few) were identified in the Early Phase (around 4500 B.C.) of Harappan sites. *O. sativa* (many) and *Panicum miliaceum* (a few) were identified in the Mature Phase (around 2600 B.C.). Then, *Setaria* species (great many), *Sorghum bicolor* (many), and *Pennisetum glaucum* (syn. *americanum*, trace) were found in the Late Phase (around 2000 B.C.). The following species were found in early South Indian sites (2300 to 1800 B.C.): *Panicum sumatrense* (trace), *Brachiaria ramosa* (many), *Setaria verticillata* (many), and *Setaria pumila* (trace). Then, traces of *Paspalum scrobiculatum* and many *Echinochloa cf. colona* (possibly *Echinochloa frumentacea*) were identified in the late sites (1800 to 1200 B.C.). Asian millets occurred historically in the following order: *Panicum miliaceum*; *Setaria* species; then *Brachiaria ramosa*, *Setaria verticillata*, *Panicum sumatrense*, and *Setaria pumila*; and *Echinochloa cf. colona* and *Paspalum scrobiculatum*. However, *Brachiaria ramosa*, *Setaria verticillata*, *Setaria pumila*, and *Echinochloa cf. colona* might have been gathered as a wild grain.

The naming scheme of millets and their relative weeds is summarized in Table 9. Farmers have four



Table 9. Naming scheme of millets and weeds by farmers in India

Stage	Awareness	Typical cases (species name) [meaning]
I	Unknown	no name: ghas, hullu [weed]
II	Non distinctive	the same name of crop as weed: ragi mawa ( <i>Eleusine coracana</i> )/ragi mawa (a weed, <i>E. indica</i> ) kodo ( <i>Paspalum scrobiculatum</i> ) /kodo (the weed) kukuru lange ( <i>Setaria pumila</i> )/kukury lange (the m in ic weed) [dog's tail]
III	Identified	
1.	a specific word (most crop has several specific names called by each language group)	madua ( <i>E. coracana</i> )/khadua ( <i>E. indica</i> ) gruji suau ( <i>Echinochloa frumentacea</i> )/dhera (a weed, <i>E. colona</i> ) merendo, kodowar (a m in ic weed, <i>P. scrobiculatum</i> )/matwali kharasam i (a weed, <i>Paspalum</i> sp.)
2.	added a few adjective words	
2.1 meaning "weed"		lingudi ( <i>Setaria pumila</i> )/ghas lingudi (the weed) kodo/kodo ghas,
2.2 like "another crop"		same melatti (a m in ic weed, <i>B. ramosa</i> ) [like little millet] akkihullu (a m in ic weed, <i>P. sumatrense</i> ) [weed like rice]
2.3 indicating a morphological trait		ragikaddi (a weed, <i>E. indica</i> ) [finger millet with spike like a stick] bilai lange (a weed, <i>S. pumila</i> ) [cat's tail]
2.4 indicating an ecological trait		samulu ( <i>Panicum sumatrense</i> )/yerri arasamulu (the weed with grain shattering) same ( <i>P. sumatrense</i> )/samuru korra ( <i>S. pumila</i> ) [foxtail millet growing in little millet field] varagu sakkalathi ( <i>S. pumila</i> ) [a m in ic weed, second wife of kodo millet] sakkalathisame (a m in ic weed, <i>B. ramosa</i> ) [second wife of little millet] same ( <i>P. sumatrense</i> )/pilsame ( <i>Brachiaria ramosa</i> ) [for fodder],
2.5 indicating a utility		
IV	Classified into some landraces	marua ( <i>E. coracana</i> ): three varieties: agat- [early], madhyam- [medium] and pichhat- [late] /maruani ( <i>E. indica</i> ). sama ( <i>P. sumatrense</i> ): four varieties: manchi- [summer], pala- [short], ara- [tall] and varagu- [sowing in January].

stages of awareness of the symbiotic process between them and plants. They are unknown (stage I), non-distinctive (II), identified (III), and classified into some local varieties (IV). In stage I, the farmers have no name for wild/weed plants and call them ghas and hullu. In stage II, the farmers use the same name for the crop (*ragi*) and weed (*ragi*). In stage III, the farmers identified and called millets a specific name, for instance, *madua* for *Eleusine coracana* (domesticated) and *khadua* for *Eleusine indica* (weed). Furthermore, farmers added a few adjective words to the root of the millet name, for example, to mean "weed" (*ghas lingudi*, meaning weed of *Setaria pumila*) and "like another crop" (*same melatti*, meaning mimic weed like little millet), and to indicate a morphological (*bilai lange*, meaning cat's tail) or ecological trait (*yerri arasamulu*, meaning weed with grain shattering) and a utility (*pil sama*, meaning *Brachiaria ramosa* for fodder). In stage IV, farmers classified the millets into some local varieties, for example, *Eleusine coracana* was known as *marua* and was classified into the varieties *agat-* (early), *madhyam-* (medium), and *pichhat-* (late); and a weed, *Eleusine*

*indica*, was known as *maruani*. As a consequence of this survey, farmers appear to have an appropriate awareness of the status of millets and their relatives, even though they sometimes use the same names for millets in different places.

In conclusion, the domestication process of millets based on field observations (Kimata et al. 2000), experimental results (Kimata 2015a, 2015b), and these linguistic sources is illustrated in Fig. 2. This domestication center of millets covered the Eastern Ghats and Southern Deccan Plateau. Although this process is quite complicated among millets and their relatives, it is very effective for understanding the domestication by a secondary origin via weed and mimic companion weed types. Oats and rye were the secondary crops of wheat that developed cold tolerance (Vavilov 1926), while Indian millets were secondary crops of upland rice that developed drought tolerance. *Brachiaria ramosa* tolerates drought better than *Setaria pumila*, and it became an independent crop. *Setaria pumila* is almost always grown with little millet, but it seems to grow singly when little millet fails to grow

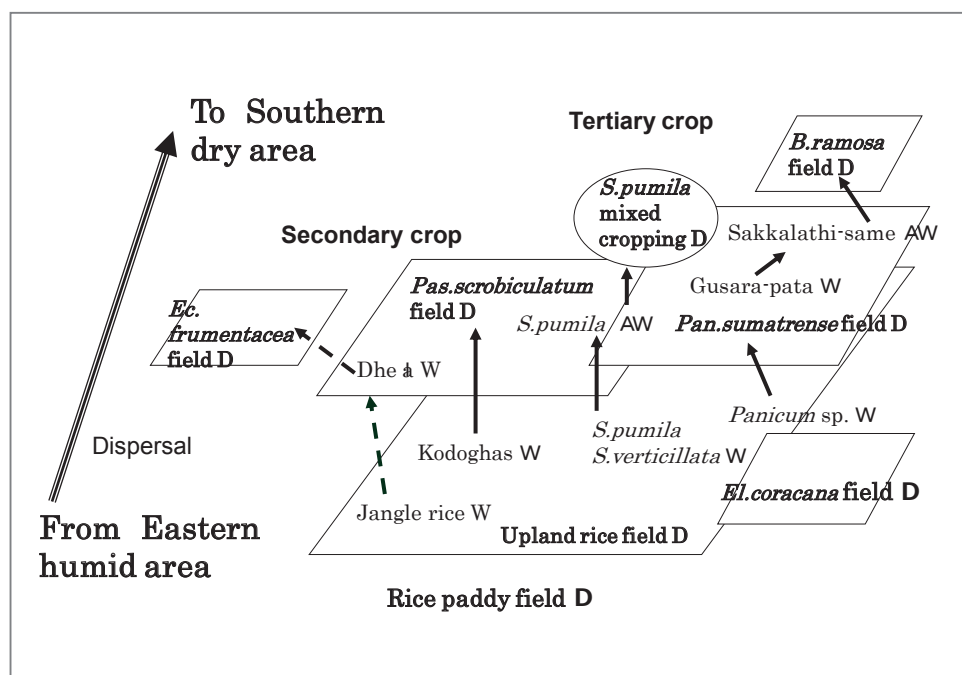


Fig. 2. Domestication process of millets in the Indian subcontinent

in severe droughts. Both species are so-called tertiary crops, meaning, they are a double secondary crop for the other millets and upland rice. The millet domestication process indicates the importance of weed-crop complexes and basic agricultural complexes as a plant-man symbiosis.

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# The tertiary domestication process of *korati*, *Setaria pumila* (Poaceae), through the mimicry of other grain crops in the Indian subcontinent

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In South India, one domesticated type of *Setaria pumila* is always cultivated in mixed stands along with *Panicum sumatrense*, whilst the others, and the weed types, are grown mostly with *Paspalum scrobiculatum*, sometimes *Eleusine coracana*, and upland rice, *Oryza sativa*, in diverse agro-ecological niches in East India. Several botanical traits of *S. pumila* indicate that the domesticated type is descended from the weed types, and that these traits have become evolutionarily synchronized with those of *P. sumatrense* and/or other cereals. This domestication process has been promoted morphologically through mimicry of other cereal species and acts as a means of adapting to the arid climate. Moreover, the pigmentation of leaves and leaf sheaths in terms of anthocyanin composition (HPLC analysis) is involved in mimicry among the other grain crops and the closely-related weeds. The weed and companion weed types are used as fodder for cattle and as an insurance crop for farmers in times of famine. The grains of *S. pumila* are always mixed with other millet grains, used to make six traditional foods as a supplementary ingredient, and in turn related to diversification of the basic agricultural complex. This tertiary domestication of *S. pumila* has proceeded from inter- and intraspecific mimicry by natural hybridization and artificial selection in sympatric fields.

Key words: adaptation, hybridization, millet, mimic companion weed, tertiary crop

## Introduction

Human beings had domesticated more than 30 grass species, as cereal crops, in several parts of the world,

possibly as long as 12,000 years ago. However, several species are threatened and in spite of their potential food value in their native habitats, have disappeared or have hardly been cultivated. This is because the three major crops of wheat, rice, and maize have rapidly increased in their yield and production, due to huge technical innovation in crop improvement programs. The other grain crops, that is to say, millets, have decreased gradually during the previous century, resulting in genetic erosion of their local varieties. Today, we need recognize their value as exploitable and underutilized genetic resources, based on their adaptability to stress-prone environments. These species of millet are mostly C<sub>4</sub> plants, which are early to mature, and can be cultivated under conditions of severe drought and harsh sunlight.

Local farmers continue to cultivate a few useful varieties of millet even today. These indigenous varieties are excellent materials for investigating crop evolution, particularly the origin and dispersal route of domesticated plants. In the Indian subcontinent, a few small millets are still undergoing the domestication process (Kimata et al. 2000; Singh and Arora 1972). While crop evolution can be reconstructed mostly from botanical data, the aspects of geographical origin and dispersal will become clear from the information on the basic agricultural complex offered by local farmers.

Vavilov (1926) showed the domestication process from weeds associated with wheat to the secondary crops in two genera, *Avena* and *Secale*. For example, *Secale cereale* L. had built up strong resistance to cold in high altitude and/or latitude areas, and, subsequently, this species had been able to grow under more severe



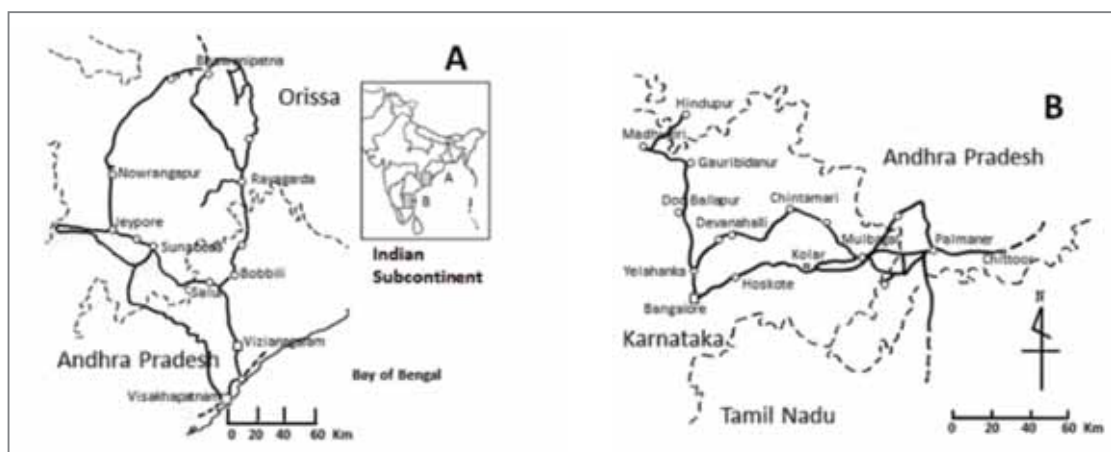


Fig. 1. Field survey: a) in Karnataka and Andhra Pradesh (1985, 1996, 2001); and b) Orissa (1987, 2001), Indian subcontinent.

conditions than those under which wheat can grow. Kobayashi (1987, 1989) proposed an integrating model of the domestication process of Indian millets as secondary crops from mimic companion weeds associated with *Oryza sativa* L.

*O. sativa* had been spread first from wetlands to uplands, secondarily, in the Indian subcontinent. Their ancestral weedy plants had invaded paddy and upland rice fields in turn. These are *Panicum sumatrense* Roth. (little millet), *Paspalum scrobiculatum* L. (kodo millet), *Echinochloa frumentacea* Link (Indian barnyard millet), *Brachiaria ramosa* (L.) Stapf. (*korne*), *Digitaria crusiata* (Nees) A. Camus (*raishan*), and *Setaria pumila* (Poir.) Roem. & Schult. (*korati*; syn. *S. glauca* (L.) P. Beauv.) (Chandra and Koppa 1990; de Wet et al. 1983a, b, c). *Pas. scrobiculatum*, *P. sumatrense*, and *E. frumentacea* were subsequently domesticated by local farmers as secondary crops to upland rice, because these had put up stronger resistance to drought than upland rice in Eastern India. In this region, several species of millet were domesticated.

Recently, archeological studies have shown very useful data in the Indian subcontinent. The material of millet grasses came from archaeological levels, Phases II (2300–1800 cal. BC) and Phases III (1800–1200 cal. BC) in the Southern Neolithic chronology. They have been identified as being primarily from two species, browntop millet, *Brachiaria ramosa*, and bristly foxtail millet-grass, *Setaria verticillata*. Yellow

foxtail millet, *Setaria pumila* was present in limited quantities, possibly gathered from the wild (Fuller et al. 2001). The first occurrence of cereals in the Harrappan Civilization had been wheat, barley, and oats in the Early phase (before 2600 BC); *Eleusine* sp. (problematic, *E. coracana*), *Setaria* sp., and *Panicum* sp. in the Mature phase (2600–2000 BC); and *Paspalum* sp., *Echinochloa* sp., *Sorghum* sp., and *Pennisetum* sp. in the Late phase (more recent than 2000 BC) (Fuller and Madella 2000; Weber 1992).

*S. pumila* is a weedy annual growing 30–60 cm tall. The inflorescence is cylindrical, densely flowered, spike-like raceme, 2.5–10 cm long, usually yellow, or more rarely purplish or pale green. It is a fairly common grass, especially in cultivated lands, along the roadsides, and in cleared forests, up to altitudes of 700 m. The spikelet (c.a. 3-mm long) is pale green or brownish-green. Cattle are fond of it (Acharyar 1921; Singh 1988). *S. pumila* is a multiple polyploid species ( $2n=18, 36, 72$ ) and an unknown genome constitution (almost genome D) (Zhao et al. 2013). The present paper is concerned with the tertiary domestication process of *S. pumila* through the mimicry that is related ecologically and genetically to the relative weeds and several grain crops in the Indian subcontinent.

## Materials and Methods

Many local varieties and relative weeds of *Setaria pumila* (Poir.) Roem. & Schult. (syn. *S. glauca* (L.) P.

Table 1. Materials used of *Setaria numila*

Collection no.	Sample no. & Status	Main crop and remarks	Locality
85-10-31-3-12	1D s-A	<i>Panicum sumatrense</i>	Duggam vapalli, Andhra Pradesh
k87-9-28-9-4	2W s-M	<i>P. sumatrense</i>	Kumbharoshi (800m), Maharashtra
k87-9-28-9-6	3W s-M	<i>P. sumatrense</i>	
k87-10-1-7-8	4D s-M	<i>P. sumatrense</i>	16km from Lanja (200m), Maharashtra
k87-10-3-3-1	5W -M	none	Gabi (650m), Maharashtra
k87-10-3-5-7	6W s-M	<i>P. sumatrense</i>	Nadagao village (541m), Maharashtra
k87-10-4-6-7	7W -M	<i>Oryza sativa</i>	8km W from Kohapur (600m), Maharashtra
k87-10-5-10-5	8W -M	<i>Setaria italica</i>	Udtare village (652m), Maharashtra
k87-10-5-10-6	9W -M	<i>S. italica</i>	Udtare village (653m), Maharashtra
k87-10-9-1-1	10M s-O	<i>P. sumatrense</i>	Sunabeda (895m), Orissa
k87-10-9-1-6	11M s-O	<i>P. sumatrense</i>	
k87-10-9-1-7	12M s-O	<i>P. sumatrense</i>	
k87-10-9-1-8	13M s-O	<i>P. sumatrense</i>	
k87-10-9-2-2	14W sk-O	<i>P. sumatrense</i> mixed	Kundali village (875m), Orissa
k87-10-9-5-6	15W s-O	<i>P. sumatrense</i>	Potang (895m), Orissa
k87-10-10-2-1	16W -O	none	7km from Sunabeda (900m), Orissa
k87-10-10-5-5b	17W s-O	<i>P. sumatrense</i>	2km of Boiparigurha (608m), Orissa
k87-10-10-5-6b	18W s-O	<i>P. sumatrense</i>	
k87-10-10-5-10d	19W s-O	<i>P. sumatrense</i>	
k87-10-10-5-13A	20W s-O	<i>P. sumatrense</i>	
k87-10-10-5-13B	21W s-O	<i>P. sumatrense</i>	
k87-10-10-5-14e	22D s-O	<i>P. sumatrense</i>	
K87-10-10-5-16A	23D s-O	<i>P. sumatrense</i>	
k87-10-10-5-16B	24D s-O	<i>P. sumatrense</i>	
k87-10-10-6-8	25W s-O	<i>P. sumatrense</i>	Beragaon, 12km of Koraput (605m), Orissa
k87-10-11-2-2	26M k-O	<i>Pas. scrobiculatum</i>	Anchaluda village, 20km of Koraput (870m), Orissa
k87-10-11-2-3	27D k-O	<i>Pas. scrobiculatum</i>	
k87-10-11-2-5	28M k-O	<i>Pas. scrobiculatum</i>	
k87-10-11-6-7	29W s-O	<i>P. sumatrense</i>	Damaniganda village (728m), Orissa
k87-10-11-6-8	30M s-O	<i>P. sumatrense</i>	
k87-10-12-2-3	31W -O	none	Sagada village (240m), Orissa
k87-10-12-2-7	32W -O	none	
k87-10-12-5-4	33W s-O	<i>P. sumatrense</i>	47km NW of Bhawanapatna (690m), Orissa
k87-10-12-5-5	34W s-O	<i>P. sumatrense</i>	
k87-10-12-5-7	35M s-O	<i>P. sumatrense</i>	
k87-10-12-5-8	36W s-O	<i>P. sumatrense</i>	
k87-10-12-6-2	37W p-O	<i>Oryza sativa</i> mixed	Balsora village (690m), Orissa
k87-10-12-6-3	38M p-O	<i>O. sativa</i> mixed with	
k87-10-12-6-4	39M p-O	<i>O. sativa</i> mixed with	
k87-10-12-7-4	40W s-O	<i>P. sumatrense</i>	Duliguda village, 11km of Gopabur (922m), Orissa
k87-10-12-7-5	41W s-O	<i>P. sumatrense</i>	
k87-10-12-8-4	42W s-O	<i>P. sumatrense</i>	Dakuta (937m), Orissa
k87-10-13-4-14	43W k-O	<i>Pas. scrobiculatum</i>	Pudapali village (269m), Orissa
k87-10-13-5-6	44M k-O	<i>Pas. scrobiculatum</i>	12km of Kharhar (272m), Orissa
k87-10-13-5-11	45M k-O	<i>Pas. scrobiculatum</i>	
k87-10-14-2-1	46W -O	none	Mandapadar village (139m), Orissa
k87-10-14-2-3	47W -O	none	
k87-10-14-2-4	48W -O	none	
k87-10-14-4-3	49M k-O	<i>Pas. scrobiculatum</i>	Budhitadar village (146m), Orissa
k87-10-15-1-6	50M k-O	<i>Pas. scrobiculatum</i>	Ram isarda Tilemal (149m), Orissa
k87-10-16-2-3	51M s-O	<i>P. sumatrense</i>	Kolarapali village (766m), Orissa
k87-10-16-2-4	52M s-O	<i>P. sumatrense</i>	
k87-10-16-3-4	53M k-O	<i>Pas. scrobiculatum</i>	Bekarakhol village, 30km of Phulabani (522m), Orissa
k87-10-16-5-4	54M s-O	<i>P. sumatrense</i> mixed with	4km from Tikabali (569m), Orissa
k87-11-7-0-26	55W -W	none	Kalimpong, West Bengal
96-11-5-1a-2	56D k-K	Domesticated type. a	Kalidevapura, Karnataka
96-11-5-2b-6	57D s-K	A few mixed with <i>P. sumatrense</i>	Madhagiri, Karnataka
96-11-5-7-2	58D k-K	A little shattering.	
97-4-12-2-2	59D s-A	<i>P. sumatrense</i>	Jalripalli, Andhra Pradesh
97-4-12-2-3	60D s-A	<i>P. sumatrense</i>	

Sample number and status: W, weed type; M, minor weedy medium type; D, domesticated type. Main crop: s, samai (*Panicum sumatrense*); k, kodo (*Paspalum scrobiculatum*); p, paddy (*Oryza sativa*); o, other species. Locality: A, Andhra Pradesh; K, Karnataka; M, Maharashtra; O, Orissa; P, Pakistan; T, Tamil Nadu; U, Uttar Pradesh; W, West Bengal

Table 2. Materials used of *Setaria pumila* and other millet species

Collection no.	Cultivation no.	Species	Status	Locality	Remarks observed in the field
96-11-5-1a-1	ps1	<i>Paspalum scrobiculatum</i>	dom est	Site 5 Kalidevapura village, Tumkur, Karnataka	main crop
96-11-5-1a-2	st56	<i>Setaria pumila</i>	medium		a few mixed
96-11-5-2b-1	pn1	<i>Panicum sumatrense</i>	dom est	Site 6 Kalidevapura village, Tumkur, Karnataka	main crop
96-11-5-2b-4	br1	<i>Brachiaria ramosa</i>	dom est		a few mixed with weedy type
96-11-5-2b-6	st57	<i>Setaria pumila</i>	medium		a few mixed
96-11-5-7-1	ps2	<i>Paspalum scrobiculatum</i>	dom est	Site 7 Kodigenahalli Hogli, Tumkur, Karnataka	pure stand
96-11-5-7-2	st58	<i>Setaria pumila</i>	dom est		1 plant mixed, small seed, compact spike
97-4-12-2-1	pn2	<i>Panicum sumatrense</i>	dom est	Site 8 Jalarpali village, Andhra Pradesh	mixed cropping
97-4-12-2-2	st59	<i>Setaria pumila</i>	dom est		mixed cropping, brown seed
97-4-12-2-3	st60	<i>Setaria pumila</i>	dom est		mixed cropping, black seed
01-10-8-1-1	pn3	<i>Panicum sumatrense</i>	dom est	Thatigul village, Kolar, Andhra Pradesh	main crop, purple disperse spike, yellow seed
01-10-8-1-2	pn4	<i>Panicum sumatrense</i>	dom est		green disperse spike, gray-yellow seed
01-10-8-1-3	pn5	<i>Panicum sumatrense</i>	dom est		green dense spike, gray-yellow seed
01-10-8-1-4	pn6	<i>Panicum sumatrense</i>	dom est		purple dense spike, yellow seed
01-10-8-1-5	st61	<i>Setaria pumila</i>	dom est		a few mixed, black seed
01-10-8-1-6	st62	<i>Setaria pumila</i>	weed		shattering black seed
01-10-8-2-1	pn7	<i>Panicum sumatrense</i>	dom est	Site 1 Ilur village, Chittoor, Andhra Pradesh	main crop, green disperse spike, gray-yellow seed
01-10-8-2-3	pn8	<i>Panicum sumatrense</i>	medium		green disperse spike, dark gray-yellow seed
01-10-8-2-5	st63	<i>Setaria pumila</i>	weed		short spike
01-10-8-2-6	st64	<i>Setaria pumila</i>	medium		a few mixed, pale green dense spike, pale green seed
01-10-8-2-7	st65	<i>Setaria pumila</i>	medium		a few mixed, purple spike, black seed
01-10-8-2-8	st66	<i>Setaria pumila</i>	dom est		
01-10-9-2-1	pn9	<i>Panicum sumatrense</i>	dom est	Dombarpally village, Palanur, Andhra Pradesh	main crop, gray-yellow seed
01-10-9-2-4	st67	<i>Setaria pumila</i>	dom est		many mixed, black seed
01-10-9-3b-3	st68	<i>Setaria pumila</i>	dom est	Punganuru, Andhra Pradesh	mixed with <i>P. sumatrense</i> , pale green seed
01-10-9-3b-4	br2	<i>Brachiaria ramosa</i>	dom est		dense spike
01-10-9-3b-5	br3	<i>Brachiaria ramosa</i>	medium		disperse spike
01-10-10-1	ps3	<i>Paspalum scrobiculatum</i>	dom est	Jalarpali village, Andhra Pradesh	
01-10-17-1	st69	<i>Setaria pumila</i>	weed	Site 3 Kundivillage, Orissa	mixed with <i>E. coracana</i> , small black seed
01-10-17-2c	ors	<i>Oryza sativa</i>	dom est		upland rice
01-10-17-4	sw	<i>Setaria sp.</i>	weed		
01-10-18-1-1	orr	<i>Oryza rufipogon</i>	weed	Bhawanipatna, Orissa	growing near rice paddy
01-10-18-1-2	psw	<i>Paspalum sp.</i>	weed		growing near rice paddy
01-10-19-2a-1	pn10	<i>Panicum sumatrense</i>	dom est	West Polehorebrd village, Bhawanipatna, Orissa	mixed with <i>E. coracana</i> , pale brown seed
01-10-19-2a-2	el	<i>Eleusine coracana</i>	dom est		small seed
01-10-19-2a-3	st70	<i>Setaria pumila</i>	weed		small seed
01-10-19-2b-1	ps4	<i>Paspalum scrobiculatum</i>	dom est	West Polehorebrd village, Bhawanipatna, Orissa	mixed with upland rice field
01-10-19-2b-2	ef	<i>Echinochloa frumentacea</i>	dom est		mixed with upland rice field

medium = associated in many weedy type

Beauv.) have been collected through field surveys of the Indian subcontinent since 1983. Concentrated field surveys were conducted in Karnataka, Andhra Pradesh, and Orissa in 1985, 1987, 1996, and 2001 as illustrated in Fig. 1. At the same time, the component species of millets and weeds were examined in five plots (1 m<sup>2</sup>) each in four typical cropping fields (sites) through the quadrat method. Voucher herbarium specimens and grain samples were collected along the entire survey route and deposited at Tokyo Gakugei University and the University of Agricultural Sciences (Bangalore). The information on agricultural practices, grain processing, food preparation, and vernacular names was obtained from local farmers.

As part of these accessions, 60 experimental strains were selected and grown in a glasshouse at Tokyo Gakugei University, Japan, in order to compare their morphological and ecological characters in 1998 (Table 1) and in 2002 (Table 2). These 10 grains of 60 strains were sown with a row spacing of 8 cm and seed spacing of 2 cm in a box on June 8, 1998 and June

10, 2002. Two weeks after sowing, germinated plants were transplanted with row spacing of 30 cm and plant spacing of 15 cm in the glasshouse. Chemical fertilizer [N:P:K = 8:8:5 (g)] was supplied at 100 g per m<sup>2</sup>. Five plants of *S. pumila*, each of the weed type, companion weed, and mimic companion weed types associated with *Pas. scrobiculatum* and other cereals, and the domesticated type mixed with *P. sumatrense* were measured for number of tillers, plant height, spike length, duration to flowering, length and width of the flag leaf, last internode diameter, number of leaves on the main culm, and number of seeds germinated every 10 days after sowing. Plant color was assessed using the PANTONE Formula Guide. These data were analyzed statistically using IBM SPSS (version 21).

Additionally, the anthocyanin composition included in the leaf and leaf sheath was analyzed by high-performance liquid chromatography (HPLC) in 2013. The materials were *S. pumila* (5 accessions) from site 5 to 8, *P. sumatrense* (8), *Pas. scrobiculatum* (2), *B. ramosa* (1), and *S. viridis* (2, fresh and dried). In

order to identify the retention time (Rt) and measure the content of each anthocyanin, natural pigments of cyanidin, pelargonidin, and malvidin were used. The experimental method was as follows. The extraction of anthocyanins from leaf and leaf sheath was performed according to the method reported by Mochioka et al. (1995), Tsuda et al. (2009), and Chiba et al. (2010), with some modifications. Briefly, liquid nitrogen was added to leaves (300 mg) that had been stored at  $-30^{\circ}\text{C}$  and these were then ground using a ceramic mortar. The ground material was placed into a safety-rock tube (1.5 ml), followed by the addition of 300  $\mu\text{l}$  50% methanol containing 5% acetic acid. The tube was allowed to stand in a sonicator for 30 min, and the solution was filtered through a membrane filter (UST-5, ADVANTC). The solution of standard pigments was also filtered through the same membrane filter. After the treatment, the solution was placed in a refrigerator at  $6^{\circ}\text{C}$  overnight. The anthocyanin composition of the leaves was identified by the retention time and the content was calculated using a calibration curve. The HPLC system employed to analyze the anthocyanins was a Shimazu system CLASS-M10A equipped with a Shimazu chromatography data station, including pump, column oven, and absorbance detector SPD-10A for monitoring at 520 nm. For the column, Shin-Pak (4.6  $\times$  250 mm, PREP-ODS(H)KIT; Shimazu) was used at  $40^{\circ}\text{C}$ . Linear gradient elution was performed with solution A (1.5% phosphoric acid) and solution B (1.5% phosphoric acid, 20% acetic acid, and 25% acetonitrile) delivered at a flow rate of 1.0 ml/min as follows: 80% of solution A initially; 15% A for the next 40 min; 80% A for a further 5 min; and finally 80% A for 15 min (P.MAX; 200 kgf/cm<sup>2</sup>: P.MIN; 10 kgf/cm<sup>2</sup>). The injection volume for the extract was 20  $\mu\text{l}$ .

## Results

### Morphological and ecological diversity of *S. pumila*

*S. pumila* is still cultivated through mixed cropping mostly with *P. sumatrense* in restricted regions in peninsular India as shown in Fig. 2e and 2f. The weed types and mimic companion weed types are also used

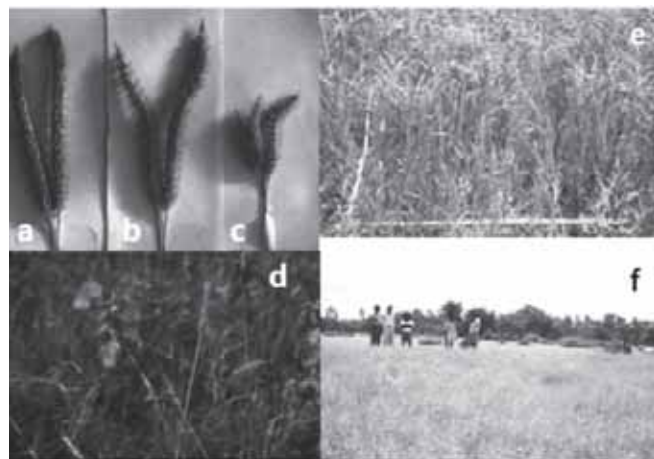


Fig. 2. Panicle types of *Setaria pumila*: a) and b) domesticated types (Dk) mixed with *Paspalum scrobiculatum*; c) domesticated type (Ds) mixed with *Panicum sumatrense* and d) weed type shattering seed grains; e) and f) cropping fields mixed with *Panicum sumatrense* and *Setaria pumila*: at Illur village near Chittoor in Andhra Pradesh.

together as a wild grain for food and forage today. Their spikes show a large variability, for example, in the domesticated type (Dk) mixed with *Pas. scrobiculatum* (Fig. 2a and 2b), another domesticated type (Ds) mixed with *P. sumatrense* (Fig. 2c), and the weed type (W) of *S. pumila* (Fig. 2d)

The morphological characteristics and the duration to flowering of *S. pumila* (60 accessions) were compared among weed, companion weed, mimic companion weed, and domesticated type mixed with the other crops (Fig. 3). The plant height of weed types had a large range (from 81 to 220 cm), and the height of the mimic companion weed and domesticated types were within the same range. The number of tillers showed very broad variability from 10 to over 60, but mostly 10 to 25, irrespective of the type. The spike length was 5 to 14 cm in weed types, and a little longer (9 cm to over 16 cm) in mimic companion weed and domesticated types. The duration to flowering of many strains was ranged from 121 to 140 days, but that of domesticated types showed a bimodal pattern, 81 to 100 days and 121 to 150 days. The ratio of length/width of the flag leaf had a modest range from 21 to 31, but that of domesticated types had a broad variation of range from 21 to 70. The last internode diameter was 1.1 to 2.5 mm in weed



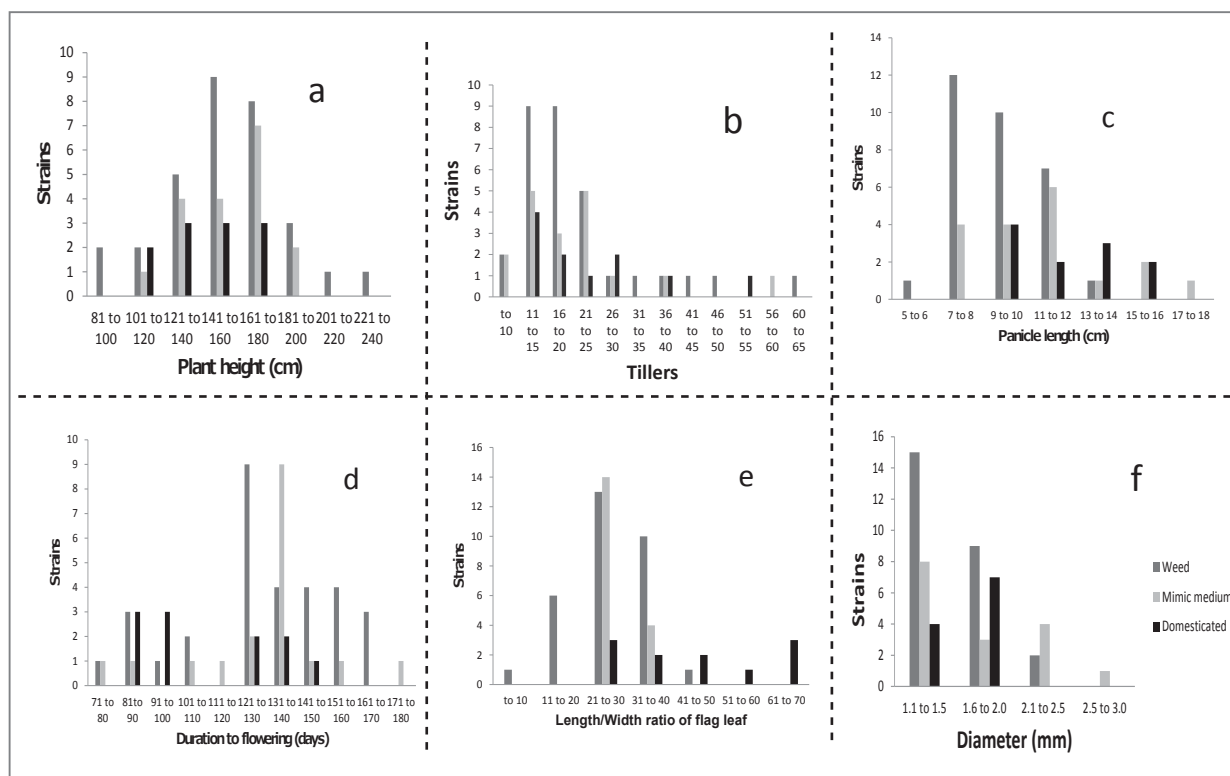


Fig. 3. Morphological and ecological characters of 60 accessions in *Setaria pumila*: a) plant height (cm), b) number of tillers, c) spike length (cm), d) duration of flowering (days), e) length/width ratio of flag leaf, and f) last internode diameter (mm).

Table 3. Component species per m<sup>2</sup> of four millet fields (sites)

Site no.	Locality	<i>Panicum sumatrense</i>	<i>Setaria pumila</i>	<i>Fleusine coracana</i>	<i>Brachiaria sp.</i>	<i>Digitaria sp.</i>	Total
Site 1	01-10-8-2 (805malt.) Cittoor, Andhra Pradesh						
	No. of plants	163.5	90.75	0	22	0.25	276.5
	s.d.	76.43	36.48		24.99	0.5	75.54
	Range	78–264	55–141		0–56	0–1	191–355
	%	59.13	32.82	0	7.96	0.09	100
	Highest plant (cm)	77.38	66.88				
	s.d.	7.63	10.17				
Site 2	01-10-9-1 (690malt.) Cittoor, Andhra Pradesh						
	No. of plants	105.5	312.25	0	0.75	1	419.5
	s.d.	68.83	60.91		0.5	0.82	68.98
	Range	30–172	240–368		0–1	0–2	352–517
	%	25.15	74.43	0	0.18	0.24	100
	Highest plant (cm)	76	68.25				
	s.d.	24.07	15.37				
Site 3	01-10-17-1 (855malt.) Kundli, Orissa						
	No. of plants	1.75	1.5	42.25	0	0.25	45.75
	s.d.	0.96	1	6.85		0.5	26.12
	Range	1–3	1–3	34–50		0–1	46–101
	%	3.83	3.28	92.35	0	0.55	100
Site 4	01-10-19-3 (375malt.) West Polehorebride, Orissa						
	No. of plants	40.5	2	0	0	0	45.75
	s.d.	8.23	1.63				20.59
	Range	30–50	0–4				40–86
	%	95.29	4.71	0	0	0	100

types, 1.1 to 3.0 mm in mimic companion weed types, and 1.1 to 2.0 mm in domesticated types.

Species component of millet and weed grown in four

cropping fields (sites)

The species components (per m<sup>2</sup>) of four millet cultivation fields are shown in Table 3. At site 1, the percentages of *P. sumatrense*, *S. pumila*, and weed

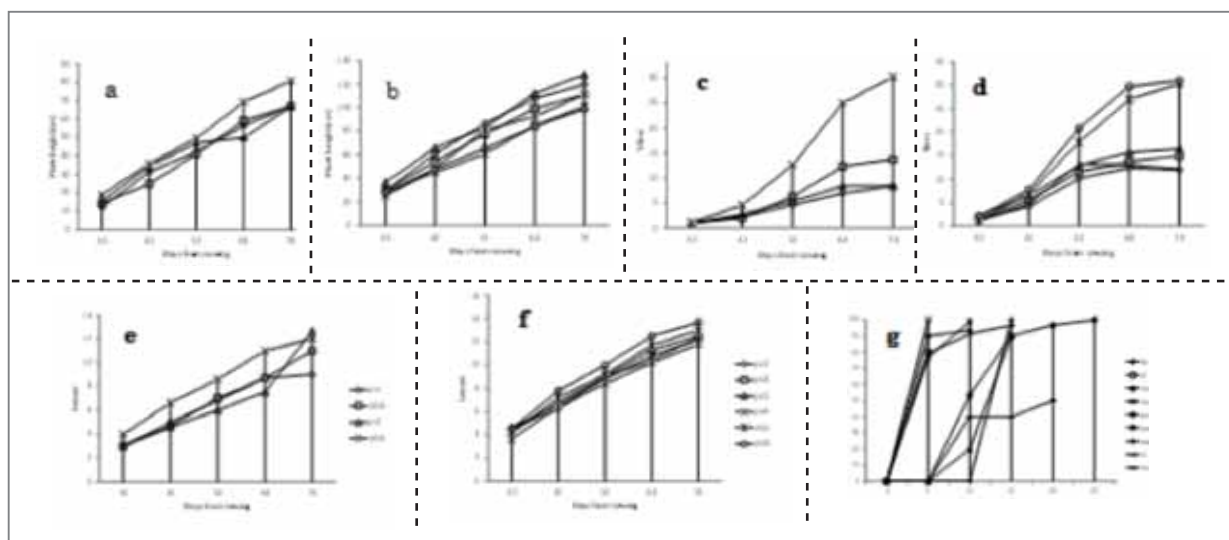


Fig. 4. Early growing patterns of seedling in *S. pumila*, *P. sumatrense* and *Pas. scrobiculatum*: a/b) plant height, c/d) number of tillers and e/f) number of leaves on main culm and g) seed germination.

*Brachiaria* sp. were 59%, 33%, and 8%, respectively, while at the nearby site 2, the percentages were 25%, 74%, and trace. At site 3, a single stand of *E. coracana*, and at site 4, a single stand of *P. sumatrense*, the weed type of *S. pumila*, had invaded significantly, but represented only 3–5% into both cropping fields.

#### Comparison of early growing among companion weeds and crops

With respect to early growing during the period of 30 to 74 days after sowing, five characteristics were compared among *S. pumila* (2, Mk-st56 and Dk-st58) and *Pas. scrobiculatum* (2, Dk-ps1 and Dk-ps2) collected at site 5 and 7 in Tumkur, Karnataka, and *S. pumila* (Ds-st61 and Ws-st62) and *P. sumatrense* (D-pn3 to D-pn6) in Kolar, Andhra Pradesh (Table 2). The early growth of the number of tillers of *S. pumila* (st58 from Karnataka) showed a marked increase, but there was little difference in the plant height or the number of leaves among the four strains (Fig. 4a-c-e). For the strains from Andhra Pradesh, the number of tillers of *S. pumila* (st61, st62) was also markedly increased 52 days after sowing, while there were little difference in plant height or the number of leaves among the six strains (Fig. 4b-d-f). On the other hand, the seed germination rates of *O. sativa*, *B. ramosa*, *E. coracana*, *P. sumatrense* and *S. pumila* were approximately 80% by 5 days, and

nearly 100% by 10 days, but the germination of *Pas. scrobiculatum* (D-pas, W-pasw), *Setaria* sp. (W-stw) and *O. rufipogon* (ancestral W-orr) was only starting at 5 days and the rates were still increasing at 15 days (Fig. 4g).

#### Mimicry in the color of leaf and leaf sheath

The leaf and leaf sheath colors of *S. pumila* were the same green (370c~371c) and reddish purple (206c~209c), respectively, using the PANTONE Formula Guide, as a mixed cropping *Pas. scrobiculatum* at site 5 in Karnataka (Table 4 and 5). The colors of *S. pumila* were also the same green (363c~371c) and reddish purple (206c~208c), respectively, at site 7 in Karnataka. At site 6 in Karnataka, the colors of *S. pumila* and *P. sumatrense* were the same green (369c~377c) and reddish purple (206c~207c), except for the leaf sheath color of *B. ramosa* (green, 374c). Among the control strains used, the colors of *P. sumatrense* ranged from green (366c~370c) to pink (203c), but those of *S. viridis* ranged from green (leaf 371c) to purple (leaf sheath 209c~5195c).

The anthocyanin composition of leaf and leaf sheaths was analyzed by HPLC as illustrated in Fig. 5. The leaf sheath of *S. pumila* showed many peaks (present on each one) on Rt (Fig. 5a), while those of *P. sumatrense* (Fig. 5b) and *Pas. scrobiculatum* (Fig. 5c) indicated only

**Table 4. Comparison of leaf and leaf sheath color based on PANTONE formula guide in four millet cultivation fields (sites)**

Site no.	Collection no.	Cultivation no.	Species	Leaf developed	Leaf undeveloped	Under part of leaf sheath
Site 5	96-11-5-1a-1	ps1	<i>Paspalum scrobiculatum</i>	371c-green	370c-green	208/209c-reddish purple
	96-11-5-1a-2	st56	<i>Setaria pumila</i>	371c-green	371c-green	206c-reddish purple
Site 6	96-11-5-2b-1	pn1	<i>Panicum sumatrense</i>	377c-green	371c-green	206c-reddish purple
	96-11-5-2b-4	br1	<i>Brachiaria ramosa</i>	371c-green	377c-green	374c-green
	96-11-5-2b-6	st57	<i>Setaria pumila</i>	371c-green	369c-green	205/207c-reddish purple
Site 7	96-11-5-7-1	ps2	<i>Paspalum scrobiculatum</i>	371c-green	370c-green	208c-reddish purple
	96-11-5-7-2	st58	<i>Setaria pumila</i>	371c-green	363c-green	206/207c-reddish purple
Site 8	97-4-12-2-1	pn2	<i>Panicum sumatrense</i>	371c-green	377c-green	374c-green
	97-4-12-2-2	st59	<i>Setaria pumila</i>	371c-green	377c-green	198/202c-reddish purple
	97-4-12-2-3	st60	<i>Setaria pumila</i>	371c-green	377c-green	198/202c-reddish purple

**Table 5. Samples used for HPLC**

Collection no.	Site no.	Species name	Organ	Panton formula guide
96-11-5-1a-1	Site 5	<i>Paspalum scrobiculatum</i>	Leaf sheath	208c/209c
96-11-5-1a-1			Leaf	371c/370c
96-11-5-1a-2		<i>Setaria pumila</i>	Leaf sheath	206c
96-11-5-1a-2			Leaf	371c
96-11-5-2b-1	Site 6	<i>Panicum sumatrense</i>	Leaf sheath	206c
96-11-5-2b-1			Leaf	277c
96-11-5-2b-4		<i>Brachiaria ramosa</i>	Leaf sheath	374c
96-11-5-2b-4			Leaf	371c
96-11-5-2b-6		<i>Setaria pumila</i>	Leaf sheath	205c/207c
96-11-5-2b-6			Leaf	371c
96-11-5-7-1	Site 7	<i>Paspalum scrobiculatum</i>	Leaf sheath	208c
96-11-5-7-1			Leaf	371c
96-11-5-7-2		<i>Setaria pumila</i>	Leaf sheath	206c (207c)
96-11-5-7-2			Leaf	371c
97-4-12-2-1	Site 8	<i>Panicum sumatrense</i>	Leaf sheath	374c
97-4-12-2-1			Leaf	371c
97-4-12-2-2		<i>Setaria pumila</i>	Leaf sheath	198/202c
97-4-12-2-2			Leaf	371c
97-4-12-2-3		<i>Setaria pumila</i>	Leaf sheath	198/202c
97-4-12-2-3			Leaf	371c
85-10-12-6-1		<i>Panicum sumatrense</i>	Leaf sheath	366c
85-10-12-6-1			Leaf	370c
85-10-12-6-2		<i>Panicum sumatrense</i>	Leaf sheath	203c
85-10-12-6-2			Leaf	370c
85-10-12-6-4		<i>Panicum sumatrense</i>	Leaf sheath	203c
85-10-12-6-4			Leaf	370c
85-10-19-3-1		<i>Panicum sumatrense</i>	Leaf sheath	366c
85-10-19-3-1			Leaf	370c
85-10-27-3-9		<i>Panicum sumatrense</i>	Leaf sheath	366c
85-10-27-3-9			Leaf	370c
85-10-31-3-1		<i>Panicum sumatrense</i>	Leaf sheath	203c
85-10-31-3-1			Leaf	370c
12-11-19		<i>Setaria viridis</i>	Leaf sheath	209c
12-11-19			Leaf	371c
12-11-19		<i>Setaria viridis</i> (dried)	Leaf sheath	5195c
12-11-19			Leaf	5185c

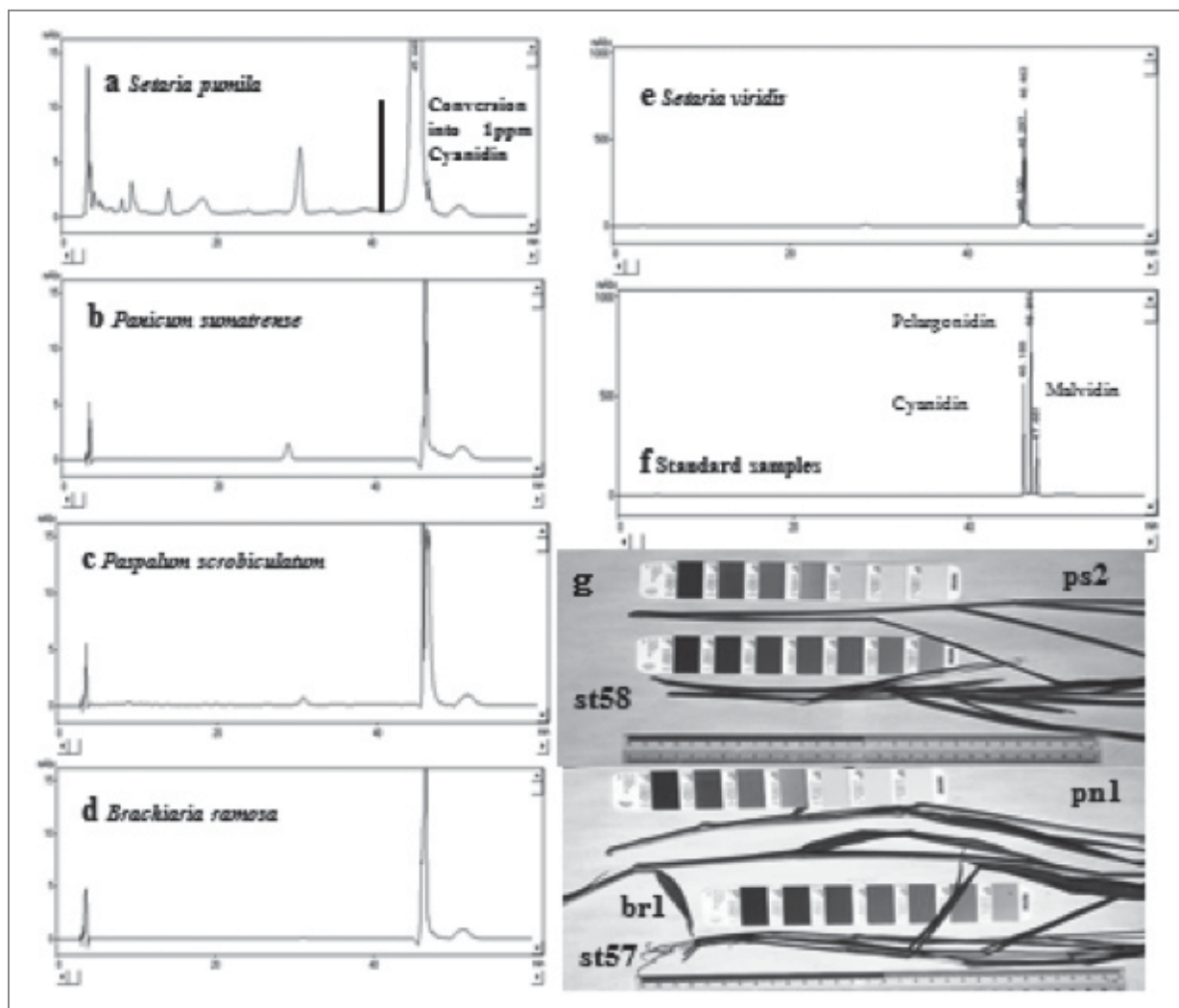


Fig. 5. HPLC analysis and comparison between plant pigmentations through PANTON Formula Guide. a) *S. pumila*, b) *P. sumatrense*, c) *Pas. scrobiculatum*, d) *B. ramosa*, e) *S. viridis*, f) standard samples and g) in a field of *Pas. scrobiculatum*: ps2, *Pas. scrobiculatum*; st58, *S. pumila*; in a field of *P. sumatrense*: pn1, *P. sumatrense*; br1, *B. ramosa*; st57, *S. pumila*.

a small peak (Rt around 30) except for some occasional peaks (around 45.6). However, that of *B. ramosa* showed no peak at all around Rt (30) (Fig. 5d). Only the Rt (46.1) of anthocyanin contained in *S. viridis* (dried matter, Fig. 5e) concurred with natural cyanidin's Rt (46.2), but most of the Rts of anthocyanins contained in samples did not coincide with the Rt of three natural pigments (Fig. 5f). Therefore, cyanidin was used as an indicator of anthocyanin content. By means of cluster analysis (Ward method), these samples were categorized into two groups as illustrated in Fig. 6. Cluster I consisted of five samples (st56~st60), which were only the leaf sheath of *S. pumila*. The color was reddish purple (198/202/205/206/207c in

the PANTONE Formula Guide). Sub-cluster IIa (11 samples) consisted of the green leaf of *S. pumila* (1, st57), the green leaf (1, ps1) and leaf sheath (2, ps1 and ps2) of *Pas. scrobiculatum*, which were reddish purple color (208/209c), the leaf sheath of *P. sumatrense* (3, pn1-reddish purple, green pn2 and the other), the green leaf sheath of *B. ramosa* (1, br1) and the green leaf (1) and leaf sheath (2) of *S. viridis*. Moreover, Sub-cluster IIb (20) consisted of the green leaf of *S. pumila* (4, st56, st58, st59 and st60), *Pas. scrobiculatum* (1, ps2), *S. viridis* (1), *P. sumatrense* (8, pn1, pn2 and so on), and *B. ramosa* (1, br1).

Seed color mimicry was found in the mixed grains of *P. sumatrense* and *S. pumila* at Illur village near



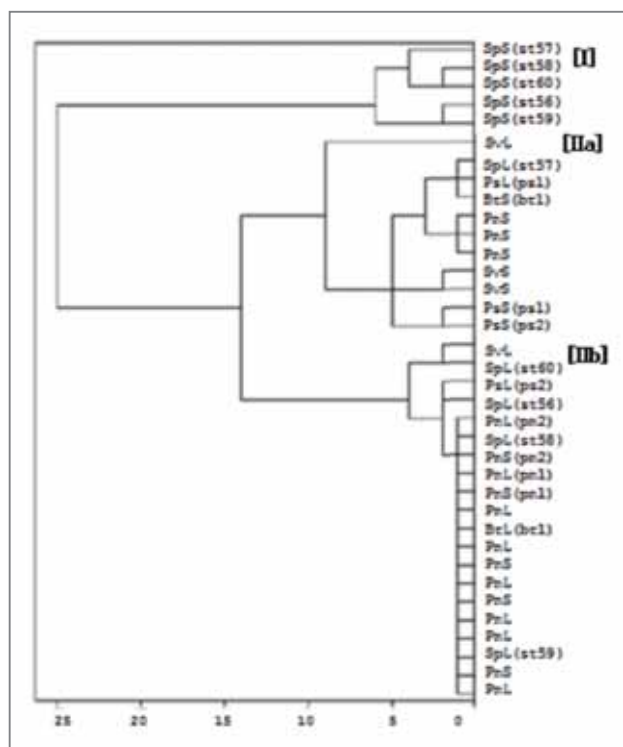


Fig. 6. Dendrogram based on the pigmentation of leaf and leaf sheath in five species.

Chittoor in Andhra Pradesh as shown in Fig. 7a. The seed grains of *P. sumatrense* (Fig. 7b) had a very similar pale brown color to the seed grains of *S. pumila* (Fig. 7c), except for their black seed grains (Fig. 7d). However, it was possible to distinguish the seed grains of *P. sumatrense* from those of *S. pumila* in detail, because of their glossy lemmata. Here, villagers have made three foods from *S. pumila*. They are boiled grain, *annamu* (Fig. 7e), flour porridge, *sankati* (Fig. 7f) and semi-solid porridge, *uppitu* (Fig. 7g).

## Discussion

The domestication process of *S. pumila* may have passed through four steps as illustrated in Fig. 8. The first step was a weed that had grown along roadsides and other unstable habitats and then invaded upland rice fields. The second step was an evolutionary process to obtain an agro-ecological niche out of weed status, using for fodder, in order to get the companion weed status growing in upland rice and some millet fields. The third step was a process of advancing from the mimic companion weed status to a semi-domesticated

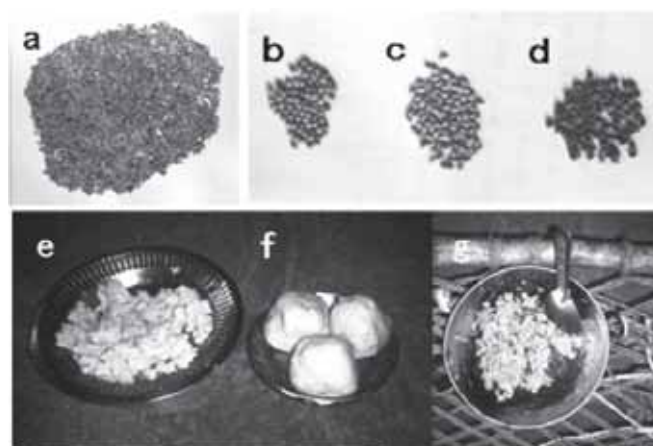


Fig. 7. Seed mimicry of *S. pumila* to *P. sumatrense* and three foods made from their mixed grains at Jalaripali village, Andhra Pradesh: a) mixed grains harvested and sold; after identified them, b) brown seeds of *P. sumatrense*, c) brown seeds and d) black seeds of *S. pumila*; e) *annamu* (boiled grain), f) *sankati* (thick flour porridge) and g) *uppitu* (semi-solid porridge).

and insurance crop, used in case of famine, under mixed cropping with *Pas. scrobiculatum*, *E. coracana*, and *P. sumatrense*. The weed types after their invasion into upland rice and millet fields obtained mimicry associated with a particular crop, and made a close weed-crop complex under the severe weed control measures practiced by farmers. In the fourth and final step, the mimic companion weed forms were used not only a fodder source for cattle, but also as a supplementary grain to the main cereal species. In the case of *S. pumila*, too strict weeding was avoided as a means of crop insurance in years of extreme drought in the Deccan Plateau. This possibly led to *S. pumila* growing taller with larger spikes and large seeds, accompanied with less shattering, and gradually progressing toward domestication. Actually, *S. pumila* has obtained mimic traits such as long leaf, a few tillers, and tall plant height in the field of *P. sumatrense* as shown in Figs. 3 and 4. The morphological and ecological characteristics of the 60 strains in *S. pumila* were very variable, as shown in Fig. 3. The plant height (cm) indicated a trend toward higher tallness in the domesticated type than in the weed type (Fig. 3a). The number of tillers showed a slight reduction in the domesticated type compared to the weed type, excluding two exceptional strains (Fig.

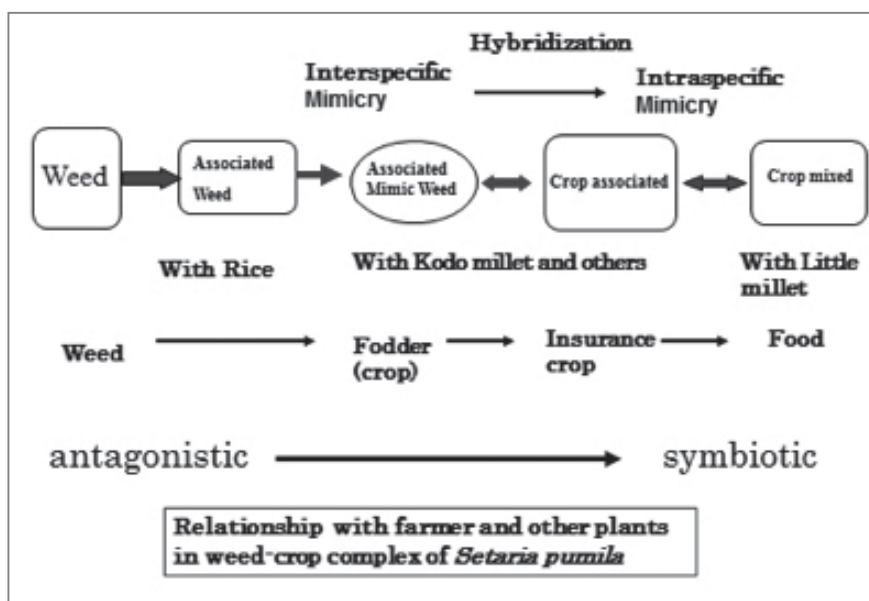


Fig. 8. Domestication process of *Setaria pumila*

3b). The spike length (cm) clearly increased more in the domesticated type than in the weed type (Fig. 3c). The duration to flowering (days) showed a bimodal pattern: early and late (Fig. 3d). The early domesticated type was similar to the weed type, while the late domesticated type was similar to the mimic companion weed type mixed with other cereals. The length/width ratio of the flag leaf showed two trends, wide and slender, as shown in Fig. 3e. The last internode diameter (mm) was clearly thick in the domesticated type than in the weed type (Fig. 3f). The domesticated type mixed with *P. sumatrense* had a higher ratio than the others, which had a medium ratio. It was morphologically clear that spikes had become longer and the last internode diameter had become bolder in the domestication process.

It was very difficult for farmers to detect the difference among mimic companion weeds and domesticated types in sympatric fields during the early growing stage, because at this stage they resemble each other very closely. The seed germination of domesticated and annual plants was usually rapid and uniform, but that of *Pas. scrobiculatum*, perennial plants, and weeds was a little late and irregular.

At the same time, *S. pumila* diversified their traits in totality through hybridization among the types under natural and artificial selection in the severely

arid environment. The mimic companion weeds were harvested together with other millet, and sown involuntarily again next season. In the third step, farmers changed their hostile weed control into a friendly one. Recently, during the fourth step, this situation was followed by mixed cropping. *S. pumila* is termed a tertiary crop in relation to its associated plants, which were secondary crops, such as *P. sumatrense*, *Pas. scrobiculatum*, with respect to rice.

The species ratio composition of each mixed cropping field was variable annually, according to some field conditions such as summer precipitation (Table 3). At the early growing stage, it was very difficult to recognize morphological differences from each other in a set of plant species collected from the same cropping field. The inter- and intra-specific mimic variation had occurred not only in the morphological characteristics e.g., plant height, leaf size and number of tillers, but also in the ecological ones, e.g., seed germination pattern, seed color, and leaf sheath color. It was clear that the leaf sheath color of *P. sumatrense* and *Pas. scrobiculatum* (Sub-cluster IIa) was mimicry related to that of *S. pumila* (Cluster I) as shown in Fig. 5. The glume color of *S. pumila* was also mimicry of the glume of *P. sumatrense*. The domestication process and dispersal of *S. pumila* has developed by means of elaborate mimicry

in several characteristics of other crops to itself as shown in Fig. 5, 6, and 7.

*Pas. scrobiculatum* is perennial and the seed germination, tillering, and plant height elongation are usually slow. Therefore, *Pas. scrobiculatum* was distinguished relative to the other species. Among others, because these characters were synchronized to each other, it was very difficult to distinguish them, especially plant height and the number of leaves on main culm in the early growing stage. The domesticated type of *S. pumila* was adjustable to its associated mimic species in morphological characters, ecological traits in early growth, and plant pigmentation as shown in Table 4 and Fig. 6. It indicated mimicry of leaf and leaf sheath by way of color among *S. pumila*, *Pas. Scrobiculatum*, and *P. sumatrense*, but not *B. ramosa*. However, both leaf color of *S. pumila* (Ds) and *P. sumatrense* were the same green (371c~377c), while the leaf sheath color of *S. pumila* was reddish purple (198c~202c) in spite of a finding of green color (206c~207c) in *P. sumatrense* at site 8 in Andhra Pradesh. This case did not indicate mimicry of leaf sheath color.

Moreover, *S. pumila* has been domesticated as a tertiary crop, by way of the other millet species, to upland rice, because it has built up the strongest resistance to frequent droughts in the Deccan Plateau. The domesticated type of *S. pumila* is commonly cultivated in mixed stands mostly along with *P. sumatrense* in South India today, while the semi-domesticated crop and mimic companion weed types are not only grown with *P. sumatrense*, but also mainly with *Pas. scrobiculatum*, *E. coracana*, and upland rice in diverse agro-ecological niches in Orissa. The weed type of *S. pumila* grows widely through the India subcontinent and tropical and temperate Northern Hemisphere. The various types have adapted to arid conditions and agro-ecological niches in the Deccan Plateau during their distribution from eastern humid areas to southern dry areas in the Indian subcontinent (Sehgal et al. 1992).

The domesticated types of *S. pumila* have broadly promoted the biocultural diversity through the mimicry

of other grain crops. The domesticated type of *S. pumila* was always sown, harvested, and consumed together with *P. sumatrense* as shown in Table 7e, 7f, and 7g. Farmers called the mixed grains *tela samuru* (meaning white little millet) in Telugu. The proportion of grains purchased at a local market was 70% of *P. sumatrense* and 27% of *S. pumila*, respectively, in 1997 (Kimata et al. 2000). These authors are of the opinion that in severe drought, *S. pumila* provides a reasonable harvest while *P. sumatrense* might fail completely. This situation recommends the domestication process of secondary crops in other cereal fields against an arid climate. These crops are used to make six traditional foods in total, including *ganji* (thin flour porridge), *kheer* (sweet gruel) and *roti* (unleavened bread), as a supplementary ingredient (Kimata and Sakamoto 1992, Kimata et al. 2000).

Furthermore, this domestication process is supported by the linguistic recognition of their various vernacular names by farmers. For example, a mimic companion weed or semi-domesticated plant occurring with *Pas. scrobiculatum* was called *varagu korali*, meaning just the same as kodo millet, while a mimic companion weed or semi-domesticated plant occurring with *P. sumatrense* was called *samuru korali*, meaning also just the same as little millet. The domesticated type was called various vernacular names (e.g., *korati*, *kora samuru*, *korin*) in each local language and region. The linguistic differentiation shows a close relationship to the domestication process (Chandra and Koppar 1990; Kawase 1987; Kimata et al. 2000, Kimata 2015c; Kobayashi 1987, 1989).

*B. ramosa* is cultivated under pure single cropping as a sole tertiary crop, while *S. pumila* is still cultivated under mixed cropping with *P. sumatrense* as a minor domesticated plant. *B. ramosa* tolerates drought better than *S. pumila*, and has been undergoing a specializing adaptation to arid regions, and has nearly attained the tertiary domesticated phase. On the other hand, the landraces of *S. pumila* have adapted to drier fields in South India than in Orissa. *S. pumila* was almost always grown with *P. sumatrense*, but seemed to grow

singly when the later fail to grow in severe droughts, as was observed in our survey of 1987. This possibly suggests that *S. pumila* could become an independent crop.

In this case of multiple polyploidy species, *S. pumila* indicated that diversity had been increased mainly by mimicry and inter- and intra-specific hybridization under natural and artificial selection. This domestication process has been promoted as a means of imparting adaptation to an arid climate, and also produced a symbiotic relationship among weeds, other crops, and farmers, while departing from an antagonistic one. The domestication process of *S. pumila* indicates the importance of weed-crop complexes and biocultural diversity as a plant-man symbiosis. The diversity of *S. pumila* and its relatives should be conserved both *in situ* and *ex situ*, especially in on-farm conservation sites.

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# Domestication process of *korati*, *Setaria pumila* (Poaceae), in the Indian subcontinent on the basis of cluster analysis of morphological characteristics and AFLP markers

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The endemic landraces and related weeds were collected in field surveys around the Deccan in India since 1983, to explain the domestication process of *Setaria pumila* (Poir.) Roem. et Schult. (Poaceae) through its mimicry of other grain crops. The domestication process of *Setaria pumila* in relation to the weed-crop complex was comparatively investigated using statistical and AFLP analyses. It was clear on the basis of these results that the domestication process had progressed through the four stages according to geographical trends in morphological (artificial selection) and genetic variation (neutral DNA markers). Under the complex process, the 4 stages were as follows: weed, companion weed, mimic companion weed and domesticated type to the secondary crop. The paddy rice had dispersed from Assam, the humid east toward Deccan, the dry south in the Indian subcontinent. Several species of Indian millet were domesticated by local farmers as the secondary crop of rice along the climatic trend and dispersal route. In South India, one domesticated type of *S. pumila* was cultivated only in mixed stands mostly along *Panicum sumatrense*. Around Orissa, the other types and the related weeds were grown in the sympatric fields with *Paspalum scrobiculatum*, *Eleusine coracana*, and upland rice (*Oryza sativa*) in diverse agro-ecological niches. Therefore, *S. pumila* became exactly a tertiary crop to the other Indian millet (secondary crop to rice).

Keywords: AFLP markers, artificial selection, domestication process, mimicry, mixed stand, tertiary crop

## Introduction

Humans have domesticated more than 30 grass species as grain crops in several parts of the world, possibly as long as 12,000 years ago. However, several species are threatened and, despite their potential food value in their native habitats, have disappeared or have not been extensively cultivated. This is because the yield and production of the three major crops: wheat, rice, and maize, have rapidly increased due to technological innovations in crop-improvement programs. Cultivation of other grain crops (e.g., millets) has decreased gradually during the 20th century, resulting in loss of genetic diversity of local varieties. It is currently necessary to recognize the value of these neglected species as exploitable and underutilized genetic resources that exhibit adaptability to stress-prone environments. In this paper, we focus on millet species, which are mostly  $C_4$  plants, are early to mature, and can be cultivated under conditions of severe drought and harsh sunlight.

Small-scale farmers continue to cultivate a few useful local varieties of millet. These indigenous varieties are excellent materials for investigating crop evolution, particularly the origin and dispersal routes of domesticated plants. In the Indian subcontinent, a few millet species are still undergoing domestication (Kimata et al. 2000; Singh and Arora 1972). While crop evolution can be reconstructed mostly from botanical data, details on geographic origin and dispersal will become clear from information on the basic agricultural complex offered by local farmers. This basic agricultural complex consists mainly of cultivation, processing and cooking such as biocultural diversity.

Vavilov (1926) illustrated the domestication process from companion weeds associated with wheat to secondary crops in two genera, *Avena* and *Secale*. For example, *Secale cereale* L. acquired strong resistance to cold in high altitude or latitude areas, and subsequently was able to grow under more severe conditions than those under which wheat can grow. Kobayashi (1987, 1989) proposed an integrating model of the domestication of Indian millet (e.g. *P. sumatrense*, *Echinochloa frumentacea*) as a secondary crop from mimic companion weeds associated with *Oryza sativa* L. Farmers have manipulated the domestication process by selecting for desired growth, visual, and palatability traits, e.g. yield, early maturation, color, sugar content. However, natural selection and hybridization have occurred among closely related weeds during domestication.

The growing area of *O. sativa* expanded from wetlands to establish secondarily in uplands in the Indian subcontinent. In turn, weedy ancestral plants invaded paddy and upland rice fields. Local farmers subsequently domesticated *Panicum sumatrense* Roth. (little millet), *Paspalum scrobiculatum* L. (kodo millet), and *Echinochloa frumentacea* Link (Indian barnyard millet), as secondary crops, because these species demonstrated stronger resistance to drought than upland rice in Eastern India. Several additional species of millet were domesticated in this region: *Brachiaria ramosa* (L.) Stapf. (*korne*, browntop millet), *Digitaria cruciata* [Nees] A. Camus (*raishan*), and *Setaria pumila* (Poir.) Roem. & Schult. (*korati*, yellow foxtail millet; syn. *Setaria glauca* [L.] P. Beauv.) (Chandra and Koppar 1990; de Wet et al. 1983a, b, c).

Recently, archeological studies in the Indian subcontinent have provided useful data on the ancient history of various grains. Millet materials were identified from two archaeological levels in the Southern Neolithic chronology: Phase II (2300–1800 cal BC) and Phase III (1800–1200 cal BC). These materials were identified primarily as two species, *B. ramosa* and *Setaria verticillata* (bristly foxtail millet-grass). *S. pumila* was present in limited quantity,

possibly gathered from the wild (Fuller et al. 2001). The first known occurrences of various cereals in the Harrappan Civilization are reported as wheat, barley, and oats in the Early phase (before 2600 BC); *Eleusine* sp. (problematic, *E. coracana*), *Setaria* sp., *Panicum* sp. in the Mature phase (2600–2000 BC); and *Paspalum* sp., *Echinochloa* sp., *Sorghum* sp., and *Pennisetum* sp. in the Late phase (more recent than 2000 BC) (Fuller and Madella 2000; Weber 1992).

Many new techniques using DNA markers, including SSR (simple sequence repeat), RAPD (random amplified polymorphic DNA), RFLP (restriction fragment length polymorphism), and AFLP (amplified fragment length polymorphism analysis), have been conducted for the genus *Setaria* (Benabdelmouna et al. 2001; d'Ennequin et al. 2000; Fukunaga et al. 2002; Lin et al. 2012). Intraspecific polymorphic variability revealed with RAPD and RFLP marker systems was negligible. AFLP has gained wide acceptance for enabling a high degree of resolution and reproducibility in genetic analysis (Lakshmi et al. 2002). AFLP has a number of other relevant applications and advantages for analysis of plant genomes in general. A large number of DNA loci can be assayed in each reaction, and a large number of fragments can be assayed with a relatively small number of primers. Intergeneric polymorphism revealed by AFLP markers was very high (94.4%). At inter-specific level, it was not significant enough AFLP analysis recorded a higher level of variation, 66.5%, between *Panicum miliaceum* and *P. sumatrense* (Bai et al. 1999). Information on intraspecific diversity and species relationships could form the basic foundation for further research on crop-improvement programs (Lakshmi et al. 2002).

GISH (Genomic in situ hybridization) patterns revealed that two diploid species ( $2n = 18$ ), *S. viridis* and *S. italica*, bore genome AA and a tetraploid species ( $2n = 36$ ), *S. verticillata*, had genome AABB. The genomic composition of *S. pumila* (polyploid species,  $2n = 18, 36, 72$ ) was unknown (Benabdelmouna et al. 2001).

*S. pumila* is a cosmopolitan weed distributed worldwide. This weed grows sympatrically on roadsides,

uplands, and the levees of lowlands; four intraspecific types of *S. pumila* have been identified based on ecological habit: weed type (W), companion weed type accompanied by crops (Wx), mimic companion weed type accompanied by crops (Mx), and domesticated type mixed with crops (Dx). Kimata et al. (2000 and 2015a) have shown the biocultural diversity of morphological and ecological characteristics in *S. pumila*, and the intraspecific differentiation of vernacular names (linguistic data). The present paper concerns the domestication process of *S. pumila*, which is related ecologically to weeds and several grain crops in the Indian subcontinent, based on cluster analysis of morphological characteristics and AFLP markers.

### Materials and Methods

Many local varieties and relative weeds of *Setaria pumila* (Poir.) Roem. & Schult. (syn. *S. glauca* [L.] P. Beauv.) have been collected from the Indian subcontinent since 1983 in field surveys (Fig. 1). Concentrated surveys were conducted in Karnataka, Andhra Pradesh, and Orissa (Fig. 2). At the same time, accompanying millet and weed species were examined in five plots (1 m<sup>2</sup>) in each of four typical cropping fields (sites) using the quadrat method. Voucher herbarium specimens and grain samples were collected along the survey route and deposited at Tokyo Gakugei University (Tokyo, Japan) and University of Agricultural Sciences (Bangalore, India). Information on agricultural practices, grain processing, food preparation, and vernacular plant names was gathered from local farmers.

The experimental strains (n = 78, Table 1) were selected from these accessions and grown in the greenhouse at Tokyo Gakugei University to compare their morphological and ecological characteristics. In addition, three relative species of *S. pumila*: *S. italica* (n = 6, from Japan), *S. viridis* (n = 2, from Kazakhstan and Uzbekistan), and *S. verticillata* (n = 3, from India) were grown using the same methods.

Ten grains each of 60 strains were sown in a seeding box with row spacing of 8 cm and seed spacing of 2 cm on early June 6, 2002. Two weeks after

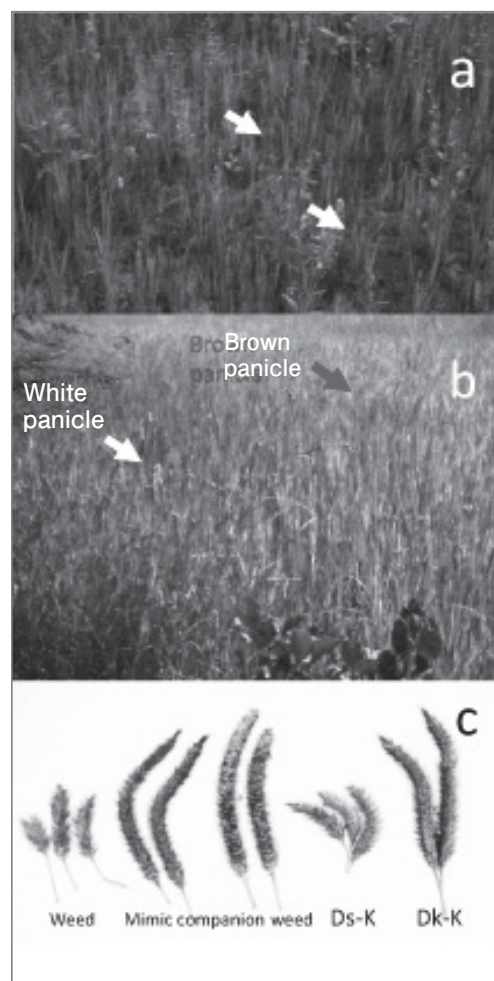


Fig. 1. Fields of *Setaria pumila* mixed with *Pas. scrobiculatum* (a) and with *P. sumatrense* (b) in South India, and spikes of *S. pumila* (c): weed; mimic companion weeds; Ds-K, domesticated type mixed with *P. sumatrense*, and Dk-K mixed with *Pas. scrobiculatum* in Karnataka.

sowing, germinated plants were transplanted into the greenhouse, with 30-cm row spacing and 15 cm between plants. Chemical fertilizer (N:P:K = 8:8:5) was supplied at 100 g·m<sup>-2</sup>. The following parameters of five types of *S. pumila* were measured at the each full-ripe stage: number of tillers, plant height, length and width of spike, length and width of flag leaf, last internode diameter, and duration to flowering. These types were three weed types; W, Wx, Mx associated with other grain crops, and two domesticated types; Dx mixed with *Paspalum scrobiculatum* and *Panicum sumatrense*. The lowercase character “x” indicates a main crop mimic of *S. pumila* as follows: “p” (paddy, *O. sativa* L.), “k” (*kodora*, *P. scrobiculatum*), “s” (*samai*, *P. sumatrense*),



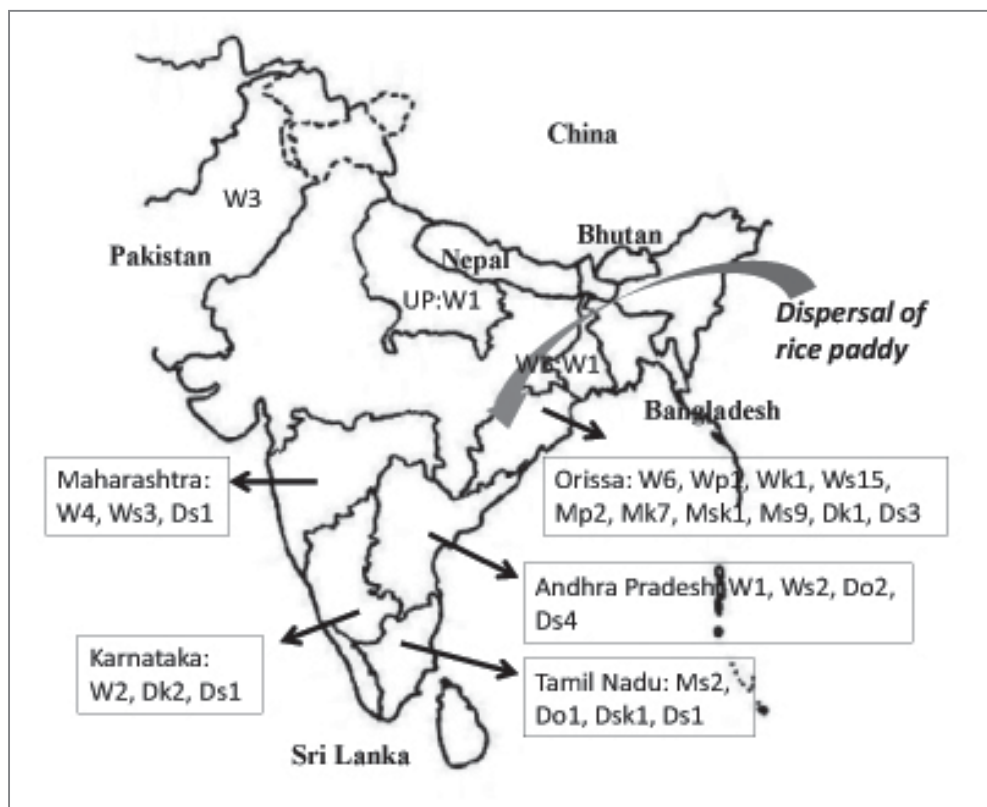


Fig. 2. Sites from which *S. pumila* and the related species were collected in the Indian subcontinent.

and “o” (others, e.g., *Eleusine coracana*). These data were analyzed statistically using partial correlation coefficients and hierarchical cluster analysis (Ward method) by SPSS version 21 (IBM Corp).

Ten grains of 78 strains were sown by the same method above-mentioned on Oct. 4, 2007. DNA extraction was performed on young leaf tissue ground in liquid nitrogen and incubated in 1.5-ml tubes containing 0.5 ml of buffer A for 10 min at 60 °C using CTAB (hexadecyl-trimethyl-ammonium bromide) methods (Murray and Thompson 1980). Buffer A contained 2% CTAB, 1% PVP (polyvinylpyrrolidone), 1.4 M NaCl, 0.25 M sucrose, 0.2% 2-mercaptoethanol, 20 mM EDTA, and 100 mM TRIS-HCl (pH 8.0); ultra pure water was added to bring the solution to 100 ml. We then added 0.5 ml of buffer B into the tube, suspended the mixture and then centrifuged it for 10 min at 10,000 g. Buffer B contained 2% CTAB, 1% PVP, 1.4 M NaCl, 1.1 M sucrose, 0.2% 2-mercaptoethanol, 20 mM EDTA, and 100 mM TRIS-HCl; water was added to bring the solution to 100 ml.

The supernatant (approximately 700  $\mu$ l) was transferred to a new tube containing 700  $\mu$ l of chloroform/isoamyl alcohol (24/1), and the tubes were shaken gently for 5 min and then centrifuged for 10 min at 10,000 g. The supernatant (approximately 650  $\mu$ l) was transferred to a new tube containing 700  $\mu$ l of chloroform/isoamyl alcohol, and the tubes were shaken for 5 min and then centrifuged for 10 min at 10,000 g. The supernatant (approximately 600  $\mu$ l) was transferred to a new tube containing 700  $\mu$ l of isopropanol to precipitate DNA for 20 min. DNA pellets were collected by centrifugation at 14,000 g for 10 min, and then were washed in 70% ethanol, dried twice, and resuspended in 30  $\mu$ l TE buffer (1 $\times$ ) containing RNase at 4 °C for 3 to 4 d, followed by storage at -20 °C. TE buffer (800  $\mu$ l) was added to 16  $\mu$ l of RNase (10 mg/ml).

#### AFLP procedure

The AFLP procedure was performed according to Applied Biosystems (2005), Bai et al. (1999), and Suyama (2001) with some modifications. Briefly, 1  $\mu$ l of

Table 1. Materials used of *Setaria pumila*

Sample no. & Status	Main crop and remarks	Collection no.	Locality
1D s-A	<i>Panicum sumatrense</i> mixed with <i>Eleusine coracana</i>	85-10-31-3-12	Duggam vapalli Andhra Pradesh
2W s-M	<i>P. sumatrense</i>	k87-9-28-9-4	Kum bharoshi (800m), Maharashtra
3W s-M	<i>P. sumatrense</i>	k87-9-28-9-6	
4D s-M	<i>P. sumatrense</i>	k87-10-1-7-8	16km from Lanja (200m), Maharashtra
5W -M	none	k87-10-3-3-1	Gabi (650m), Maharashtra
6W s-M	<i>P. sumatrense</i>	k87-10-3-5-7	Nadagao village (541m), Maharashtra
7W -M	<i>Oryza sativa</i>	k87-10-4-6-7	8km W from Kohapur (600m), Maharashtra
8W -M	<i>Setaria italica</i>	k87-10-5-10-5	Udtare village (652m), Maharashtra
9W -M	<i>S. italica</i>	k87-10-5-10-6	Udtare village (653m), Maharashtra
10M s-O	<i>P. sumatrense</i>	k87-10-9-1-1	Sunabeda (895m), Orissa
11M s-O	<i>P. sumatrense</i>	k87-10-9-1-6	
12M s-O	<i>P. sumatrense</i>	k87-10-9-1-7	
13M s-O	<i>P. sumatrense</i>	k87-10-9-1-8	
14W sk-O	<i>P. sumatrense</i> mixed with <i>Paspalum scrobiculatum</i>	k87-10-9-2-2	Kundali village (875m), Orissa
15W s-O	<i>P. sumatrense</i>	k87-10-9-5-6	Potang (895m), Orissa
16W -O	none	k87-10-10-2-1	7km from Sunabeda (900m), Orissa
17W s-O	<i>P. sumatrense</i>	k87-10-10-5-5b	2km of Bopargurha (608m), Orissa
18W s-O	<i>P. sumatrense</i>	k87-10-10-5-6b	
19W s-O	<i>P. sumatrense</i>	k87-10-10-5-10d	
20W s-O	<i>P. sumatrense</i>	k87-10-10-5-13A	
21W s-O	<i>P. sumatrense</i>	k87-10-10-5-13B	
22D s-O	<i>P. sumatrense</i>	k87-10-10-5-14e	
23D s-O	<i>P. sumatrense</i>	K87-10-10-5-16A	
24D s-O	<i>P. sumatrense</i>	k87-10-10-5-16B	
25W s-O	<i>P. sumatrense</i>	k87-10-10-6-8	Beragaon, 12km of Koraput (605m), Orissa
26M k-O	<i>Pas. scrobiculatum</i>	k87-10-11-2-2	Anchaluda village, 20km of Koraput (870m), Orissa
27D k-O	<i>Pas. scrobiculatum</i>	k87-10-11-2-3	
28M k-O	<i>Pas. scrobiculatum</i>	k87-10-11-2-5	
29W s-O	<i>P. sumatrense</i>	k87-10-11-6-7	Damaniganda village (728m), Orissa
30M s-O	<i>P. sumatrense</i>	k87-10-11-6-8	
31W -O	none	k87-10-12-2-3	Sagada village (240m), Orissa
32W -O	none	k87-10-12-2-7	
33W s-O	<i>P. sumatrense</i>	k87-10-12-5-4	47km NW of Bhawanapatna (690m), Orissa
34W s-O	<i>P. sumatrense</i>	k87-10-12-5-5	
35M s-O	<i>P. sumatrense</i>	k87-10-12-5-7	
36W s-O	<i>P. sumatrense</i>	k87-10-12-5-8	
37W p-O	<i>Oryza sativa</i> mixed with <i>Pas. scrobiculatum</i>	k87-10-12-6-2	Balsora village (690m), Orissa
38M p-O	<i>O. sativa</i> mixed with <i>Pas. scrobiculatum</i>	k87-10-12-6-3	
39M p-O	<i>O. sativa</i> mixed with <i>Pas. scrobiculatum</i>	k87-10-12-6-4	
40W s-O	<i>P. sumatrense</i>	k87-10-12-7-4	Duliguda village, 11km of Gopapur (222m), Orissa
41W s-O	<i>P. sumatrense</i>	k87-10-12-7-5	
42W s-O	<i>P. sumatrense</i>	k87-10-12-8-4	Dakuta (937m), Orissa
43W k-O	<i>Pas. scrobiculatum</i>	k87-10-13-4-14	Pudalavillage (269m), Orissa
44M k-O	<i>Pas. scrobiculatum</i>	k87-10-13-5-6	12km of Kharhar (272m), Orissa
45M k-O	<i>Pas. scrobiculatum</i>	k87-10-13-5-11	
46W -O	none	k87-10-14-2-1	Mandapadar village (139m), Orissa
47W -O	none	k87-10-14-2-3	
48W -O	none	k87-10-14-2-4	
49M k-O	<i>Pas. scrobiculatum</i>	k87-10-14-4-3	Budhitadar village (146m), Orissa
50M k-O	<i>Pas. scrobiculatum</i>	k87-10-15-1-6	Ram sarda Talimal (149m), Orissa
51M s-O	<i>P. sumatrense</i>	k87-10-16-2-3	Korapaju village (766m), Orissa
52M s-O	<i>P. sumatrense</i>	k87-10-16-2-4	
53M k-O	<i>Pas. scrobiculatum</i>	k87-10-16-3-4	Bekarkhol village, 30km of Phulabani (522m), Orissa
54M s-O	<i>P. sumatrense</i> mixed with <i>E. coracana</i>	k87-10-16-5-4	4km from Takaball (569m), Orissa
55W -W	none	k87-11-7-0-26	Kalimpong, West Bengal
56D k-K	Domesticated type, a few mixed in <i>Pas. scrobiculatum</i>	96-11-5-1a-2	Kalidevapura, Karnataka
57D s-K	A few mixed with <i>P. sumatrense</i>	96-11-5-2b-6	Madhagiri, Karnataka
58D k-K	A little shattering, only one plant mixed with <i>Pas.</i>	96-11-5-7-2	
59D s-A	<i>P. sumatrense</i>	97-4-12-2-2	Jalarpalli Andhra Pradesh
60D s-A	<i>P. sumatrense</i>	97-4-12-2-3	
61W -U	weed mixed with <i>Echinochloa frumentacea</i>	96-11-17-0-1	Ranichauri Uttar Pradesh
63W s-A	<i>P. sumatrense</i>	01-10-8-1-5	Mubagal Andhra Pradesh
64W s-A	<i>P. sumatrense</i>	01-10-8-2-5	Palmner, Andhra Pradesh
66D s-A	<i>P. sumatrense</i>	01-10-9-2-4	Dombarpally, Andhra Pradesh
69W s-O	<i>P. sumatrense</i>	01-10-19-2a-3	Polehorebdrle, Orissa
70D s-T	<i>P. sumatrense</i>	85-10-28-1-1	Morumu, Tamil Nadu
71D o-A	mixed stand	85-11-10-1-11	Gandrapalli Andhra Pradesh
72D o-A	mixed stand	85-11-10-1-16	
73W -A	mixed stand	85-11-10-1-18	
75W -P	<i>Vigna mungo</i>	85-9-15-5-2	39km from Abbottabad to Hazara, Pakistan
76W -P	mixed stand	89-9-29-3-3-5	47km from Muzafabad, Pakistan
762W -P	mixed stand	89-9-29-3-3-6	
77D sk-T	<i>P. sumatrense</i> and <i>Pas. scrobiculatum</i>	89-10-25-3-7	Bawalavillage, Madia, Tamil Nadu
81W -K	<i>S. pumila</i> ssp. <i>pallide-fusca</i> , mixed stand	85-10-16-3-2	Namahalil, Karnataka
82W -K	<i>S. pumila</i> ssp. <i>pallide-fusca</i> , mixed stand	85-10-17-3-3	Honnava, Karnataka
84D o-T	mixed stand	85-10-27-3-6	Vellakadai (Goundar tribe), Tamil Nadu
85M s-T	<i>P. sumatrense</i>	85-10-23-2-15	Kollimalai (Kotha tribe), Tamil Nadu
86M s-T	<i>P. sumatrense</i>	85-10-23-2-7	

Sample number and status: W, weed type; M, medium type; D, domesticated type. Main crop: s, *setaria* (*Panicum sumatrense*); k, *kodo* (*Paspalum scrobiculatum*); p, paddy (*Oryza sativa*); o, other species. Locality: A, Andhra Pradesh; K, Karnataka; M, Maharashtra; O, Orissa; P, Pakistan; T, Tamil Nadu; U, Uttar Pradesh; W, West Bengal

Table 2. Partial correlation coefficients of morphological characters in *Setaria dumila*

characteristics	tillers	plant height	spike length	spike width	sl/sw	flag leaf length	flag leaf width	fl/flw	first node diameter	duration to flowering
tillers	1	-0.142	-0.055	-0.410*	0.221	0.166	-0.289	0.301	-0.239	-0.095
plant height	-0.142	1	0.256	-0.001	0.086	-0.224	0.404*	-0.517**	0.388*	0.211
spike length	-0.055	0.256	1	0.151	0.739**	0.664**	0.584**	0.166	0.716**	-0.242
spike width	-0.410*	-0.001	0.151	1	-0.455*	-0.132	0.254	-0.251	0.227	-0.091
sl/sw	0.221	0.086	0.739**	-0.455*	1	0.704**	0.172	0.488*	0.292	-0.227
flag leaf length	0.166	-0.224	0.664**	-0.132	0.704**	1	0.194	0.720**	0.311	-0.544**
flag leaf width	-0.289	0.404*	0.584**	0.254	0.172	0.194	1	-0.508**	0.882**	0.122
fl/flw	0.301	-0.517**	0.166	-0.251	0.488*	0.720**	-0.508**	1	-0.35	-0.561**
first node diameter	-0.239	0.388*	0.716**	0.227	0.292	0.311	0.882**	-0.35	1	0.171
duration to flowering	-0.095	0.211	-0.242	-0.091	-0.227	-0.544**	0.122	-0.561**	0.171	1

Control variables : grain size, shattering

each genomic DNA (was digested with 0.3  $\mu$ l of *Eco*RI adapter (TAKARA), 0.3  $\mu$ l of *Mse*I adapter (New England), 2.0  $\mu$ l of 10 $\times$  reaction buffer H, and 7.4  $\mu$ l of H<sub>2</sub>O in a final volume of 20  $\mu$ l for 3 h at 37 °C. After incubation, ligation of adapters corresponding to the sticky ends of both enzymes was performed. Adapter mix (*Eco*RI, *Mse*I, 2.0  $\mu$ l), 0.5  $\mu$ l of T4 DNA ligase (TAKARA), 1.5  $\mu$ l of 10 $\times$  reaction buffer, and 3.5  $\mu$ l H<sub>2</sub>O were added to 7.5  $\mu$ l of the digested DNA. The resulting reaction mix was incubated for 5 min at 95 °C.

A preselective amplification step using non-selective primers was then performed in a total volume of 20  $\mu$ l containing 15  $\mu$ l of the AFLP Amplification Core Mix, 1  $\mu$ l of preselective primer pair (Eco A/*Mse* C), and 4  $\mu$ l of ligation mixture (diluted 5 times in 10 mM Tris buffer, pH 8.0). The core mix contains all of the components necessary to amplify modified target sequences, e.g. buffer, nucleotides, and AmpliTaq DNA polymerase. The polymerase chain reaction (PCR) program was the same as that described by AFLP Plant Mapping Protocol (Applied Biosystems 2005) using a PCR thermal cycler (TAKARA TP3000). Selective amplifications were performed in a 20- $\mu$ l final volume containing 3  $\mu$ l of pre-amplification products (diluted in 10 mM Tris buffer) with primers having three additional 3' nucleotides. Amplification reactions were performed according to the same protocol. Five primers associated with *Eco*RI (E+AAC; E+AAG; E+AGG; E+ACT; E+ACA) were used in combination with 5 primers

associated with *Mse*I (M+CAG; M+CTG; M+CTA; M+CAT; M+CAA). Five microliters of amplification products were loaded onto a 5.75% denaturing polyacrylamide gel (LONZA) and electrophoresed in 1 $\times$  TBE for 1 h. Bands were detected using the silver staining protocol described by Cho et al. (1996).

#### Data analysis

The bands were detected on the gel at the finest level of sensitivity by Lane Analyzer (ATTO), the raw data were adjusted, and then the visible and reproducible bands were scored for accessions as present (1) or absence (0). The dendrogram of the AFLP markers was constructed using the neighbor-joining method and bootstrap analysis (PAUP\* version 4.0) on all data matrices (Nei and Kumar 2000).

#### Results

##### Morphological characteristics

Results of statistical analyses of partial correlation coefficients of the ten characteristics (number of tillers, plant height, length (pl) and width (pw) of spike, the ratio of pl/pw, length (fl) and width (flw) of flag leaf, the ratio of fl/flw, last internode diameter, and duration to flowering, are shown in Table 2. Those characteristics have been strongly affected by artificial selection during the domestication process. The controlled variables were seed size and seed shattering in this analyses. Statistical significance at the 1% level was found for the following

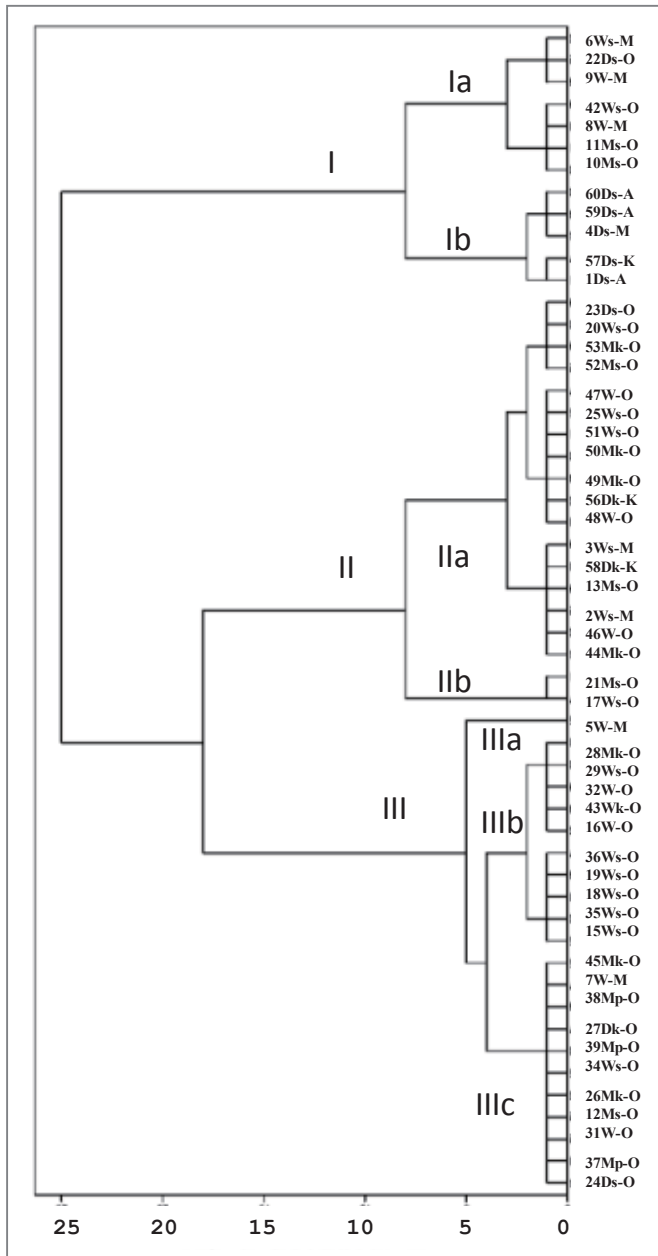


Fig. 3. Dendrogram of cluster analysis based on morphological characteristics.

results: ratio of length/width of flag leaf to plant height (-0.517); ratio of spike length/width (0.739), length of flag leaf (0.664), width of flag leaf (0.584), and diameter of last internode (0.716) to spike length; spike length (0.739) and length of flag leaf (0.704) to the ratio of spike length/width; spike length (0.664), the ratio of spike length/width (0.704), the ratio of length/width of the flag leaf (0.720), and the duration to flowering (-0.544) to length of flag leaf; spike length (0.584), the ratio of length/width of the flag leaf (-0.508), and the

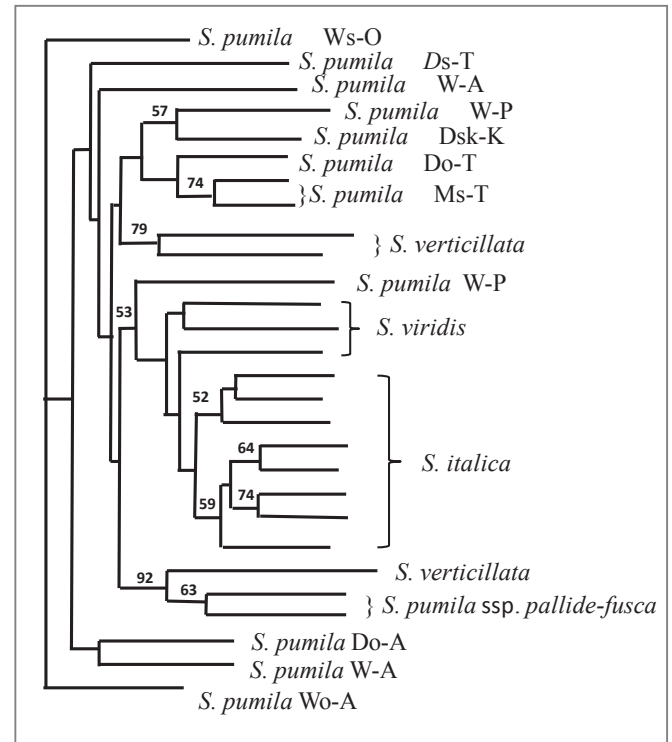


Fig. 4. Dendrogram of neighbor-joining method based on AFLP markers of genus *Setaria*

last internode diameter (0.882) to width of flag leaf; plant height (-0.517), length of flag leaf (0.720), width of flag leaf (-0.508), and the duration to flowering (-0.561) to the ratio of length/width of the flag leaf; spike length (0.716) and width of flag leaf (0.882) to the last internode diameter; and length of flag leaf (-0.544) and the ratio of length/width of the flag leaf (-0.561) to the duration to flowering. There were no significant ( $p < 0.01$ ) correlations between the number of tillers and the last internode diameter.

Cluster analysis of six morphological characteristics (number of tillers, plant height, spike length, length and width of flag leaf, and flag leaf length/width ratio) and the duration to flowering are illustrated in Fig. 3. Using the Ward method, 60 accessions were categorized into three clusters and several sub-clusters. Cluster I contained sub-clusters Ia and Ib. Subcluster Ia (7 accessions) included weed type (W2); companion weed type (Ws1) from Maharashtra; companion weed type (Ws1); mimic companion weed type (medium, Ms2); and domestication type mixed with *samai* (*P. sumatrense*, Ds1) from Orissa. Sub-cluster Ib



Table 3. AFLP analysis of 72 accessions of *Setaria pumila* using 4 combinations of primer pairs

EcoRI/MseI	Total no. of bands	No. of polymorphic	Percent polymorphism
AAC/CAG	59	52	88.1
ACT/CAT	60	49	81.7
AGG/CTA	68	64	94.1
AAG/CTG	76	71	93.4
Total	263	236	89.7

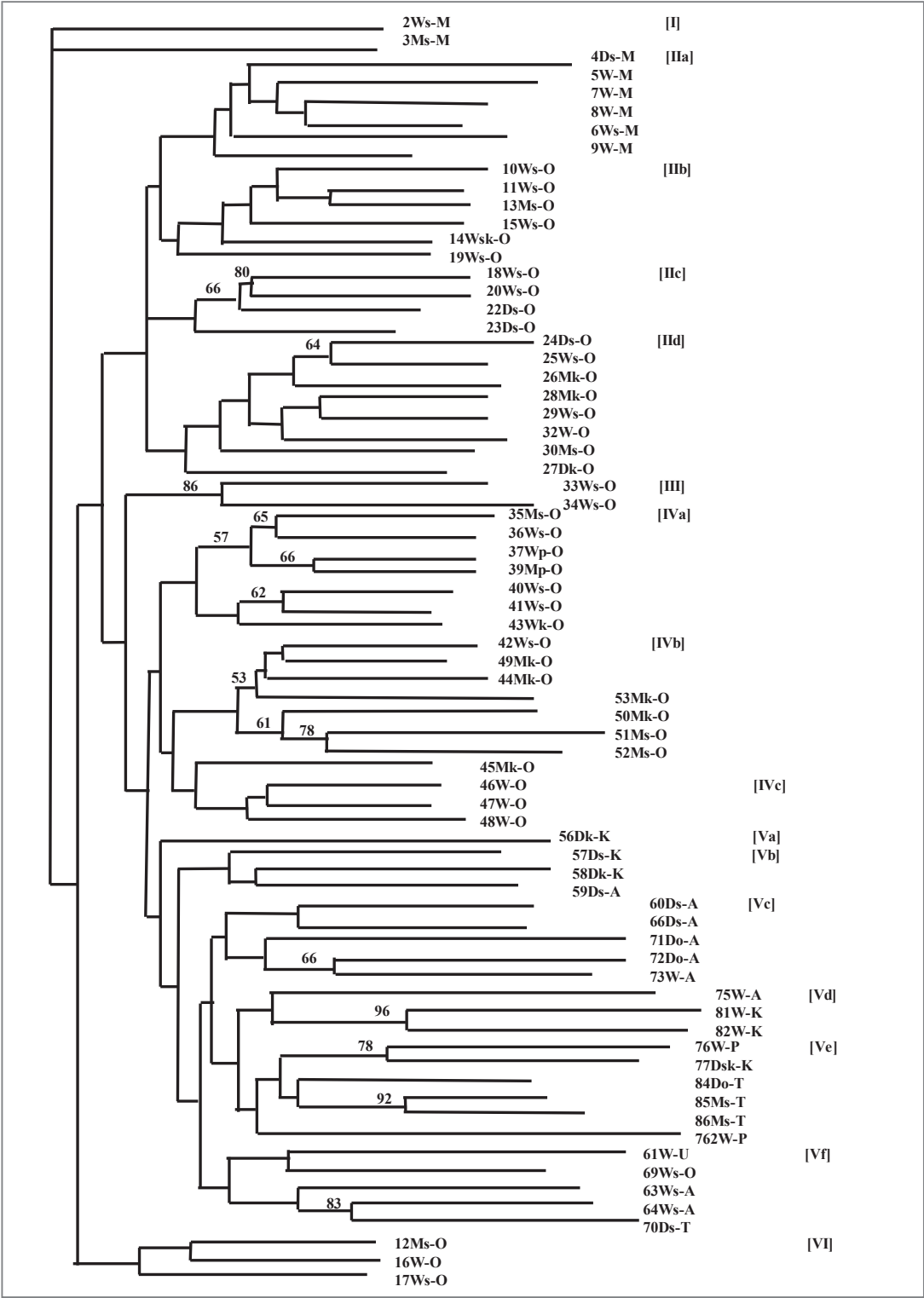


Fig. 5. Dendrogram of neighbor-joining method based on AFLP markers of *S. pumila*.

(5 accessions) included Ds5 from Andhra Pradesh (3), Karnataka (1), and Maharashtra (1). Cluster II contained sub-clusters IIa and IIb. Sub-cluster IIa (17 accessions) included: Ds1, Ms2, Mk4, Ws3, and W3 from Orissa; Dk2 from Karnataka; and Ws2 from Maharashtra. Sub-cluster IIb (2 accessions) included Ms1 and Ws1 from Orissa. Cluster III contained sub-clusters IIIa–c. Sub-cluster IIIa (1 accession) comprised W1 from Maharashtra. Sub-cluster IIIb (10 accessions) included Mk1, Ws6, Wk1, and W2 from Orissa. Sub-cluster IIIc (11 accessions) included Ds1, Dk1, Ms1, Mk2, Mp3, Ws1, and W1 from Orissa, and W1 from Maharashtra. The "W" type of *S. pumila* was distributed around the Indian subcontinent as a cosmopolitan weed.

#### Variation of AFLP markers

The results of AFLP on 72 accessions from the Indian subcontinent are shown in Table 3. Most bands showed polymorphic more than 81.7% to 94.1% polymorphisms, excluding the main bands were detected more than 70% of all accessions. Each combination of *Eco*RI and *Mse*I detected from 59 to 76 fragments based on the four primer pairs selected, and were used for analysis as follows: E+AAG/M+CTG, E+AGG/M+CTA, E+ACT/M+CAT, and E+AAC/M+CAG. Those primer combinations revealed 263 visible polymorphic bands. The dendrogram accounted for accessions of related species on one hand (Fig. 4) and the accessions of *S. pumila* on the other (Fig. 5).

The diversity of AFLP markers was compared among relative species (28 accessions) of *S. pumila* (14 including *ssp. pallide-fusca* 2), domesticated *S. italica* (8 from Japan), the ancestral weed *S. viridis* (3 from Central Asia), and the weed *S. verticillata* (3 from India). The dendrogram constructed with the neighboring-joint method is illustrated in Fig. 4. The clusters of *S. pumila* were composed, successively, of Ws1 from Orissa; Wo1, Do1, and W1 from Andhra Pradesh; Ds1 from Tamil Nadu; and W1 from Andhra Pradesh. The other clusters included W1 from Pakistan, Dsk1 from Karnataka, and Do1 and Ms2 from Tamil Nadu. *S. pumila* ssp.

*pallide-fusca* (2) from Karnataka and *S. verticillata* (1) from Andhra Pradesh formed a cluster. W1 of *S. pumila* from Pakistan was located as the neighbor of *S. viridis*. *S. verticillata* (2) was located in the cluster of *S. pumila*, but *S. viridis* (3) and *S. italica* (8) were located in the same cluster. The location of species within clusters was not significant at  $p \leq 0.05$  based on the bootstrap test, but the species were clearly categorized.

*S. pumila* (72 accessions) were divided into six clusters including 16 sub-clusters based on AFLP marker data as shown in Fig. 5. Cluster I contained Ws1 and Ms1 from Maharashtra; Cluster III consisted of Ws2; and Cluster VI contained W1, Ws1, and Ms1 from Orissa. These clusters did not contain a domesticated type.

Cluster II (4 sub-clusters, 23 accessions) consisted of sub-cluster IIa (6), W4, Ws1, and Ds1 from Maharashtra; sub-cluster IIb (6), Ws (4), Ms1, and Wsk1 from Orissa; sub-cluster IIc (4), Ws2 and Ds2 from Orissa; and sub-cluster IId (8), W1, Ws2, Ms1, Ds1, Mk2, and Dk1 from Orissa. Cluster IV (three sub-clusters, 18 accessions from Orissa) consisted of sub-cluster IVa (7), Wp1, Mp1, Wk1, Ws3, and Ms1; sub-cluster IVb (7), Ws1, Ms2, and Mk4; sub-cluster IVc (4), W3, and Mk1. Cluster V (6 sub-clusters, 23 accessions) consisted of sub-cluster Va (1), Dk1 from Karnataka; Vb (3), Ds1, Dk1 from Karnataka, and Ds1 from Andhra Pradesh; Vc (5), W1, Do2 and Ds2 from Andhra Pradesh; Vd (3), W1 from Andhra Pradesh and W2 from Karnataka; Ve (6), W2 from Pakistan, Ms2, Dsk1, and Do1 from Tamil Nadu; Vf (5), W1 from Uttar Pradesh, Ws1 from Orissa, Ws2 from Andhra Pradesh, and Ds1 from Tamil Nadu.

#### Discussion

The domestication process for each species was a complex combination of natural and artificial selection, mimicry, hybridization, and polyploidy. Pioneer farmers required plants some to have some degree of tolerance to conditions (e.g., cold, hot, drought, harsh sunlight). Farmers continue to gather wild cereals in dry areas of Africa and the Indian subcontinent. For example,

*Secale cereale* L. has acquired strong resistance to cold in high altitude or latitude areas, and farmers have been able to grow *S. cereale* mixed with wheat as a secondary crop as a companion weed under severe conditions (Vavilov 1926). Kobayashi (1987, 1989) proposed an integrated model of the domestication process of several millet species as secondary crops derived from weeds by mimicking companion weeds associated with *Oryza sativa* in the Indian subcontinent.

Increasing the size and shattering resistance in seeds are important factors in the domestication process. The partial correlation coefficients that describe control of seed size and shattering (Table 2) explain that the cylindrical spike has become longer, the last internode diameter of the main culm has thickened, and the flag leaf has widened for effective photosynthesis as a result of artificial selection by farmers.

The low coefficient between the number of tillers and the other characteristics reveals that the number of tillers in Dk has decreased during domestication by processes such as mimicry of *Pas. scrobiculatum*, while the number of tillers of Ds has increased as the mimicry of *P. sumatrense*. Separate selection processes functioned to both decrease and increase the number of tillers (Kimata 2015a). The low coefficients for length of flag leaf and ratio of length/width of the flag leaf to duration of flowering indicate that artificial selection has operated on the flag leaf, causing it to become narrower and to mature early under domestication.

The negative correlation between ratio of length/width of the flag leaf to plant height demonstrated that the flag leaf has become longer and narrower, while plant height has increased, as in Ds. The Ds of *S. pumila* matures early and has a relatively long and narrow flag leaf due to artificial selection, reflected in the significant negative correlations between length of flag leaf and the ratio of length/width of the flag leaf in relation to duration to flowering. In addition, Ds has acquired a relatively long and narrow flag leaf as a result of taller plant height, as seen in the significant negative correlation between plant height and length/width of flag leaf.

During the evolutionary process from companion weed to secondary crop, which involved morphological mimicry of other species (Mo), *S. pumila* (Ds) became a slender-type mimic with long-narrow leaves as in *P. sumatrense*, while *S. pumila* (Do) became a thick-type mimic with wide leaves as in *Pas. scrobiculatum* and other species. Based on the PANTONE Formula Guide (Pantone Inc.), it was clear that the leaf, leaf sheath, culm, and glume of *S. pumila* exhibited mimetic coloration among species and demonstrated mimicry of coloration of *P. sumatrense* and *Pas. scrobiculatum*, according to anthocyanin composition revealed by HPLC analysis (Kimata 2015a).

From the cluster analysis, *S. pumila* cluster I clearly showed that the domestication process of *S. pumila* has occurred continuously in fields of *P. sumatrense* and other grain crops around the Deccan. Cluster II consisted of sub-cluster IIa; Ds1, Ms2, Mk4, Ws3 and W3 from Orissa, Dk2 from Karnataka, Ws2 from Maharashtra, and sub-cluster IIb; Ms1 and Ws1 from Orissa. Cluster II gives an example of the domestication process by mimicry, which *S. pumila* has become Dsk mixed with *P. sumatrense* and *Pas. scrobiculatum* in each fields. Cluster III revealed that the W type of *S. pumila* was distributed around the Indian subcontinent as a cosmopolitan weed.

The domestication process of *S. pumila*, Dsk, has taken a route from weed type to companion weed and then to mimic companion weed with *O. sativa*, *P. sumatrense*, and *Pas. scrobiculatum* in Orissa. Therefore, the domestication process of *S. pumila* has moved forward as follows. First, the mimic companion weeds (Mks, mainly in Orissa) and second, the domesticated type (Do) evolved and moved south to the Deccan Plateau via Andhra Pradesh. After that, the domesticated type progressed from Dk to Ds in Karnataka and Tamil Nadu.

The natural intraspecific hybrids of *S. pumila* occurred continually in sympatric fields among weeds, companion weeds, mimic companion weeds, and domesticated types, as revealed by a geographic bias in both morphological characteristics and AFLP markers

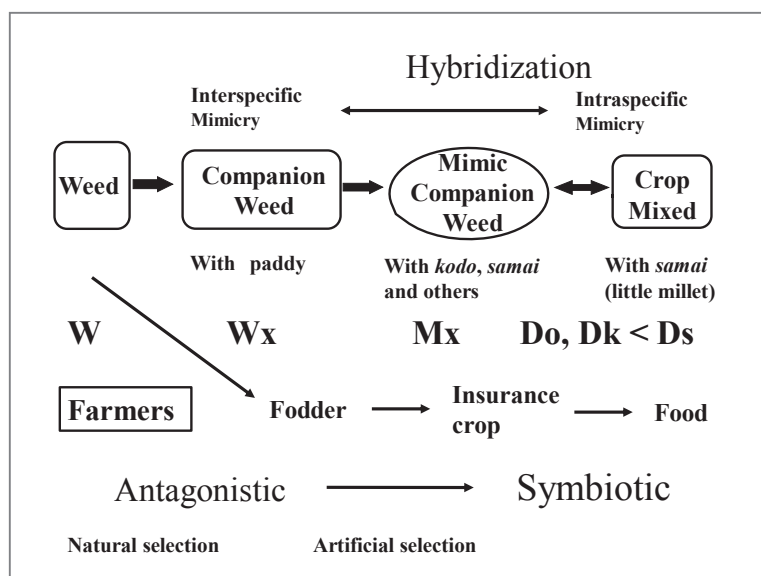


Fig. 6. Domestication process of *S. pumila* in relation to the weed-crop complex.

(Figs. 3 and 5). There were two cases of mimicry, interspecific and intraspecific, in this domestication process. Interspecific mimicry was found in the mimic companion weed with *O. sativa*, *Pas. scrobiculatum*, and *P. sumatrense* and other species. The intraspecific mimicry occurred by continuous natural hybridization between weed and domesticated type and also though natural or artificial selection by farmers. The mimic companion weed type was quite similar to the domesticated type, but farmers were able to differentiate between the two by seed shattering.

The diversity of AFLP markers was compared among relative species of *S. pumila*, domesticated *S. italica*, the ancestral weed *S. viridis*, and another weed, *S. verticillata* (see dendrogram in Fig. 4). Recently, Wang et al. (2009) and Zhao et al. (2013) indicated that the genome constitution of *S. verticillata* had diploid (BB) and tetraploid (AABB) forms based on GISH, while *S. glauca* (syn. *S. pumila*) was identified genome 'D,' but its genomic constitution was not known. Based on the dendrograms by Bayesian analyses for 5s rDNA and kn1 sequences, the A genome included *S. italica*, *S. viridis*, and *S. verticillata*; the B genome comprised *S. verticillata*, and the D genome consisted of *S. glauca* (syn. *S. pumila*). *S. pumila* (W-P) from Pakistan was located the neighbor of *S. viridis* in Fig. 4. *S. pumila* ssp. *pallide-*

*fusca* from Karnataka and *S. verticillata* from Andhra Pradesh made a cluster. The irregular positions in which *S. pumila* was located related to its multiple ploidy levels and obscure genomic constitution.

The AFLP methodology gave highly reproducible bands, and polymorphisms among individuals within accessions were very low (d'Ennequin et al. 2000). Small millet species including *S. pumila* have shown remarkable genetical variation (Lakshmi et al. 2002) because of its polyploidy and natural hybridization. The AFLP variation in *S. pumila* was generally high because of the grouping of many sub-clusters, but the bootstrap values were low in each sub-cluster. Intraspecific morphological differentiation was easily detected, but the variation in AFLP was reduced by natural hybridization. Therefore, based on the AFLP dendrogram, which was not directly influenced by the artificial selection by farmers, it was obvious that there was a regional bias; many accessions of mimic companion weed type were located in sub-cluster IVb, and the most accessions of the domesticated type were in Cluster V with little significance in bootstrap value. Moreover, Cluster IV, from Orissa only, did not include the domesticated type but contained the most accessions of mimic companion weed type. Cluster II from Maharashtra and Orissa indicated that the companion/



mimic companion weeds coexist with the domesticated type mixed with other crops.

The domestication process of *S. pumila* may have passed through four steps as illustrated in Fig. 6. The first step consisted of a weed that had grown along roadsides and other unstable habitats moving to invade upland rice fields. The second step was an evolutionary process of obtaining an agro-ecological niche as use for fodder, to attain companion weed status in upland rice and millet fields. The third step was a process of advancing from mimic companion weed status to a semi-domesticated insurance crop in case of famine, under mixed cropping with *P. scrobiculatum*, *E. coracana*, and *P. sumatrense*. After their invasion into upland rice and millet fields and under the severe weed control measures practiced by farmers, weeds evolved to mimic particular crops and to create a close weed-crop complex. In the third step, farmers reduced the aggressiveness of their weed-control practices. In the fourth step, mimic companion weeds were used as both a fodder source for cattle and as a supplementary grain to the main cereal species. In the case of *S. pumila*, overly strict weeding was avoided as a means of crop insurance in years of extreme drought in the Deccan. This may have led to *S. pumila* growing taller with larger spikes and seeds accompanied by less shattering, and gradually progressing towards domestication. *S. pumila* has obtained mimetic traits such as a long leaves, a few tillers, and tall height, in fields of *P. sumatrense* (Fig. 2 and Table 2). The pigmentation of leaves and leaf sheaths by anthocyanin creates the mimicry among grain crops and closely related weeds in mixed crop stands (Kimata 2015a, Kimata et al. 2000).

*S. pumila* concurrently diversified its traits entirely through hybridization among the four types under natural and artificial selection in severely arid environments. Mimic companion weeds were harvested together with other (crop) millet, and were sown again involuntarily the following season. Recently, at the fourth step, this situation was followed by mixed cropping. *S. pumila* is termed a “tertiary crop” in relation to its associated plants, secondary crops such

as *P. sumatrense* and *Pas. scrobiculatum*, with respect to rice. The domestication process of *S. pumila*, a tertiary crop mixed with other grain crops, proceeds from inter- and intraspecific mimicry by natural and artificial selection in sympatric fields. This process has occurred by adaptation to aridity as a result of the spread of *S. pumila* from the east to the south in the Indian subcontinent.

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# Domestication and dispersal of *Panicum miliaceum* L. (Poaceae) in Eurasia

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*Plants and People Museum*

Common millet (*Panicum miliaceum* L.) was the most important grain crop in Eurasian civilization for several thousand years starting from the Neolithic era. It is still cultivated and has various uses around the world. Although it is one of the oldest domesticated plants in Eurasia, the ancestral plant and place of origin have yet to be definitively determined. A series of studies was started based on the plant's morphological and ecological characteristics, followed by studies of its genetic characteristics and secondary compounds, to elucidate its domestication process and dispersal in Eurasia. Accessions (650 local varieties obtained from local farmers) and herbarium specimens collected by field surveys were used for observations and experiments on morphological and ecological characteristics, crossability, amplified fragment length polymorphism of total DNA, phenol and iodine color reactions of seeds, fatty acid component in seeds, traditional food styles, and archeolinguistic data. The botanical origin, domestication process, and geographical dispersal of common millet are discussed and then integrated through the characteristics mentioned above. In conclusion, common millet was domesticated from a wild population of *P. miliaceum* subsp. *ruderales* in Central Asia, specifically from the Aral Sea to the Southwest Tien Shan Mountains. Since the Neolithic era, the millet has been dispersed eastward to China, westward to Europe, southward to the Indian subcontinent, and northward to Siberia by nomadic groups.

Key words: common millet, dispersal, domestication, Eurasia, local varieties, original place

## Introduction

The genus *Panicum* (Poaceae) consists of about 500 species. These species have been used for wild grains, fodder, and medicine up to the present day, while three cereals, *P. miliaceum* L. (common millet), *P. sumatrense* Roth. (*samai*, little millet), and *P. sonorum* Beal. (*sau*, panic grass), were domesticated in different places and times. These are C<sub>4</sub> plants endowed with strong drought resistance, early maturation, and high nutrient content. *P. sumatrense* was domesticated from an ancestral species, *P. sumatrense* subsp. *psilopodium*, after around 2200 BC on the Indian subcontinent (Weber 1992), while *P. sonorum* was domesticated from *P. hirticaule* around 600 BC in northwestern Mexico (Nabhan and de Wet 1984). On the other hand, common millet was the most important grain crop that supported civilization around Eurasia over several thousand years starting in the Neolithic era. It is still cultivated and has various uses around the world. Although it is one of the oldest domesticated plants in Eurasia, the ancestral plant and place of origin have yet to be definitively determined. The place of origin of common millet has been discussed for many years (e.g., Bellwood 2005, Church 1886, de Candolle 1886, Gerard 1597, Harlan 1995, Jones 2004, Kimata 2009, Sakamoto 1987, Vavilov 1926). Vavilov (1926) proposed that the original place was North China, and Chun et al. (2004) suggested that common millet was domesticated in the southern part of the middle reaches of the Yellow River 8000–7000 years BP.

Harlan (1975) suggested that the two homelands were North China and eastern Europe. Nesbitt (2005) also suggested that it might have been domesticated

independently in each area. Although both the wild ancestor and the place of domestication of common millet are unknown, it first appeared as a crop in both Transcaucasia and China about 6000 BC. Zohary and Hopf (2000) suggested that common millet may have originated somewhere between the Caspian Sea and Xinjiang. The earliest sites bearing remains of common millet are in China and Europe from the seventh millennium BC, on opposite sides of the Eurasian continent (Jonse 2004). Furthermore, Sakamoto (1987) indicated that the area was located within Central Asia and the northwestern parts of the Indian subcontinent. Common millet was found from the sixth millennium BC at Tepe Gaz Tavilla in southeastern Iran (Meadow 1986). One explanation for its domestication could be an altered climate earlier in the Holocene. Meadow (1986) suggested that it might have been grown using floodwater runoff to supplement rainfall in this dry area as a spring or autumn crop. Similarly, farmers grow common millet in the Ganga area after winter floods. Detailed local analyses of this kind should underpin future considerations of common millet's origin in Central Asia to determine its possible routes of spread through this critical but underexplored area (Hunt and Jones 2006). However, the ancestor and original place of common millet have yet to be clearly determined.

Bellwood (2005) summarized recent thinking on the origin and spread of common millet based on recent archaeological contributions as follows. Common millet perhaps originated in Central Asia (Sakamoto 1987, Zohary and Hopf 2000). Neolithic settlers may have migrated from there to Afghanistan, the Russian steppes, or even western China. Common millet has been reported widely in the Neolithic cultures of Europe and the Eurasian steppes, but it would appear that the oldest known dates of cultivation are from North China from about 6500 BC onward. The first known occurrence in southeastern Iran was in the sixth millennium BC (Meadow 1986), c. 1550 BC in northwestern Iran (Nesbitt and Summers 1988), and about 2600 BC in South Asia (Fuller et al. 2001).

A series of studies was started on common millet's

morphological and ecological characteristics, followed by studies of the secondary compounds in the grain (Kimata and Negishi 2002, Kimata et al. 2007). The present paper is concerned with the ancestor, domestication, and geographical dispersal of common millet in Eurasia. The purpose is to examine these questions using all botanical characteristics, including biocultural diversity (traditional food styles and archeolinguistic data) and genetic characteristics (crossability, F<sub>1</sub> hybrids and AFLP markers).

### Materials and Methods

Many endemic varieties and relatives of *Panicum miliaceum* L. have been collected from all of Japan and the Eurasian continent through field surveys since 1973. Grain samples (650 accessions) were collected along the survey route and the voucher herbarium specimens were deposited at Tokyo Gakugei University (Tokyo, Japan). Information on agricultural practices, grain processing, food preparation, and vernacular names was gathered from local farmers.

Some of these accessions, 441 local varieties, were selected and grown at the greenhouse of Tokyo Gakugei University, Japan to compare their morphological and ecological characteristics starting on July 10, 1986. These local varieties included 132 from Japan, 39 from eastern Asia, 78 from the former USSR, 90 from southern Asia, 26 from western Asia, 43 from Europe, two from Africa, and one from Canada (Kimata and Negishi 2002).

Ten grains of each strain were sown in a seeding box with a row spacing of 8 cm and seed spacing of 2 cm. Two weeks after sowing, germinated plants were transplanted into the greenhouse, with 30-cm row spacing and 15 cm between plants. Chemical fertilizer (N:P:K = 8:8:5) was supplied at 100 g/m<sup>2</sup>. Five plants of each strain were measured for traits, including the duration to flowering (days), number of leaves on the main culm, number of productive tillers, hairiness of the uppermost internode, panicle type, lemma color, pistil stigma color, and others. These morphological and ecological data were analyzed statistically using partial



Table 1. Materials used of *Panicum miliaceum* and the relative species

Area collected	Sample no.	Total
Japan	p1, p2, p30, p37, p38, p39, p60	7
Korea	p3, p4, p23,	3
China	p5, p14, p15, p19, p29, p51	6
Mongolia	p18, p20,	2
Nepal	p13, p16, p52	3
Bangladesh	p50	1
Uzbekistan	p68, p69, p70	3
Afghanistan	p6, p7,	2
India	p53, p54, p55, p56, p57, p61; ( <i>P. sumatrense</i> ) pm 2, pw 1, pw 68	9
Pakistan	p58, p59, p62, p63, p64, p65, p66, p67	8
Turkey	p17, p33, p91 (weed)	3
Greece	p36,	1
Romania	p9, p10, p24, p31, p32, p34, p35	7
Czechoslovakia	p21	1
Yugoslavia	p40	1
USSR-E	p41, p43, p46, p49	4
USSR-CA	p42, p45, p48	3
Poland	p44	1
Bulgaria	p22	1
Germany	p25, p26, p27, p28,	4
Belgium	p8	1
France	p11	1
Spain	p12	1
Canada	p47	1
USA	( <i>P. sonorum</i> ) p111	1
Total		75

correlation coefficients and hierarchical cluster analysis in SPSS (ver. 21, IBM Corp).

Moreover, 70 local varieties, including six pollen testers, were selected and grown in the greenhouse from 1990 to 1995. These accessions included 21 from eastern Asia, 8 from Central Asia, 19 from southern Asia, 21 from Europe, and one weed, *P. miliaceum* subsp. *ruderales*, from Romania. The crossability among the 70 Eurasian varieties and the morphological characteristics of their F<sub>1</sub> hybrids were examined in the six pollen testers from France, Central Asia, India, China, Japan, and a weed.

Ten grains of each of 75 accessions were sown by the same method as above on Oct. 4, 2007 (Table 1). DNA extraction was performed on young leaf tissue ground in liquid nitrogen and incubated in 1.5-ml tubes containing 0.5 ml of buffer A for 10 min at 60 °C by using CTAB (hexadecyl-trimethyl-ammonium bromide) methods (Murray and Thompson 1980). The AFLP procedure was performed according to Applied Biosystems (2005), Bai et al. (1999), and Suyama (2001) with some modifications. Amplification reactions were performed according to the same protocol. Five primers



Fig. 1. Foods from common millet in Uzbekistan and Inner Mongolia. a, milk tea with roasted grains in Inner Mongolia; b, colored grains for a topping of bread in Uzbekistan; c, milk porridge for healthful lunch at a nursery school in Uzbekistan.

associated with *EcoRI* (E+AAC, E+AAG, E+AGG, E+ACT, and E+ACA) were used in combination with 5 primers associated with *MseI* (M+CAG, M+CTG, M+CTA, M+CAT, and M+CAA). Five microliters of amplification products were loaded onto a 5.75% denaturing polyacrylamide gel (LONZA) and electrophoresed in 1× TBE for 1 h. Bands were detected using the silver staining protocol described by Cho et al. (1996). The bands were detected on the gel at the finest level of sensitivity by Lane Analyzer (ATTO), the raw data were adjusted, and then the visible and reproducible bands were scored for accessions as present (1) or absent (0). The dendrogram of the AFLP markers was constructed using the neighbor-joining and UPGMA methods (Nei and Kumar 2000) with the bootstrap

Table 2. Foods made from common millet around Eurasia

Locality	glutinous/no n- glutinous	grain				coarse- ground flour	ground flour			drinks	
		boiled	steamed	porridge	<i>mochi</i>	porridge	dumpling	gruel	bread	non- alcohol	alcohol
Japan	non-glutinous	○		○			○	○			
	glutinous		○		○		○				○
Korea	non-glutinous	○									
	glutinous		○		○						○
China	non-glutinous	○		○					○		○
	glutinous		○		○				○		○
Taiwan	non-glutinous	○									
	glutinous		○		○		○				○
Bataan Isles	non-glutinous					○					
Halmahera	non-glutinous					○					
India	non-glutinous	○				○		○	○		
Pakistan	non-glutinous	○							○		
Afghanistan	non-glutinous					○	○		○		
Uzbekistan	non-glutinous					○			○		
Kazakhstan	non-glutinous					○					
Caucasia	non-glutinous					○				○	
Turkey	non-glutinous					○					
Ukraine	non-glutinous					○				○	
Bulgaria	non-glutinous					○				○	
Romania	non-glutinous					○			○		
Germany	non-glutinous					○					
Belgium	non-glutinous					○					
Italy	non-glutinous					○					

analysis (PAUP\* ver. 4.0) and the hierarchical cluster analysis (group average method, SPSS ver. 21) on all data matrices of 75 local varieties.

## Results

### Food preparation and secondary compounds in grain

The Eurasian foods made from common millet are classified into four processing methods: grain, coarse-ground flour, fine flour, and drinks. Asian people cook boiled grain and porridge from the polished grains of non-glutinous varieties (Table 2). Especially, East Asians cook steamed grain and *mochi* (a kind of cake) from the polished grains of glutinous varieties and ferment alcoholic drinks from polished grains of both non-glutinous and glutinous varieties. Inner Mongolians drink daily milk tea with roasted grains (Fig. 1a). Uzbeks top *non* (a kind of bread) with colored grains (Fig. 1b) and cook milk porridge from non-glutinous varieties for lunch at a nursery school (Fig. 1c). Europeans cook milk porridge from coarse-ground flour, bread from fine flour, and ferment non-alcoholic drinks from polished grains of only non-glutinous varieties. Based on the endosperm starch in seed grains, the varieties were divided into two glutinous or non-glutinous categories.

The distribution of glutinous varieties of common millet and *Setaria italica* were restricted to eastern Asia. On the contrary, the geographical distribution of phenol color reaction to seed coats in *S. italica* was very similar to that of *Oryza sativa*, but the distribution in common millet was different from the trends in *S. italica* and *O. sativa* (Sakamoto 1982, Kawase and Sakamoto 1982, Kimata and Negishi 2002).

The four types of local varieties of common millet were categorized by the composition of the minor fatty acids arachidic, behenic, and eicosapentaenoic acid. If the ancestral prototype was the weedy AE type containing arachidic and eicosapentaenoic acids, the AB type (arachidic and behenic acid) may have been bred both in Europe and Asia, while the ABE (all three fatty acids) and O (no fatty acids) types may have originated around Central Asia and then spread to both Europe and Asia (Kimata et al. 2007).

### Vernacular names

The linguistic data are as follows (Table 3). Prefixes for the word for “common millet” were mainly “*ki-*,” “*che-*,” “*va-*,” or “*ba-*” in East and South Asia, but several variations were noted in China. The prefixes were widely

Table 3. Vernacular names of common millet around Eurasia

Region	Country	Modern name	Ancient name
East Asia	China	chi huangm i nianm i shu, shuzi	shu
	Inner Mongolia	hore i bata	
	Korea	kian	
	Japan	nak bi k bi kok bi	kim i sh ipsh i-kepp
Central Asia	Kazakhstan	psheno	
South Asia	Afghanistan	arzan	
	Pakistan		
	North	bau, cheena, ch i na, o lea n, onu	
	South	tzetze	
	India		
	North	chara i cheena, ch i n, ch i na, saw an, w orga	unoo, vree lb-heda, vreeh b-heda
	South	baragu, cheena, , katacuny, pan i baragu, tane, variga, varagu, w ari	
	Nepal	ch i na	
	Sri Lanka	me ne'ri	
	West Asia		
	Arabia	dokhn, kosae b, kos ae b	
	Turkey	dari, kundari	
	Israel	dokhan	
Africa	Egypt	dokhn	
Europe	Greece		kegchros
	Hungary	ko" les	
	Russia	proso	
	Poland	proso	
	Croatia	proso	
	Lithuania		sora
	Netherlands	g ierst	
	Germany	rispen hirse	
	Italy	m i l ium	m i g l i o
	Spain	m i p comm un	
	France	m i l l e t comm un	
	United Kingdom	common m i l l e t	m i l l

cf. Kawase 1991, Sakamoto 1986, and many dictionaries.

diverse in Central Asia and the mountainous area of Pakistan. It was mainly “d-” in western Asia and Egypt. There were also many European prefixes, including “mi-” and “proso.” Because the vernacular names of common millet were remarkably diverse around all Eurasia, this indicates that the crop was domesticated and/or broadly dispersed starting in a very ancient period. However, common millet is called “cheena,” “chiena,” or “chin” in the Indian subcontinent. Based on the Farming/Language Dispersal Hypothesis (Bellwood and Renfrew 2002), these vernacular names might be derived from China and “Qin” (an ancient Chinese Empire), indicating that common millet was dispersed from China to the Indian subcontinent through a route

via Nepal.

### Taxonomy

Fig. 2 shows typical panicle types such as sparse (a1), compact (a2), and dense (a3). It also shows a domestic type (b1) and an escaped weed (b2) in Pakistan; a domestic type (b3) and a weed, ssp. *rudera le* (b4), in Romania; a domestic type (b5) and a weed, subsp. *agricolum* (b6), in Uzbekistan; a crop-like weedy biotype, subsp. *miliaceum* (c1); and an F<sub>1</sub> hybrid between a domestic type and the subsp. *rudera le* in Pakistan (c2), with both sparse and shattering panicles. It also shows a weed, subsp. *rudera le*, in Inner Mongolia (d, taken in 2004) and European common millet (e1 and

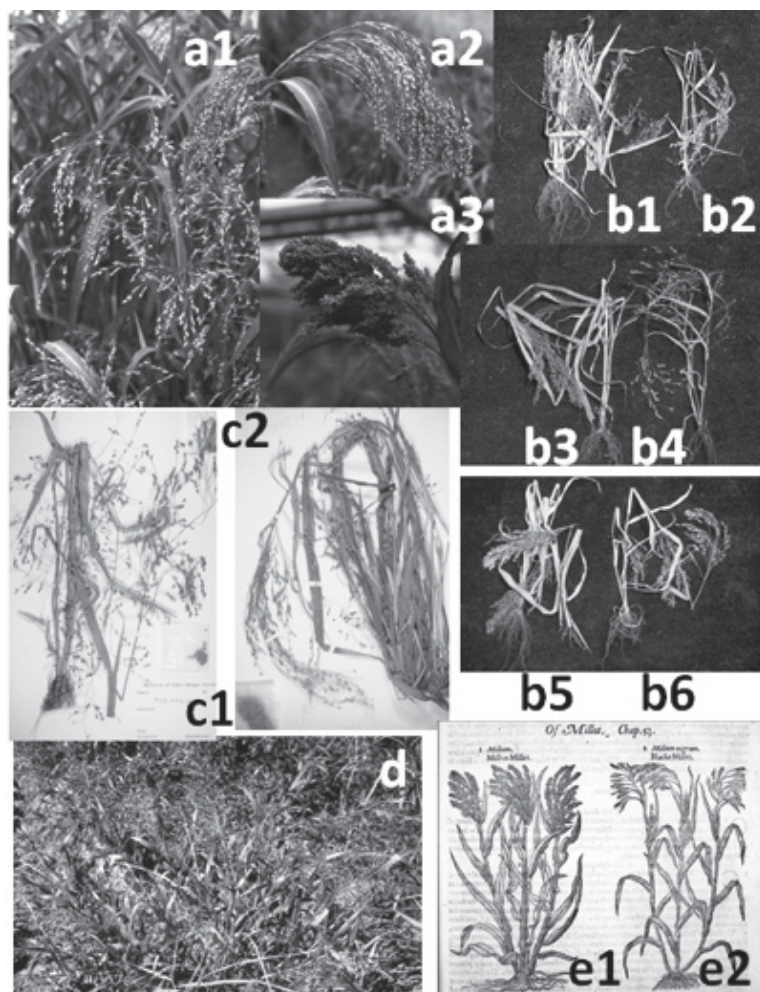


Fig. 2. Morphology of common millet, *Panicum miliaceum*. Types of panicle: a1, sparse; a2, compact; a3, dense. Domestic type and mimic weed in Central Asia: b1, b3 and b5, subsp. *miliaceum*; b2, an escaped weed; b4 and d, subsp. *rudemale*; and b6, subsp. *agricolum*. c1, a crop-like weedy biotype in Pakistan and c2, a F<sub>1</sub> hybrid between subsp. *miliaceum* and subsp. *rudemale*. e1 and e2, European common millet in 17th century (Gerarde 1597).

e2) illustrated in a book (Gerarde 1597). The panicles of common millet can be divided into five types: sparse, compact, dense, and two intermediate types (relatively sparse or dense). Common millet is generally a densely piliferous plant, but the hairiness of the uppermost internode is very variable. This trait can be divided into four types: glabrous, sparsely, moderately and densely piliferous.

Lyssov (1968, 1975) classified *P. miliaceum* L. into five groups based on the panicle types as follows. The panicle of race *miliaceum* was similar to that of a wild species. *Race patentissimum* had long, slender, and sparse panicles (a1), but it was very difficult to divide these two races, which were distributed from Eastern Europe to

Japan. *Race contractum* had a droopy, compact panicle (a2). *Race compactum* had a cylindrical, erect panicle. *Race ovatum* had an oval, dense panicle (a3). Because these morphological characteristics did not clearly show a geographical cline, this classification was not indicative of their taxonomical characteristics. The taxonomy of common millet needs to identify intra-specific differentiation through a matrix of various characteristics. Scholz and Mikoláš (1991) classified *P. miliaceum* into three subspecies: *miliaceum*, *rudemale*, and *agricolum*. Subsp. *miliaceum* consisted of the cultivar form (b1, b3, b5) and crop-like weedy biotype (c1) in Pakistan, and also in Austria, Slovakia, and Canada, respectively. Subsp. *rudemale* (b4, d) was an



Table 4. Partial correlation coefficients of 14 characteristics

	Days for flowering	No. of tillers	Plant height	No. of leaves on main culm	Length of flag leaf	Width of flag leaf	FL/FW	Panicle length	Diameter of uppermost internode	Panicle type	Lemma color	Stigma color	Hairiness of uppermost internode	Shattering
DF	1.000	0.005	0.835**	0.916**	0.501**	0.503**	-0.032	-0.400**	0.569**	0.363**	-0.055	0.131	0.078	0.027
TN	0.005	1.000	-0.203	-0.173	-0.216	-0.347**	0.297*	-0.259	-0.375**	-0.157	-0.118	-0.045	-0.008	-0.048
PH	0.835**	-0.203	1.000	0.907**	0.746**	0.736**	-0.095	-0.024	0.804**	0.543**	-0.030	0.015	0.036	0.057
LN	0.916**	-0.173	0.907**	1.000	0.594**	0.640**	-0.145	-0.310*	0.713**	0.372**	-0.009	0.172	0.056	0.066
FL	0.501**	-0.216	0.746**	0.594**	1.000	0.787**	0.164	0.179	0.726**	0.382**	0.039	-0.012	0.049	0.221
FW	0.503**	-0.347**	0.736**	0.640**	0.787**	1.000	-0.451**	0.170	0.814**	0.515**	-0.127	-0.123	-0.104	0.186
FL/FW	-0.032	0.297*	-0.095	-0.145	0.164	-0.451**	1.000	-0.052	-0.254	-0.226	0.217	0.123	0.202	0.002
PL	-0.400**	-0.259	-0.024	-0.310	0.179	0.170	-0.052	1.000	0.169	0.235	0.061	-0.240	0.052	-0.116
DI	0.569**	-0.375**	0.804**	0.713**	0.726**	0.814**	-0.254	0.169	1.000	0.548**	-0.033	-0.079	0.082	0.081
PT	0.363**	-0.157	0.543**	0.372**	0.382**	0.515**	-0.226	0.235	0.548**	1.000	-0.043	-0.335	-0.128	-0.142
LC	-0.055	-0.118	-0.030	-0.009	0.039	-0.127	0.217	0.061	-0.033	-0.043	1.000	0.358	0.102	0.043
SC	0.131	-0.045	0.015	0.172	-0.012	-0.123	0.123	-0.240	-0.079	-0.335*	0.358**	1.000	0.124	-0.011
HI	0.078	-0.008	0.036	0.056	0.049	-0.104	0.202	0.052	0.082	-0.128	0.102	0.124	1.000	0.053
SH	0.027	-0.048	0.057	0.066	0.221	0.186	0.002	-0.116	0.081	-0.142	0.043	-0.011	0.053	1.000

Controlled value is Iodine color reaction; \* 5%, \*\* under 1% level significance.

escaped weed from subsp. *miliaceum* (b2) around the world, with the small grains shattering easily on its sparse panicle. Subsp. *agricolum* (b6) was a mutant race with characteristics intermediate between the domestic form and subsp. *rudérale*. This subspecies grew in maize fields because of its strong tolerance to herbicide. The two types of European common millet in the sixteenth century might have been the races *ovatum* (e1) and *patentissimum* (e2). A F<sub>1</sub> hybrid (c2) between subsp. *miliaceum* and subsp. *rudérale* was grown.

### Morphological characteristics

The heading of common millet often occurred irregularly. Because the panicle flowered inside the leaf sheath 4–5 days before heading, the duration (days) to flowering from sowing was observed instead of the heading date. Generally, the duration of local varieties from high latitude areas was brief, but the number of days was remarkably variable. The varieties from China, Mongolia, the former USSR, Europe, and Japan (Hokkaido) flowered very early, by 40 days after sowing, while those from India and southern Japan flowered late, a third of them by 80 days. The varieties from China, Mongolia, the former USSR, Europe, and Japan (Hokkaido) had fewer leaves (5–10) on the main culm than those of southern and western Asia, Korea, and southern Japan (11 to 16). All of the varieties from Japan, Korea, and Nepal had only a few productive tillers (1 to 3), while the varieties from southern and western Asia, the former USSR (including Central

Asia), and Europe indicated very broad variation (1–6), up to an extreme of 9 in 6.9% of samples from India.

Common millet is a densely piliferous plant. The hairiness of the uppermost internode was divided into four types: glabrous, sparse, moderate, and dense. Most varieties were glabrous or sparse, while the others were dense in Hokkaido (40.0%), western Asia (26.1%), and Europe (20.0%). The panicle was divided into five types: sparse, dense, compact, and intermediate values (Kimata unpublished). Most of the local varieties from Japan (Hokkaido), China, India, western Asia, the former USSR, and Europe were the sparse type, while the remaining varieties from Japan, Korea, and Nepal were the dense type. Only a few varieties from western Asia, the former USSR, and Europe were the compact type.

The lemma color on mature plants was classified into six colors: dark brown, brown, pale brown, ivory, orange, and grayish-green. The varieties from the former USSR and Europe showed large variations in color. Most grains from Japan (Hokkaido) and China were dark brown, but others from southern Japan were brown, pale brown, or ivory. In India, the grain color included grayish-green (45.6%) in addition to pale brown and ivory. The stigma color of the pistil in the mature stage was one of three colors: white, faint purple, or purplish-red. About 70% of the varieties showed the former two colors. Especially, in southern Japan and Nepal all the varieties had white stigmas except one. However, in Japan (Hokkaido), India, and western Asia over 73% of varieties had purplish-red stigmas. In Europe 28% of the varieties had

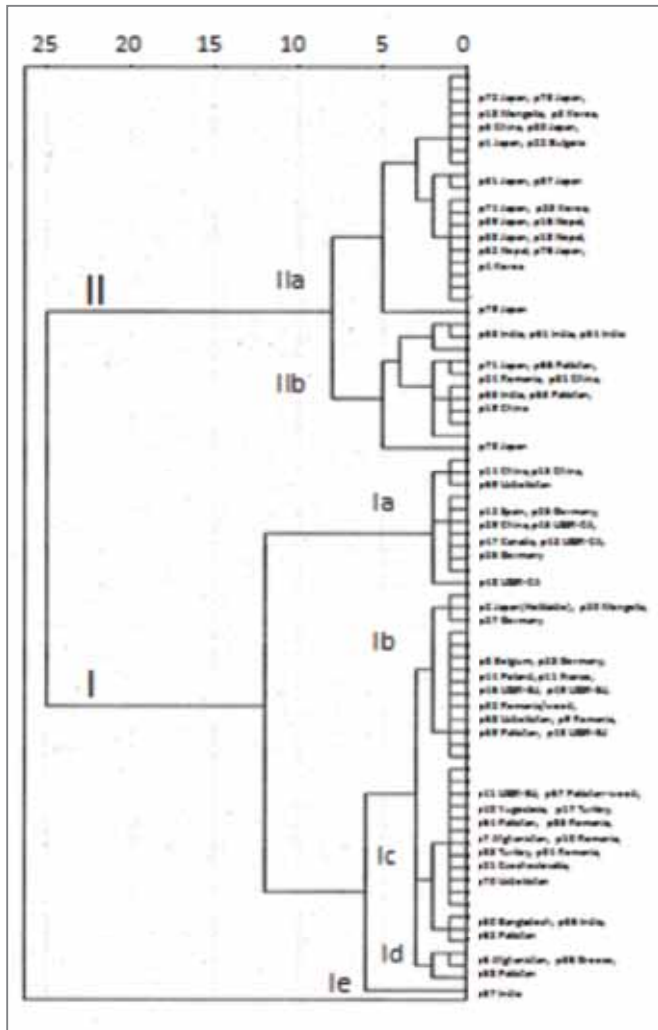


Fig 3. Cluster analysis of morphological characteristics.

purplish-red stigma (Kimata unpublished).

The partial correlation coefficients of 14 characteristics are shown in Table 4. The coefficients greater than 0.6 under a 1% significance level were PH (plant height) and LN (number of leaves on the main culm) to days for flowering (DF). The DF, LN, FL and FW (length and width of flag leaf), and diameter of uppermost internode (DI) to PH; DF, PH, FW and DI to LN; PH, LN, and FL and FW to each other; DI to FL & FW; and PH, LN, FL, and FW to DI. The others, namely, number of tillers (TN), panicle length (PL), panicle type (PT), lemma color (LC), stigma color (SC), hairiness of uppermost internode (PI), and SH (shattering) were not highly statistical significant. Therefore, the domestic varieties with late maturity are tall with many leaves, a large flag leaf that maintains

effective photosynthesis during the growing season, and a bold culm that holds a heavy panicle.

The hierarchical cluster analysis of eight morphological characteristics and earliness is illustrated in Fig. 3 (by using the group average method of SPSS). The 75 local varieties were divided into two major clusters, I, with five sub-clusters, and II, with two sub-clusters. Sub-cluster Ia consisted of 11 varieties, from Central Asia (3 varieties, former USSR), Uzbekistan (1), China (3), Spain (1), Germany (2), and Canada (1); Ib came mostly from Western Europe, including a few from Japan (Hokkaido), Mongolia, Uzbekistan, and Pakistan; Ic came mostly from Eastern Europe, including a few from Uzbekistan and the Indian subcontinent; Id consisted of three varieties from Afghanistan, Greece, and Pakistan; and Ie consisted of only one variety from India. Sub-cluster Iia consisted of 20 varieties, mostly from East Asia but including a few from Nepal (3) and Bulgaria (1). Iib consisted of 11 varieties, mostly from the Indian subcontinent and also a few from China (2), Japan (2), and Romania (1). The distribution of morphological characteristics generally showed two geographical trends, from Central and South Asia toward Europe via Asia Minor, and from China toward India via Nepal (to the south) and Japan via Korea (to the far east).

#### Crossability among Eurasian varieties and morphological characteristics of F<sub>1</sub> hybrids

The crossability among six testers was estimated by their fructification rates. The florets (range 5 to 50, average 17.0) on panicles (1 to 3, average 1.2) were artificially crossed with the tester pollen of each variety, yielding an average fructification rate of 4.8%. Crossing tests were conducted between 351 combinations yielding 117 F<sub>1</sub> hybrids fructified. The artificial cross pollination of common millet was technically very difficult because the quite irregular flowering happened often before heading, and anther dehiscence was very sensitive to daily weather conditions and it did not open entirely under wet conditions on rainy days. Because of this, the observed crossability was relatively low, ranging from 0

Table 5. Crossability (%) among local varieties

Locality	Ovum No. of varieties	Pollen					
		France	p32 Weed	Central Asia	India	p51 China	p60 Japan
East Asia	21	23.5	16.7	58.8	33.3	45.0	45.0
Central Asia	8	16.7	28.6	20.0	0	0	37.6
South Asia	19	26.7	35.7	29.4	30.8	25.0	38.9
Europe	20	41.2	16.7	17.6	17.6	45.0	21.1
Canada	1	0	0	+	0	0	0
Weed type (Romania)	1	0	0	0	0	0	0
Total combinations	70	56	58	47	65	67	58

+, with another variety.

to 63.9%. The F<sub>1</sub> hybrid was obtained from 18 varieties. The crossability of ovum parents was lower than that of pollen parents among the testers. One to 15 seed grains were obtained from each variety, and the germination ratio was observed in only 105 strains of the F<sub>1</sub> hybrid. Most seeds germinated well, while the others did not germinate or necrotized immediately after germination. All of the F<sub>1</sub> hybrid plants had good pollen fertility of over 78%.

Crossability among varieties was summarized to each country and region as shown in Table 5. The French tester had the largest number of sound F<sub>1</sub> plants (41.2%) with European varieties. The Central Asian tester made F<sub>1</sub> plants (58.8%) only with East Asian varieties. The Indian tester made F<sub>1</sub> plants with East Asian (33.3%) and South Asian (30.8%) varieties. The Chinese tester (p51) made F<sub>1</sub> plants with East Asian (45.0%) and European (45.0%) varieties. The Japanese tester (p60) made F<sub>1</sub> plants with East Asian (45.0%), Central Asian (37.6%), and South Asian (38.9%) varieties. The weed tester (p32, subsp. *ruderalis* from Romania) made F<sub>1</sub> plants with South Asian (35.7%) and Central Asian (28.6%) varieties. The pollens of subsp. *ruderalis* could artificially fertilize the ovum of domestic varieties, but the counter practices could not at all. Notably, a domestic variety with sparse and shattering panicles (PC57-2 from Hokkaido, Japan) made F<sub>1</sub> hybrids with the testers from Central Asia, India, and Japan, but not with the others.

The French tester made the largest number of fertile F<sub>1</sub> hybrids with European varieties, the Central Asian tester with East Asian varieties, the Indian tester with East and South Asian varieties, and the Chinese tester with East Asian and European varieties (Table. 5).

Central Asian varieties were infertile when crossed with Indian or Chinese ovum parents similar to that when crossed with a weed (p32). These data suggested that common millet was dispersed from Central Asia to China and Europe, respectively, and then dispersed indirectly to South Asia and East Asia. The weed (p32) was not a crop-like weedy biotype because it was isolated reproductively and made no fertile hybrids as an ovum parent, notwithstanding the assured fructification among varieties from all regions in the reverse as a pollen parent. However, it might still be possible that subsp. *ruderalis* was an ancestor, since it made fertile F<sub>1</sub> hybrids between the other varieties.

The panicle type of F<sub>1</sub> hybrids with the sparse-panicled Indian tester was also sparse. The F<sub>1</sub> hybrids with the dense-panicled Japanese tester (p60) had sparse panicles when combined with sparse varieties and dense panicles when combined with dense varieties. The F<sub>1</sub> hybrids between varieties with middle-type panicles generally also had middle-type panicles.

Common millet is generally a densely piliferous plant, but the hairiness of the uppermost internode was highly variable. This trait was divided into four types: glabrous, sparsely, moderately and densely piliferous. The F<sub>1</sub> hybrids between the moderate varieties (e.g., p9, p11, and p56) had a moderate internode except for p8 (glabrous). The F<sub>1</sub> hybrids with the glabrous testers from Central Asia, China, and Japan mostly had a glabrous internode except for a few in p2, p53, and p9 (moderately). The F<sub>1</sub> hybrids between the moderate or dense varieties and the dense Indian tester were varied widely between glabrous, sparsely and moderately, while an F<sub>1</sub> hybrid between a glabrous variety from Japan (Hokkaido) and the moderate Indian tester had a

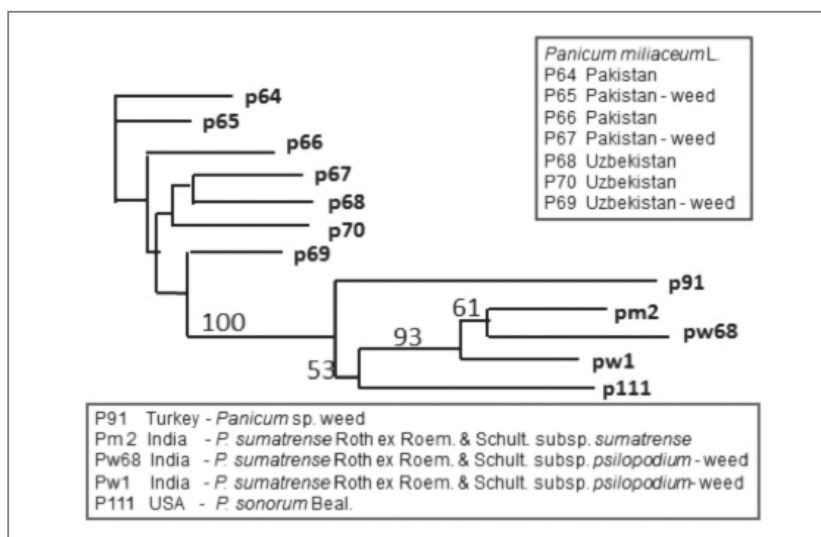


Fig. 4. Interspecific dendrogram of three domestic species in genus *Panicum* by AFLP markers.

glabrous internode.

#### AFLP markers

The AFLP markers of 75 local varieties were analyzed by PAUP\* ver. 4.0 and SPSS ver. 21, including neighboring joint and UPGMA methods with the bootstrap test. The interspecific differentiation of *Panicum miliaceum*, *P. sumatrense*, *P. sonorum*, and their relatives is illustrated in Fig. 4 (neighboring joint tree, PAUP\*). Clear interspecific differentiation among these species of *Panicum* were noted, including the domestic and weed types of *P. miliaceum* from Pakistan and Uzbekistan, and the other species, *P. sumatrense* and *P. sonorum* in the bootstrap test. However, the phylogenetic differentiation of common millet was not as clear among varieties based on the bootstrap test (200 replicates), as shown in Fig. 5 (UPGMA tree, PAUP\*), although there was a geographical trend in the dendrogram.

The 75 varieties were divided into two major clusters: I with six sub-clusters and II with three sub-clusters. Sub-cluster Ia consisted of five varieties from Germany, Romania (subsp. *ruderalis*), China, and Japan (2 varieties). Ib consisted of seven varieties from Turkey, Greece, Romania (2), and Japan (3). Ic1 consisted of six varieties from Yugoslavia, the European portion of the former USSR (USSR-EU, 2), the Central Asian portion

of the former USSR (USSR-CA, 2) and Poland. Ic2 consisted of ten varieties from Canada, USSR-EU (2), USSR-CA, China, Nepal, Bangladesh, and India (3). Ic3 consisted of eight varieties from India (3), Pakistan (4), and Japan. Id consisted of seven varieties, including Pakistan (4, with two weed types) and Uzbekistan (3, with one weed type). Sub-cluster IIa consisted of only two varieties from Afghanistan. I Ib consisted of 9 varieties from China (2), Nepal (2), Romania (2), France, Spain, and Belgium. I Ic consisted of 11 varieties from China, Korea, Mongolia (2), Turkey, Bulgaria, Romania, Czechoslovakia, and Germany (3). The distribution of AFLP markers generally showed two geographical trends, from Afghanistan and Mongolia toward Europe and Nepal via China (to the west and east), and from Uzbekistan and Pakistan toward India and Eastern Europe via USSR-CA/EU (to the south and west).

On one hand, based on the hierarchical cluster analysis (group average method, SPSS), only two clusters were detected among 51 varieties. Cluster I consisted of five varieties, including three weed types from Pakistan and Uzbekistan, while Cluster II consisted of 46 varieties from the other regions.

#### Discussion

The botanical origin, domestication, and

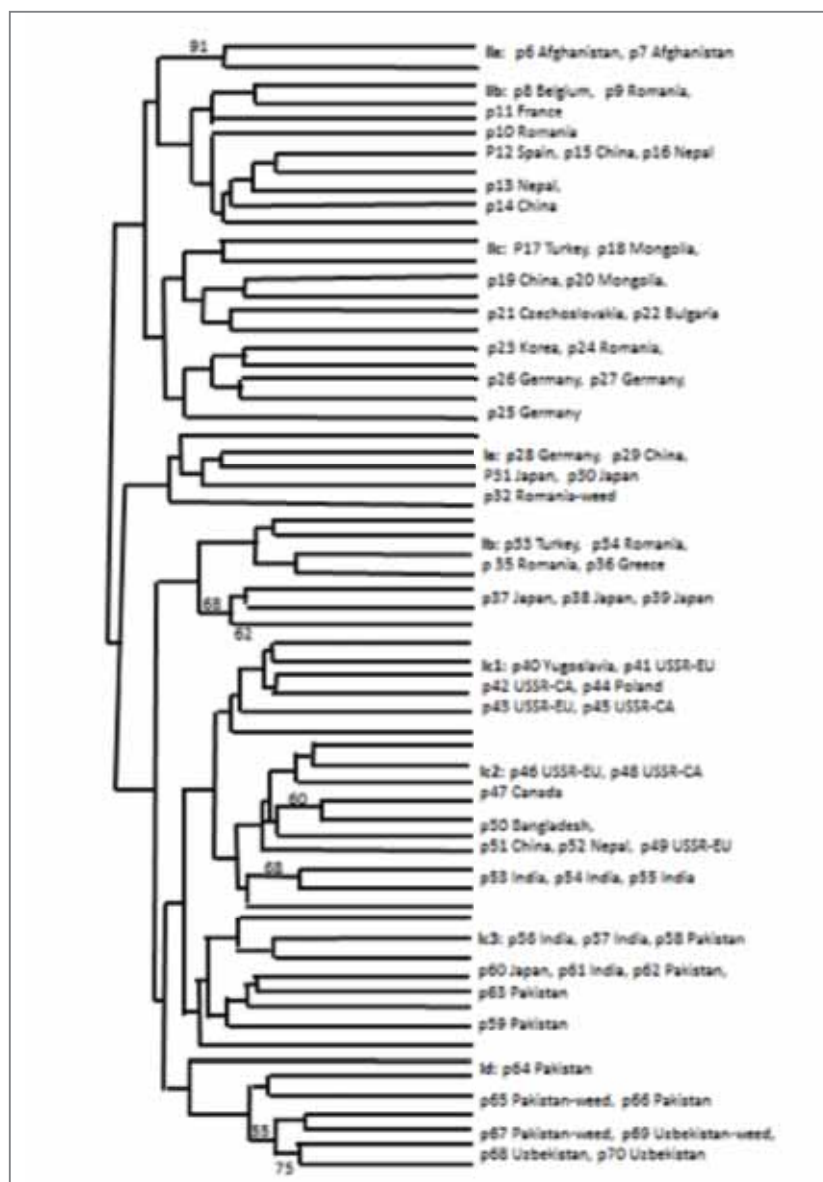


Fig. 5. Intraspecific dendrogram of common millet by AFLP markers.

geographical dispersal of common millet were discussed and then integrated through the results mentioned above. The following working hypothesis might well-explain the place of origin and dispersal of common millet with respect to recent archaeological contributions (e.g., Fuller et al. 2001, Hunt and Jones 2006, Jones 2004, Nesbitt 2005). This hypothesis is supported by the crossability among varieties in Eurasia and the geographical variation of several genetic characteristics (Table 5), although this needs further detailed study, especially the phylogeny of common millet and its close relatives. The early domestication process began in Central Asia and then progressed

with a continuous process of dispersal toward China. The domestic type then dispersed from Central Asia to South Asia, directly to Europe, and indirectly to southeastern Europe via West Asia. On the other hand, this grain crop might have dispersed from China to Japan and Southeast Asia. The ancient farmers who had cultivated barley and wheat in the Near East area had not necessarily accepted common millet. However, the nomads who had moved around the Eurasian steppe had gladly accepted the millet as the food source, the same as the present day Mongolian herdsman, because of its early maturation within the short summer season and its value as fodder for the livestock. They dispersed





Fig. 6. Dispersal routes of common millet through the Eurasia. I, original place and II, secondary dispersal center; solid lines, ancient routes from Middle Asia; dotted lines, the 13th century AD routes from China.

common millet from Central Asia to China and Europe. Common millet might have dispersed faster to Europe in an east/west direction at similar latitudes than to southeastern Europe in a south/north direction across different latitudes. It matured early in summer, but barley and wheat grew slowly in winter.

The traditional varieties cultivated by the Ainu people in Hokkaido, Japan are similar to the varieties from North China and Mongolia in their panicle type and the duration to flowering, while the other Japanese varieties are similar to the varieties from Korea and Nepal in their panicle type and stigma color (Kimata et al. 1986). The same large variability in lemma color and panicle type was shown in varieties from both the former USSR and Europe. Indian and West Asian varieties had very large variation in many characteristics (Fig. 3 and Table 4).

As compared with the other varieties through Eurasia, the varieties around Afghanistan, Pakistan, India, and Central Asia had a large diversity of characteristics, including sparse panicles and many tillers. The geographical distribution of characteristics was useful information including the biocultural

diversity, particularly foods and vernacular names (Tables 2 and 3) to reconstruct the domestication process and dispersal routes (Kimata 2015c).

An ancestral form of common millet might have had early maturation, remarkable grain shattering, sparse panicles, small grains, many tillers, pale brown lemmas, white stigmas, glabrous uppermost internodes, and non-glutinous starch. Usually, the domestic form of cereals has fewer productive tillers than wild forms. Many varieties from Central Asia and the Indian subcontinent show many of the ancestral characteristics. There is only a little information on the mimic weed type associated with the domestic type of common millet (Sakamoto 1988, Scholz and Mikoláš 1991), but several weed types with remarkable grain shattering have been found in Pakistan, Uzbekistan, and Kazakhstan (Kimata 1994, 1997). These seeds were mixed with those of the domestic type. Because the varieties around Central Asia show large variation and their related weedy subspecies still grow today, this area is appropriate to be the place where common millet had been domesticated. Moreover, the weed types were classified into two subspecies, *ruderalis* and *agricolum*, and a crop-like

weedy biotype escaped from the domestic type. It would seem that *rudérale* was an ancestor, while *agricolum* became a weed by hybridization between these two subspecies.

Common millet was domesticated from a wild variety of *P. miliaceum* subsp. *rudérale* in Central Asia including the northern mountains of Afghanistan and Pakistan, especially from the Aral Sea to the Southwest Tien Shan Mountains. It was dispersed both eastward to China and westward to Europe, and both southward to the Indian subcontinent (de Wet 1995) and northward to Siberia by nomadic groups since the Neolithic era (Fig. 6). Moreover, when the Mongolian army invaded Europe in the thirteenth century, they carried with them common millet (Carpine 1246). It suggests the dispersal of common millet by Mongolian that a few Chinese varieties are mingled with European varieties in the clusters of morphological characteristics (Fig. 3) and AFLP markers (Fig. 5). Additionally, the traditional varieties cultivated by the Ainu people in Japan (Hokkaido) are similar to the varieties from North China and Mongolia in their panicle type and early duration to flowering, while the other Japanese varieties are similar to the varieties from Korea and Nepal in their panicle type, stigma color, and phenol reaction of young lemmas (Kimata et al. 1986, Kimata and Negishi 2002). A northern route from North China into Hokkaido is suggested by the fact that PC57-2 (Hokkaido, Japan) made fertile hybrids among the testers from Central Asia, India, and Japan.

An ancestor of common millet may have been a wild type of *P. miliaceum* subsp. *rudérale*. The early domestication process began around Central Asia and then progressed in a continuous dispersal process toward China. Furthermore, the domestic type dispersed from Central Asia to South Asia, directly to Europe, and indirectly to southeastern Europe via West Asia.

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## Appendix: International Forum for Promotion and Development of Minor Cereals(1997)

資料：国際フォーラムの提案 (1997)

Phone : { Off : 3332387  
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PROJECT COORDINATION CELL  
ALL INDIA COORDINATED SMALL MILLETS IMPROVEMENT PROJECT  
INDIAN COUNCIL OF AGRICULTURAL RESEARCH  
University of Agricultural Sciences, GKVK Campus, Bangalore - 560 065, India.

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**Dr. A. SEETHARAM**  
Project Coordinator (Small Millets)

Ref. No. PC (SM) /  
Date : **Dr. M. KIMATA**  
Visiting Professor

June 3, 1997

Dear Sir,

In Asia and several countries around the world, many kinds of small millets (Minor cereals) are grown. They are finger millet (*Eleusine coracana*), italian millet (*Setaria italica*), kodo millet (*Paspalum scrobiculatum*), proso millet (*Panicum miliaceum*), little millet (*Panicum sumatranse*), barnyard millet (*Echinochloa frumentacea/E.colana*), grain-amaranth (*Amaranthus sp.*) and buck wheat (*Fagopyron spp.*). There are other minor cereals like teff (*Eragrostis tef*) and fonio (*Digitaria spp.*) which are important in Africa.

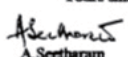
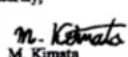
Research on these crops is in progress in many countries but it is scattered and localized. As a result, there is difficulty in finding access to the valuable research information available elsewhere. The scientists working on these crops are handicapped for want of a common forum for discussion of issues of mutual interest. The two International Workshops held in 1986 in India and 1991 in Zimbabwe (Africa) has helped in documenting the available information at global level on some of the above cereals. But, this has not helped much in filling the vacuum. Recognizing the importance of these minor cereal crops in food security at the farm/regional level and its role in World Agriculture it is thought appropriate to launch an **International Forum for Promotion and Development of Minor Cereals**. The proposed forum will cover 10 crop species - finger millet, italian millet, proso millet, little millet, kodo millet, Japanese/Indian barnyard millet, grain-amaranth, buck wheat, teff and fonio.

**The forum intends to provide:**

- 1) A common platform for scientists working to discuss issues related to conservation, improvement and promotion of these crops.
- 2) To bring out International Journal to serve as promotional media for exchange and dissemination of information.
- 3) To support organizing International/Regional Seminars and Workshops on these crops and assist to identify areas of research and development for the common benefit.

Through this letter we are enlisting your support for launching of such a forum/society by end of the December 1997 and your willingness to serve as one of the founder members. We would be grateful if you could kindly circulate this letter among the interested scientists/colleagues in your country and help us to know their response. We look forward for your suggestions in this regard.

Thanking you,  
With regards,

Yours sincerely,  
   
A. Seetharam M. Kimata

**Kindly send your suggestions to:**

- 1) Dr. M. Kimata, Professor of Ethnobotany and Environmental Studies, Tokyo Gakugei University, Koganei, Tokyo 184, Japan.
- 2) Dr. A. Seetharam, Project Coordinator (Small Millets), University of Agricultural Sciences, GKVK, Bangalore-560 065 (India).





## あとがき

私の第2の人生は、環境教育学を確立するという義務を優先し、教育実践研究に多くの時間をかけた。雑草や雑穀の調査研究・実験は、趣味という位置づけだった。義務と趣味によって、私生活は経済的にも時間的にも、さらに精神的にも甚だしく犠牲にした。自分の家族の世話をしないで、他家の子どもたちのお世話に時間をかけた。「アンパンマンの正義は、自己犠牲だ。自己犠牲を伴わない正義はない」と、やなせたかしは言っている。自己の信条や信仰に従うとはそのことであろう。すべては自己の内にあり、足るを知ることなのだろう。第3の人生では義務はほとんどなく、さらに自由になり、趣味と家族に暮らしている。人生に何の恨みも残さず、足るを知って彼岸に行くことだと思うので、今は調査研究などのアーカイヴズ作り、すなわち売らない文筆作業、3家族分の有機無農薬の食料作り、刺繍など、趣味の仕事に勤しんでいる。

第9号の特集は、主にインド亜大陸の雑穀についてである。本来、雑草の進化研究を志したが、老師阪本寧男の誘導により、雑穀研究にも憑りつかれてしまった。初めは文化人類学の野外調査程度だったが、次第に深間にはまり、キビの起源と伝播の研究を進めることになった。インド亜大陸調査では、優秀な隊員たちとの研究分担のバランスで、食文化を主な対象とした。ところが、畏友小林央往が、西アフリカの野外調査で、マラリアに斃れた。インドで一緒に調査旅行を繰り返した親友の志を継ぎ、インド起源の雑穀の研究を追加することにした。彼の卓見に導かれながらも、能力不足で、十分な成果を挙げられたとは思えない。

この特集の拙い論文は、定年退職を間近に控えながら、国際誌に投稿する努力によって生まれたものである。残念ながら受理されるまで、あるいは投稿するまでには及ばなかった。しかし、第2の人生において膨大な労力を費やし、拙いとはいえ、二度と余人がなせる仕事量ではないので、残しておくべき研究成果であると考えた。また、小林の遺志であるとも思った。トルストイが言っているように、人はいずれ死を遁れられず、仕事は忘れ去られて行く。しかし、内村鑑三が言ったように、小さな個人の最大遺産としての「人生」ではある。「読む人知らず」であっても、第3の人生の足るを知るために書いておきたい。

木俣美樹男

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