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Intraspecific Variation and Systematics of Cultivated *Setaria italica*, Foxtail Millet (Poaceae)¹

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Foxtail millet (Setaria italica) is grown as a cereal in southern Europe and in temperate, subtropical, and tropical Asia. Its closest wild relative is S. italica ssp. viridis (green foxtail). Green foxtail is native to temperate Eurasia, but was introduced and became widely established as a weed in temperate and warmer parts of the Americas. Spontaneous and cultivated S. italica cross to produce fertile hybrids. Derivatives of such crosses, resembling foxtail millet in some inflorescence traits but with efficient natural seed dispersal, accompany the cereal across its range of cultivation. Giant green foxtail of Europe and the American corn belt is a weed of hybrid origin. Foxtail millet was domesticated in the highlands of central China; remains of cultivated foxtail millet are known from the Yang-shao culture period dating back some 5,000 yrs. Comparative morphology suggests that foxtail millet spread to Europe and India as a cereal soon after its domestication. Three cultivated races are recognized. Moharia, from Europe and southwestern Asia, includes cultivars with 5–52 culms, each bearing several, small, more or less erect inflorescences. Cultivars in race maxima are characterized by plants with 1–8 usually unbranched culms that bear large inflorescences; they occur in Transcaucasian Russia and the Far East. Race indica is intermediate in culm number (ave. 6.6) and inflorescence size between races moharia and maxima, and is cultivated in southern Asia.

The genus *Setaria*, widely distributed in warm and temperate parts of the world, is a member of the subfamily Panicoideae and the tribe Paniceae. Its spikelets are subtended by one to several bristles that persist even when the spikelets fall at maturity. The genus is of significant agricultural importance. The annuals *S. faberi* Herrm., *S. pumila* (Poir.) Roem. & Schult., *S. verticillata* (L.) P. Beauv., and *S. italica* (L.) P. Beauv. subsp. *viridis* (L.) Thell. [*S. viridis* (L.) P. Beauv.], are aggressive colonizers in their native Old World and have become widely established as weeds in the Americas. In Africa, *S. sphacelata* (Schum.) Stapf & Hubb. is harvested as a wild cereal across African savannas (Dalziel 1937), and *S. pallide-fusca* (Schum.) Stapf & Hubb. is harvested by the Kasonke of Burkina Faso (Chevalier 1913). A panicle of *S. verticillata* found in a garland excavated at El Lahum dates back to the 12th Egyptian dynasty (Dixon 1969). In the Philippines *S. palmifolia* (Koen.) Stapf is harvested as a wild cereal (Monsalud et al. 1966), and in New Guinea the species is vegetatively propagated for the edible young shoots, which are cooked as a green vegetable (Barrau 1958; Bulmer 1964). An unidentified *Setaria* species was used as a cereal in pre-Colombian Mexico but was eventually replaced by *Zea mays* L. (Smith 1968). During the 2 millennia that *Setaria* was cultivated in Tamaulipas, grain size increased significantly (Callen 1965, 1967), probably as a result of selection pressures associated with harvesting

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and sowing. Two Old World species, *S. pumila* and *S. italica*, are presently cultivated as cereals. Korali (*S. pumila*) is occasionally sown across southern India. Cultivated kinds differ from wild *S. pumila*, which naturally colonizes cultivated fields, primarily in degree of efficient natural seed dispersal. Large grains, colonizing ability, and ease of harvesting make this species a favorite wild cereal across southern Asia (Bor 1960). Foxtail millet (*S. italica*), a major food crop native in temperate Eurasia, has become widely adapted as a cereal also in tropical and subtropical Asia.

MATERIALS AND METHODS

The 1,195 accessions of *S. italica* in the germplasm bank at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) were grown under irrigation at Patancheru, Andhra Pradesh, India, during the dry season 1983. These included 55 collections from Europe and southwestern Asia, 801 from India and Nepal, 67 from Transcaucasian USSR, 60 from China, Japan, and Mongolia, and 212 of uncertain origin. Data collected from 10 living plants of each accession were compared with data from specimens filed with the Crop Evolution Herbarium at the University of Illinois (CEL), the Royal Botanic Gardens, Kew (K), and the Rijksherbarium, Leiden (L). Quantitative characters measured in the nursery were length and width of flag leaf, length of flag-leaf sheath, length of terminal inflorescence, width of inflorescence, weight of mature inflorescence, length of peduncle to terminal inflorescence, height of plant, number of basal tillers per plant, and days to flowering. Discriminant function analyses using these data (Nie et al. 1975) were used to assess a racial classification based on geographic distribution and inflorescence shape. Data on growth habit, fruit color, degree of lodging, days to maturity, and disease resistance, together with the quantitative data, are filed at ICRISAT as a descriptor base for each accession. Herbarium specimens of selected accessions studied are filed with CEL in Urbana.

TAXONOMY

Cultivated foxtail millets were recognized by Linnaeus (1753) as *Panicum italicum*. Variants within the species were later recognized as *Panicum germanicum* Mill. and *P. glomeratum* Moench (Mansfeld 1952). These taxa were transferred to *Setaria* and combined into *S. italica* (foxtail millets) by Beauvois (1812), who also transferred the weedy *P. viride* L. (green foxtail) to *Setaria*. Foxtail millet and the weedy green foxtail are morphologically and genetically allied. Some cultivars of *S. italica* in southeastern Europe and in Afghanistan resemble green foxtail except for their lack of efficient natural seed dispersal. Foxtail millet also crosses naturally (de Wet et al. 1979) and experimentally with green foxtail (Li et al. 1942; Li et al. 1945) to produce fertile hybrids. For these reasons green foxtail and foxtail millet are taxonomically considered to be conspecific; following the suggestion of Harlan and de Wet (1971), the cultivated taxa are recognized as *S. italica* ssp. *italica* and the spontaneous taxa as *S. italica* ssp. *viridis*.

Setaria italica ssp. *viridis* is based on *S. viridis*. Synonymy is discussed by Rominger (1962). Spontaneous green foxtail is extensively variable, widely distributed in temperate Eurasia, and extensively naturalized as a weed in the temperate parts of the New World. It is primarily an urban weed, but a robust race

is an obnoxious weed of agricultural land in the American Corn Belt (Pohl 1966). Green foxtail is typically a small, erect or decumbent plant up to 1.5 m tall, with several culms that are strongly branched (de Wet et al. 1979). Leaf blades are linear-lanceolate, essentially glabrous, and up to 29 cm long, but usually shorter. Panicles are spike-like and densely flowered, usually less than 10 cm long, with 0.5–1.5 cm long branches bearing clusters of several spikelets, each subtended by one to three bristles that exceed the 2.0–2.5 mm long spikelets in length. Spikelets are elliptic, with the lower glume about one third the length of the spikelet, and the upper glume about as long as the lemma. Spikelets disarticulate from the rachis below the glumes. The single grain is tightly enclosed by the indurate lemma and palea.

Giant green foxtail, a weed foxtail of corn fields in the American Midwest, also occurs across the species range in Eurasia (Rominger 1962). It is more robust (1.0–2.5 m tall) than common green foxtail and has larger panicles (up to 20 cm long), elongated panicle branches (up to 4 cm long), and an erect growth habit. Pohl (1951) suggested that giant green foxtail originated from cultivated foxtail millets through mutations that introduced natural seed dispersal. They more likely represent derivatives of hybrids between wild and cultivated *S. italica* (de Wet et al. 1979). Foxtail millet is highly autogamous, but natural hybrids between wild and cultivated taxa do occur. Hybrids produced by Li et al. (1945) were about 50% sterile although meiotic chromosome behavior was regular. Similar hybrids produced by de Wet et al. (1979) were fully fertile, and derivatives of these crosses resembled spontaneous giant green foxtail in morphological detail. Genetic studies indicate that spikelet disarticulation is controlled by two complementary dominant genes, and hybrids as well as some of their derivatives were characterized by wild-type seed dispersal. Weeds of hybrid origin are common in cereal species (Harlan et al. 1973; de Wet and Harlan 1975). *Representative specimens*: China: Shanxi province, weed in cultivated fields, grown at Urbana, IL, Aug 1980, UI 5340 (CEL); Afghanistan: weed in Kabul, grown at Urbana, IL, Aug 1980, UI 5344 (CEL); Japan: weed on Hatoma Island, grown at Urbana, IL, Aug 1980, UI 4598 (CEL).

Setaria italica ssp. *italica* is based on *S. italica*. Including all cultivated foxtail millets, it differs consistently from ssp. *viridis* only in having lost the ability of natural seed dispersal. It depends on man for sowing in suitable habitats. Foxtail millet is morphologically variable and widely grown as a cereal across temperate, subtropical, and tropical Eurasia.

The species has undergone extensive morphological changes under domestication. As in other cereals, the primary phenotypic change was a loss of efficient natural seed dispersal. Persistent spikelets at maturity facilitate harvesting. Those cultivars from southeastern Europe and from Afghanistan that resemble wild foxtail millet in vegetative and inflorescence structure differ from it in that their spikelets do not disarticulate at maturity. A second universal characteristic of domesticated cereals is a tendency toward uniform plant maturity. This is achieved through a combination of synchronized tillering and apical dominance. The number of tillers is usually reduced under domestication, as are number of inflorescence-bearing branches on each culm. Apical dominance can lead to a loss of all but one culm and to the production of a single terminal inflorescence. In foxtail millets, primitive cultivars have numerous, strongly branched culms as is char-

acteristic of spontaneous green foxtail, while highly evolved cultivars produce a single culm with a large, solitary inflorescence (Table 1). Reduction in number of inflorescences per plant is usually associated with an increase in inflorescence size. This is due to an increase in the length of the primary axis and an increase in number of spikelets on each inflorescence branch. Kruse (1972) demonstrated that the number of fertile spikelets per inflorescence is correlated with an increase in number of branches and degree of inflorescence branching. The primary branches elongate to accommodate the increased number of spikelets, and in some cultivars secondary branches become so crowded as to give the inflorescence a lobed appearance. *Representative specimens* (all grown at Patancheru, India, Oct 1982): Afghanistan, widely cultivated along foothills of the mountains, ICRISAT 502-82, moharia (CEL); USSR, cultivated in Georgia, ICRISAT 998-82, moharia (CEL); China, cultivated in Shanxi province, UI 4050, maxima (CEL); India, cultivated in Assam, ICRISAT 389-82, maxima (CEL); India, Andhra Pradesh, grown by tribal people around Kurnool, ICRISAT 015-82, indica (CEL).

DOMESTICATION OF FOXTAIL MILLET

The antiquity of foxtail millet as a cultivated cereal is uncertain. It probably evolved from spontaneous green foxtail (*S. italica* ssp. *viridis*) under a regime of harvesting and sowing. The species could have been domesticated anywhere across its natural range extending from Europe to Japan. It has been grown in China for about 5,000 yrs (Ho 1975). It was an important cereal in the highlands during Yang-shao times (Chang 1973; Nai 1963). Jars filled with husks of *S. italica* were found at an early farming site at Ban-po in Shanxi. The abundance of this cereal in storage and the farming implements associated with Yang-shao cultures strongly suggest that the cereal was cultivated rather than harvested in the wild. The name of the legendary ancestor of the Chow tribe of the loess highlands, Hou Chi, translates literally to mean "Lord of Millets" (Bray 1981). It is possible that the name refers to *Panicum miliaceum* L. (broomcorn millet), another early cultivated millet of China. Foxtail and broomcorn millets were probably domesticated in China at about the same time (Ho 1975). Wang Xiangjin of the Ming dynasty, however, recorded that northerners relied on foxtail millet for their daily food (Bray 1981).

Foxtail and broomcorn millets also occur in early agricultural sites from Switzerland and Austria dating back some 3,000 yrs (Werth 1937). The progenitor of broomcorn millet is native to Manchuria, and this species was probably introduced to Europe as a domesticated cereal. Green foxtail millet, native to southern Europe and temperate Asia, could have been independently domesticated in Europe and China. Neuweiler (1946) dated the European neolithic site at Baldegy, in which foxtail millet grains occur, to around 3600 B.P. The species, however, became widely cultivated in Europe only during the Bronze Age, when the more cold tolerant broomcorn millet spread rapidly across northern Europe (Hjelmquist 1955; Van Zeist 1970). These millets are absent from known neolithic settlements in the Far East (Braidwood et al. 1971), from ancient Egypt (Woenig 1897), and from neolithic India (Mittre 1968). The single millet grain pictured by Milojević et al. (1962) from an early farming site in Turkey is neither foxtail nor broomcorn millet. The absence of foxtail millet from known prehistoric farming sites in India,

TABLE 1. MORPHOLOGY OF CULTIVATED FOXTAIL MILLETS DIVIDED ON THE BASIS OF GEOGRAPHICAL DISTRIBUTION (*MOHARIA*: EUROPE, RUSSIA, NEAR EAST, AFGHANISTAN; *INDICA*: INDIA, SRI LANKA, PAKISTAN, NEPAL; *MAXIMA*: FAR EAST).

Character	Moharia \bar{x} (SD) range	Indica \bar{x} (SD) range	Maxima \bar{x} (SD) range
Days to flowering	39.6 (4.9) 32-50	57.0 (4.3) 43-70	40.5 (4.3) 32-57
Plant height	59.4 (15.4) 25-100	122.2 (170) 65-175	84.8 (19.3) 45-100
No. tillers	12.4 (8.6) 5-52	6.6 (3.4) 1-25	2.5 (1.6) 1-8
Leaf length	177.5 (54.6) 60-340	321.2 (56.8) 30-500	257.9 (47.0) 160-400
Leaf width	14.6 (4.7) 5-30	21.8 (5.1) 10-40	25.2 (5.7) 15-40
Sheath length	94.6 (25.3) 50-260	149.1 (23.5) 50-260	143.5 (26.7) 80-240
Peduncle length	266.6 (70.6) 100-460	310.5 (48.4) 80-500	303.8 (65.2) 90-500
Infl. length	81.5 (35.9) 20-200	180.0 (37.7) 60-300	149.5 (39.4) 60-300
Infl. width	11.8 (3.2) 5-30	21.0 (6.0) 10-50	22.2 (6.0) 15-40
	N = 229	N = 726	N = 94

however, does not necessarily indicate a late introduction of this cereal into the tropics of southern Asia. The wide distribution and morphological variation of foxtail millet in India suggest the opposite.

RACIAL CLASSIFICATION OF CULTIVATED FOXTAIL MILLETS

Foxtail millet are commonly divided into two cultivar complexes on the basis of inflorescence structure (Körnicke and Werner 1885). Cultivars with large, pendulous inflorescences are included in group maxima, and those with smaller, erect inflorescences, in group moharia (*germanicum*). Within groups, cultivars are recognized on the basis of fruit color, bristle length, and length of lateral inflorescence branches (Hubbard 1915). Dekapreleovich and Kasparian (1928) classified foxtail millets into ssp. *moharium* to include cultivars with numerous culms and small, cylindrical inflorescences, and ssp. *maxima* to include cultivars with one or a few culms and large inflorescences. They indicated that *maxima* cultivars are grown from Russian Georgia (Transcaucasia) to Japan, while *moharium* cultivars are the principal foxtail millet in Europe.

The present study of collections from across the range of *S. italica* cultivation suggests three morphologically distinct complexes. These complexes are recognized as races. They are artifacts of man's agricultural activities and do not deserve formal taxonomic status. Discriminant function analysis reveals that phenotype is closely correlated with distribution. Race moharia is centered in Europe and southwestern Asia, maxima in Transcaucasian Russia and the Far East, and indica in India and the rest of southern Asia. Gammie (1911) suggested, on the basis of comparative morphology, that Indian cultivars were derived from primitive Manchurian foxtail millets.

Race moharia

Cultivars of race moharia often resemble members of wild ssp. *viridis* (green foxtail) in phenotype, except that they have lost the ability of natural seed dispersal. Plants are 25-100 cm tall, with 5-52 (av. 8.6) tillers per plant. Tillers are usually branched to produce a well-developed terminal inflorescence and several, smaller

lateral inflorescences. Terminal inflorescences are erect or nodding at maturity and 5–20 cm long. Panicle branches are short and compactly arranged on the primary axis. Bristles are well developed or more rarely shorter than the spikelets. At Patancheru (India) these cultivars start to flower 32–50 days after sowing. Race moharia is cultivated in southeastern Europe, southwestern Russia, Afghanistan, and Pakistan. Cultivars from Afghanistan have small inflorescences with unusually large grains. Phenotypically similar cultivars occur in Manchuria and northeastern China (Gritzenko 1960). Discriminant function analysis suggests close affinities with primitive Manchurian cultivars as well as with the race indica.

Race maxima

This race, extensively variable, is characterized by spikelets closely arranged on elongated lateral branches, giving the inflorescence a lobed appearance. Plants are 45–100 cm tall, with 1–8 (av. 1.6) unbranched tillers, each bearing a terminal inflorescence. Two inflorescence types are recognized (Gritzenko 1960). Plants from eastern China, Japan, and Korea are tall, with large, pendulous inflorescences 12–30 cm long. They commonly have well-developed bristles. Plants with smaller, essentially erect inflorescences occur in northwestern China and Mongolia. These commonly have short bristles and often have the panicle branches tightly packed along the primary axis. Race maxima was introduced into the United States, where it is grown as bird feed. It also occurs in Nepal and Assam, along the southern foothills of the Himalaya, and in Russian Georgia.

Race indica

Foxtail millet is well adapted to dryland agriculture across tropical and subtropical southern Asia. It is particularly important as a cereal among hill tribes of the western and eastern Ghats of Central India and in Sri Lanka. Foxtail millet is frequently grown as a secondary crop with *Sorghum bicolor* (L.) Moench (grain sorghum). It is extensively variable in India, and race indica was probably derived from a combination of moharia cultivars from southwestern Asia and maxima cultivars from China.

Foxtail millet in India is typically a robust plant with 1–25 (av. 3.4) culms. Inflorescences are 6–30 cm long, with the elongated lateral branches loosely arranged along the primary axis. Peduncles are erect or nodding, with larger inflorescences becoming curved at maturity because of the weight of their grains. Bristles are usually well developed. Some collections from northern India belong typically with race maxima and are introduced from China. Collections from Meghalaya have long, slender inflorescences with small spikelets, and those from Assam commonly have short, compact inflorescences. Plants in which the bristles bear a spikelet at the tip occur across the range of foxtail millet cultivation in India. Two collections from Karnataka have stiffly erect, slender panicles with short lateral branches, somewhat resembling cultivated yellow foxtail, *S. pumila*, in inflorescence and spikelet structure. Foxtail millet has one to three bristles below each spikelet, whereas yellow foxtail millet has four or more bristles supporting each spikelet. One to three bristles occur below the spikelet in the Karnataka cultivar.

GENERAL DISCUSSION

Phenotypic evolution is rapid under domestication. Disruptive selection effectively isolates genotypes under domestication from their wild progenitors. Domesticated cereals are adapted to habitats created for them by man and cannot successfully invade the habitats of their wild relatives. It is only when the progenitor species becomes weedy and spontaneously invades the man-made habitat that additional isolating barriers between spontaneous and cultivated races of cereals become selectively advantageous. Wild *S. italica* is highly autogamous, as are weedy and cultivated complexes. Individual genotypes are in effect reproductively isolated with less than 2% natural outcrossing in continuous populations. Nevertheless, sterility barriers are evolving in China where the species has been cultivated for several thousand years, and where wild and domesticated taxa are naturally sympatric. Li et al. (1945) demonstrated up to 50% sterility in crosses between members of cultivated race maxima and of spontaneous green foxtail from China. Similar sterility barriers occur between cultivated Asiatic rice (*Oryza sativa* L.) and its wild progenitor (Hinata and Oka 1962) where these taxa compete for the same habitat. In African cultivated rice (*Oryza glaberrima* Steud.), a complex genetic system prevents gene exchange with its wild progenitor (Chu and Oka 1972). Hybrids between wild and cultivated taxa do occur and are fully fertile. Hybrid derivatives, however, are rare and introgression does not occur. Dominant alleles of two complementary genes determine survival in hybrids and derivatives. One dominant allele is carried by cultivated *O. glaberrima* and the other by its wild progenitor, *O. barthii* Chevalier. Few if any domesticated species have evolved completely effective reproductive isolation between wild and spontaneous taxa, and cereals are often characterized by weeds that mimic cultivars.

Domestication not only leads to rapid phenotypic differentiation between wild and cultivated taxa, but also to rapid evolution among cultivars. A farmer selects for adaptation to cultivation and to suit his individual fancies and needs. Man also transports domesticated species beyond their natural ranges, and spatial isolation allows for racial evolution. Races of domesticated species commonly have geographic and phenotypic unity. Grain sorghum [*Sorghum bicolor* (L.) Moench], as an example, is classified into races guinea from tropical West Africa, kafir from the African savannas, durra from the African Sahel, caudatum from the Sudan-Chad region, and the widely distributed bicolor, which represents relics of the original cultivated complex (de Wet 1978). Within races, morphological variation is extensive, but essentially continuous (Snowden 1936). Foxtail millets are equally variable. The range of variation that characterizes race indica often occurs in a single cultivated field from the eastern Ghats of Andhra Pradesh in India. Variation is maintained by farmers selecting a range of phenotypes for sowing with different ripening times. This allows for harvesting over an extended period of time and eliminates the necessity of prolonged seed storage. Racial evolution is largely directed by man through his agricultural activities. Domestication, on the other hand, results from natural selection pressures associated with harvesting and sowing. In seed crops, such a farming regime automatically leads to loss of natural seed dispersal, uniform population maturity, uniform individual plant maturity, increased fecundity, adaptation to man-made habitats and the phenotypic changes associated with these adaptations (Harlan et al. 1973).

Selection by man accelerates these adaptive and phenotypic changes, and disruptive selection maintains the unity of type in the wild and cultivated complexes of domesticated species.

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