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CEREALS FOR THE SEMI-ARID TROPICS

J.M.J. DE WET

International Crops Research Institute
for the Semi-Arid Tropics,
Patancheru, Andhra Pradesh,
India

Abstract

CEREALS FOR THE SEMI-ARID TROPICS.

The region of semi-arid tropics is the most famine prone area of the world. This region with nearly one billion people extends across some 20 million square kilometres. Major domesticated cereals adapted to semi-arid regions are sorghum (*Sorghum bicolor* (L.) Moench), foxtail millet (*Setaria italica* (L.) P. Beauv.) and pearl millet (*Pennisetum glaucum* (L.) R. Br.). Several minor cereals are grown as speciality crops, or harvested in the wild in times of severe drought and scarcity. Important in the African Sahel are the fonios *Digitaria iburua* Stapf, *D. exilis* (Kapist) Stapf and *Brachiaria deflexa* (Schumach.) C.E. Hubbard. These species are aggressive colonizers and are commonly encouraged as weeds in cultivated fields. Sown genotypes differ from their close wild relatives primarily in the lack of efficient natural seed dispersal. The fonios lend themselves to rapid domestication. Several wild cereals extend well beyond the limits of agriculture into the Sahara. Commonly harvested are the perennial *Stipagrostis pungens* and *Panicum turgidum*, and the annual *Cenchrus biflorus* (kram-kram). Kram-kram yields well under extreme heat and drought stress, and holds promise as a domesticated cereal. Sauwi millet (*Panicum sonorum*) is promising cereal in arid northwestern Mexico.

1. INTRODUCTION

Feeding the ever increasing human population is a major challenge facing mankind. This is particularly true in the semi-arid tropics which include the African savanna and Sahel, and significant parts of Asia, Australia and the Americas, an area of some 20 million square kilometres with nearly one billion people.¹ Cereals associated with the green revolution of the last two decades (rice, wheat and maize) are poorly adapted to the nutrient poor soils, limited rainfall and unpredictable climate of this vast region. Principal cereals are pearl millet (*Pennisetum glaucum* (L.) R. Br.), sorghum (*Sorghum bicolor* (L.) Moench) and foxtail millet (*Setaria italica* (L.) P. Beauv.). Yields of the cereals are low in comparison with yields of cereals

¹ One billion = 10⁹.

adapted to the wet tropics and temperate climates. Yield potentials, however, are excellent under conditions of limited environmental stress. To achieve self-sufficiency of cereal production within the semi-arid tropics, genotypes with tolerance, particularly to extreme conditions of drought and heat, need to be developed. There are three possible ways in which this can be accomplished. The genotypes of wheat, rice and maize must be altered to fit into the agro-ecosystems of the semi-arid tropics; native wild and semidomesticated cereals that are well adapted to a semi-arid climate must be brought into cultivation; or the genotypes of fully domesticated cereals native to the semi-arid regions must be improved to provide high and stable yields under the fluctuating environmental conditions of the region.

2. THE POTENTIAL OF WILD AND SEMIDOMESTICATED CEREALS

Wild grasses are commonly harvested as famine food. They usually produce a harvest even when the sympatric crop fails completely. Some of these wild cereals accompany crops as weeds, and are often encouraged to invade cultivated fields and under adverse conditions may yield as much as, or better than, the principal crop.

Dryland cultivation of major cereals becomes unproductive when rainfall drops much below 300 mm during the growing season. Numerous grass species extend well beyond this limit of agriculture, and several are harvested as cereals by nomadic cattle herders in Africa and Asia. Significant for potential domestication are *Stipagrostis pungens* (Desf.) de Winter that is harvested by the Tuareg of the Sahara, *Panicum turgidum* Forssk. that extends on sandy soils from arid North Africa to India, *Oryzopsis hymenoides* (Roem et Schult.) Ricker of arid North America, and *Cenchrus biflorus* Roxb. that has been used as a wild cereal in the African Sahel since prehistoric times [1-3].

The first three species mentioned are perennials, and perennial grasses are notorious for their low seed yield. They are, however, aggressive colonizers of disturbed habitats and Chevalier [2] recorded that one adult can gather 10 kg of *Panicum* florets in a morning's effort. Threshing of 10 kg of florets provides 1-2 kg of grain, a fair yield for a morning's work. *Stipagrostis pungens* is easier to harvest. The spikelets have three plumose awns that allow disarticulated spikelets to stick together and form large balls as they are dispersed by the wind. These balls are gathered by nomads in the African Sahel and the floral parts are removed by burning:

Kram-kram (*Cenchrus biflorus*) is an annual which yields well for a wild grass and is relatively easy to harvest. Grains are enclosed by thorny fascicles which disarticulate at maturity, stick together and are readily collected from around plants. The species is abundant in the African savanna and Sahel and extends into the adjacent Sahara. It is an aggressive colonizer and often occurs in large, almost pure stands. Barth [4] recorded that at Gogo on the Niger he provisioned himself and his horses with kram-kram, since no other cereal was available in the market at that time.

Several grass species that are harvested as wild cereals in the semi-arid tropics became semidomesticated [5]. They are widely distributed as natural colonizers of cultivated fields, and are consciously sown in parts of their ranges. Sown races have lost the ability of efficient natural seed dispersal. They lend themselves to rapid improvement under cultivation.

Two species of crabgrass, *Digitaria iburua* Stapf (black fonio) and *D. exilis* (Kapist) Stapf (true fonio), are cultivated in West Africa as minor cereals [6-8]. Grains are small, but yields are acceptable, and fonio is an important item of trade. Another savanna grass, *Brachiaria deflexa* (Schumach.) C.E. Hubbard (animal fonio) is extensively harvested as a wild cereal, and is cultivated in arid West Africa as a famine crop [2]. It frequently invades cultivated fields where it is harvested as a wild cereal. Fonios are frequently grown in mixtures with sorghum or pearl millet, and are harvested long before the major cereal matures. Black fonio (*D. iburua*) is an important cereal between Jos and Zaria in Nigeria. It is also sporadically grown around Zinder in Niger, in the Côte d'Ivoire, Kande and Atalote in Togo Republic, and between Birni and Nititingou in Benin [9]. True fonio (*D. exilis*) and animal fonio (*B. deflexa*) are cultivated primarily in northern Nigeria, but extend into northern Togo and adjacent Benin, northwestern Mali, Guinea, eastern Sierra Leone, Senegal and the Gambia [10]. The fonios are native to the West African savanna and Sahel, and some genotypes are extremely drought tolerant. They yield a crop under adverse conditions where sorghum and even pearl millet fail completely. Little is known about their yield potential. Their rapid life cycle makes them potential major crops in areas with a short growing season owing to limited rainfall.

Sauwi millet (*Panicum sonorum* Beal) of the New World is another promising cereal for the semi-arid tropics. Wild and weedy races occur naturally from southern Arizona to Honduras. In northwestern Mexico and adjacent Arizona, the species favours open woodlands and barrancas. Palmer [11] recorded that it also grew on bars and moist sites of the Colorado River. It is relished by grazing animals and was harvested as a wild cereal by Indian tribes on the flood plains of the Colorado at least until the beginning of the twentieth century [12]. Sauwi is grown as a cereal in Mexico by Mayo farmers of the Sonora and adjacent Chihuahua [13, 14]. The species is extremely drought tolerant and competes well as a secondary crop in maize fields. Grains are small (1.8-3.0 mm long), but under ideal conditions a single plant produces as many as 2500 spikelets.

Domestication of wild cereals is no easy task [15]. This is particularly true of perennials. Among wild cereals of the African Sahel and Sahara, *Cenchrus biflorus* holds the most promise. It is an aggressive natural colonizer of cultivated fields. It lacks excessive seed dormancy, and selection for loss of efficient natural seed dispersal should be feasible. The hard, thorny floral structures that surround the grain will pose an initial problem in domestication. The closely related *Cenchrus ciliaris* L., however, has races with thorny or plumose fascicles, suggesting that plumose genotypes may also occur in kram-kram.

The semidomesticated fonios and sauwi millet lend themselves to rapid improvement by modern plant breeding techniques. They are adapted to cultivation and have lost the ability of efficient natural seed dispersal, essential adaptations for successful domestication. They are further adapted to cultivation in a mixture with other crops and are highly competitive with weeds, both advantageous adaptations for cultivation in subsistence agro-ecosystems.

3. MINOR CEREALS AS SECONDARY CROPS IN THE SEMI-ARID TROPICS

Food production in the semi-arid tropics depends to a large degree on the efficiency of the farmer whose primary concern is self-sufficiency. Surpluses depend as much on improved farming systems and genetically improved cultivars, as on incentives for increased production. An integral part of successful subsistence farming is multicrop cultivation in which minor cereals are playing an ever increasingly important role. Minor cereals are grown for home consumption together with a major cereal or other crop that is harvested to supply cash income.

Interplanting sorghum or pearl millet with fonios (*Digitaria exilis*, *D. iburua* and *Brachiaria deflexa*) in Africa, and with foxtail millet (*Setaria italica*) or pigeon pea (*Cajanus cajan*) is common in India. In the Eastern Ghats of India, sorghum or pearl millet is often interplanted with sawa millet (*Echinochloa colona* (L.) P. Beauv.), kodo millet (*Paspalum scrobiculatum* L.), sama millet (*Panicum sumatrense* Roth. ex Roem. et Schult.), korali millet (*Setaria pumila* (Poir.) Roem. et Schult.) or peda sama (*Brachiaria ramosa* (L.) Stapf.). These minor cereals are not truly drought tolerant, but genotypes grown in multicrop systems have such short growing cycles that they mature within the short low stress period of usually adequate moisture. These minor cereals are also interplanted with finger millet (*Eleusine coracana* (L.) Gaertn.).

Finger millet is native to the highlands of eastern Africa, but is widely grown in India and South East Asia. Along the western foothills of the Eastern Ghats of Andhra Pradesh, finger millet is germinated in nurseries and seedlings are transplanted to fields with the first rains to mature before moisture stress becomes severe. Somewhat similar techniques are practised elsewhere in the world. In the Dire-Goundam-Lake Faguibine area of Mali, with a rainfall of about 250 mm annually, sorghum and pearl millet are sown on the flood plains of the Niger and Bani rivers. To make use of all available arable lands, areas that dry late in the season are planted with nursery grown sorghum plants [16]. Hopi farmers of arid New Mexico and Arizona plant maize in pits several feet² deep and add soil as the seedlings emerge and the stems elongate to make efficient use of available moisture

² One foot = 30.48 cm.

Minor millets are not the only crops that are interplanted with sorghum, pearl millet and maize. Grain legumes are important in multicrop farming systems. Beans (*Phaseolus* species) are interplanted with maize in the New World, in Africa the cowpea (*Vigna unguiculata* (L.) Wasp) is grown with sorghum or maize, and in India pigeon pea (*Cajanus cajan*) is an integral part of subsistence cereal farming in combination with sorghum or pearl millet. Experiments at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) demonstrated that monoculture of sorghum or groundnut (*Arachis hypogaea*) under ideal conditions yields 5000 kg/ha, but only 100 to 900 kg/ha under severe stress. Intercropping groundnut with sorghum results in yields which drop less rapidly than sole crop yields when stress increases. Under severe drought and heat stress, intercropping produces individual yields well above those of either sorghum or groundnut in monoculture [17].

4. MAJOR CEREALS FOR THE SEMI-ARID TROPICS

Three major cereals, sorghum (*Sorghum bicolor*), pearl millet (*Pennisetum glaucum*) and foxtail millet (*Setaria italica*) are naturally adapted to cultivation in arid habitats. Maize (*Zea mays* L.) has potential in some areas of the semi-arid tropics, but yields of available drought tolerant genotypes are low.

The closest wild relative of foxtail millet is *Setaria italica* ssp. *viridis* (L.) Thell. (green foxtail). This natural colonizer is native to temperate Eurasia and has become established as an introduced weed in temperate parts of the New World.

Derivatives of hybrids between green and cultivated foxtail millets are obnoxious weeds in Europe, Asia and the American cornbelt. The species was domesticated as a cereal in Asia and has been grown in the loess highlands of Central China for at least 7000 years. Comparative morphology suggests that this cereal spread to Europe soon after domestication. Foxtail millet has been grown in Austria and Switzerland for at least 3000 years [18, 19]. The date when foxtail millet was introduced and became adapted to the semi-arid tropics of South Asia is not known. It is now cultivated across temperate Eurasia and tropical India, Sri Lanka and South East Asia.

Foxtail millet is extensively variable in habitat preference and morphology [20, 21]. Races *moharia*, *indica* and *maxima* are recognized [22]. *Moharia* resembles wild *S. italica* ssp. *viridis* in inflorescence morphology, tillering of individual plants, and culm branching with each branch bearing an inflorescence. *Moharia* cultivars differ from wild green foxtail primarily in loss of efficient natural seed dispersal and more synchronized tillering. These traits allow for ease in harvesting under cultivation. A majority of inflorescences matures at the same time and spikelets disarticulate tardily. *Moharia* is adapted to a temperate agro-ecosystem.

Race *maxima* is an important cereal in northwestern China and adjacent Mongolia. It is also grown in the Democratic People's Republic of Korea, the

Republic of Korea and Japan, and to a limited extent in southern China. Plants tiller infrequently, with each culm bearing a large and usually solitary inflorescence. This race yields well in single crop cultivation, but does poorly in competition with other crops or under conditions of stress. It is not adapted for cultivation in the tropics.

Tropical cultivars of foxtail millet belong to race *indica*. They are intermediate in morphology between cultivars of races *moharia* and *maxima*. Cultivars from Nepal and Assam appear to be derivatives of hybrids between races *maxima* and *indica*. Race *indica* is grown as a single crop in commercial planting where rainfall is as low as 600 mm during the kharif (rainy) season. It is also extensively grown as a secondary crop with sorghum or pearl millet. The number of days to flowering ranges from 32–57 and early maturing kinds are harvested before the major cereal comes into flower.

Grain sorghum is native to the African savanna. It was introduced to India and the rest of Asia before historical times [23]. It is grown in areas with as little as 500 mm of annual rainfall, but is best adapted to areas with substantially higher rainfall during the growing season. The wild progenitor of grain sorghum is *S. bicolor* ssp. *verticilliflorum* (Steud.) Piper. The closest wild relative of grain sorghum is the savanna race *verticilliflorum*. Wild ssp. *verticilliflorum* extends into tropical forests (race *arundinaceum*) and the Sahel (race *aethiopicum*). These wild sorghums cross with grain sorghum to produce fertile hybrids, and can possibly be used to increase the agronomic fitness of the crop in the semi-arid tropics.

Grain sorghum is classified into five ecogeographic races [24–26]. Race *bicolor* resembles wild ssp. *verticilliflorum* in inflorescence morphology. Cultivars are low yielding, rarely important as a crop, and widely distributed across the natural range of grain sorghum in Africa. Race *caffra* is the most important native cereal in the African savanna. It is closely related to race *caudatum* of Chad and adjacent Sudan, Nigeria and Uganda. Derivatives of hybrids between races *caffra* and *caudatum* are grown across the African savanna and form the basis of high yielding commercial cultivars. Race *guinea* is the principal sorghum of high rainfall areas of West and Eastern Africa. It is also grown in Asia. Introgression with race *durra* in northern Nigeria gave rise to high yielding cultivars with excellent drought tolerance. The most drought tolerant grain sorghums belong to race *durra*. This race is widely grown in the Sahel, West Asia and arid parts of India.

Farmers in the semi-arid tropics produce some 55% of the world's sorghum. World production of sorghum in 1984 was 71 898 000 t [27]. Asia produced 21.8 million t and Africa produced 9 million t. It has been estimated that as much as 65% of total annual sorghum production in Africa and Asia is by subsistence farmers. Yield potential of sorghum is well above 7000 kg/ha. Average yields in the semi-arid tropics, however, are 587 kg/ha in Africa, and 715 kg/ha in India [27]. Lowest average yields in 1984 were 171 kg/ha in Botswana, and 235 kg/ha in Niger. In these countries sorghum is planted up to its limit of natural drought tolerance in regions with less than 500 mm of annual rainfall.

Pearl millet is the best adapted of major cereals to drought prone areas. Its closest wild relatives, *P. violaceum* (Lam.) L. Rich and *P. fullax* (Fig. and de Not.) Stapf and C.E. Hubbard are distributed across the West African savanna and Sahel in areas with a mean annual rainfall of 250–850 mm [10]. Pearl millet was domesticated some 3000 years ago along lake edges in what is now the Sahara [3, 28]. It is the most important cereal in the dry Sahel zone bordering the Sahara, and in the arid regions of India.

Pearl millet is extensively variable and was divided into races *typhoides*, *nigritarum*, *globosum* and *leonis* on the basis of grain shape [28, 29]. *Typhoides* cultivars have obovate grains and occur across the Sahel and the savanna. They are also extensively grown in India. Inflorescences are cylindrical or elliptical in shape. Race *nigritarum* has obovate grains as is typical for *typhoides*, but the grains are angular rather than obtuse in cross-section. Inflorescences range from 10 cm to 120 cm in length. Their centre of distribution stretches from northern Nigeria to western Sudan. Race *globosum* has spherical grains. It occurs across the millet zone of West Africa, with a center of importance in the central Sahel. Race *leonis* is characterized by acute, oblanceolate grains, and its cultivation is centered in Sierra Leone. Distribution and morphological variations of West African pearl millet are discussed by Clement [30].

Pearl millet is extensively grown in regions with an annual rainfall of between 400 mm and 1000 mm. In more favourable climates, it is replaced by sorghum or maize. It can be successfully grown in areas with as little as 250 mm of annual rainfall. Average yields in 1984 ranged from 70 kg/ha in Botswana to 1800 kg/ha in Sierra Leone [27]. Subsistence farmers of the semi-arid tropics produce some 95% of the world's annual pearl millet harvest. In West Africa alone about 6.7 million t of pearl millet are produced on some 11.5 million ha.

5. BREEDING

Cereal yields in the semi-arid tropics are affected by several environmental factors. Rainfall and temperature are important, but so are diseases and pests, competition with weeds, soil fertility, choice of species and farming practices. Superimposed on the subsistence agro-ecosystem of this region is the economics of cereal production. Average yields of sorghum in the United States of America increased from around 2300 kg/ha in 1960 to 3300 kg/ha in 1970, to around 3500 kg/ha in 1980. In Africa and India, average yields during this period remained essentially stable at around 700 kg/ha. The rise in yield in the USA resulted from a combination of breeding and improved farming practices.

In Africa and India, urban consumers prefer rice, wheat or maize, and the prices for sorghum and pearl millet are substantially lower than those of the preferred cereals. For the subsistence farmer to produce a surplus of sorghum or pearl millet

an input of resources is often required that cannot profitably be recovered through higher yields. Sorghum and pearl millet are therefore grown primarily where more desirable cereals fail because of environmental conditions.

Breeding strategies must take into account farming practices. Economic policies exclude a drastic change in farming practices during the foreseeable future. Genotypes are needed with an acceptable yield under conditions of minimum resource input and high environmental stress. Yields will never be as high as those achieved under ideal farming conditions. Percentage yield increases, however, are possible.

ICRISAT has in its geoplasm bank some 1500 collections of foxtail millet, 18 000 of pearl millet and 28 000 of sorghum [31]. During the last decade the Office de la recherche scientifique et technique outre-mer (ORSTOM) has collected cereal germplasm across West Africa [30]. Collections of foxtail and other millets are also being assembled by the Zentralinstitut für Genetik und Kulturpflanzenforschung der Akademie der Wissenschaften of the German Democratic Republic. Scientists are systematically screening this germplasm for agronomic fitness traits. Resistance to grain mould, leaf diseases, shoot fly, stem borer, head bug, midge and *Striga*, as well as drought and heat tolerance, have been identified in cultivated or wild accessions of sorghum and pearl millet. High yielding land races are now being converted into genotypes with relatively short stature and day-long insensitivity. Also, disease and pest resistance traits are being introduced into standard sorghum and pearl millet breeding lines by plant breeders.

Genotype improvement is a long term and often unrewarding task. Progress is based on well established breeding techniques, but speed of progress is to some degree determined by chance. The genetics of disease and insect resistance, competitive ability, grain quality and yield are to a large extent unknown in sorghum and pearl millet. Furthermore, breeding of cultivars adapted to an agro-ecosystem with high and variable stress is far more difficult and time consuming than breeding for high yield under ideal farming conditions.

High yielding sorghum and millet are based on genetic heterosis derived from highly selected inbreds. Hybrids are genetically uniform and display high agronomic fitness to a predictable and environmentally uniform agricultural habitat. Farmers who can afford to buy hybrid seeds, supply nutrients to the soil, and apply herbicides and pesticides when necessary obtain yields of sorghum of over 4 t/ha and 2 t/ha of pearl millet. Hybrids are easy to produce. Cytoplasmic male sterility is available in both sorghum and pearl millet.

Subsistence farmers, on the other hand, often have only the financial resources to purchase seeds and prepare the land for planting. Fertilizers are rarely used, and herbicides and pesticides are seldomly available. Genetically uniform cultivars are generally not well adapted to such an agro-ecosystem. Genetically buffered cultivars with yield stability in the form of mixed genotypes need to be developed. They will never yield as well as genetically uniform hybrids, but a balanced population system can yield well under conditions of variable stress as well as under ideal conditions.

Natural selection will maintain this balanced genetic system during periods of average stress. Ideally the population will have disease and pest resistance, have high competitive ability, tolerance to climatic fluctuations, and yield well.

REFERENCES

- [1] DUVEYRIER, H., *Les Touareg du Nord*, Challamel Aine, Libraire-Editeur, Paris (1864).
- [2] CHEVALIER, A., *Ressources vegetales du Sahara et de ses confins nord et sud*, Mus. d'Hist. Nat. d'Agron. Colon., Paris (1932) 256.
- [3] MUNSON, P.J., "Archaeological data on the origins of cultivation in southwestern Sahara and their implications for West Africa", *Origins of African Plant Domestication* (HARLAN, J.R., DE WET, J.M.J., STEMLER, A.B.L., Eds), Mouton Press, The Hague (1976) 187-209.
- [4] BARTH, H., *Travels and Discoveries in North and Central Africa*, 3 vols, Harper Bros., New York (1857).
- [5] DE WET, J.M.J., *Species concepts and systematics of domesticated cereals*, *Kulturpflanzen* 29 (1981) 177-198.
- [6] BUSSON, F., *Plantes alimentaires de l'ouest Africain*, L'Imprimerie Leconte, Marseille (1965).
- [7] JARDIN, C., *List of Foods Used in Africa*, FAO Rome Publ. (1967) 320.
- [8] PORTERES, R., "African cereals: *Eleusine*, fonio, black fonio, teff, *Brachiaria*, *Paspalum*, *Pennisetum* and African rice", *Origins of African Plant Domestication* (HARLAN, J.R., DE WET, J.M.J., STEMLER, A.B.L., Eds), Mouton Press, The Hague (1976) 409-452.
- [9] PORTERES, R., *Les cereales mineures du genre *Digitaria* en Afrique et Europe*, *J. Agric. Trop. Bot. Appl.* 2 (1955) 349-675.
- [10] CLAYTON, W.D., "Gramineae", *Flora of West Tropical Africa* (HUTCHINSON, J., DALZIET, J.M., Eds), 2nd edn., Vol. 3 (1972) 349-574.
- [11] PALMER, E., *Food products of the North American Indians*, Rep. Commiss. Agric. 1870 (1981) 404-428.
- [12] FORBES, R.H., *The Colorado river west, Ariz. Mon.* 6 (1904) 119-126.
- [13] CENTRY, H.S., *The Warihio Indians of Sonora-Chihuahua: an ethnographic survey*, *Bur. Am. Ethnol. Bull.* 186 (1963) 61-144.
- [14] NABHAN, G., DE WET, J.M.J., *Panicum sonorum* in Sonoran desert agriculture, *Econ. Bot.* 38 (1984) 65-82.
- [15] HARLAN, J.R., DE WET, J.M.J., PRICE, E.G., *Comparative evolution of cereals*, *Evolution* 27 (1973) 311-325.
- [16] HARLAN, J.R., PASQUEREAU, J., *Decrue Agriculture in Mali*, *Econ. Bot.* 23 (1969) 70-74.
- [17] WILLEY, R.W., RAO, M.R., REDDY, M.S., NATARAJAN, M., "Cropping systems with sorghum", *Sorghum in the Eighties* (HOUSE, L.R., MUGHOGHO, L.K., PEACOCK, J.M., Eds), *International Crops Research Institute for the Semi-Arid Tropics*, Patancheru (1982) 477-490.

- [18] HEER, O., Pflanzen der Pfahlbauten, Neujahrblatt Naturforsch. Gesellsch., Zurich (1866).
- [19] WERTH, E., Zur Geographie and Geschichte der Hirsen, Angewandte Bot. 19 (1937) 42-88.
- [20] DEKAPRELEVICH, L.L., KASPARIAN, A.S., A contribution to the study of foxtail millet (*Setaria italica* P. Beauv. *maxima* Alf.) cultivated in Georgia (western Transcaucasia), Bull. Appl. Bot. Plt. Breed. 19 (1928) 533-572.
- [21] GRITZENKO, R.J., Chumiza (Italian millet) taxonomy (*Setaria italica* (L.) P. Beauv. ssp. *maxima* Alef.), Bull. Appl. Bot. Genet. Plt. Breed 32 (1960) 145-182.
- [22] DE WET, J.M.J., DESTRY-STIDD, L.L., CUBERO, J.I., Origins and evolution of foxtail millets (*Setaria italica* (L.) P. Beauv.), JATBA 26 (1979) 53-64.
- [23] HARLAN, J.R., STEMLER, A., "The races of sorghum in Africa", Origins of African Plant Domestication (HARLAN, J.R., DE WET, J.M.J., STEMLER, A.B.L., Eds), Mouton Press, The Hague (1976) 465-478.
- [24] DE WET, J.M.J., HUCKABAY, J.P., The origin of *Sorghum bicolor*. II. distribution and domestication, Evolution 21 (1967) 787-802.
- [25] HARLAN, J.R., DE WET, J.M.J., A simplified classification of cultivated sorghum, Crop Sci. 12 (1972) 172-176.
- [26] DE WET, J.M.J., Systematics and evolution of *Sorghum* section *Sorghum* (Gramineae), Am. J. Bot. 65 (1978) 477-484.
- [27] FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS, FAO Production Year Book 38 (1984) 120-121.
- [28] BRUNKEN, J.N., DE WET, J.M.J., HARLAN, J.R., The morphology and domestication of pearl millet, Econ. Bot. 31 (1977) 163-174.
- [29] BRUNKEN, J.N., A systematic study of *Pennisetum* section *Pennisetum* (Gramineae), Am. J. Bot. 64 (1977) 161-176.
- [30] CLEMENT, J.C., Les mils Penicillaires de l'Afrique de l'ouest, International Board of Plant Genetic Resources, Rome (1985) 231.
- [31] MENGESHA, M.H., PRASADA RAO, K.E., "Current situation and future of sorghum germplasm", Sorghum in the Eighties (HOUSE, L.R., MUGHOGHO, L.K., PEACOCK, J.M., Eds), International Crops Research Institute for the Semi-Arid Tropics, Patancheru (1982) 323-334.

- [18] HEER, O., Pflanzen der Pfahlbauten, Neujahrblatt Naturforsch. Gesellsch., Zurich (1866).
- [19] WERTH, E., Zur Geographie and Geschichte der Hirsen, Angewandte Bot. 19 (1937) 42-88.
- [20] DEKAPRELEVICH, L.L., KASPARIAN, A.S., A contribution to the study of foxtail millet (*Setaria italica* P. Beauv. *maxima* Alf.) cultivated in Georgia (western Transcaucasia), Bull. Appl. Bot. Plt. Breed. 19 (1928) 533-572.
- [21] GRITZENKO, R.J., Chumiza (Italian millet) taxonomy (*Setaria italica* (L.) P. Beauv. ssp. *maxima* Alef.), Bull. Appl. Bot. Genet. Plt. Breed 32 (1960) 145-182.
- [22] DE WET, J.M.J., DESTRY-STIDD, L.L., CUBERO, J.I., Origins and evolution of foxtail millets (*Setaria italica* (L.) P. Beauv.), JATBA 26 (1979) 53-64.
- [23] HARLAN, J.R., STEMLER, A., "The races of sorghum in Africa", Origins of African Plant Domestication (HARLAN, J.R., DE WET, J.M.J., STEMLER, A.B.L., Eds), Mouton Press, The Hague (1976) 465-478.
- [24] DE WET, J.M.J., HUCKABAY, J.P., The origin of *Sorghum bicolor*. II. distribution and domestication, Evolution 21 (1967) 787-802.
- [25] HARLAN, J.R., DE WET, J.M.J., A simplified classification of cultivated sorghum, Crop Sci. 12 (1972) 172-176.
- [26] DE WET, J.M.J., Systematics and evolution of *Sorghum* section *Sorghum* (Gramineae), Am. J. Bot. 65 (1978) 477-484.
- [27] FOOD AND AGRICULTURAL ORGANIZATION OF THE UNITED NATIONS, FAO Production Year Book 38 (1984) 120-121.
- [28] BRUNKEN, J.N., DE WET, J.M.J., HARLAN, J.R., The morphology and domestication of pearl millet, Econ. Bot. 31 (1977) 163-174.
- [29] BRUNKEN, J.N., A systematic study of *Pennisetum* section *Pennisetum* (Gramineae), Am. J. Bot. 64 (1977) 161-176.
- [30] CLEMENT, J.C., Les mils Penicillaires de l'Afrique de l'ouest, International Board of Plant Genetic Resources, Rome (1985) 231.
- [31] MENGESHA, M.H., PRASADA RAO, K.E., "Current situation and future of sorghum germplasm", Sorghum in the Eighties (HOUSE, L.R., MUGHOGHO, L.K., PEACOCK, J.M., Eds), International Crops Research Institute for the Semi-Arid Tropics, Patancheru (1982) 323-334.