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Millets: Genetic and Genomic Resources

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ABSTRACT

Small-grained millets, comprising ten annual grasses from the family Poaceae and grown for grain, contribute ~13% of annual global cereal production. Some are widely grown, while cultivation of others is restricted. They differ in ploidy, genome size, and breeding system, but their grains are all highly nutritious. Their most common nonfood uses are in brewing and as livestock feeds. Millets are C₄ plants adapted to marginal lands in hot, drought-prone arid and semiarid regions. Selection for plant phenology and architecture, panicle shape, spikelet structure and reduced shattering, seed dormancy, and seed coat hardness contributed to their domestication. Approximately 161,708 millet accessions are preserved in gene banks globally. These show exceptional diversity associated for phenology, photoperiod sensitivity, tolerance to abiotic stresses, resistance to biotic stresses, seed storability and shelf life, and specific grain characteristics associated with end user preferences. Contributions from wild relatives' toward enhancing cultivated gene pools have been limited to pearl millet and foxtail millet. Core or minicore/reference collections have been used to identify new sources of biotic stress resistances and abiotic stress tolerances. Waxy mutants have been selected in barnyard millet, foxtail millet, and proso millet for specific food uses. Pearl millet hybrids and open pollinated varieties (OPVs) with high iron and zinc grain densities will soon be available in India. While no transgenic work has reached field level, DNA markers are routinely used to assess millets' population structure and genetic diversity. Genetic maps of varying density are reported in finger millet, foxtail millet, pearl millet, proso millet, and tef. Major quantitative trait loci associated with resistance to downy mildew, rust, and blast and tolerance to terminal drought stress have been backcrossed into elite inbred pearl millet hybrid parents. Marker-assisted backcrossing has been used to improve downy mildew resistance in pearl millet. Cytoplasmic-genetic male sterility (CMS)-based hybrids of pearl millet are extensively cultivated, and CMS systems for foxtail millet are under development. An aligned genome sequence of foxtail millet will be released in the near future as this millet is closely related to several polyploid bioenergy grasses. This foxtail millet genome sequence is highly syntenic with those of rice, sorghum, and maize, which should allow comprehensive surveys of genetic diversity for identifying and conserving diversity in grass germplasm with bioenergy crop potential.

KEYWORDS: diversity; domestication; genetic markers; genome syntenicity; phylogeny; population structure; quantitative trait loci; stress tolerance

LIST OF ABBREVIATIONS

- I. INTRODUCTION
 - II. NUTRITIONAL QUALITY AND FOOD, FEED, MEDICINAL, AND OTHER USES
 - III. DOMESTICATION, PHYLOGENETIC, AND GENOMIC RELATIONSHIPS
 - IV. ASSESSING PATTERNS OF DIVERSITY IN GERMPLASM COLLECTIONS
 - V. IDENTIFYING GERMPLASM WITH BENEFICIAL TRAITS
 - A. Resistance to Biotic Stresses
 1. Phenotypic Screening
 2. Natural Genetic Variation
 3. Pathogen Variability, Mechanism, and Genetics of Resistance
 - B. Tolerance to Abiotic Stresses
 1. Drought
 2. Salinity
 3. Low Temperature
 4. Lodging
 5. Waterlogging
 - C. Seed Quality
 - VI. GENOMIC RESOURCES
 - A. Markers and Genetic Linkage Maps
 - B. Characterization and Functional Validation of Genes Associated with Important Traits
 - C. Genomic and Genetic Tools to Sequence the Foxtail Millet Genome
 - VII. ENHANCING USE OF GERMPLASM IN CULTIVAR DEVELOPMENT
 - A. Core, Mini-Core and Reference Sets for Mining Allelic Diversity and Identifying New Sources of Variation
 - B. Assessing Population Structure and Diversity in Germplasm Collections
 - C. Promoting Use of Male Sterility as an Aid in Crossing
 - VIII. FROM TRAIT GENETICS TO ASSOCIATION MAPPING TO CULTIVAR DEVELOPMENT USING GENOMICS
 - A. Markers/QTL Associated with Agronomic Traits, Abiotic Stress Tolerance, Biotic Stress Resistance, and Product Quality
 - B. Marker-Aided Introgressions of Disease Resistance
 - C. Marker-Aided Introgressions to Enhance Drought Tolerance
 - D. Use of Rice, Maize, Sorghum, and Foxtail Millet Genome Sequences to Strengthen Molecular Breeding Tools
 - E. Exploiting Variation at Waxy Locus to Diversify Food Uses
 - F. Foxtail Millet, Sorghum and Maize Genome Sequences as Resources for Identifying Variation Associated with High Biomass Production in Bioenergy Grasses
 - IX. CONCLUSIONS AND FUTURE PROSPECTS
- ACKNOWLEDGMENTS
- LITERATURE CITED

LIST OF ABBREVIATIONS

AFLP	Amplified fragment length polymorphism
AICPMIP	All India Coordinated Pearl Millet Improvement Project
BEP	Bambusoideae, Ehrhartoideae, Pooideae
BP	Before present
Bp	Base pair
cDNA	Complementary deoxyribonucleic acid
cDNA–AFLP	Complementary deoxyribonucleic acid–amplified fragment length polymorphism
CISP	Conserved intron scanning primers
CMS	Cytoplasmic-genetic male sterility
CO ₂	Carbon dioxide
DArT	Diversity arrays technology
DNA	Deoxyribonucleic acid
DM	Downy mildew
EST	Expressed sequence tag
FAO	Food and Agriculture Organization
WHO	World Health Organization
Fe	Iron
GBSS I	Granule-bound starch synthase I
GCP	Generation Challenge Program
HDL	High-density lipoprotein
ISSR	Inter-simple sequence repeats
ITS	Internal transcribed spacer
LDL	Low-density lipoprotein
LG	Linkage group
MABC	Marker-assisted backcrossing
Mbp	Million base pair
MRL	Maximum root length
mRNA	Messenger ribonucleic acid
Na	Sodium
NC7	North Central Regional PI Station
NSSL	National Center for Genetic Resource Preservation
OA	Osmotic adjustment
PACCAD	Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Aristidoideae, Danthonioideae
PCR	Polymerase chain reaction
PGQO	Plant Germplasm Quarentine Program
P5C	Pyrroline-5-carboxylate
QTL	Quantitative trait loci
QTL-NIL	QTL near-isogenic line

RAPD	Rapid amplified polymorphic DNA
rDNA	Ribosomal deoxyribonucleic acid
RFLP	Restriction fragment length polymorphism
RILs	Recombinant Inbred Lines
S9	Southern Regional PI Station
SNP	Single-nucleotide polymorphism
SSCP–SNP	Single-strand conformation polymorphism–single nucleotide polymorphism
SSR	Simple sequence repeat
TILLING	Targeting Induced Local Lesions in Genomics
Tr	Transpiration rate
UPGMA	Unweighted pair group method arithmetic mean
VPD	Vapor pressure deficit
W6	Western Regional PI Station
WUE	Water use efficiency
Zn	Zinc

I. INTRODUCTION

Cereals (rice, wheat, maize, barley, sorghum, millets, oats, rye, and triticale) contributed on average 255.1 million tonnes annually to world food production during the period from 2004 to 2008, of which the millet share was 12.7% (32.3 mt). Millets are comprised of a number of small-grained, annual cereal grasses that include several distinct species: pearl millet (*Pennisetum glaucum*), finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), proso millet (*Panicum miliaceum*), little millet (*Panicum sumatrense*), barnyard millet [*Echinochloa crus-galli* (Japanese) and *E. colona* (Indian)], kodo millet (*Paspalum scrobiculatum*), tef (*Eragrotis tef*), fonio [*Digitaria exilis* (white fonio) and *D. iburua* (black fonio)], guinea millet (*Brachiaria deflexa*), and Job's tears (*Coix lacrym-jobi*). Taxonomically, these millets belong to the Poaceae but differ either at species, genus, tribe, or subfamily hierarchy; ploidy levels (pearl millet and foxtail millet are diploids; finger millet, proso millet, tef, fonio, and Job's tears are tetraploids; barnyard millet is hexaploid); genome size [foxtail millet has the smallest genome, 490 million base pair (Mbp) (Bennett et al. 2000) while finger millet, 2509 Mbp (Bennett and Leitch 1995) and pearl millet, 2352 Mbp (Bennett et al. 2000) have the largest genomes among other millets studied for genome size variation]; and breeding systems (pearl millet being highly outbreeding, Job's tears with mixed mating—inbreeding and outbreeding, and the

remaining millets with high levels of inbreeding with some outcrossing (0.3%– 4%) in foxtail millet, *Setaria italica*, and its wild ancestor, *S. viridis* (Li et al. 1945; Till-Bottraud et al. 1992) (Table 5.1). Natural outcrossing in the range of 0.2% to 1% has also been reported for tef (Ketema 1993). Wild relatives of these millets possess even greater taxonomic diversity. For example, barnyard millet relatives vary from tetraploid to octaploid; those of finger millet are all diploid; relatives of foxtail millet and Job's tears vary from diploid to octaploid; those of pearl millet from diploid to hexaploid; while kodo millet, little millet, proso millet, and tef are tetraploid (Table 5.2). Furthermore, both sexual and asexual (apomictic) forms of reproduction have been reported among pearl millet's wild relatives. Most of these wild species are annuals; however, some of the foxtail millet and pearl millet wild relatives have both annual and perennial life-forms (Table 5.2). Other minor millets include *Brachiara ramosa*, *Setaria glauca*, *Echinochloa turneriana*, *Echinochloa oryzicola*, and *Panicum hirticaule* var. *hirticaule* (Hirosue and Yabuno 2002; Kimata et al. 2000). *Brachiara ramosa* is cultivated in pure stands while *Setaria glauca* in mixed stands along with little millet, and the grains are used as traditional foods in southern India (Kimata et al. 2000). The cultivated form of *E. oryzicola* is characterized by large spikelets with nonshattering habit and no innate dormancy (Hirosue and Yabuno 2002).

The millets have abundant within-species racial diversity. In finger millet, there are five races (*coracana*, which resembles the subsp. *africana*, *vulgaris*, *compacta*, *plana*, and *elongata*) (Dida and Devos 2006) and 10 subraces (*laxa*, *reclusa*, and *sparsa* in *elongata*; *seriata*, *confundera*, and *grandigluma* in *plana*; *liliacea*, *stellata*, *incuriata*, and *digitata* in *vulgaris*). The race *compacta* in finger millet has no subraces. Foxtail millet has three races (*moharia*, *maxima*, and *indica*) and ten subraces (*aristata*, *fusiformis*, and *glabra* in *moharia*; *compacta*, *spongiosa*, and *assamense* in *maxima*; and *erecta*, *glabra*, *nana*, and *profusa* in *indica*). Proso millet has five races: *miliaceum*, *patentissimum*, *contractum*, *compactum*, and *ovatum*, while little millet (subsp. *sumatrense*) has two races, *nana* and *robusta*, each with two subraces: *laxa* and *erecta* in the former and *laxa* and *compacta* in the latter. Barnyard millet has two cultivated species, the Indian barnyard millet (*Echinochloa colona*) and Japanese barnyard millet (*E. crus-galli*), each with two ssp.: *colona* and *frumentacea* in the former and *crus-galli* and *utilis* in the latter. Subspecies *colona* has no races, while ssp. *frumentacea* has four races: *stolonifera*, *intermedia*, *robusta*, and *laxa*. Both ssp. *crus-galli* and *utilis* each have two races: *crus-galli* and *macrocarpa* in the former and *utilis* and *intermedia* in the latter. The three races in kodo millet are

Table 5.1. Taxonomic relationships of ten cereals belonging to millets group of crops.

Common name	Subfamily	Tribe	Genus	Species	Ploidy	Chrom. no.	Reference
Barnyard millet	Panicoideae	Paniceae	<i>Echinochloa</i>	<i>E. colona</i>	Hexaploid	36	Wanous 1990; de Wet et al. 1983
Finger millet	Chloridoideae	Eragrosteae	<i>Eleusine</i>	<i>E. crus-galli</i> <i>E. coracana</i>	Tetraploid	36	Wanous 1990; Bisht and Mukai 2001
Fonio	Panicoideae	Paniceae	<i>Digitaria</i>	<i>D. exilis</i> <i>D. iburua</i>	Tetraploid	36	Adoukonou-Sagbadja et al. 2007; Wanous 1990
Foxtail millet	Panicoideae	Paniceae	<i>Setaria</i>	<i>S. italica</i>	Diploid	18	Wanous 1990; Bennett et al. 2000
Job's tears	Maydeae	Andropogoneae	<i>Coix</i>	<i>C. lacryma-jobi</i>	Tetraploid	20	Clayton 1981; Wanous 1990
Kodo millet	Panicoideae	Paniceae	<i>Paspalum</i>	<i>P. scrobiculatum</i>	Tetraploid	36	Wanous 1990
Little millet	Panicoideae	Paniceae	<i>Panicum</i>	<i>P. sumatrense</i>	Tetraploid	36	Wanous 1990; Hiremath et al. 1990
Pearl millet	Panicoideae	Paniceae	<i>Pennisetum</i>	<i>P. glaucum</i>	Diploid	14	Wanous 1990; Bennett et al. 2000
Proso millet	Panicoideae	Paniceae	<i>Panicum</i>	<i>P. miliaceum</i>	Tetraploid	36	Baltensperger 1996; Hiremath et al. 1990; Zeller 2000
Tef	Chloridoideae	Eragrosteae	<i>Eragrostis</i>	<i>E. tef</i>	Tetraploid	40	Wanous 1990; Ingram and Doyle 2003

Table 5.2. Differences in ploidy level, chromosome number, reproductive behavior, mating system and life form among selected wild relatives of millets species.

Species	Ploidy	Chromosome number	Reproductive behavior	Mating system	Life form	Reference
Barnyard millet						
<i>E. colona</i>	Tetraploid, hexaploid, octaploid	36, 54, 72	Sexual	Inbreeder	Annual	Wanus 1990; de Wet et al. 1983
<i>E. crusgalli</i>	Tetraploid, hexaploid	36, 54	Sexual	Inbreeder	Annual	
<i>E. oryzoides</i>	Tetraploid	36				
Finger millet						
<i>E. indica</i> (A genome)	Diploid	18	Sexual	Not reported	Annual	NRC 1996; Bisht and Mukai 2001;
<i>E. floccifolia</i>	Diploid	18	Not reported	Not reported	Perennial	Neves et al. 2005;
<i>E. tristachya</i>	Diploid	18	Not reported	Not reported	Annual	Anderson and de
<i>E. intermedia</i>	Diploid	18	Not reported	Not reported	Perennial	Vicent 2010
<i>E. verticillata</i>	Diploid	18	Not reported	Not reported	Not reported	
<i>E. multiflora</i>	Diploid	16	Not reported	Not reported	Annual	
<i>E. jaegeri</i>	Diploid	20	Not reported	Not reported	Perennial	
<i>E. coracana</i> subsp. <i>africana</i>	Tetraploid	36	Sexual	Inbreeder	Annual	
<i>E. spontanea</i>	Not reported	Not reported	Sexual	Inbreeder	Annual	
<i>E. kigeziensis</i>	Tetraploid	36	Not reported	Not reported	Perennial	
Fonio						
<i>D. longiflora</i>	Not reported	Not reported	Not reported	Not reported	Not reported	Adoukonou
<i>D. ternata</i>	Not reported	Not reported	Not reported	Not reported	Not reported	-Sagbadja et al. 2007
<i>D. lecardii</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>D. ciliaris</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
Foxtail millet						
<i>S. viridis</i> (A genome)	Diploid	18	Sexual	Inbreeder	Annual	Hacker 1967; Till-Bottraud et al. 1992;
<i>S. faberii</i> (AB genome)	Tetraploid	36	Sexual	Inbreeder	Annual	Le Thierry d'Ennequin et al. 1998;
<i>S. verticillata</i> (AB genome)	Tetraploid and hexaploid	36, 54	Sexual	Inbreeder	Annual	Benabdelmouna et al. 2001a;
<i>S. glauca</i> (<i>S. pumela</i>) (B genome)	Complex ploidy	36–72	Sexual	Inbreeder	Not reported	Wang et al. 2007b;
<i>S. adhaerans</i> (<i>S. pumela</i>) (B genome)	Diploid	18	Sexual	Inbreeder	Annual	Jia et al. 2009a;
<i>S. holstii</i>	Diploid	18	Sexual	Inbreeder	Perennial	Wang et al. 2009;
<i>S. woodii</i>	Diploid	18	Sexual	Not reported	Perennial	http://database.prota.org
<i>S. chevalieri</i>	Tetraploid	36	Sexual	Not reported	Perennial	
<i>S. incrassata</i>	Tetraploid	36	Not reported	Not reported	Not reported	
<i>S. leiantha</i>	Tetraploid	36	Not reported	Not reported	Not reported	
<i>S. neglecta</i>	Tetraploid	36	Not reported	Not reported	Not reported	

(continued)

Table 5.2 (Continued)

Species	Ploidy	Chromosome number	Reproductive behavior	Mating system	Life form	Reference
<i>S. palmifolia</i>	Tetraploid	36	Not reported	Not reported	Perennial	
<i>S. parviflora</i>	Tetraploid	36	Not reported	Not reported	Perennial	
<i>S. sphacelata</i>	Complex ploidy	18 to 90	Sexual	Outbreeder	Perennial	
<i>S. macrostachya</i>	Hexaploid	54	Not reported	Not reported	Perennial	
<i>S. pumila</i>	Tetraploid and hexaploid	36, 54	Sexual	Inbreeder	Annual	
<i>S. finita</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>S. sphacelata</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>S. grisebachii</i> (C genome)	Diploid	18	Sexual	Inbreeder	Annual	
<i>S. queenslandica</i> (AA genome)	Tetraploid	36	Sexual	Inbreeder	Annual	
<i>S. verticillata</i> (B genome)	Diploid	18	Not reported	Not reported	Not reported	
<i>S. leucopila</i> (A genome)	Diploid	18	Sexual	Inbreeder	Annual	
Job's tears						
<i>C. aquatica</i>	Diploid	10	Not reported	Not reported	Not reported	Reviewed in Han et al. 2004
<i>C. aquatica</i>	Tetraploid	20	Not reported	Not reported	Not reported	
<i>C. aquatica</i>	Hexaploid	30	Not reported	Not reported	Not reported	
<i>C. aquatica</i>	Octaploid	40	Not reported	Not reported	Not reported	
Kodo millet						
<i>Paspalum scrobiculatum</i>	Tetraploid	49	Sexual	Inbreeder	Annual	Wanous 1990
Little millet						
<i>P. sumatrense</i>	Tetraploid	36	Sexual	Inbreeder	Annual	Wanous 1990; Hiremath et al. 1990; Wanous 1990
<i>P. psilopodium</i>	Tetraploid	36	Sexual	Inbreeder	Annual	
Pearl millet						
<i>P. glaucum</i> ssp. <i>monodii</i>	Diploid	14	Sexual	Inbreeder	Annual	Martel et al. 1997; http://croptenebank.sgrp-cgiar.org
<i>P. violaceum</i>	Diploid	14	Sexual	Inbreeder	Annual	
<i>P. mollissimum</i>	Diploid	14	Sexual	Inbreeder	Annual	
<i>P. ramosum</i>	Diploid	10	sexual and apomictic	Inbreeder	Annual, Biennial	
<i>P. purpureum</i>	Tetraploid	28	Sexual	Inbreeder	Perennial	
<i>P. setaceum</i>	Triplid	27	Apomictic	Inbreeder	Perennial	
<i>P. setaceum</i>	Hexaploid	54	Apomictic	Inbreeder	Perennial	
<i>P. villosum</i>	Tetraploid	36	Apomictic	Inbreeder	Perennial	
<i>P. pedicellatum</i>	Tetraploid	36	Sexual	Inbreeder	Annual	
<i>P. orientale</i>	Tetraploid	36	Sexual	Inbreeder	Perennial	
<i>P. meianum</i>	Diploid	16	Sexual	Inbreeder	Perennial	
<i>P. squamulatum</i>	Hexaploid	54	Apomictic	Inbreeder	Perennial	

(continued)

Table 5.2 (Continued)

Species	Ploidy	Chromosome number	Reproductive behavior	Mating system	Life form	Reference
Proso millet						
<i>P. miliaceum</i>	Tetraploid	36	Sexual	Inbreeder	Annual	Baltensperger 1996
Tef						
<i>E. pilosa</i>	Tetraploid	40	Not reported	Not reported	Not reported	http://database.prota.org
<i>E. ciliaris</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>E. curvula</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>E. cylindriiflora</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>E. gengetica</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>E. tremula</i>	Not reported	Not reported	Not reported	Not reported	Not reported	
<i>E. turgida</i>	Not reported	Not reported	Not reported	Not reported	Not reported	

regularis, *irregularis* and *variabilis*. All these races and subraces can be recognized by variation in panicle morphology (Prasad Rao et al. 1993). The two most recognized and widely cultivated species in fonio are white and black fonio, differentiated by seed color (Murdock 1959).

The millets growing area worldwide has declined by 18% over a period of 45 years, from the average of 43.7 million ha in 1964 to 1968 to 35.82 million ha in 2004 to 2008; however, production during the same period has increased by 20.5%, from 26.9 million t in 1964 to 1968 to 32.3 million t in 2004 to 2008, largely due to increased productivity, which raised from 0.61 t ha⁻¹ in 1964 to 1968 to 0.9 t ha⁻¹ in 2004 to 2008 (Table 5.3). Globally, the millets are grown in 90 countries (<http://faostat.fao.org/>). The major countries for production of millets are India, China, Nepal, Pakistan, and Myanmar in Asia; Burkina Faso, Cameroon, Chad, Ghana, Kenya, Mali, Namibia, Niger, Nigeria, Senegal, Sudan, Tanzania, Togo, Uganda, and Zimbabwe in sub-Saharan Africa; and Argentina and the United States on the American continent (Table 5.4). The production trends of 45 years (1964–2008) from these countries reveal interesting patterns. For example, China recorded the highest average annual production of 8.4 million t during the 1969–1973 period, which gradually declined to 1.7 million t in the period between 2004 and 2008. In contrast, India has shown a consistently upward trend in millets production, with marginal variation, increasing from 7.8 million t annually in the 1964 to 1968 period to 11.1 million t annually between 2004 and 2008 (i.e., an increase of ~43%). The increased production of millets in India, particularly pearl millet with substantial production, is due to large-scale adoption of hybrid cultivars with inherent resistance/tolerance to biotic and/or abiotic stresses, which

Table 5.3. Five-yearly averages of world area, production, and productivity of millets for the period from 1964 to 2008.

Year	Area (million ha)	Production (million tons)	Yield (t ha ⁻¹)
1964–1968	43.71	26.84	0.61
1969–1973	44.25	29.94	0.68
1974–1978	40.61	27.52	0.68
1979–1983	37.26	26.67	0.72
1984–1988	36.75	27.26	0.74
1989–1993	37.10	28.12	0.76
1994–1998	36.59	27.81	0.76
1999–2003	35.77	28.57	0.80
2004–2008	35.82	32.34	0.90

Source: <http://faostat.fao.org>.

Table 5.4. Five-yearly averages of the millets production from the major millets producing countries in South and Southeast Asia, sub-Saharan Africa, the American continent, and CIS countries for the period from 1964 to 2008.

Country	1964–1968	1969–1973	1974–1978	1979–1983	1984–1988	1989–1993	1994–1998	1999–2003	2004–2008
South and Southeast Asia									
Afghanistan	0.024	0.029	0.035	0.032	0.026	0.023	0.022	0.021	0.017
Bangladesh	0.050	0.056	0.043	0.055	0.088	0.064	0.057	0.028	0.016
China	7.946	8.356	6.454	6.299	5.300	3.814	3.143	2.106	1.746
India	7.791	9.901	9.491	9.677	8.754	10.009	10.102	10.227	11.142
Myanmar	0.044	0.044	0.050	0.122	0.172	0.129	0.146	0.168	0.181
Nepal	0.108	0.132	0.137	0.120	0.147	0.239	0.274	0.282	0.288
Pakistan	0.386	0.335	0.304	0.248	0.222	0.176	0.192	0.207	0.251
Sub-Saharan Africa									
Burkina Faso	0.325	0.319	0.360	0.401	0.617	0.726	0.791	0.972	1.106
Cameroon	0.082	0.083	0.090	0.090	0.047	0.061	0.064	0.052	0.060
Chad	0.290	0.236	0.241	0.163	0.238	0.216	0.282	0.378	0.497
Ghana	0.074	0.113	0.128	0.117	0.135	0.140	0.175	0.160	0.163
Kenya	0.133	0.130	0.129	0.062	0.050	0.059	0.044	0.057	0.068
Mali	0.433	0.418	0.485	0.511	0.775	0.752	0.760	0.885	1.136
Namibia	0.020	0.026	0.030	0.036	0.047	0.043	0.063	0.060	0.060
Niger	0.875	0.894	0.947	1.307	1.274	1.675	1.848	2.328	2.874
Nigeria	2.435	3.041	3.175	2.570	3.780	4.624	5.572	5.948	7.745
Senegal	0.427	0.400	0.521	0.486	0.565	0.567	0.534	0.575	0.469
Sudan	0.299	0.382	0.458	0.339	0.304	0.245	0.622	0.588	0.644
Tanzania	0.119	0.131	0.231	0.358	0.304	0.235	0.274	0.189	0.226
Togo	0.133	0.132	0.096	0.047	0.072	0.071	0.055	0.045	0.043
Uganda	0.545	0.701	0.598	0.473	0.467	0.598	0.565	0.591	0.707
Zimbabwe	0.215	0.186	0.186	0.131	0.169	0.106	0.076	0.040	0.048
American continent									
Argentina	0.188	0.167	0.278	0.214	0.112	0.081	0.051	0.035	0.014
USA	0.137	0.137	0.088	0.112	0.164	0.178	0.190	0.291	0.319
CIS countries									
Ukraine	0.000	0.000	0.000	0.000	0.000	0.260	0.220	0.268	0.200
Russia	0.000	0.000	0.000	0.000	0.000	1.331	0.617	0.773	0.660

Source: <http://faostat.fao.org>.

have shown 25% to 30% yield advantage over open-pollinated varieties (Gowda and Rai 2006), while maize largely replaced millets in large acreage in China mainly due to its high yield potential, ease of cultivation, and better agronomic management practices including use of herbicides, thus reducing production cost (Diao 2007). Production of millets in Nepal almost tripled from the 1964–1968 period to the 2004–2008 period. In sub-Saharan Africa, Burkina Faso, Chad, Niger, Nigeria, Mali, Senegal, and Uganda are the largest producing countries, recording consistently increasing production. For example, millets production increased by 218% in Nigeria and by 240% in Burkina Faso, largely because of increased productivity (Table 5.4). Although the millet production in Niger and Mali increased by 228% and 162%, respectively, this increase probably was largely due to increased acreage. In many other sub-Saharan African countries, however, production either remained stagnant or has declined since the 1960s. The millets in these countries are still grown on marginal lands, low in soil fertility, poor crop management practices adopted, and unavailability of seeds of improved cultivars. The millets production in Argentina and America also showed variable trends. Production in Argentina reached its highest peak in the 1970s and then declined rapidly, with an average annual production of only 14,000 t for the 2004–2008 period. Annual millets production in the United States, except for periods in the 1970s and early 1980s, largely remained between 137,000 t to 319,000 t, and the highest average annual production was recorded for the period between 2004 and 2008. Millets production in Ukraine remained at below 300,000 t annually for the last 20 years while production declined by 50.4% in Russia.

The economic development around the world brought dietary changes—those of hunter-gatherers containing large amounts of fiber and low amounts of sugar and fat to energy diets composed predominantly of highly processed foodstuffs, driven by a variety of culturally specific factors, including the increased production, availability, and marketing of processed foods and the complex effects of urbanization (Drewnowski and Popkin 1997; Popkin 2004, 2006; Finnis 2007). Global food consumption patterns have been shifting from food grains to high-value crops/animal products in developing countries while it is from animal/fish-based to crop-based foods in the developed countries. Worldwide, per-capita cereal consumption declined by 5.6% between 1990 to 2003 while fruit consumption increased by 55% and vegetable consumption by 26% during the same period, with more pronounced effect noted in developing than developed countries. While meat, dairy, and seafood/fish consumption increased remarkably—55%, 29%, and

44% in developing countries—it declined by 1.2%, 0.6%, and 11.5% in developed countries (https://www.ifama.org/events/conferences/2010/cmsdocs/a72_pdf). Women's opportunity cost of time—that is, the extent of women working outside the home generating income for the family—has also emerged as a key determinant in the shift from coarse-grain cereals to nontraditional grains (wheat and rice) and convenience foods (Senauer et al. 1986; Kennedy and Reardon 1994). For example, sustained economic growth, increasing population, and changing lifestyles has caused significant changes in the Indian food basket, away from staple foodgrains toward high-value horticultural products (Kumar et al. 2007; Mittal 2007). More important, the production of minor millets, for example, in the Kolli Hills region of Tamil Nadu, India, has declined substantially due to changing consumption preferences in favor of other crops, such as cassava, rice, and pineapple (Gruère et al. 2009). The erratic rainfall and drudgery associated with processing of minor millets also contributed to decline in production of these millets species (S.B. Ravi, MSS Research Foundation, Chennai, India). The changes in the dietary pattern also led to an increased demand of food grains as feed (Dikshit and BIRTHAL 2010), with a steeper decline in per-capita consumption of coarse-grain cereals than that of rice and wheat, in both rural and urban India (Kumar et al. 2009).

Millets productivity in the last five decades showed consistent increases in China, India, Burkina Faso, Nigeria, Uganda, Argentina, and the United States (Table 5.5). However, the percentage increase varied—76% in China; 132% in India; 183% in Nigeria; 80% in Uganda; 40% in Argentina; and 20% in the United States. In Kenya, productivity remained on average at 1.7 t ha^{-1} until the 1970s, but then substantially declined to 40% and 71% for the early 1980s and the last decade. In contrast, millets productivity remained constant at around 1 t ha^{-1} in Nepal. Millet yield in Namibia among the African countries remained the lowest ($0.20\text{--}0.30 \text{ t ha}^{-1}$) (Table 5.5). Isolated cases of very high grain yield under reasonably good management conditions have also been reported: finger millet grain yield as high as 4.2 t ha^{-1} in Uganda (Odelle 1993), 6 t ha^{-1} in Zimbabwe (Mushonga et al. 1993), 3.7 t ha^{-1} in Ethiopia (Mulatu and Kebebe 1993), and 4 to 6 t ha^{-1} in India (Seetharam and Prasada Rao 1989; Bondale 1993); foxtail millet grain yield as high as 9 t ha^{-1} in China (Diao and Cheng 2008), and up to 11 t ha^{-1} in breeding trial with the newly released hybrid cultivar “Zhangzagu 8” (Diao 2007).

Pearl millet, finger millet, foxtail millet, and proso millet are grown widely (pearl millet in south Asia and sub-Saharan Africa; finger millet in South and Southeast Asia and East Africa; foxtail millet in South and

Table 5.5. Five-yearly averages of the millets productivity (t ha^{-1}) from the major millets-producing countries in South and Southeast Asia, sub-Saharan Africa, the American continent, and CIS countries for the period from 1964 to 2008.

Country	1964–1968	1969–1973	1974–1978	1979–1983	1984–1988	1989–1993	1994–1998	1999–2003	2004–2008
South and Southeast Asia									
Afghanistan	0.847	0.836	0.848	0.860	0.866	0.839	0.815	0.821	0.905
Bangladesh	0.870	0.764	0.680	0.718	0.750	0.724	0.701	0.693	0.693
China	1.150	1.249	1.323	1.567	1.724	1.836	2.073	1.792	2.023
India	0.404	0.502	0.517	0.546	0.544	0.683	0.774	0.823	0.937
Myanmar	0.289	0.273	0.315	0.648	0.933	0.693	0.641	0.703	0.772
Nepal	1.108	1.125	1.111	0.966	0.933	1.147	1.060	1.081	1.100
Pakistan	0.455	0.481	0.488	0.495	0.448	0.422	0.449	0.515	0.548
Sub-Saharan Africa									
Burkina Faso	0.443	0.400	0.426	0.473	0.575	0.599	0.682	0.739	0.853
Cameroon	0.750	0.688	0.790	0.701	0.949	1.044	1.005	1.004	1.134
Chad	0.586	0.559	0.508	0.531	0.502	0.403	0.418	0.495	0.541
Ghana	0.571	0.552	0.619	0.659	0.652	0.697	0.935	0.805	0.869
Kenya	1.788	1.710	1.618	0.883	0.649	0.610	0.482	0.552	0.650
Mali	0.745	0.736	0.706	0.718	0.859	0.658	0.720	0.691	0.743
Namibia	0.225	0.226	0.232	0.251	0.309	0.285	0.236	0.252	0.245
Niger	0.482	0.399	0.394	0.429	0.394	0.378	0.367	0.428	0.463
Nigeria	0.563	0.633	0.864	1.293	1.255	1.026	1.048	1.221	1.596
Senegal	0.459	0.452	0.587	0.543	0.590	0.635	0.606	0.663	0.599
Sudan	0.503	0.458	0.390	0.303	0.178	0.200	0.240	0.243	0.301
Tanzania	0.636	0.631	0.836	1.151	0.996	0.881	1.033	0.798	0.799
Togo	0.482	0.714	0.686	0.624	0.831	0.522	0.499	0.585	0.700
Uganda	0.911	1.121	1.184	1.519	1.401	1.542	1.410	1.519	1.645
Zimbabwe	0.557	0.491	0.502	0.417	0.572	0.406	0.282	0.274	0.226
American continent									
Argentina	1.106	1.041	1.217	1.178	1.240	1.453	1.233	1.689	1.547
USA	1.284	1.308	1.217	1.327	1.439	1.501	1.501	1.431	1.546
CIS countries									
Ukraine	0.000	0.000	0.000	0.000	0.000	1.335	1.173	1.102	1.151
Russia	0.000	0.000	0.000	0.000	0.000	0.814	0.791	0.960	1.169

Source: <http://faostat.fao.org>.

Southeast Asia; proso millet in Asia, Europe, and North America), while other millets are mostly confined to specific geographic regions: for example, fonio in West Africa; tef predominantly in Ethiopia; Job's tears and barnyard millet in South and Southeast Asia; and little millet and kodo millet in South Asia (Table 5.6). India is the largest producer of pearl millet and finger millet, while China is the largest producer of foxtail and proso millet. Millets species are known by different vernacular names across regions and countries within regions (Table 5.7).

Like other cereals, millets are also adversely affected by diseases, including downy mildew, rust, smut, ergot, and leaf blight in pearl millet; blast (leaf, neck, and finger) and leaf blight in finger millet; blast, downy mildew, rust, and leaf spot in foxtail millet; and rust, head smudge, and damping-off diseases in tef (Table 5.8). Major insect pest damage has been limited in millets but does impact regions of production. Proso millet is limited to less humid environments of the United States by chinch bugs, and this impact has been reported to impact pearl millet as well (Ni et al. 2009). Stem-boring insects have also been reported in proso, foxtail, and pearl millet (Adugna and Hofsvang 2000). Aphids have been limiting to grain and forage production and interact with the spread of plant viruses (www.ars.usda.gov/Research/docs.htm?docid=8927). Foraging insects, such as grasshoppers, also occasionally have been severe for proso millet in the U.S. Great Plains (Lyon et al. 2008) and pearl millet in Mali (Coop and Croft 1993). Some pest damage has been reported in tef and fonio from Africa, or during storage conditions. Additionally, the millets grain retains viability for long periods even under poor storage conditions. Most of the millets species are considered to be hardy crops adapted to marginal lands in the hot, drought-prone arid and semiarid regions of Africa, Asia, and the American continent (http://www.underutilized-species.org/documents/millet_mssrf.pdf); however, drought and heat stresses adversely affect millets productivity. For example, postflowering drought stress in pearl millet causes substantial grain and stover yield losses (Mahalakshmi et al. 1987), and tef is highly sensitive to water stress during grain filling (Mengistu 2009). Lodging adversely affects finger millet, foxtail millet, proso millet, tef, and fonio production. Parasitic weeds, *Striga* spp., are serious constraints to finger millet, pearl millet, and fonio cultivation in Africa. Millets are C₄ plants (Roder 2006; Osborne and Freckleton 2009), which have competitive advantage (better adaptation) over C₃ plants under conditions of drought, high temperature, and nitrogen or carbon dioxide (CO₂) limitation. C₄ plants utilize their specific leaf anatomy, known as Kranz anatomy, to fix CO₂ around rubisco, thus reducing photorespiration (Osborne and Beerling 2005). Millets are considered to provide more grain

Table 5.6. Major regions/countries with substantial millets production.

Major geographical regions and countries with substantial production	Reference
Barnyard millet South and Southeast Asia: China, Korea, Japan, India	Prasad Rao et al. 1993
Finger millet South and Southeast Asia: India, China, Nepal, Myanmar, and Sri Lanka Eastern Africa: Uganda, Kenya, Sudan, and Eritrea Southern Africa: Zimbabwe, Zambia, Malawi, and Madagascar Central Africa: Rwanda and Burundi	Prasad Rao et al. 1993; http://afriprod.org.uk/paper02obilana.pdf
Fonio West Africa: Benin, Burkina Faso, Chad, Guinea, Gambia, Mali, Nigeria, Senegal, and Togo	http://underutilized-species.org
Foxtail millet China, South and Southeast Asia: India, Nepal, Afghanistan, Korea, and Japan East Asia: China Other regions/countries: Russian Federation, USA, and France	http://hort.purdue.edu/newcrop/proceedings1997/v3-182html ; Prasad Rao et al. 1993
Job's tears South and Southeast Asia: Burma, China, India, Malaysia, the Philippines, Thailand, and Taiwan South America: Brazil	Venkateswarlu and Chaganti 1973; Wanous 1990 iat.sut.ac.th/food/FIA2007/FIA2007/paper/P1-07-CP.pdf
Kodo millet South Asia: widely grown in India	Prasad Rao et al. 1993
Little millet South Asia: India (Eastern Ghats), Nepal, Myanmar, and Sri Lanka	Prasad Rao et al. 1993
Pearl millet South Asia: India (Rajasthan, Gujarat, Maharashtra, Haryana and Uttar Pradesh), Afghanistan, Bangladesh, Myanmar, and Pakistan Sub-Saharan Africa: Grown in 28 countries with Nigeria, Niger, Burkina Faso, and Mali being the largest producers	Yadav 1996a; afriprod.org.uk/paper02obilana.pdf
Proso millet India, China, Japan, Russia, Afghanistan, Iran, Iraq, Syria, Turkey, Mongolia, Romania, and USA (Nebraska, South Dakota, and Colorado)	http://hort.purdue.edu/newcrop/proceedings1997/v3-182html ; Wanous 1990

(continued)

Table 5.6 (Continued)

Major geographical regions and countries with substantial production	Reference
Tef	
Eastern and southern Africa: Ethiopia the major grain producer and the highlands of Eritrea; South Africa (both forage and grain), northern Kenya	database.prota.org
Europe and North America (small-scale grain production): USA, Canada, and the Netherlands	
Oceania: Australia (both grain and forage)	
Other countries: tef as forage in Morocco, India, and Pakistan	

per unit of water than other cereals (Briggs and Shantz 1914; Felter et al. 2006).

Millet grains are nutritious (see Section II) and commonly used for food in Asia and Africa, while in Europe and on the American continent, they are predominantly used as poultry feed. However, proso millet is a common ingredient in high-priced artisan breads sold in the United States, where there is a new “ancient grains” marketing niche. Millets straws are important sources of fodder in developing countries. Millets are also grown on the American continent as forage crops on light-textured or acidic soils throughout the tropical and subtropical lowlands and increasingly as a mulch component in no-till soybean production on the acidic soil savannahs of Latin America (<http://www.cgiar.org/impact/research/millet.html>).

Millets are an underresearched crop commodity, especially compared with maize, which continues to push into previous millet cropping systems. Pearl millet, and to a lesser extent proso millet, finger millet, foxtail millet, and tef, have received greater attention from the research community to developing genetic and genomic resources for use in breeding, while in others only limited progress has been realized to date. This chapter is focused primarily on domestication and evolution of millets vis-à-vis other cereals; nutritional quality to diversify food uses; germplasm resources; sources of resistance to biotic and abiotic stresses and of agronomic and seed quality traits; diversity pattern in germplasm collections and formation of reduced subsets representing diversity present in entire germplasm collection of a given species to identifying new sources of variation; promoting use of male sterility to exploit heterosis; and genomic resources as an aid to marker-aided

Table 5.7. Vernacular names of barnyard millet, finger millet, fonio, foxtail millet, Job's tears, kodo millet, little millet, proso millet, and tef as known in different regions.

Common name	Other vernacular names	Reference
Barnyard millet	Japanese barnyard millet (<i>Echinochloa crus-galli</i>), Indian barnyard millet (<i>E. Colona</i>), cocksbur grass, Korean native millet, prickly millet, sawa millet, and watergrass	Prasad Rao et al. 1993; Wanous 1990
Finger millet	Ragi in Hindi; tallaban in Arabic; petit mil and coracan in French; fingerhirse in German; wimbi and ulleji in Swahili; degussa in Ethiopia; telebun in Sudan; bulo in Uganda; African millet, birdsfoot, hansa ragi, koracan, madiwa	Wanyera 2007; NRC 1996; Wanous 1990
Fonio	Hungry rice in English, fonio in French; acha in Nigeria, eboniaye in Senegal, findo in Gambia, podgi in Benin; crabgrass, fundi, and raishan.	NRC 1996; Wanous 1990
Foxtail millet	Italian millet; German millet; Russian millet; Hungarian millet; awa in Japanese; Siberian millet, dawa in Indonesia, shao-mi, su and kou weitsao in China; mohar in Russia; millet des oiseaux and millet d'Italie in French; panico, milho panico, and milho panico de Itálica in Portuguese; kimanga in Swahili	http://database.prota.org ; Wanous 1990; Austin 2006
Job's tears	Hortus, magharu, shoriew, mim (arora), trigo tropical (Joyal), attabi (Bodner), wallnöfer adlay in the Philippines; hatomugi, mayuen, or Chinese pearl barley in China	http://plantsforuse.com ; http://iat.sut.ac.th/food/FTA2007/FIA2007/paper/P1-07-CP.pdf
Kodo millet	kodo in Hindi, khoddi in Urdu, arugu in Telugu, and varagu in Tamil, all Indian languages; African bastard millet grass, arika, haraka, ditch millet in New Zealand, and mandal in Pakistan	Prasad Rao et al. 1993; de Wet et al. 1983; Wanous 1990
Little millet	Samai in Tamil (India), sama (little or slender) (India)	Arunachalam et al. 2005; Wanous 1990
Pearl millet	Bajra, bajri, bulrush millet, cattail millet, babala, bulrush, seno, spiked millet, cumbu, gero, munga; dukhun in Arabic; mil a chandelles in French; mijo perla in Spanish	Yadav 1996a; Wanous 1990; http://www.sik.se/traditionalgrains/review/
Proso millet	Broomcorn millet, common millet, hog millet, Hershey millet, white millet, creeping paspalum, ditch millet, Indian paspalum, water couch, brown corn, Russian millet; huang mi, mi tzu, and shu in Chinese	Prasad Rao et al. 1993; Wanous 1990; http://www.sik.se/traditionalgrains/review/
Tef	Tef, t'ef, teff grass, and/or Williams lovegrass in English, French and Portuguese; tahf in Arabic	http://database.prota.org ; NRC 1996; Wanous 1990

Table 5.8. Major biotic constraints reported in barnyard millet, finger millet, fonio, foxtail millet, Job's tears, kodo millet, little millet, pearl millet, proso millet, and tef.

Biotic stress	Reference
Barnyard millet	
Grain smut (<i>Ustilago panici-frumentacei</i> Brefeld)	Gupta et al. 2009a
Finger millet	
Leaf, neck and finger blast (<i>Pyricularia grisea</i>); leaf blight (<i>Helminthosporium nodulosum</i>); shoot fly (<i>Atherigona milliacea</i>) and pink stem borer (<i>Sesamio inferens</i>)	Sreenivasaprasad et al. 2007; cropgene bank.sgrp.cgiar.org
Fonio	
Insect causing severe leaf and stem damage	Adoukonou-Sagbadja et al. 2006
Foxtail millet	
Blast (<i>Pyricularia setariae</i>); downy mildew (<i>Sclerospora graminicola</i>); rust (<i>Uromyces setariae-italiae</i>); smut (<i>Ustilago crameri</i>); leaf spot (<i>Helminthosporium</i> spp.); shoot fly (<i>Atherigona</i> spp.); seed smut (<i>Sorosporium bullatum</i>), kernel smut (<i>Ustilago paradoxa</i>); and wheat curl mite (<i>Eriophyes tullipae</i> Keifer) and wheat streak mosaic virus reported from USA	Brink 2006; Siles et al. 2004; http://www.hort.purdue.edu/http://database.prota.org
Job's tears	
Leaf blight (<i>Pseudocochlibolus nisikadoi</i>)	http://www.nilgs.affrc.go.jp/db/diseases/contents/de40.htm#cm%20leaf%20blight
Kodo millet	
Head smut (<i>Sorosporium paspali</i>); rust (<i>Puccinia substriata</i> Ellis and Barht); smut (<i>Ustilago crus-galli</i> , <i>U. paradoxa</i> and <i>U. panici-frumentacei</i>)	Viswanath and Seetharam 1989
Little millet	
Rust (<i>Uromyces linearis</i>)	Viswanath and Seetharam 1989
Pearl millet	
Downy mildew (<i>Sclerospora graminicola</i>); smut (<i>Moeszimyoces penicillariae</i>); ergot (<i>Claviceps fusiformis</i>); leaf blight (<i>Pyricularia grisea</i> and <i>Bipolaris setariae</i>); rust (<i>Puccinia substriata</i>); head caterpillar (<i>Heliothis albipunctella</i>); scarab beetle (<i>Pachnoda interrupta</i> (Olivier)), stem borer (<i>Acigona ignefusalis</i> (Hamps.), and striga (<i>Striga hermonthica</i>)	crop.sgrp.cgiar.org; de
Proso millet	
Head smut (<i>Sphacelotheca destruens</i>); bacterial spot (<i>Pseudomonas syringae</i>), smut (<i>Sphacelotheca panici milliacea</i>), wheat curl mite (<i>Eriophyes tullipae</i>) and wheat streak mosaic virus reported from USA	ianpubs.unl.edu/live/ec137/build/ec137.pdf; Ilyin et al. 1993; Baltensperger 1996

Table 5.8 (Continued)

Biotic stress	Reference
Tef	
Diseases: Rust (<i>Uromyces eragrostidis</i>); head smudge (<i>Helminthosporium miyakei</i>); damping off (<i>Drechslera</i> spp., and <i>Epicoccum nigrum</i>)	database.prota.org
Pest: Wollo bush-cricket (<i>Decticoides brevipennis</i>); red tef worm (<i>Mentaxya ignicollis</i>); black tef beetle (<i>Erlangerius niger</i>); grasshoppers, ants, and termites	

gene introgression of food, feed, and bioenergy traits for product development.

II. NUTRITIONAL QUALITY AND FOOD, FEED, MEDICINAL, AND OTHER USES

Millet grains are nutritionally equivalent or superior to other cereals (Mengesha 1965; FAO 1972). The grains contain high amounts of carbohydrates, proteins, minerals, and vitamins. For example, high levels of protein, calcium, iron, and zinc are found in finger millet, foxtail millet, and fonio; methionine, iron and zinc in pearl millet; methionine and/or cysteine in finger millet and fonio; iron in tef; tryptophan, lysine, methionine, phenylalanine, threonine, valine, leucine, and isoleucine in foxtail millet (Ode et al. 1993; de Lumen et al. 1993; NRC 1996; Malleshi and Klopfenstein 1998; Fernandez et al. 2003; Khairwal et al. 2004; Alaunyte et al. 2010; database.prota.org; http://www.underutilized-species.org/documents/millet_mssrf.pdf). Millets gains are therefore recommended for lactating women and for diabetic (non-insulin-dependent) and sick people (Kumari and Sumathi 2002). Diets containing proso millet protein concentrate raise plasma levels of high-density lipoprotein (HDL) cholesterol without causing an increase in low-density lipoprotein (LDL) cholesterol levels in rats and mice (Nishizawa et al. 1990; Nishizawa and Fudamoto 1995; Shimanuki et al. 2006; Park et al. 2008). Furthermore, Nishizawa et al. (2009) reported the beneficial effects of dietary Japanese barnyard millet protein on plasma levels of adiponectin, high-density lipoprotein (HDL) cholesterol, glucose, and triglycerides in obese diabetic mice.

Foxtail millet grain has high protein and iron contents compared to rice, wheat, and maize. Not only is the biological value of digestible

protein higher than in rice and wheat, seven of the eight essential amino acids, which cannot be synthesized by the human body, are higher in foxtail millet (Zhang et al. 2007a). Edible fiber is important for intestine and stomach health. Foxtail millet grain contains 2.5 times the edible fiber found in rice and thus is a promising source for edible fiber (Liang et al. 2010). Foxtail millet bran contains 9.4% crude oil and is rich in linoleic (66.5%) and oleic (13.0%) acids (Liang et al. 2010).

Millet fodders are highly nutritious and palatable and are fed to animals in Asia, Africa, and the American continent. From ancient times (>7000 years BP), foxtail millet has been in use for grain (for use by human) and hay production (for cattle and horse feeding) in China (Diao 2007). Some of the foxtail millet cultivars specifically bred for hay production in China contain as high as 15% protein (Zhi et al. 2011). Some brown-midrib (*bmr*) mutants in pearl millet have shown increased in vitro dry matter digestibility compared to normal cultivars (Cherney et al. 1988; Akin and Rigsby 1991), and have potential as sources of improved forage quality. Millets being C₄ plants have great potential for biomass production; for example, biomass of pearl millet can yield 6 to 12 t ha⁻¹ on a dry-weight basis in less than 100 days (Khairwal et al. 2004). Hall et al. (2004) reported substantial genetic variation for stover quality and quantity without detrimental effect on grain yield in pearl millet.

Millets are also considered sacred crops in some communities/regions, where they play a central role in social events and celebrations. Because of its long cultivation history and great contribution to Chinese ancient civilization, foxtail millet was named “first” among the “Five Grains of China” (Austin 2006), which also include proso millet, rice, soybean, and wheat. Foxtail millet is used even today in ancestor worship ceremonies. In developing countries, in both Africa and Asia, the dry stalks of millets are used for fuel, thatching houses, constructing fences, and making mats. Job’s tears seeds are used as decorative beads to make necklaces and rosaries (Table 5.9).

Substantial variations in seed composition of proso millet, finger millet, and foxtail millet cultivars have been reported. Ravindran (1991) reported higher seed protein (14% to 16%) and crude fat (5% to 8%) in proso millet and foxtail millet than in finger millet (protein 10% and crude fat 1.6%). Finger millet, however, had higher carbohydrate (81% to 74%), while all three millets had similar (4%) fiber contents. Ravindran (1991) also reported high calcium and potassium contents in finger millet grains, while other minerals, such sodium, magnesium, and phosphorous, were similar across these three millets. Regarding the

Table 5.9. Food, feed, medicinal and industrial uses of barnyard millet, finger millet, fonio, foxtail millet, Job’s tears, kodo millet, little millet, pearl millet, proso millet and tef grains, and stover.

Food	Feed	Medicinal uses	Beverage	Other uses	Reference
Barnyard millet Flour to make bread (chapatti); porridge; popped grains as snacks	Straw superior to rice and oat straw because of high protein and Ca content (Yabuno 1987)	Unknown	Unknown	Unknown	Taylor and Emmambux 2008
	Both grain and/or stover used for animal feed including caged birds and poultry	Highly recommended diet for lactating women, diabetic people, and sick people	Grains brewed for beer		
Finger millet Flour to make bread (chapatti); porridge; popped grains as snacks; whole grains cooked as khichadi; sprouted grains; dosa, a thin fermented pancake containing blackgram					

(continued)

Table 5.9 (Continued)

Food	Feed	Medicinal uses	Beverage	Other uses	Reference
Fonio Porridge; tuwo; fonio-beans prepared on special occasions; couscous; both black fonio and white fonio used to make couscous "wusu-wusu"; bread; popped	Straw and chaff used as fodder; hay	Grain is regarded as medicinal (i.e., anththyroid, chronic diarrhea, dysentery, chickenpox, stomachache, asthma) and healing properties; highly recommended diet for lactating women, diabetic people, and sick people	Grains brewed for beer, named locally as tchapalo, tchoukoutou, pito and burukuto	Straw and chaff mixed with clay to build houses; sacred crop that plays central role in social events/ celebrations; grains used as an important part of dowry in Sahelian communities	http://www.species.org/ ; NRC 1996; Adoukonous- Sagbadia et al. 2006
Foxtail millet Dehusked grain for steamed food and porridge or gruel; flour to make bread (chapatti); porridge; popped grains as snacks	Both grain and/or stover used for animal feed including caged birds and poultry; hay production	Pregnant and lactating women; prevention of diabetics; bran oil for skin diseases; dietary fiber for prevention of stomach and intestinal diseases	Huangjiu or yellow wine—alcoholic drink; xiaomiyin— nonalcoholic drink	Decoration; thatching houses	Sema and Sarita 2002; Li 2005; Austin 2006; Diao 2007; Zhang et al. 2007a
Job's tears Porridge	Foliage as green fodder to animals	Anodyne; anthelmintic, anti- inflammatory; antipyretic; antirheumatic; antispasmodic; cancer; hypoglycemic; diuretic; pectoral; sedative; tonic; warts; appendicitis; rheumatoid arthritis; menstrual disorders	Tea from boiled seed as drink to cure warts; soup; grains for brewing beer "dzu"; vines; coffee made from roasted grains	Seeds as decorative beads to make necklaces and rosaries; stems to make matting	http://www.pfaf.org/database/plants.php? Coix + lacryma- jobii; http://www.waynesword.palomar.edu/plapr99.htm
Kodo millet Flour used to make chapatti or flat cake/bread	Straw as fodder	Not known	Not known	Not known	
Little millet Flour to make bread (chapatti); porridge; popped grains as snacks	Both grain and/or stover used for animal feed including caged birds and poultry	Not known	Not known	Not known	

(continued)

Table 5.9 (Continued)

Food	Feed	Medicinal uses	Beverage	Other uses	Reference
Pearl millet Flour to make bread (chapatti); porridge; boiled and/or roasted grains; baked food; weaning mixture; diabetic product; couscous or arraw (steamed product)	Both grain and/or stover used for animal feed including caged birds and poultry	Gluten-free grains to use in health food	Nonalcoholic—oshikundu in Namibia and kunun zaki in Nigeria Alcoholic—ndlovo beer in Bulawayo and Zimbabwe	Dry stalks used for firewood, thatching houses, constructing fences, and making mats	Andrews and Kumar 1992; Khairwal et al. 2004; Taylor and Emmambux 2008
Proso millet Flour to make bread (chapatti); porridge; popped grains as snacks	Both grain and/or stover used for animal feed including caged birds and poultry	Birdseed	A popular alcoholic beer, bosa, in Balkans, Egypt, and Turkey	Hay	Baltensperger 1996; Lyon et al. 2008
Tef A flat, spongy, and slightly sour bread, injera; porridge; gruel (muk)	Tef straw as animal feed	Gluten-free grains for health food	Grains brewed to make alcohol	Hay	http://database.prota.org ; Stallknecht et al. 1993

trace elements, both proso millet and foxtail millet had high manganese, zinc, and iron contents, while all the three millets had similar copper contents.

Most millets grains contain some antinutrients in their seeds. The major antinutrients include polyphenols, phytic acid, and oxalic acid. Phytates decrease the bioavailability of minerals such as calcium, iron, and zinc, while oxalic acid reduces calcium availability (Reddy et al. 1982). Ravindran (1991) found that finger millet grains have less phytic acid than that present in proso millet and foxtail millet, while foxtail millet grains contain high amounts of oxalate. To date, no antinutrients from barnyard millet and kodo millet have been reported. Among all millets, Kodo millet has the highest free radical quenching potential, thus possessing good antioxidant property (Taylor and Emmambux 2008). Some people are allergic to gluten present in cereals; for example, gluten in wheat causes severe allergies. Unlike foxtail millet (Sakamoto 1987), pearl millet, tef, some proso millet, fonio, and barnyard millet grains are gluten-free and therefore offer good opportunities for their use as health foods (NRC 1996; Gulia et al. 2007b; Hoshino et al. 2010). The association of a mycotoxin with “kodua poisoning” was reported when kodo millet (*Paspalum scrobiculatum*) grains infected with *Aspergillus flavus* or *A. tamarii* were used as food or feed. Both fungi produce cyclopiazonic acid, which results in kodua poisoning in man (Rao and Husain 1985), which result sleepiness, tremors and guiddiness (Bhide 1962).

Grain from millets has also shown high potential for milling, popping, and malting. Malleshi and Desikachar (1985) demonstrated that millets could be milled to remove the outer bran (husk) and such milled grains could be easily cooked for consumption. The popped products have potential for use in development of breakfast and specialty foods (Srivastava and Batra 1998; Srivastava et al. 2001; Singh and Sehgal 2008). The millets grains, especially pearl millet, finger millet, foxtail millet, proso millet, and Job's tears, are locally brewed, both in Africa and Asia, to produce alcoholic and nonalcoholic beverages (Table 5.9). Malting and fermentation processes result in malted and brewed alcoholic or nonalcoholic products. Huangjiu, an alcoholic drink made from brewing foxtail millet or proso millet grain, was very popular in ancient China and is still popular in some parts of northern China. Malted pearl millet and finger millet are used in brewing of the traditional opaque African beer in southern and eastern Africa. Finger millet provides the best-quality malt, which is used in the brewing industry in southern and eastern Africa as well as in south and southeast Asia and for making highly digestible nutritious foods.

Foods prepared from millets are of several types that differ between countries and regions (Table 5.9). Because of their long cultivation and use as food, a number of different methods of consumption have been developed using foxtail millet and proso millet in China. The most popular dish from these millets are dehusked grain (referred to as *miaomi*) steamed or used to make gruel and porridge. Flour from foxtail millet and proso millet is used to make bread, pancakes, chapattis, and snacks. Steamed bread made from composite flour containing foxtail millet, wheat, and soybean has gained prominence in northern China; it not only tastes good but is also nutritious (Diao 2007). Food dishes from pearl millet in western Africa vary by countries: thick porridge (*tuwo*) is most popular in Sahelian countries while thin porridge and steamed products (couscous) are also consumed in Francophone countries. Tef and fonio are mostly used for porridges and flat breads. For example, *injera*, the soft, spongy, thin pancakelike bread with a sour taste made from tef flour, is the major staple food in Ethiopia. This traditional millet-based food has recently gained ground in Europe, North America, and Israel. Traditional foods made from pearl millet in India include *chapatti* or *roti*, porridges, and roasted/boiled grains eaten as snacks (Khairwal et al. 2004). European and American multigrain breads frequently use dehulled proso millet.

Grain color is an important seed quality trait that influences the overall grain quality that determines the end use pattern of millets. Grain color in pearl millet ranges from ivory, to cream, to gray and brown. The major grain colors in other millets include white and black in fonio; white, red, and brown in tef; white and brown in finger millet; yellow, red, gray, black, and white in foxtail millet; white, cream, straw, olive, red, black, and brown in proso millet; and straw, olive, brown, and gray in little millet. Moreover, variation in grain color is associated with variation in quality traits and trade value. For example, tef grains with dark color are rich in flavor (NRC 1996); white-colored finger millet grains contain higher protein and iron contents but are lower in fiber and tannins (Seetharam et al. 1984; Rao 1994); black-colored finger millet grains contain only half as much iron and one-tenth as much molybdenum as reported for white-colored finger millet grains (Fernandez et al. 2003; Glew et al. 2008); dark-colored proso millet grains have higher tannin contents than those with light color (Lorenz 1983). White-grained finger millet and foxtail millet grains get high premiums in trade (C. R. Ravishanker, pers. commun.). Red- and brown-seeded tef are harvested from plants that are hardier, faster maturing, and easier to grow (NRC 1996).

Millets have medicinal values for treating complex diseases (Table 5.9). Foxtail millet is widely used not only as an energy source for pregnant and lactating woman but also for sick people and children and especially for diabetics. It is reported to reduce blood sugar concentration in female diabetics (Sema and Sarita 2002). Job's tears grains are most popularly used in Chinese traditional medicine because of their anti tumor and anti-allergenic, probiotic, and hypolipidomic properties while fonio reportedly has healing properties. It is suggested that the low incidence of anemia in the Ethiopian population can be attributed to the high consumption levels of tef, which has high iron content (NRC 1996). Utilization of whole-meal cereals including the seed coat in food formulations is increasing worldwide, since these are rich sources of phytochemicals and dietary fiber, which offer several health benefits. Regular consumption of finger millet is known to reduce the risk of diabetes (Gopalan 1981) and gastrointestinal tract disorders (Tovey 1994), which could be attributed to polyphenols and dietary fiber present in its grains. In China, foxtail millet is used to cure rheumatism. Proso millet protein concentrate, when fed for 21 days to rats, was shown to increase plasma levels of HDL cholesterol without an increase in low-density lipoprotein (LDL) cholesterol compared with a casein diet, which (HDL) may have a beneficial effect against the risk of coronary heart disease (Shimanuki et al. 2006). Furthermore, finger millet and proso millet may prevent cardiovascular disease by reducing plasma triglycerides in hyperlipidemic rats; in contrast, sorghum increases total cholesterol and HDL and LDL cholesterol concentrations (Lee et al. 2010).

Inhabitants of southeast Asia and eastern Asia prefer sticky food. Amylose is an important starch in cereals including millets. Foods made from waxy grains are much stickier than those obtained from nonwaxy grains due to differences in amylose content. Large variations in the waxy phenotype has been reported in several cereals including foxtail millet, proso millet, and Job's tears. This presents opportunities to diversify food uses of millets using allelic variation at the waxy locus (see Section VIII.E).

III. DOMESTICATION, PHYLOGENETIC, AND GENOMIC RELATIONSHIPS

The comprehensive overview of grass phylogenetic relationships stems from the Grass Phylogeny Working Group (GPWG 2001). A simplified representation of one of the combined analyses, using morphological

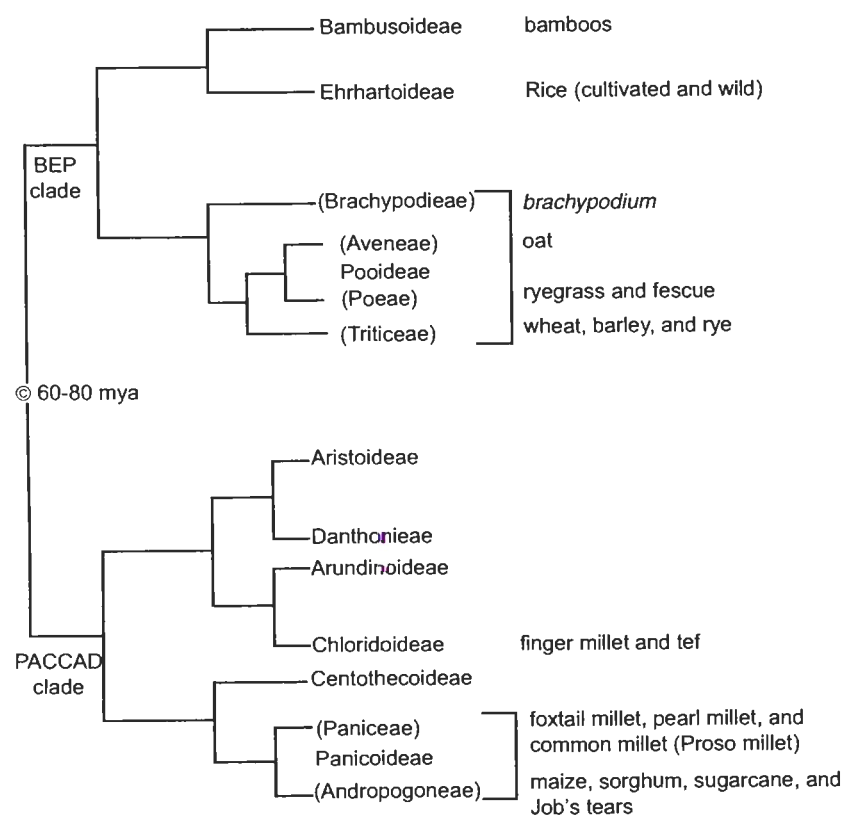


Fig. 5.1. Phylogenetic relationships of the crown group of grasses. Taxon terminal names are subfamilies, with tribes in parentheses. (Source: Adapted from Doust 2007).

and molecular data sets, revealed that the earliest diverging lineages of basal grasses were from a few species and that cereal and forage crops were domesticated from many different grass groups (Fig. 5.1). The members of “crown” (C) group of grasses, which have two large clades, the BEP and PACCAD (acronyms composed of the initial letters of the included subfamilies), diverged from one another 60 to 80 million years ago (Crepet and Feldman 1991; Prasad et al. 2005). The BEP clade is comprised of the basal subfamily Bambusoideae (bamboos) sister to Ehrhartoideae (wild and cultivated rice) and Pooideae (wheat, oats, barley, etc.). This large group of ~ 4200 species is sister to another clade (PACCAD clade) comprised of the Panicoideae, Arundinoideae, Chloridoideae, Centothecoideae, Aristidoideae, and Danthonioideae subfamilies. The Panicoideae has two tribes, the Paniceae, containing

the foxtail millet, pearl millet, and proso millet, and the Andropogoneae, containing sorghum, maize, sugarcane, and Job's tears. The Chloridoideae subfamily includes finger millet and tef (Doust 2007).

In the first 15 to 20 million years of the 60 to 80 million years of evolution, when the main cereal grass lineage separated from other flowering plants, there was little molecular divergence among grass genomes. However, marked genomic divergence has occurred in the last two-thirds (45–60 million years) of this period (Paterson et al. 2004), resulting in genome size differences that range from rice at 420 Mb to wheat at 16,000 Mb (Goff et al. 2002). Genomic evolution in grasses has been complex, with a number of rounds of genome duplications followed by gene deletions (Kellogg 2003; Malcomber et al. 2006). Cereal genomes have shown a high level of macrocollinearity (Gale and Davos 1998), while microcollinearity was disrupted or incomplete at sequence level (Xu and Zhang 2004). Finger millet, foxtail millet, and pearl millet among the millets were the only species studied for collinearity with other cereal genomes. The rice genome has shown a high degree of conserved macrocollinearity against that of foxtail millet and finger millet (Devos et al. 1998; Srinivasachary et al. 2007), while the pearl millet genome has undergone many rearrangements compared to foxtail millet and rice (Devos et al. 2000; Gale et al. 2005).

Pearl millet (*Pennisetum glaucum*) belongs to the genus *Pennisetum*, which has five sections: *Penicillaria*, *Brevivalvula*, *Gymnothrix*, *Heterostachya*, and *Eu-Pennisetum* (Stapf and Hubbard 1934) and 80 to 140 species (Donadio et al. 2009), with haploid chromosome numbers of 5, 7, 8, or 9 (Jauhar 1981) and ploidy levels ranging from diploid to hexaploid. Phylogenetic analyses revealed that *Pennisetum* (excluding *P. lanatum*) is paraphyletic as it is nested with the closely related genus *Cenchrus*. Sections *Pennisetum* and *Gymnothrix* are polyphyletic. The domesticated species *P. glaucum*, *P. purpureum* (napiergrass), *P. squamulatum*, *P. nervosum*, and *P. sieberianum* are closely related, suggesting potential use of these species in crop improvement (Martel et al. 2004; Donadio et al. 2009). The wild progenitor of pearl millet is *Pennisetum glaucum* ssp. *monodii* (Harlan 1975; Brunken 1977). Some believe that pearl millet is the product of multiple domestications (Harlan 1975; Portères 1976) while others propose a single domestication (Marchais and Tostain 1993). Evidence suggests that pearl millet domestication took place in Africa, although different geographical origins have been proposed along the Sahelian zone from Mauritania to Sudan (Harlan 1975; Portères 1976; Marchais and Tostain 1993). The earliest archaeological evidence for pearl millet domestication is from northern Ghana, some 3,500 years BP (D'Andrea and Casey 2002). Studies on

isozyme and simple sequence repeat (SSR) markers have further confirmed a monophyletic origin of pearl millet in West Africa (Ibrahima et al. 2005; Mariac et al. 2006a,b; Oumar et al. 2008; Kapila et al. 2009). Using microsatellite data from wild and cultivated accessions from Africa and Asia, Oumar et al. (2008) detected significantly higher diversity in the wild pearl millet group. The phylogenetic relationship among accessions not showing introgressions support a monophyletic origin of cultivated pearl millet in West Africa, with eastern Mali and western Niger as the most likely region of pearl millet domestication.

Introgression has played a major role in evolution of pearl millet (Brunken et al. 1977; Ibrahima et al. 2005; Miura and Terauchi 2005; Mariac et al. 2006a,b; Oumar et al. 2008). There seems to be a putative supergene or gene complex involved in the domestication syndrome that differentiates weedy and cultivated types (Miura and Terauchi 2005). Quantitative trait loci (QTL) analyses involving F_2 populations derived from crosses of cultivated pearl millet and *Pennisetum glaucum* ssp. *monodii* revealed two genomic regions on linkage groups (LGs) 6 and 7, which controlled most of the key morphological differences (Poncet et al. 1998, 2000, 2002). The importance of these two LGs reveals their central role both in the developmental control of spikelet structure and in the domestication process of pearl millet, and these genomic regions may correspond with quantitative trait loci (QTL) involved in domestication of other cereals, such as maize and rice (Poncet et al. 2000, 2002).

Foxtail millet (*Setaria italica*) is a diploid species, and its wild ancestor is *S. viridis* (Kihara and Kishimoto 1942; Li et al. 1945; Wang et al. 1995; Le Thierry d'Ennequin et al. 2000). Vavilov (1926) suggested east Asia, including China and Japan, to be the principal center of diversity for foxtail millet, while other views suggest independent domestication in China and Europe based on archaeological, isozyme, 5S rDNA, and morphological evidence (Harlan 1975; de Wet et al. 1979; Jusuf and Pernes 1985; Li et al. 1995a,b, 1998; Benabdelmouna et al. 2001a). However, diversity studies using different DNA marker systems do not support the hypothesis of two domestication centers. Using 16 restriction fragment length polymorphism (RFLP) probes, Fukunaga et al. (2002a) classified 62 landraces into five groups, with no clear geographical structure. Le Thierry d'Ennequin et al. (2000) used 160 polymorphic amplified fragment length polymorphism (AFLP) loci data on 39 *S. italica* (foxtail millet) and 22 *S. viridis* (green foxtail millet) accessions. Neither cultivated nor wild accessions showed a clear differentiation of population structure, but both domesticated and wild accessions from China were the most genetically diverse, which supports the monophyletic origin of foxtail millet in China. Previous studies

involving rapid amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) markers (Schontz and Rether 1998, 1999) or the analysis of either *waxy* or *prolamine* genes (Nakayama et al. 1999; Fukunaga et al. 2002b) were also not conclusive in supporting hypotheses of two domestication centers of foxtail millet. QTL mapping of candidate genes revealed that tillering and panicle shape were involved in domestication (Doust et al. 2004, 2005), while human selection contributed to the origin of waxy phenotype in foxtail millet (see Section VIII.D).

The genus *Setaria*, which also includes foxtail millet, has approximately 125 species widely distributed in warm and temperate parts of the world. The genome of foxtail millet and *S. viridis* is designated as AA genome (Li et al. 1945). Weedy tetraploid species *S. faberii* and *S. verticillata* have AABB genome, probably originated from a natural cross between *S. viridis* and another diploid species, *S. adhaerans* (Benabdelmouna et al. 2001a,b). *S. grisebachii* from Mexico has been identified as CC genome diploid species (Wang et al. 2009). *S. queenslandica* is the only autotetraploid (AAAA genome) species in genus *Setaria* (Wang et al. 2009) whereas other polyploid species such as *S. pumila* and *S. pallide-fusca* do not contain the AA genome (Willweber-Kishimoto 1962; Benabdelmouna et al. 2001a,b; Benabdelmouna and Darmency 2003).

Cultivated finger millet, *E. coracana* subsp. *coracana*, was domesticated some 5,000 years ago from the wild *E. coracana* subsp. *africana* ($2n = 4x = 36$) in the highland that stretches from Ethiopia to Uganda (Hilu and de Wet 1976; Hilu et al. 1979; Werth et al. 1994). Subsp. *africana* is the result of a spontaneous hybridization event between the diploid *E. indica* (AA genome) and an unknown B-genome donor (Hilu and Johnson 1992; Hiremaths and Salimaths 1992; Salimaths et al. 1995; Neves et al. 1998; Bishit and Mukai 2000). Neves et al. (2005) assessed the phylogenetic relationships in finger millet, a tetraploid species, using nuclear (internal transcribed spacer [ITS] region of the 18S-26S ribosomal DNA repeat and the 5.8S rRNA gene) and plastid (*trnT-trnF*) DNA sequences, which strongly support a monophyletic origin, but basal relationships in the genus remain uncertain, with either *E. jaegeri* or *E. multiflora* the first diverging lineage. Further, two putative ITS homologues loci (A and B loci) were identified in finger millet. *E. coracana* and its putative "A" genome donor, the diploid *E. indica*, are close allies, while the sequence data contradict the hypothesis that *E. floccifolia* is its second genome (B) donor. Thus, the "B" genome donor remains unidentified and may be extinct. More recently, Dida et al. (2008) analyzed phylogeny of finger millet landraces from Africa

and India and their wild ancestor with microsatellite markers. They confirmed that finger millet was domesticated in East Africa and dispersed into India, which became the secondary center of diversity for this crop.

Proso millet (*Panicum miliaceum*) and little millet (*P. sumatrense*) are tetraploid species (Sakamoto 1988) that belong to the genus *Panicum*, a cosmopolitan genus with approximately 450 species. *Panicum* is a remarkably uniform genus in terms of its floral characters but exhibits considerable variation in anatomical, physiological, and cytological features. Proso millet probably originated from a weedy variety, *Panicum miliaceum* var. *ruderales*, distributed from northeast China to eastern Europe (Sakamoto 1987). Vavilov (1926) suggested that China is the center of diversity for proso millet, while Harlan (1975) opined that proso millet probably was domesticated in China and Europe together with foxtail millet. Further study revealed that proso millet was domesticated somewhere in the region ranging from central Asia to northwestern India together with foxtail millet (Sakamoto 1987). Current evidence suggests that proso millet was the first millet domesticated, some 10,000 years BP in Neolithic China, where it appears to have been the earliest dry-farming crop (Lu et al. 2009). Using molecular data of the chloroplast *ndhF* gene, Aliscioni et al. (2003) assessed infrageneric classifications and proposed a robust phylogenetic tree of *Panicum*; however, genome origin of proso millet and little millet has not been analyzed. RAPD analysis differentiated North American wild proso and cultivated species (Colosi and Schaal 1997).

Barnyard millets *Echinochloa crus-galli* (Japanese) and *E. colona* (Indian), both hexaploid species, are from eastern Asia and India. *E. crus-galli* originated from the hybridization between tetraploid *E. oryzicola* and an unknown diploid species. The genetic relationship between *E. crus-galli* and *E. oryzicola* using nuclear DNA (nrDNA) ITS and the chloroplast DNA (cpDNA) *trnT-L*, *trnL* intron, and *trnL-F* regions clearly separated the New World *E. crus-galli* from Eurasian *E. crus-galli* and showed a close relationship to the American taxa, *E. crus-pavonis* and *E. walteri*. The nuclear DNA ITS sequences further indicated no differentiation between the Eurasian *E. crus-galli* and *E. oryzicola*, in contrast to their clear divergence in the cpDNA sequence, suggesting that *E. oryzicola* is the male donor of *E. crus-galli* (Aoki and Yamaguchi 2008). Further, phylogenetic analysis of the homologous copy sequences of *Oryza sh4* gene (controlling shattering nature of the spikelets) in *Echinochloa* showed genomic relationship between the Asian *Echinochloa* species, which supports the theory that the allohexaploid *E. crus-galli* shares two genomes with its parental donor, *E. oryzicola*. The Asian

perennial tetraploid species, *E. stagnina*, shares one genome with *E. oryzicola* and possesses an unknown genome. *E. crus-pavonis*, from the New World, shows a close affinity of two genomes with *E. crus-galli* and *E. oryzicola*, while *E. colona* shows distinct affinities in all homologous copies (Aoki and Yamaguchi 2009).

Ethiopia is the center of origin and diversity for tef (*Eragrostis tef*) (Vavilov 1951), and farmers in Ethiopia have greatly contributed to domesticating this unique cereal as a food crop. Tef is an allotetraploid cereal crop whose origin within the large genus *Eragrostis* was investigated by Ingram and Doyle (2003). Phylogenetic analysis of sequence data from the nuclear gene *waxy* and the plastid locus *rps16* strongly supports the widely held hypothesis of a close relationship between tef and *E. pilosa*, a wild allotetraploid. *Eragrostis heteromera*, another previously proposed progenitor, is shown by the *waxy* data to be a close relative of one of the tef genomes. Other putative progenitors included in the taxon sample were not supported as closely related to tef. The *waxy* phylogeny also resolves the relationships among other allopolyploids, supporting a close relationship between the morphologically similar disomic tetraploid species *E. macilentia*, *E. minor*, and *E. mexicana*. *Eragrostis cilianensis*, another morphologically similar disomic polyploid, appears to have shared one diploid progenitor with these species but derived its other genome from an unrelated diploid. Both *E. tef* and *E. pilosa* are disomic tetraploid species, cross compatible, and have similarity in karyotype and morphological traits; however, the two differ in spikelet shattering. The multifloreted spikelets of *E. pilosa* readily break apart at maturity as a natural mechanism of seed dispersal, whereas they remain attached to the rachis at maturity in *E. tef* (Phillips 1995).

Job's tears (*Coix lacryma-jobi*), a native to tropical Asia, belongs to the Andropogoneae tribe. The genus *Coix* consists of four species, *Coix aquatica*, *C. gigantea*, *C. lacryma-jobi*, and *C. puellarum*. *C. lacryma-jobi* is further divided into four taxa, var. *mayuen*, var. *lacryma-jobi*, var. *monilifer*, and var. *sternocarpa*. *C. lacryma-jobi* is widely distributed in Africa, Oceania, east Asia, and America (Bor 1960; Koyama 1987). Var. *mayuen* is cultivated as a cereal or medicinal plant in east Asia, southeast Asia, and south Asia, whereas other taxa are wild and some are used as medicine or beads. Murakami and Harada (1958) reported that *mayuen* is cultivated as a cereal and domesticated from *lacryma-jobi*, but the two differ in hardness of seed coats; *mayuen* is softer than *lacryma-jobi*. Job's tears probably were domesticated as a cereal in the continental parts of southeast Asia (Arora 1977; Sakamoto 1988).

Enomoto et al. (1985) used restriction endonuclease of cpDNAs to study the phylogenetic relationship among crops in tribe Gramineae and

showed that the phylogenetic tree is in complete agreement with that reported by Tateoka (1957) except that the genetic distance between the chloroplast genomes of sorghum (*Sorghum bicolor*) and maize (*Zea mays*)/Job's tears (*Coix Lacryma-jabi*), is closer than that between maize and Job's tears despite sorghum belongs to different tribe from maize and Job's tears. Thus, the two genera, *Zea* and *Coix*, should be placed in separate tribes. More recently, Leseberg and Duvall (2009) also demonstrated that the position of Job's tears in a phylogenetic tree coincides with the broadly delimited Andropogoneae (GPWG 2001) but contradicts earlier studies that classified Job's tears in a putative sister tribe, Maydeae, with *Zea mays* (Kellogg and Birchler 1993).

The genus *Digitaria* has 230 species, widely distributed in the tropics and subtropics (Clayton and Renvoze 1986). Of these species, *D. exilis* (white-seeded fonio) and *D. iburua* (black-seeded fonio) are domesticated and cultivated in West Africa (Portères 1976), with the former being most diverse and widely cultivated, while the latter is restricted to northern Nigeria, Benin, and Togo (Murdock 1959; NRC 1996). The putative wild relatives of cultivated fonio are probably *D. horizontalis* and *D. longiflora*; the latter has many interesting agronomic traits (erect habit, resistant to lodging, long panicle full of grains and large-size seeds) and appears useful for improving cultivated fonio (Dansie et al. 2010).

IV. ASSESSING PATTERNS OF DIVERSITY IN GERMPLASM COLLECTIONS

Ex situ seed storage is the most widely used method to conserve millets genetic resources. To date, 161,708 accessions of millets species are preserved in gene banks across the globe, 98.1% cultivated and 1.9% wild types (Table 5.10). Finger millet, foxtail millet, pearl millet, and proso millet form the largest collection of cultivated millets germplasm, while fonio and Job's tears form the smallest (Tables 5.11–13). In addition, the U.S.-based GRIN database contains 306 accessions of 18 *Echinochloa* species from 33 countries housed at the National Center for Genetic Resources Conservation (Fort Collins, Colorado; NSSL); 1,468 accessions of eight *Eleusine* species from 20 countries housed at NSSL and Southern Regional PI Station (Griffin, Georgia; S9); 1,014 accessions of 36 *Setaria* species from 52 countries housed at the North Central Regional PI Station (Ames, Iowa; NC 7); 1,616 accessions of 38 *Panicum* species from 52 countries housed at NC 7, NSSL, the Plant Germplasm Quarantine Program (Beltsville, Maryland; PGQP), S9, and the Western

Table 5.10. List of cultivated and wild relatives of barnyard millet, finger millet, fonio, foxtail millet, Job's tears, kodo millet, little millet, proso millet, and tef germplasm preserved worldwide in national and international gene banks in Africa, America, Asia, Europe, and Oceania.

Crop	Africa	America	Asia	Europe	Oceania	Total
Cultivated germplasm						
Barnyard millet			749		67	816
Finger millet	7,766	1,453	24,308	48	21	33,596
Fonio	285					285
Foxtail millet	985	1,368	38,429	4,643	336	45,761
Kodo millet			4,025		227	4,252
Job's tears		1	154	4		159
Little millet			1,017			1,017
Pearl millet	11,105	13,213	13,252	4,088	252	41,910
Proso millet		1,134	8,547	14,918	245	24,844
Tef	4,747	768	420	46	20	6,001
Total	24,888	1,7937	90,901	23,747	1,168	158,641
Wild relatives						
Barnyard millet	27					27
Finger millet	930	19	130			1,079
Foxtail millet	143	21	388			552
Job's tears			8		1	9
Pearl millet	286	57	1,025	1		1,369
Tef	1	5	1	24		31
Total	1,387	102	1,552	25	1	3,067

Source: http://apps3.fao.org/wIEWS/germplasm_query.htm.

Regional PI Station (Pullman, Washington; W6); and 1,401 accessions of 69 *Paspalum* species from 44 countries housed at NSSL, PGQP, and S9 gene banks (<http://www.ars-grin.gov/npgs/stats/>). The largest collections of finger millet can be found in India in Asia and in Ethiopia, Kenya, and Uganda in Africa; China, France, India, and Japan have the largest collections of foxtail millet; China, Russia, and Ukraine have the largest collections of proso millet; India has the largest collections of kodo millet and little millet; India and Japan have the largest collections of barnyard millet; Benin has the largest collection of fonio; Japan has the largest collection of Job's tears; Brazil, Canada, China, France, India, Namibia, Niger, Nigeria, and Pakistan have the largest collections of pearl millet; and Ethiopia has the largest collections of tef germplasm. Evidence suggests that some of the fonio germplasm has already been lost. The main reason for fonio genetic erosion is due to difficulties in its harvesting and postharvest processing (Adoukonou-Sagbadja et al. 2004). Likewise, diversity in barnyard millet has fast eroded due

Table 5.11. Number of cultivated germplasm accessions of finger millet, foxtail millet, pearl millet and proso millet preserved globally in national and international gene banks.

Country	Institute	No. accessions			
		Finger millet	Foxtail millet	Pearl millet	Proso millet
Asia					
Bangladesh	Bangladesh Agr. Res. Inst., Joydebpur, Gazipur		515		209
China	Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences (ICGR-CAAS), Beijing	300	26,233	103	6,517
India	All India Coordinated Small Millet Project, UAS, Bangalore	6,257	2,512		577
	CSK HP Krishi Vishvavidyalaya, Palampur, Himachal Pradesh	30			
	CCS Haryana Agricultural University, Hisar, Haryana			875	
	Indian Grassland and Fodder Research Institute(ICFRI), Jhansi, Uttar Pradesh			734	
	International Crop Research Institute for the Semi-Arid Tropics, Patancheru	5,852	1,488		849
	Indian Grass and Fodder Research Institute			568	
	National Bureau of Plant Genetic Resources (NBPGR), New Delhi	9,522	4,330	3,294	
	Regional Station Akola, NBPGR, Maharashtra	455	349		
	Regional Research Center, Jodhpur			5,772	
Japan	Department of Genetic Resources I, National Institute of Agrobiological Sciences (NIAS), Tsukuba-shi	565	2,450	133	296
	National Grassland Research Institute (NGRI), Nasu-gun, Tochigi-ken	74			
	Plant Germplasm Institute, Faculty of Agriculture, Kyoto University (KYOPGI), Mozume-cho - Muko-shi, Kyoto	58	274		62
Nepal	Central Plant Breed. & Biotechnol. Division, Nepal Agric. Res. Council (CPBBD), Kathmandu	869	30		16
Pakistan	Plant Genetic Resources Institute, Natl. Agric. Res. Centre, Islamabad		138	1,377	21
Sri Lanka	Fodder Research Institute, Sargodha			333	
	Seed Conservation Unit, Plant Genetic Resources Centre, Gannoruwa, Peradeniya	295	110		
Thailand	Dry Zone Agricultural Research Institute, Maha-Illuppallma	31			
	National Corn and Sorghum Research Center, Kasetsart University, Pak Chong - Nakhon Ratchasima			63	
Africa					
Angola	Centre National des Ressources Phytogénétiques, Ministère de l'Agriculture et du Développement Rural (CNRF), Luanda			135	
Benin	Centre de Recherches Agricoles Sud (CRAS), Attogon			27	
Botswana	Department of Agricultural Research, Sebele Agricultural Research Station, Gaborone			61	
Burkina Faso	Centre de Recherches Agricoles de Farako-Ba (CRA), Bobo-Dioulasso			112	
Ethiopia	Inst. Biodiversity Conserv (IBC), Addis Ababa	2,156		166	
Kenya	Natl. Gene Bank of Kenya, Crop Plant Genet. Resour. Centre (KARI-NGBK), Muguga	2,875	772	499	
Malawi	Chitedze Agr. Research Station			47	
Mali	Station de Recherche Agronomique de Cinzana (SRAC), Cinzana, Ségou			243	
Niger	Institut National de la Recherche agronomique du Niger (INRAN), Niamey			2,052	
Nigeria	ICRISAT, Niamey			2,817	
Namibia	Nat. Centre Genet. Resour. Biotechnol., Moor Plantation—Ibadan		45	46	
	National Plant Genetic Resources Center, National Botanical Research (NPGRC) Institute		5	1,416	
Senegal	Unité de Recherche en Diversité Génétique et Culture In-vitro (URCI), Dakar			44	

(continued)

Table 5.11 (Continued)

Country	Institute	No. accessions			
		Finger millet	Foxtail millet	Pearl millet	Proso millet
South Africa	Division of Plant and Seed Control, Dept. Agriculture, Pretoria	3	41	69	
Tanzania	National Plant Genetic Resources Centre (NPGRC), Arusha	74		48	
Uganda	Serere Agric. & Animal Prod. Res. Inst.,(SAARI) Soroti	1,231	122	2,142	
Zambia	Mt. Makulu Central Res. Station, Chilanga	390			
	SADC Plant Genet. Resour. Centre, Lusaka	1,037		785	
Zimbabwe	Zambia Agriculture Research Institute (ZARI), Chilanga			323	
	Genetic Resources and Biotechnology Institute, Ministry of Agriculture, Mechanization and Irrigation Development (GRBI), Causeway—Harare			73	
Americas					
Brazil	Embrapa Milho e Sorgo (CNPMS), Sete Lagoas			7,225	
	Embrapa Recursos Genéticos e Biotecnologia (CENARGEN), Brasília			161	
Canada	Plant Genet. Resour. of Canada, Saskatoon Research Centre, Agr. & Agri-Food Canada, Saskatoon, Saskatchewan	3	18	3,764	21
Mexico	Estación de Iguala, Instituto Nacional de Investigaciones Agrícolas, (INIA), Iguala		350		400
USA	North Central Reg. Plant Introd. Station, USDA-ARS, NCRPIS, Iowa State Univ. Ames, IA		1,000		713
	National Center for Genetic Resources Preservation, Fort Collins Colorado	702			
	Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS, Griffin, GA	748		2,063	
Europe					
Austria	AGES Linz—Austrian Agency for Health and Food Safety/Seed Collection, Wieningerstrasse 8, Linz	10			
Bulgaria	Inst. Plant Genet. Resour. “K.Malkov” (IPGR), Sadovo, Plovdiv				97
Czech Republic	Res. Inst. Crop Production, Praha		34		162
France	Biologie Végétale Appliquée, Institut Louis Pasteur (IUT), 3 rue de l’Argonne-Strasbourg		850		
Germany	ORSTOM-MONTP, Montpellier Cedex		3,500	4,059	
	Gene Bank, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Corrensstrasse 3, Gatersleben	27	124	29	
Hungary	Institute for Agrobotany (RCA), Kulsomezo 15, Tápíószele	11	27		20
Poland	Bot. Garden of Plant. Breed. & Acclimatization Inst., Bydgoszcz		82		721
Romania	Res. Inst. Cereals and Technical Plants Fundulea, Fundulea, Calarasi				65
Russian Federation	N.I. Vavilov All-Russian Scientific Res. Inst. of Plant Industry, St. Petersburg				8,778
Slovakia	Res. Inst. Plant Production, Piestany				53
Ukraine	Inst. Plant Prod. V.Y. Yurjev of UAAS, Kharkiv		14		1,046
	Ustymivka Experimental Station of Plant Production, S. Ustymivka				3,976
United Kingdom	Institute of Biological, Environmental & Rural Sciences, Aberystwyth University (IBERS-GRU), Ceredigion, Wales		12		
Oceania					
Australia	Australian Medicago Genetic Resources Centre, South Australian Research and Development Institute (AMGRC), SARDI, PRC GPO Box 397, Adelaide	8			
	Australian Tropical Crops & Forages Collection, Australian Plant Genetic Resource Information Service, Biloela	13	336	252	245
Total		33,596	46,070	41,910	24,844

Source: http://apps3.fao.org/wIEWS/germplasm_query.htm.

Table 5.12. Number of cultivated germplasm accessions of barnyard millet, kodo millet, and little millet preserved globally in national and international gene banks.

Country	Institute	No. accessions		
		Barnyard millet	Kodo millet	Little millet
Asia				
India	All India Coordinated Minor Millet Project, UAS, Bangalore		1,111	544
	ICRISAT, Patancheru	749	665	473
	NBPGR, New Delhi		2,170	
	NBPGR Regional Station, Akola, Maharashtra		79	
Oceania				
Australia	Tropical Crops & Forages Collection, Australian Plant Genetic Resource Information Service, Biloela	67	227	
Total		816	4,252	1,017

Source: http://apps3.fao.org/wIEWS/germplasm_query.htm.

to considerable reduction in acreage and changing sociocultural and economic dimensions of the farming community in India (Maikhuri et al. 2001). Foxtail millet, finger millet, and pearl millet have extensive collections of their wild relatives preserved in ex situ seed gene banks. No wild relatives are reported for fonio, kodo millet, and little millet (Table 5.14). In addition, some of the pearl millet wild relatives are maintained by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in an ex situ field gene bank at Patancheru, India, as they do not set seed. Among global gene banks, China has the largest collection of wild relatives of foxtail and proso millet; India has the largest collection of finger millet; and France and India have largest collections of pearl millet. A German gene bank contains the largest number of the few accessions of tef's wild relatives available.

Descriptor lists were developed and used to characterize barnyard millet (IPGRI 1983), finger millet (IBPGR 1985a), foxtail millet (IBPGR 1985b), kodo millet (IBPGR 1983), proso and little millets (IBPGR 1985c), pearl millet (IBPGR/ICRISAT 1993), and tef (Ketema 1997) germplasm for sets of morphological and agronomic traits. This information, along with passport data, was used to assess patterns of diversity in millets germplasm collections and has revealed many interesting facts about the utility of such germplasm in millets breeding and

Table 5.13. Number of cultivated germplasm accessions of fonio, Job's tears, and tef millets preserved globally in national and international gene banks.

Country	Institute	No. accessions		
		Fonio	Job's tears	Tef
Asia				
China	National Key Laboratory of Crop Genetic Improvement, Huazhong Agr. Univ., Wuha		14	
India	National Bureaue Plant Genetic Resources, New Delhi			253
Japan	CCS Haryana Agr. Univ., Hissar Department of Genetic Resources I, National Institute of Agrobiological Sciences (NIAS)		140	137
	National Inst. Crop Sci., Tsubuka			30
Africa				
Ethiopia	Institute of Biodiversity Conservation, P.O.Box 30726			4,741
Benin	Laboratory of Genetics and Biotechnology, Univ, Aboney-Calvi, Cotonou	261		
Ghana	Sabana Agr. Res. Inst., Tamale	24		
Kenya	National Gene Bank of Kenya, Crop Plant Genetic Resources Centre, Muguga			3
South Africa	Division of Plant and Seed Control, Dept. Agr, Technical Service			3
Americas				
Brazil	Centro de Pesquisa Agropecuaria dos Cerrados (CPAC), Planaltina			400
USA	Western Regional Plant Introduction Sta., USDA-ARS, Washington State Univ. North Central Regional Plant Introduction Station, USDA-ARS, NCRPIS		1	368
Europe				
Germany	Gene Bank, Leibniz Institute of Plant Genetics and Crop Plant Research Federal Center for Breeding Researcg on cultivated plants (BAZ), Braunschweig			12 30
UK	Welsh Plant Breeding Station, Genetic Resources Unit, Institute of Grassland and Environmental Research		2	2
Hungary	Institute for Agrobotany		2	2
Oceania				
Australia	Australian Tropical Crops & Forages Genetic Resources Centre			20
Total		285	159	6,001

Source: http://apps3.fao.org/wIEWS/germplasm_query.htm.

Table 5.14. Number of wild relative accessions of barnyard millet, finger millet, foxtail millet, Job's tears, pearl millet, and tef preserved globally in national and international gene banks.

Country	Institute	No. accessions				
		Barnyard millet	Finger millet	Foxtail millet	Job's tears	Pearl millet Tef
Asia						
Armenia	Laboratory of Plant Gene Pool and Breeding(LPGPB), Yerevan					42
	Scientific Center of Agrobiotechnology (SCAPP), Echimiadzin					30
China	Institute of Crop Germplasm Resources, Chinese Academy of Agricultural Sciences, Beijing			173		
	National Key Laboratory of Crop Genetic Improvement, Huazhong Agricultural University, Wuha				7	
India	International Crops Research Institute for the Semi Arid Tropics, Patancheru		105	54		
	National Bureaue Plant Genetic Resources, New Delhi			62		78
	CCS Haryana Agric. University, Hissar					875
Japan	Department of Genetic Resources I, National Institute of Agrobiological Sciences (NIAS), Tsukuba-shi		25	81	1	
Pakistan	Plant Genet. Resour. Inst., Natl. Agric. Res. Centre, Islamabad			18		
Yemen	Agricultural Research and Extension Authority (AREA), Dhamar					1
Africa						
Ethiopia	Int. Livestock Res. Inst. (ILRI), Addis Ababa	27	11	119		203
	Institute of Biodiversity Conservation (IBC), Addis Ababa		17	6		1
Kenya	Agricultural Research Centre (KARI), Kitale			13		59
	National Gene Bank of Kenya, Crop Plant Genetic Resources Centre(KARI-NGBK), Muguga		56	5		
Malawi	Chitedze Agricultural Research Station, Lilongwe		156			
South Africa	RSA Plant Genetic Resources Centre, Pretoria		21			
Tanzania	National Plant Genetic Resources Centre (NPGRC), Arusha		286			8
Zambia	SADC Plant Genet. Resour. Centre, Lusaka					10
	Zambia Agriculture Research Institute, Chilanga		383			
American continent						
Canada	Plant Genetic Resources of Canada, Saskatoon Res. Center, Agric. and Agri-Food		3			25
Colombia	CIAT, Cali, Valle del Cauca			21		27
USA	Western Regional Plant Introduction Station, USDA-ARS, Washington State University					3
	Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS, Griffin		16			
Uruguay	INIA La Estanzuela					5
Europe						2
Germany	Gene Bank, Leibniz Institute of Plant Genetics and Crop Plant Research (IPK), Corrensstrasse 3, Gatersleben		9	30		31
Austria	AGES Linz—Austrian Agency for Health and Food Safety/Seed Collection, Wientingerstrasse 8, Linz					1
France	Biologie Végétale Appliquée, Institut Louis Pasteur (IUT), Strasbourg			250		
	ORSTOM-MONTP, Montpellier Cedex					131
Hungary	Institute for Agrobotany (RCA), Kulsomezo 15, Tápiószele		4	15		
Slovakia	Botanical Garden, University of Agriculture, Nitra					1
United Kingdom	Seed Conservation Department, Royal Botanic Gardens (RBG), Kew, Wakehurst Place		23	57		250
Oceania						
Australia	Australian Medicago Genetic Resources Centre, South Australian Research and Development Institute (AMGRC), SARDI, PRC GPO Box 397, Adelaide		18	2		7
	Australian Tropical Crops & Forages Genetic Resources Centre (ATCFRC), Biloela				1	
Total		27	1,133	906	9	1,781
						32

Source: http://apps3.fao.org/wIEWS/germplasm_query.htm.

genetics (Table 5.15). For example, accessions belonging to *laxa* race of barnyard millet, endemic to Sikkim state of India, are not represented in the ex situ collections preserved at the ICRISAT gene bank in Patancheru, India. Thus, there is an urgent need to collect this race before it becomes extinct. Likewise, the germplasm accessions from tef-growing regions of Hararghe, Arsi, Wellega, and Bale in Ethiopia are not represented in the gene bank of the Institute of Biodiversity Conservation in Ethiopia (Demissie 2001). Fonio landraces collected from Ghana and Togo have immense diversity with respect to agroecological adaptation and preferences of the tribes that maintain and cultivate these landraces: for example, landraces from the northern zone of Togo are better adapted to dry conditions; those from the Kara region in the north had the most landrace diversity, with greatest landrace diversity being maintained by the Lamba tribe. The later-maturing fonio landraces from Ghana have lighter seeds (1,000-seed weight) while early-maturing types have heavier seeds. Furthermore, earliness, ease in processing, and long shelf life (e.g., seeds of “Saranu” landrace could be stored up to eight years without loss of quality or viability) were the basis for farmer selection of landrace variability in fonio. More recently, Dansi et al. (2010) grouped 15 farmer-named landraces collected from the fonio production zones of Benin into five morphotypes, of which four belong to *D. exilis* (white fonio) and one to *D. iburua* (black fonio), and identified eight preference criteria of farmer-preferred fonio varieties: earliness, culinary characteristics, ease of harvesting and processing, productivity, grain size, storability, and drought tolerance. This study further revealed that farmers preferred the early-maturing landrace “Tinting” as it help them to bridge the food shortage period when no other crops are ready for harvest and consumption. Likewise, the preference for the “Sémbré” landrace was mainly due to its ease in processing (husking) of the grains, while most farmers disliked landraces “Tamaou” and “Fôlôm” because of their long growth period and difficulties in husking their grains. Foxtail millet (*Setaria italica*) accessions from Afghanistan, Iran, and Lebanon, one of the three possible (putative) centers of domestication and diversity in foxtail millet, resemble green foxtail millet (*S. viridis*), the wild progenitor species of cultivated *S. italica*. In pearl millet, landraces from Yemen are a source of variation for early maturity, cold tolerance, short stature, and large seeds. Landraces from western and central Africa show exceptional buffering against environmental variability, and landraces from Cameroon, Togo, and Ghana are good sources for earliness and/or large seeds. Early flowering, profuse tillering, more panicles plant⁻¹, and larger seed size are the characteristics of some landraces from northwestern India. Some of the landraces from this Indian region exhibit no trade-off

Table 5.15. Summary of the pattern of diversity as assessed in barnyard millet, finger millet, fonio, foxtail millet, pearl millet, proso millet, and tef germplasm.

Accessions/traits studied	Pattern of diversity discerned	Reference
Barnyard millet 194 accessions from India and 14 traits	Assessing pattern of phenotypic diversity among accessions collected from different ecogeographical regions of India revealed no accession represented race <i>laxa</i> , endemic to Sikkim in India	Gupta et al. 2009
Finger millet 909 germplasm from southern and eastern Africa and 7 traits	Early-flowering accessions from Kenya while later-flowering types from Tanzania and Zaire; accessions with narrowest inflorescence width from Kenya and Zimbabwe while those with the widest inflorescence width from Nepal, Ethiopia, and Tanzania; accessions with no panicle exertion can be found in Kenya, Nepal, and Zimbabwe while those with full panicle exertion from Tanzania and Zaire	Upadhyaya et al. 2007a
Fonio 13 landraces from Ghana and 5 traits	Phenology—a major determinant of diversity among landraces: those from Nyankpala matured earlier than those from eastern part of northern region; late-maturing types had lighter 1000-seed weight while early-maturing types heavier seeds	Clottey et al. 2006a
11 landraces from farmers barns in Ghana	Earliness, ease of processing and storage quality the basis for farmers' selection of landrace variability, i.e., Nomba, Fefeka, and Kiyo landraces selected for early maturity; Yadema for ease in processing; Sarannu for long shelf life (8 years without loss of quality and viability); and Nankapando for drought resistance	Clottey et al. 2006b

(continued)

Table 5.15 (Continued)

Accessions/traits studied	Pattern of diversity discerned	Reference
95 accessions representing 34 landraces collected from 7 ethnic groups in Togo	Landraces from the northern zone better adapted to dry conditions than those cultivated in the south, which are adapted to a relatively wet climate; landraces from Kara region in the north have the most diversity followed by Plateaux in the south and Savanes in the north; at ethnic level, the Lamba tribe maintained maximum landrace diversity followed by the Akposso, Losso-Nwada, and Tamberma	Adoukonou-Sagbadja et al. 2004
Foxtail millet 1535 accessions from 26 countries and 6 traits	Greater diversity for flowering in Sri Lankan germplasm, while narrowest in Russian germplasm; accessions from China dwarf while those from India tall; accessions with maximum panicle exertion from Russia; accessions with longest and widest inflorescence from India	Reddy et al. 2006
2907 accessions from 16 provinces of China + 22 countries and 9 traits	Accessions of Chinese origin highly diverse, while those from Afghanistan, Iran, and Lebanon less diverse and characterized by short plant height with more tillers and smaller panicles, resembling green foxtail millet (wild type)	Li et al. 1995a
Pearl millet 145 inbreds derived from 122 WCA landraces	Flowering, relative response to photoperiod and panicle length significantly impacted, population structure differentiation but not the environmental factors such as latitude, temperature, or precipitation	Stich et al. 2010
169 landraces from India evaluated for grain and stover yield	Significant differences among landraces for biomass, grain, and stover yield; several landraces outperformed controls in both grain and stover yields; no trade-off between stover and grain yields under arid zone conditions	Yadav and Bidingar 2008
20,844 germplasm from 51 countries and 23 traits	Diversity in flowering ranges from 33 to 159 days; plant height from 30 cm to 490 cm; tillers from 1 to 35; 100-seed weight from 1.5 to 21.3 g; forage type 141 accessions; 9 panicle shapes, 5 seed shapes, and 10 seed colors	Upadhyaya et al. 2007b
5197 germplasm from India and 8 traits	Climate variables impacted pattern of diversity: arid zone as the promising source of early flowering, short height, and large seeds; semiarid zone for thick panicles and high panicle exertion; subhumid zone for tall and long panicles	Upadhyaya et al. 2007c
424 landraces from West and Central Africa (WCA) evaluated for flowering	Exceptional buffering capacity (both at individual and population level) against environmental variability, due to variation in photoperiod sensitivity and intravarietal heterogeneity for flowering, confer adaptive advantages under variable climatic conditions, thus, a good resource to enhance adaptation of pearl millet under similar scenarios in other agroecological zones as found in WCA	Haussman et al. 2007
229 germplasm from Yemen and 12 traits	Yemen has extreme variation in elevation, temperature, and rainfall, which significantly impacted variability in pearl millet: germplasm from high elevation good source for early maturity, cold tolerance, short plant height, and large seeds; accessions from lower elevation have longer panicle while increasing elevation have accessions with thinner panicle	Reddy et al. 2004
105 landraces from northwestern India and 8 traits	Large variation in flowering, plant height, panicle length and panicles plant ⁻¹ among landraces; more than 2-fold difference in grain and stover yield; phenotypic diversity spread into 9 clusters, some with specific attributes: i.e., landraces from cluster 9 were highest yielding due to early flowering, more panicle plant ⁻¹ , and larger seed size while cluster 4 landraces provided highest stover yield but flowered late and produced less grain	Yadav et al. 2004b
918 accessions including wild relatives from Cameroon and 8 traits	A good source for more reproductive tillers, large compact spikes, and larger ivory- and cream-colored grain besides its potential for forage; early-maturing types (Mouri) adapted to low rainfall, while late-maturing types (Yadiri) in high rainfall regions	Rao et al. 1996
227 landrace populations from Ghana and 18 traits	Mixtures of various morphological types were the common features of landrace populations grown by the farmers and good source of genes for earliness and large grain size	Rao et al. 1985

(continued)

Table 5.15 (Continued)

Accessions/traits studied	Pattern of diversity discerned	Reference
Proso millet 842 germplasm from 27 countries and 9 traits	Early-flowering accessions from Syria while late-flowering from India; dwarf accessions from Mexico and tall from Sri Lanka; accessions with good panicle exertion from Australia and China while those with shorter panicle from former USSR and of longer panicle from Nepal	Reddy et al. 2007
Tef 144 heterogeneous germplasm from Ethiopia and 18 traits	Regions and altitudes have had no substantial effect on genetic diversity; higher intraregional genetic diversity (between tef germplasm from the same region and altitude) than interregional diversity	Adnew et al. 2005
3000 panicle derived lines from 60 germplasm of Ethiopia and 17 traits	Detected regional and clinal (altitude zone) diversity patterns in tef germplasm; all the 6 regions remain separate and unclustered at 75% similarity, while at 50% level of similarity Shewa, Wellega, and Keffa clustered together and the remaining 3 regions remained distinct and ungrouped	Assefa et al. 2003a
60 germplasm and 6 traits	Germplasm from high altitudes (>2400 m.a.s.l.) differed significantly from those either lowland (<1800 m.a.s.l.) or midaltitude (1800–2400 m.a.s.l.)	Assefa et al. 2002
1080 germplasm (36 populations) from 6 central/northern regions of Ethiopia and 14 traits	Large variations within populations as well among populations within regions and altitude zones providing immense potential for the genetic improvement through breeding	Assefa et al. 2001

between stover and grain yields and thus provide potential resource for producing dual-purpose hybrids adapted to arid-zone environments. Tef landraces from Ethiopia have revealed greater intraregional diversity than interregional diversity, clearly indicating that regions and altitudes have had no substantial effect on genetic diversity in tef populations.

Unlike other cereals, there are very limited collections of millets wild relatives in gene banks. Wild relatives are not utilized in crop improvement programs, probably because sufficient variability already is present in the cultivated gene pool and there is a lack of resources for introgression work to eliminate weedy characteristics. However, some wild relatives have been reported to contribute beneficial traits to the cultivated gene pool. For example, resistance to herbicides (triazine, sethoxydim, dinitroaniline, and trifluralin) from *Setaria viridis* (green foxtail millet), controlled by one to two major genes with some modifier effects, has been successfully transferred into *S. italica* (the cultivated type) (Darmency and Pernes 1985; Jasieniuk et al. 1994; Wang et al. 1996; Wang and Darmency 1997). Likewise, *Pennisetum glaucum* subsp. *monodii* accessions (PS# 202, 637, 639, and 727) are good sources of resistance to *Striga hermonthica*, a serious cereal parasitic weed in sub-Saharan West Africa. PS 202 is also resistant to downy mildew, a devastating disease of pearl millet (Wilson et al. 2004). Other wild pearl millet accessions have been used as sources of rust resistance (Hanna et al. 1985) and alternative cytoplasmic male sterility systems (Hanna 1989). Clearly, more research is needed to find useful traits locked into the genetic backgrounds of wild relatives of millets to expand their cultivated gene pools.

Targeting induced local lesions in genomics (TILLING) is a novel nontransgenic PCR-based technology that uses chemically mutated populations. It has been successfully implemented to improve crops and identify gene function in maize, barley, and wheat (reviewed in Dwivedi et al. 2007). Lodging is a serious constraint to tef production, and there is no genetic variation reported for this trait in germplasm collections. Recently, an Ethiopian researcher at the University of Bern, Switzerland, has developed a tef-based TILLING assay. The assay will be transferred to the technology platform of the Biosciences Eastern and Central Africa in Nairobi, Kenya, for use in tef with the initial objective of developing dwarf tef plants resistant to lodging (<http://www.syngenta-foundation.org>). Ecotilling has also been applied on 500 nonmutanized accessions to detect useful genetic variations in natural populations of tef (Assefa et al. 2010). Likewise, researchers at ICRISAT have developed a TILLING population in pearl millet that can be studied to identify mutants with beneficial traits or identify specific genes contributing substantially to variation in specific traits (e.g., downy mildew and rust resistance) for use in pearl millet improvement (ICRISAT 2009).

V. IDENTIFYING GERMPLASM WITH BENEFICIAL TRAITS

A. Resistance to Biotic Stresses

Like other cereals, the millets are also affected by several fungal diseases. The most prominent among these are blast in finger millet, foxtail millet, and pearl millet; downy mildew in pearl millet and foxtail millet; ergot in pearl millet; rust in pearl millet, foxtail millet, and tef; smut in barnyard millet, foxtail millet, Job's tears, pearl millet, and proso millet; and wheat curl mite (*Eriophyes tullipae*), the carrier for wheat streak mosaic virus, and the virus itself in proso millet (Table 5.8). Their effects range from mild symptoms to catastrophes when large areas are destroyed. For example, India harvested a record grain production of 8.2 million t of pearl millet during the 1970–1971 season, but production declined to 4.6 million t in 1971–1972 season due to a severe epidemic of downy mildew on a popular single-cross hybrid, HB3, grown on a large scale in India at the time. Tift 23A (which had no resistance to downy mildew) was the only cytoplasmic male sterile (CMS) line used as a female parent to develop the first commercialized pearl millet hybrids in India including HB3 (Singh 1995). Subsequent studies (Yadav 1996b) have clearly demonstrated that the male-sterile cytoplasm itself is not associated with increased susceptibility to downy mildew; instead, the nuclear genotype controls downy mildew reaction in pearl millet. The deployment of genetic resistance is the most sustainable way to minimize losses in grain yield and quality due to pest and diseases. Precise phenotyping, presence of natural variation in crop germplasm (including wild relatives), pathogen variability, and understanding the mechanism and genetics of resistance are very important to finding and using new genes for host plant resistance to biotic stresses.

1. Phenotypic Screening. Researchers at ICRISAT and elsewhere have developed phenotypic screens (field and/or greenhouse) for resistance to downy mildew (Williams et al. 1981; Singh and Gopinath 1985; Singh et al. 1997; Jones et al. 2002; Thakur et al. 2008), ergot (Thakur and Williams 1980; Thakur et al. 1982), rust (Singh et al. 1997), and smut (Thakur et al. 1983; Thakur and King 1988c) in pearl millet; to blast (neck and finger) in finger millet, foxtail millet, and pearl millet (R. P. Thakur, pers. commun., ICRISAT); and to grain smut in barnyard millet (Gupta et al. 2009a). These screenings allow identification of millet disease-resistant germplasm.

2. Natural Genetic Variation. Pearl millet, finger millet, foxtail millet, and probably proso millet germplasm collections have been most extensively evaluated for resistance to major diseases. There are several sources of resistance to downy mildew, ergot, rust, blast, and smut in pearl millet; to blast in finger millet; to blast, downy mildew, rust, and smut in foxtail millet; to smut in proso millet and barnyard millet. These resistances in many cases have been transferred into improved genetic backgrounds (Table 5.16). Clearly, more research input is needed to identify sources of resistance to rust in tef and smut in barnyard millet and Job's tears.

3. Pathogen Variability, Mechanism, and Genetics of Resistance.

Downy mildew (*Sclerospora graminicola*) is the major pathogen of pearl millet in Asia and Africa. It is heterothallic and reproduces both sexually and asexually, with pathogen populations from West Africa earlier reported to be highly virulent compared to those from south Asia and eastern and southern Africa. This disease has demonstrated potential to shorten the useful life of genetically uniform single-cross hybrids (Singh 1995; Thakur et al. 2002, 2004). Host plant resistance to downy mildew can be dominant over susceptibility, additive, recessive, or even exhibit (pseudo-) overdominance. Partial host plant resistance to the causal pathogen of downy mildew is controlled by one or more major genes with some modifiers (Singh et al. 1993; Jones et al. 1995, 2002; Hash and Witcombe 2001; Breese et al. 2002). Six major putative pathotypes, based on disease incidence across a set of differential lines, have been reported on pearl millet in India (Thakur et al. 2006), while additional pathogenic variation is present in sub-Saharan Africa (Jones et al. 1995). Inter-simple sequence repeats (ISSR) primers have been used to characterize variability among 22 *S. graminicola* isolates. The 19 inter-simple sequence repeats (ISSR) primers were able to distinguish all these isolates, which formed four major clusters, accounting for 70% of the marker-based variation among isolates (Sudisha et al. 2009), while Jogaiah et al. (2008), based on RAPD and ISSR marker profiling data, grouped the 27 downy mildew isolates into six distinct pathotypes. However, clustering of six pathotypes within groups was not similar when RAPD and ISSR-based dendograms were compared. More recently, Sharma et al. (2010) reported a high level of variation among 46 downy mildew isolates from India for disease incidence, latent period, and virulence index. Based on reaction on a set of nine pearl millet lines, they classified 46 isolates into 21 pathotypes, with pathotype P11 the most virulent, infecting all the nine host differentials. Furthermore, there was little correspondence between the two dendograms generated by the average linkage cluster analysis: The virulence index-based dendogram

Table 5.16. Germplasm and cultivars reported resistance to major diseases in barnyard millet, finger millet, foxtail millet, Job's tears, pearl millet, proso millet, and tef.

Sources of resistance to major diseases in millets crops	Reference
Barnyard millet	
Grain smut (<i>Ustilago panici-frumentacei</i> Brefeld)	
Large range variation, from highly resistant, to moderately resistant to highly susceptible category, were reported among 257 accessions tested for grain smut spores at anthesis	Gupta et al. 2009
Finger millet	
Blast (<i>Magnaporthe grisea</i>)	
GE# 281, 568, 669, 705, 1044, 1293, 1409, 1546, 1855, 3022, 3024, 3058, 3060 and MR 6; IE 287 and IE 976; IC 43335; MR 33, KMR 9 and KMR 3; Gulu E, Seremi 1, Seremi 2, Pese 1, SX8, SEC915; KNE# 620, 629, 688, 814, 1034, and 1149; VL 149, VL 146, Gautami, GPU 28,	Seetharam 1989, 1998; Gowda et al. 1999; Jain and Yadav 2004; Madhukeshwara et al. 2004; Wanyera 2007; Sreenivasaprasad et al. 2007
Foxtail millet	
Downy mildew (<i>Setosphaeria graminicola</i>)	
Meera (SR 16), Longgu 28, Jingu 16, Jingu 11, Lugu No 7, Yugu No 3, Lujin 3, Beihuang, Zhenggu 2	Jiyaju 1989; Jiyaju and Yuzhi 1993; Maloo et al. 2001
Blast (<i>Pyricularia setariae</i>)	
K74-10-4-4, 73-10-24-15, 72-12-6-3, 77-10-7-9, 77-10-7-24, 7-6-22-21	
Nenxian 13, Jigu 1, Jingu 16, Jingu 11, Jingu 1, Lugu No 7, Yugu No 3, Minquangingu	Nakayama et al. 2005
Smut (<i>Ustilago crameri</i>)	Jiyaju and Yuzhi 1993
Jingu 16, Lugu No 7, K8763 (<i>P.1</i> , gene donor for smut resistance), Saratovskoye 2, Saratovskoye 3, Saratovskoye 6, Veselepodolanskoye 632, Barnaulskoye 80, Gorlinka	
Rust (<i>Uromyces setariae-italicae</i>)	
Lugu No 7, Yugu No 2, Yugu No 3	Jiyaju and Yuzhi 1993
Job's tears	
Leaf blight	
Akisizuku	Tetsuka et al. 2008
Smut (<i>Ustilago coicis</i>)	
Mayuen	Chang and Tzeng 1999
Pearl millet	
Downy mildew (<i>Sclerospora graminicola</i>)	
ICML #12, 13, 14, 15, 16, and 22; IP #16438 and 16762; P 310-17 and P 1449-3; IP18292; IP18293; 700651; ICMP #312, 423, and 85410; 7042S; 841A; IP #9, 55, 104, 253, 262, 336, 346, 498, 545, and 558; landrace such as Ardi-Beniya Ka Bas, Dhodsar local and Desi Bajri-Chomu	Singh et al. 1997; Khairwal and Yadav 2005; Thakur et al. 2006; Sharma et al. 2007
Rust (<i>Puccinia</i> sps.)	
ICML #5, 6, 7, 8, 9, and 10; ICML #17, 18, 19, 20 and 21; Tift 3 (PI 547035) and Tift 4 (PI 547036); Tift 65 (resistant to rust and leaf spot); Tifleaf 3	Bourland 1987; Thakur and King 1988a; Wilson and Burton 1991; Burton and Wilson 1995; Hanna et al. 1997
Ergot (<i>Claviceps fusiformis</i>)	
ICML #1, 2, 3, 4, 5, 6, 7, 8, 9, 10; ICMA 92666 and ICMB 92666 (resistant to ergot, smut, and downy mildew); ICMA #91333, 91444, and 91555; ICMPE #13-6-30, 134-6-9, 134-6-34, 13-6-27, 37, and 71	Thakur et al. 1982; Willingale et al. 1986; Thakur and King 1988a,b; Thakur et al. 1992; Rai et al. 1998a; Khairwal and Yadav 2005
Smut (<i>Moesziomyces penicillariae</i>)	
SSC 46-2-2-1, SC 77-7-2-3-1, SSC 18-7-3-1; ICMV 8282, ICMV8283; ICMA 88006A and ICMA 88006B (resistant to smut and downy mildew); ICMA #91333, 91444 and 91555; 44 accessions selected from the screening of 1747 germplasm; ICML #5-10; ICMPs #100-5-1, 700-1-5-4, 900-1-4-1, 900-3-1, 900-9-3, 1300-2-1-2, 1400-1-6-2, 1600-2-4, 1500-7-3-2, 1800-3-1-2, and 2000-5-2; SSC FS 252-S-4, ICI 7517-S-1, ExB 132-2-S-5-2-DM-1, ExB 46-1-2-S-2, ExB 112-1-S-1-1, and P-489-S-3	Thakur et al. 1986; Thakur and King 1988c; Yadav and Duhan 1996; Rai et al. 1998b; Khairwal and Yadav 2005
Proso millet	
Smut (<i>Sphacelotheca panici millii</i> pers (Bubak))	
K8763 (<i>P.1</i> , gene donor for smut resistance), Saratovskoye 2, Saratovskoye 3, Saratovskoye 6, Veselepodolanskoye 632, Barnaulskoye 80, Gorlinka; 'Ilnovskoe' (having <i>Sph2</i> -resistant gene)	Ilyin et al. 1993; Zolotukhin et al. 1998
Tef	
Rust (<i>Uromyces eragrostidis</i>)	
Lower levels of rust severity reported in 22 landraces	Dawit and Andrew 20005

grouped the isolates into eight clusters while the AFLP-based dendrogram formed seven clusters; four isolates could not be clustered into any of these groups.

Ergot (*Claviceps fusiformis*) infection in pearl millet occurs mainly through the stigmas, and stigma receptivity influences the infection of pearl millet florets by *C. fusiformis* conidia (Thakur and Williams 1980). For infection to occur, it is essential that the stigmas remain fresh long enough to enable ergot conidia to germinate and for penetrating hyphae to pass down through the stigma to the ovary. The period required for a stigma to be infected by *C. fusiformis* is approximately between 36 and 48 hours in the tropics. Stigmas that remain fresh for 48 hours or more in the absence of cross- or self-pollination are potentially at risk from ergot. However, escape from ergot becomes likely if the stigma remains receptive for a few hours only (Willingale et al. 1986). Further, postpollination stigmatic constriction, ubiquitous among pearl millets, provides a mechanical barrier to invasion of the fertilized ovary by the fungal pathogen. Pollination thus provides protection against ergot infection as it induces rapid withering of stigmas. Pollen-based escape mechanisms must be avoided while screening for other forms of resistance to ergot. To do that, plants at the boot-leaf stage should be bagged so that the inflorescences emerge into a pollen-free and inoculum-free environment. Such panicles should be inoculated with a conidial suspension containing 1×10^6 conidia milliliter⁻¹ and bagged immediately after inoculation. Very low levels of resistance to ergot have been reported in pearl millet; however, when such germplasms were intermated and the progenies evaluated for ergot resistance during succeeding generations, from F₂ to F₆, using an improved screening technique, the resistance level increased steadily when individual inoculated inflorescences with little or no ergot were selected to provide selfed seed for the next generation (Thakur et al. 1982, 1985). No major genes for ergot resistance have been reported in pearl millet. Resistance is recessive and polygenic (Thakur et al. 1983). To the authors' knowledge, there has been no pathogenic variability reported in *C. fusiformis*. Likewise, resistance to smut (*Moesziomyces penicillariae*) in most of the ergot susceptible lines is independent of the timing of flowering events, while in ergot-resistant lines, it could be closely related to flowering events (Thakur 1989). Resistance to smut is controlled by a few dominant genes with additive effects (Chavan et al. 1988), although the recessively inherited trichomeless mutation (*tr*), which removes most aerial trichomes, including stigmatic hairs, is reported to confer partial resistance to smut (Wells et al. 1987; Wilson and Hanna 1998). To our best knowledge, there are no

definite indications of any pathogenic variation in *M. penicillariae* populations.

Blast (*Magnaporthe grisea*) is the major disease of finger millet and foxtail millet and damages the leaf, neck, and finger or panicles. This fungus can also be an important disease of pearl millet grain and forage crops and cause disease on many other grasses, including rice. Using a PCR-based method and marker profiling of 328 *M. grisea* isolates, Srinivasaprasad et al. (2007) demonstrated that *M. grisea* isolates from East Africa were genetically distinct from those of Asia, and identified 243 haplotypes from 328 *M. grisea* isolates. Cluster analysis of these haplotypes showed continuous genetic variation and lack of clonal lineage among the blast pathogen populations from East Africa. Some of the shared haplotypes identified were common between countries while others were restricted to one country. Likewise, some of the shared haplotypes represented *M. grisea* isolates from different parts of the finger millet plant, indicating genetic similarity of isolates capable of causing different types of blast. Furthermore, some of the shared haplotypes also represented *M. grisea* isolates both from cultivated and wild finger millet, suggesting their genetic similarity; thus, wild finger millets could serve as an alternate host in the field. Pathogenicity tests have further confirmed that all *M. grisea* isolates caused susceptible blast reactions on finger millet varieties, with variation in aggressiveness.

Preliminary genetic analysis of blast resistance to four Japanese fungus isolates suggests that resistance to blast is controlled by more than two dominant genes in foxtail millet (Nakayama et al. 2005).

B. Tolerance to Abiotic Stresses

All crops are affected by abiotic stresses, and millets are no exception. However, these crops are generally considered well adapted (at least compared to most other cereals) to drought, salinity, high temperature, water logging, soil Al⁺⁺⁺ saturation, and poor soil fertility stresses (Zegada-Lizarazu and Iijima 2005). In addition, the thinner-stemmed millets, such as finger millet, foxtail millet, proso millet, and fonio, are often affected by lodging, especially under conditions of high soil fertility. Lodging is often less problematic in pearl millet, especially in improved cultivars, although some commercialized single-cross hybrids and their parental lines are highly prone to lodging. In addition, the parasitic weed *Striga* has become a major constraint to finger millet production in Africa (N. Wanyera, NASARRI, Soroti, Uganda, pers. comm.).

Identification and utilization of undiscovered variation for abiotic stress tolerance could enhance the adaptation of cereal crops. World-wide, over 161,708 gene bank accessions of the ten millets species preserved in national and international gene banks (see Section IV) provide researchers a unique resource for the discovery and characterization of genetic variation for abiotic stress tolerance that can eventually be harnessed in crop improvement programs. Precise phenotyping is the key to finding and exploiting new genes for abiotic stress tolerance. Phenotypic screens for drought, salinity, and high temperature stresses have been developed by ICRISAT to identify tolerant germplasm (Krishnamurthy et al. 2007; ICRISAT 2009). Further, improved understanding of the physiological and molecular basis of tolerance mechanisms will contribute toward developing more stress-tolerant crops.

Unlike other cereals, these millets have received limited research attention to identify sources of resistance to abiotic stresses. More of the research priority was on identifying drought and salinity tolerance in pearl millet, which as a species is also reasonably tolerant to Al toxicity (Flores et al. 1991); drought tolerance in fonio; drought, salinity, low temperature, lodging, and water-logging tolerance in foxtail millet; and drought and salinity tolerance in proso millet (Table 5.17). In a limited way, there have been some gains in understanding the physiological basis of abiotic stress tolerances and the genomic regions associated with control to some of these abiotic stresses (see Section VIII.A); for example, research teams have started developing more drought-tolerant pearl millet inbred lines and hybrids using marker-assisted backcrossing (MABC) (Serraj et al. 2005).

1. Drought. Using seedling survival following repeated drought stress, Li (1991, 1997) grouped 17,799 foxtail millet accessions (17,313 landraces and 486 elite cultivars) into five grades of drought tolerance, with grade 1 accessions being the most drought tolerant and including more elite cultivars than landraces. Using a similar screening procedure, Wen et al. (2005) identified several drought-tolerant landraces and cultivars from Shanxi Province in China. Researchers in China developed a quick and simple screen for drought tolerance using mannitol or polyethylene glycol (PEG-6000) tests and identified relative water content and germination rate under osmotic stress as indicators of drought tolerance at the seedling stage in foxtail millet (Zhang et al. 2005; Zhu et al. 2008). Foxtail millet is most sensitive to drought at the inflorescence and spikelet development stage (about 35 to 50 days after sowing).

When comparing water use efficiency (WUE) of the six millet species under waterlogging, well-watered (control), and drought conditions,

Table 5.17. Germplasm/cultivars reported resistant/tolerant to abiotic stresses in finger millet, foxtail millet, Job's tears, pearl millet, proso millet, and tef.

Abiotic stress and sources of resistance/tolerance	Reference
DROUGHT	
Finger millet	
MR-2 (high-yielding dual-purpose cultivar), AK132-1	Gowda et al. 1998; Seetharam 1998
Foxtail millet	
Longgu 28, Nenxian 13, Chingu No 4, Jingu 11; Longgu 25, Longfu 92170, Nuanxuan 8, Chigu 4, Yugu 1, Yugu 2, Zheng 173, Jigu 11, Chengu 7, Jingu 9, Jingu 10, Jingu 16, Yapoché, Dongfangliang, Liutiaoqing, Paosima, Yintianhan, Liutiaoqing, Kaoshanhuang, Shengzitou	Chen and Qi 1993; Li 1997
Pearl millet	
CZP 9802; 863B, ICMP 83720, ICMV 9413, ICMV 94472, and PRLT 2/89-33	Yadav 2004; Dwivedi et al. 2010
Tef	
DZ-Cr-37, 237186, 237131 and 212928; Ada and DZ-01-99; Kaye Murri and Ada (35% longer maximum root length under drought stress); Fesho had largest osmotic adjustment	Ayele et al. 2001; Degu et al. 2008; Asfaw and Itanna 2009
SALINITY	
Finger millet	
TRY1	Seetharam 1998
Foxtail millet	
Prasad; Honggu, Xiaohuanggu, and Sanbianchou (tolerant at germination and seedling stage)	Sreenivasulu et al. 1999; Tian et al. 2008
Pearl millet	
10876 and 10878 (Sudan), 18406 and 18570 (Namibia), and ICMV93753 and ICMV 94474 (India); 863-B, CZI 98-11, CZI 9621, HTP 94/54, ICMB 02111, ICMB 94555, ICMB 95333, ICMB 00888, ICMB 01222, ICMP 451, IP 3732, IP 3757, IP8210, and PRLT 2/89-33	Ali et al. 2004; Dwivedi et al. 2010
Proso millet	
008211, 008214, 008215, 0080220, and 008226 (tolerant at seedling stage)	Sabir and Ashraf 2007, 2008
LODGING	
Foxtail millet	
Longgu 28, Nenxian 13, Jingu 11, Yugu No. 1, Yugu No 2, Yegu 5, Yanggu, Liuyuexian 2, Cang 155, Gufeng 1, An 4844, Heng 8735, Ji 9409, Pin 324, Zheng 9188, Pin 540, Cang 409, An 7169, An 9217, Bao 182	Chen 1989; Chen and Qi 1993; Tian et al. 2010
Job's tears	
Akisizuku	Tetsuka et al. 2008

(continued)

Table 5.17 (Continued)

Abiotic stress and sources of resistance/tolerance	Reference
WATERLOGGING	
Foxtail millet	
Lugu No. 7	Chen and Qi 1993
LOW TEMPERATURE	
Foxtail millet	
Liggu No. 26 (adapted to very cold region, which extended foxtail millet cultivation some 385 km farther north to 54°; normally, the northern limit of foxtail millet cultivation in China was 50°N)	Chen and Qi 1993

Zegada-Lizarazu and Iijima (2005) found that waterlogging significantly reduced WUE in all millets species but drought did not. The ratio of WUE under stress to that under the control conditions indicated that pearl millet had the highest and lowest tolerances to drought and waterlogging conditions, respectively, while barnyard millet was tolerant to both stresses.

Postflowering drought (also termed as terminal drought) is the major form of drought that causes substantial reduction in grain and stover yields in pearl millet (Mahalakshmi et al. 1987; Winkel et al. 1997; Bidinger and Hash 2004). Genotypes that flower early, have few but effective basal tillers, are low in biomass, and have a high harvest index (including panicle harvest index) perform better under terminal drought stress (Yadav et al. 2003b; Bidinger et al. 2005). Landraces or traditional cultivars provide a rich source of diversity for tolerance to abiotic stresses in pearl millet (see Section IV.D). Farmers of the drought-prone arid zone of northwestern India (Rajasthan, Gujarat, and Haryana) prefer sowing these traditional landraces or landrace-based materials because of their grain and stover yield advantages over conventionally bred materials (Bidinger et al. 2009). For example, CZP9802, the first open-pollinated variety of pearl millet derived from the landraces of Rajasthan, combines a high level of adaptation to drought stress and outyielded controls—Pusa 266 (grain yield 0.98 t ha^{-1} ; stover yield 2.1 t ha^{-1}) and ICTP 8203 (grain yield 1.14 t ha^{-1} ; stover yield 2.7 t ha^{-1})—by producing 14% to 33% higher grain and 18% to 36% higher stover yield in arid zone environment (<400 mm of seasonal rainfall) of northwestern India (Yadav 2004). It flowers within 48 days of sowing and matures in 75 days, and thus has the ability to escape terminal droughts that are very frequent in these arid zone environments. Okashana 1, another early-maturing pearl millet variety, selected by the farmers in Namibia from ICRISAT-bred populations, is cultivated on about 50% of the pearl millet area in Namibia (Daisuke 2005). The *Iniadi*

landrace from West Africa is early maturing (70 to 85 days), relatively photoperiod insensitive, and productive with lustrous, bold grain and well-exserted, compact, conical panicles. It has contributed to development of large numbers of pearl millet cultivars worldwide (Andrews and Kumar 1996), including ICMV 88904 (released as ICMV 221) (Witcombe et al. 1997), which was bred by recurrent selection for a combination of improved grain yield potential, terminal drought tolerance, and downy mildew resistance, and has been released for cultivation in India, Kenya, Uganda, Eritrea, and Ethiopia.

More recently, preliminary results from the screening of finger millet and foxtail millet core collection accessions, using mini lysimeter (cylinders 25 cm diameter and 200 cm long, containing 124 kg of well-fertilized Alfisol) in a partly controlled environment, revealed genotypic differences in response to drought tolerance, with several accessions performing well under drought stress conditions (L Krishnamurthy, ICRISAT, pers. comm.).

The genus *Eragrostis* is widely distributed in dry habitats of tropical, subtropical, and temperate zones of both hemispheres (Boechat and Longhi-Wagner 2000). One of the well-known adaptive features of plants established in dry habitats is the ability to form slime-producing (mycospermatic, mucilaginous) diaspores (e.g., fruits or seeds), which are involved in plant dispersal (Huang et al. 2000; Penfield et al. 2001). Recently, Kreitschitz et al. (2009) reported the presence of slime cells, a type of modified epidermal cell, covering the fruit of tef, which is exclusively composed of pectins. The pectin forms uniform layers on the cell wall inner surface, which in the presence of water quickly hydrate and cause swelling of the slime cells. The ability of the slime to absorb and maintain moisture around the grain is probably an adaptive feature for tef, which may create conditions suitable for rapid germination in dry habitats. Furthermore, grain-filling is the most sensitive growth stage to water stress, and severe water stress has caused significant reduction in physiological performance of tef (Mengistu 2009). Species within the genus *Eragrostis* differ greatly in their ability to tolerate water stress and had a positive correlation between leaf tensile strength and drought tolerance. Leaf tensile strength strongly correlated with differences in leaf architecture and cell wall chemistry. Leaf tensile properties differed according to the measured position along the lamina (Balsamo et al. 2006). More recently, Degu et al. (2008) found that tef cultivars 'Kaye Murri' and 'Ada' under drought stress conditions had about 35% longer maximum root length (MRL) compared with that under irrigated conditions, while cultivar 'Fesho' had the largest osmotic adjustment (OA) value 1.38 Mpa under similar conditions. In contrast,

'Balami' and 'Alba' had decreased MRL and low OA under drought stress conditions, which reveals that the ability to increase MRL and increased OA contributes to better performance under drought conditions (Degu et al. 2008). Baltensperger, working in Nebraska on proso and foxtail millets, developed several proso millet cultivars. Baltensperger, working in nebraska on proso millet and foxtail millet, developed several proso millet cultivars (Baltensperger et al. 1995a,b, 1997, 2004a,b) and foxtail millet germplasm (Siles et al. 2004). Much of this was attributed to early maturity avoidance.

2. Salinity. There has been only limited research reported on response to soil salinity in finger millet, foxtail millet, pearl millet, and proso millet germplasms/cultivars, unlike other cereals (Table 5.18). Whole-plant tolerance to salinity in pearl millet is associated with reduced shoot N content and increased K^+ and Na^+ contents, while K^+/Na^+ and Ca^{++}/Na^+ ratios are of lesser importance. Genetic variation exists for shoot biomass ratio (shoot biomass under salinity/shoot biomass from nonsaline control), associated with salt tolerance, and shoot Na^+ concentration could be considered as a potential nondestructive selection criterion for vegetative-stage screening (Krishnamurthy et al. 2007).

Salt-tolerant proso millet accessions produced high biomass but accumulated low amount of Na^+ in their shoots and roots under saline conditions, while salt-sensitive accessions accumulated a high amount of Na^+ under saline conditions. The salt-tolerant accessions also maintained higher K^+/Na^+ ratios than the salt-sensitive accessions (Sabir and Ashraf 2007).

Using relative germination rate at 1.0% and 1.5% NaCl concentration, Zhi et al. (2004) screened 260 foxtail millet landraces and cultivars and detected a large range of variation: 0% to 20% in 29 accessions; 21% to 50% in 45 accessions; 51% to 90% in 153 accessions; and over 90% in 33 accessions. Glutamine synthetase (GS) and pyrroline-5-carboxylate (P5C) reductase are important for proline synthesis. Veeranagamallaiah et al. (2007) studied the changed expression profile of glutamine synthetase and pyrroline-5-carboxylate (P5C) reductase under saline conditions using salt-sensitive (Lepakshi) and salt-tolerant (Prasad) foxtail millet cultivars. Salt stress resulted in significant accumulation of proline in seedlings of both the cultivars; however, proline accumulation was more in the tolerant than in the sensitive cultivar and was positively correlated with increased glutamine synthetase and P5C reductase activities.

More recently, preliminary results from the screening of finger millet and foxtail millet core collections accessions in pot (23 cm diameter) culture using Alfisol (11 kg well-fertilized soil) in a partly controlled

Table 5.18. Summary of DNA-based markers available in barnyard millet, finger millet, foxtail millet, pearl millet, proso millet, and tef from 2002 to 2010.

Summary of DNA markers reported	Reference
Barnyard millet	
3 of 5 SSR loci isolated from <i>Echinochloa colona</i>	Danquah et al. 2002; Nozawa et al. 2006
Finger millet	
3 EST-derived SSR	Nnaemeka 2009
9 of 31 EST-derived SSRs polymorphic in finger millet producing 2 alleles, while 11 EST-SSRs polymorphic in pearl millet	Arya et al. 2009
Foxtail millet	
~1000 SNPs by sequencing pools of RILs (<i>S. italica</i> acc. B100 × <i>S. viridis</i> acc. A10)	http://www.plantbio.uga.edu/media/2010_grad_symposium(1).pdf
12 EST-derived SSR	Nnaemeka 2009
100 polymorphic SSRs developed from 2 genomic DNA libraries	Jia et al. 2009b
Job's tears	
17 polymorphic SSRs isolated from a microsatellite-enriched library of Job's tears	Ma et al. 2006
Pearl millet	
>100 polymorphic EST-SSR markers mapped in 1 or more of 4 pearl millet RIL populations	Rajaram et al. 2010
~250-280 DArT markers polymorphic in each of 3 pearl millet RIL populations	Senthilvel et al. 2010
11 of 31 finger millet EST-derived SSR primer pairs detected polymorphism in pearl millet	Arya et al. 2009
4 EST-SSRs and 9 CIPs detecting polymorphism in 1 or more of 4 pearl millet biparental mapping populations	Yadav et al. 2008
A set of 21 polymorphic EST-SSRs and 6 genomic SSRs	Senthilvel et al. 2008
19 EST-derived SSR primer pairs, of which 11 gave amplification products and 4 detected polymorphism on agarose gels	Yadav et al. 2007
16 EST-derived polymorphic SSRs	Mariac et al. 2006h
SSCP-SNP primer pairs developed by comparison of rice and pearl millet EST sequences	Bertin et al. 2005
36 SSRs derived from from genomic library	Qi et al. 2004
18 SSRs derived from genomic library	Budak et al. 2003; Allouis et al. 2001; Qi et al. 2001
Proso millet	
46 polymorphic SSRs from rice, wheat, oat, and barley	Hu et al. 2009

(continued)

Table 5.18 (Continued)

Summary of DNA markers reported	Reference
Tef	
262 polymorphic SSR markers	Zeid et al. 2010
80 EST-derived SSRs	Yu et al. 2006b
8 <i>MseI</i> - and 8 <i>EcoRI</i> -based AFLP primers; 8 ISSR markers; 22 EST-derived SSRs and 10 SSRs from rice	Chanyalew et al. 2005
8 polymorphic ISRs	Assefa et al. 2003b

environment revealed genotypic differences for salt (100 mM concentration saturating the soil to field capacity) tolerance, with several accessions outyielding the controls (L. Krishnamurthy, ICRISAT, pers. comm.).

3. Low Temperature. The northern limit of the foxtail millet cultivation in China was 50° N. However, researchers in China have developed a foxtail millet cultivar (Table 5.17) that is tolerant to extreme cold and thus extended the cultivation of foxtail millet 385 km farther north to 54° (Chen and Qi 1993).

4. Lodging. Lodging is a constraint in many crops, including millets, causing substantial losses in grain yield and quality. Both crop management and environmental factors impact lodging (Berry et al. 2005). Finger millet, foxtail millet, proso millet, tef, and the fonio are reported to suffer from lodging. The use of lodging-resistant cultivars along with good crop husbandry is the most effective way to minimize losses due to lodging. Knowledge of traits associated with lodging and identifying a suitable method to assess lodging are essential steps to select for lodging resistance and to predict the risk of lodging in a cultivar. A lodging coefficient based on stem and root traits associated with lodging is found to be a suitable indicator of field selection for lodging resistance in foxtail millet (Tian et al. 2010). Further, the study revealed that mechanical strength of the stem and plant height were the most important contributors to lodging coefficient in the landraces, whereas the weights of the aboveground and underground tissues in combination with mechanical strength of the stem were most important in the improved cultivars. A number of landraces and improved cultivars that resist lodging have been reported in foxtail millet from China (Table 5.17), which could be used as a resource of this trait to transfer into new breeding lines. Most recent proso millet lines developed in

the United States have had strong selection for lodging resistance (Baltensperger et al. 1995a,b, 2004a).

5. Waterlogging. There are relatively few reports on waterlogging in millets. Based on the changes in dry-matter production and transpiration coefficient under varying soil moisture conditions, Kono et al. (1987) classified cereal crops into four groups: rice and Job's tears are susceptible to drought but tolerant to waterlogging; finger millet and Japanese barnyard millet are relatively tolerant to both drought and waterlogging; proso millet, pearl millet, sorghum, and maize are relatively susceptible to waterlogging but tolerant to drought; and foxtail millet is highly susceptible to waterlogging but tolerant to drought. Further studies under prolonged waterlogging stress detected substantial reduction in number of roots in foxtail millet and slight reductions in proso millet and pearl millet. However, total root numbers increased in rice, finger millet, Job's tears, Japanese barnyard millet, sorghum, and maize (Kono et al. 1988). No systematic study on waterlogging has been reported on other millet crops, but 'Lugu 7' foxtail millet has been found tolerant to waterlogging (Chen and Qi 1993).

C. Seed Quality

Seed size, seed color, protein and fat contents, and minerals and vitamins are important traits that influence grain quality in cereals including millets, and various procedures have been developed to measure these effectively (Gomez et al. 1997). Variations in amino acid composition influence the protein quality. Various reports indicate sufficient genetic variation for seed quality traits, which has been exploited to develop cultivars with high protein or fat content in some millet crops. For example, Chinese cultivars of foxtail millet 'Anzhenhuanggu', 'Baocao-honggu', 'Gouweisu', 'Huangshugu 01724', 'Huiningdaheigu', 'Lazhu-taigu 013611', 'Pin114', 'Pingliangmaocaogu', and 'Xiaohonggu 015147' have high seed protein (15%–18%) and fat (5%) (He et al. 2002; Dong and Cao 2003; Zhu et al. 2004). Finger millet germplasm accessions with high seed protein include GE 2500, 1168, MS 174 and MS 2869, while those with high seed calcium are Malawi 1915 and CO 11 (Vadivoo et al. 1998). More recently, researchers at ICRISAT identified finger millet germplasm accessions with relatively high seed protein (8.5%–12.7%), calcium (3.2–5.2 g kg⁻¹ seed), iron (41–56 mg kg⁻¹ seed), and zinc (26–31 mg kg⁻¹ seed) contents, which were higher than the best controls (protein 8.2%; Ca 3.1 g kg⁻¹ seed; Fe 40.3 mg kg⁻¹ seed; and Zn 22.9 mg kg⁻¹). Likewise, some foxtail millet accessions had higher seed protein (17.8%), calcium

(288 mg kg⁻¹ seed), iron (59 mg kg⁻¹ seed), and zinc (74 mg kg⁻¹ seed) contents than the controls (protein 13.4%, Ca 152.8 mg kg⁻¹ seed, Fe 48.6 mg kg⁻¹ seed, and Zn 52 mg kg⁻¹ seed) (ICRISAT 2009). An early-maturing foxtail millet germplasm, Super Early Maturation No. 2, has been developed that has high protein (14.4%), fat (6.2%), and iron (54.1 mg kg⁻¹) contents and requires 1650°C heat units to mature at approximately 1,400 m altitude in Bashang, China (Liu et al. 2006). Chinese researchers have also reported large variation in vitamin E content (2.74 µg g⁻¹–90.97 µg g⁻¹) among foxtail millet landraces Huangbangtuo, Huangtenggu, Xiaohuanggu, and Yazuinian (Li et al. 2009).

Pearl millet grain contains 17.4% protein, 6.3% fat, 2.8% fiber, and 2.2% ash (Sawaya et al. 1984). Pearl millet landraces of diverse origin differ in fatty acid composition, with linoleic acid (45%), oleic acid (23%), and palmitic acid (22%) being the dominant fatty acids (Jellum and Powell 1971). More recently, pearl millet germplasm and advanced lines with high iron and zinc contents, which are positively correlated, have been identified (<http://www.harvestplus.org>). Some newly developed hybrids had more than 70 ppm grain Fe and in excess of 50 ppm Zn contents, with two hybrids showing 80 to 85 ppm Fe and 70 ppm Zn, which are higher than those reported in improved cultivars of other cereal crops (ICRISAT 2009).

Chinese proso millet accessions Dabairuanmi 0673, Taianhuangmi 2657 and Yongchanghuangmi 2659 showed high protein content (17%–19%), whereas 80-4064, Dahuangshu 2643 and Heimizi 4392 had high fat (~5.5%); and Edanbai 0885, Hongmizi, and Ziganhong had both high protein and fat contents (Wang et al. 2007a). Proso millet cultivar 'Tololanskoe' is reported to contain high protein content (13.6%) (Kalinova and Moudry 2006). The protein content of Japanese barnyard millet ranged from 11.1% to 13.9% (Monteiro et al. 1987). Significant work at utilization of the waxy trait has been conducted in the United States to improve specific food quality in proso (Heyduck et al. 2008; Graybosch and Baltensperger 2009).

Millet and other cereals are deficient in some of the essential amino acids, such as lysine (Geervani and Eggum 1989). The lysine content in foxtail millet germplasm ranges from 0.20% to 0.30% (Zhu et al. 2004; Tian et al. 2009); however, there are some high-lysine foxtail millet cultivars (e.g., 'Gouweisu 27531', 'Gouweisu 27510', and 'Xiaomi 27516') (Zhu et al. 2004). Compared to other millets, proso millet grains are richer in essential amino acids (leucine, isoleucine, and methionine) and contain about 3.3 g kg⁻¹ of the limiting amino acid lysine (Vadivoo et al. 1998). High lysine content has been reported in proso millet

cultivar 'Belgorodskoe' (Kalinova and Moudry 2006). Black and grey seeded foxtail millet germplasm often have higher lysine contents (He et al. 2002).

Pearl millet seeds are relatively larger than other millets, with 1,000-seed mass ranging from 1.5 g to 21.3 g and averaging 8 g to 12 g among germplasm accessions (Upadhyaya et al. 2007b; Loumerem et al. 2008). Foxtail millet grains are relatively small compared with other cereals, with 1,000-seed mass ranging from 1.9 g to 3.6 g (Liang and Quan 1997). Finger millet 1,000-seed mass averaged 2.6 g (Vadivoo et al. 1998). Proso millet seeds are larger (3–10 g 1,000-seed mass, average ~7.0 g) than foxtail millet but smaller than pearl millet. Nonwaxy proso millet cultivars usually have larger seed than waxy types (Wang 2006). Much of the selection for proso millet and foxtail millet in the United States has been based on large seed size (Baltensperger et al. 1995a,b).

Variation in seed color can influence seed quality. For example, white-seeded finger millet accessions had higher protein content than brown-seeded types, while white-grained types had higher prolamin and lower glutelin levels than those with brown-grain types (Vadivoo et al. 1998). Black- and grey-seeded foxtail millet germplasm have high protein content (He et al. 2002). Ethiopian farmers overwhelmingly selected a very white-seeded tef variety, DZ-01-196 (Magna), which gets a premium price in the market, although variation in seed color has no effect on agronomic or nutritional traits (Belay et al. 2006).

Foxtail millet has been cultivated in China for a very long time, with ancient farmers selecting landraces with better taste and cooking quality. Foxtail millet landraces with superior cooking characteristics are Jinmin, Jiugenqi, Qinzhouhuang, and Taohuami (Dong et al. 2003). Most foxtail millet landraces and cultivars in China are yellow-seeded, the preferred seed color. More recently, however, white-seeded cultivars have been bred to meet diversified market demands (Diao 2007).

Grains of pearl millet, finger millet, fonio, proso millet, foxtail millet, and tef are brewed to produce beer. Genotypic differences in brewing quality have been reported. For example, a preponderance of β-amylase as the major starch-degrading enzyme has been found in fonio millet cultivars 'Nock 2', 'KN 3', and 'Chori 1', which is similar to the enzyme profile in barley (Nzelibe et al. 2000). Further, malt of 'Chori 1' has α-amylase content similar to that in barley (Nzelibe and Nwasike 1995; Nzelibe et al. 2000). Finger millet malt is prized for its high diastatic power and is second only to that of barley in its ability to hydrolyze starches (NRC 1996).

VI. GENOMIC RESOURCES

A. Markers and Genetic Linkage Maps

The discovery of DNA markers and construction of genetic linkage maps in millets lagged behind other cereals such as rice, wheat and maize (reviewed in Dwivedi et al. 2007). Pearl millet, foxtail millet, finger millet, Job's tears and tef among the millets have been investigated for development of PCR-based markers (Table 5.18) and construction of genetic linkage maps (Table 5.19). The foxtail millet has the largest collection of single-nucleotide polymorphisms (SNPs) and a high-density SNP-based genetic map, with ~1,000 SNP markers evenly mapped to all nine chromosomes ([http://www.plantbio.uga.edu/media/2010_grad_symposium\(1\).pdf](http://www.plantbio.uga.edu/media/2010_grad_symposium(1).pdf)). An consensus genetic map (418 cM) of pearl millet, based on four crosses, mapped 353 RFLP and 65 SSRs into seven linkage groups, with ~85% of the markers occupying less than a third of the total map length (Qi et al. 2004). Recently, an array of about 6,900 Diversity Array Technology (DART™) clones was developed using *PstI/BanII* complexity reduction and is now available for mapping low-cost, high-throughput DART markers in pearl millet (Senthilvel et al. 2010). Further, Senthilvel et al. (2010) also identified 256 to 277 polymorphic DART markers in three pearl millet recombinant inbred lines (RIL) populations, which they have integrated with simple sequence repeat (SSR) data to construct individual genetic maps, each with >300 marker loci. Over 200 DART markers were mapped in more than one population, and their mapping positions were reasonably consistent across maps. Among these, 32 DART markers representing all seven pearl millet linkage groups were mapped in all three RIL populations, permitting the development of a well-saturated pearl millet consensus linkage map combining DART and SSR markers.

Recently some DNA markers from rice, wheat, oat, and barley have shown polymorphism in proso millet (Hu et al. 2009). More recently, Reddy et al. (2010) isolated 41 resistant gene homologues from a popular finger millet cultivar, 'UR762', which showed strong homology to NBS-LRR type R-genes of other crop species. The molecular cloning of these resistant gene homologues may provide new ways to deploy these genes against biotic stresses. Clearly, more directed efforts are needed to develop markers in other millets. One way to overcome the paucity of DNA markers in these millets is to try markers from other cereals, as both macro- and micro-synteny have been reported among cereals (Devos et al. 2000; Srinivasachary et al. 2007; Yadav et al. 2008; also see Section VIII.D). Recent work on switchgrass (*Panicum virgatum*) has shown

Table 5.19. Summary of genetic linkage maps reported in finger millet, foxtail millet, pearl millet, and tef from 1994 to 2007.

Summary of linkage maps reported	Reference
Finger millet	
131 markers mapped to 16 LGs on A genome, with a total map distance 721.4 cM, while 196 markers to 9 LGs on B genome covering 786.8 cM map distance	Dida et al. 2007
332 loci from 266 primers mapped into 26 LGs. 13 on A-genome and 9 on B-genome LGs assembled into 9 homologous groups, 6 six of these corresponding to a single rice chromosome each, while remaining 3 were orthologous to 2 rice chromosomes; gene orders between rice and finger millet highly conserved	Srinivasachary et al. 2007
Foxtail millet	
A high-density genetic map with ~1000 SNPs evenly mapped to all 9 chromosomes; a number of chromosomal rearrangements, including several previously unknown rearrangements, relative to sorghum and rice genomes	http://www.plantbio.uga.edu/media/2010_grad_symposium(1).pdf
81 SSR and 20 RFLP markers mapped to 9 LGs, with a total map length of 1654 cM, and marker density of 16.4 cM	Jia et al. 2009b
160 RFLP loci mapped to 9 LGs, with a total map distance of 964 cM	Wang et al. 1998
Job's tears	
80 AFLP and 10 RFLP markers mapped to 10 LGs, with a total map length of 1339.5 cM, average marker density 14.88 cM	Qin et al. 2005
Pearl millet	
A map with 55 RFLP and 32 genomic SSR and 17 EST-SSR loci spanning 675 cM	Senthilvel et al. 2008
An integrated genetic map, based on 4 crosses, mapped 353 RFLP and 65 SSRs into 7 linkage groups (LGs), ~85% of the markers occupying less than a third of the total map length	Qi et al. 2004
A map with 61 RFLP and 30 SSR loci spanning 476 cM	Yadav et al. 2004a
181 RFLP loci mapped to 7 LGs, with a total map length of 303 cM and ~2 cM marker density	Liu et al. 1994
A map with 38 RFLP markers covering 280 cM	Jones et al. 1995
Tef	
252 SSR loci mapped to 30 LGs, with a total map length of 1277.4 cM (78.7% genome coverage), averaged marker density 5.7 cM	Zeid et al. 2010
156 loci from 121 markers (RFLP, SSR, SNP/INDEL, IFLP, ISSR) mapped to 21 LGs, with a total map length of 2081.5 cM and 12.3 cM marker density	Yu et al. 2006a
166 markers (AFLP, ISSR, and SSR) mapped to 20 LGs, covering 2112.3 cM and marker density of 12.7 cM.	Chanyalew et al. 2005

(continued)

Table 5.19 (Continued)

Summary of linkage maps reported	Reference
149 RFLP loci mapped to 20 LGs, with a total map distance of 1489 cM and marker density of 9.99 cM; alignment of tef RFLP map with the rice RFLP map shows synteny and collinear gene order between the 2 genomes	Zhang et al. 2001
211 AFLP loci mapped to 25 LGs, with a total map distance of 2149 cM, marker density of 10.4 cM	Bai et al. 1999

many common expressed sequence tag (EST) markers with proso millet (Tobias et al. 2008).

B. Characterization and Functional Validation of Genes Associated with Important Traits

A number of QTLs have been identified and mapped for resistance to downy mildew, drought tolerance, grain yield and yield components, and for stover quality in pearl millet and for agronomic traits in foxtail millet and tef (see Section VIII.A). Linkage analysis in most of these studies allowed identification of genes/QTLs at a distance as large as 10 to 40 cM from the nearest markers, which may not be suitable for either marker-assisted breeding or for identification/cloning of candidate genes. Unlike other cereals such as rice, maize, and barley (Table 5.20), the only studies reported on functional validation of genes associated with agronomic traits in millets are for the *tb1* and *ba1* genes associated with branching (basal and axillary) in foxtail millet (Doust and Kellogg 2006); *PHYC* gene associated with flowering time and morphological variation (spike length and stem diameter) (Saïdou et al. 2009); a major drought-tolerance QTL on linkage group 2 (Sehgal et al. 2009) in pearl millet; and the *SiOPRI* gene associated with osmotic adjustment and improved drought tolerance in foxtail millet (Zhang et al. 2007b). Further, toward identifying candidate genes for salt tolerance in foxtail millet, Jayaraman et al. (2008) used the cDNA-AFLP technique to compare gene expression profiles of salt-tolerant and salt-sensitive cultivars in foxtail millet, and identified 27 nonredundant differentially expressed cDNAs unique to genes involved in metabolism, cellular transport, cell signaling, transcriptional regulation, messenger ribonucleic acid splicing, seed development and storage in the salt-tolerant cultivar 'Prasad'. The expression patterns of seven such genes showed a significant increase in 'Prasad' after 1 hour of salt stress in comparison to the salt-sensitive cultivar 'Lepakshi'. More recently,

Table 5.20. Summary of quantitative trait loci (QTL) or gene association with important traits and their validation in barley, foxtail millet, maize, pearl millet, and rice from 1995 to 2009.

Trait	QTL/gene	Validation	References
Barley			
Flowering time	<i>Ppd-H1</i>	Association	Stracke et al. 2009
Foxtail millet			
Drought (osmotic adjustment)	<i>SiOPRI</i>		Zhang et al. 2007b
Vegetative branching (basal and axillary)	<i>tb1</i> and <i>ba1</i>		Doust and Kellogg 2006
Maize			
Plant architecture	<i>Tb1</i>	Complementation	Doebley et al. 1995, 1997
Yield	<i>lcyE</i>	Mutagenesis	Harjes et al. 2008
Pearl millet			
Flowering time, plant and spike morphology	<i>PHYC</i>	Association	Saïdou et al. 2009
Rice			
Heading time	<i>Hd1/Se1</i>	Transformation	Yano et al. 2000
	<i>Hd3a</i>	Transformation	Kojima et al. 2002
Grain number	<i>Gn1/CKX2</i>	Transformation	Ashikari et al. 2005
Seed shattering	<i>qSH-1/RPL</i>	Complementation	Konishi et al. 2006
	<i>sh4</i>	Transformation	Li et al. 2006
Salt tolerance	<i>SKC1</i>	Transformation	Ren et al. 2005
UV resistance	<i>qUVR-10</i>	Transformation	Ueda et al. 2005
Submergence tolerance	<i>Sub1</i>	Transformation	Xu et al. 2006

Lata et al. (2010) detected above 2.5-fold variation in nine up-regulated transcripts between drought-tolerant and susceptible cultivars upon dehydration stress. The induction of these genes suggests their function in regulation of dehydration tolerance in foxtail millet. These researchers therefore initiated cloning of full-length copies of some of the known and unknown up-regulated genes and will analyze their functions to identify candidate genes for drought tolerance in foxtail millet.

In summary, the limited published research on QTL mapping and validation among millets has been restricted only to foxtail millet, pearl millet, and tef and research on gene expression for abiotic stresses tolerance has been limited to pearl millet and foxtail millet, largely because of the nonavailability of DNA markers or sequences in most of the other millets. Clearly, more efforts should be directed toward the development of large numbers of genic and genomic markers to conduct

association genetics for identification and validation of candidate genes associated with important traits.

C. Genomic and Genetic Tools to Sequence the Foxtail Millet Genome

Foxtail millet has a highly conserved genome structure relative to the ancestral grass lineage (Devos et al. 1998). It is a diploid grass with a relatively small genome (490 Mb) and is closely related to bioenergy grasses, such as switchgrass (*Panicum virgatum*), napiergrass (*Pennisetum purpureum*), and pearl millet. It is an ideal model crop to investigate plant architecture, genome evolution, and physiology in the bioenergy grasses (Doust et al. 2009). In 2008, the Joint Genome Institute of the U.S. Department of Energy announced support for developing genomic and genetic tools to complement sequencing of the foxtail millet genome and for the improvement of biomass production for bioenergy crops (<http://GenomicScience.energy.gov/research/DOEUSDA>). Four U.S. universities along with the Hudson Alpha Institute for Biotechnology of Huntsville, Alabama, and the Joint Genome Institute of Walnut Creek, California, are involved in sequencing of the foxtail millet genome and development of the complementary tool sets. The latest report from this group revealed that draft genome sequencing of foxtail millet has been completed to $8.3 \times$ coverage, with the aligned sequence showing a high degree of synteny to rice and sorghum, even though these lineages last shared a common ancestor more than 50 million years ago (Mitros et al. 2010). The ongoing genetic and genomic research on foxtail millet includes annotation and mining of the full genome sequence, development of foxtail millet bacterial artificial chromosome (BAC) and expressed sequence tag (EST) resources, comparative analysis with sorghum and rice, characterization of orthologous copies of genes controlling biomass in other grass groups, establishment of efficient transformation protocols, creation of new mapping populations, and QTL analyses to identify new candidate genes for plant architectural variation. In addition, resequencing of several diverse green foxtail millet accessions will provide a data set that allows measurement of the overall genetic variability present within the wild and cultivated crop and will be a source of markers for mapping and biodiversity studies (Doust et al. 2009, 2010; see Section VII.A). Other genomic tools available for foxtail millet research include the availability of >100 SSRs and the genetic map (see Section VI.A), ~1,500 SNPs, the genome sequences from other cereals (see Section VIII.D), the QTL associated with agronomic traits (see Section VIII.A), and candidate genes

associated with agronomic traits (see Section VI.B). All of these resources are expected to support molecular breeding in foxtail millet.

VII. ENHANCING USE OF GERMPLASM IN CULTIVAR DEVELOPMENT

A. Core, Mini-Core and Reference Sets for Mining Allelic Diversity and Identifying New Sources of Variation

Core (~10% accessions of the entire collection) and mini-core (~10% accessions of the core collection or ~1% of entire collection) collections are cost-effective sources to identify accessions with desirable agronomic traits, including resistance to biotic and abiotic stresses. To date, core and mini-core collections (based on phenotypic characterization and evaluation data) are reported in finger millet, foxtail millet, little millet, pearl millet, and tef (Table 5.21). Limited evaluation of finger millet and foxtail millet core collections has resulted in identification of germplasm accessions that mature early, produce more grain or fodder in comparison to control cultivars, or differ in panicle shape and size and seed color and of a few accessions tolerant to drought or salinity. Many of accessions with grains having high seed protein, calcium (Ca), iron (Fe), and/or zinc (Zn) contents were also identified (ICRISAT 2009). Moreover, the core or mini-core collections are dynamic in nature, and these must be augmented, as recently done in pearl millet.

Researchers at ICRISAT have developed a global composite collection in pearl millet, finger millet, and foxtail millet, which were genotyped (using SSRs and high-throughput assay, ABI3700) to determine population structure and diversity prior to formation of reference germplasm sets. This reference set captured between 87% to 95% allelic diversity of the composite collections (www.generationcp.org; ICRISAT 2009). Clearly, more research is needed to develop these subsets in other millets or to augment the existing subsets to make them more relevant to the changing needs of crop breeding.

B. Assessing Population Structure and Diversity in Germplasm Collections

Vast collections of millets germplasm are maintained worldwide in gene banks (see Section IV), and in many cases core or mini-core collections have been formed (see Section VII.A), representing diversity present in the entire collection of a given species. Such reduced subsets are ideal resources to dissect population structure and diversity (both at

Table 5.21. Core collection, mini-core subset, and genotype-based reference set reported in finger millet, foxtail millet, little millet, pearl millet, and tef.

Crop	No. accessions	Reference
Core collection		
Finger millet	622	Upadhyaya et al. 2006
	551	Gowda et al. 2007
Foxtail millet	155	Upadhyaya et al. 2008
Little millet	55	Gowda 2008
Pearl millet	1600	Bhattacharjee et al. 1997
	2094 (revised core)	Upadhyaya et al. 2009
Tef	320	http://www.database.prota.org
Mini-core collection		
Finger millet	80	Upadhyaya et al. 2010
Foxtail millet	35	ICRISAT unpublished data
Pearl millet	238	Upadhyaya et al. 2011
Genotype-based reference set		
Finger millet	300	ICRISAT unpublished data
Foxtail millet	200	ICRISAT unpublished data
Pearl millet	300	ICRISAT unpublished data

phenotypic and molecular level), to identify new sources of variation, and to conduct association mapping, which provides insights to marker-trait association. In the last few years, there have been greater efforts to develop PCR-based markers, especially microsatellites and SNPs, and/or DArT markers (see Section VI.A), which were employed to assess population structure and diversity in barnyard millet, common millet, finger millet, foxtail millet, Job's tears, pearl millet, and tef germplasm collections (Table 5.22). For example, barnyard millet accessions belonging to var. *esculenta* were less diverse than those of var. *crus-galli* or var. *formosensis* (Nozawa et al. 2006), and the molecular profile of tetraploid *E. oryzicola* is different from that of hexaploid *E. crus-galli* var. *formosensis* (Nozawa et al. 2004). Microsatellites differentiated finger millet subsp. *africana* accessions from those of subsp. *coracana* originating either from Africa or Asia (Dida et al. 2008). Wang et al. (2010) detected a low level of genetic diversity in *Setaria viridis* (green foxtail millet) in comparison to its cultivated form, *Setaria italica*. In addition, they also found that despite a 55% loss of its wild diversity, *S. italica* still harbors a considerable level of diversity when compared to rice and sorghum. Likewise, the level of linkage disequilibrium in *S. italica* extends to 1 kb; it decayed rapidly to a negligible level within 150 bp in *S. viridis*. The 17 SSRs differentiated most of the Chinese Job's tears accessions from those of Korean accessions, and the Chinese accessions

Table 5.22. Assessment of population structure and diversity as reported in barnyard millet, common millet, finger millet, foxtail millet, and tef germplasm.

Accessions and markers	Pattern of population structure and diversity	Reference
Barnyard millet 155 accessions and 3 SSRs	The 155 accessions included 49 from var. <i>esculenta</i> , 94 from var. <i>crus-galli</i> , and 12 from var. <i>formosensis</i> . SSR markers clustered the var. <i>esculenta</i> accessions into 2 groups (either from central and northeastern Japan or northern and southern Japan), <i>crus-galli</i> accessions into 12 groups, and <i>formosensis</i> accessions into 6 groups. <i>E. esculenta</i> were less diverse than either of <i>crus-galli</i> or <i>formosensis</i> accessions.	Nozawa et al. 2006
170 accessions and 13 SSRs	The var. <i>esculenta</i> accessions grouped into 2 classes, while those from var. <i>crus-galli</i> into 11 classes. Marker EC1 discriminated <i>E. oryzicola</i> (a tetraploid species) from the hexaploid species <i>E. crus-galli</i> var. <i>formosensis</i> .	Nozawa et al. 2004
Finger millet 109 accessions including wild types and 45 SSRs	<i>E. coracana</i> germplasm grouped into 3 distinct clusters: subsp. <i>africana</i> , subsp. <i>coracana</i> originating from Africa, and subsp. <i>coracana</i> originating from Asia, with few accessions showing introgression between the African and Asian cultivated germplasm pools, and lower diversity in Asian subpopulation probably due to small number of founder plants involved in its origin.	Dida et al. 2008
Foxtail millet 77 <i>S. italica</i> and 40 <i>S. viridis</i> accessions, rDNA IGS	PCR-based length polymorphism and sequence polymorphism of rDNA intergenic spacer (IGS) clearly demonstrated genetic differentiation between cultivated and wild forms from northern Pakistan and Afghanistan; cultivated forms to some extent showed genetic differentiation between different areas, while wild forms clearly showed differentiation between regions in northern Pakistan.	Fukunaga et al. 2010

(continued)

Table 5.22 (Continued)

Accessions and markers	Pattern of population structure and diversity	Reference
50 <i>S. italica</i> and 43 <i>S. viridis</i> accessions, sequence variation at 9 loci	DNA sequence variation at 9 loci revealed low level of genetic diversity in wild green foxtail ($\theta = 0.0059$). Despite of a 55% loss of its wild diversity, the cultivated foxtail millet still harbored a considerable level of diversity ($\theta = 0.0027$) compared to rice ($\theta = 0.0024$) and sorghum ($\theta = 0.0034$). LD in domesticated foxtail millet extends to 1 kb, while it decayed rapidly to a negligible level within 150 bp in wild green foxtail millet.	Wang et al. 2010
62 landraces and 16 RFLP markers	Landraces grouped into 5 major clusters: cluster I and II and to some extent cluster IV contain landraces from East Asia including China; cluster III from subtropical and tropical regions in Asia; cluster V from central and western regions of Eurasia; Chinese landraces highly variable among the germplasm studied.	Fukunaga et al. 2002b
81 accessions and AFLP markers	Chinese accessions were highly diverse, consistent with the hypothesis of a center of domestication in China, while accessions from eastern Europe and Africa form 2 distinct clusters. The genetic relatedness within <i>S. viridis</i> or between <i>S. viridis</i> and <i>S. italica</i> is probably due to consequence of gene flow between the two subspecies.	Le Thierry d'Ennequin et al. 2000
39 <i>Setaria</i> species and 19 RAPD markers	RAPD analysis revealed that <i>S. italica</i> more closely related to <i>S. viridis</i> , supporting idea that the former originated from the latter. <i>Setaria italica</i> and <i>S. glauca</i> differ considerably. <i>S. glauca</i> and <i>S. sphacelata</i> distinct from <i>S. italica</i> , implying that it will be difficult to transfer some of the beneficial traits from <i>S. glauca</i> and <i>S. sphacelata</i> to <i>S. italica</i> .	Li et al. 1998
Job's tears 79 accessions (Korea and Japan) and 17 SSRs	Most Chinese accessions genetically distinct from Korean accessions; genetic relatedness and place of collection not related; greater within population polymorphism in Chinese accessions, potentially a reservoir of novel alleles for crop improvement.	Ma et al. 2010
Pearl millet 145 WCA inbreds and 20 SSRs	STRUCTURE analysis detected 5 subgroups and 1 admixed group. Plotting the STRUCTURE results on the geographic map revealed no obvious association either of country of origin or agroecological zone of origin.	Stich et al. 2010
2000 lines and 24 SSRs	Established a diversity panel of 288 genotypes. 4 maturity groups representing the whole breadth of genetic variation in the pearl millet germplasm pool from Africa and Asia.	Yadav et al. 2010
22 inbreds and 627 markers	267 of the 627 markers (100 pearl millet genomic SSRs, 60 pearl millet EST SSRs, 410 intron sequence haplotypes, and 57 exon sequence haplotypes) were polymorphic among the 22 inbred lines, which were grouped into 3 clusters with most of the inbreds derived from landrace <i>Iniadi</i> in cluster I; high correlation ($r > 0.97$, $P < 0.05$) between the patterns of diversity exposed by different marker systems.	Thudi et al. 2010
72 inbreds (70 B-lines and 2 R-lines) and 34 SSR primer pairs	The 72 hybrid parental lines included 70 phenotypically diverse B-lines developed at ICRISAT-Patancheru from diverse germplasm and breeding materials of African, Asian, and American origin, and 2 elite R-lines. Genetic similarity estimates among these inbreds varied from 0.05 (ICMR 356 and ICMB 01666) to 0.73 (ICMB 97444 and ICMB 95555), with a mean of 0.29. Five major clusters were detected, with the smallest comprised of R-line ICMR 356, 2 older B-lines (81B and ICMB 841) and 2 more recent B-lines (ICMB 95333 and ICMB 98777). The second cluster included 30 B-lines, including 843B, arranged in 4 major subclusters. The third cluster appeared to contain elite R-line ICMR 451 and 5 B-lines including 863B and ICMB 88004. The fourth and fifth cluster included 17 B-lines each, arranged in 3 subclusters.	Kapila et al. 2009

(continued)

Table 5.22 (Continued)

Accessions and markers	Pattern of population structure and diversity	Reference
467 accessions including 46 wild species and 25 SSRs	The cultivated accessions showed significantly lower number of alleles and lower gene diversity than wild types. Wild accessions from the central region of Niger showed introgression of cultivated alleles, while cultivated accessions from the western, central, and eastern Niger showed introgressions of wild alleles, wild populations thus interesting source of new alleles and new allele combinations, which could be useful to broaden the genetic base of cultivated pearl millet.	Mariac et al. 2006a
39 landraces + 12 controls; AFLP markers	The material included 14 and 13 landraces from western and eastern Rajasthan and 12 control cultivars. The diversity analysis revealed much higher variation within landrace population than between regional samples. Variation between landrace groups bearing a specific name from eastern Rajasthan was higher than intragroup variation. Greater gene flow among landrace populations of western Rajasthan due to frequent exchange of seed materials among farmers.	vom Brocke et al. 2003
53 accessions and 30 SSRs	Two major and 8 minor clusters formed involving 53 lines, the genetic distance ranged from 0.28 to 0.92, and few unique lines with potentially important new sources of alleles identified for enhancing trait value.	Budak et al. 2003
10 landraces and 16 RFLP markers	High within accession (30.9%) and between accessions (69.1%) variability among 10 landraces of Indian origin, selected from the pearl millet landrace core collection (504 accessions).	Bhattacharjee et al. 2002
Proso millet 118 accessions and 46 SSRs	118 accessions grouped into 5 clusters that parallel with their known geographical distribution; accessions from the Loess Plateau ecotype were more genetically diverse than other 5 ecotypes reported from China.	Hu et al. 2009
38 accessions and 3 intron splice junction (ISJ) primers	Geographical origin and glutinous vs. nonglutinous trait associated with the pattern of clustering of 38 accessions, with majority of the landraces forming 5 clusters while cultivars or breeding lines from Inner Mongolia 3 clusters.	Hu et al. 2008
Cultivated/wild and weedy types (12) and AFLP markers	Cultivated and weedy biotypes formed 2 distinct clusters without any geographic association: a group formed only by weedy biotypes and another composed of domesticated and weedy biotypes displaying domesticated traits, while the typical wild types clustered separately. The most distinct biotypes were Colorado-Weld county black-seeded and Wyoming-Platte county type. Differences in aggressiveness and nutrient accumulation were also noticed: Canada-Rosemount biotype being more aggressive than Colorado biotype while Canada Rosemount and Colorado tan seeded biotypes showed differences in nutrient accumulation.	Karam et al. 2004
Tef 92 lines and 8 ISSR markers	UPGMA resulted formation of 6 major clusters of 2 to 37 lines with further 8 lines remained ungrouped, and all the improved cultivars grouped in cluster 1.	Assefa et al. 2003b
59 cultivated, wild types and RAPD markers	High polymorphism among wild relatives but low polymorphism among cultivated accessions. The RAPD primers differentiated <i>E. pilosa</i> from <i>E. curvula</i> , both wild relatives, with former more closely related to cultivated tef.	Bai et al. 2000
3 species and AFLP markers	AFLP analysis differentiated the species, <i>E. tef</i> , <i>E. pilosa</i> and <i>E. curvula</i> , from one another, with <i>E. pilosa</i> being the most diverse followed by <i>E. curvula</i> and <i>E. tef</i> ; however, <i>E. pilosa</i> more closely related with <i>E. tef</i> than <i>E. curvula</i> . Within tef germplasm, Rubicunda and DZ-01-1093 were distantly related to the rest of the tef accessions.	Ayele and Nguyen 2000

exhibited greater within-population polymorphism, thus they form a potential reservoir of novel alleles for crop improvement (Ma et al. 2010). Pearl millet cultivars and landraces in Niger had a significantly lower number of microsatellite alleles and lower gene diversity than that of their wild relatives, with wild populations from western and central Niger showing introgression of cultivated alleles; thus the wild relatives provide an interesting source for new alleles and new allelic combinations to broaden the genetic base of cultivated pearl millet (Mariac et al. 2006a). RFLP and AFLP markers detect high within-accessions and between-accessions variability among pearl millet landraces from India (Bhattacharjee et al. 2002; vom Brocke et al. 2003) or substantial gene flow among pearl millet landrace populations due to frequent exchange of seed materials among farmers in western Rajasthan, India (vom Brocke et al. 2003). More recently, Yadav et al. (2010) used 24 SSRs distributed over seven pearl millet linkage groups to identify a “diversity panel” of 288 genotypes of four maturity groups from a composite collection of 2,000 diverse pearl millet breeding lines and accessions from Africa and Asia. This diversity panel of accessions represented the whole breadth of genetic variation in the pearl millet germplasm pool; the researchers are further studying it to identify gene-based markers tightly linked to the drought-tolerant QTL on LG2.

In order to elucidate the relationship between foxtail millet and its wild ancestor green foxtail, d’Ennequin (2000) used AFLP markers. They indicated that both foxtail millet and green foxtail accessions originating in China were much more diverse than those from eastern Europe and Africa. Their results provide evidence that China is the center of foxtail millet domestication. More recently, with the development of microsatellites, the population structure of foxtail millet germplasm collections has been further detailed. For example, Jia et al. (2009a) reported close relationships among newly released cultivars except those from Shanxi Province in China, while Zhu et al. (2010) classified 120 landraces into four clusters coincident with their geographical origin: North-west Inland group, Loess Plateau and Inner Mongolia group, North China Plain Landrace group, and North China Plain Cultivar group. Furthermore, Li et al. (2011) used ISSRs to demonstrate that foxtail millet landraces from China are not only highly diverse but also that they, along with landraces from Europe, are closely related with a group of green foxtail millet accessions originating in the central and western region of the Yellow River basin in China, where substantial archaeological evidence for ancient cultivation has been recovered (Lee et al. 2007). Wang et al. (2010) used nine genomic DNA fragment sequences to study relationships among 50 foxtail millet and 34 green

foxtail millet accessions collected worldwide and found a relatively low level of genetic diversity in wild green foxtail millet ($\theta = 0.0059$). They further reported that despite 55% loss of diversity as compared to green foxtail millet, the cultivated foxtail millet (*S. italica*) germplasm still harbors considerable diversity ($\theta = 0.0027$) comparable to that reported in rice ($\theta = 0.0024$) and sorghum ($\theta = 0.0034$). Wang et al. (2010) also observed linkage disequilibrium extending to 1 kb in foxtail millet, while it decayed rapidly to a negligible level at 150bp in the wild green millet.

C. Promoting Use of Male Sterility as an Aid in Crossing

Most of the millet crops, except for pearl millet, are self-pollinated, and all possess small flowers that are difficult to emasculate for crossing and hybrid seed production (Siles et al. 2001). In the case of pearl millet, protogyny can be exploited for manual crossing without emasculation, small-scale seed production of experimental hybrids, or production of chance hybrids. Male sterility thus becomes an important genetic tool to facilitate crossing and to facilitate production of sufficient hybrid seed to permit exploitation of hybrid vigor. Although male sterility is a common phenomenon in the plant kingdom (Kaul 1988), so far among millets, it is routinely used to produce seed of hybrid cultivars in only pearl millet and to some extent experimented in foxtail millet and finger millet.

The CMS in pearl millet has been widely exploited for grain-producing hybrids in India and for forage (and to a lesser extent grain) hybrid production in the United States. Several sources of male-sterility-inducing cytoplasms—for example, A_1 (Burton 1965), A_2 and A_3 (Burton and Athwal 1967), A_v (Marchais and Tostain 1985), A_4 (Hanna 1989), Ex-bornu = A_g (Aken’ova 1985), A_5 (Rai et al. 1998c), and A_{egg} (Delorme et al. 1997)—have been identified in pearl millet. Most of the pearl millet hybrids in India are based on the A_1 CMS source, which has been clearly shown as not increasing the vulnerability of these hybrids to downy mildew (Yadav 1996b; Rai et al. 1998a,b), despite earlier concerns that this might be the case. Further studies have shown that A_4 , once a commercially unexploited CMS source, is not associated with downy mildew susceptibility and can safely be used as an alternative to the A_1 cytoplasm (Yadav 1996a). Unfortunately, the A_2 , A_3 , and A_g CMS systems do not reliably maintain male sterility in seed production environments, so they cannot be exploited for commercial hybrid seed production.

CMS is a maternally inherited phenotype characterized by an ability to produce sterile pollen, while female fertility and vegetative

development are unaffected. Cytological observation indicates that pollen mother cell/microspore/pollen degeneration in A-lines occurred at different stages of anther development in pearl millet CMS lines. Each cytoplasm had its unique influence on microsporogenesis and anther development, as evidenced by different developmental pathways leading to pollen abortion. The cause of pollen abortion differed from line to line, from floret to floret within a spikelet, from anther to anther within a floret, and in some cases even from locule to locule within an anther. This could be one of the reasons for greater instability of male sterility in the A₂ and A₃ systems and greater stability of male sterility in the A₁ and A₄ systems (Chhabra et al. 1997). More recently, Rai et al. (2009) compared stability of male sterility among A₁, A₄, and A₅ CMS lines, which revealed that the A₅ CMS source is the most stable, followed by A₄ and A₁. Hybrids based on A₁ and A₅ CMS sources had no significant difference in grain yield, which implies that seed parents' breeding efficiency will be the greatest with the A₅ CMS system. The previous work also revealed that grain yield of hybrids based on A₂, A₃, and A₄ cytoplasm was either similar to or significantly higher than that of their counterpart hybrids with A₁ cytoplasm (Yadav 1996b). Hybrids based on A₃ and A₄ cytoplasm produced, on average, 8% more grain compared with those based on A₁ cytoplasm. These studies indicate that the A₄ and A₅ CMS sources can be used as alternatives to A₁ cytoplasm to widen the cytoplasmic base (and thereby the nuclear genetic base) of pearl millet hybrids.

The CMS phenotype is associated with mutations in the mitochondrial genome (Hanson 1991) and rearranged mitochondrial genes are frequently co-transcribed with standard mitochondrial genes (Dewey et al. 1986; Laver et al. 1991; Bonhomme et al. 1992). Delorme et al. (1997) characterized cytoplasmic diversity, using mitochondrial gene-specific DNA probes in combination with eight restriction endonucleases, among five pearl millet isonuclear CMS lines as compared to the isonuclear fertile cytoplasm; their study revealed that five CMS cytoplasm (81A₁, 81A_v, 81A₄, 81A_{egg}, and 81A₅) can be distinguished from each other and from the isonuclear fertile cytoplasm (81B). Further, based on *cox1*, *cox3*, *apt6*, and *apt9* polymorphisms, these lines can be classified into two major groups: one corresponds to A₅, A_{egg}, A_v and A₁ cytoplasm, and the other consists of the A₄ cytoplasm. The rearrangement involving the *cox1* gene might be related to CMS in the former group, whereas rearrangement within the *atp6/cox3* cluster region might be related to CMS in the latter group. ChandraShekara et al. (2005) used mitochondrial DNA polymorphism to differentiate A₁, A₂, and A₃ CMS lines from A₄ and A₅ CMS lines. Spontaneous fertility reversion in the

CMS A₁ line of pearl millet occurs rarely (0.01% frequency), observed as a single pollen-shedding panicle surrounded by fully male-sterile panicles in a CMS plant (Smith et al. 1987). More recently, Feng et al. (2009) compared mitochondrial genome configurations between the male-sterile A₁ line and the fertile revertants to demonstrate that this low frequency might be controlled by the substoichiometric nature of junction molecule *CoxI-3-2*, which appears to be essential to initiate the reversion phenomenon.

Genetic male sterility in foxtail millet is controlled either by single recessive or dominant genes (Cui et al. 1979; Hu et al. 1986, 1993; Diao et al. 1991) and used to develop hybrid cultivars, such as 'Suanxi 28×Zhangnong 10' and 'Jigu 16' (Cui et al. 1979; Du and Wang 1997). Herbicide resistance in foxtail millet (Darmency and Pernes 1985), which is dominant in nature (Wang and Darmency 1997), has been used to identify true hybrids while pseudo- (false) hybrids could be easily removed by spraying herbicide. Using this system, a few foxtail millet hybrid cultivars (F₁), such as 'Zhangzagu 8' and 'Zhangzagu 10', were bred that showed grain yield up to 9 t ha⁻¹ in China (Diao and Cheng 2008).

Researchers in China have used both physical and chemical mutagens as well as wide hybridization to discover a CMS system in foxtail millet (Hu et al. 1986; Zhou et al. 1988; Luo et al. 1993; Zhu and Wu 1997; Wu and Bai 2000). However, to date, no successful CMS line has been developed for commercial exploitation of hybrid vigor in foxtail millet. More recently, Zhi et al. (2007) reported a CMS material in a cross involving green foxtail and foxtail millet; the hybrid and BC₁ plants were all male sterile. Further work is in progress to perfect this CMS system for the exploitation of hybrid vigor in foxtail millet. Heterosis for grain yield up to 68% has been reported, which reveals that heterozygosity could provide a significant yield benefit over nonhybrid cultivars in foxtail millet (Siles et al. 2004).

Gupta (1999) developed a genetic male-sterile line, INFM 95001 (PI 595204), from the finger millet germplasm line IE 3318, using ethyl methanesulfonate. Genetic study involving INFM 95001 with its sister male-fertile line (IE 3318) and three unrelated male-fertile lines (FMV 1, FM 2, and SDFM 957) revealed that male sterility in INFM 95001 is controlled by a major recessive gene (Gupta 1999). Exploitation of the male-sterility gene present in INFM 95001 would facilitate crossing for the production of finger millet hybrid progenies to generate new segregants, to enhance genetic recombination in recurrent selection programs, and to facilitate exploitation of background selection in marker-assisted backcrossing programs.

So far male-sterility systems in other millets have not been reported. Clearly, more research is needed to discover a CMS-based system because of the problems associated with the use of nuclear gene-based male sterility systems in hybrid seed production. However, genetic male-sterility systems still would be useful as breeding tools to facilitate production of segregating populations derived from controlled crosses, particularly in small-flowered self-pollinated species such as most millets, where it is otherwise difficult to produce large numbers of seeds from crosses required for efficient recurrent selection or back-crossing programs.

VIII. FROM TRAIT GENETICS TO ASSOCIATION MAPPING TO CULTIVAR DEVELOPMENT USING GENOMICS

A. Markers/QTL Associated with Agronomic Traits, Abiotic Stress Tolerance, Biotic Stress Resistance, and Product Quality

Pearl millet, finger millet, foxtail millet., and tef have sufficient genetic and genomic resources (see Section VI.A) to identify QTL associated with beneficial traits. Of these, pearl millet has been extensively investigated to identify QTL associated with agronomic traits, including resistance to biotic (Jones et al. 1995, 2002; Morgan et al. 1998; Hash and Witcombe 2001; Breese et al. 2002; Gulia et al. 2007a) and abiotic stresses (Yadav et al. 2002, 2004a; Biding et al. 2005, 2007; Sharma et al. 2010) as well as the association of QTL for flowering time with genotype \times environment interaction of grain and stover yield in favorable production environments (Yadav et al. 2003a). More recently, Kholova et al. (2009) investigated whether the control of water loss under nonlimiting conditions is involved in terminal drought tolerance in pearl millet. Using test crosses of drought-tolerant and sensitive inbred lines together with QTL–near-isogenic line (NIL) introgression lines containing a terminal drought-tolerance QTL, they demonstrated that upon exposure to water deficit, transpiration began to decline at lower fraction of transpirable soil water in the tolerant than in the sensitive genotypes, while the transpiration rate (Tr) under well-watered conditions was lower in test crosses of the tolerant than in those of the sensitive parental genotypes. The fraction of transpirable soil water and Tr of the QTL near-isogenic line (QTL-NIL) test crosses followed patterns similar to their drought-tolerant parent. Further, Tr measured in detached leaves from the field-grown plants of the parental test crosses showed lower Tr values in test crosses of tolerant parents and the

differences in Tr between genotypes were not related to the stomatal density, which further demonstrates that constitutive traits controlling leaf water loss under well-watered conditions correlate with expression of this terminal drought-tolerance QTL in pearl millet, which may lead to more water being available for grain filling under terminal drought conditions. Furthermore, Kholova et al. (2010) investigated whether this pearl millet terminal drought-tolerance QTL confers high leaf abscisic acid (ABA), limiting transpiration at high vapor pressure deficit (VPD), thus leading to transpiration efficiency differences. ABA levels under well-watered conditions were higher in drought tolerant testcross genotypes, including those of the QTL-NILs, than in test crosses of sensitive genotypes. ABA levels did not increase significantly under water stress in any of the test crosses, while well-watered Tr was lower in tolerant than in sensitive genotypes at all vapor pressure deficit (VPD) levels. This finding supports the hypothesis that water-saving (avoidance) mechanisms (i.e., a low Tr even at low VPD), which may relate to leaf ABA or sensitivity to higher VPD that further restricts Tr, may operate under well-watered conditions in drought-tolerant pearl millet. Both constitutive traits (higher leaf ABA levels and lower Tr), which did not lead to transpiration efficiency differences, could contribute to absolute water saving, which would become critical for grain filling under conditions of limited total water availability and deserve consideration in breeding for pearl millet genotypes tolerant to terminal drought stress when grown on soils capable of retaining water for use during grain filling. Interestingly, this same major drought-tolerant QTL from PRLT 2/89-33 also confers a positive effect under salinity stress by limiting Na^+ accumulation in pearl millet leaves (Sharma et al. 2010).

Variation in grain mineral contents (Fe and Zn) has been reported in pearl millet germplasm, improved cultivars, and elite hybrid parental lines (ICRISAT 2009). Genetic mapping using an existing RIL population recently identified five putative QTLs for grain Fe density and two for grain Zn density in this crop, with favorable alleles for grain densities of both minerals from 863B-P2 (high Fe and Zn) at a major QTL mapped on LG3, while LG6 alleles from ICMB 841-P3 (moderate Fe and Zn) were favorable for both minerals (Kumar et al. 2010). Ruminant nutritional value of pearl millet straw (i.e., stover quality) is a genetically complex trait (Hash et al. 2003). Marker-aided identification of genomic regions would facilitate identification of progenies with better stover quality. Blümmel et al. (2003) reported sufficient genetic variation in cell wall digestibility and stover yield in pearl millet germplasm/parental lines. The stover quality on dry matter basis is determined by its gas volume (mL) produced after 24 h of in vitro digestion of dry matter (GAS24), in

vivo organic matter digestibility, nitrogen content, metabolic energy content, and sugar content. Nepolean et al. (2006) identified two genomic regions on LG2 and LG6 associated with stover quality and three genomic regions on LG3, LG5, and LG6 associated with stover yield in a set of mapping population progeny test crosses. Further, the genomic region on LG2 also contains another major QTL associated with terminal drought tolerance (Yadav et al. 2004a) and thus is a good candidate region to improve terminal drought tolerance and better stover quality. More recently, the researchers at ICRISAT have validated a stover quality QTL in LG4, and found that this QTL cosegregates with dominantly inherited host plant resistance to the foliar disease blast caused by *Pyricularia grisea*. The donor parent for this stover quality/blast resistance QTL is 863B-P2. Further, an improved version of the previously released hybrid HHB 146 containing this QTL is now being tested by the All India Coordinated Pearl Millet Improvement Project (AICPMIP) for its adaptation in India (Nepolean et al. 2010).

The domesticated foxtail millet (*Setaria italica*) has fewer branches than its wild progenitor (*Setaria viridis*), a phenomenon similar to maize (*Zea mays*) when it domesticated from its wild ancestor, teosinte (Doebley and Stec 1993). The basal branching (four QTL, one each on chromosomes I and V and two on chromosome III, together contributed 66%–73% phenotypic variation) and axillary branching (four QTL, one each on chromosomes VI and IX and two on chromosome V, together contributed 65%–99% phenotypic variation) is partially controlled by separate loci, and the orthologue of *teosinte branched1*, the major gene controlling branching phenotype in maize, has only a minor and variable effect. Other candidate genes for control of branching were a number of hormone biosynthesis pathway genes (Doust et al. 2004). They also detected that some of the variation in basal branching is controlled by loci separate from those controlling axillary branching, which is similar to what is reported in pearl millet (Poncet et al. 2000), a species more closely related to foxtail millet (Doust and Kellogg 2002) than either is to maize. Doust and Kellogg (2006) further found that branch number in F_{2:3} progenies of a cross between two species varies with genotype, planting density, and other environmental variables, with significant genotype × environment interactions, and the likely candidate genes underlying the QTL include *teosinte branched1* and *barren stalk1*; however, much variation in branching is explained by QTL that do not have obvious candidate genes from maize or rice.

QTL analysis in *tef* detected several genomic regions associated with yield and yield components, with majority of the QTL concentrated in 4 to 6 clusters on a few linkage groups, suggesting pleiotropic effects of a

few major genes (Chanyalew et al. 2005; Yu et al. 2007). *Tef* suffer from lodging that reduces grain yield and quality. Using F₉-generation derived RIL from an interspecific cross (*Eragrostis tef* × *E. pilosa*), Zeid et al. (2010) mapped 83 QTL (phenotypic variation ranged from 4.8% to 33.0%) on 20 LGs for lodging, grain yield, and 15 other related traits. They detected two major clusters of QTL on LG6 and LG7, with LG7 harboring the largest number of QTL for eight traits. Furthermore, seven QTL for grain yield on five LGs together explained 64.7% variance. QTL for panicle length, panicle weight, and panicle seed weight were collocated with QTL for grain yield on LG7 and LG23.

B. Marker-Aided Introgressions of Disease Resistance

Downy mildew (DM) is one of the most important diseases of pearl millet, with diverse virulent pathogen populations reported from Africa and Asia (Singh et al. 1993). HHB 67 was a highly popular (<65 days from sowing to grain maturity) and widely grown (~500,000 ha) pearl millet hybrid in northwestern India following its release in 1989. However, like all popular single-cross hybrids before it, this hybrid became susceptible to DM (up to 30% incidence in farmers' fields), with potential to cause substantial grain and stover yield losses to farmers in the state of Haryana. Resistance to DM is multigenic in nature and controlled by both major and minor QTL. All pearl millet DM-resistance QTL detected to date confer partial resistance that is pathogen-population specific, although in rare cases only a single major QTL of large effect can be detected in screens of a particular host mapping population against a particular pathogen isolate. Researchers at ICRISAT, in collaboration with partners from Haryana Agricultural University (which had bred and released the original HHB 67) and U.K.-based teams at the University of Wales used both marker-aided backcross and conventional backcross systems to incorporate additional DM resistance into the parental lines of HHB 67. Toward this end, they employed marker-assisted backcross transfer of DM resistance (two major QTL) from donor parent ICMP 451 to male parent H 77/833-2 (Breese et al. 2002), while they used conventional backcross to transfer DM resistance in female parent 843A/B from the donor parent ICML 22. Using these improved parental sources, an improved version of HHB 67 was developed, tested, and released as "HHB 67 Improved." Not only does it show substantially improved resistance to DM, but it also produced higher grain and stover yields (5%–10%) than the original hybrid HHB 67. After 3 years (2002–2004) of rigorous testing under AICPMIP, "HHB 67 Improved" was released in 2005 for cultivation in Haryana. It can be easily recognized from the

original HHB 67 because of its long, thin panicles with short bristles. It was the first public sector-bred marker-assisted breeding product to be commercialized in India (Hash et al. 2006) and has been widely and rapidly adopted by the seed industry and pearl millet producers in that country. Furthermore, introgression lines containing downy mildew resistance QTL in other elite hybrid parent genetic backgrounds, such as J 2340, will soon be available for evaluation in India.

C. Marker-Aided Introgressions to Enhance Drought Tolerance

Pearl millet research at ICRISAT led to identification of a major QTL on LG2 associated with increased grain yield and harvest index under terminal drought stress in PRLT 2/89-33 (Yadav et al. 2002). The QTL marker-assisted selection-derived topcross hybrids moderately but significantly outyielded the field-based topcross hybrids under varying moisture stress conditions. However, this advantage under stress was at the cost of lower yield of the same hybrids under nonstressed environment. The hybrids flowered earlier and had limited effective basal tillers, low biomass, and high harvest index, similar to that of PRLT 2/89-33 (Bidinger et al. 2005). More recently, Serraj et al. (2005) and Witcombe et al. (2008) reported results of marker-assisted backcrossing by ICRISAT and its U.K.- and India-based partners to produce a set of near-isogenic version of elite pollinator H 77/833-2 (drought sensitive but widely used source for producing hybrids in India, including HHB 67 referred to earlier) with and without the LG2 drought-tolerance QTL from the donor parent PRLT 2/89-33. Field screening in carefully managed field environments revealed that hybrids produced on QTL introgression lines with the QTL yielded up to 21% more grain under postflowering drought stress conditions with no adverse effect on grain yield under nonstressed conditions. Furthermore, several of these introgression lines had a significant positive general combining ability for grain yield under terminal stress due to high panicle harvest index. Thus, these marker-assisted breeding products have greater value for both water-limited and assured moisture conditions than either parental line. More recently, it has been shown that the drought-tolerance QTL contributed by PRLT 2/89-33 exerted favorable effects on growth and productivity traits under salt stress by limiting Na^+ accumulation in leaves (Sharma et al. 2010) and that the mechanism of this terminal drought-tolerance QTL appears to be constitutively higher leaf ABA levels that reduce transpiration rate, altering the dynamics of crop water use so that there is still moisture left deep in the soil profile to support grain filling, at least under the managed terminal drought stress conditions in which this QTL was originally

detected (Kholova et al. 2009, 2010). Thus, breeding line PRLT2/89-33 and its backcross derivatives provide important genetic resources for improving drought and salinity tolerance in pearl millet.

Testing of products of the pyramiding of LG2 terminal drought-tolerance QTL from PRLT 2/89-33 with two downy mildew resistance QTL (on LG1 and LG2) from donor parent ICMP 451-P6 in the genetic background of elite pollinator H 77/833-2 (male parent of released pearl millet hybrids HHB 60, HHB 67, and HHB 68) has recently been initiated (C. T. Hash, pers. commun.).

D. Use of Rice, Maize, Sorghum, and Foxtail Millet Genome Sequences to Strengthen Molecular Breeding Tools

In the last 25 years, most of the genomic and molecular breeding research of cereals concentrated on major crops such as maize, rice, sorghum, and wheat because of their significance in world food production. Similar genomic research on millets has been very limited during the same period. Therefore, availability of genomic resources is very limited in the millets except for pearl millet, finger millet, foxtail millet, and tef. In recent years, genomic research has intensified in these millets due to their potential in sustainable farming in the era of climate change and global warming. Nevertheless, comparative genomics have great potential to speed up development of genomic tools in these millets to support molecular breeding using genome sequences of rice, maize, sorghum, and foxtail millet.

The earliest evidence of conservation of map position and order of DNA markers between chromosomal regions across different genomes in plants were reported between tomato and potato (Bonierbale et al. 1988). Soon after, comparative studies in grasses revealed a high degree of synteny of many DNA markers between chromosomal regions of different grass genomes, which had differences of 60 million years in evolutionary divergence times and up to 40-fold variation in genome sizes (Devos and Gale 1997; Gale and Devos 1998; Keller and Feuillet 2000). As a result, a series of early studies on genomic comparisons between members of grass family (Poaceae) were reported between rice and maize (Ahn and Tanksley 1993); rice and wheat (Kurata et al. 1994); rice, maize, wheat, and oat (Van Deynze et al. 1995); foxtail millet and rice (Devos et al. 1998); foxtail millet and maize (Doust et al. 20004); and pearl millet, rice, and foxtail millet (Devos et al. 2000). The comparative genomics approach was successful for map-based prediction of genes underlying the QTL that determine key traits for genetic improvement of the crops (Paterson et al. 1995; Doust and Kellogg 2006). Moore et al. (1995)

published the first comparative genome map of seven different grass species using rice as reference map; their map subsequently was further refined (Gale and Devos 1998; Devos and Gale 2000). Although divergence of rice from other grass species occurred about 60 to 80 million years ago, fewer than 30 rice linkage blocks would be enough to represent all these genomes (Moore et al. 1997). Comparative mapping in grasses has resulted in the most comprehensive data set of comparative genomics in a plant family to date.

Genome conservation is not limited only to a large region of chromosome, which is called macrocolinearity. Similar conservation was also observed at DNA sequence level (called microcolinearity) within orthologous regions in different members of the grass family. Ramakrishna et al. (2002) reported one such microcolinearity of orthologous regions in barley, rice, sorghum, and wheat based on bacterial artificial chromosome sequence analysis. However, within microcolinear regions, different types of sequence rearrangements (small inversions, gene duplications, deletions, and translocations) occurred during grass genome evolution (Paterson et al. 2010). For example, comparative analysis of finger millet and rice genomes reveals that six of the nine finger millet homologous groups correspond to a single rice chromosome each, while each of the remaining three finger millet groups are orthologous to two rice chromosomes, and in all three cases one rice chromosome was inserted into the centromeric region of a second rice chromosome to give the finger millet chromosomal configuration. Gene orders between rice and finger millet were highly conserved, with rearrangements being limited to single marker transpositions and small putative inversions encompassing at most three markers (Srinivasachary et al. 2007). Although these regions will appear as collinear at the genetic map level, some microrearrangements, such as deletions and translocations, can greatly complicate genome analysis at small regions. Although collinearity at the map level can be used in taxonomy and as a predictive tool, comparative map-based gene isolation requires highly conserved gene orders at the 100-kb to 1-Mb level (Devos and Gale 2000). Thus, the use of rice, maize, sorghum, finger millet, and foxtail millet for the map-based isolation of genes from other millet genomes often may be complicated by such local genome rearrangements. Consequently, approaches based on collinearity between grass genomes must also be performed using more closely related species (e.g., within tribes or subtribes).

Finger millet is an excellent source of seed calcium (376–515 mg per 100 g), with a level far above that of the other cereals and millets (Barbeau and Hilu 1993). More recently, Nath et al. (2010) cloned the *CaM* gene, a calcium sensor, of finger millet along with other cereals (barley, maize,

oat, rice, and sorghum) and millets (barnyard millet, kodo millet, little millet, and proso millet) to identify the structural similarity of *CaM* genes with their possible role in calcium signaling and calcium accumulation in cereals. The *CaM* sequences among these crops ranges from 579 to 623 bp, which could be due to amplification of variable length of the genomic sequence by same *CaM* specific primer. Multiple sequence alignment reveals a high degree of sequence conservation, although the authors detected some alterations that might be partially due to *CaM* sequence variation, 579 to 623 bp in cereals and millets. The *in silico* three-dimensional structural analysis of cloned sequences showed similar structures and reveals a high degree of conserved *CaM* in cereals and millets, with finger millet and barley *CaM* having closed evolutionary relationships as compared to others.

The small millets and other major cereals (rice, wheat, barley, oat, corn, and sorghum) belong to the same family, Poaceae, but to different subfamilies (see Section I). Phylogenetic relationship among cereals and millets based on chloroplast and nuclear genes showed close relationships (Giussani et al. 2001; Doust 2007; Paterson et al. 2009a; also see Section IV), and the subfamily Panicoideae includes two small groups of millets: Pearl millet, foxtail millet, proso millet, and little millet belong to one group, while maize, sorghum, sugarcane and Job's tears belong to the other group. Members within the group are more similar than across the group. The subfamily Chloridoideae includes finger millet and tef (Doust 2007). Rice, however, belongs to the subfamily Ehrhartoideae, and phylogenetically it is located far from maize, sorghum, sugarcane, and other millets (Doust 2007). Determination of the phylogenetic relationship between millets and other cereals will be helpful to identify the grass cereal species closest to the target millet for comparative genomics studies.

Availability of genome sequences of foxtail millet (Doust et al. 2009) will be extremely valuable for genome mapping, marker development, and molecular breeding of pearl millet, proso millet, and little millet because of their taxonomic closeness (Doust 2007), as will genome sequence availability of corn and sorghum will be equally useful for genome analysis of sugarcane and Job's tears. Finger millet and tef genome analysis will also be aided by genome sequences of these cereals of Panicoideae.

Even in the absence of local microcolinearity, the overall good collinearity observed between the grass genomes still offers the possibility of increasing the number of markers in a targeted region using RFLP and EST probes without the need to develop additional markers from the species of interest. Molecular markers derived from orthologous regions

in different grass species can be used to increase the map density at specific genetic loci and facilitate map-based cloning of genes in millets (Kilian et al. 1997). Comparative genomics studies of millets using available grass sequences can help in understanding the molecular mechanisms of genome evolution in the grasses, which is necessary to define the best strategies and the tools necessary to isolate genes of agronomic importance from large and complex cereal genomes.

Comparative genomics and genome sequence database of rice (Goff et al. (2002), maize (Schnable et al. 2009), sorghum (Paterson et al. 2009b), and foxtail millet (Doust et al. 2009; Mitros et al. 2010) can be used to align EST and other DNA markers of millets. Millets markers can be mapped on the linkage groups of these species, then located on the millets linkage group by comparative genetics mapping among rice, maize, sorghum, or foxtail millet and the genome of other millets. The aligned EST information should be available for further study on genomics and gene cloning. Such approaches have already been used successfully to saturate different genomic regions of sugarcane, barley, and wheat (Kilian et al. 1997; Roberts et al. 1999; Asnaghi et al. 2000; Druka et al. 2000). In sorghum, EST-SSR were developed based on rice-sorghum syntenies to enrich the sorghum genetic linkage map (Ramu et al. 2009). Microsatellite markers from subtracted drought stresses EST were also developed in sorghum (Srinivas et al. 2009). In maize, 364,385 ESTs and 27,455 full-length complementary deoxyribonucleic acids (FLcDNAs) are in a database (Soderlund et al. 2009). A new type of DNA marker, single-strand conformational polymorphism (SSCP)-SNP, has been developed in pearl millet using annotated rice genomic sequences to initially predict the intron-exon borders in millet ESTs and then to design primers that would amplify across the introns (Bertin et al. 2005). ESTs-SSRs in pearl millet were developed based on comparative genomics using the rice genome sequence (Senthilvel et al. 2008). Using the rice genome sequence as base, a comparative genomics approach was applied to develop new types of DNA markers, conserved intron scanning primers (CISPs), and tested across several grasses (rice, sorghum, pearl millet, and tef) (Feltus et al. 2006). A similar approach can be used to develop such markers in other millets using available genome sequences of sorghum, maize, and foxtail millet. The current genetic linkage maps and available RFLP, AFLP, EST, and SSR markers in finger millet and tef can be aligned to the foxtail millet genome sequence for development of more markers to saturate the genome (Yu et al. 2006a,b; Dida et al. 2007). In finger millet, SSRs are being developed from the available 1740 ESTs, which will be useful in a comparative genomics study for developing more genomic tools

(Arya et al. 2009). Although genome synteny among cereals is well established, the linking information between different genomes is still too sparse to accurately pinpoint candidate homologous genes except in the few cases where the similarities in phenotypes are obvious. Soon the grasses, including all of the major cereals and minor millets, will be able to be considered a single entity, and all of the information available on gene structure, gene action, metabolism, physiology, and phenotype accumulated over the past century in the different species will be pooled. An immediate practical implication is that breeders need no longer be restricted to their own species in their search for exploitable variation. Homologous genes and all of their alleles in all species will be available to the cereal breeder/genetic engineer of the early 21st century.

E. Exploiting Variation at Waxy Locus to Diversify Food Uses

Endosperm starch of cereals consists of amylose and amylopectin. Wild type (nonwaxy) endosperm starch consists of 20% or more of amylose and 80% of amylopectin whereas waxy type consists of 100% amylopectin and lacks amylose. Nonwaxy (*Wx*) phenotype is dominant over waxy phenotype (*wx*). Endosperm starch of the waxy type has a stickier texture than that of the non-waxy type. Both types of endosperm have been reported among the landraces of sorghum, rice, foxtail millet, maize, common millet, barley, and Job's tears (Sakamoto 1996). The waxy types of these cereals are found in east and southeast Asia but are rare in India and farther westward. A core area where people show a strong ethnobotanical preference for waxy cereals, which extends from southern China through northern Thailand to Assam, has been identified (Sakamoto 1996; Yoshida 2002). In adjacent countries such as Taiwan, Japan, and Korea, waxy cereals are grown mainly on upland soils and are used in traditional rituals or eaten only on special occasions. This trait is apparently associated with ethnological preferences in the region (Fogg 1983; Takei 1994).

Waxy endosperm arises through the disrupted expression or loss of function of the *waxy* (*GBSS 1*) gene that encodes granule-bound starch synthase I (*GBSS I*) (Sano 1984). Waxy-type cereals are characterized by little or no starch amylose, which constitutes about 20% or more of the total starch in the nonwaxy endosperm. This character has often been neglected in other regions, although waxy maize, which was first reported (Collins 1909) in Chinese landraces, is now globally used for the production of waxy corn starch.

Molecular basis of naturally occurring *wx* mutants in foxtail millet has been well characterized. The waxy foxtail millet probably evolved from

the nonwaxy type after domestication, since the wild ancestor (*S. italica* ssp. *viridis*) has a nonwaxy endosperm (Nakayama et al. 1998). In addition to those two types, an intermediate or low-amylose type foxtail millet germplasm has also been reported (Sakamoto 1987). Amylose content is positively correlated with amounts of GBSS 1 protein among the three phenotypes (Afzal et al. 1996) and is genetically controlled by waxy (GBSS 1) alleles (Nakayama et al. 1998). No other genes that regulate amylose content, such as *du* in rice (Okuno et al. 1983), are known in foxtail millet. Fukunaga et al. (2002a) determined the sequence of the full-length cDNA and the genomic structure of the *waxy* (GBSS 1) gene, which revealed multiple origins of the waxy endosperm in foxtail millet. Kawase et al. (2005) classified 841 landraces of foxtail millet into 11 groups based on PCR analysis of the gene to conclude that waxy foxtail millet originated four times independently and low-amylose foxtail millet three times by insertions of transposable elements. More recently, Van et al. (2008) reported several SNPs and small indels in *waxy* gene in foxtail millet.

The waxy phenotype has also been reported in proso millet germplasm from east Asia, with complex inheritance due to the tetraploid nature of this species (Sakamoto 1996; Graybosch and Baltensperger 2009). The waxy trait is being introduced into locally adapted proso millet cultivars in the central Great Plains of the United States (Heyduck et al. 2008). Further, molecular basis of waxy endosperm phenotype in this species revealed 15-bp deletion in one of the *waxy* loci and the insertion of an adenine residue, which causes a reading frame shift or a point mutation causing a cysteine/tyrosine amino acid polymorphism in other loci (Hunt et al. 2010).

Nearly all the cultivated Job's tears cultivars have waxy phenotype, while the waxy trait has not been reported in its wild relatives (Okuyama et al. 1989). Molecular characterization of the gene is under way, and mutation conferring waxy phenotype may be due to partial deletion of the gene (T. Hachiken and K. Fukunaga, Prefectural University of Hiroshima, Japan, pers. commun.).

There are no waxy landraces in Japanese barnyard millet due to the allohexaploid nature of this crop (Yabuno 1987), which requires mutations in three different waxy loci to permit expression of the waxy phenotype. However, several Japanese landraces with approximately half the level of amylose have been reported. Hoshino et al. (2010) used a low-amylose landrace (Noge-Hie) and γ -ray radiation to produce a waxy Japanese barnyard millet cultivar ('Chojuro-mochi'), with its waxy phenotype originating from the partial deletion of waxy genes. Grain of this genotype may be used for making cookies and other foods in Japan.

The waxy phenotype has not been reported in pearl millet, finger millet, tef, kodo, or fonio (Sakamoto 1996). However, it is possible to develop waxy cultivars in these species through mutations by mutagens such as ethyl methanesulfonate, γ -ray, or ion beam, or by transgenic events. Thus, the waxy cultivars of such cereals will be new sticky food sources for human consumption.

F. Foxtail Millet, Sorghum and Maize Genome Sequences as Resources for Identifying Variation Associated with High Biomass Production in Bioenergy Grasses

Some of the photosynthetic-efficient C_4 bioenergy crops include sugarcane, maize, sorghum, foxtail millet, pearl millet, switchgrass, and napiergrass (Perlack et al. 2005; Ragauskas et al. 2006; Carpita and McCann 2008; Doust et al. 2009). These species differ in genome size (1C) [foxtail millet: 490 Mb; sorghum: 730 Mb; pearl millet: 2,352 Mb; maize: 2,605–2,798 Mb; switchgrass (1,372–1,666 Mb in $4\times$, 1,960–2,058 Mb in $6\times$, 2,352–3,136 Mb in $8\times$); napiergrass: 2254 Mb (Bennett and Leitch 1995; Bennett et al. 2000; Doust et al. 2009; Paterson et al. 2009b)], ploidy levels (diploid: foxtail millet, pearl millet, and sorghum; tetraploid: napiergrass; tetraploid, hexaploid, octaploid: switchgrass), breeding systems (inbreeder: foxtail millet; outbreeder: maize, pearl millet, switchgrass, and napiergrass; mixed mating: sorghum) and life-forms (annual: foxtail millet, maize, pearl millet, and sorghum; perennial: napiergrass and switchgrass).

Many forms of feedstocks, including maize, rice, sorghum, wheat, barley, and oat, are available for biofuel production. Cereal grains are high in starch content and therefore good feedstock for conversion to biofuels and other bio-based products, with ethanol being commercially produced from these feedstocks in the United States and elsewhere. Among the millet species, pearl millet grain has also been explored for production of ethanol in the United States. The grains contain about 70% starch, which gives it a theoretical ethanol yield of 0.43 L kg^{-1} , comparable to barley and oat but inferior to maize, rice, sorghum, and wheat grains (0.52 – 0.57 L kg^{-1}) (<http://www.mhprofessional.com/downloads/products/0011487492/DrapchoCh4.pdf>). Furthermore, the fermentation efficiencies of pearl millets, on the basis of starch, are comparable to those of maize and sorghum grains (Wu et al. 2006). Pearl millet therefore could be a potential feedstock for fuel production in areas too dry or too hot to grow maize and sorghum.

The genomic relationships among cereals have been established (Gale and Devos 1998). The high degree of genetic synteny among grass

genomes should facilitate the translation of gene-function discovery in bioenergy model crops (maize and sorghum) (Carpita and McCann 2008; Doust et al. 2009), which have abundant genetic and genomic resources (reviewed in Dwivedi et al. 2007) and their genomes have been recently sequenced (Paterson et al. 2009b; Schnable et al. 2009). Foxtail millet has been recently identified as an experimental model crop to investigate many aspects of plant architecture, genome evolution, and physiology in the bioenergy grasses (Doust et al. 2009). More recently, significant progress has been announced toward sequencing the foxtail millet genome, which is closely related to bioenergy grasses (Doust et al. 2010; Mitros et al. 2010). With the release of maize, sorghum, and foxtail millet genome sequences and the availability of next-generation sequencing technologies (Varshney et al. 2009), genomic and genetic approaches can be explored to study the molecular basis of biomass production, cell wall modification using brown midrib mutants (*bmr* in maize or *bmr* in sorghum, which alter the cell wall composition, particularly lignin subunit composition) (reviewed in Vermerris et al. 2007), or accumulation of sugar in sweet sorghums and its relationship with grain and biomass production (Rao et al. 2009). Furthermore, sequence variation would also allow a comprehensive survey of genetic diversity to identify and conserve germplasm diversity with bioenergy traits.

IX. CONCLUSIONS AND FUTURE PROSPECTS

Gene banks around the world have a large collection of germplasm for most of the millets species. However, more effort is needed to collect landraces of barnyard millet, fonio, tef, and Job's tears before these priceless genetic resources vanish forever from their habitats. Access to genetic diversity contained in large germplasm collections continues to be a significant challenge. A reduced subset of germplasm in the form of a conventional core or genotype-based "diversity panel" is the ideal pool of diverse germplasm resources for studying population structure and diversity. Landrace diversity in pearl millet and fonio has been found to possess several agronomically beneficial traits. More efforts are therefore needed to collect and characterize landrace in other millets to identify potential germplasm resources for use in crop improvement programs.

Precise phenotyping is the key to finding and introducing new genes for biotic and abiotic tolerances. An effective phenotypic screen for lodging and temperature tolerance is urgently needed in millets to identify lodging and high-temperature-tolerant germplasm resources

for use in breeding. Downy mildew in pearl millet and blast in finger millet have shown large pathogen variability, with some pathotypes being more virulent than others. There is a continuing need to monitor pathogen variability and take effective measures to deploy cultivars with resistance to multiple pathotypes to contain these diseases in farmers' fields.

Among the millets, pearl millet is the only crop in which heterosis has been exploited using CMS-based hybrids for large-scale commercial cultivation in India, the American continent, and Oceania. In years to come, foxtail millet has great potential to exploit heterosis for total biomass and grain yield. Researchers in China have discovered CMS materials, which are being further studied to develop stable CMS seed parents and reliable fertility restorers for the development of hybrids in foxtail millet.

As of now, eight angiosperm genomes, including maize, rice, and sorghum, have been sequenced (Paterson et al. 2010). The draft genome sequencing of foxtail millet (*Setaria italica*) has been completed to 8.3× coverage; it has shown a high degree of synteny to rice and sorghum, suggesting that foxtail millet genome sequences will soon be available to the research community (Mitros et al. 2010). By comparing the genome sequences of maize, rice, and sorghum with that of foxtail millet—all of which are used as food, feed, and biofuel crops—we should be able to find sequence variation across species and relate these differences to beneficial traits. Furthermore, it should be feasible to resequence the elite genetic stocks with contrasting phenotypes of a given crop species. Sequence variation among these genetic stocks could then be related to phenotypic differences, as detected in maize inbreds and hybrids (Lai et al. 2010). With the development of next-generation sequencing technologies, identification and tracking of genetic variations has become so efficient and precise that thousands of variants can be tracked within large populations at a much-reduced cost (Varshney et al. 2009). Moreover, the availability of DNA sequence information should enable the discovery of genes and molecular markers associated with diverse agronomic traits, creating new opportunities for crop improvement (Edwards and Batley 2010).

Millets as a group are C₄ plants, mostly adapted to marginal lands in the hot, drought-prone arid and semiarid regions of Africa, Asia, and the Americas. The gains in productivity associated with C₄ photosynthesis include improved water and nitrogen use efficiencies. Engineering C₄ traits into C₃ grasses is an attractive target for crop improvement. However, the lack of a small, rapid-cycling genetic model system to study C₄ photosynthesis has limited progress in dissecting the regulatory

networks using the C₄ pathway. *Setaria viridis* (genome size 510 Mb), the wild ancestor of foxtail millet (*S. italica*) and a close relative of several feed, fuel, and bioenergy grasses, uses the nicotinamide adenine dinucleotide phosphate (NADP)-malic enzyme subtype C₄ photosynthetic system to fix carbon and is therefore a potential model system for dissecting C₄ photosynthesis (Brutnell et al. 2010). The only major hurdle yet to overcome with *S. viridis*, however, is to develop an effective transformation and regeneration system. Some progress has already been reported toward regenerating plants from seed callus and establishing a transient transformation system in *S. viridis*. Engineering C₄ traits into C₃ plants will go a long way to sustain and stabilize food production, particularly in the developing world, in view of global warming due to climate change.

PCR-based markers have been used to assess the structure of genetic diversity in some millets; such studies are needed in other species. Genetic maps of varying density are available for pearl millet, finger millet, foxtail millet, and tef and QTL associated with various agronomic traits have been reported for pearl millet, foxtail millet, and tef. Marker-aided breeding is being practiced to incorporate biotic and abiotic stress resistance into the improved genetic background of pearl millet. Pearl millet hybrid with enhanced resistance to downy mildew is widely grown in India. Pearl millet introgression lines combining terminal drought-tolerant QTL (on LG2) and downy mildew-resistant QTL (on LG1 and LG4) are being tested for their agronomic performance in India. There is, however, urgent need to develop genomic resources (markers and genetic maps) for fonio and Job's tears, two underresearched millets. Lodging is a serious problem in fonio and little positive variability has been identified for this trait in fonio germplasm evaluated so far. Tef-based TILLING has been perfected and is currently used to identify dwarf tef plants from mutagenetically ionized tef populations.

Even though grain from millets is more nutritious than most major starch crop and has some medicinal value, production in traditional millets growing areas has been declining in favor of other crops, such as rice, wheat, and cassava. The decline in production has resulted in reduced consumption, which could also be related to changing lifestyle due to overall economic development. Government policies, in addition to erratic rainfall and drudgery associated with processing of minor millets, also contributed to the decline in production of these millets species. An all-front attempt is needed to bring production back to the levels these species were grown to and consumed during the 1960s and 1970s. Doing so includes increasing public awareness of the nutritional value of these millet species to overall human health; enhanced research

on issues associated with production, processing, and utilization; value addition by developing new products; and government support for marketing and inclusion of millets to distribution through public systems so it reaches needy people. Collective action involving diverse players will be required to develop a promotional strategy for demand expansion to ensure that production of these millets is solidly anchored and sustained in the long run.

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