GENETIC AND GENOMIC RESOURCES FOR GRAIN CEREALS IMPROVEMENT

EDITED BY
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Academic Press is an Imprint of Elsevier

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125, London Wall, EC2Y 5AS, UK
525 B Street, Suite 1800, San Diego, CA 92101-4495, USA
225 Wyman Street, Waltham, MA 02451, USA
The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK

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British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloging-in-Publication Data
A catalog record for this book is available from the Library of Congress

ISBN: 978-0-12-802000-5

Publisher: Nikki Levy
Acquisition Editor: Nancy Maragioglio
Editorial Project Manager: Billie Jean Fernandez
Production Project Manager: Julie-Ann Stansfield
Designer: Mark Rogers

Typeset by Thomson Digital

Printed and bound in the United States of America

Pearl millet

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6.1 Introduction

Pearl millet [*Pennisetum glaucum* (L.) R. Br., Syn. *Cenchrus americanus* (L.) Morrone] is the sixth most important cereal worldwide and the main food source in the semiarid regions of Asia and Africa. Globally, pearl millet is cultivated on 30 million ha with majority of the crop in Africa (~18 million ha) and Asia (>10 million ha) (Yadav and Rai, 2013). It is mainly grown for food and forage in India and Africa, while as a forage crop in the Americas. India is the single largest producer of pearl millet (7.95 million ha, 8.90 Mt) with seven major growing states (AICPMIP, 2014). Pearl millet is a C_4 plant with very high photosynthetic efficiency, dry matter production capacity, short duration, and high degree of tolerance to heat and drought. It is also adapted on saline, acidic, and aluminum toxic soils (Yadav and Rai, 2013).

Pearl millet grain is a staple food for around 90 million people in the Sahelian region of Africa and northwestern India, with majority of the produce being used as food (www.icrisat.org). It is consumed primarily as a thick porridge (toh), but it is also milled into flour to prepare unfermented breads and cakes (roti), steam-cooked dishes (couscous), fermented foods (kisra and gallettes), nonalcoholic beverages, and snacks. Roasted young earheads are a popular food for children. In the Sahelian countries like Senegal, Mali, Niger, and Burkina Faso, pearl millet is consumed in preference to sorghum. In northern Nigeria, pearl millet is used in making a popular fried cake known as *masa* (Girgi and O'Kennedy, 2007).

Pearl millet is a "high-energy" cereal that contains carbohydrates, protein, and fat, rich in vitamins B and A, high in calcium, iron, and zinc, and also contains potassium, phosphorus, magnesium, zinc, copper, and manganese. Feeding trials conducted in India have shown that pearl millet is nutritionally superior to maize and rice (NRC, 1996; DeVries and Toenniessen, 2001). Pearl millet grains are gluten-free and the biological value of its protein is superior over wheat. Grain has no tannin, contains oil (5–7%), and has higher protein and energy levels than maize or sorghum and more balanced amino acid profile compared to sorghum and maize (Rai et al., 2008). In India, although grains are mainly used for human consumption, alternative uses have increased (55%) mainly as animal feed for dairy (in rural parts of western Rajasthan) and to some extent in poultry, alcohol industry, starch industry, processed food industry, and export demand (Basavaraj et al., 2010). Both green fodder and dry stover are used for cattle.

Genetic and Genomic Resources for Grain Cereals Improvement. http://dx.doi.org/10.1016/B978-0-12-802000-5.00006-X

Stover has excellent forage quality with lower hydrocyanin content; green fodder is rich in protein, calcium, phosphorus, and other minerals with safer limits of oxalic acid.

6.2 Origin, distribution, and diversity

P. glaucum subsp. *monodii*, found in the Sahelian region of Africa, is the progenitor of cultivated pearl millet (Harlan, 1975; Brunken, 1977). Domestication of pearl millet has been suggested to have occurred through single or multiple events (Harlan, 1975; Portères, 1976) and the earliest archeologic evidence for pearl millet domestication is from northern Ghana, ~3000 years BP (D'Andrea and Casey, 2002). Domestication followed by migration of aboriginal populations in sub-Saharan regions and secondary diversification in the eastern Sahel has been suggested (Tostain et al., 1987; Tostain, 1992). Early-flowering types may have domesticated around Lake Chad, which is considered as a secondary center of diversification. Furthermore, the late flowering, new early-flowering varieties, pearl millet varieties from East and South Africa and India could have originated from this region (Robert et al., 2011). Monophyletic origin of pearl millet has been suggested based on similarity among domestic and wild forms for isozymes and simple sequence repeats (SSRs) (Tostain, 1993; Mariac et al., 2006a, 2006b; Oumar et al., 2008; Kapila et al., 2008).

Molecular profiling revealed that cultivated pearl millet contains 81% of the alleles and 83% of the genetic diversity of the wild pearl millet (Oumar et al., 2008), suggesting that domestication has decreased genetic diversity. The gene flow between domestic and wild forms could later have contributed to increase in genetic diversity of the domestic genepool (Robert et al., 2011). A large number of spontaneously occurring weedy and intermediate form plants, which mimic the cultivated plants in their vegetative and floral morphologies called "shibras" (=*Pennisetum stenostachyum*), are observed throughout West African Sahel. The *stenostachyum* is considered as a product of postdomestication hybridization between pearl millet and its wild ancestor (Brunken et al., 1977). Its widespread occurrence outside the natural area of its wild progenitor suggests its persistence over long times.

Quantitative trait loci (QTL) analyses using F_2 populations of crosses between pearl millet and its wild progenitor (*P. glaucum* subsp. *monodii*) identified two genomic regions on linkage groups (LG) 6 and 7, which control most of the key morphologic differences between wild and cultivated types (Poncet et al., 1998, 2000, 2002). These genomic regions have a prime role in the developmental control of spikelet structure and domestication process of pearl millet, which may also correspond with QTLs involved in domestication of other cereals like maize and rice (Poncet et al., 2000, 2002). Furthermore, Miura and Terauchi (2005) proposed the occurrence of a putative supergene or gene complex during domestication that differentiated weedy and cultivated pearl millet.

6.2.1 Taxonomy and diversity

The genus *Pennisetum* (bristle grass) is the largest and important genera belonging to the subtribe Panicinae, tribe Paniceae, subfamily Panicoideae of the family Poaceae. The genus is mainly characterized by its inflorescence, a false spike with spikelet on contracted

axes, or spikelets fascicled in false spikes, always surrounded by involucres, which are crowded with slender, basally free, glabrous to plumose bristles; the spikelets are sessile or pedicillate, falling with the involucres, only persistent in the cultivated species (Watson and Dallwitz, 1992). The *Pennisetum* genus includes over 80–140 species (Brunken, 1977; Clayton and Renvoize, 1986), which differ in their duration (annual or perennial), reproduction (sexual or asexual/apomictic), somatic chromosome number ($2n$ = 10–78), basic chromosome number (x = 5, 7, 8, or 9; Jauhar, 1981a, 1981b), chromosome size (92–395 Mbp), genome size (1Cx = 0.75–2.49 pg) (Martel et al., 1997), and ploidy levels (diploid to octoploid) (Table 6.1). Aneuploids are fairly common (Schmelzer, 1997) and frequent occurrence of B chromosomes was reported in many species (Vari et al., 1999).

Diversity in basic chromosome number, different chromosome sizes between species with larger size for those with low basic chromosome number (Jauhar, 1981a), reflect "chromosome repatterning" within the genus during evolution. Different hypotheses were proposed for ancestral basic chromosome number in *Pennisetum*. Jauhar (1981a) and Rao et al. (1989) based on chromosome pairing observations in *Pennisetum*, suggested an increase in basic chromosome number from x = 5. But, frequent occurrence of x = 9 in *Pennisetum* and closely related genera like *Cenchrus*, *Panicum*, and *Setaria* suggests a decrease in "x" from ancestral number (x = 9) (Robert et al., 2011). In the genus *Pennisetum*, nearly 3/4th of the species are polyploids (Jauhar, 1981a). Cultivated species (*Pennisetum glaucum*) is essentially a diploid, though both spontaneous and induced polyploids have been reported. Based on meiotic chromosome pairing studies in section *Brevivulvula*, species *Pennisetum pedicellatum* and *Pennisetum polystachyon* were reported to be autoploid or autoalloploid or segmental alloploid. Similarly, many species such as *Pennisetum subangustatum*, *Pennisetum atrichum*, *Pennisetum setosum*, and *Pennisetum squamulatum*, were suggested to be autoalloploids (for details see Robert et al., 2011). However, *P. squamulatum* is suggested to be an octoploid (Kaushal et al., 2008).

6.2.1.1 Sections

Based on morphological differences, genus *Pennisetum* is divided into five sections (Stapf and Hubbard, 1934), that is, *Penicillaria* (tropical Africa and India), *Brevivulvula* (pan-tropical), *Gymnothrix* (pan-tropical), *Heterostachya* (northeast Africa), and *Eupennisetum* (tropical and subtropical Africa and India), each having several species (Table 6.1). The differences between sections were often not very strong as more than one morphological section consisted of taxa with one common basic chromosome number and also one section included taxa from different basic chromosome number groups. Section *Penicillaria* represents species with x = 7 and include cultivated pearl millet (*P. glaucum*) and napier/elephant grass (*P. purpureum*), while Brunken (1977) included them under a different section *Pennisetum*. Other sections comprise 22 species in *Gymnothrix*, 5 in *Pennisetum*, and 3 each in *Heterostachya* and *Brevivulvula*.

6.2.1.2 Genepool

The classification of genepool for pearl millet and its wild relatives was proposed based on the genetic relationship between species (Harlan and de Wet, 1971). Later, it was

Table 6.1 Characteristics of *Pennisetum* species

Genepool/section/species/ subspecies/common name	Mode of reproduction, plant habit*	Geographic range	Chromosome number**			2C value (pg)
			n	2*n*	*x*	
I. Primary genepool (GP1)						
Section *Penicillaria/Pennisetum*†			7	14	7	
P. glaucum (L.) R. Br.						
1. *P. glaucum* ssp. *glaucum* (Pearl millet)	Sex, A	Wide	7	14(2*x*)	7	4.71
2. *P. glaucum* ssp. *monodii*						
Two ecotypes:						
(a) *P. violaceum*	Sex, A	Africa	7	14(2*x*)	7	4.52
(b) *P. mollissimum*	A	West Africa	–	14(2*x*)	–	4.51
II. Secondary genepool (GP2)						
Section *Penicillaria/Pennisetum*†			7–28	21–28	7	
P. purpureum (Elephant grass)	Sex/Apo, Inb, P, SP	Wide	7, 14, 28	28(4*x*), 27, 21	7	4.59
Section *Heterostachya*				54–56	7, 9	
P. squamulatum	Apo, Inb, P, C, RSE	Africa	–	54(6*x*), 56(8*x*)	7, 9	9.56
III. Tertiary genepool (GP3)						
Section *Brevivulvula*			9–36	18–78	9	
Pennisetum hordeoides	Apo, A	Africa, Asia-tropical	9	36, 54	9	–
P. pedicellatum (Hairy fountaingrass)	Apo, Inb, A	Africa, Asia-tropical, Australasia, South America	14, 18, 27	54(6*x*), 36(4*x*), 24, 30, 32, 35, 42, 45, 48, 53	9	5.61
1. ssp. *pedicellatum*						
2. ssp. *unispiculum*						
P. polystachion (Missiongrass)	A/P, C	Wide	27	54(6*x*)	9	5.66
1. ssp. *polystachion*	Apo	–	18, 36	18, 24, 32, 36, 45, 48, 52, 53, 54, 56, 63, 78	9	–
2. ssp. *atrichum*	P, A	South, West and East Africa	–	36(4*x*)	9	4.25

Section *Eupennisetum/Pennisetum*[†]			9–27	18–68	9, 17	
Pennisetum clandestinum (Kikiyugrass)	Apo/Sex, P, MF, RE, SP	Africa, Asia-temperate, Asiatropical, Australasia, Pacific, America, Antarctic	18, 27	36	9	2.30
P. flaccidum (Himalayan fountaingrass)	Apo/Sex, P, C, RS	Asia-temperate, Asia-tropical	9, 18, 27	18, 36	9	–
Pennisetum foermeranum	P, RE	Southern Africa	–	–	–	–
P. setaceum (Tender fountaingrass)	Apo, Inb, P, C	Europe, Africa, Asia-temperate, Australasia, Pacific	18	27(3*x*), 54(6*x*), 68	9, 17	2.78, 5.28
Pennisetum sieberianum	A	Africa, Asia-temperate	–	–	–	–
Pennisetum villosum (Feathertop)	Apo, Inb, P, MF, RE	Cosmopolitan	27	36(4*x*), 18, 27, 45, 54	9	3.47
Section *Gymnothri*			5–18	10–72	5, 8, 9	
Pennisetum alopecuroides (Chinese fountaingrass)	Sex, P, C	Asia-temperate, Asia-tropical, Australasia	18	18(2*x*), 22	9	1.90
Pennisetum basedowii	A, C, CL	Australasia	–	54	9	–
Pennisetum chilense	P, C, RE	South America	–	–	–	–
Pennisetum frutescens	Apo, P, CE, RE	South America	–	63	9	–
Pennisetum hohenackeri	P, C, CD	Africa, Asia-tropical	9	18 (2*x*)	–	1.69
Pennisetum latifolium (Uruguay fountaingrass)	Apo, P, RS	Australasia, South America	–	36	9	–

(Continued)

Table 6.1 Characteristics of *Pennisetum* species *(cont.)*

Genepool/section/species/subspecies/common name	Mode of reproduction, plant habit*	Geographic range	Chromosome number**			2C value (pg)
			n	2*n*	*x*	
Pennisetum macrourum (Waterside Reed)	Apo, P, RE	Africa, Asia-temperate, Australasia	–	36, 54	9	–
Pennisetum massaicum	Apo/Sex, P, RS, K	Africa	–	16, 32	8	–
Pennisetum mezianum	Apo, Inb, P, RS, K	Africa, Asia-tropical	–	16, 32	8	3.01 (4*x*)
Pennisetum montanum	P	South America	16	32	8	–
Pennisetum nervosum (Bentspike fountaingrass)	P, RSE	America	–	36, 72	9	–
P. ramosum (unresolved sp.)	Sex/Apo, Inb, A, C	Africa	5	10(2*x*), 20	5	4.04
Pennisetum sphacelatum	P, C	Africa	–	18	9	–
Pennisetum thunbergii	P, C, RE	Africa, Asia-temperate, Asia-tropical, Australasia	–	18	9	–
Pennisetum trachyphyllum	P	Africa	–	–	–	–
Pennisetum tristachyum	P, C	America	–	–	–	–
Pennisetum unisetum	P, C	Africa, Asia-temperate	–	18	9	–
Section *Heterostachya*			9–18	14–56	7, 9	
P. orientale (White fountaingrass)	Sex/Apo, Inb, P, C, RS	Africa, Asia-temperate, Asia-tropical, Pacific, South America	9, 18	36(4*x*), 45, 27, 56	9	3.77
P. schweinfurthii (=*Pennisetum tetrastachyum*)	Sex, A	Africa	–	14(2*x*)	7	4.97

Section unknown						
Pennisetum advena (Foreign fountaingrass)	P, C	North America	–	–	–	–
Pennisetum annuum	A	South America	–	–	–	–
Pennisetum articulare	P, C	Pacific	–	–	–	–
Pennisetum bambusiforme	P, C	America	–	36	–	–
Pennisetum beckeroides	P, RS	Africa	–	–	–	–
Pennisetum caffrum	P, C, CD	Africa Indian ocean	–	–	–	–
Pennisetum centrasiaticum	P	Asia-temperate	–	36	–	–
P. ciliare (syn. *Cenchrus ciliaris*) (Buffelgrass)	Apo/Sex, P, C, RE	Africa, West Asia, India	9, 18	32, 34, 36, 40, 45, 52, 54	9	–
Pennisetum complanatum	P, RE	Pacific, North America	–	–	–	–
Pennisetum crinitum	P, C	North America, Mexico	–	–	–	–
Pennisetum distachyum	P, C	North America, South America	–	36	–	–
Pennisetum divisum	P, RS, K	Africa, Asia-temperate, Asia-tropical	18, 27	36	–	–
Pennisetum domingense	P	South America	–	–	–	–
Pennisetum durum	P	North America, Mexico	–	–	–	–
Pennisetum glaucifolium	P, CE, RS	Africa, Asia-temperate	–	–	–	–
Pennisetum gracilescens	P, C, RS	Africa	–	–	–	–
Pennisetum henryanum	P, C	Pacific	–	–	–	–
Pennisetum humile	P, C, RE	Africa	–	–	–	–
Pennisetum intectum	P	South America	–	–	–	–

(Continued)

Table 6.1 Characteristics of *Pennisetum* species *(cont.)*

Genepool/section/species/ subspecies/common name	Mode of reproduction, plant habit*	Geographic range	Chromosome number**			2C value (pg)
			n	2*n*	*x*	
Pennisetum lanatum	P, C, RE	Asia-temperate, Asia-tropical	18	–	9	–
Pennisetum laxius	A	Africa	–	–	–	–
Pennisetum ledermannii	P	Africa	–	–	–	–
Pennisetum longissimum	P	Asia-temperate	–	54	–	–
Pennisetum longistylum	P, MF, CE, RE	Africa	–	45	–	–
Pennisetum macrostachyum (Pacific fountaingrass)	P, C	Asia-tropical, Pacific	–	54	–	–
Pennisetum mildbraedii	P, C, RE	Africa	–	–	–	–
Pennisetum monostigma	P, C	Africa	–	18	–	–
Pennisetum nodiflorum	P	Africa	–	–	–	–
Pennisetum nubicum	A	Africa, Asia-temperate	–	–	–	–
Pennisetum occidentale	P	South America	–	–	–	–
Pennisetum pauperum	P, C	South America	–	–	–	–
Pennisetum peruvianum	P	South America	–	–	–	–
Pennisetum petiolare	A	Africa	–	–	–	–
Pennisetum pirottae	P	Africa	–	–	–	–
Pennisetum procerum	P	Africa	–	–	–	–
Pennisetum prolificum	P, C	North America	–	–	–	–
Pennisetum pseudotriticoides	P, C	Africa	–	–	–	–
Pennisetum pumilum	P, C	Africa	–	–	–	–
Pennisetum qianningense	P, C	Asia-temperate	–	36	–	–
Pennisetum rigidum	P, RE	South America	–	–	–	–
Pennisetum riparium	P, MF, RE	Africa	–	–	–	–
Pennisetum rupestre	P, RE	South America	–	–	–	–
Pennisetum sagittatum	P	South America	–	–	–	–

*Pennisetum setigerum (*syn. *Cenchrus setiger)* (Birdwoodgrass)	P	North-east Africa, India	–	34 (2*x*)	–	–
Pennisetum shaanxiense	P	Asia-temperate	–	–	–	–
Pennisetum sichuanense	P, RS	Asia-temperate	–	–	–	–
Pennisetum stramineum	P, C	Africa, Asia-temperate	–	–	–	–
Pennisetum tempisquense	P, C	South America	–	–	–	–
Pennisetum thulinii	P, C, CD	Africa	–	–	–	–
Pennisetum trisetum	P	Africa	36	–	–	–
Pennisetum uliginosum	P, C, CL, RE	Africa	–	–	–	–
Pennisetum weberbaueri	P	South America	–	–	–	–
Pennisetum yemense	P, C, CD, RSE, RS/RE	Africa, Asia-temperate	–	–	–	–

* Mode of reproduction: Sex, sexual; Apo, apomictic; Inb, inbreeder. Plant habit: A, annual; P, perennial; C, caespitose; CD, clumped densely; CE, cataphylls evident; CL, clumped loosely; K, knotty; MF, mat forming; RE, rhizomes elongated; RS, rhizomes short; RSE, root stock evident; SP, stolons present.
** Range of chromosome numbers given for sections.
† Brunken (1977) grouped them under section *Pennisetum.*
Sources: Robert et al. (2011); Chemisquy et al. (2010); Clayton et al. (2006); www.theplantlist.org.

extended to the concept of "complex of species" (Pernès, 1984) based on crossability of wild species with domesticated form and also the amount of gene flow occurring between all the members of the genepool. This classification includes primary, secondary, and tertiary genepools. Primary genepool (GP1) includes two subspecies: (1) cultivated pearl millet (*Pennisetum glaucum* ssp. *glaucum*, $2n = 2x = 14$, AA) with distinctly stalked and persistent involucres at maturity, and (2) wild progenitor (*P. glaucum* subsp. *monodii*: two ecotypes, *Pennisetum violaceum* and *Pennisetum mollissimum*) with subsessile, deciduous involucres at maturity (Robert et al., 2011). The intermediate weedy forms, "shibras" (=*P. stenostachyum*) are found throughout West African Sahel. Members of GP1 are not reproductively isolated and can cross-hybridize in sympatric condition forming fertile hybrids with normal chromosome pairing. Despite this gene flow, mechanisms like linkage, gametophytic competition, and phenology contribute to the maintenance of the genetic structure of the species (Robert et al., 2011).

The secondary genepool (GP2) includes napier/elephant grass (*Pennisetum purpureum* Schum., $2n = 4x = 28$, A′A′BB), and recently included apomictic, octoploid species *P. squamulatum* ($2n = 8x = 56$), whose genome size is similar to *P. purpureum*. Cytogenetic analysis like crossability, DNA content, genetic relatedness, and cytology of advanced hybrids supported the placement of *P. squamulatum* in GP2 (Kaushal et al., 2008). Napier grass is a rhizomatous perennial with desirable traits like resistance to most pests, vigorous growth, and outstanding forage potential; most of these characteristics appear to be on B genome (Hanna, 1987). *P. purpureum* and *P. squamulatum* can be easily crossed with cultivated pearl millet but their hybrids are highly sterile. The tertiary genepool (GP3) includes the remaining *Pennisetum* spp., which are true biological species compared to GP1 and GP2 species. Several *Pennisetum* species in the GP3 are of economic importance, namely *Pennisetum flaccidum*, *P. mezianum*, and *P. setaceum* (ornamental), *P. squamulatum*, *P. polystachyon*, *P. pedicellatum*, and *Pennisetum orientale* (forage). A strong reproductive barrier occurs between members of GP3 with GP1 and GP2 affecting gene flow and occurrence of hybrids. Gene transfer is possible through radical manipulations involving *in vitro* techniques or by using complex hybrid bridges. GP3 species with $x = 9$ cross more readily with pearl millet than those with $x = 5$ (*P. ramosum*) and $x = 8$ (*P. mezianum*) (Dujardin and Hanna, 1989a).

6.2.1.3 Races

Brunken et al. (1977) classified the world collection of cultivated pearl millet based on seed shapes into four races:

1. *typhoides*: It occurs from Senegal to Ethiopia, and northern to southern Africa. It is the only basic race found outside Africa, and predominantly grown in India. It is widely distributed and morphologically most variable among the four races. Caryopses are obovate in frontal and profile views, and obtuse and terete in cross-section. Grains are occasionally shorter and enclosed by floral bracts. Inflorescences are variable in length and more or less cylindrical, but rarely short inflorescences with elliptic shape are also found (Appa Rao and de Wet, 1999).
2. *nigritarum*: It is found from western Sudan to northern Nigeria, probably native to eastern Sahel and its isolated occurrences in western Sahel due to recent migration events. The caryopsis is angular in cross-section with three and six facets. Grains apex is usually

truncate with purple tinge and mature grain is elongated and protrudes beyond the floral bracts. Inflorescence is candle-shaped.

3. *globosum*: It occurs from central Burkina Faso to western Sudan and is most commonly found in central Nigeria, Niger, Ghana, Togo, and Benin. This large-seeded race has experienced a great degree of migration in recent times. The caryopses are characteristically spherical with each of its dimensions equal, otherwise terete and obtuse, and grain depth always exceeds 2.4 mm. It has candle-shaped inflorescence.
4. *leonis*: It is mainly found in Sierra Leone, infrequently observed in Senegal, southern Mauritania, and the hilly areas of southern India. Caryopsis is oblanceolate and terete with acute apex due to remnants of stylar base. Grains are elongated and nearly oblanceolate from all lateral perspectives. At maturity, 1/3 of the grain protrudes beyond the floral bracts. It has candle-shaped inflorescence.

There are arguments that patterns of racial variation observed in crops are the result of several independent domestications (Portères, 1976). Although independent domestications cannot be ruled out, it appears that migration events, very early in the history of pearl millet, followed by a combination of geographic and ethnographic isolation are responsible for the present-day pattern of variation in seed morphology of the crop (Appa Rao and de Wet, 1999).

6.2.1.4 Genomic relationships

The study of genomic relationships provides information on phylogenetic relations and evolution, and it is also useful in breeding programs seeking gene introgression. GP1 species (*P. glaucum*, *P. violaceum*, and *P. mollissimum*) are reported to have similar amount of DNA per basic chromosome set (Martel et al., 1997). Genomic relationships between *Pennisetum* species were investigated by studying variations in chloroplast DNA (Clegg et al., 1984; Renno et al., 2001), mitochondrial DNA (Chowdhury and Smith, 1988), and repetitive DNA sequences (Ingham et al., 1993). Significant relationships were noticed between *P. glaucum*, *P. purpureum*, and *P. squamulatum* suggesting a common origin. Homeology between A (pearl millet) and A′ (*P. purpureum*) genomes has been established earlier by conventional cytogenetic techniques (Jauhar, 1981a), and B genome was found dominant over A′ genome that masks genetic variability (Hanna, 1987). Recent investigations using genomic *in situ* hybridization revealed homeology between the genomes of pearl millet (A) and *P. purpureum* (A′, B), and also differences in the distribution and proportion of homologous regions (dos Reis et al., 2014). Despite differences in ploidy levels, *P. purpureum* (4*x*) and *P. glaucum* (2*x*) have almost the same 2C values (4.59, 4.71 pg, respectively), but different monoploid genome size (1C*x* = 1.15, 2.35 pg, respectively). The *P. purpureum* chromosomes (~80 Mbp) are half the size of *P. glaucum* (~165 Mbp) showing important chromosomal changes linked to divergence of these species (Martel et al., 1997).

Phylogenetic relationships in *Pennisetum* suggest an ancestral small chromosome (*x* = 9), but reduced chromosome number (decreasing dysploidy) (*x* = 5, 7, or 8) and increased chromosome size (Martel et al., 2004; Robert et al., 2011) rather than increase in basic chromosome number (ascendant dysploidy) (Jauhar, 1981b;

Jauhar et al., 2006). Molecular phylogenetic studies using ribosomal and chloroplast DNA sequences suggest the genus *Pennisetum* as paraphyletic (a taxonomic group that includes some but not all of the descendants of a common ancestor) (Martel et al., 2004; Donadio et al., 2009) with the species *Cenchrus ciliaris* (=*Pennisetum cenchroides*/*Pennisetum ciliare*) nested within it (Doust et al., 2007). Close genomic relationships were observed between *P. squamulatum* and aposporous apomictic species *Cenchrus ciliaris*, which also showed complete macrosynteny at the apospory-specific genomic region governing apomixes in these species (Goel et al., 2006). Chromosomal and genomic characteristics combined with phylogenetic relationships favor the inclusion of *Cenchrus* species within the genus *Pennisetum*. Hence, it was proposed to reconsider the taxonomic position of *Cenchrus* species and to rename them as *Pennisetum* species as previously known (Robert et al., 2011).

6.3 Erosion of genetic diversity and gene flow

The success of any plant-breeding program depends on the germplasm diversity available in the crop. Conserving the rich diversity of crop varieties and related wild species is essential for providing farmers and plant breeders with diverse sources to improve and adapt crops to meet future challenges. The genetic variability accumulated over centuries is fast eroding, mainly due to the replacement of landraces by improved cultivars, natural catastrophes (droughts, floods, fire hazards, etc.), industrialization, human settlement, overgrazing, and destruction of plant habitats for irrigation projects and dams (Upadhyaya and Gowda, 2009). Changes in the diversity of landraces in centers of diversity of cultivated plants need to be assessed in order to monitor and conserve agrobiodiversity. This notably applies in tropical areas where factors, such as increased population, climate change, and shifts in cropping systems, are hypothesized to cause varietal erosion.

Pearl millet landraces are fast disappearing in most states of India due to large-scale adoption of improved cultivars. For example, a popular landrace from Punjab, “Gullisita” is no longer found in its original form. Recurring droughts in a region enforce the farmers to introduce new cultivars from elsewhere, resulting in loss of local landraces. With the availability of irrigation, pearl millet is being replaced by more remunerative crops like rice, pigeonpea, and cotton in Punjab, India; coconut in Srikakulam district of Andhra Pradesh, India; cassava and cotton in the Central African Republic; wheat, maize, and other commercial crops in Yemen; and early maturing maize in northern Togo, southern Africa, and Nigeria (Appa Rao et al., 1993, 1994; Appa Rao, 1999).

A rapid survey was undertaken (2000–2005) by AICPMIP (pearl millet) in Rajasthan (India) to measure and monitor the genetic erosion of pearl millet landraces through participatory approach under an FAO project (www.globalplanofaction.org), which revealed narrowing of genetic diversity. Diversity in major cereals/millet crops including pearl millet was found decreasing at a local level in India (NBPGR, 2007). Genetic

erosion of crop landraces was found increasing in southern Tunisia (Mohamed, 1998). Improved cultivars were found replacing traditional varieties in different geographical regions of Tanzania (Appa Rao et al., 1989a) and Yemen (Muallem, 1987). Based on comparison of diversity in pearl millet varieties collected in 79 villages spanning the entire cereal-growing zone of Niger over a 26 year period (1976–2003), high diversity of pearl millet varieties was confirmed (Bezançon et al., 2009). Genetic erosion was not observed suggesting that farmers' management could preserve the diversity of millet varieties in Niger despite recurrent and severe drought periods and major social changes.

Gene flow within the GP1 species of *Pennisetum* has been assessed by some workers. Weedy plants with intermediate (domesticated × wild) phenotypes occur in most pearl millet fields in West Africa, even in the absence of wild populations. Under experimental conditions, hybrid (domesticated × wild) frequency decreased steadily during germination (42%), at emergence (37%), and thinning (17%) by the farmer, and finally only 11% of mature plants were hybrids (Couturon et al., 2003). This shows that under the combined pressures of natural and human selection, the frequency of hybrids in the field declined drastically up to maturity without completely preventing the introgression of wild pearl millet genes into the cultivated genome. Morphologic and AFLP marker data suggest some introgression from the wild to the weedy population but very low gene flow between the parapatric wild and domesticated populations (Mariac et al., 2006b). Analyses of introgressions between cultivated and wild accessions using microsatellite markers showed modest introgressions. Wild accessions in the central region of Niger showed introgressions of cultivated alleles, while accessions of cultivated pearl millet showed introgressions of wild alleles in the western, central, and eastern parts of Niger (Mariac et al., 2006a).

6.4 Germplasm resources conservation

Germplasm of *Pennisetum* spp. (cultivated and wild) is conserved as 66,682 accessions in 97 genebanks across 65 countries, while germplasm of related genera *Cenchrus* spp. is conserved (3758 accessions) in 50 genebanks across 32 countries (www.genesys-pgr.org). Eleven major genebanks hold almost 90% of the pearl millet germplasm (Table 6.2). The ICRISAT genebank at Patancheru (India) has the largest collection (22,888 accessions) from 52 countries, including 794 wild germplasm belonging to 27 *Pennisetum* species. At Patancheru, majority of these accessions are conserved as base/active collections under cold storage. However, several accessions of wild species, which either do not produce seed or produce very less seed, are maintained alive in a field genebank. In addition, three regional genebanks of ICRISAT (Niamey, Niger; Nairobi, Kenya and Bulawayo, Zimbabwe) together conserve 14,272 accessions of pearl millet. ICRISAT has contributed 20,527 accessions of pearl millet as safety duplication to the Svalbard Global Seed Vault (SGSV), Norway, while nine other genebanks with small collections have deposited 1459 accessions of *Pennisetum* and *Cenchrus* spp. at SGSV.

Table 6.2 Major genebanks conserving cultivated and wild pearl millet germplasm

Institute/genebank	*Pennisetum* spp.		Total
	Cultivated	Wild	
Embrapa Milho e Sorgo, Sete Lagoas, Brazil	7,225	–	7,225
Plant Gene Resources of Canada, Saskatoon Research Centre, Agriculture and Agri-Food Canada, Saskatoon, Canada	3,543	263	3,806
Laboratoire des Ressources Génétiques et Amélioration des Plantes Tropicales, ORSTOM, Montpellier Cedex, France	3,620	798	4,418
International Crop Research Institute for the Semi-Arid Tropics, Patancheru, India	22,094	794	22,888
National Bureau of Plant Genetic Resources, New Delhi & Jodhpur, India	9,144	327	9,471
National Plant Genetic Resources Centre, National Botanical Research Institute, Windhoek, Namibia	1,419	2	1,421
Institut national de la recherche agronomique du Niger, Niamey, Niger	2,052	–	2,052
International Crops Research Institute for Semi-Arid Tropics, Niamey, Niger	2,817	–	2,817
Plant Genetic Resources Program, Islamabad, Pakistan	1,377	–	1,377
Serere Agriculture and Animal Production Research Institute, Serere, Uganda	2,142	–	2142
Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, University of Georgia, USDA-ARS, Griffin, USA	1,090	973	2,063

Source: https://www.genesys-pgr.org/; genebanks with >1000 accessions considered for listing.

At ICRISAT, the short-term storage is maintained at 18–20°C, 30–40% RH, and used for temporary holding of seeds for drying and preparation for subsequent transfer to medium- and long-term storage. Active collections are conserved under medium term (4°C, 20% RH) for 15–20 years by drying seeds up to 7–9% moisture content and stored in aluminum cans with screw caps having rubber gaskets. Base collections

are conserved under long term (–20°C) for >50 years by drying seeds up to 4–6% moisture content and storing in hermetically sealed laminated aluminum foil packets to extend viability (Upadhyaya and Gowda, 2009).

6.5 Germplasm characterization and evaluation

Germplasm collection is of little value unless it is characterized, evaluated, and documented properly toward their enhanced utilization in crop improvement.

6.5.1 Agronomic traits

A total of 21,461 accessions have been characterized at ICRISAT for 23 morphoagronomic traits using the descriptors for pearl millet (IBPGR and ICRISAT, 1993). These accessions showed large phenotypic diversity for almost all quantitative traits (Table 6.3). Likewise, diversity for qualitative traits, such as panicle shape (nine classes), seed shape (five classes), and seed color (10 classes), was also observed. Predominant types found were those with candle-shaped panicles, short-bristled panicles, globular seed shape, grey seed color, and seeds with partly corneous endosperm texture. Several accessions were identified as a promising source for green fodder yield (147), while some others for seed yield potential (6). Enormous diversity reported for morphoagronomic traits among landraces and wild relatives from India, west and central Africa, Cameroon, Yemen, and Ghana has been summarized by Dwivedi et al. (2012).

Table 6.3 Range variation for morphoagronomic traits observed in core collection and entire collection evaluated during rainy season at Patancheru, India

Characters	Range		Mean	
	Entire collection*	Core collection (Upadhyaya et al., 2009a)**	Entire collection	Core collection (Upadhyaya et al., 2009a)
Days to flowering	33–159	33–157	72.7	72.7
Plant height (cm)	30–490	35–490	248.5	243.3
Total tillers (no.)	1–35	1–35	2.7	2.7
Productive tillers (no.)	1–19	1–19	2.1	2.1
Panicle exsertion (cm)	−45 to 29	−32 to 22	3.5	3.5
Panicle length (cm)	5–135	5–120	28.9	28.2
Panicle width (cm)	8–58	10–55	24.0	23.9
1000 grain weight (g)	1.5–21.3	2.9–19.3	8.5	8.5

* Entire collection: 21,461 accessions.
** Core collection: 2,094 accessions.

6.5.2 Abiotic stress tolerance

Drought is the primary constraint for pearl millet production in the drier semi-arid and arid regions of south Asia and Africa. Traditional landraces from drier regions are good sources of drought adaptation (Table 6.4) and they could produce significantly greater biomass, grain, and stover yields than elite populations (Yadav, 2008). Under severe moisture stress, high tillering and small-panicled landraces produce higher grain yield than low tillering and large-panicled landraces (Van Oosterom et al., 2006). Drought-tolerant genotypes extract less water prior to anthesis and more water after anthesis resulting in better yield (Vadez et al., 2013). High-temperature stress at seedling and reproductive stages has an impact on crop establishment and yield of pearl millet. Genetic variation has been observed for heat tolerance at seedling and reproductive stage among germplasm (Table 6.4). A recent study for reproductive-stage heat tolerance over 3–4 years could identify tolerant breeding lines and germplasm line (IP 19877) having equivalent seed set as that of tolerant check 9444 (Gupta et al., 2015). Low-temperature stress at vegetative stage causes increased basal tillering and grain yield; at elongation stage, it leads to reduced spikelet fertility, inflorescence length, and decreased grain yield; at grain development stage, it leads to increase in grain yield (Fussell et al., 1980). Pearl millet germplasm tolerant to salinity have been reported (Table 6.4). Pearl millet is often cultivated in less-fertile soils with low amount of organic matter and low to medium levels of available phosphorus (Yadav and Rai, 2013). Pearl millet production on acid sandy soils of the Sahel is limited by low-P status. For low-P tolerance, both seedling and mature plant traits were found useful for selection as secondary traits (Gemenet et al., 2015). Diverse germplasm including breeding lines, varieties, and landraces with resistance to abiotic stresses has been summarized by Dwivedi et al. (2012).

6.5.3 Biotic stress tolerance

Resistance to major diseases like downy mildew, blast, smut, ergot, and rust have been reported in pearl millet germplasm (Table 6.4). At ICRISAT, evaluation of a large number of germplasm accessions has led to the identification of resistant/tolerant sources for downy mildew (54), smut (397), ergot (283), and rust (332) (Upadhyaya et al., 2007). Several germplasms with multiple disease resistance to major diseases have also been identified (Table 6.4). Diverse germplasm including breeding lines, varieties, and landraces showing resistance to biotic stresses have been summarized by Dwivedi et al. (2012). GP1 wild species, *P. glaucum* ssp. *monodii* is a good source for smut resistance, while ssp. *stenostachyum* is a good source for rust and leaf blast resistance. Some of the accessions of GP3 species were found immune to rust, while a group of accessions showed resistance to several fungal diseases including blast (Wilson and Hanna, 1992). A large number of accessions (223) belonging to 12 wild *Pennisetum* species were free from downy mildew, while most of the *Pennisetum schweinfurthii* accessions were free from downy mildew and also found resistant to rust (Singh and Navi, 2000). *Striga* [*Striga hermonthica* (Del.) Benth.] is

Table 6.4 Sources of resistance to major abiotic and biotic stress among pearl millet landraces and derivatives of landraces or wild relatives

Resistant landraces or derivatives*	References
Abiotic stress	
Drought: CZMS 44A (landrace 3072); IP 8210; landraces 220, 184, 235, 238	Manga and Yadav (1997); Kusaka et al. (2005); Yadav (2010)
Heat: IP 3201; IP 19877	Howarth et al. (1997); Gupta et al. (2015)
Salinity: 93613, KAT/PM-2, Kitui, Kitui local, 93612; 10876, 10878, 18406, 18570; IP 3757, 3732; Birjand pearl millet; IP 6112; IP 3616, 6104, 6112; ZZ ecotype	Ashraf and McNeilly (1992); Ali et al. (2004); Krishnamurthy et al. (2007); Kafi et al. (2009); Esechie and Al-Farsi (2009); Nadaf et al. (2010); Radhouane (2013)
Biotic stress	
Downy mildew: 18 resistant progenies (IP 2696); P 310, 472, 1564, 700516, D322/1/-2-2, P1449-3, P 8695-1, 8896-3, 3281; DMRP 292 (IP 18292); Gwagwa; 62 accessions resistant to 2 or more pathotypes	Singh et al. (1988); Singh (1990); Singh and Talukdar (1998); Wilson et al. (2008); Sharma et al. (2015)
Blast: Tift $85D_2B_1$ (*monodii*); landrace 122, 162, 192; Acc. 36, 41, 46, 71; 32 IP acc. (resistant to one or more pathotypes), IP 7846, 11036, 21187 (resistant to four pathotypes)	Hanna et al. (1987); Wilson et al. (1989a); Wilson et al. (1989b); Sharma et al. (2013)
Smut: Selections from germplasm (6); landrace 133, 224, 192; SSC 46-2-2-1, SC 77-7-2-3-1, SC 18-7-3-1	Thakur et al. (1986); Wilson et al. (1989a); Yadav and Duhan (1996)
Ergot: 27 F_6 lines (intermating of 20 acc.); 16 acc.	Thakur et al. (1982); Kumar et al. (1997)
Rust: *monodii* (3 acc.); 2696-1-4; landrace 192; ICML 17, 18, 19, 20, 21 (selected from bulk germplasm); Tift 3, Tift 4 (landrace from Burkina Faso); Tift $89D_2$ (Se Fa); Tift 65 (*monodii*); 7042-1-4-4, IP 8695-4, 700481-27-5	Hanna et al. (1985); Andrews et al. (1985); Wilson et al. (1989a); Singh et al. (1990); Wilson and Burton (1991); Hanna and Wells (1993); Burton and Wilson (1995); Pannu et al. (1996)
Striga: Serere 2A9, 80S224, P2671, P2950; Buduma-Chad; PS 202, 637, 639, 727	Roger and Ramaiah (1983); Gworgwor (2001); Wilson et al. (2004)
Multiple disease resistant**	
DM, ER, RU, BL: Tift #5S1 (Bulk of 114 acc. of *monodii*)	Hanna et al. (1993)
DM, ER, RU: 7 inbreds and 6 bulk populations (Intermating between landraces and pedigree selection)	Thakur et al. (1985)
DM, SM: ICML 5 to 10	Thakur and King (1988)
DM, RU: IP 1481-L-2, P2895-3, IP 8877-3, 700481-5-3; ICML 11 (IP 2696)	Singh (1990); Singh et al. (1987b)
BL, RU: Acc. 122, 162; Tift 86DB/A; Tift 65	Wilson et al. (1989a); Hanna and Wells (1989); Burton and Wilson (1995)
BL, SM: Acc. 192	Wilson et al. (1989a)
SM, RU: Acc. 133, 224	Wilson et al. (1989a)

* Content in bracket indicates derived from the landrace or wild relative.
** DM, downy mildew; ER, ergot; RU, rust; BL, blast; SM, smut.

a serious constraint for pearl millet production in West Africa. Few landraces with less susceptibility and some *monodii* accessions with resistance to *Striga* have been identified (Table 6.4). Shibras have been found to show resistance to *Striga* in the field (Parker and Wilson, 1983).

6.5.4 Seed nutritional quality

Enormous variability has been found in pearl millet germplasm collection for protein (up to 24.3%) among 260 accessions (Singh et al., 1987a) and micronutrient concentrations, namely Fe (51–121 mg/kg) and Zn (46–87 mg/kg) among 191 accessions (Rai et al., 2015).

6.5.5 Source of male sterility

Cytoplasmic male sterility (CMS) sources in pearl millet were identified in populations of crosses involving genetically diverse parents, for example, A_1 (Burton, 1958), A_3 CMS (Athwal, 1966); or derived from diverse germplasm accessions, for example, A_2 (Athwal, 1961) and several unclassified CMS sources (Appa Rao et al., 1989b); or identified from broad-based genepools, for example, A_{egp} CMS in early genepool (Sujata et al., 1994), A_5 CMS in large-seeded genepool (Rai, 1995). CMS sources have also been identified in populations derived from crosses between GP1 wild relative [*P. glaucum* subsp. *monodii* (=*P. violaceum*)] as female parent and cultivated pearl millet as male parent, for example, germplasm accessions from Senegal were identified as source of A_v (Marchais and Pernès, 1985) and A_4 CMS (Hanna, 1989).

6.6 Germplasm regeneration and documentation

Germplasm regeneration is essential to produce uncontaminated and representative seed samples of the original accessions in sufficient quantities for subsequent evaluation, distribution, and conservation. Methods suggested for regeneration of pearl millet germplasm (Burton, 1979) are described next.

6.6.1 Intercrossing

Intermating of 100 or more plants in isolation would help to maintain an accession close to its original form. Limited availability of isolations does not permit this. Hence, manual intercrossing among 100 or more plants of an accession without allowing for outcrossing from other accessions is practiced. Pollination of receptive panicle on each plant with mixture of pollen from an accession is an effective method (Appa Rao, 1999).

6.6.2 Cluster bagging

To regenerate thousands of landraces at ICRISAT, cluster-bagging method is being used to prevent unwanted genetic contamination and avoid hand pollination (Upadhyaya and Gowda, 2009). About 160 plants per accession are grown in four rows. Before stigma emergence, the main stem panicle from two to four adjacent plants in a row is covered in a single parchment paper bag. All the plants of an accession are covered with bags in this fashion. Cross-pollination takes place among the diverse plants covered in a single bag, thereby reducing the inbreeding depression. During harvesting, one such bagged panicle per plant from at least 120 plants per accession is taken and an equal quantity of seeds from each plant is used to reconstitute the accession.

6.6.3 Selfing

Selfing of plants that are used to describe an accession is the most convenient way to obtain large amounts of seed of a new accession (Burton, 1985). At ICRISAT, inbreds and genetic stocks are maintained by selfing (Upadhyaya and Gowda, 2009).

6.6.4 Genepools

Various accessions of similar maturity coming from the same region/country are grown as a mixture of equal quantities of seeds from all accessions in isolation to intermate and seed is harvested from a part or all of the plants. Germplasm pools that are increased each year and contain many accessions offer an easy way to handle germplasm (Burton, 1979). It allows breaking undesirable linkages, resulting in the emergence of new recombinants and improves adaptation. To ensure proper representation of accessions entering the genepools, it is desirable to group accessions based on maturity, specific morphologic characters, and region of origin. Accessions are evaluated and chosen to create trait-specific genepools (TSG). For genetic resource purposes, TSGs are best maintained without any selection pressure to allow for local adaptation. At ICRISAT, TSGs have been developed by random mating (four to six generations) of a large number of germplasm accessions, for example, early genepool (1143 acc.), high tillering genepool (1093), large-grain genepool (887), large-panicle genepool (804); INMG 1 (123 acc.), INMG 2 (208), INMG 3 (73), INMG 4 (51), INMG 5 (69) (Rai et al., 1997; Singh and Jika, 1988).

At ICRISAT, good-quality seed is regenerated for conservation during the post-rainy season with regular monitoring by pathologists to have healthy seeds. Physiologically mature seeds are harvested, seed moisture brought down to 5–7% by drying in cool and dry atmospheres, or in the drying cabinets at 18°C and 16% RH. For pearl millet, the recommended sample size per accession in a base collection is 12,000 seeds, with a minimum of 3,000 seeds (IBPGR, 1985). At ICRISAT, about 12,000 seeds of pearl millet are used for long-term conservation and stored in hermetically sealed containers to maintain low seed moisture content with a view to control humidity. Prior to conservation, seed viability is recorded initially for

all accessions and also randomly monitored during storage by drawing samples at regular intervals of 6 months for their germinability. Accessions that show <85% viability or below critical quantity of 50 g are routinely regenerated. Proper documentation allows rapid accessioning of new samples, answer queries on the conserved germplasm, and monitor quality and quantity of stored material to carry out regeneration and distribution. Hence, a computerized data handling system is ideal for a genebank.

6.7 Gap analyses of germplasm

Identifying the gaps in germplasm collections of genebanks helps to plan for collecting landraces that are not represented in genebanks. Toward this at ICRISAT, gap analyses of cultivated pearl millet germplasm from different geographical regions like west and central Africa (WCA), Asia, and east and southern Africa (ESA) and also for wild relatives like *P. glaucum* ssp. *monodii* and *P. pedicellatum* (Deenanath grass) were made to identify the missing diversity in germplasm assembled in its genebank (Upadhyaya et al., 2009b, 2010, 2012, 2014a, 2014b). The WCA region, being the center of diversity for pearl millet, has germplasm sources for resistance to biotic and abiotic stresses. Gap analysis using passport and characterization data and geographical information system tools could identify gaps in cultivated germplasm in the provinces of Chad, Ghana, Nigeria, Burkina Faso, Mali, and Mauritania in WCA; provinces of India and Pakistan in Asia; provinces of Sudan, Uganda, and seven countries in southern Africa. Similarly, gaps were identified in 86 provinces of 8 countries in the primary center of origin for *P. glaucum* subsp. *monodii*, while 194 provinces in 21 countries of Asia and Africa for *P. pedicellatum*. This information would be helpful in assembling poorly represented or totally missing germplasm from these regions of diversity to avoid genetic erosion and ensure their conservation and utilization in crop improvement.

6.8 Limitations in germplasm use

The use of available genetic resources in crop improvement is the most neglected part of germplasm conservation (de Wet, 1989). A very large gap exists between actual utilization of the germplasm and availability of collection in the genebanks (Wright, 1997; Upadhyaya et al., 2006). Germplasm resources would not be used if the information needed by crop improvement scientists is not readily available. Extensive use of fewer and closely related parents and their derivatives in crop improvement is contrary to the very purpose of establishing large germplasm collections. Representative subsets, in the form of core collection (Frankel, 1984) or minicore collection (Upadhyaya and Ortiz, 2001), has been suggested as an entry point for germplasm utilization in crop breeding. Core and minicore collections (Upadhyaya et al., 2009a, 2011) and reference sets (Upadhyaya, 2009) are now available in

pearl millet. Evaluation of core collection has led to the identification of new sources of variation for grain and fodder traits (Khairwal et al., 2007), while evaluation of minicore collection led to identification of sources of resistance to blast and downy mildew (Sharma et al., 2013, 2015). More targeted evaluation of these subsets for morphoagronomic traits, resistance to various abiotic and biotic stresses, and their molecular profiling will lead to mining of allelic variation associated with agronomically beneficial traits.

6.9 Germplasm uses in pearl millet improvement

6.9.1 Cultivated germplasm

The greatest achievement is conserving the vanishing pearl millet germplasm and making it available for crop improvement. At ICRISAT, to enhance the utilization of pearl millet germplasm, core and minicore collections and reference sets have been developed (Bhattacharjee et al., 2007; Upadhyaya et al., 2009a, 2011; Upadhyaya, 2009), which would allow their extensive evaluation for identification of trait-specific germplasm and widely adaptable accessions across locations. Trait-specific genepools have been developed earlier for early maturity, high tillering, large panicle, and large grain to provide breeders with useful variability for utilization. Recently, a *Striga*-resistant genepool was developed by recurrent selection (Kountche et al., 2013).

In general, Indian pearl millet landraces have earliness, high tillering, high harvest index, and local adaptation, whereas African landraces are good sources of high head volume, large seed size, and disease resistance. Significant progress has been made with regard to utilization of germplasm in pearl millet improvement. Early maturing accessions like IP 4021 and IP 3122 were supplied most frequently. Pearl millet germplasm has been widely used in developing composites, which include a wide range of germplasm and improved breeding lines. The *Iniadi* germplasm from the Togo–Ghana–Burkina Faso–Benin regions of western Africa is most commonly used in pearl millet breeding programs worldwide (Andrews and Anand Kumar, 1996). The most successful example of the use of pearl millet landraces is ICTP 8203, a large-seeded and high-yielding open-pollinated variety bred at ICRISAT, Patancheru as a selection within the large-seeded *Iniadi* landrace (IP 17862) from northern Togo (Rai et al., 1990). This variety was released in India as MP 124 in Maharashtra and Andhra Pradesh and as PCB 138 in Punjab, while as Okashana 1 in Namibia and as Nyankhombo [ICMV 88908] in Malawi.

Direct selection within the landrace has led to the development of a large-seeded and downy mildew resistant male sterile line ICMA 88004 in India (Rai et al., 1995); varieties IKMP 3 (IP 11381) and IKMP 5 (IP 11317) in Burkina Faso; open-pollinated variety ICMV-IS 88102 (IP 6426) in Burkina Faso, while as Benkadi Nio in Mali; IP 6104 and IP 19586 released in Mexico as high forage yielding varieties. Some varieties were developed by crosses involving at least one of the parents as landrace, for example, Okashana 2 and Kangara (SDMV 92040) varieties

in Namibia and PMV 3 in Zimbabwe (Obilana et al., 1997). ICRISAT has contributed genetic material to public and private institutions, which has helped in breeding high-yielding varieties/hybrids with resistance to biotic and abiotic factors. Using pearl millet germplasm from ICRISAT, a large number of varieties/hybrids have been released by NARS across the world (163) including India (80) as of December 2010 (Anonymous, 2011).

Donor parents like 863B (IP 22303), P 1449-2 (IP 21168), ICMB 90111 (IP 22319), ICMP 451 (IP 22442), and IP 18293 were identified as sources of gene for resistance against different pathotypes of downy mildew in India (Upadhyaya et al., 2007). Several promising germplasm accessions have been identified for resistance to downy mildew (IP #9645, 14537, 18292), blast (IP 7846), smut and heat tolerance (IP #19799, 19843, 19877), multiple disease resistance (IP #21268, 21296), salinity tolerance (IP #3732, 3757, 22269), high Fe and/or Zn content (IP #9198, 11535, 12364, 17672), and yellow endosperm with high beta-carotene content (IP #15533, 15536) in seed. Germplasm with earliness, resistance to abiotic and biotic stresses, new dwarfing genes, high iron and zinc, sweet stalk, yellow endosperm, and so on, are widely used in crop improvement programs in different countries. Several new and useful traits, such as narrow leaf, glossy leaf, brown midrib leaf, and leaf color variants, have been used extensively in academic studies.

6.9.2 Wild relatives

There has been a general lack of interest in using wild species because of the large amount of genetic variability already available in pearl millet landraces. However, *P. glaucum* ssp. *monodii* for new source of cytoplasmic-nuclear male sterility (CMS), *P. purpureum* for forage, stiff stalk and restorer genes of the A_1 CMS system, *P. mezianum* for drought tolerance, *Pennisetum orientale* for drought tolerance and forage, *P. schweinfurthii* for large seeds, *P. pedicellatum* and *P. polystachion* for downy mildew resistance, and *P. squamulatum* for apomictic gene are useful (Rai et al., 1997).

Intersubspecific, interspecific, and intergeneric hybridization have been attempted to expand the cultigen genepool in pearl millet (Table 6.5). Intersubspecific crosses involving ssp. *glaucum* (cultivated), *monodii* (wild relative), and *stenostachyum* (weedy relative) have been successful in transferring desirable traits like rust resistance, male sterility, and alleles for enhancing yield components from GP1 to pearl millet. Interspecific hybridization between *P. glaucum* and *P. purpureum* has led to development of forage hybrids with high biomass and better quality (Table 6.5). The A′ genome from *P. purpureum* contributes excellent genetic variability for inflorescence and plant types, maturity, and fertility restoration of the sterile cytoplasm, which has been transferred to pearl millet (Hanna, 1983, 1990). *P. squamulatum* has desirable traits like perenniality, apomixis, disease resistance, tolerance to drought and frost, and so on, which could be transferred to pearl millet. Crosses between members of GP1 with GP3 showed incompatibility at pollen germination or at stylar or ovarian level, but in some cases, hybrids could be recovered through embryo rescue but often showing male sterility (Table 6.5). Efforts of intergeneric hybridiza-

Table 6.5 Attempts of wide crosses involving *Pennisetum* spp.

Crosses	Details	References
Intersubspecific/interspecific		
Within GP1		
*P. glaucum** × *P. glaucum* ssp. *monodii*	Normal pollen germination and growth in stigmatic tract	Kaushal and Sidhu (2000)
	Transferred rust resistance and thermosensitive genetic male sterility	Hanna et al. (1985), Kaushal et al. (2004)
	Frequency of natural hybrids decreased up to 11% at maturity	Couturon et al. (2003)
P. glaucum ssp. *monodii* × *P. glaucum*	Transferred cytoplasmic male sterility	Marchais and Pernès (1985), Hanna (1989), Rai et al. (1996)
P. glaucum × *P. mollissimum*	Inheritance of domestication traits studied; Transgressive segregants obtained for panicle length and width	Poncet et al., 1998, 2000
P. glaucum × *P. stenostachyum*	Some introgression from wild to weedy population, but very low gene flow between wild and domesticated populations	Mariac et al. (2006b)
Between GP1 and GP2		
P. glaucum × *P. purpureum*	Homeology between A and A′ genome confirmed based on meiotic studies and genomic *in situ* hybridization	Jauhar (1981b), Jauhar and Hanna (1998), dos Reis et al. (2014)
	High frequency of meiotic abnormalities in F_1's resulting in sterile pollen	Techio et al. (2006)
	Hybrids with improved forage potential and quality produced	Hanna et al. (1984), Obok et al. (2012), Obok (2013), Kannan et al. (2013)
	Genes controlling earliness, long inflorescence, leaf size, and male fertility restoration transferred from *P. purpureum*	Hanna (1983)
P. glaucum (2*x*/4*x*) × *P. squamulatum*	Recovered partially fertile hybrids	Dujardin and Hanna (1983, 1989a), Marchais and Tostain (1997)
	Transfer of gene/s controlling apomixis through crosses and backcrosses	Dujardin and Hanna (1985)
(*P. glaucum* × *P. squamulatum*) × (*P. glaucum* × *P. purpureum*)	Double cross hybrid used to transfer apomixis from *P. squamulatum* into a backcross derivative	Dujardin and Hanna (1989b)

(Continued)

Table 6.5 Attempts of wide crosses involving *Pennisetum* spp. *(cont.)*

Crosses	Details	References
Between GP1 and GP3		
P. glaucum/*P. glaucum ssp. monodii** × *P. orientale*/*P. setaceum*/*P. schweinfurthii*/*Pennisetum ramosum*/*P. pedicellatum*/*P. polystachyon*	Incompatibility observed at pollen germination, pollen tube growth or fertilization level	Kaushal and Sidhu (2000), Chaix and Marchais (1996)
P. glaucum × *P. schweinfurthii*/*P. ramosum*	Hybrids recovered by embryo rescue but normally male sterile and partially female fertile	Marchais and Tostain (1997), Nagesh and Subrahmanyam (1996)
P. glaucum × *P. mezianum*	Hybrids recovered by embryo rescue/ embryo cloning and showed low pollen fertility	Nagesh and Subrahmanyam (1996), Marchais and Tostain (1997)
P. glaucum × *P. macrourum*	Failed to get any hybrid although germinating pollen abundant on stigma	Dujardin and Hanna (1989a)
P. glaucum (2*x*/4*x*) × *P. ramosum*	Embryo rescue could recover hybrids only from tetraploid crosses	Nagesh and Subrahmanyam (1996), Marchais and Tostain (1997)
P. glaucum × *P. orientale*	Partial homology between the genomes	Jauhar (1981b)
	Male fertility of F_1 restored by chromosome doubling	Dujardin and Hanna (1987)
	Embryo rescue used to obtain hybrids	Nagesh and Subrahmanyam (1996)
	Backcrossing resulted in hybrids with varying chromosome numbers	Hanna and Dujardin (1982), Dujardin and Hanna (1989b)
P. glaucum × *P. setaceum*	Obligate apomictic interspecific hybrids recovered but did not allow further progress	Dujardin and Hanna (1989a)
P. glaucum × *P. pedicellatum*/*P. polystachyon*	Miniature hybrid seeds formed that failed to germinate; embryo culture might be useful for recovering hybrids	Dujardin and Hanna (1989a)
P. glaucum × *P. dubium*	Single hybrid obtained but no homology between parental genomes	Gildenhuys and Brix (1961)
P. glaucum × *P. cenchroides*	Incompatibility for pollen tube growth in stylar region	Mohindra and Minocha (1991)
	High frequency of proembryos with large undifferentiated endosperm; hybrid obtained was completely sterile	Read and Bashaw (1974), Chaix and Marchais (1996); Marchais and Tostain (1997)

Table 6.5 Attempts of wide crosses involving *Pennisetum* spp. *(cont.)*

Crosses	Details	References
Within GP3		
Cenchrus ciliaris × *P. orientale*	Hybrid with excellent forage potential	Hussey et al. (1993)
P. flaccidum × *P. mezianum*	Hybrids of (2*n* + *n*) type were more winter hardy and produced more forage than (*n* + *n*) type	Burson and Hussey (1996)
Between GP2 and GP3		
P. purpureum × *P. squamulatum*/*P. schweinfurthii*/*P. ramosum*/*P. pedicellatum*/*P. polystachyon*	Incompatibility at pollen germination, pollen tube growth or fertilization level	Chaix and Marchais (1996)
P. schweinfurthii × *P. purpureum*	Hybrid obtained due to fertilization between unreduced (2*n*) and normal (*n*) gamete	Vidhya and Fazlullah Khan (2003)
Intergeneric		
P. glaucum × *Panicum maximum*/*Zea mays*	Low compatibility and pollen tubes arrested in the style	Chaix and Marchais (1996)
Oryza sativa × *P. orientale*	Hybrid recovered were regenerated vegetatively and completely sterile	Wu and Tsai (1963)
Triticum aestivum × *P. glaucum*	Hybrid embryos produced haploid wheat due to elimination of pearl millet chromosomes	Laurie (1989), Gernand et al. (2005)
Hordeum vulgare × *P. glaucum*	Globular embryos obtained	Zenkteler and Nitzsche (1984)
Avena sativa × *P. glaucum*	Hybrids obtained at low frequency but pearl millet chromosomes lost in embryo or plant	Matzk (1996)
P. glaucum × *Zea mays*/*Triticale*/*Sorghum bicolor*	Haploid induction rate (HIR) varied in crosses	Gugsa et al. (2013)

* *Pennisetum glaucum* syn. *Pennisetum typhoides*/*Pennisetum americanum*; *P. glaucum* ssp. *monodii* syn. *P. violaceum*; *Cenchrus ciliaris* syn. *P. cenchroides*; 2*x*, diploid; 4*x*, tetraploid.

tion and somatic hybridization have shown little success. Concerted efforts need to be made for utilization of GP2 and GP3 species through the development of wide crosses by utilizing special techniques and generation of prebreeding populations for use by breeders.

6.9.3 Chromosome segment substitution lines

Development of chromosome segment substitution lines (CSSLs), originating from crosses between cultivated and wild types, will be a most useful resource as each of these lines will have different genomic regions from wild germplasm introgressed in cultivated genotypic background. Characterization of these populations for different traits and genotyping helps in exploitation of useful alleles found in wild germplasm. CSSLs based on crosses between cultivated pearl millet and its wild relatives are not yet available. However, at ICRISAT, a set of CSSLs (1492) based on a cross between two agronomically elite parental lines differing for several important agronomic traits have been developed (Ramana Kumari et al., 2014). CSSLs will be an ideal set of genetic stocks for mapping and fine-mapping the multitude of traits for which their parents differ.

6.10 Genomic resources in management and utilization of germplasm

Pearl millet has a genome of ~2350 Mb (Bennett et al., 2000) and haploid genome content of 1C*x* = 2.36 pg (Martel et al., 1997). Genomic resources like molecular markers, genetic linkage maps, and genes associated with specific traits developed in pearl millet using diverse genetic material and their utilization for assessing diversity or population structure and genetic mapping have been summarized by Dwivedi et al. (2012). Toward utilization of molecular markers in management and utilization of germplasm, they have been employed for assessing diversity among and within pearl millet landraces. Genetic diversity analysis of representative accessions of Indian origin (10) from core collection (504 accessions) using highly polymorphic RFLP probes (16) revealed high variability within-accession (30.9%) and also between accessions (69.1%) (Bhattacharjee et al., 2002). Landraces from western and eastern Rajasthan revealed higher variation within landrace population than between regional samples as assessed by AFLP markers (Vom Brocke et al., 2003). Genetic diversity assessed among wild (46) and cultivated (421) pearl millet accessions from Niger using microsatellites (25) revealed lower number of alleles and lower gene diversity in cultivated than wild accessions and a strong differentiation between cultivated and wild groups (Mariac et al., 2006a). Similarly, wild (84) and cultivated (355) accessions originating from the whole pearl millet distribution area in Africa and Asia analyzed by microsatellite loci (27) revealed higher diversity in the wild pearl millet group (Oumar et al., 2008). The cultivated pearl millet sample possessed 81% of the alleles and 83% of the genetic diversity of the wild pearl millet sample.

Next-generation sequencing (NGS) technologies offer efficient and cost-effective sequencing of a large number of samples for organisms, which provide opportunity to relate sequence differences with phenotypes of diverse accessions in comparison with decoded reference genome. The role of NGS technologies to enhance efficiency of different genebank activities need to be established. For collection management, NGS technologies could be useful to basically support all management areas (Van Treuren and Van Hintum, 2014). For example, DNA sequence data of genebank ac-

cessions may be used to determine the genetic structure of collections and to improve the composition thereof by eliminating redundancies (Van Treuren et al., 2009). Ample sequence data of the existing collection allows genebank curators to take more informed decisions about acquisition by evaluating potentially interesting materials for their added value to the genetic diversity already present in the collection (Van Treuren et al., 2008). One can consider removal of accessions that contribute least to the genetic diversity of the collection (Van Treuren et al., 2009). NGS data could also be used to monitor the regeneration of accessions in order to ensure the maintenance of genetic integrity thereof, for example, by comparing sequence data of samples before and after regeneration (Van Hintum et al., 2007).

6.11 Conclusions

Pearl millet is gaining importance as a climate-resilient and health-promoting nutritious crop. Recent evidences using microsatellites suggest the monophyletic origin of pearl millet and its further migration and secondary diversification leading to enormous diversity. Genetic erosion of landraces has been evident in different pearl millet growing regions due to replacement with modern cultivars. Large variability found in pearl millet germplasm has been conserved in several genebanks. Toward enhancing the utilization of pearl millet germplasm, available subsets like core and minicore collections and reference sets should be extensively evaluated to identify trait-specific germplasm and also develop genomic resources to associate sequence differences with trait variations. Although transfer of desirable traits from primary wild relatives has been successful, concerted efforts are needed to broaden cultivated genepool by utilizing secondary and tertiary genepool toward developing climate-resilient cultivars. Development of genomic resources is expected to rise as the genome sequence of pearl millet is due for release and also due to faster developments in NGS technologies that could be efficiently utilized for management and utilization of pearl millet germplasm and in turn for crop improvement.

References

AICPMIP, 2014. Project Coordinator's Review. Available from: www.aicpmip.res.in/pcr2014.pdf

Ali, G.M., Khan, N.M., Hazara, R., McNeilly, T., 2004. Variability in the response of pearl millet (*Pennisetum americanum* (L.) Leeke) accessions to salinity. Acta Agron. Hung. 52, 277–286.

Andrews, D.J., Anand Kumar, K., 1996. Use of the West African pearl millet landrace *Iniadi* in cultivar development. Plant Genet. Resour. Newsl. 105, 15–22.

Andrews, D.J., Rai, K.N., Singh, S.D., 1985. A single dominant gene for rust resistance in pearl millet. Crop Sci. 25 (3), 565–566.

Anonymous, 2011. Available from: http://www.thehindubusinessline.com/industry-and-economy/agri-biz/icrisat-germplasm-crops-contributing-to-global-food-security-nars-report/article2047506.ece

Appa Rao, S., 1999. Genetic Resources. In: Khairwal, I.S., Rai, K.N., Andrews, D.J., Harinarayana, G. (Eds.), Pearl Millet Breeding. Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi, pp. 49–81.

Appa Rao, S., de Wet, J.M.J., 1999. Taxonomy and Evolution. In: Khairwal, I.S., Rai, K.N., Andrews, D.J., Harinarayana, G. (Eds.), Pearl Millet Breeding. Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi, pp. 29–47.

Appa Rao, S., House, L.R., Gupta, S.C., 1989a. A Review of Sorghum, Pearl Millet and Finger Millet Improvement in SADCC Countries. SADCC/ICRISAT, Bulawayo, Zimbabwe.

Appa Rao, S., Mengesha, M.H., Rajagopal Reddy, C., 1989b. Development of cytoplasmic male-sterile lines of pearl millet from Ghana and Botswana germplasm. In: Manna, G.K., Sinha, U. (Eds.), Perspectives in Cytology and Genetics. Kalyani Publishers, India, pp. 817–823.

Appa Rao, S., Murked, A.W., Mengesha, M.H., Amer, H.M., Reddy, K.N., Alsurai, A., et al., 1993. Collecting crop germplasm in Yemen. Plant Genet. Resour. Newsl. 94/95, 28–31.

Appa Rao, S., Mengesha, M.H., Nwasike, C., Ajayi, O., Olabanji, O.G., Aba, D., 1994. Collecting crop germplasm in Nigeria. Plant Genet. Resour. Newsl. 97, 63–66.

Ashraf, M., McNeilly, T.M., 1992. The potential for exploiting variation in salinity tolerance in pearl millet (*Pennisetum americanum* (L.) Leeke). J. Plant Breed. 108 (3), 234–240.

Athwal, D.S., 1961. Recent developments in the breeding and improvement of bajra (pearl millet) in the Punjab. Madras Agric. J. 48, 18–19.

Athwal, D.S., 1966. Current plant breeding research with special reference to *Pennisetum*. Indian J. Genet. Plant Breed. 26A, 73–85.

Basavaraj, G., Parthasarathy Rao, P., Bhagavatula, S., Ahmed, W., 2010. Availability and utilization of pearl millet in India. J. SAT Agric. Res. 8, 1–6.

Bennett, M.D., Bhandol, P., Leitch, I.J., 2000. Nuclear DNA amounts in angiosperms and their modern uses-807 new estimates. Ann. Bot. 86, 859–909.

Bezançon, G., Pham, J.-L., Deu, M., Vigouroux, Y., Sagnard, F., Mariac, C., et al., 2009. Changes in the diversity and geographic distribution of cultivated millet (*Pennisetum glaucum* (L.) R. Br.) and sorghum (*Sorghum bicolor* (L.) Moench) varieties in Niger between 1976 and 2003. Genet. Resour. Crop Evol. 56, 223–236.

Bhattacharjee, R., Bramel, J., Hash, T., Kolesnikova-Allen, A., Khairwal, S., 2002. Assessment of genetic diversity within and between pearl millet landraces. Theor. Appl. Genet. 105 (5), 666–673.

Bhattacharjee, R., Khairwal, I.S., Bramel, P.J., Reddy, K.N., 2007. Establishment of a pearl millet [*Pennisetum glaucum* (L.) R. Br.] core collection based on geographical distribution and quantitative traits. Euphytica 155 (1–2), 35–45.

Brunken, J.N., 1977. A systematic study of *Pennisetum* sect. *Pennisetum* (Gramineae). Am. J. Bot. 64 (2), 161–176.

Brunken, J.N., de Wet, J.M.J., Harlan, J.R., 1977. The morphology and domestication of pearl millet. Econ. Bot. 31, 163–174.

Burson, B.L., Hussey, M.A., 1996. Breeding apomictic forage grasses. In: Williams, M.J. (Ed.), Proceedings of the American Forage and Grassland Council, Vancouver BC, Canada, June 13–15, AFGC, Georgetown, TX, pp. 226–230.

Burton, G.W., 1958. Cytoplasmic male sterility in pearl millet (*Pennisetum glaucum*) (L.) R. Br. Agron. J. 50, 230–231.

Burton, G.W., 1979. Handling cross-pollinated germplasm efficiently. Crop Sci. 19, 685–690.

Burton, G.W., 1985. Collection, evaluation and storage of pearl millet germplasm. Field Crops Res. 11, 123–129.

Burton, G.W., Wilson, J.P., 1995. Registration of Tift 65 parental inbred line of pearl millet. Crop Sci. 35 (4), 1244.

Chaix, G., Marchais, L., 1996. Diversity of Pennicillarian millets (*Pennisetum glaucum* and *P. purpureum*) as for the compatibility between their gynoecia and pollens from some other Poaceae. Euphytica 88, 97–106.

Chemisquy, M.A., Giussani, L.M., Scataglini, M.A., Kellogg, E.A., Morrone, O., 2010. Phylogenetic studies favour the unification of *Pennisetum*, *Cenchrus* and *Odontelytrum* (Poaceae): a combined nuclear, plastid and morphological analysis, and nomenclatural combinations in *Cenchrus*. Ann. Bot. 106 (1), 107–130.

Chowdhury, M.K.V., Smith, R.L., 1988. Mitochondrial DNA variation in pearl millet and related species. Theor. Appl. Genet. 76, 25–32.

Clayton, W.D., Renvoize, S.A., 1986. Genera Graminum, Grasses of the World, Kew Bulletin. Her Majesty's Stationery Office, London, p. 389, Additional Series XIII.

Clayton, W.D., Harman, K.T., Williamson, H., 2006. GrassBase – The Online World Grass Flora. Available from: http://www.kew.org/data/grasses-db.html

Clegg, M.T., Rawson, J.R.Y., Thomas, K., 1984. Chloroplast DNA variation in pearl millet and related species. Genetics 106, 449–461.

Couturon, E., Mariac, C., Bezançon, G., Lauga, J., Renno, J.F., 2003. Impact of natural and human selection on the frequency of the F_1 hybrid between cultivated and wild pearl millet (*Pennisetum glaucum* (L.) R. Br.). Euphytica 133, 329–337.

D'Andrea, A.C., Casey, J., 2002. Pearl millet and Kintampo subsistence. Afr. Arachaeol. Rev. 19, 147–173.

de Wet, J.M.J., 1989. Cereals for the semi-arid tropics. In: Plant Domestication by Induced Mutation. Proceedings of an Advisory group meeting on the possible use of mutation breeding for rapid domestication of new crop plants. Joint FAO/IAEA Division of Nuclear techniques in Food and Agriculture, 17–21 Nov. 1986, Vienna, p. 79–88.

DeVries, J., Toenniessen, G., 2001. Securing the Harvest: Biotechnology, Breeding and Seed Systems for African Crops. CAB International, Wallingford.

Donadio, S., Giussani, L.M., Kellogg, E.A., Zuloaga, F.O., Morrone, O., 2009. A preliminary molecular phylogeny of *Pennisetum* and *Cenchrus* (Poaceae-Paniceae) based on the *trnL-F*, *rpl16* chloroplast markers. Taxonomy 58, 392–404.

dos Reis, G.B., Mesquita, A.T., Torres, G.A., Andrade-Vieira, L.F., Pereira, A.V., Davide, L.C., 2014. Genomic homeology between *Pennisetum purpureum* and *Pennisetum glaucum* (Poaceae). Comp. Cytogenet. 8 (3), 199–209.

Doust, A.N., Penly, A.M., Jacobs, S.W.L., Kellogg, E.A., 2007. Congruence, conflict, and polyploidization shown by nuclear and chloroplast markers in the monophyletic "bristle clade" (Paniceae, Panicoideae, Poaceae). Syst. Bot. 32, 531–544.

Dujardin, M., Hanna, W.W., 1983. Apomictic and sexual pearl millet × *Pennisetum squamulatum* hybrids. J. Hered. 74, 277–279.

Dujardin, M., Hanna, W.W., 1985. Cytology and reproductive behavior of pearl millet – Napier grass hexaploids × *Pennisetum squamulatum* trispecific hybrids. J. Hered. 76, 382–384.

Dujardin, M., Hanna, W.W., 1987. Inducing male fertility in crosses between pearl millet and *Pennisetum orientale* Rich. Crop Sci. 27, 65–68.

Dujardin, M., Hanna, W.W., 1989a. Crossability of pearl millet with wild *Pennisetum* species. Crop Sci. 29 (1), 77–80.

Dujardin, M., Hanna, W.W., 1989b. Developing apomictic pearl millet – characterization of a BC_3 plant. J. Genet. Breed. 43, 145–149.

Dwivedi, S., Upadhyaya, H., Senthilvel, S., Hash, C., Fukunaga, K., Diao, X., et al., 2012. Millets: genetic and genomic resources. In: Janick, J. (Ed.), Plant Breeding Reviews, vol. 35, John Wiley & Sons, USA, pp. 247–375.

Esechie, H.A., Al-Farsi, S.M., 2009. Performance of elite pearl millet genotypes under salinity stress in Oman. Crop Res. (Hisar) 37 (1/3), 28–33.

Frankel, O.H., 1984. Genetic perspectives of germplasm conservation. In: Arber, W., Llimensee, K., Peacock, W.J., Starlinger, P. (Eds.), Genetic Manipulation: Impact on Man and Society. Cambridge University Press, Cambridge, Part III, Paper No. 15.

Fussell, L.K., Pearson, C.J., Norman, M.J.T., 1980. Effect of temperature during various growth stages on grain development and yield of *Pennisetum americanum*. J. Exp. Bot. 31 (121), 621–633.

Gemenet, D.C., Hash, C.T., Sanogo, M.D., Sy, O., Zangre, R.G., Leiser, W.L., et al., 2015. Phosphorus uptake and utilization efficiency in West African pearl millet inbred lines. Field Crops Res. 171, 54–66.

Gernand, D., Rutten, T., Varshney, A., Rubtsova, M., Prodanovic, S., Bru, C., et al., 2005. Uniparental chromosome elimination at mitosis and interphase in wheat and pearl millet crosses involves micronucleus formation, progressive heterochromatinization, and DNA fragmentation. Plant Cell 17, 2431–2438.

Gildenhuys, P., Brix, K., 1961. Cytogenetic evidence of relationship between the $x = 7$ and $x = 9$ groups of *Pennisetum* species. Zuchter 31, 125–127.

Girgi, M., O'Kennedy, M., 2007. Pearl millet. Transgenic crops. Biotechnol. Agric. Forest. 59, 119–127.

Goel, S., Chen, Z., Akiyama, Y., Conner, J.A., Basu, M., Gualtieri, G., et al., 2006. Comparative physical mapping of the apospory-specific genomic region in two apomictic grasses: *Pennisetum squamulatum* and *Cenchrus ciliaris*. Genetics 173 (1), 389–400.

Gugsa, L., Haussmann, B.I.G., Kumlehn, J., Melchinger, A., 2013. Towards a protocol for double haploid production in pearl millet using wide hybridisation. In: Agricultural development within the rural-urban continuum, Tropentag, Stuttgart-Hohenheim, September 17–19, p. 1.

Gupta, S.K., Rai, K.N., Singh, P., Ameta, V.L., Gupta, S.K., Jayalekha, A.K., et al., 2015. Seed set variability under high temperatures during flowering period in pearl millet (*Pennisetum glaucum* (L.) R. Br.). Field Crops Res. 171, 41–53.

Gworgwor, N.A., 2001. Evaluation of pearl millet varieties for resistance to *Striga hermonthica*. Int. Sorghum Millets Newsl. 42, 85–87.

Hanna, W.W., 1983. Germplasm transfer from *P. purpureum* to *P. americanum*. Agronomy Abstracts. ASA, Madison, WI, p. 66.

Hanna, W.W., 1987. Utilization of wild relatives of pearl millet. In: Proceedings of the International Pearl Millet Workshop, April 7–11, 1986, ICRISAT, pp. 33–42.

Hanna, W.W., 1989. Characteristics and stability of a new cytoplasmic-nuclear male sterile source in pearl millet. Crop Sci. 29, 1457–1459.

Hanna, W.W., 1990. Transfer of germplasm from the secondary to the primary gene pool in *Pennisetum*. Theor. Appl. Genet. 80, 200–204.

Hanna, W.W., Dujardin, M., 1982. Apomictic interspecific hybrids between pearl millet and *Pennisetum orientale* L.C. Rich. Crop Sci. 22, 857–859.

Hanna, W.W., Wells, H.D., 1989. Inheritance of *Pyricularia* leaf spot resistance in pearl millet. J. Hered. 80 (2), 145–147.

Hanna, W.W., Wells, H.D., 1993. Registration of parental line Tift $89D_2$, rust resistant pearl millet. Crop Sci. 33 (2), 361–362.

Hanna, W.W., Gaines, T.P., Gonzalez, B., Monson, W.G., 1984. Effect of ploidy on yield and quality of pearl millet × napiergrass hybrids. Agron. J. 76 (6), 969–971.

Hanna, W.W., Wells, H.D., Burton, G.W., 1985. Dominant gene for rust resistance in pearl millet. J. Hered. 76, 134.

Hanna, W.W., Wells, H.D., Burton, G.W., 1987. Registration of pearl millet inbred parental lines, Tift $85D_2A_1$ and Tift $85D_2B_1$. Crop Sci. 27 (6), 1324–1325.

Hanna, W.W., Wilson, J.P., Wells, H.D., Gupta, S.C., 1993. Registration of Tift #5 S-1 pearl millet germplasm. Crop Sci. 33 (6), 1417–1418.

Harlan, J.R., 1975. Crops and Man. American Society of Agronomy – Crop Science Society of America, Madison, WI, USA.

Harlan, J.R., de Wet, J.M.J., 1971. Toward a rational classification of cultivated plants. Taxonomy 20, 509–517.

Howarth, C.J., Pollock, C.J., Peacock, J.M., 1997. Development of laboratory-based methods for assessing seedling thermotolerance in pearl millet. New Phytol. 137 (1), 129–139.

Hussey, M.A., Bashaw, E.C., Hignight, K.W., Wipff, J., Hatch, S.L., 1993. Fertilisation of unreduced female gametes: a technique for genetic enhancement within the *Cenchrus*–*Pennisetum* agamic complex. In: Baker, M.J., et al. (Eds.), Proceedings of the Seventeenth International Grassland Congress, Palmerston North, New Zealand, February 8–21, pp. 404–405.

IBPGR, 1985. Documentation of genetic resources: information handling systems for genebank management. In: Konopka, J., Hanson, J. (Eds.), Proceedings of a Workshop at the Nordic Gene Bank, Alnarp, Sweden, November 21–23, 1984, p. 87.

IBPGR and ICRISAT, 1993. Descriptors for Pearl Millet [*Pennisetum glaucum* (L.) R. Br.]. IBPGR/ICRISAT, Rome.

Ingham, L.D., Hanna, W.W., Baier, J.W., Hannah, L.C., 1993. Origin of the main class of repetitive DNA within selected *Pennisetum* species. Mol. Genet. 238, 350–358.

Jauhar, P.P., 1981a. Cytogenetics and Breeding of Pearl Millet and Related Species. Alan R. Liss, New York, p. 91.

Jauhar, P.P., 1981b. Cytogenetics of pearl millet. Adv. Agron. 34, 407–470.

Jauhar, P.P., Hanna, W.W., 1998. Cytogenetics and genetics of pearl millet. Adv. Agron. 64, 1–26.

Jauhar, P.P., Rai, K.D., Ozias-Akins, P., Chen, Z., Hanna, W.W., 2006. Genetic improvement of pearl millet for grain and forage production: cytogenetic manipulation and heterosis breeding. In: Singh, R.J., Jauhar, P.P. (Eds.), Genetic Resources, Chromosome Engineering, and Crop Improvement, vol. 2, Cereals. CRC, Taylor & Francis, Boca Raton, FL, pp. 281–307.

Kafi, M., Zamani, G., Ghoraishi, S.G., 2009. Relative salt tolerance of south Khorasan millets. Desert 14 (1), 63–70.

Kannan, B., Valencia, E., Altpeter F., 2013. Interspecific hybridization between elephantgrass and pearl millet and selection of hybrids with high-biomass production and enhanced biosafety. International Annual Meetings: Water, Food, Energy & Innovation for a Sustainable World. American Society of America (ASA), Crop Science Society of America (CSSA) and Soil Science Society of America (SSSA), Tampa, Florida, pp. 165.

Kapila, R.K., Yadav, R.S., Plaha, P., Rai, K.N., Yadav, O.P., Hash, C.T., et al., 2008. Genetic diversity among pearl millet maintainers using microsatellite markers. Plant Breed. 127, 33–37.

Kaushal, P., Sidhu, J.S., 2000. Pre-fertilization incompatibility barriers to interspecific hybridizations in *Pennisetum* species. J. Agric. Sci. 134, 199–206.

Kaushal, P., Roy, A.K., Zadoo, S.N., Choubey, R.N., 2004. Cytogenetic analysis of thermosensitive genic male sterility (TGMS) recovered from *Pennisetum glaucum* (L.) R. Br. × *P. violaceum* (Lam.) Rich cross. Cytologia 69, 409–418.

Kaushal, P., Khare, A., Zadoo, S.N., Roy, A.K., Malaviya, D.R., Agrawal, A., et al., 2008. Sequential reduction of *Pennisetum squamulatum* genome complement in *P. glaucum* ($2n = 28$) × *P. squamulatum* ($2n = 56$) hybrids and their progenies revealed its octoploid status. Cytologia 73 (2), 151–158.

Khairwal, I.S., Yadav, S.K., Rai, K.N., Upadhyaya, H.D., Kachhawa, D., Nirwan, B., et al., 2007. Evaluation and identification of promising pearl millet germplasm for grain and fodder traits. J. SAT Agric. Res. 5 (1), 1–6.

Kountche, B.A., Hash, C.T., Dodo, H., Laoualy, O., Sanogo, M.D., Timbeli, A., et al., 2013. Development of a pearl millet *Striga*-resistant genepool: response to five cycles of recurrent selection under *Striga*-infested field conditions in West Africa. Field Crops Res. 154, 82–90.

Krishnamurthy, L., Serraj, R., Rai, K.N., Hash, C.T., Dakheel, A.J., 2007. Identification of pearl millet [*Pennisetum glaucum* (L.) R. Br.] lines tolerant to soil salinity. Euphytica 158 (1–2), 179–188.

Kumar, S., Thakur, D.P., Singh, R., Arya, S., 1997. Reaction of pearl millet germplasm to ergot disease under natural field conditions. Ann. Biol. (Ludhiana) 13 (2), 297–298.

Kusaka, M., Ohta, M., Fujimura, T., 2005. Contribution of inorganic components to osmotic adjustment and leaf folding for drought tolerance in pearl millet. Physiol. Plant. 125 (4), 474–489.

Laurie, D.A., 1989. The frequency of fertilization in wheat × pearl millet crosses. Genome 32, 1063–1067.

Manga, V.K., Yadav, O.P., 1997. Development of a landrace based male-sterile line (CZMS 44A) of pearl millet. Crop Improv. 24 (1), 125–126.

Marchais, L., Pernès, J., 1985. Genetic divergence between wild and cultivated pearl millets (*Pennisetum typhoides*) I. Male sterility. Z. Pflanzenzüchtg 95, 103–112.

Marchais, L., Tostain, S., 1997. Analysis of reproductive isolation between pearl millet (*Pennisetum glaucum* (L.) R. Br.) and *P. ramosum*, *P. schweinfurthii*, *P. squamulatum*, and *Cenchrus ciliaris*. Euphytica 93, 97–105.

Mariac, C., Luong, V., Kapran, I., Mamadou, A., Sagnard, F., Deu, M., et al., 2006a. Diversity of wild and cultivated pearl millet accessions (*Pennisetum glaucum* [L.] R. Br.) in Niger assessed by microsatellite markers. Theor. Appl. Genet. 114, 49–58.

Mariac, C., Robert, T., Allinne, C., Remigereau, M.S., Luxereau, A., Tidjani, M., et al., 2006b. Genetic diversity and gene flow among pearl millet crop/weed complex: a case study. Theor. Appl. Genet. 113 (6), 1003–1014.

Martel, E., De Nay, D., Siljak-Yakovlev, S., Brown, S., Sarr, A., 1997. Genome size variation and basic chromosome number in pearl millet and fourteen related *Pennisetum* species. J. Hered. 88, 139–143.

Martel, E., Poncet, V., Lamy, F., Siljak-Yakovlev, S., Lejeune, B., Sarr, A., 2004. Chromosome evolution of *Pennisetum* species (Poaceae): implication of ITS phylogeny. Plant Syst. Evol. 249, 139–149.

Matzk, F., 1996. Hybrids of crosses between oat and Andropogoneae or Paniceae species. Crop Sci. 36, 17–21.

Miura, R., Terauchi, R., 2005. Genetic control of weediness traits and the maintenance of sympatric crop-weed polymorphism in pearl millet (*Pennisetum glaucum*). Mol. Ecol. 14, 1251–1261.

Mohamed, L., 1998. Inventory of some cultivated landraces threatened by genetic erosion in southern Tunisia. Plant Genet. Resour. Newsl. 113, 8–12.

Mohindra, V., Minocha, J.L., 1991. Pollen-pistil interactions and interspecific incompatibility in *Pennisetum*. Euphytica 56, 1–5.

Muallem, A.S., 1987. Genetic resources of cereal crops in PDR Yemen. 2. Barley, millet and maize. Plant Genet. Resour. Newsl. 72, 32–33.

Nadaf, S.K., Al-Hinai, S.A., Al-Farsi, S.M., Al-Lawati, A.H., Al-Bakri, A.N., 2010. Differential response of salt tolerant pearl millet genotypes to irrigation water salinity. In: Mushtaque, A., Al-Rawahy, S.A., Hussain, N. (Eds.), A Monograph on Management of Salt-Affected Soils and Water for Sustainable Agriculture. Sultan Qaboos University, Oman, pp. 47–60.

Nagesh, C.H., Subrahmanyam, N.C., 1996. Interspecific hybridization of *Pennisetum glaucum* (L.) R. Br. with wild relatives. J. Plant Biochem. Biotechnol. 5, 1–5.

NBPGR, 2007. State of Plant Genetic Resources for Food and Agriculture in India (1996–2006): A Country Report. National Bureau of Plant Genetic Resources, New Delhi.

NRC, 1996. Lost Crops of Africa, vol. 1: Grains. Board on Science and Technology for International Development. National Research Council/National Academy Press, Washington, DC, pp. 372.

Obilana, A.B., Monyo, E.S., Gupta, S.C., 1997. Impact of genetic improvement in sorghum and pearl millet: developing country experiences. In: Proceedings of the International Conference on Genetic improvement of Sorghum and Pearl Millet, September 22–27, 1996, Lubbock, Texas, USA. Collaborative Research Support Program on Sorghum and Pearl Millet, Lincoln, Nebraska, USA, pp. 119–141.

Obok, E.E., 2013. Mineral contents of selected pearl millet (*Pennisetum glaucum* (L.) R. Br.) × elephant grass (*Pennisetum purpureum* (Schum.)) interspecific hybrids of Nigerian origin. J. Plant Stud. 2 (2), 22–27.

Obok, E.E., Aken'Ova, M.E., Iwo, G.A., 2012. Forage potentials of interspecific hybrids between elephant grass selections and cultivated pearl millet genotypes of Nigerian origin. J. Plant Breed. Crop Sci. 4 (9), 136–143.

Oumar, I., Mariac, C., Pham, J.L., Vigouroux, Y., 2008. Phylogeny and origin of pearl millet (*Pennisetum glaucum* [L.] R. Br) as revealed by microsatellite loci. Theor. Appl. Genet. 117, 489–497.

Pannu, P.P.S., Sokhi, S.S., Aulakh, K.S., 1996. Resistance in pearl millet against rust. Indian Phytopathol. 49 (3), 243–246.

Parker, C., Wilson, A.K., 1983. *Striga*-resistance identified in semi-wild 'Shibra' millet (*Pennisetum* sp.). Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Genetics 48 (4), 1111–1117.

Pernès, J., 1984. Plant Genetic Resources Management vol. 1. ACCT, Paris, France.

Poncet, V., Lamy, F., Enjalbert, J., Joly, H., Sarr, A., Robert, T., 1998. Genetic analysis of the domestication syndrome in pearl millet (*Pennisetum glaucum* L., Poaceae): inheritance of the major characters. Heredity 81, 648–658.

Poncet, V., Lamy, F., Devos, K.M., Gale, M.D., Sarr, A., Robert, T., 2000. Genetic control of domestication traits in pearl millet (*Pennisetum glaucum* L., Poaceae). Theor. Appl. Genet. 100, 147–159.

Poncet, V., Martel, E., Allouis, S., Devos, M., Lamy, F., Sarr, A., et al., 2002. Comparative analysis of QTLs affecting domestication traits between two domesticated × wild pearl millet (*Pennisetum glaucum* L., Poaceae) crosses. Theor. Appl. Genet. 104 (6–7), 965–975.

Portères, R., 1976. African cereals: *Eleusine*, fonio, black fonio, teff, *Bracharia*, *Paspalum*, *Pennisetum* and African rice. In: Harlan, J.R., de Wet, J.M.J., Stemler, A.B.L. (Eds.), Origins of African Plant Domestication. Mouton, The Hague, The Netherlands.

Radhouane, L., 2013. Agronomic and physiological responses of pearl millet ecotype (*Pennisetum glaucum* (L.) R. Br.) to saline irrigation. Emirates J. Food Agric. 25 (2), 109–116.

Rai, K.N., 1995. A new cytoplasmic-nuclear male sterility system in pearl millet. Plant Breed. 114, 445–447.

Rai, K.N., Anand Kumar, K., Andrews, D.J., Rao, A., Raj, A.G.B., Witcombe, J.R., 1990. Registration of ICTP 8203 pearl millet. Crop Sci. 30, 959.

Rai, K.N., Rao, A.S., Hash, C.T., 1995. Registration of pearl millet parental lines ICMA 88004 and ICMB 88004. Crop Sci. 35, 1242.

Rai, K.N., Virk, D.S., Harinarayana, G., Appa Rao, S., 1996. Stability of male-sterile sources and fertility restoration of their hybrids in pearl millet. Plant Breed. 115, 494–500.

Rai, K.N., Appa Rao, S., Reddy, K.N., 1997. Pearl millet. In: Fuciillo, D., Sears, L., Stapleton, P. (Eds.), Biodiversity in Trust: Conservation and Use of Plant Genetic Resources in CGIAR Centers. Cambridge University Press, Cambridge, pp. 243–258.

Rai, K.N., Gowda, C.L.L., Reddy, B.V.S., Sehgal, S., 2008. The potential of sorghum and pearl millet in alternative and health food uses. Compr. Rev. Food Sci. Food Saf. 7, 340–352.

Rai, K.N., Velu, G., Govindaraj, M., Upadhyaya, H.D., Rao, A.S., Shivade, H., et al., 2015. Iniadi pearl millet germplasm as a valuable genetic resource for high grain iron and zinc densities. Plant Genet. Resour. 13 (1), 75–82.

Ramana Kumari, B., Kolesnikova-Allen, M.A., Hash, C.T., Senthilvel, S., Nepolean, T., Kavi Kishor, P.B., et al., 2014. Development of a set of chromosome segment substitution lines in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Crop Sci. 54 (5), 2175–2182.

Rao, Y.S., Rao, S.A., Mengesha, M.H., 1989. New evidence on the phylogeny of basic chromosome number in *Pennisetum*. Curr. Sci. 58 (15), 869–871.

Read, J.C., Bashaw, E.C., 1974. Intergeneric hybrid between pearl millet and buffelgrass. Crop Sci. 14 (3), 401–403.

Renno, J.F., Mariac, C., Poteaux, C., Bezancon, G., Lumaret, R., 2001. Haplotype variation of cpDNA in the agamic grass complex *Pennisetum* section *Brevivalvula* (Poaceae). Heredity 86, 537–544.

Robert, T., Khalfallah, N., Martel, E., Poncet, V., Remigereau, M., Rekima, S., et al., 2011. *Pennisetum*. In: Kole, C. (Ed.), Wild Crop Relatives: Genomic and Breeding Resources, vol. 9, Springer, Heidelberg, Berlin, pp. 217–255.

Roger, Z.G., Ramaiah, K.V., 1983. Screening of pearl millet cultivars for resistance to *Striga hermonthica*. Proceedings of the Second International Workshop on *Striga*, Ouagadougou, Upper Volta, October 5–8, 1981, pp. 77–81, 83–86.

Schmelzer, G.H., 1997. Review of *Pennisetum* section *Brevivalvula* (Poaceae). Euphytica 97, 1–20.

Sharma, R., Upadhyaya, H.D., Manjunatha, S.V., Rai, K.N., Gupta, S.K., Thakur, R.P., 2013. Pathogenic variation in the pearl millet blast pathogen *Magnaporthe grisea* and identification of resistance to diverse pathotypes. Plant Dis. 97 (2), 189–195.

Sharma, R., Upadhyaya, H.D., Sharma, S., Gate, V.L., Raj, C., 2015. Identification of new sources of resistance to multiple pathotypes of *Sclerospora graminicola* in the pearl millet mini core germplasm collection. Crop Sci. 55 (4), 1619–1628.

Singh, S.D., 1990. Sources of resistance to downy mildew and rust in pearl millet. Plant Dis. 74 (11), 871–874.

Singh, B.B., Jika, N., 1988. Five pearl millet genepools in Niger. Plant Genet. Resour. Newsl. 73/74, 29–30.

Singh, S.D., Navi, S.S., 2000. Genetic resistance to pearl millet downy mildew. II. Resistance in wild relatives. J. Mycol. Plant Pathol. 30 (2), 167–171.

Singh, S.D., Talukdar, B.S., 1998. Inheritance of complete resistance to pearl millet downy mildew. Plant Dis. 82 (7), 791–793.

Singh, P., Singh, U., Eggum, B.O., Anand Kumar, K., Andrews, D.J., 1987a. Nutritional evaluation of high protein genotypes of pearl millet (*Pennisetum americanum* (L.) Leeke). J. Sci. Food Agric. 38, 41–48.

Singh, S.D., Andrews, D.J., Rai, K.N., 1987b. Registration of ICLM 11 rust resistant pearl millet germplasm. Crop Sci. 27, 367–368.
Singh, S.D., Williams, R.J., Reddy, P.M., 1988. Isolation of downy mildew resistant lines from a highly susceptible cultivar of pearl millet. Indian Phytopathol. 41 (3), 450–456.
Singh, S.D., King, S.B., Reddy, P.M., 1990. Registration of five pearl millet germplasm sources with stable resistance to rust. Crop Sci. 30 (5), 1165.
Stapf, O., Hubbard, C.E., 1934. *Pennisetum*. In: Prain, D. (Ed.), Flora of Tropical Africa, vol. 9, Reeve & Co. Ltd, Ashford, Kent, pp. 954–1070, Part 6.
Sujata, V., Sivaramakrishnan, S., Rai, K.N., Seetha, K., 1994. A new source of cytoplasmic male sterility in pearl millet: RFLP analysis of mitochondrial DNA. Genome 37, 482–486.
Techio, V.H., Davide, L.C., Pereira, A.V., 2006. Meiosis in elephant grass (*Pennisetum purpureum*), pearl millet (*Pennisetum glaucum*) (Poaceae, Poales) and their interspecific hybrids. Genet. Mol. Biol. 29 (2), 353–362.
Thakur, R.P., King, S.B., 1988. Registration of six smut resistant germplasms of pearl millet. Crop Sci. 28 (2), 382–383.
Thakur, R.P., Williams, R.J., Rao, V.P., 1982. Development of resistance to ergot in pearl millet. Phytopathology 72 (4), 406–408.
Thakur, R.P., Rao, V.P., Williams, R.J., Chahal, S.S., Mathur, S.B., Pawar, N.B., et al., 1985. Identification of stable resistance to ergot in pearl millet. Plant Dis. 69 (11), 982–985.
Thakur, R.P., Rao, K.V.S., Williams, R.J., Gupta, S.C., Thakur, D.P., Nafade, S.D., et al., 1986. Identification of stable resistance to smut in pearl millet. Plant Dis. 70 (1), 38–41.
Tostain, S., 1992. Enzyme diversity in pearl millet (*Pennisetum glaucum*), wild millet. Theor. Appl. Genet. 83, 733–742.
Tostain, S., 1993. Evaluation de la diversité des mils pénicillaires diploïdes (*Pennisetum glaucum* (L.) R. Br.) au moyen de marqueurs enzymatiques. Etudes des relations entre formes sauvages et cultivées. PhD Thesis, Université Paris XI, Orsay, France.
Tostain, S., Riandey, M.F., Marchais, L., 1987. Enzyme diversity in pearl millet (*Pennisetum glaucum*), West Africa. Theor. Appl. Genet. 74, 188–193.
Upadhyaya, H.D., 2009. Reference set of pearl millet. Grain Legumes, 1, http://oar.icrisat.org/4197/1/Web_Art_2009_Reference_Set_of_Pearl_Millet.pdf.
Upadhyaya, H.D., Gowda, C.L.L., 2009. Managing and Enhancing the Use of Germplasm – Strategies and Methodologies. Technical Manual No. 10. ICRISAT, Patancheru.
Upadhyaya, H.D., Ortiz, R., 2001. A mini-core collection for capturing diversity and promoting utilization of chickpea genetic resources in crop improvement. Theor. Appl. Genet. 102, 1292–1298.
Upadhyaya, H.D., Gowda, C.L.L., Buhariwalla, H.K., Crouch, J.H., 2006. Efficient use of crop germplasm resources: identifying useful germplasm for crop improvement through core and mini-core collections and molecular marker approaches. Plant Genet. Resour. 4 (1), 25–35.
Upadhyaya, H.D., Reddy, K.N., Gowda, C.L.L., 2007. Pearl millet germplasm at ICRISAT genebank – status and impact. J. SAT Agric. Res. 3 (1), 1–5.
Upadhyaya, H.D., Gowda, C.L.L., Reddy, K.N., Singh, S., 2009a. Augmenting the pearl millet core collection for enhancing germplasm utilization in crop improvement. Crop Sci. 49 (2), 573.
Upadhyaya, H.D., Reddy, K.N., Irshad Ahmed, M., Gowda, C.L.L., Haussmann, B.I.G., 2009b. Identification of geographical gaps in the pearl millet germplasm conserved at ICRISAT genebank from West and Central Africa. Plant Genet. Resour. 8 (1), 45–51.

Upadhyaya, H.D., Reddy, K.N., Irshad Ahmed, M., Gowda, C.L.L., 2010. Identification of gaps in pearl millet germplasm from Asia conserved at the ICRISAT genebank. Plant Genet. Resour. 8 (3), 267–276.

Upadhyaya, H.D., Yadav, D., Reddy, K.N., Gowda, C.L.L., Singh, S., 2011. Development of pearl millet minicore collection for enhanced utilization of germplasm. Crop Sci. 51 (1), 217.

Upadhyaya, H.D., Reddy, K.N., Irshad Ahmed, M., Gowda, C.L.L., 2012. Identification of gaps in pearl millet germplasm from East and Southern Africa conserved at the ICRISAT genebank. Plant Genet. Resour. 10 (3), 202–213.

Upadhyaya, H.D., Reddy, K.N., Singh, S., Gowda, C.L.L., Irshad Ahmed, M., Kumar, V., 2014a. Diversity and gaps in *Pennisetum glaucum* subsp. *monodii* (Maire) Br. germplasm conserved at the ICRISAT genebank. Plant Genet. Resour. 12 (2), 226–235.

Upadhyaya, H.D., Reddy, K.N., Singh, S., Irshad Ahmed, M., Vinod, K., Ramachandran, S., 2014b. Geographical gaps and diversity in Deenanath grass (*Pennisetum pedicellatum* Trin.) germplasm conserved at the ICRISAT genebank. Indian J. Plant Genet. Resour. 27 (2), 93–101.

Vadez, V., Kholová, J., Yadav, R.S., Hash, C.T., 2013. Small temporal differences in water uptake among varieties of pearl millet (*Pennisetum glaucum* (L.) R. Br.) are critical for grain yield under terminal drought. Plant Soil 371 (1–2), 447–462.

Van Hintum, T.J.L., van de Wiel, C.C.M., Visser, D.L., van Treuren, R., Vosman, B., 2007. The distribution of genetic variation in a *Brassica oleracea* genebank collection related to the effects on diversity of regeneration, as measured with AFLPs. Theor. Appl. Genet. 114, 777–786.

Van Oosterom, E.J., Weltzien, E., Yadav, O.P., Bidinger, F.R., 2006. Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones. Field Crops Res. 96 (2/3), 407–421.

Van Treuren, R., Van Hintum, T.J.L., 2014. Next-generation genebanking: plant genetic resources management and utilization in the sequencing era. Plant Genet. Resour. 12 (3), 298–307.

Van Treuren, R., Van Hintum, T.J.L., Van de Wiel, C.C.M., 2008. Marker-assisted optimization of an expert-based strategy for the acquisition of modern lettuce varieties to improve a genebank collection. Genet. Resour. Crop Evol. 55, 319–330.

Van Treuren, R., Engels, J.M.M., Hoekstra, R., Van Hintum, T.J.L., 2009. Optimization of the composition of crop collections for *ex situ* conservation. Plant Genet. Resour. 7, 185–193.

Vari, A.K., Sidhu, J.S., Minocha, J.L., 1999. Cytogenetics. In: Khairwal, I.S., Rai, K.N., Andrews, D.J., Harinarayana, G. (Eds.), Pearl Millet Breeding. Oxford and IBH Publishing Co. Pvt. Ltd, New Delhi, pp. 83–117.

Vidhya, K., Fazlullah Khan, A.K., 2003. Hybrid between *P. schweinfurthii* and Napier grass. Cytologia 68 (2), 183–190.

Vom Brocke, K., Christinck, A., Eva-Weltzien, R., Presterl, T., Geiger, H.H., 2003. Farmers seed system and management practices determine pearl millet genetic diversity in semiarid regions of India. Crop Sci. 43, 1680–1689.

Watson, L., Dallwitz, M.J., 1992. The Grass Genera of the World. CAB International, Wallingford, pp. 674–676.

Wilson, J.P., Burton, G.W., 1991. Registration of Tift 3 and Tift 4 rust resistant pearl millet germplasms. Crop Sci. 31 (6), 1713.

Wilson, J.P., Hanna, W.W., 1992. Disease resistance in wild *Pennisetum* species. Plant Dis. 76 (11), 1171–1175.

Wilson, J.P., Burton, G.W., Wells, H.D., Zongo, J.D., Dicko, I.O., 1989a. Leaf spot, rust and smut resistance in pearl millet landraces from central Burkina Faso. Plant Dis. 73 (4), 345–349.

Wilson, J.P., Wells, H.D., Burton, G.W., 1989b. Inheritance of resistance to *Pyricularia grisea* in pearl millet accessions from Burkina Faso and inbred Tift 85DB. J. Hered. 80 (6), 499–501.

Wilson, J.P., Hess, D.E., Hanna, W.W., Kumar, K.A., Gupta, S.C., 2004. *Pennisetum glaucum* subsp. *monodii* accessions with *Striga* resistance in West Africa. Crop Prot. 23, 865–870.

Wilson, J.P., Sanogo, M.D., Nutsugah, S.K., Angarawai, I., Fofana, A., Traore, H., et al., 2008. Evaluation of pearl millet for yield and downy mildew resistance across seven countries in sub-Saharan Africa. Afr. J. Agric. Res. 3 (5), 371–378.

Wright, B., 1997. Crop genetic resource policy: the role of *ex situ* genebanks. Aust. J. Agric. Resour. Econ. 41, 81–115.

Wu, S., Tsai, C., 1963. Cytological studies on the intergeneric F_1 hybrid between *Oryza sativa* L. × *Pennisetum* sp. Acta Bot. Sin. 11 (4), 293–307.

Yadav, O.P., 2008. Performance of landraces, exotic elite populations and their crosses in pearl millet (*Pennisetum glaucum*) in drought and non-drought conditions. Plant Breed. 127 (2), 208–210.

Yadav, O.P., 2010. Evaluation of landraces and elite populations of pearl millet for their potential in genetic improvement for adaptation to drought-prone environments. Indian J. Genet. Plant Breed. 70 (2), 120–124.

Yadav, M.S., Duhan, J.C., 1996. Screening of pearl millet genotypes for resistance to smut disease. Plant Dis. Res. 11 (1), 95–96.

Yadav, O.P., Rai, K.N., 2013. Genetic improvement of pearl millet in India. Agric. Res. 2 (4), 275–292.

Zenkteler, M., Nitzsche, W., 1984. Wide hybridization experiments in cereals. Theor. Appl. Genet. 68, 311–315.