Genetic insights in pearl millet breeding in the genomic era: challenges and prospects

Mandeep Singh1 · Usha Nara1

Received: 23 July 2021 / Revised: 30 April 2022 / Accepted: 17 May 2022 / Published online: 6 June 2022 © Korean Society for Plant Biotechnology 2022

Abstract
Pearl millet, a vital staple food and an important cereal, is emerging as crop having various end-uses as feed, food as well as fodder. Advancement in high-throughput sequencing technology has boosted up pearl millet genomic research in past few years. The available draft genome of pearl millet providing an insight into the advancement of several breeding lines. Comparative and functional genomics have untangled several loci and genes regulating adaptive and agronomic traits in pearl millet. Additionally, the knowledge achieved has far away from being applicable in real breeding practices. We believe that the best path ahead is to adopt genome-based approaches for tailored designing of pearl millet as multi-functional crop with outstanding agronomic traits for various end uses. Presently review highlight several novel concepts and techniques in crop breeding, and summarize the recent advances in pearl millet genomic research, peculiarly genome-wide association dissections of several novel alleles and genes for agronomically important traits.

Keywords Cereal crop · Genetic gain · Genomic approaches · Pearl millet · Tailored designing

Introduction
The rising global population, integrated with climate changes striking natural disasters more frequently impose remarkable challenges and pressure on global food security. To meet the food demands, we need to produce 70% more food as the world population is exceed to 9.7 billion by 2050 (Tripathi et al. 2019). Due to the COVID-19 pandemic, additionally, 83–132 million people in the world will become undernourished, and that further exacerbates insecurity of global food production and poses a hindrance in achieving the goal of Zero Hunger, indicated by a recent FAO report (FAO 2020). To avoid global food insecurity, it is necessary to manage important crop ideotypes to enhance crop production.

Pearl millet (Pennisetum glaucum), is an important cereal crop in the arid and semiarid ecologies of Sub-Saharan Africa and South Asia where the temperature is high and also challenged by erratic rainfall. It has the capacity to withstand extreme conditions and also built-in adaptation to low fertility soils, and is an excellent crop for shorter growing season because of its short development stages, high growth rate, and high photosynthetic efficiency (Yadav and Rai 2013; Serba et al. 2020). Pearl millet is emerging as an important crop for feed, relay crop, fodder, and food in Canada, North Africa, United States, Mexico, Central Asia, and Brazil. Pearl millet has significant importance because of its nutrient-rich grains for human consumption, and dry Stover as well as green fodder for livestock (Rai et al. 2008).

Pearl millet breeding has made enormous progress and is often referred to as one of the considerable success stories in agriculture but the average grain yield of pearl millet is still very low as compared to other cereals (Yadav et al. 2019). Globally, the average yield of millet in 2018/2019 was only ~0.94 MT/ha, which is much lower than that of wheat (~3.39 MT/ha), maize (~5.86 MT/ha), and rice (~4.58 MT/ha) (FAOSTAT 2020; Tang and Cheng 2018). Yield levels of pearl millet are greatly influenced by genotype and environment and its yield varies significantly among different countries. In this review, we first introduce molecular breeding approaches and systems. We also review the current advances in pearl millet genomic and genetic research. Main emphasis is on important genes and allelic variations focusing agronomic traits with immense potential in pearl millet breeding. Moreover, novel cutting-edges breeding...
Cutting edge molecular breeding approaches and systems

Breeding and genetic improvement of crops aim at enhancing genetic gain, defined as the enhancement in performance achieved via artificial selection over generations. In the era of molecular breeding, conventional breeding approaches including phenotypic selection, have transformed into molecular approaches to enhance genetic gain (Moose and Mumm 2008; Xu et al. 2017). Crop breeding and genetic improvement have been elaborated by exploiting and integrating the concepts of DNA markers, genetic engineering, and marker-assisted breeding (MAB) as anticipated by more accurate background and foreground selection, shortening of breeding cycle (MARS), and utilization and discovery of diverse genetic resources (Bruce 2012). We know that agronomically important traits are governed by multiple genes (polygenic), which restrict breeding on a molecular basis. So, the success of molecular plant breeding of traits having genes with major effect is limited due to: unavoidable linkage drag linked with larger chromosomal regions selection, the underlying hindrance of lower genome coverage of molecular markers, and difficulties in utilizing a wider range of crop genetic resources. Hence, advancements in theoretical configuration and technologies are in need to boost the breeding system (Gupta et al. 2010). Since time immemorial, the emergence of novel molecular approaches such as next-generation sequencing techniques, genome editing, molecular modules, genome-wide association studies, genomic selection, marker-assisted breeding, and high throughput phenomics, has reformed the scope of crop breeding, authorize much more productive utilization of artificial and naturally created variation, and phenotyping (Zhou et al. 2018; Chen et al. 2019; Xu et al. 2020). Marker assisted selection (MAS) stand out to be an intensive approach providing the breeders an efficient tool to use his skill. In pearl millet, it has been utilized for development of lines tolerant to drought stress, thus improving overall genetic gain (Rani et al. 2021). Here we review the concepts of genomic selection and molecular modules and up-to-date reviews can be found for marker-assisted recurrent selection (Singh et al. 2021a).

Genomic selection (GS)

Genomic selection (GS) has been authenticated with immense potential to increase genetic gain in breeding of crop plants but also used extensively in animal breeding (Weller et al. 2017; Mehrban et al. 2017). GS breeding programs require adequate and affordable genotyping platforms, availability of pedigree records, and a less structured population. One of the major aims of using GS is enabling genomic selection per se with improved predictive accuracy. Prediction accuracy is highly affected by population size, marker density, population structure, genetic models, TP-BP (Training Population-Breeding Population) relationship, and heritability. It can be expressed using the formula:

\[ r_{GM} = ay_1 + by_2 + cy_3 + dy_4 + ey_5, \]

where \( y_1 \) is related to marker density, \( y_2 \) is population size, \( y_3 \) is TP-BP relationship, \( y_4 \) is heritability, and \( y_5 \) is a genetic model and \( a \) to \( e \) are the constants related with variables \( y_1 \) to \( y_5 \). Marker density is one of the important factors in prediction of accuracy. The number of markers should be high to ensure that the maximum number of QTLs associated with trait should be in strong LD with at least one marker (Daetwyler et al. 2010) whereas low-density markers may be helpful in predicting genomic estimated breeding value (GEBVs) with less accuracy (Singh and Singh 2015; Xu et al. 2020).

Unlike marker-assisted selection, genomic selection uses information from whole genome-wide marker data whether they are related with a marker of interest or not, showing advantage of genomic selection over marker-assisted selection in reducing cost of genotyping and phenotyping. It is noteworthy that GS does not need any data related to phenotyping of the breeding population and no need to identify the QTLs associated with target trait (Xu et al. 2020). At whole genome level, major and minor genes effect can be estimated by exploiting the genotype-to-phenotype relationship thus helping in reducing time cycle and cost thereby enhancing genetic gain of every cycle (Singh and Singh 2015; Guo et al. 2019). In recent years, genomic selection has been utilized in breeding of major crops such as maize, rice, and wheat (Crossa et al. 2014; Schrag et al. 2019; Spindel et al. 2015). In a study, Liang et al. (2018), characterize the inbred pearl millet lines, developed by ICRISAT, and evaluated the utility of genomic selection using two genotypic strategies viz., GBS and RAD-seq. It has been reported that genomic prediction scheme (RR-BLUP) generated median predictions that ranges for different traits viz., grain yield (0.48–0.51), 1000 grain weight (0.73–0.74), plant height (0.72–0.73), and days to flowering (0.87–0.89), when used hybrid data but can also be improved moderately by incorporating inbred phenotypic data sets (Liang et al. 2018). In pearl millet, GS was mainly emphasized model training using several training populations such as inbred for GCA and SCA, and test cross hybrids. By combining the GCA and SCA concepts, we can enhance our power for identification of superior cultivars (Jarquin et al. 2020). In ICRISAT, efforts are being made to exploit the available whole-genome resequencing
(WGRS) data of PMiGAP lines along with phenotyping data for different traits for genomic selection.

Over the past years, various machine learning methods and statistical models have been advocated for genomic selection such as random forest, rrBLUP, RKHS, and BayesA/B. The selection of the model is entirely relying on the purposes for which they are used and it may be different for different traits. Although the models may be different, the values of prediction accuracy were substantially alike and rrBLUP method appears to be more popular (Yu et al. 2016).

Pearl millet genetic resources and populations

Pearl millet germplasm

The United States Department of Agriculture’s National Plant Germplasm System (USDA-NPGS) and International Crops Research Institute for Semi-Arid Tropics (ICRISAT) are the two major pearl millet germplasm banks, housing more than 26,000 accessions including landraces, wild relatives, historic accessions, and breeding lines. In addition, the National Bureau of Plant Genetic Resources (NBPRG) in India has got 8291 collections, The Institut de Recherche Pour le Développement (IRD, France) holds about 3968 accessions, and the Canadian Genetic Resources Program, Saskatoon holds about 3821 accessions.

Genus *Pennisetum* represents 55 taxa, out of which 53 are wild species and 2 are intra-specific taxa. These taxa are classified according to their relatedness with *P. glaucum* using the model given by Maxted and Kell (2009). They are classified into primary, secondary, and tertiary wild relatives, in which *P. glaucum* cultivars and landraces *P. glaucum subsp. stenostachyum* and *P. glaucum subsp. monodii* and are included in primary wild relatives, *P. purpureum* and *P. squamulatum* come under secondary wild relatives and all other species in the genus are included in the tertiary wild relatives.

The center of domestication and geographical origin of pearl millet is located in Western Africa. In India, it was introduced dating back to 2000 B.C., and records reveal cultivation of pearl millet into Brazil in 1960s and into the United States in 1850s. The earliest finding of wild and domesticated pearl millet was recorded at about 1459 BC in Birimi in northern Ghana (D’Andrea et al. 2001), and the domesticated pearl millets was catalogued at about 3500 B.C. (Amblard and Pernes 1989). Whether pearl millet has a single center of the origin or more than one center of origin, called “non-centers”, there was a dispute among the scholars in several regions. According to latter hypothesis, these non-centers of pearl millet include whole Sahel from Mauritania to western Sudan (Clark 1962; Harlan 1971).

Diversity panels

Developing a core collection to represents diversity is an efficient pathway to increase the utilization of germplasm in crop improvement. The core collection of pearl millet consisting of 1600 accessions which are selected from 16,000 accessions characterized in 1998 at the ICRISAT Gene bank. This was supplemented by addition of 501 accessions that represent 4717 accessions and the revised core collection consisting of 2094 accessions (Upadhyaya 2009). The core collection was far too huge, making crop inefficient and expensive. To overcome these difficulties, a mini core collection of pearl millet consisting of 238 accessions (Table 1) was organized by evaluating core collection of 2094 accessions of pearl millet for 18 morpho agronomic traits. The mini core collection was designed in a way that represents majority of the variation present in core collection and its reduced size provides an insight in a more economical point of view for exploitation of genetic resources of pearl millet for crop improvement (Upadhyaya 2011). Based on genotypic data, a subset of 300 diverse accessions were selected from composite collection to reduce the redundancy between units thus limits diversity losses. This reference subset of pearl millet accession, comprising 230 accessions from composite collection, were evaluated for drought stress and other agronomically important traits to enhance yield potential. These reference sets are available from ICRISAT gene bank by signing on SMTA (Standard Material Transfer Agreement). A set of germplasm material from Africa and India having diverse phenotypic characters such as grain size, panicle size, tillering, etc. was exploited for broadening genetic base of restorer and seed parents (Yadav et al. 2012; Patil et al. 2020).

Mutagenized populations

After successful exploitation of Targeting Induced Local Lesions IN Genomes (TILLING) approach in Arabidopsis plant, this approach has been extended in cereals such as maize (Till et al. 2004), wheat (Slade et al. 2005), and rice (Horst et al. 2007). In a study, the seeds of pearl millet (*Pennisetum typhoides* (Burn) Stapf. Var.Co (CU)-9 were mutated for chlorophyll and morphological mutation using ethyl methane sulfate (EMS). The results revealed EMS as an effective chemical mutagen which induce mutation that can be used in breeding programmes. (Ambli and Mullainathan 2015). Application of TILLING in mutation breeding plays a significant role in improvement of particular traits using radiation or chemical treatment (Szurman-Zubrzycka et al. 2018). Some of the key applications of TILLING to some important traits include
| Sr. No. | Accession ID | Accession name          | Material type/country | Sr. No. | Accession ID | Accession name          | Material type/country | Sr. No. | Accession ID | Accession name          | Material type/country |
|---------|--------------|-------------------------|-----------------------|---------|--------------|-------------------------|-----------------------|---------|--------------|-------------------------|-----------------------|
| 1       | IP 196       | B 90                    | L/Kenya               | 81      | IP 8155      | GS 138                  | B/India               | 161     | IP 13623     | L/India                 |                       |
| 2       | IP 277       | No. 8                   | B/Congo               | 82      | IP 8205      | P 7-1                   | L/Nigeria             | 162     | IP 13624     | L/India                 |                       |
| 3       | IP 446       | IC 5462                 | L/India               | 83      | IP 8220      | GS 163                  | B/India               | 163     | IP 13636     | Etah type               | L/India               |
| 4       | IP 869       | Georgia inbred 37       | B/U.S. A              | 84      | IP 8245      | IP 228-2                | B/India               | 164     | IP 13760     | PEN 578-1-1             | B/Germany             |
| 5       | IP 952       | –                       | L/India               | 85      | IP 8276      | IP 2130-1/CG 51         | B/India               | 165     | IP 13875     | 60                      | L/Burkina Faso         |
| 6       | IP 1060      | Moti Mehrana            | L/India               | 86      | IP 8288      | IP 535-1                | B/India               | 166     | IP 13991     | –                       | L/Zimbabwe             |
| 7       | IP 1098      | Bajra Tadpang           | L/India               | 87      | IP 8350      | Acc No. 21              | L/India               | 167     | IP 14294     | –                       | L/Cameroon             |
| 8       | IP 1405      | Bajra Chakpaki          | L/India               | 88      | IP 8418      | E 127                   | L/Nigeria             | 168     | IP 14428     | –                       | L/Cameroon             |
| 9       | IP 1536      | Bajri Rampahari         | L/India               | 89      | IP 8472      | D 172 C-2               | L/Niger               | 169     | IP 14522     | –                       | L/Cameroon             |
| 10      | IP 1566      | Bajra Hirasda           | L/India               | 90      | IP 8529      | –                       | L/India               | 170     | IP 14537     | Yadir                   | L/Cameroon             |
| 11      | IP 1625      | –                       | L/India               | 91      | IP 8540      | –                       | L/India               | 171     | IP 14542     | –                       | L/Cameroon             |
| 12      | IP 1834      | Anand No. 5            | L/India               | 92      | IP 8562      | –                       | L/India               | 172     | IP 14599     | –                       | L/Cameroon             |
| 13      | IP 1917      | Anand No. 77           | L/India               | 93      | IP 8672      | 30 K                    | L/Sudan               | 173     | IP 14753     | –                       | L/Cameroon             |
| 14      | IP 2083      | No. 13                  | L/South Africa        | 94      | IP 8707      | 49 KA Darfur-2          | L/Sudan               | 174     | IP 14776     | –                       | L/Cameroon             |
| 15      | IP 2167      | CPI 26307               | B/Australia           | 95      | IP 8818      | 5 LUP                   | L/Zimbabwe            | 175     | IP 14787     | –                       | L/Cameroon             |
| 16      | IP 2246      | N 6                     | L/Nigeria             | 96      | IP 8863      | –                       | L/Zambia              | 176     | IP 15095     | –                       | L/India                |
| 17      | IP 2322      | Sz 36                   | L/Nigeria             | 97      | IP 8913      | Sanio                   | L/Gambia              | 177     | IP 15119     | –                       | L/India                |
| 18      | IP 2704      | BAM-C 130              | L/Chad                | 98      | IP 9000      | P3 Kolo P-1/1/1         | B/Niger               | 178     | IP 15256     | –                       | L/India                |
| 19      | IP 2761      | Antia                   | L/Burkina Faso        | 99      | IP 9026      | Sanio                   | L/Gambia              | 179     | IP 15273     | Kattu cumbu             | L/India                |
| 20      | IP 2789      | Mousse                  | Mauritania            | 100     | IP 9157      | –                       | L/India               | 180     | IP 15372     | –                       | L/India                |
| 21      | IP 3110      | –                       | L/India               | 101     | IP 9198      | SB 21                   | L/India               | 181     | IP 15448     | –                       | L/India                |
| 22      | IP 3329      | Karauli                 | L/India               | 102     | IP 9449      | –                       | L/Ghana               | 182     | IP 15556     | 162                     | L/Burkina Faso         |
| 23      | IP 3432      | Chadi local             | L/India               | 103     | IP 9464      | –                       | L/Ghana               | 183     | IP 15829     | –                       | L/Tanzania             |
| 24      | IP 3489      | Oong                    | L/India               | 104     | IP 9492      | –                       | L/Ghana               | 184     | IP 15836     | –                       | L/Tanzania             |
| 25      | IP 3525      | Podi cumbu              | L/India               | 105     | IP 9527      | –                       | L/Ghana               | 185     | IP 15953     | Sajjalu                 | L/India                |
| 26      | IP 3626      | Peria cumbu             | L/India               | 106     | IP 9596      | 126                     | L/Yemen               | 186     | IP 16402     | Sifimbata               | L/Zimbabw              |
| 27      | IP 3642      | Kulan                   | L/India               | 107     | IP 9617      | PI 337492               | B/Brazil              | 187     | IP 16489     | –                       | L/Zimbabw              |
| 28      | IP 3646      | –                       | L/India               | 108     | IP 9645      | PI 286842               | L/Nigeria             | 188     | IP 16540     | –                       | L/Zimbabw              |
| 29      | IP 3706      | –                       | L/India               | 109     | IP 9692      | PI 286979               | L/Nigeria             | 189     | IP 16754     | –                       | L/Zimbabw              |
| 30      | IP 3852      | –                       | L/India               | 110     | IP 9795      | UI 1639                 | L/United states       | 190     | IP 16863     | –                       | L/Zimbabw              |
| 31      | IP 4177      | –                       | L/India               | 111     | IP 9813      | Mexioera                | L/Mozambique          | 191     | IP 17396     | –                       | L/Central African      |
| 32      | IP 4291      | –                       | L/India               | 112     | IP 9934      | Acc 229                 | L/Sudan               | 192     | IP 17465     | –                       | L/Algeria              |
| 33      | IP 4363      | –                       | L/India               | 113     | IP 10085     | P 5439                  | L/Mali                | 193     | IP 17490     | –                       | L/Tunisia              |
| 34      | IP 4488      | –                       | L/India               | 114     | IP 10151     | P 5521                  | L/Mali                | 194     | IP 17532     | –                       | L/Togo                 |
| 35      | IP 4747      | Meerut 30               | L/India               | 115     | IP 10263     | P 5684                  | L/Mali                | 195     | IP 17775     | –                       | L/Togo                 |
| 36      | IP 4903      | NEP 218-5081            | B/Lebanon             | 116     | IP 10371     | EC 134848               | L/Nigeria             | 196     | IP 18040     | –                       | L/Pakistan             |
### Table 1 (continued)

| Sr. No. | Accession ID | Accession name | Material type/country | Sr. No. | Accession ID | Accession name | Material type/country | Sr. No. | Accession ID | Accession name | Material type/country |
|---------|--------------|----------------|-----------------------|---------|--------------|----------------|-----------------------|---------|--------------|----------------|-----------------------|
| 37      | IP 4979      | 700164         | L/Nigeria             | 117     | IP 10399     | Purple dwarf   | B/India               | 197     | IP 18353     | –              | L/Namibia             |
| 38      | IP 5085      | 700706         | L/Nigeria             | 118     | IP 10437     | P 3908         | L/Benin             | 198     | IP 18545     | –              | L/Namibia             |
| 39      | IP 5153      | D 70           | L/Niger               | 119     | IP 10467     | Bikita         | L/Zimbabwe          | 199     | IP 18579     | –              | L/Namibia             |
| 40      | IP 5185      | D 46           | L/Niger               | 120     | IP 10601     | M’Boneri       | L/Mali              | 200     | IP 18657     | –              | L/Namibia             |
| 41      | IP 5261      | D 222          | L/Niger               | 121     | IP 10632     | CMM 465        | L/Mali             | 201     | IP 18824     | –              | L/Namibia             |
| 42      | IP 5298      | D 219-1        | L/Niger               | 122     | IP 10665     | Haini          | L/Mali             | 202     | IP 18854     | –              | L/Namibia             |
| 43      | IP 5389      | P 2672         | L/Niger               | 123     | IP 10713     | Acc 447        | L/Sudan            | 203     | IP 18900     | –              | L/Namibia             |
| 44      | IP 5407      | P 2693         | L/Niger               | 124     | IP 10729     | Acc 473        | L/Sudan            | 204     | IP 19072     | –              | L/Namibia             |
| 45      | IP 5438      | P 2727         | L/Niger               | 125     | IP 10761     | Acc 516        | L/Sudan            | 205     | IP 19141     | –              | L/Namibia             |
| 46      | IP 5455      | P 2745         | L/Niger               | 126     | IP 10925     | Acc 772        | L/Sudan            | 206     | IP 19305     | –              | L/Namibia             |
| 47      | IP 5581      | P 2877         | L/Niger               | 127     | IP 10953     | BM 8           | L/Kenya            | 207     | IP 19415     | TCD 115        | L/Namibia             |
| 48      | IP 5711      | 45-347         | L/Nigeria             | 128     | IP 11010     | –              | L/India            | 208     | IP 19425     | –              | L/Republic of the Congo |
| 49      | IP 5719      | 45-359         | L/Nigeria             | 129     | IP 11036     | –              | L/India            | 209     | IP 19448     | –              | L/Namibia             |
| 50      | IP 5793      | WJR 8/28530    | B/Russia             | 130     | IP 11044     | Gullisita      | L/India            | 210     | IP 19629     | C 90–136       | L/Niger             |
| 51      | IP 5869      | P 1471/SI165   | L/Senegal            | 131     | IP 11113     | –              | L/India            | 211     | IP 19722     | ICMSR 45       | B/India             |
| 52      | IP 5957      | P 1565/SI395   | L/Senegal            | 132     | IP 11247     | Rushambo       | L/Zimbabwe          | 212     | IP 19816     | ICMSR 147      | B/India             |
| 53      | IP 5964      | P 1572/SI419   | L/Senegal            | 133     | IP 11268     | –              | L/Zimbabwe          | 213     | IP 19851     | ICMSR 183      | B/India             |
| 54      | IP 6057      | P 172          | L/Central African Republic | 134     | IP 11405     | CVP 508        | L/Burkina Faso     | 214     | IP 19913     | ICMSR 247      | B/India             |
| 55      | IP 6113      | P 965          | L/Niger               | 135     | IP 11428     | CVP 610        | L/Burkina Faso     | 215     | IP 19964     | ICMSR 299      | B/India             |
| 56      | IP 6193      | P 89           | L/Cameroon           | 136     | IP 11546     | P 6008        | L/Burkina Faso     | 216     | IP 20249     | –              | L/Yemen             |
| 57      | IP 6275      | P 246          | L/Mali                | 137     | IP 11666     | Millet 181    | L/United Kingdom   | 217     | IP 20274     | –              | L/Yemen             |
| 58      | IP 6278      | P 249          | L/Mali                | 138     | IP 11799     | Pitta ganti    | L/India            | 218     | IP 20409     | Dauro         | L/Nigeria             |
| 59      | IP 6324      | P 304          | L/Mali                | 139     | IP 11811     | Pedda sajja    | L/India            | 219     | IP 20576     | Dauro         | L/Nigeria             |
| 60      | IP 6340      | P 333          | L/Mali                | 140     | IP 11930     | Belenguine     | L/Sierra Leone    | 220     | IP 20577     | Dauro         | L/Nigeria             |
| 61      | IP 6517      | P 552          | L/Mali                | 141     | IP 11943     | Tasur          | L/Sierra Leone    | 221     | IP 20611     | Maiwa         | L/Nigeria             |
| 62      | IP 6769      | –              | L/Malawi             | 142     | IP 12221     | Maiwa          | L/Nigeria          | 222     | IP 20715     | –              | L/Nigeria             |
| 63      | IP 6798      | –              | L/Malawi             | 143     | IP 12364     | –              | L/Nigeria          | 223     | IP 20768     | –              | L/Nigeria             |
| 64      | IP 6805      | –              | L/Malawi             | 144     | IP 12374     | –              | L/Nigeria          | 224     | IP 20929     | Maiwa         | L/Nigeria             |
| 65      | IP 7118      | Haram Type     | L/India              | 145     | IP 12418     | Fes MAR       | L/Morocco          | 225     | IP 20955     | Gero          | L/Nigeria             |
| 66      | IP 7259      | –              | L/India              | 146     | IP 12431     | SA. Anter 11004 | B/Cabo Verde     | 226     | IP 21066     | 62            | Myanmar             |
| 67      | IP 7358      | –              | L/India              | 147     | IP 12498     | C 3-4         | L/India            | 227     | IP 21093     | PI 331692     | Ethiopia            |
| 68      | IP 7522      | Uwele          | L/Tanzania           | 148     | IP 12533     | MB 6939       | L/India            | 228     | IP 21127     | 90-20-DVP-Dwarf PO | B/United States     |
starch synthesis in wheat (Slade et al. 2012); plant architecture in rice for salt-tolerance (Hwang et al. 2017); high number of tillers in barley (Marzec et al. 2016); powdery mildew resistance in wheat (Acevedo-Garcia et al. 2017); resistance to northern corn leaf blight in maize (Severune et al. 2015); for other yield-related parameters such as waterlogging tolerance and DNA repair in barley (Mendiondo et al. 2016). Maryono et al. (2020) studied the M3 population of pearl millet for performance and estimation of genetic variability. Population treated with different doses of gamma rays showed high heritability for the traits such as panicle diameter, number of nodes per plant and stem diameter (Maryono et al. 2020).

Although ICRISAT and other institutes collected thousands of accessions of pearl millet, the majority of the accessions lack genotyping and phenotypic data. With the advent of new sequencing techniques, all accessions can be genotyped and phenotyped at low cost both effectively and efficiently. Additionally, wild relatives of pearl millet offer excellent sources of genes for agronomic traits and various abiotic stresses (Yadav et al. 2021).

**MAGIC and NAM populations**

Molecular breeding for second generation platforms brought about a shift in population linkage mapping from bi-parental to the multi-parental population, such as multi-parent advanced generation inter-cross (MAGIC) population (Kover et al. 2009) and nested association mapping (NAM) population, to exploit allelic diversity in the fine mapping of QTLs for traits of interest. These populations utilize the supremacy of both association mapping and linkage analysis thereby reducing the limitations of both and facilitating high-resolution mapping using a multi-parental population (Tibbs et al. 2021). NAM population was first reported in Zea mays and MAGIC population was first reported in Arabidopsis and both offer potential for exploiting the structure of the genome and improving breeding populations. MAGIC populations have been utilized in various crops including maize (Dell’Acqua et al. 2015), wheat (Huang et al. 2012), sorghum (Ongom and Ejeta 2018), and rice (Bandillo et al. 2013). The information about the NAM and MAGIC population in pearl millet to decode allelic variations for stress tolerance and yield-related traits is lacking. Accessions of pearl millet exhibit novel alleles and can be conquered through the exploitation of a multi-parental populations. MAGIC and NAM populations should be developed in such a way that they consolidate diverse parents crossed with a common parent (Fig. 1).
Genomic research in pearl millet

Pearl millet domestication

Sequencing of pearl millet genome provides an insight to assess the domestication origin of pearl millet. Moreover, it enables breeders and researchers to improve this staple food for agronomically important traits as well as against various biotic and abiotic stresses. Pearl millet domestication was related to the modification of plant architecture and spike morphology like that observed in maize crop (Schnable et al. 2009). Lakis et al. (2012) studied three flowering genes namely \( \text{PgHd3a} \), \( \text{PgDwarf8} \) and \( \text{PgPHYC} \) that involved in domestication of pearl millet. \( \text{PgDwarf8} \) and \( \text{PgPHYC} \) genes were found to show significant differentiation between wild and domestic populations but such differentiations were not found for \( \text{PgPHYC} \) gene. Results revealed lack of differentiation between early and late landraces on the basis of three candidate genes (Lakis et al. 2012). For pearl millet domestication, 221 accessions of traditional varieties and wild forms were structured into 3 major geographic groups. Several genomic regions have been identified that showed reduced diversity in cultivated species only. A total of 140 genomic regions have been identified with values above 95% threshold for loss of differentiation and diversity (Gaut et al. 2018). Out of 24 genomic regions, 8 were located on pg7,6 on pg6 and 5 on pg1. Linkage group 6 and 7 carrying QTLs have been identified previously which explained the majority of phenotypic differences between cultivated and wild germplasm (Poncet 2000; Poncet 2002).

Domestication syndrome can be defined as set of traits that blemishes a divergence of crop from its wild relatives (Purugganam 2019). A linkage map has been obtained which revealed genes that are involved in qualitative traits of spikelet namely abscission layer (AL); pedicel length (PL); seed coating (Ct); Length of involucre bristle (BL); and presence
of longer bristles (PB). Additionally, a QTL for length of glumes (GL), tillering, and spike morphology (WeS) and these genes have been identified on segment II (Poncet et al. 1998). However, only a few genes for pearl millet domestication have been reported. Domestication genes can also be uncovered using parallel selection theory (Purugganan 2019; Rendon-Anaya and Herrera-Estrella 2018).

Pearl millet draft genome

Pearl millet is a diploid (2n = 2x = 14) crop species having relatively non-duplicated and large genome (1.76 Gb). The genome of pearl millet was sequenced using whole-genome shotgun (WGS) and bacterial artificial chromosome (BAC) technique. Tift 23D2B1-P1-P5 genotype was used to construct 13 large inserts (~ 2, 5, 10, 20 and 40 kb) and 10 small inserts (~ 170, 250, 500, 800 bp) of WGS libraries and these libraries were sequenced on the IlluminaHiSeq 2000 and 520 Gb of sequence data. From Tift 23D2B1-P1-P5, genotype two BAC libraries were constructed using HindIII and EcoR1 having an average insert size of ~ 120 kb. It has been estimated that the genome of pearl millet was about 1.76 Gb indicating that about 90% of the genome was assembled along with 50% of scaffolds (Varshney et al. 2017). About 77.2% of the repetitive sequences were found in the assembled genome. The true percentage of the repetitive sequence was about 80% (0.18 Gb) which is similar to the proportion of repetitive DNA found in the 466-Mb rice genome (~42%) (Yu 2002), ~ 400-Mb foxtail millet (~46%) (Ben-netzen 2012), ~ 730-Mb sorghum (~61%) (Paterson 2009) and ~2.3 Gb maize (> 85%) (Schnable et al. 2009). Another study revealed a total of 69,398 transcriptome assembled contigs (TACs) in pearl millet using transcriptome sequence (Rajaram et al. 2013). The length of the CDS, mRNA, exon and introns in pearl millet were similar with those reported for other cereal crops genome. CEGMA analysis revealed that among 458 of the conserved genes, 437 genes were complete, 8 genes were not found in the genome sequence, 8 genes were not included in the gene set, and 5 genes has more than 1 copy (possibly fragmented genes). In addition, BUSCO analysis for 956 genes revealed that 96.7% genes were annotated and 95.4% of these were complete. Gene models of rice were chosen to investigate the completeness of pearl millet genes because of closely relatedness showing 90.86% homology with rice gene model than Arabidopsis gene model.

Population structure and genetic diversity

Population genomics is a widespread approach to understand the linkage disequilibrium, population structure, migration, genetic basis of adaptation, and relatedness at genome level. Pearl millet is an important cereal crop with wider adaptability and long cultivation history. Agronomic adaptation and speciation of pearl millet could facilitate breeding at molecular level and is also helpful in understanding this concept for other crops as well. Availability of diverse resources for pearl millet including geographical and genetic resources offers material worth for genomic research.

In pearl millet breeding, genetic diversity is an important basis for exploitation of complex traits. For better elucidation of genetic diversity and population structure, 994 lines of pearl millet were re-sequenced, including 260 inbred male sterility maintainer (B-) and 320 male fertility restorer (R-) lines, 345 PMiGAP (Pearl Millet Inbred Germplasm Association) lines, 31 wild accessions and 38 inbred parents of mapping populations (Varshney et al. 2017). In this, a total of 1.16 Tb whole-genome resequencing (WGRS) on PMiGAP lines and 116 Gb WGRS on parental lines of mapping populations were performed. Additionally, 78.9 Gb data for PMiGAP lines were generated using GBS (genotyping by sequencing) (Elshire 2011) and R- and B- lines were generated using RAD sequencing (Miller et al. 2007). In the pearl millet genome sequence, 88,256 simple sequence repeats (SSR) were identified using MicroSAtellite program (Thiel et al. 2003) and the primers were designed for 74,891 SSR-containing sequences which can be utilized for breeding and genetic applications. A total of 29,542,173 single nucleotide polymorphisms (SNPs) were identified in PMiGAP lines, including 3,844,446 insertions and deletions, and 423,118 genome-wide structural variations (Varshney et al. 2017).

Genome-wide single-Nucleotide polymorphism discovery identified 82,112 SNPs markers distributed over all 7 chromosomes. From identified SNPs, majority of the SNPs were found on chromosome 1 (38,71) and 2 (36,854) whereas 35,714 SNPs were mapped to the scaffolds. Genome-wide Linkage disequilibrium (LD) in west African population was shorter than in all other subpopulations (South Africa, Middle East, East Africa, USA and India) (Serba et al. 2019). To explore the diversity of different pearl millet races, Kanfany et al. (2020) analyzed the 309 genotypes of pearl millet. They found lowest genetic distance (0.09) between ICML197458 and ICML197279 which were developed from landraces of Nigeria and India, respectively whereas highest genetic distance (0.33) was observed between ICML197390 and ICML197314.

GWAS in pearl millet

GWAS is a powerful tool to dissect the architecture of complex agronomically important traits of crops using genome-wide single nucleotide polymorphism (SNPs) markers. The discovery of pearl millet draft genome has unlocked numerous possibilities to dissect various QTLs along with the functions of its related genes having diverse traits. Association mapping analysis and QTL-mapping/interval mapping
are two techniques that can be utilized for construction of genetic maps. Association mapping greatly reduces time and labor requirement as breeders can skip the hectic task of generating a mapping population through hybridization, continuous selection, and recurrent crossing. Instead, diverse germplasm accessions are employed as mapping panel to identify relationship between markers and trait under study. Since, these diverse accessions were the results of the plethora of random meiotic events amongst these accessions, relatedness for recombination events are uncontrolled (Verdeprado et al. 2018). Due to uncontrolled meiotic recombination within diverse accessions, association mapping approach can be suited well for high resolution identification of genes or QTLs with high resolution (100–1000 kb) which are tightly linked to diverse phenotypic traits (Mackay et al. 2009). Pearl millet germplasm accessions have very high levels of heterozygosity and heterogeneity which poses difficulty in association mapping, and hence, limited strategies were delivered to dissect genetic diversity (Kannan et al. 2014). Association study conducted on pearl millet reveals factors responsible for flowering time variation at phytochrome C (PHYC) locus (866 bp). A significant association between genetic variation and phenotypic traits was observed using a linear mixed model (Saidou et al. 2009). Further, accessions were explored using an association study that revealed an extra 100 bp region adjoining the PHYC genes using MCMC (Markov chain Monte Carlo) method for identification of tightly linked markers (75 SNPs and INDELS) adjoining 6 kb (PHYC) genomic region (Saidou et al. 2014).

GWAS study on three germplasm sets of pearl millet was conducted by using Genome-wide SNP data to compute linkage disequilibrium decay (LDD). GWAS on 288 testcross progenies of PMiGAP lines were carried out for 20 traits, and about 1054 marker-trait associations (MTAs) have been identified for 15 traits including panicle yield (9), stover dry matter yield (5), tillers per plant (147), grain number per panicle (91), fresh stover yield (38), grains per square meter (75) panicle diameter (1), panicle length (3), panicle harvest index 1), plant population (68), panicle number (246), 1000 grain weight (10), plant height (344), grain harvest index (5), and grain yield (11). Moreover, these MTAs explained 9–27% of the total phenotypic variation, and the selected markers were found on pg1 and pg5 commonly for yield-related parameters and stresses (Varshney et al. 2017). MTAs between 250 SSR and 17 genetic markers with grain zinc and iron content was developed using 130 diversified lines of pearl millet revealed that markers Xipes0224, Apsmp2213 and Xpsmp2086 showed significant association with zinc content in grain on LG6 and LG4, and marker Xicmp3092 had a strong association with iron content on LG7 (Anuradha et al. 2017; Gemenet et al. 2015). Moreover, GWAS analysis using 34 SSR markers and 250 full-sib progenies revealed that marker allele Xpsmp2237_230 was associated with grain yield on LG7. Xpsm2224_157 was linked with plant height on LG7, Xicmp3058_193 was strongly associated with stover dry matter yield on LG6, and marker alleles Xpsmp2224_157, Xpsm2233_260, and Xpsmp2077_136 were associated with panicle length on LG7, LG5, and LG2, respectively (Kannan et al. 2014). Another association analysis study was conducted under high and low phosphorus conditions in West Africa with the available 285 DArT markers using phenotypic data of 151 PMiGAP lines. The results indicated that the pgpb12954 marker showed a strong association with grain yield and the pgpb11603 DArT marker showed a significant association with time of flowering (Gemenet et al. 2015).

Comparative genomics in pearl millet

The first published map of pearl millet had a genetic length of only 303 cM (Liu et al. 1994). Comparative genetic maps were constructed of pearl millet genome with foxtail millet and used to describe homoeology between genomes of pearl millet, foxtail millet and rice (Devos et al. 2000). Pearl millet genome is differentiated from rice genome by several structural rearrangements while strong relatedness has been observed between foxtail millet and pearl millet. Pearl millet genome carried one or probably two duplications in linkage group 1 (LG1) and group 4 (LG5). Endogenous gibberellic acid levels suggested that genes d1, d2, and d4 are recessive dwarfing genes which may be similar to the rye dwarfing genes ct1 and ct2 (Devi et al. 1994) and these genes were mapped in the centromeric regions of rye chromosomes 7R and 5R (long arm), respectively. Similarly, these regions are homoeologous to LG4 and LG2 segments of pearl millet, respectively (Devos et al. 2000). Comparative analysis of global accessions and landraces of pearl millet was carried out using 500 pearl millet accessions consisting of 252 global accessions, and 248 Senegalese landraces using genotyping by sequencing (GBS) technique of Pstl-Mspl reduced representation libraries. A total of 83,875 SNPs were identified as a genomic resource for population improvement for pearl millet. Comparative genomics for population improvement will provide an insight for the improvement of these climate-resilient crops (Hu et al. 2015). The genomic analysis of elephant grass (Cenchrus purpureus) provides an insight in discovery of enzyme-coding gene families responsible for biosynthesis of anthocyanidins and flavonoids content. Evolutionary analysis revealed that the subgenome A of elephant grass and pearl millet may have originated from common ancestor (Yan et al. 2021).
Transcriptome analysis in pearl millet

The draft genome of pearl millet has been sequenced in 2017, but short reads cannot be mapped due to incomplete genome annotations. Next-generation sequencing such as PacBio sequencing (single-molecule real-time sequencing), enables the production of full-length transcript making it ideal for transcript recovery (Abdelghany et al. 2016; Wang et al. 2017) but this has the limitations of low throughput (Rhoads and Au 2015). Transcription profiling in pearl millet identified 10 differentially expressed genes that validated for drought tolerance, namely Calmodulin-like proteins, Aspartic proteinase Oryzasin, DnaJ-like protein, Rab7, Glyoxalase, Putative beta-1,3-glucanase, Inosine-5’-monophosphate, Ascorbate peroxidase, and Abscisic stress ripening protein (Choudhary and Padaria 2015). Two sequencing techniques were used to study the differences and similarities in response of pearl millet under drought and heat stress. A total of 63,090 new transcripts and 26,299 new genes were identified and functional annotations were boosted by 20%. The results revealed regulation of 5039 DEGs and 4603 DEGs under drought and heat stress, respectively. Under drought and heat stress, 6484 and 6920 genes were expressed differentially and 1881 genes were expressed under both stresses (Sun et al. 2020). Likewise, RNA-Seq approach was used to understand the pathways involved in response to drought stress in pearl millet using two inbred lines ICMB843 (drought tolerant) and ICMB 863 (less tolerant), which were procured from ICRISAT. About 25 up-regulated genes in ICMB843 and 8 genes in ICMB 863 were found to be involved in photosynthesis and its related pathways. Pathway and gene function analysis revealed that drought response in pearl millet was mainly regulated by pathways related to photosynthesis, plant hormone signal transduction and mitogen-activated protein kinase signaling. Results obtained from the analysis revealed molecular mechanisms dealing with drought stress for genetic improvement of pearl millet crop (Dudhate et al. 2018).

Genetic analysis of important adaptive and agronomic traits in pearl millet

With the advancement of sequencing and phenotyping techniques, various important genetic loci and genes which are agronomically important have in the past few decades been identified in pearl millet using several technologies like GWAS, QTL mapping, genotyping by sequencing in past few decades (Table 2). The regulatory mechanisms of the genes are still unknown and our understanding of genetic resources provides an opportunity for designing of super pearl millet for various purposes (Fig. 2). Below we summarized in detail the genome-wide dissection of agronomically important traits and their related genes.

Grain yield and grain quality

A three major QTLs with less QTL * environment interaction for grain yield were identified in a post-flowering moisture environment (Bidinger et al. 2007). Results obtained from association mapping in pearl millet accessions indicated that the SNP101 of PHYC gene showed a significant association for grain yield-related parameters (Saidou et al. 2009). Association studies on pearl millet revealed that Xibmsp11/AP6.1, a known SNP marker that is present on an acetyl CoA carboxylase gene, is highly associated with yield traits (Grain harvest index and grain yield). InDels markers, Xibmcpo9/AP10.2 and Xibmcpo9/AP10.1, present on chlorophyll a/b binding protein genes, are strongly associated with stay green and grain yield traits (Gemenet et al. 2015). Much emphasis should be given on grain quality and grain yield-related traits to dissect the variability present among pearl millet accessions.

Plant height and flowering

A significant association between PHYC gene and flowering time has been reported in pearl millet inbred lines which is having a major role in pearl millet adaptation in different regions (Saidou et al. 2009). Further analysis of PHYC locus revealed association of Pg7830 and Pg7840 genes with flowering time in pearl millet but none of them were found to be associated with plant height (Saidou et al. 2014). Polymorphism of PgMADS11 associated with phenotypic variation has been identified and it might be possible that polymorphism can also be located in the neighbouring region that is in linkage disequilibrium with the revealed polymorphism. Actual sequenced data revealed that INDEL polymorphism is located in the intron of PgMADS11, although it is highly similar to a MADS-box gene family (Mariac et al. 2011). Pearl millet accessions collected in different years were evaluated for early flowering for PHYC gene (Vigouroux et al. 2011). Fifteen flowering genes and 20 random genes were amplified in 33 cultivated and 13 wild relatives of pearl millet. The results indicated that all flowering genes showed high density which was identified using BLASTn. Flowering genes in pearl millet accessions include: PgEMF2, PgFY, PgGFI, PgHD1, PgHD3a, PgHD6, PgLFL1, PgMADS11, PgPHYA, PgPHYB, PgPHYC, PgPIPK1, PgPRR73, PgPRR95 and PgTFL1 (Clotault et al. 2012). Another study was conducted on three flowering candidate genes namely, PgPHYC, PgDwarf8, and PgHd3a, and results suggested that PgDwarf8, and PgHd3a were targeted through selection in the course of domestication. The gene, PgHd3a has been the target of selection in domestic population because this
Table 2 Major QTLs genes for important input and output traits in Pearl millet

| Trait                  | Markers                   | Gene name                                      | Linkage group | Phenotype/pathways                  | References               |
|------------------------|---------------------------|------------------------------------------------|---------------|-------------------------------------|--------------------------|
| **Flowering time**     | Xibmsp27                  | Alanine glyoxylate aminotransferase           | LG2           | Causes variation in the flowering time | Sehgal et al. (2012)    |
|                        | Xibmsp9                   | Uridylate kinase                              | LG2           |                                     |                          |
|                        | Xibmsp12                  | Acyl CoA oxidase                              | LG2           |                                     |                          |
|                        | Xibmsp60                  | MADS-box                                      | LG2           |                                     |                          |
|                        | Xibmsp14                  | Serine-threonine protein kinase               | LG2           |                                     |                          |
|                        | Xibmsp24                  | Ubiquitin conjugating enzyme                  | LG2           |                                     |                          |
|                        | Xibmsp31                  | HD3                                           | LG2           |                                     |                          |
|                        | Xibmsp15                  | Zinc finger C×8-C×5-C×3-H type                | LG2           |                                     |                          |
|                        | SNP                       | PgMADS11                                      |               | Characterization of early and late flowering in landraces | Diack et al. (2017)   |
|                        | InDel                     | PgPHYC                                        |               |                                     |                          |
|                        | Xibmsp27                  | Alanine glyoxylate aminotransferase           | LG2           | Responsible for enhanced grain yield | Sehgal et al. (2012)    |
|                        | Xibmsp9                   | Uridylate kinase                              | LG2           |                                     |                          |
|                        | Xibmsp12                  | Acyl CoA oxidase                              | LG2           |                                     |                          |
|                        | Xibmsp60                  | Dipeptidyl peptidase IV                      | LG2           |                                     |                          |
|                        | Xibmsp34                  | MADS-box                                      | LG2           |                                     |                          |
|                        | Xpsm592-Xpsm356           |                                                | LG2 (6.91)    | Enhanced grain yield                | Yadav et al. (2004)     |
|                        | Xpsm464-Xpsm716           |                                                | LG4 (2.32)    |                                     |                          |
|                        | Xpsm588-Xpsm514           |                                                | LG6(2.21)     |                                     |                          |
| **Grain quality biofortification** | Xpsm2214-Xipes142        | Zinc (Zn)                                     | LG3 (4.68)    | Increased Zinc level in the accessions | Kumar et al. (2016, 2017)|
|                        | ppgb10531-ppgb9130        |                                                | LG1 (25.36)   |                                     |                          |
|                        | Iron (Fe)                 | Xpsm588-Xpsm716                               | LG4B          | Enhanced Iron content level         | Kumar et al. (2016, 2017)|
|                        | ppgb9502-ppgb6039         |                                                | LG7           |                                     |                          |
|                        | ppgb6825-Xipes195         |                                                |               |                                     |                          |
| **Plant Height**       | D1/d1                     |                                                | LG1           | Responsible for the plant height of pearl millet | Kumar et al. (2017); Kannan et al. (2014)|
|                        | D2/d2                     |                                                | LG4           |                                     |                          |
|                        | Pgbpb6112-pgbpb9106       |                                                | LG1           |                                     |                          |
|                        | Pgbpb9498-Xipes017        |                                                | LG1           |                                     |                          |
|                        | Xipes203-Xpsmp2273        |                                                | LG1           |                                     |                          |
| **Biomass**            | Xpsm592-Xpsm443           |                                                | LG2           | Increased biomass production        | Yadav et al. (2003)     |
|                        | Xpsm716-Xpsm265           |                                                | LG4           |                                     |                          |
|                        | Xpsm87.1-Xpsm514          |                                                | LG6           |                                     |                          |
| Trait                  | Markers          | Gene name                  | Linkage group | Phenotype/pathways                                                                 | References                                                                 |
|------------------------|------------------|----------------------------|---------------|-----------------------------------------------------------------------------------|-----------------------------------------------------------------------------|
| Leaf rolling           | Xibmsp60         | *Dipeptidyl peptidase IV*  | LG2           | Identified genes conferring leaf rolling in pearl millet                           | Sehgal et al. (2012)                                                       |
|                        | Xibmsp34         | *Serine-threonine protein kinase* | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp14         | *Ubiquitin conjugating enzyme* | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp24         | *HD3*                      | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp31         | *Acetyl CoA carboxylase*    | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp11         | *Zinc finger C-x8-C-x5-C-x3-H type* | LG2           |                                                                                   |                                                                             |
| Delayed leaf senescence| Xibmsp15         | *Photolyase*                | LG2           | Identified locus in the linkage group conferred delayed leaf senescence           | Sehgal et al. (2012)                                                       |
|                        | Xpsmp2066        |                            | LG2           |                                                                                   |                                                                             |
| Panicle Length         | los1             |                            | LG1           |                                                                                   | Ponct et al. (2000);                                                        |
|                        | los2             |                            | LG2           |                                                                                   | Kumar et al. (2017)                                                        |
|                        | pgpb9647-Xicmp3027|                            | LG5           |                                                                                   |                                                                             |
|                        | Xicmp3056        |                            | LG2           |                                                                                   |                                                                             |
| Drought tolerance      | Xpsmp2237        |                            | LG2           | Conferring drought tolerance                                                     | Sehgal et al. (2012); Choudhary and Padaria (2015)                         |
|                        | Xctm03           |                            | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp53         |                            | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp55         |                            | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp51         |                            | LG2           |                                                                                   |                                                                             |
|                        | Xpsmp2072        |                            | LG2           |                                                                                   |                                                                             |
|                        | Xpsmp2237        | *Aux/IAA, GH3 & SAUR GIDI, PIF* | LG2           |                                                                                   | Dudley et al. (2018)                                                       |
|                        | Xpsmp2237        | *PP2C, SnRK2, ABF*         | LG2           |                                                                                   |                                                                             |
|                        | Xctm03           | *ETR, TRE, MKK6 &ChiB*     | LG2           |                                                                                   |                                                                             |
|                        | Xibmsp53         | *PVR, MAP3K17/18, CAT1, MAPK1 & MAPK6* | LG2           |                                                                                   |                                                                             |
|                        | S3_216179591     |                            | LG7           | Aerial Biomass                                                                    | Debieu et al. (2018)                                                       |
|                        | S6_64437341      |                            | LG6           |                                                                                   |                                                                             |
|                        | S3_13047576      |                            | LG6           |                                                                                   |                                                                             |
|                        | Pgl_GLEAN_10002188 | *Salt stress protein*    | LG2           |                                                                                   | Shivhare et al. (2020)                                                      |
|                        | Pgl_GLEAN_10005403 | *Glutamine synthetase root isozymes* | LG2           |                                                                                   |                                                                             |
|                        | Pgl_GLEAN_10011050 | *Lateral root formation*  | LG2           |                                                                                   |                                                                             |
|                        | GAPDH and EF-1α  |                            | LG3           | Involved in primary metabolism and cellular processes                              | Shivhare and Lata (2016)                                                   |
A gene plays a very well-known function in flower transition (Lakis et al. 2012). Seeds from 16 early-flowering, 13 late-flowering, and 16 wild relatives of pearl millet were used to characterize the early and late-flowering in accessions using microsatellite loci (Dussert et al. 2015). Landraces of pearl millet from Senegal were used for characterization of early- and late-flowering using SSRs markers. Allelic diversity of \( \text{PgPHYC} \) and \( \text{PgMADS11} \) genes were assessed in landraces of pearl millet and the results revealed that the early flowering landraces carried allele for early flowering at \( \text{PgPHYC} \) locus and \( \text{PgMADS11} \) locus showed significant differences in genotype frequencies (Diack et al. 2017). In another study, Diack et al. (2020) identified one SNP that is located on \( \text{PgPPR} \) gene encodes a pentatricopeptide repeat protein belonging to ATP DNA-binding cassette family involved in plant resistance and defense. Additionally, they identified one SNP on \( \text{PgAAO1} \) gene that encodes an indole-3-acetaldehyde oxidase.

**Tillering, spike length, and other agronomic traits**

Tillering and spike length are agronomically important traits in pearl millet breeding. A study showed that the SNP101 of \( \text{PHYC} \) gene was significantly associated with spike length and basal diameter. Moreover, most of the \( \text{PHYCSNPs} \) were tightly linked, so the same association was found for the whole \( \text{PHYC} \) amplified region (Saidou et al. 2009). Association mapping in pearl millet revealed that there was a significant marker traits association for various agronomic traits such as stover dry matter yield, fresh stover yield, panicle harvest index, spike length, and so on (Varshney et al. 2017). For tillering, one SNP on \( \text{PgHK4} \) gene was identified which...
encodes a histidine kinase but no SNPs were identified for biomass (Diack et al. 2020).

### Biotic stress tolerance

Pearl millet is a robust crop and has a low vulnerability to insect-pests and diseases in comparison to other crops. Downy mildew, blast, smut, and ergot are common pearl millet diseases which causes severe damage and ultimately reduces crop yield. To this end, host plant resistance (HPR) is an effective and efficient strategy to cope up with biotic stresses and it does not incur an additional cost.

Downy mildew disease of pearl millet, caused by *Sclerospora graminicola* is causing economic damage in Africa and India. Screening of breeding lines and germplasm accessions provides an insight for the identification of various sources of resistance (Singh et al. 1997). QTLs from the resistant parent were mapped to linkage groups 1, 2, and 4 and it has been observed that these QTLs are effective against pathogen isolates from Sudan, Mali, Nigeria and India. After the mapping of QTLs, marker-assisted selection is supposed to be an effective approach for breeding against pathogens (Breese et al. 2003). SCAR marker was used for screening of downy mildew in parents (ICMR-01004 and ICMR-01007), F₁, F₂, and F₃ progenies. Primer pair ISSR-22 was found to be polymorphic with a fragment of 1.4 kb band in both parents and F₂ populations, and it was then cloned, catalogued and sequenced and linkage map was established on linkage group 4 (LG4) (Jogaiah et al. 2014).

The leaf spot or blast disease, caused by *Pyricularia grisea*, has arisen as a serious disease of pearl millet (Rai et al. 2012). Screening of breeding and germplasm accessions of pearl millet led to the identification of resistant lines which can be further used for development of blast-resistance hybrids (Sharma et al. 2013; Goud et al. 2016).

Six blast resistance genotypes (ICMB 97222, ICMB93333, ICMR 11003, IP 21187-P1 and ICMR 06222) of pearl millet were crossed with two susceptible genotypes (ICMR-01004 and ICMR-01007) for rust resistance (Thakur et al. 2011). The advent of molecular markers emerged as a tool for dissecting QTL associated with resistance. A mapping population of 168 F₇ RILs was used for the construction of DArT- and SSR-based linkage maps and screened for rust resistance. Three QTL on linkage groups 1, 4 and 7 were identified for pearl millet rust resistance explaining 58% of the observed phenotypic variation in rust reaction. Linkage group 1 (LG1), was novel QTL identified for rust resistance and is thought to confer a durable slow-rusting phenotype (Ambawat et al. 2016).

### Abiotic stress tolerance

#### Drought tolerance

Drought, caused by low rainfall and its erratic distribution, adversely affect the growth and development of crop plants. In pearl millet drought tolerance has remained a strategic research issue, so pearl millet response to drought has been studied exhaustively. QTL for drought tolerance has been found to contribute to differences in photosynthetic pigments and ROS scavenging enzymes in pearl millet accessions. From studied QTL, APX activity was found to be increased in tolerant genotypes but the SOD and CAT activity remain unchanged. The presence or absence of drought-related QTL did not contribute to photosynthetic pigment molecules (Kholova et al. 2011).

Grain filling stage in pearl millet is the most sensitive stage to drought stress leading to reduction in grain size and grain number (Fussell et al. 1991). Pearl millet germplasm association panel was established recently and exploited for association mapping of drought tolerance traits. SNP in *CoA carboxylase* genes showed a significant association with panicle yield, grain harvest index and grain yield whereas an InDel was found to be significantly associated with grain yield and stay green traits under drought conditions (Sehgal et al. 2015). Four QTLs contributing to enhanced transpiration have been identified in accessions of...
Illumina data of pearl millet (Sun et al. 2020). The data were used as a reference sequence to examine the identified using RNA sequencing and Pacbio-sequencing. Under drought condition, Debieu et al. (2018) evaluated 188 inbred lines for the identification of QTLs associated with agronomic traits using genotyping by sequencing (GBS). After filtering of 3,168,971 unfiltered SNPs, 392,493 have been identified with an average density of 2.5 per 10 kb. Four marker-trait associations were identified on chromosome 6 for stay greens trait and two SNPs were found to be significantly associated with biomass production under early drought stress conditions. Out of the two SNPs identified for biomass production, one SNP was mapped between two predicted genes *Pgl_GLEAN_10037359* and *Pgl_GLEAN_10037360* whereas the second SNP was mapped being located between two predicted genes *Pgl_GLEAN_10036946* and *Pgl_GLEAN_10036945*. It has been observed that early drought stress in lines led to reduction in grain and biomass production but limited changes were observed in grain weight (Debieu et al. 2018). The first report on validation of reference genes in pearl millet was given by Shivhare and Lata (2016), and result revealed two best reference genes whose specificity was confirmed by relative expression of *PgAP2 like-ERF* gene. This study can facilitate fastidious discovery of genes related to stress-tolerance (Shivhare and Lata 2016).

Transcriptomic analysis of pearl millet identified 6799 and 1253 differentially expressed genes (DEGs) in ICMB 843 and ICMB 863 respectively, and RNA sequencing for drought-responsive genes confirmed 7 genes using reverse-transcription PCR (Dudhate et al. 2018). Transcriptomic analysis conducted by Jaiswal et al. (2018) revealed 19,983 differentially expressed genes, 7595 transcription factors, and a hub of 45 genes having a regulatory gene network. Moreover, 34,652 putative markers, 4192 SSRs, 12111SNPs and 6249 InDels were reported and the results were validated using qPCR for 13 selected genes. Shivhare et al. (2020), identified 1129 DEGs on all the seven chromosomes of pearl millet except chromosome 4. The majority of genes were found to be present and mapped on chromosome 2 (196) followed by chromosome 3 (171), chromosome 5 (168), chromosome 6 (164), chromosome 7 (140) and chromosome 4 (108). A recent report on transcriptome analysis identified 2792 transcription factors and, 1223 transcriptional regulators, from which 315 transcription factors and 128 transcriptional regulators were expressed under drought condition and a total of 6484 genes for drought stress were identified using RNA sequencing and Pacbio-sequencing. The data were used as a reference sequence to examine the Illumina data of pearl millet (Sun et al. 2020).

In a recent study, Zhang et al. (2021) explored the mechanism of drought tolerance of pearl millet by comparing physiological and transcriptomic data under drought and controlled condition. It has been reported that during stress, a total of 12 genes were upregulated in which some genes are associated with drought stress in other species such as *ADH1*, *FisH*, and *CCCH*. Additionally, genes namely *SnRK2* and *PP2C* were found to have changes in their expression level that participate in ABA Signaling pathways (Zhang et al. 2021).

**Heat tolerance**

Reproductive and seedling stages are greatly affected by high temperature as the optimum temperature for normal crop growth is 33–34 °C. In southern and western Africa and India, the temperature of soil surfaces often exceeds 45 °C and may sometimes reaches up to 60 °C, causing poor plant growth because the pearl millet seedlings are more prone to high temperature during their first ten days of seedling (Peacock et al. 1993). Pearl millet has emerged as a remunerative and productive crop in western and northern parts of India (Yadav and Rai 2013). High temperature during flowering stage of pearl millet causes flower sterility, and ultimately leading to extreme reduction in seed set, lowering of grain yield (Gupta et al. 2015; Djanaguiraman et al. 2018). A clone from pearl millet heat stress-responsive EST database was used as a DNA probe, as it showed maximum homology to *PgHsc70* gene, for screening of *Pennisetum* heat stress cDNA library using plaque hybridization method. Nucleotide sequencing of the 5′ flanking promoter region of the gene identified a heat-shock element and a protective activity was observed against the damage caused by heat stress (Reddy et al. 2010). Another gene, *PgHsp90* consisting of three exons and three introns, was identified, characterized, cloned and the sequence was analysed for heat stress in pearl millet (Reddy et al. 2011). Nitnavare et al. (2016) reported a gene, *PgHsp10* from pearl millet and characterized for heat stress using qRT-PCR analysis for gene expression in response to abiotic stresses with special reference to heat stress and it has been revealed that this gene consists of two introns and three exons. A recent report on transcriptome analysis identified 2792 transcription factors, 1223 transcriptional regulators, from which 318 transcription factors and 149 transcriptional regulators were expressed under heat stress condition and a total of 6920 genes for heat stress were identified using RNA sequencing and Pacbio-sequencing data as a reference sequence to examine the Illumina data of pearl millet (Sun et al. 2020). Recently, a study was conducted in pearl millet roots to explored the changes both at physiological and transcriptional level under heat stress. It has been observed that trehalose was accumulated in roots at 3 h to 7 h of heat stress. Additionally, POD activity increased gradually from 3 to 7 h of heat stress. At transcriptional
level, HSFs, bZIP and bHLHs were main identified transcription factors expressed under heat stress. A total of 16 bZIPS, 7 HSFs and 18 bHLH genes were identified which were expressed differentially under heat stress condition (Sun et al. 2021).

Salinity tolerance

Salinity stress severely limit the crop production. The adverse effects of salinity on plants includes osmotic stress, oxidative stress, nutrient constraints and ion toxicity (Singh et al. 2021c; Shrivastava and Kumar 2015). According to a study, the reduced shoot nitrogen content and enhanced sodium and potassium content are related with salinity stress tolerance in pearl millet (Dwivedi et al. 2011). Various salinity stress-related genes have been identified in pearl millet but function of only some salinity-responsive genes such as \(PgDH\) (dehydrin), \(PgNH\) (Na+/H+ antiporter), \(PgV-\)

DAC (voltage-dependent anion channel), and \(PgLEA\) (late embryogenesis abundant) have been studied (Agarwal et al. 2010; Reddy et al. 2012; Singh et al. 2015; Verma et al. 2007). To understand the mechanism of salinity tolerance at physiological and molecular level, pearl millet salinity tolerant (ICMB 01222) and susceptible (ICMB 081) line were subjected to de novo transcriptomic profiling. A total of 11,627 DGEs have been identified in both lines. In the tolerant line, 2965 unigenes were found to be upregulated whereas 2964 were downregulated whereas in susceptible line, 2243 unigenes were upregulated and 3473 were downregulated. Physiological analysis showed that soluble sugar content was higher in tolerant line under salt stress (Shinde et al. 2018).

Hybrid development in pearl millet

Hybrid development in pearl millet was initiated after recognition of cytoplasmic male sterile lines viz., Tift18A and Tift23A, and these lines being released as male sterile lines led to the development of hybrid breeding. The first pearl millet hybrid, HB1, was released by PAU in India in 1965 (Burton 1907, 1965; Burton and Athwal 1967). Genetic male sterility, caused by nuclear genes, has been identified in several crops like maize, rice, soybean and others, but little information is available in pearl millet (Yadav et al. 2010; Gupta et al. 2012). In pearl millet, genetic male sterility has been studied in male sterile lines, Vg 272 and IP 482, and the variation in the expression of sterility has been observed when crossed with different isogenic and non-isogenic lines, leading to an alteration in \(ms_2\) allele (Rao and Devi 1983).

Cytoplasmic male sterility (CMS) has been studied well in pearl millet and is used commonly for hybrid seed production (Yadav and Rai 2013). CMS systems in pearl millet were developed using genetic crosses, not protoplast fusion. For commercial hybrid production, this system requires male sterile (A-), maintainer (B-), and restorer (R-) lines in which male sterility is controlled by sterility factors and fertility restorer (rf) allele (Islam et al. 2015). Restriction fragment length polymorphism (RFLP) analysis in pearl millet identified five CMS cytoplasm that was different from each other because of the rearrangement of mitochondrial genes. The formation of \(A_4\), \(A_1\), \(A_3\), and \(A_{egp}\) CMS system was due to rearrangement of \(coxl\) gene whereas the \(atp6\) and \(cox3\) gene alterations led to formation of \(A_4\) CMS system (Delorme et al. 1997). Additionally, two CMS sources 66A and 67A were identified as a genetic stock at PAU which were later named as \(A_2\) and \(A_3\) CMS sources (Athwal 1965). Subsequently, various other CMS sources have been reported by different centers in different genetic stocks. Gero, a CMS source, was identified by Ibadan Nigeria (Aken'Ova and Chheda 1981), and two novel sources, PT732A and \(A_5\), \(A_{egp}\), were discovered from genetic pools and genetic sources of IC RISAT (Appadurai et al. 1982; Rai 1995). Moreover, a new CMS source ex-Bornu, a cross between wild relatives of pearl millet and landrace from Senegal and \(A_4\), was identified which is different from the existing CMS sources and is utilized for hybrid seed production (Govindaraj et al. 2019).

Conclusion and future prospects of pearl millet breeding

With an increasing population, global demand for feed, energy and food is increasing day by day thereby posing an opportunity for exploitation and development of sustainable food for various end uses. Pearl millet is an important cereal crop with immense potential but breeding has been lagging, compared to other cereals. Genomic approaches should be encouraged in pearl millet breeding programs. Genomics could be helpful for a better understanding of genetic and genomic insights of pearl millet by investigating the genetic diversity present in the wild species or germplasm accessions (Fig. 3). Moreover, populations for functional genomics, such as mapping populations, natural diverse panels, molecular modules, GWAS and genetic engineering could help dissect the useful variations present in the population (Singh et al. 2021b). Targeted genes/genomic regions/alleles, through introgression and breeding selection, can be replaced in the elite varieties via screening of breeding lines or genetic stocks with the help of genomic selection and functional genomics. During the past decades, considerable progress in pearl millet molecular breeding and genomics has been made, but still more work is needed to comprehensively design pearl millet as a multi-purpose crop.

Firstly, attention should be paid to the validation and identification of genes controlling important agronomic
traits, especially molecular modules, which are emerging topics in the post-genomic era. For example, flowering time and plant height are the two important traits of pearl millet and major genes and QTL have been identified controlling flowering time and plant height but their association between stay green and grain size is poorly understood. Brown midrib in pearl millet is associated with decreased lignin content and this trait offers greater palatability and digestibility (Sattler et al. 2010) but QTL associated with brown midrib are unknown yet. Moreover, purple foliage of pearl millet is controlled by three alleles Rp1 Rp2, and rp (Hanna and Burton 1992) and the association analysis of pearl millet genotypes revealed that the foliar color locus was mapped in the linkage group 4 (LG4) (Azhaguvel et al. 2003). More QTL controlling brown color foliage should be mapped from the wild relatives, elite varieties or germplasms of pearl millet.
The long bristle of panicle is an important trait providing an advantage in deterring birds feeding on grain. It has been reported that the bristle panicle trait is controlled by the dominant genes but none of the genes have been identified thereby proving an opportunity to identify the genes and map them in the linkage groups. In future, in-depth examination should be conducted for unravelling the genetic variations, phenotypic variations, and characterization of novel alleles for agronomically important genes.

Secondly, more pearl millet genome sequences are needed because their utilization and exploitation in pearl millet are far from enough when compared to wheat, maize and rice genomes. Sequencing of landraces, wild relatives and improved cultivars of pearl millet will provide novel genomic variability for the study of pearl millet diversification and domestication of various end - uses. As a multi-purpose crop, pearl millet has a unique form of evolution. Therefore, domestication is a good model for evolutionary study purposes. The genetic basis of complex agronomic traits is essential to understand various end-use pearl millet improvements. Single genome sequence does not represent the whole genomic structure of a species. But pan-genome analysis, collecting genes at clad level, provides an opportunity to identify the genetic variability present in the whole genome with the help of sequencing of multiple individuals of a species.

Finally, it is necessary to consolidate the genome-based tools and technologies in pearl millet breeding programs thereby provide an opportunity for the development of “Super pearl millet” with key traits. The most common input traits are to improve the resistance against abiotic (drought, heat, and salt) stresses and biotic (diseases and insect pests) whereas output traits include grain yield, grain quality, flowering time, and plant height. Precision molecular breeding of pearl millet should be implemented based on different traits viz., pearl millet grain is characterized by low lignin content for easy digestibility and palatability and biofortification of pearl millet for high nutrient content. The future breeding goal is to enhance the protein and starch content and reduce lignin content. Improvement in the low crude protein, high starch content, and reduced tannin content is the major breeding objective of forage pearl millet breeding whereas increasing the tillering, multi-cut, and rapid growth should also be considered in the breeding program.

Moreover, modern emerging approaches can accelerate the breeding cycle of pearl millet and encourage breeders to develop superior varieties for various end uses but still, there is a long way to go. Identification and pyramiding of supper alleles controlling agronomically important traits using molecular modules at genome level is still a task for pearl millet breeding. Genomic selection should be carried out for genotyping and phenotyping of pearl millet accessions and the model should be selected according to the type of population and gene-environment interactions. Genome editing, an emerging tool in the genomic era, plays a significant role in the identification of genes and their function for crop improvement but there is lack of published work in pearl millet breeding. The application of this system is greatly relying on the transformation efficiency and is still much lower in crops like sorghum than those of other major crops. Optimization of the transformation system is essential to advance the CRISPR/Cas9 application in pearl millet breeding. CRISPR/Cas9 can be used to control the expression of miRNA genes through genetic modifications for crop improvement. Thus, there is a great scope for research on pearl millet in reducing anti-nutrients, thus making it further enriched cereal.

The journey of plant breeding has significantly transcended from the large resource-intensive field trials to the molecular level. With the dawn of molecular markers, several techniques have found their way towards population improvement. Although tremendous progress has been achieved in the identification of genetic loci underlying various agronomically important traits, the epigenomes, pan-genomes, and other disciplines should be integrated for dissection of genetic diversity and the superior alleles underlying complex agronomic traits. Moreover, efficient breeding techniques should be incorporated with the novel breeding approaches to bring beneficial changes to the genetic breeding of pearl millet

Authors contributions MS conceptualized the study and wrote the manuscript. UN prepared the original draft and edited the manuscript.

Data availability Not applicable.

Declarations

Conflict of interest The authors have no competing financial interests.

Consent to participate Not applicable.

Consent for publication Not applicable.

Ethics approval Not applicable.

References

Abdelghany SE, Hamilton M, Jacobi JL, Ngam P, Devitt N, Schilkey F, Benhur A, Reddy ASN (2016) A survey of the sorghum transcriptome using singlemoleculelong reads. Nat Commun 7:11706
Abraham P, Alimpia PD, Bdiyya BS (2019) Inheritance of resistance to ergot disease in a diallel cross of pearl millet (Pennisetum glaucum (L.) R. Br.). Tanzania J Agric Sci 18:50–58
Acevedo-Garcia J, Spencer D, Thieron H, Reinstädl er A, Hammond-Kosack K, Phillips AL, Panstruga R (2017) mlo-based powdery mildew resistance in hexaploid bread wheat generated by a non-transgenic TILLING approach. Plant Biotechnol J 15:367

Agarwal P, Agarwal PK, Joshi AJ, Sopory SK, Reddy MK (2010) Overexpression of PgDREB2A transcription factor enhances abiotic stress tolerance and activates downstream stress-responsive genes. Mol Biol Rep 37(2):1125–1135

Aken’Ova ME, Chhedra HR (1981) A new source of cytoplasmic—genic male sterility in pearl millet I. Crop Sci 21:984–985

Ambawat S, Senthivel S, Hash CT, Nepolean T, Rajaram V, Eshw ar K, Srivastava RK (2016) QTL mapping of pearl millet rust resistance using an integrated DAR-T- and SSR-based linkage map. Euphytica 209(2):461–476

Amblard S, Pernez J (1989) The identification of the cultivated pearl millet (Pennisetum) amongst plant impressions on pottery from Oued Chebbi (Dhar Oualata, Mauritania). Afr Archaeol Rev 7:117–126

Ambli K, Mullainathan L (2015) Chlorophyll and morphological mutants of pearl millet (Pennisetum tphoides (Burn.) stapf. Var. CO (cu) 9. Eur J Exp Bio 5(3):72–77

Anuradha N, Satyavathiti CT, Bharadwaj C, Nepolean T, Sankar SM, Singh SP (2017) Deciphering genomic regions for high grain iron and zinc content using association mapping in pearl millet. Front Plant Sci 8:242

Aparna K, Nepolean T, Srivastava RK, Kholová J, Rajaram V, Kumar S, Vadez V (2015) Quantitative trait loci associated with constitutive traits control water use in pearl millet [Pennisetum glaucum (L.) R. Br.]. Plant Biol 17(5):1073–1084

Appadurai R, Raveendran TS, Nagarajan C (1982) A new male sterility system in pearl millet. Indian J Genet Plant Breed 52:832–834

Athwal DS (1965) Hybrid baija-1 marks a new era. Ind Farm 15:6–7

Azhaguvel P, Hash CT, Rashangamy S, Sharma A (2003) Mapping the d1 and d2 dwarfing genesand the purple foliage color locus P in pearl millet. J Hered 94:155–159

Bandillo N, Raghavan C, Muyco PA, Sevilla MAL, Lobina IT, Dilla-Errmita CJ, Tung CW, McCouch S, Thomson M, Mauleon R, Singh RK, Gregorio G, Redoña E, Leung H (2013) Multi-parent analyses of isonuclear male-sterile lines. Theor Appl Genet 126:961–968

Devi KU, Rao MK, Croker SI, Hedden P, Rao SA (1994) Coleoptile length, gibberellin sensitivity and concentrations in five non-allelic dwarf mutants of pearl millet—Pennisetum glaucum (L.) R. Br. Plant Growth Regul 15(3):215–221

Devos KM, Pittaway TS, Reynolds A, Gale MD (2000) Comparative mapping reveals a complex relationship between the pearl millet genome and those of foxtail millet and rice. Theor Appl Genet 100(2):190–198

Diack O, Kane NL, Leaver CJ (1997) Cytoplasmic-nuclear male sterility in pearl millet: comparative RFLP and transcript analyses of isonuclear male-sterile lines. Theor Appl Genet 95:961–968

Diack O, Kanfany G, Gueye MC, Sy O, Fofana A, Barnaud A (2017) New genetic insights into pearl millet diversity as revealed by characterization of early-and late-flowering landraces from Senegal. Front Plant Sci 8:818

Diack O, Kanfany G, Gueye MC, Sy O, Fofana A, Tall H, Kane NA (2020) GWAS unveils features between early-and late-flowering pearl millets. BMC Genom 21(1):1–11

Djanguguiram M, Perumal R, Ciampitti IA, Gupta SK, Prasad PVV (2018) Quantifying pearl millet response to high temperature stress:thresholds, sensitive stages, genetic variability and relative sensitivity of pollenan pistil. Plant Cell Environ 41:993–1007

Dudhate A, Shinde H, Tsugama D, Liu S, Takano T (2018) Transcriptional profiling in pearl millet (Pennisetum glaucum LR Br.) for identification of differentially expressed drought responsive genes. Physiol Mol Biol Plants 21(2):187–196

Choudhary M, Padaria JC (2015) Transcriptional profiling in pearl millet (Pennisetum glaucum LR Br.) for identification of differentially expressed drought responsive genes. Physiol Mol Biol Plants 21(2):187–196

Clark JD (1962) The spread of food production in sub-Saharan Africa. J Afr Hist III 2:211–228

Clotault J, Thuillet AC, Buiron M, De Mita S, Couderc M, Haussmann BI, Vigneur Y (2012) Evolutionary history of pearl millet (Pennisetum glaucum [L.] R. Br.) and selection on flowering genes since its domestication. Mol Biol Evol 29(4):1199–1212

Crossa J, Perez P, Hickey J, Burgueno J, Ornella L, Ceron-Rojas J, Zhang X, Dreisigacker S, Babu R, Li Y, Bonnett D, Mathews K (2014) Genomic prediction in CIMMYT maize and wheat-breeding programs. J Hered 112:48–60

D’Andrea AC, Klee M, Casey J (2001) Archaeological evidence for pearl millet (Pennisetum glaucum) in Sub-saharan West Africa. Antiquity 75:341–348

Dauwyler HD, Pong-Wong R, Villanueva B, Woolliams JA (2010) The impact of genetic architecture on genome-wide evaluation methods. Genet 185:1021–1031

Debieu M, Bine S, Passot S, Grondin A, Akata E, Gangashetty P, Laplaze L (2018) Response to early drought stress and identification of QTLs controlling biomass production under drought in pearl millet. PLoS ONE 13(10):e0201635

Devi Acquà M, Gatti DM, Pea G, Cattonaro F, Coppons F, Magris G et al (2015) Genetic properties of the MAGIC maize population: a new platform for high-definition QTL mapping in Zea mays. Genome Biol 16(1):1–23

Delorme V, Keen CL, Rai KN, Leaver CJ (1997) Cytoplasmic-nuclear male sterility in pearl millet: comparative RFLP and transcript analyses of isonuclear male-sterile lines. Theor Appl Genet 95:961–968

Dwivedi S, Upadhyaya H, Senthivel S, Hash C, Fukunaga K, Diao X, et al (2011) Millets: genetic and genomic resources. Plant Genet Resour: crop Evolution 6:117–126

Elshire RJ (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS ONE 6:e19379

FAO (2020) The State of Food Security and Nutrition in the World FAOSTAT 2020 Food and Agriculture organization of the United Nations. FAOSTAT statistical database. https://www.fao.org/faostat

Fussell GK, Bidinger FR, Bieler P (1991) Crop physiology and breeding for drought tolerance. Res Dev Field Crops Res 27:183–199

FAOSTAT (2020) Food and Agriculture organization of the United Nations. FAOSTAT statistical database. https://www.fao.org/faostat

Springer
Jogaiah S, Sharathchandra RG, Raj N, Vedamurthy AB, Shetty HS, Jarquin D, Howard R, Liang Z, Gupta SK, Schnable JC, Crossa J (2020) Jaiswal S, Antala TJ, Mandavia MK, Chopra M, Jasrotia RS, Tomar A, Islam A, Mian MA, Rasul G, Bashar K, Johora FT (2015) Developing phosphorus uptake and utilization efficiency in West African pearl millet inbred lines. Field Crops Res 171:54–66

Goud TY, Sharma R, Gupta SK, Uma Devi G, Gate VL, Boratankar M (2016) Evaluation of designated hybrid seed parents of pearl millet for blast resistance. Indian J Plant Protect 44:83–87

Govindaraj M, Rai KN, Cherian B, Pteier WH, Kanatti A, Shivade H (2019) Breeding biofortified pearl millet varieties and hybrids to enhance millet markets for human nutrition. Agriculture 9:106

Guo TT, Yu XQ, Li XR, Zhang HZ, Zhu CS, Flint-Garcia S, McMullen MD, Holland JB, Szalma SJ, Wisser RJ, Yu JM (2019) Optimized designs for genomic selection in hybrid crops. Mol Plant 12:390–401

Gupta PK, Kumar J, Mir RR, Kumar A (2010) Marker-assisted selection as a component of conventional plant breeding. Plant Breed Rev 33:145–217

Gupta S, Rai KN, Govindaraj M, Rao A (2012) Genetics of fertility restoration of the A4 cytoplasm-nuclear male sterility system in pearl millet. Czech J Genet Plant Breed 48:87–92

Gupta SK, Rai KN, Singh P, Ameta VL, Gupta SK, Jayalekha AK (2015) Seed set variability under high temperatures during flowering period in pearl millet (Pennisetum glaucum L. (R. Br.). Field Crops Res 171:41–53

Hanna WW, Burton GW (1992) Genetics of red and purple plant color in pearl millet. J Hered 83:386–388

Harlan JR (1971) Agricultural origins: centres and non-centres. Science 174:468–474

Hort S, Welham T, Kelly S, Kaneko T, Sato T, Tabata S, Parinske M, Wang TL (2007) TILLING mutants of Lotus japonicus reveal that nitrogen assimilation and fixation can occur in the absence of nodules-enhanced sucrose synthase. Plant Physiol 144:806–820

Hu Z, Mbacké B, Guèye MC, Sy O, Bouchet S, Morris GP (2015) Population genomics of pearl millet (Pennisetum glaucum (L.) R. Br.): Comparative analysis of global accessions and Senegalese landraces. BMC Genomics 16(1):1–12

Huang BE, George AW, Forrest KL, Kilian A, Hayden MJ, Morell MK, Cavanagh CR (2012) A multiparent advanced generation intercross population for genetic analysis in wheat. Plant Biotechnol J 10(7):826–839

Hwang JE, Jang DS, Lee KJ, Ahn JW, Kim SH, Kang SY, Kim DS, Kim JB (2017) Identification of gamma ray irradiation-induced mutations in membrane transport genes in a rice population by TILLING. Genes Genet Syst 91:245–256

Islam A, Mian MA, Rasul G, Bashkar H, Jhohara FT (2015) Development of component lines (CMS, maintainer and restorer lines) and their maintenance using diversified cytosources of rice. Rice Res 3:1–5

Jaiswal S, Antala TJ, Mandavia MK, Chopra M, Jasrotia RS, Tomar RS, Kumar D (2018) Transcriptomic signature of drought response in pearl millet (Pennisetum glaucum (L.) and development of web-genomic resources. Sci Reports 8(1):1–16

Jarquin D, Howard R, Liang Z, Gupta SK, Schnable JC, Cossa J (2020) Enhancing hybrid prediction in pearl millet using genomic and/or multi-environment phenotypic information of inbreds. Front Genet 10:1294

Jogaih S, Sharathchandra RG, Raj N, Vedamurthy AB, Shetty HS (2014) Development of SCAR marker associated with downy mildew disease resistance in pearl millet (Pennisetum glaucum L.). Mol Biol Rep 41(12):7815–7824

Kanfany G, Serba DD, Rhodes D, Amand PS, Bernardo A, Gangashetty PI, Bai G (2020) Genomic diversity in pearl millet inbred lines derived from landraces and improved varieties. BMC Genom 21(1):1–12

Kannan B, Senapathy S, Bhasker Raj AG, Chandra S, Muthiah A, Dhanapal AP, Hash CT (2014) Association analysis of SSR markers with phenology, grain, and stover-yield related traits in pearl millet (Pennisetum glaucum (L.) R. Br.). Sci World J 2014:562327

Khokhlova J, Hash CT, Kočová M, Vadez V (2011) Does a terminal drought tolerance QTFL contribute to differences in ROS scavenging enzymes and photosynthetic pigments in pearl millet exposed to drought? Env Exp Bot 71(1):99–106

Kover PX, Valdar W, Trakalo J, Scarcelli N, Ehrenreich IM, Puruganan MD et al (2009) A multiparent advanced generation inter-cross to fine-map quantitative traits in Arabidopsis thaliana. PLoS Gen 5(7):e1000551

Kumar S, Hash CT, Thirunavukkarasu N, Singh G, Rajaram V, Rathore A, Senapathy S, Mahendrakar MD, Yadav RS, Srivastava RK (2016) Mapping quantitative trait loci controlling high iron and zinc content in self and open pollinated grains of pearl millet [Pennisetum glaucum (L.) R. Br.]. Front Plant Sci 7:1636

Kumar S, Hash CT, Nepolean T, Satyavathi CT, Singh G, Mahendrakar MD, Yadav RS, Srivastava RK (2017) Mapping QTFLs controlling flowering time and important agronomic traits in pearl millet. Front Plant Sci 8:1731

Lakis G, Navascués M, Rekima S, Simon M, Remigereau MS, Leveugle M, Robert T (2012) Evolution of neutral and flowering genes along pearl millet (Pennisetum glaucum) domestication. Front Genet 3:170

Liang Z, Gupta SK, Yeh CT, Zhang Y, Ngu DW, Kumar R (2018) Phenotypic data from inbred parents can improve genomic prediction in pearl millet hybrids. G3: Genes Genomes Genet 8(7):2513–2522

Liu CJ, Witcombe JR, Pittaway TS, Nash M, Busso CS, Hash CT, Gale MD (1994) An RFLP-based genetic map of pearl millet (Pennisetum glaucum). Theor Appl Genet 89:481–487

Mackay TF, Stone EA, Ayroles JF (2009) The genetics of quantitative traits: challenges and prospects. Nat Rev Genet 10:565–577

Maganal SJ (2018) Linkage and QTL mapping for blast resistance in pearl millet (Pennisetum glaucum (L.) R. Br.) 2507 (Doctoral dissertation, JAU, JUNAGADH)

Mariac C, Jehin L, Saindou AA, Thuillier AC, Coulenc M, Sire P, Vigoouroux Y (2011) Genetic basis of pearl millet adaptation along an environmental gradient investigated by a combination of genetic scan and association mapping. Mol Ecol 20(1):80–91

Maryono MY, Indriatama WM, Human S (2020) Performance and estimation genetic variability of M3 pearl millet (Pennisetum glaucum) populations. In: IOP conference series: earth and environmental science, vol 484, no 1, pp 012021. IOP Publishing

Marzec M, Gruszka D, Tylec P, Szarejko I (2016) Identification and functional analysis of the HvD14 gene involved in strigolactone signaling in Hordeum vulgare. Physiol Plant 158:341–355

Maxted N, Kell SP (2009) Establishment of a Global Network for the In Situ Conservation of Crop Wild Relatives: Status and Needs. FAO Commission on Genetic Resources for Food and Agriculture, Rome. pp 266

Mehran H, Lee DH, Moradi MH, Cho C, Nasseri-Kheil M, Ibáñez-Escriche N (2017) Predictive performance of genomic selection methods for carcass traits in Hanwoo beef cattle: impacts of the genetic architecture. Genet Sel Evol 49(1):1–13

Mendiondo GM, Gibbes DJ, Szurman-Zubrzycka M, Korn A, Marquez J, Szarejko I, Maluszynski M, King J, Axcell B, Smart K (2016) Enhanced water-logging tolerance in barley by manipulation of expression of the N-end rule pathway E3 ligase PROTEOLYSIS 6. Plant Biotechnol J 14:40–50
Miller MR, Dunham JP, Amores A, Cresko WA, Johnson EA (2007) Rapid and cost-effective polymorphism identification and genotyping using restriction site associated DNA (RAD) markers. Genome Res 17:240–248

Moose SP, Mumm RH (2008) Molecular plant breeding as the foundation for 21st century crop improvement. Plant Physiol 147:969–977

Morgan RN, Wilson JP, Hanna WW, Ozias-Akins P (1998) Molecular markers for rust and undecaryllicaria leaf spot disease resistance in pearl millet. Theor Appl Genet 96:413–420

Nituavare RB, Yeshvekar RK, Sharma KK, Vadez V, Reddy MK, Reddy PS (2016) Molecular cloning, characterization and expression analysis of a heat shock protein 10 (Hsp10) from Pennisetum glaucum (L.), a C 4 cereal plant from the semi-arid tropics. Mol Biol Reports 43(8):861–870

Ongom PO, Ejeta G (2018) Mating design and genetic structure of a multi-parent advanced generation intercross (MAGIC) population of sorghum (Sorghum bicolor (L.) Moench). G3: Genes, Genomes, Genetics 8(1):331–341

Paterson AH (2009) The Sorghum bicolor genome and the diversification of grasses. Nature 457:551–556

Patil KS, Gupta SK, Marathi B, Danam S, Thatikunta R, Rathore A (2020) African and Asian origin pearl millet populations: genetic diversity pattern and its association with yield heterosis. Crop Sci 60:3035–3048

Peacock JM, Soman P, Jayachandran R, Rani AU, Howarth CJ, Thomas A (1993) Effects of high soil surface temperature on seedling survival in pearl millet. Exp Agric 29:215–225

Poncet V (2000) Genetic control of domestication traits in pearl millet (Pennisetum glaucum L., Poaceae). Theor Appl Genet 100:147–159

Poncet V (2002) Comparative analysis of QTLs affecting domestication traits between two domesticated x wild pearl millet (Pennisetum glaucum L., Poaceae) crosses. Theor Appl Genet 104:965–975

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(6):648–658

Poncet V, Lamy F, Devoz KM, Gale MD, Sarr A, Robert T (2000) Genetic control of domestication traits in pearl millet (Pennisetum glaucum L., Poaceae). Theor Appl Genet 100:147–159

Punnum SM, Wallace JG, Knoll JE, Hyma KE, Mitchell SE, Buckler ES, Varshney RK, Singh BP (2016) Development of a high-density linkage map and tagging leaf spot resistance in pearl millet using genotyping-by-sequencing markers. Plant Genome 9:1–13

Purugganan MD (2019) Evolutionary insights into the nature of plant domestication. Cur Biol 29:705–R714

Rai KN (1995) A new cytoplasmic-nuclear male sterility system in pearl millet. Plant Breed 114:445–447

Rai KN, Gowda CLL, Reddy BVS, Sehgal S (2008) The potential of sorghum and pearl millet in alternative and health food uses. Comp Rev Food Sci Food Saf 7:340–352

Rai KN, Yadav OP, Gupta SK, Mahala RS, Gupta SK (2012) Emerging research priorities in pearl millet. J SAT Agric Res 10:1–4

Rajaram V et al (2013) Pearl millet [Pennisetum glaucum (L.) R. Br.] consensus linkage map constructed using four RIL mapping populations and newly developed ESTSSSRs. BMC Genomics 14:159

Rani A, Taunk J, Jangra S, Yadav RC, Yadav NR, Yadav D, Yadav HP (2021) Development of advance pearl millet lines tolerant to terminal drought stress using marker-assisted selection. Vegetus 1–11

Rao MK, Devi KU (1983) Variation in expression of genic male sterility in pearl millet. J Hered 74:34–38

Reddy PS, Mallikarjuna G, Kaul T, Chakradhar T, Mishra RN, Sopory SK, Reddy MK (2010) Molecular cloning and characterization of gene encoding for cytoplasmic Hsc70 from Pennisetum glaucum may play a protective role against abiotic stresses. Mol Genet Genom 283(3):243–254

Reddy PS, Thirulugachandar V, Vaishnavi CS, Aakrati A, Sopory SK, Reddy MK (2011) Molecular characterization and expression of a gene encoding cytosolic Hsp90 from Pennisetum glaucum and its role in abiotic stress adaptation. Gene 474(1–2):29–38

Reddy PS, Reddy GM, Pandey P, Chandrasekar K, Reddy MK (2012) Cloning and molecular characterization of a gene encoding late embryogenesis abundant protein from Pennisetum glaucum: protection against abiotic stresses. Mol Biol Rep 39(6):7163–7174

Rendon-Anaya M, Herrera-Estrella A (2018) The advantage of parallel selection of domestication genes to accelerate crop improvement. Genome Biol 19:147–149

Rhoads A, Au KF (2015) PacBio sequencing and its applications. Genom Proteom Bioinf 13(5):278–289

Saidou AA, Mariaic C, Luong V, Pham JL, Bezançon G, Vigouroux Y (2009) Association studies identify natural variation at PHYC linked to flowering time and morphological variation in pearl millet. Genet 182:899–910

Saidou AA, Cloutard J, Couderc M, Mariaic C, Devos KM, Thuillet AC (2014) Association mapping, patterns of linkage disequilibrium and selection in the vicinity of the PHYTOCHROME C gene in pearl millet. Theor Appl Genet 127:19–32

Sanghani JM, Sanghani AO, Kothari VV, Raval SS, Kahodariya JH (2018) The SSR based linkage map construction and identification of QTLs for blast (Pyricularia grisea) resistance in pearl millet (Pennisetum glaucum (L.) r. br.). J Pharmacog Phytochem 7(2):3057–3064

Sattler SE, Funnell-Harris DL, Pedersen JF (2010) Brown midrib mutations and their importance to the utilization of maize, sorghum, and pearl millet lignocellulosic tissues. Plant Sci 178:229–238

Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Presting GG (2009) The B73 maize genome: complexity, diversity, and dynamics. Science 326(5956):1112–1115

Schrag TA, Schipprack W, Melchinger AE (2019) Across-years prediction of hybrid performance in maize using genomics. Theor Appl Genet 132:933–946

Sehgal D, Rajaram V, Armstead IP, Vadez V, Yadav YP, Hash CT, Yadav RS (2012) Integration of gene-based markers in a pearl millet genetic map for identification of candidate genes underlying drought tolerance quantitative trait loci. BMC Plant Biol 12(1):1–13

Sehgal D, Skot L, Singh R, Srivastava RK, Das SP, Taunk J et al (2015) Exploring potential of pearl millet germplasm association panel for association mapping of drought tolerance traits. PLoS ONE 10(5):e0122165

Serba DD, Muleta KT, St. Amand P, Bernardino A, Bai G, Perumal R, Bashir E (2019) Genetic diversity, population structure, and linkage disequilibrium of pearl millet. Plant Genome 12(3):e018091

Serba DD, Yadav RS, Varshney RK, Gupta SK, Mahalingam G, Srivastava RK (2020) Genomic designing of pearl millet: a resilient crop for arid and semi-arid environments. In: Kole C (ed) Genomic designing of climate-smart cereal crops. Springer, Cham, pp 221–286

Severune H, Daniela S, Simon GK, Bettina K, Thomas W, Gerhard H, Mirjam NF, James B, Thomas P, Miliena O (2015) The maize disease resistance gene Htn1 against northern corn leaf blight encodes a wall-associated receptor-like kinase. Proc Natl Acad Sci USA 112:8780–8785

Sharma R, Upadhyaya HD, Manjunatha SV, Rai KN, Gupta SK, Thakur RP (2013) Pathogenic variation in the pearl millet blast pathogen, Magnaporthe grisea and identification of resistance to diverse pathotypes. Plant Dis 97:89–195
Shivhare R, Asif AH, Lata C (2020) Comparative transcriptome analysis of response of pearl millet root to heat stress. J Agro Crop Sci. https://doi.org/10.1111/jac.12496

Szurman-Zubrzycycka ME, Zbiesczyk J, Marzec M, Jelonek J, Chmielewska B, Kurowska MM, Krok M, Daszkowska-Golec A, Guzy-Wrobelka J, Gruszczka D (2018) HorTILLUS—a rich and renewable source of induced mutations for forward/reverse genetics and pre-breeding programs in barley (Hordeum vulgare L.). Front Plant Sci 9:216

Tang D, Cheng ZK (2018) From basic research to molecular breeding—Chinese scientists play a central role in boosting world rice production. Genom Proteom Bioinf 16:389–392

Thakur RP, Sharma R, Rao VP (2011) Screening Techniques for Pearl-Millet Diseases. Information Bulletin No. 89. Patancheru: National Crops Research Institute for the Semi-Arid Tropics, 56.

Thiel T, Michalek W, Varshney RK, Graner A (2003) Exploiting EST databases for the development and characterization of gene-derived SSR-markers in barley (Hordeum vulgare L.). Theor Appl Genet 106:411–422

Tibbs Cortes L, Zhang Z, Yu J (2021) Status and prospects of genomewide association studies in plants. Plant Genome 14(1):e20077

Till BJ, Reynolds SH, Weil C, Springer N, Burtner C, Young K, Bowers E, Codomo CA, Enns LC, Odden AR, Greene EA, Comai L, Henikoff S (2004) Discovery of induced point mutations in maize genes by TILLING. BMC Plant Biol 4:12–19

Tripathi AD, Mishra R, Maurya KK, Singh RB, Wilson DW (2019) Estimates for world population and global food availability for global health. In: Singh RB, Watson RR, Takahashi T (eds) The role of functional food security in global health. Academic Press, Cambridge, pp 3–24

Upadhyaya (2009) Augmenting the pearl millet core collection for enhancing germplasm utilization in crop improvement. Crop Sci 49:573–580

Upadhyaya (2011) Development of pearl millet minicore collection for enhanced utilization of germplasm. Crop Sci 51:217–223

Varshney RK, Chetani, Thudi M, Mariac C, Wallace J, Qi P, Xu X (2017) Pearl millet genome sequence provides a resource to improve agronomic traits in arid environments. Nature Biotechnol 35(10):969–976

Vrederop H, Kretzschmar T, Begum H, Raghavan C, Joyce P, Lakshmanan P (2018) Association mapping in rice: basic concepts and perspectives for molecular breeding. Plant Produc Sci 21:159–176

Verma D, Singla-Pareek SL, Rajagopal D, Reddy MK, Sopory SK (2007) Functional validation of a novel isoform of Na(+)-H+ antiporter from Pennisetum glaucum for enhancing salinity tolerance in rice. J Biosci 32(3):621–628

Vigouroux Y, Mariac C, de Mita S, Pham JL, Gérard B, Kapran I (2011) Selection for earlier flowering crop associated with climatic variations in the Sahel. PLoS ONE 6:e19563

Wang M, Wang P, Liang F, Ye Z, Li J, Chen C, Pei L, Wang F, Hu J, Tu L (2017) A global survey of alternative splicing in allopolyploid cotton: landscape, complexity and regulation. New Phytol 217(1):163

Weller JL, Ezra E, Ron M (2017) Invited review: a perspective on the future of genomic selection in dairy cattle. J Dairy Sci 100(11):8633–8644

Xu YB, Li P, Zou C, Lu YL, Xie CX, Zhang XC, Prasanna BM, Olsen MS (2017) Enhancing genetic gain in the era of molecular breeding. J Exp Bot 83:2641–2666

Xu YB, Liu XS, Fu JJ, Wang HW, Wang JK, Huang CL, Prasanna BM, Olsen MS, Wang GY, Zhang AM (2020) Enhancing geneticgain through genomic selection: from livestock to plants. Plant Comm 1:100005

Yadav OP, Rai KN (2013) Genetic improvement of pearl millet in India. Agric Res 2:275–292

Yadav R, Bidinger F, Hash C, Yadav Y, Yadav O, Bhatnagar S, Howarth C (2003) Mapping and characterization of QTLs in interactions
for traits determining grain and stover yield in pearl millet. Theor Appl Genet 106:512–520
Yadav RS, Hash CT, Bidinger FR, Devos KM, Howarth CJ (2004) Genomic regions associated with grain yield and aspects of post-flowering drought tolerance in pearl millet across stress environments and tester background. Euphytica 136:265–277
Yadav D, Gupta SK, Kulkarni VN, Rai KN, Behl RK (2010) Inheritance of A1 system of cytoplasmic-nuclear male sterility in pearl millet [Pennisetum glaucum (L.) R. Br.]. Cereal Res Commun 38:285–293
Yadav OP, Rai KN, Rajpurohit BS, Hash CT, Mahala RS, Gupta SK (2012) Twenty-five years of pearl millet improvement in India. In: All India Coordinated Pearl Millet Improvement Project (Jodhpur). 122
Yadav OP, Singh DV, Dhillon BS, Mohapatra T (2019) India’s evergreen revolution in cereals. Curr Sci 116:1805–1808
Yadav OP, Gupta SK, Govindaraj M, Sharma R, Varshney RK, Srivastava RK, Mahala RS (2021) Genetic gains in Pearl Millet in India: insights into historic breeding strategies and future perspective. Front Plant Sci 12:396
Yan Q, Wu F, Xu P, Sun Z, Li J, Gao L et al (2021) The elephant grass (Cenchrus purpureus) genome provides insights into anthocyanin accumulation and fast growth. Mol Eco Res 21(2):526
Yu J (2002) A draft sequence of the rice genome (Oryza sativa L. ssp. indica). Science 296:79–92
Yu XQ, Li XR, Guo TT, Zhu CS, Wu YY, Mitchell SE, Roozeboom KL, Wang DH, Wang ML, Pederson GA, Tesso TT, Schnable PS, Bernardo R, Yu JM (2016) Genomic prediction contributing to a promising global strategy to turbocharge gene banks. Nat Plants 2:16150
Zhang A, Ji Y, Sun M, Lin C, Zhou P, Ren J et al (2021) Research on the drought tolerance mechanism of Pennisetum glaucum (L.) in the root during the seedling stage. BMC Genomics 22(1):1–14
Zhou XC, Bai XF, Xing YZ (2018) A rice genetic improvement boom by next generation sequencing. Curr Issues Mol Biol 27:109–126

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.