World Journal of Advanced Research and Reviews
eISSN: 2581-9615 CODEN (USA): WJARAI
Cross Ref DOI: 10.30574/wjarr
Journal homepage: https://wjarr.com/

(Research Article)

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The role of scientific research in pearl millet improvement and its impact in Sub-Saharan Africa (SSA)

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World Journal of Advanced Research and Reviews, 2025, 28(03), 678-688

Publication history: Received on 28 October 2025; revised on 05 December 2025; accepted on 08 December 2025

Article DOI: https://doi.org/10.30574/wjarr.2025.28.3.4079

Abstract

Pearl millet is an essential food cereal for the SSA countries with regards to its fundamental role in food security and its impact on the rural economy. History enlightens us that pearl millet is a crop linked to this part of Africa. This paper investigates pearl millet genetic improvement in SSA focusing on breeding evolution in West Africa. The objectives of paper are (i) to illustrate genetic progress on pearl millet, (ii) to assess the existing technologies on pearl millet, and (iii) to assess the contribution of genetic improvement on pearl millet yield, area and production in SSA. Through documents research, the analysis revealed that most authors describe pearl millet as a species originated in SSA and the domestication of this crop dates back to 3000? BC. It is fundamental to understand that pearl millet yielded less than 200kg/ha to more than 900kg/ha due to scientific efforts. The National Agricultural Research Institutes in collaboration with ICRISAT have contributed to pearl millet development in Sub-Saharan Africa. Research contributed to establishing gene bank, tools for selection and species improvement and the use of pearl millet as a model in agricultural improvement technology. The development and application of high-throughput genomic tools speeded pearl millet improvement. Varietal selections move from population varieties to the development of high-performance hybrids. These efforts have resulted in the release of approximately 178 pearl millet varieties in 5 majors producing countries by 2023.

Keywords: Pearl millet; Breeding; Research; Yield; Biotechnologies, History; Sub-Saharan Africa

1. Introduction

The domestication of species appeared in several areas and its evolution has continued according to needs and cultural choices. However, Vavilov's concept of center of origin was coined to locate the geographical origin of species. It seems that the origin of pearl millet is at the time Africa and Asia. Many researchers concluded that this crop has been domesticated 4000 to 5000 yr ago in Sub-Saharan Africa (Harlan,1971; Munson, 1975; Brunken *et al*., 1977; Yadav and Rai, 2013) [1,2,3,4]. Several studies indicate that pearl millet has a cultural link with this part of Africa. Among crops in Africa, pearl millet is one of the most resilient to climate change. Today, Serba *et al.* (2020) and FAOSTAT (2021) [5,6] report that 29 million tons, which is the equivalent to a whole year maize production in the United States, is produced in these areas. The increase of pearl millet production covered 19.7 M ha in West Africa, of which 7 M ha in SSA. Thanks to support of technological progress in pearl millet production, and particularly cereal yields increased substantially. The mean yield increase to <0.74 tons ha^{-1}. This growth in pearl millet production is achieved with the contribution of the National agricultural research systems (NARS) and international institutions research (Evenson and Gollin, 2007) [7]. Indeed, the development of varietal creation and good cultivation practices for pearl millet played a central role in the development of this crop. It is to be noted that six major countries lead the breeding research programs on pearl millet in West Africa (ECOWAS-WAEMU-CILSS, 2016, 2018 ,2021) [8,9,10].

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However, the low support of many African countries for Norman Borlaug's Green Revolution over the past fifty years (1960-1990 period) has limited scientific research on pearl millet in Africa compared to India. As a result, SSA countries have not been able to build national research centers focused on biotechnologies. Finally, we conclude that the Green Revolution bypassed Sub-Saharan Africa countries (Pingali,2012) [11]. In many West Africa countries, the programs of plants breeding started with the research institutes of France as IRAT, CIRAD and IRD. Additionally, ICRISAT helped to build pearl millet program breeding in SSA with research projects on pearl millet and the creation a research center to Niger (1972 period). Scientific studies on the research programs over the last three decades have been focusing on crop genetic improvements with diverse new biotechnologies as hybrids creation and crop management technologies.

Furthermore, there are some new biotechnologies tools on pearl millet which started in 1991 by DFID-JIC-ICRISAT project (Gale *et al.,* 2005) [12]. The success of these tools has been the construction of the genetic linkage map of pearl millet (Liu *et al.*, 1994) [13]. Today the international efforts to increase genetic progress on pearl millet enabled to sequence and analyze its genome (Varshney *et al.,* 2017; Niazian and Niedbała, 2020; Mundada *et al*.,2022) [14,15,16]. So, the scientific research helped to increase pearl millet breeding (Yadav *et al*., 2021; Jency *et al*., 2021) [17,18]. Currently, new breeding techniques as gene editing (GE), epigenetic modification, and heritable targeted mutation are applied for pearl millet improvement (Burgarella *et al.,* 2018; Yan *et al*., 2023) [19,20]. The deepening of scientific research on plant improvement has become an essential component of breeding programs and proven to be useful for identifying novel genes for important traits (Yu *et al.,* 2008; Davey *et al.,* 2011; Serba and Yadav,2016) [21,22,23].

Most scientific studies of pearl millet have been conducted in Sub-Saharan Africa and India. Through the literature, little scientific research on pearl millet was found in Africa despite the full evolution that led to a strong dynamic in the crop. This paper traces the contributions of scientific research on the evolution of pearl millet in Sub-Saharan Africa.

2. Materials and Methods

For accomplishment of this work, articles from databases as Web of Science, Scopus, Science Direct, Google Scholar and others were consulted. The papers are from *Advanced in Agronomy*, *Field Crops Research;* The *American Jurgery* reviews. The decision on the inclusion or exclusion of websites was based on a set of criteria: literature from credible sources; specialized google search engine for academic literature; search across a number of journals on pearl millet. The keywords used in the research included "Works Done in world on Pearl Millet''**;** "Works Done in SSA on Pearl Millet *"*;" pearl millet breeding in West Africa"; "genetic progress of pearl millet", "pearl millet area and yield in SSA"; or "*pearl millet improvement in Sub-Saharan* '' or "*pearl millet gene pool*". The study was conducted in English and French. The bibliography of the selected papers was screened to identify additional papers.

2.1. History of research programs on pearl millet in Sub-Saharan Africa

The global research in SSA on agriculture was established by France. The research institutes involved are INERA (Burkina Faso), IER (Mali); INRAN (Niger) ITRAD (Tchad) and ISRA (Senegal). According to Balma (1992) [24], the history of pearl millet breeding program was initiated by IRAT in SSA. In 1960, the ongoing breeding programs in several countries of SSA decided to establish a regional cooperative for pearl millet grain yield trials. Between 1969-1974, pearl millet was collected and preserved by IBPGR in collaboration with ORSTOM and with the establishment of ICRISAT-Mali-Niger (Gill, 1991; Witcombe, 1999) [25,26]. To strengthen pearl millet program an active participation and collaboration with NARS staff on training, research and selection was essential. Evenson and Gollin (2007) [7] reported that the goal of national centers was to generate crop improvement. ICRISAT was entrusted with pearl millet genetic resources for the organization of scientific research on crops in the world (Upadhyaya *et al.,* 2007) [27]. One of nine collaborative research programs on pearl millet has been supported by the United States Agency for International Development on 34 years of research (1979-2013) as mentioned in the review INTSORMIL (2015). This program worked with 15 Africa countries on mass and recurrent selections for pearl millet breeding. The big part of the literature shows that pearl millet breeding program is set to improve the yields and to reduce harmful effects drought (Shetty *et al.*,1991; Balma,1992) [28,24]. A cereal adapted to high temperature; the collection of local materiel was important milestones. Several studies have analyzed the impact associated with the landrace *Iniadi* from SSA and the development a large-seeded and downy mildew resistant male sterile using through in world (Rai *et al.,*1995; Andrew and Kumar, 1996 and Manga, 2015) [29,30,31]. Indeed, the history of pearl millet research in SSA include the objectives presented in Table 1.

Table 1 West Africa program on pearl millet

West Africa Program on pearl millet	**Objectives**
	improvement pearl millet
	yield stability
	Agronomic techniques
	physiology of crop establishment and climate change
	Pearl millet protection
	Rotation and monoculture system, soil biological, composting techniques and manure;
	weeds as striga;
	germplasm collection
	germplasm conservation

2.2. Strengthening pearl millet research in taxonomic classification

Many efforts have been done over time to understand pearl millet center of origin, taxonomical position, genetic resource diversity and conservation for effective utilization in breeding programs as reported by Bisht *et al.* (2019) [32]. A better understanding of pearl millet taxonomy reveals that gene pools are crucial for genetic improvement. Despite recent taxonomic studies on pearl millet *Pennisetum glaucum* (*2n = 2x = 14*), placed *Pennisetum* within the genus *Cenchrus*, making *Cenchrus americanus* the accepted name for this species, (Hubbard 1954, Bor 1960, DeLisle 1963, Clayton 1972 and Gould 1975) [33,34,35,36,37], *Pennisetum* and *Cenchrus* as often treated as separate genera. It is among the oldest cereals that described since 1753 to 1809, in six different genera as, *Panicum, Holcus, Alopecuros, Cenchrus, Penicillaria,* and *Pennisetum.* Prem *et al.* (1998) [38] reported that *Pennisetum genus* contains chromosome numbers multiples of 5, 7, 8, and 9, i.e, *P. ramosum* (2*n* = 10), *P. typhoides* (2n = 14) and *P. purpureum* (2*n* = 28), *P. massaicum* (2*n* = 16, 32), and *P. orientate* (2*n* = 18, 36, 54). Research conducted by many authors in 1972 proposed a grouping of millets. This description has enabled to classify the different pearl millet cultivated. Indeed, three gene pools were found in millets as proposed by Harlan and Wet (1974 & 1982) [39,40]. Cytogenetics studies have classified cultivated and wild forms into different chromosomes. Bezançon *et al.* (1997) [41], Appa Rao et De Wet (1999) [42], Hanna (1986 &1987) [43,44] have shown that pearl millet primary gene pool has two subspecies with same number chromosomes (x=7), while the secondary gene pool also has two subspecies with different chromosomes (x=7 and x=9). The tertiary gene pool has five subspecies with same number chromosomes (x=9). Only the *P. purpurem* subspecies (x=7) from the secondary gene pool are fertile with primary gene pool subspecies. According in the literature, the primary gene pool appears to have been successful to transfer desirable traits, compared to the others gene pools. The relationships that exist between pearl millet and others neighboring species carried out by historians and archaeologists, in which one method is used alongside another, and then combined and assessed according to their relative value (Figure 1).

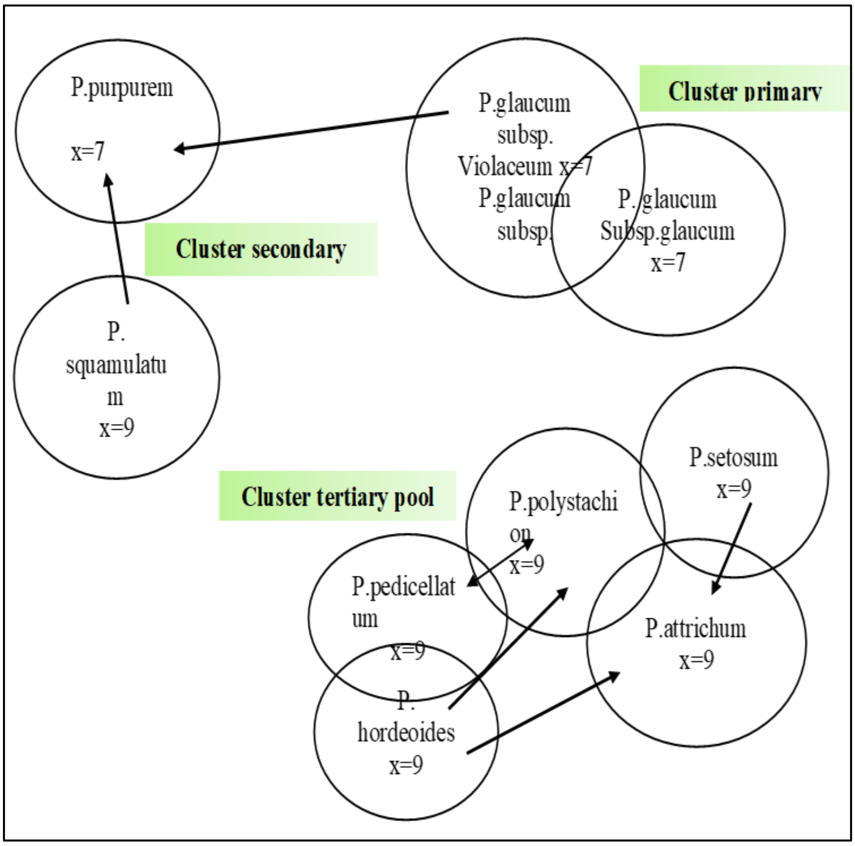

Figure 1 Pearl millet botanic classification (Bezançon *et al*.,1997, [41]

2.3. Efforts of genetic improvement accomplishments on pearl millet

The studies carried out by the International Agricultural Research Centers (IARCs), the Universities and national research programs have led to important advances on pearl millet improvement (Table 2). West African countries have provided genetic material to public and private institutions in increasing the research studies on pearl millet to develop resistance to biotic and abiotic factors as well as scientific tools (Manga, 2015; Varshney *et al.,* 2017) [45,14]. Starting from the 1970s, population improvement of pearl millet has been carried out by different institutes (ICRISAT, IRAT, ERA, ORSTOM) in Sub-Saharan Africa focusing on the development of improved open-pollinated varieties. Pearl millet has been used as model plant to understand quantitative genetic and heritability (Burton, 1951& 1959; Bilquez and LeComte, 1969; Virk, 1988; IPGRI and ICRISAT,1983; Pucher et al., 2016) [46,47,48,49,50,51]. With quantitative genetic of pearl millet, molecular markers to identify the genes that cause genetic variation in quantitative traits have been developed. Over the last twenty years, new analysis tools have become available to characterize pearl millet diversity, and most recently, the availability of the pearl millet genetic map (Liu *et al.,* 1994) [52]. Pearl millet genomic resources have been diversified, driven by rapid advancements in next-generation sequencing technologies, which will enhance germplasm management and crop improvement efforts. Now, RAPD, RFLP, DArT, SSR, ITS, ISSRs, SCAR marker, SRAPs molecular markers and SNPs methods have been used as a molecular screening tool in pearl millet (Qi *et al.,* 2004; Pedraza-Garcia *et al.,* 2010; Supriya *et al.,* 2011; Rajaram *et al.,* 2013; Vengadessan *et al.,* 2013; Jogaiah *et al.,* 2014; Mariac *et al.,* 2011; Kumar *et al.,* 2016) [53,54,55,56,57,58,59,60]. With the advancement in genome and transcriptome sequencing, pearl millet reference genome has been completed (Varshney *et al.,* 2017) [14]. Recently, Yan *et al.* (2023) [20] developed the pan-genome of pearl millet which may complement the current reference genome. Salson *et al.* (2023) [61] has shown that genetic resources of pearl millet in Africa allowed the improved assembly of the pearl millet reference genome. Several pearl millet DNA sequences are available in digital library platforms such as NCBI. The meteoric evolution of pearl millet in terms of scientific knowledge has enabled its genetic improvement. More than 1,318 research results on the quantitative genetics of pearl millet have been made available in the Science Direct database between 2001 and 2025. Research results associated with pearl millet in the *PubMed* database resulted with 2,012 research works between 1945 and 2025 (pubmed.ncbi.nlm.nih.gov/? term=pearl millet).

Table 2 Molecular markers developed for genotyping applications in pearl millet

Markers	Methods	Major finding	reference
AFLP, RAPD, RFLP, DArT, SSRs, ITS, ISSRs, SCAR, SRAPs, SNPs, Genomic SSRs, Whole-genome sequencing,	Association mapping, Genotyping-by-sequencing Whole-genome NGS GWAS, MWAS and mGWAS GBS-ddRAD approach Genome-wide identification genotyping-by-sequencing (GBS) Gene editing	Mapping QTLs, identified new polymorphic SSRs and SNPs, reference genome, identification about 1.76 Gb as size of genome, predicted 38,579 genes, 600 identical proteins groups, QTLs agronomic traits including leaf blast resistance, Genomic selection, Evolutionary genomic, epigenetics, haplotype-based breeding, genomic edition; Validation of the major QTL using NILs; improving drought tolerance	Li *et al.,* 1994 [13];; Varshney, *et al.*, 2017 [14]; Jogaiah *et al.,* 2014 [58]; Mariac *et al.,* 2011 [59]; Kumar *et al.,* 2016[60]; Yan *et al.,*2023 [61] Srivastava *et al.*, 2020 [62] Oumar *et al.*, 2008[63];

2.4. Pearl millet gene bank and distribution efforts

Scientists and farmers in SSA have contributed to pearl millet genetic resources activities including collection, exploration and evaluation. For some collection, the International Agricultural Research Centers and the Universities have provided funds for activities. Sub-Saharan Africa countries have been the cradle of pearl millet genetic resources collection as the realization of application of the precautionary principle in the management of pearl millet because the rate of collection is important. Pearl millet important germplasm collection in the Sahelian region began in 1975 thanks to international funding and under the direction of IBPGR. Collection missions were carried out in collaboration with national organizations and the ORSTOM. Nowadays, Yadav et al., (2017) [64] reported that 7.4 million accessions of various crops conserved in more than 1,750 gene banks, including 56,580 accessions of pearl millet in 70 gene banks of 46 countries. This diverse germplasm, also available in the countries where it was collected, provides significant variability for crop improvement. For example, pearl millet germplasm collected includes landraces and Wilds. From 1979 to 2009, the pearl millet germplasm collected was maintained at ICRISAT gene bank (Genesys, 2014; Yadav et al., 2017) [65,64]. Since 1980, more than 13,185 accessions have been received by the ICRISAT from SSA (Figure 2). Many research indicate that 22,888 pearl millet germplasm accessions come from 51 countries in 97 gene banks (Genesys,2016; Upadhyaya et al., 2016) [65,25]. In SSA, Burkina Faso has contributed with approximately 860 pearl millet accessions (Yadav et al., 2017; Table 3) [64]. The distribution of pearl millet germplasm to researchers and breeders in India and throughout the world is an important part of the activities of national research programs in SSA.

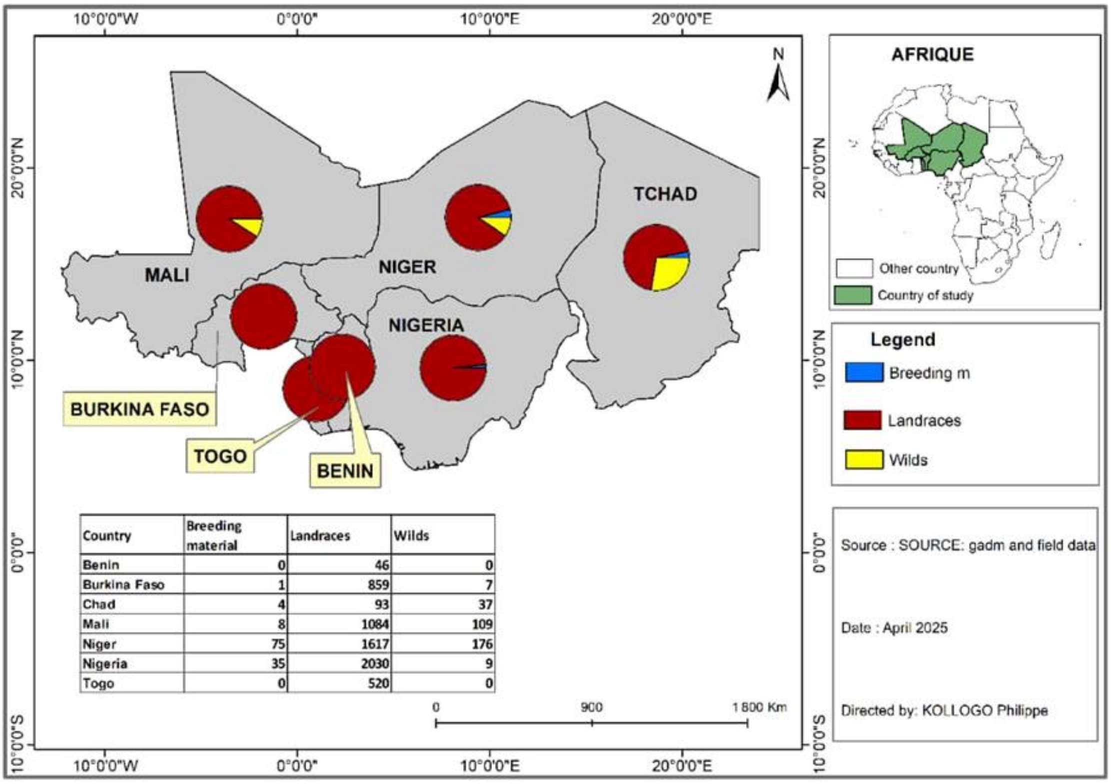

Figure 2 Contribution of few West Africa to ICRISAT genbank

Table 3 Germplasm collections in Burkina Faso details

Years	Institutions
1960	IRAT
1975	IPGRI/ICRISAT
1980	ICRISAT
1981	IPGRI/INERA/U. O/DSA/IRD
1982	IPGRI/BirminghamUniv/INERA/DSA /Ouagadougou Univ
1984-1986	IPGRI/U.O/INERA/IRD
1981-1986-1987	Around 350 accessions, including 3 wild populations (*Pennisetum monodii*)

2.5. Works Done in SSA on Pearl Millet OPVs and Hybrid Breeding

Research on the role of IARCs and NARS programs have been important on the development of pearl millet. Particularly in SSA, two varieties have been developed including OPVs and hybrids. Several studies indicated that the ICRISAT is the main partner of NARS programs for pearl millet breeding in SSA since the 1970s. Between 1976 and 1986, the United Nations Development Program has made concerted effort to fund different programs in Nigeria, Niger, Burkina Faso, Senegal and Sudan. Research conducted show that, six major countries with a research program on pearl millet are in West Africa (Niger, Nigeria, Mali, Chad, Burkina Faso and Senegal). Recently, the majority of literature indicates that pearl millet yield in SSA is around 917kg ha^{-1} (FAOSTAT 2021, cited by Bastos et al., 2022) [66,67]. In addition, 178 varieties were developed through this selection and disseminated in several countries via research program (ECOWAS-WAEMU-CILSS, 2008; Sattler & Haussmann, 2020) [68,69]. Hybrids are long-term plans in SSA with a total of 3 hybrids released in catalog. Research shows that the history of pearl millet breeding in SSA provided an important result to improve food security. Over the past 50 years history of pearl millet breeding, the exploitation of heterosis has permitted significant breakthroughs, leading to a substantial increase in production worldwide (Figure 3). Exploitation of heterosis in pearl millet was initiated in Africa by IRAT in the late 1970s, with the use of numerous top-crosses derived solely from parents of local cultivars. ICRISAT also engaged in the investigation of the exploitation of hybrid vigor in SSA. This trial included 10 TCH hybrids, their respective pollinators and two controls, was carried out in 9 sites in the West African sub-region. The first set of hybrids introduced in West Africa seed catalog. A total of 3 hybrids were released (ECOWA-WAEMU-CILSS, 2008; Sattler & Haussmann, 2020) [68,69] showing the low popularity of pearl millet hybrids in SSA.

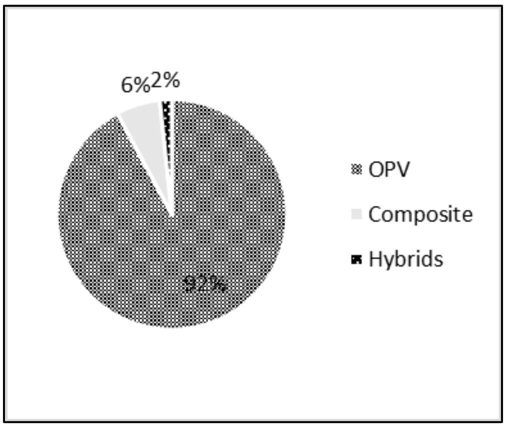

Figure 3 Details of genetic nature developed from different countries

2.6. The impact of genetic progress on yield, area and production of pearl millet in SSA

Over the past 20 years, genetic progress in pearl millet yields has increased in all Sub-Sahara African countries (Figure 4). National agricultural research institutions have been the key to effective efforts for development of pearl millet in West Africa. Effective deployment of pearl millet genetic improvements has led to the remarkable gains in productivity, from only 10 kg grain $ha^{-1}yr^{-1}$ (http://www.earthtrends.wri.org) in the 1965s, to 1188 kg ha^{-1} or less. The annual yield variation of pearl millet in SSA changed from -0.3% between 1987-1997 to 5.6% in 2007. During the same period, both the area under cultivation and total production of pearl millet also increased significantly." From 1984 to 2003, the area to pearl millet increased by 76% and production by 197% thanks to the access to disease resistant varieties (mildew, a real pearl millet disease) and improved pearl millet production.

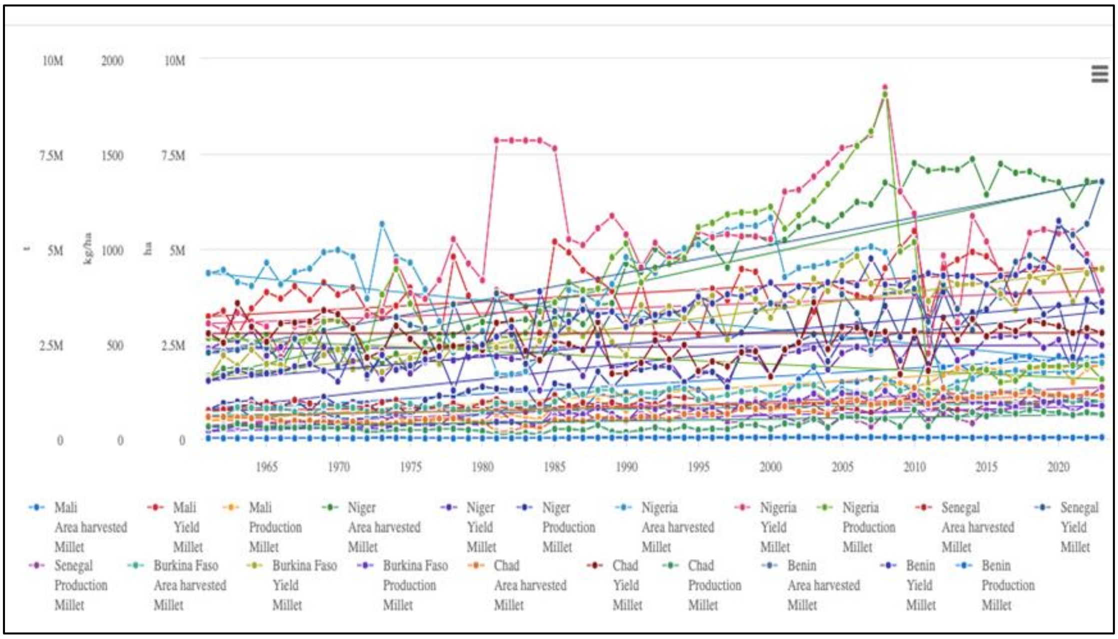

Figure 4 Changes of yield, area and production quantities of pearl millet in SSA between 1965-2025 (FAOSTAT)

3. Conclusion

The genetic improvement of pearl millet has been dynamic at the international level as in West African research programs. The strengthening of international collaborations, particularly in West Africa, has played a key role in pearl millet production systems. Several scientific contributions have been made on pearl millet with a view to its genetic improvement. The level of bioinformatics research for this species has increased knowledge on its traits of interest. Scientific research has increased pearl millet progress in yield, area and production in SSA during the last 20 years. There is a pipeline of pearl millet varieties available to growers. The existence of a large *ex situ* and *in situ* collection means that core collections can still be created for genetic improvement programs. However, we can keep in mind that these new varietal creation technologies are progressing slowly in Sub-Saharan Africa. Despite the contributions of advanced research on pearl millet, the crop benefits from few favorable development conditions in SSA. Given that it is considered as an ancestral and resilient crop, the lack of agricultural credit and adequate equipment, as is the case for maize and rice, this limits and sometimes wipes out scientific contributions. Technological innovations developed in controlled environments have not taken into account the agricultural realities of this crop in SSA. Pearl millet is still grown for human and animal consumption in SSA, and remains more diverse and complex. For a research program to serve rural development, it is essential to take into account this diversity of agricultural needs.

Compliance with ethical standards

Acknowledgments

The authors thank Joseph KI-ZERBO University and the Dept. of Genetic and plant breeding Research for supporting this work.

Disclosure of conflict of interest

All authors declare their consent for publication.

Author contribution:

The manuscript was edited and revised by all authors.

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