

Research and developmental strategies to hasten the improvement of orphan crops

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ABSTRACT

To feed the world's expanding population, crop breeders need to increase agricultural productivity and expand major crops base. Orphan crops are indigenously important crops with great potential because they are climate resilient, highly nutritious, contain nutraceutical compounds, and can improve the livelihood of smallholder farmers and consumers, but they have received little or no scientific attention. This review article examines several research and developmental strategies for hastening the improvement of these crops so that they can effectively play their role in securing food and nutrition. The integration of both research and developmental approaches will open up modern opportunities for crop improvement. We summarized ways in which advanced tools in phenotyping and genotyping, using high-throughput processes, can be used to accelerate their improvement. Finally, we suggest roles the genebanks can play in improving orphan crops, as the utilization of plant genetic resources is important for the genetic improvement of a crop.

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Introduction

With the exponentially growing population rate and the lack of available arable land, humanity is facing enormous challenges that have resulted in food security being threatened.¹ Due to the limited number of staple crops and their ability to withstand climate change, scientists and breeders have shifted focus to looking at alternative methods of ensuring future food security. Breeders have discovered germplasm (local landraces or crop wild relatives) with advantageous traits and have introduced the adaptive alleles into superior varieties. Despite significant efforts and numerous breakthroughs in developing climate-resilient crops, yields have begun to plateau due to the adverse effects of extreme weather conditions in some years and some regions of the world.² Neglected, orphan, underutilized, or opportunity crops offer an important connection in the ongoing problem of food security. These scientifically ignored crops are specially adapted to the local environmental circumstances, are used as part of local meals, and have contributed to the

economic stability of farmers.³ They serve as a large gene pool for advancing crops in the future and are crucial to the world's food and nutrition security. They may also help in ensuring the sustainability of food systems in the face of climate change.⁴

Research attention is shifting toward orphan crops as a result of a renewed awareness of their potential as nutrient-dense, adaptable to a variety of food systems, and tolerant of suboptimal growing conditions.⁵ The potential orphan crops possess has made them important in ensuring food and nutritional security as well as agricultural sustainability. They are well suited for sustainable agriculture since they are more resilient to biotic and abiotic stressors and make better use of water and soil nutrients. The climate resilience traits some orphan crops possess have made them significant in ensuring the continued production of food in these climate-changing times.⁶ Due to their nutritious nature, they have the potential to improve nutritional security and their inclusion to complement

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major crops in diet and farming practices ensure food system and agricultural diversification. Additionally, some of them contribute to sustainable and healthy diets as they possess medicinal properties, exemplifying functional foods, thereby highlighting their value in transforming food systems.⁷ Furthermore, they can strengthen the economies of emerging nations because they require low input to cultivate therefore, are a good source of income for small and marginal farmholders.⁸

Specialized breeding initiatives are needed to identify these crops and their potential cultivars and ensure their commercial viability. Orphan crops are seldom taken into consideration in industrialized nations where breeding programs run by private businesses predominate over public ones, due to the ongoing high research interest in major crops and their widespread distribution, minor crops and their related indigenous knowledge are lost, and the development of true-breeding, high-yielding cultivars of potential significance for global food systems are slowed down by this lack of investment.^{9,10} However, if all these hurdles are overcome, the inclusion of orphan crops in our food system can help double food production by 2050, diversify and build a climate-resilient food system, and improve the diet of the populace as well as the income of small farm owners.^{6,11} To achieve continued research and development on orphan crops, the collection of both ex-situ and in-situ germplasm is vital, followed by their exhaustive characterization. Although bodies like the International Institute of Tropical Agriculture (IITA), Alliance of Bioversity International, International Center for Tropical Agriculture (CIAT), African Orphan Crops Consortium (AOCC), and some other international agencies are making significant efforts, more organizations need to intensify their efforts toward continued research and development on these crops.^{5,12} The objective of this review is to underscore research and developmental strategies as well as suggest pre-breeding programs that can be carried out in the genebanks to accelerate the improvement of orphan crops. These methods may help fast-track the improvement of orphan crops without affecting their valuable traits.

Recent research areas, achievements, and gaps in crop improvement of some orphan crops

Hyacinth Bean (Lablab Purpureus L. Sweet)

This is a grain legume of African origin that grows well in diverse environmental conditions and is extremely resistant to drought. As a result, it is commonly grown throughout Asia and Africa's tropical and subtropical climates. It was confirmed that domesticated Lablab had dual origin: the widely distributed four-seeded type and the locally confined (to Ethiopia) two-seeded type are genetically distinct from one other, and domestication processes have occurred in both of these groups.^{13,14} Described an inclusive African-led project to generate a high-quality reference genome for lablab, a versatile and climate-resilient crop. In addition to highlighting some intriguing and significant aspects of the lablab genome, as well as its domestication and population diversity, the chromosome-scale assembly of Lablab improves upon the prior assembly in a number of ways.^{15,16} Identified 22 and 2567 SSR markers, some of which were used in the population genetics that clearly showed a distinction between the 2-seeded and 4-seeded pod.¹⁷ The use of molecular markers for the breeding of this crop is still in its early stages. The identification of single gene traits such as bruchid resistance, maturity, and photoperiod sensitivity, as well as the development of a variety that combines both abiotic and biotic stresses, should be the focus of the breeding program for Lablab. In addition, the assembly and annotation of a more complete reference genome should be targeted.¹⁴

Winged Bean (Psophocarpus Tetragonolobus (L.) DC.)

Winged bean is cultivated mainly for its pods, seeds, and tubers. It is one of those crops that has benefited from selective breeding by creating lines that are less photoperiod-vulnerable.¹⁸ All parts of the plant are highly nutritious and it serves as a substitute for soybean in the tropics because it can thrive in areas where the cultivation of soybean is difficult. In addition, its protein content is comparable to that of soybean.^{19,20} This crop is however faced with the problem of low yield. In recent times, the de novo transcriptome of winged bean was generated by Vatanparast et al.²¹ They

identified Single Sequence Repeats (SSR) and Single Nucleotide Polymorphism (SNP) that can provide new resources for gene discovery and marker development. 18 SSR markers have also been validated for genetic diversity in winged bean by Wong et al.²² Further identification of trait-specific markers was studied by Chankaew et al.²³ using linkage mapping. They discovered 31 QTLs controlling pod length, pod color, pod anthocyanin content, flower color, and seed color in winged bean. Despite the information obtained from these studies and several others, there is still a lack of trait-specific markers and improved varieties for yield.

Zombi Pea (*Vigna Vexillata* (L.) A. Rich)

Zombi pea, an orphan legume is the least known of the domesticated *Vigna* spp. It is known to be of African origin and it exists in two forms (i.e. seeds and tubers (storage roots). Zombi pea is also grown in Southeast Asia, Australia, and India.^{24,25} It is believed that the tuber type originated in Asia, whereas the seed type originated in Africa.²⁵ Compared to sweet potatoes and tapioca, the protein content of Zombi pea tubers was found to be up to eight times higher. The *Vigna vexillata* tuber is one of the domesticated *Vigna* species that has received the least attention in terms of genetic resource research, particularly in India. Despite their worth, collections from Africa have drawn greater interest than those from Southeast Asia, which includes India.²⁶ The genetics of domestication traits in zombi pea were investigated using QTL analysis.^{25,27} Other QTLs detected in Zombi pea include those for salt tolerance,²⁸ and bruchid resistance.²⁹ More QTLs for abiotic and biotic stresses need to be identified to initiate marker-assisted selection for breeding programs.

African Yam Bean (*Sphenostylis Stenocarpa* (Hochst. Ex A. Rich))

African yam bean (AYB) is a neglected legume that can also contribute toward alleviating food insecurity in sub-Saharan Africa.³⁰ It is grown mainly for the nutritious seeds in western Africa while the tubers are utilized in eastern and central Africa. It is also a source of animal feed.³¹ AYB is consumed by some

hypertensive, diabetic patients who have cardiovascular diseases in Nigeria.³² The low amount of sodium present in AYB seeds makes them suitable for consumption among hypertensive patients. Also, AYB is the right choice for diabetic patients because the rate of digestion is prolonged, avoiding the accumulation of sugar in the blood.³³ The ability of African yam bean to be used during inter-cropping is of great benefit because it establishes nitrogen fixation in the soil.^{34,35} Reported that the lectins extracted from African yam bean are insecticidal. Recent findings revealed SNP alleles associated with some nutritional traits and seed size traits have been identified in AYB.^{36,37} Other studies recently carried out on AYB include (i) further studies to identify genetic diversity among some AYB accessions toward crop improvement,^{36,38,39} (ii) identification of diseases/infections such as bean common mosaic virus (BCMV) which limit the yield of AYB;⁴⁰ (iii) mutation in AYB.⁴¹⁻⁴³

Despite the amount of research that has been carried out on orphan crops, there is still a long way to go in developing better varieties of these crops without compromising their inherent ability to meet the standards of foods in the food system. Also, the conservation of orphan crop landraces is necessary for additional assessments, and modern breeding initiatives should be used to enhance promising landraces and their attributes.³⁸ We have identified some research gaps (Table 1) for some orphan crops. If these gaps are addressed, then these crops can help in achieving food and nutritional security quickly.

Research strategies for improvement

There are ongoing efforts to see orphan crops together with major crops in the global food basket. However, there is a need for more strategies that can speed up the improvement of orphan crops to remove the inherent natural barrier that causes them to stay orphan not just from conventional plant breeders alone, but also from biochemists, plant geneticists, botanists, and traditional farmers.⁷⁴ The use of high-throughput phenotyping such as Ground Based Imaging, Unmanned Aerial Vehicle (UAV) imaging, and satellite imaging has shown promises in increasing the speed of genetic gain by the precise measurements of

Table 1. Some orphan crops, their potential trait for crop improvement, research gaps and genome sequence status.

Crop [Common name]	Scientific name	Potential	Genomic Markers	Genome Sequence Status	Chromosome Number	Genome Size	Breeding Effort	Available Genomic Tools	Availability Transformation system	Research Gap	References
Hyacinth bean	<i>Labiab purpureus</i> L.	Drought and salinity tolerance, nutritious, nutraceutical properties	EST-SSRs, RAPD, EST-SNP, InDel.	No	2 n = 2x = 24	367Mb	Improved photoperiod insensitive and development of determinate pureline varieties	Linkage map, QTL mapping	Nil	No superior cultivars and resistant varieties to pest and weeds	44,45
Zombi pea	<i>Vigna vexillata</i> (L.) A. Rich	Nutritious, biotic and abiotic stresses resistance	RAD-seq, SSR, SNP	No	2 n = 2x = 22	803Mb	Identification of candidate gene, VtAxI for Bruchid resistance	QTL mapping	Nil	No improved zombi pea for abiotic stress resistance	24,46,47
African Yam Bean	<i>[Sphenostylis stenocarpa</i> (Hochst ex. A. Rich.) Harms]	Nutritious, versatile	AFIP, ISSR, SSR, SNP	77–81%	2 n = 2x = 22	> 649Mb	Identification of various agronomic traits	Association mapping	Nil	There is need to improve crop yield, shorten the cooking and maturity periods, and increase the crop's resilience to pests and diseases.	48,39
Winged bean	<i>Psophocarpus tetragonolobus</i> (L.) DC.	Nutritious, versatile, adaptable to diverse soil types	AFIP, RAPD, SSR, SNP	98.9%	2 n = 2x = 18	1.22Gb	Identification of quantitative trait loci (QTLs) for traits such as pod and seed characteristics	Cloning, transcriptomics, Genetic linkage maps	Nil	Little or no information on how to improve the long maturation period, indeterminate growth habit, low seed yield, and the need for a stake to support the vigorously growing vines	19,49
Bambara groundnut	<i>Vigna subterranea</i> (L.) Verdc	Nutritious, climate-resilient, versatile, adaptable to diverse environment	ISSR, SSR, SNP	No	2 n = 2x = 22	550Mb	Identification of QTL for some agronomic traits	Whole Genome Sequencing, Transcriptome sequencing	Nil	No improved line for yield and adaptation to moisture stress	44,50,51
Finger millet	<i>Eleusine coracana</i>	Resilience to adverse climatic conditions, high nutritional content, versatile	EST-SSR, ISSR, SSR, SNP	100%	2 n = 4x = 36	1.45Gb	Development of lines with improved agronomic traits	Linkage mapping, QTL mapping, Whole Genome sequencing, Reference genome, Transcriptomic, Proteomics, RNA-Seq	Agrobacterium-mediated transformation and particle bombardment [biolistics]	Identification of novel genes for abiotic stress tolerance and nutritional traits	52,53
Chickpea	<i>Cicer arietinum</i>	Nutritious, adaptability to diverse climates	AFIP, ISSR, InDel, ISM, ILP, SSR, SNP	73.8%	2 n = 2x = 16	738Mb	Identified loci associated with yield, drought tolerance, and resistance to diseases	Linkage mapping, QTL mapping, GWAS, Whole Genome sequencing, Reference genome, Proteomics, RNA-Seq, DGE, CRISPR/Cas9	Agrobacterium-mediated transformation and particle bombardment [biolistics]	Selection of accessions that can be used as parental material in breeding programs. Lack of drought-tolerant cultivars.	54,55
Foxtail millet	<i>Setaria italica</i>	High nutritional content, environmental resilience, and potential health benefits	KASP, AFIP, RAPD, InDel, SSR, SNP	100%	2 n = 2x = 18	490Mb	Identification of genetic loci associated with drought resistance, plant height, flowering time, grain yield, and nutritional quality	Linkage mapping, QTL mapping, GWAS, Whole genome Sequencing, Comparative Genomics, CRISPR Cas9, DGE, TILLING, MAS, GS	Agrobacterium-mediated transformation and particle bombardment [biolistics]	Lack of high yielding varieties	56,57
Grass pea	<i>Lathyrus sativus</i>	Ability to thrive in adverse conditions, high nutritional value	AFIP, RAPD, EST-SSR, KASP, SSR, SNP	100%	2 n = 2x = 14	6.3Gbp	Identification of stress-responsive genes	Draft Genome Assemblies, Transcriptome sequencing [RNA-Seq], Comparative Genomics, Gene Knockout, TILLING	Nil	Lack of genetic improvement through GWAS and MAS	58,59

(Continued)

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Crop [Common name]	Scientific name	Potential	Genomic Markers	Genome Sequence Status	Chromosome Number	Genome Size	Breeding Effort	Available Genomic Tools	Availability Transformation system	Research Gap	References
Horsegram	<i>Macrotyloma uniformum</i>	Nutritional and therapeutic properties, resilience to harsh environmental conditions	RAPD, ISSR, SSR, SNP, ILP, COS	83.53%	2 n = 2x = 20 or 22	400Mb	Identification of genes involved in metabolic process. Identification of candidate gene involved in environmental adaptation	Linkage mapping, QTL mapping, Whole Genome Sequence, Transcriptome sequencing, Comparative Genomics, GWAS, DEG	Nil	Candidate genes underlying functional traits has not been identified	60,61
Pigeon pea	<i>Cajanus cajan</i>	Nutritious, versatile, nutraceutical properties, adaptability to marginal environments, drought resistance	SSAP, REMAP, SCAO, SSR, SNP	100%	2 n 2x = 22	833Mb	Identification of regions associated with Fusarium wilt resistance, sterility mosaic disease resistance, drought tolerance, and pod yield	Whole Genome sequence, GWAS, MAS, Transcriptomics, Comparative Genomics, CRISPR	Agrobacterium- mediated transformation	Lack of breeding for high yielding pure line and hybrid	62,63
Moth bean	<i>Vigna aconitifolia</i>	Nutritious, adaptability to harsh climates, nutraceutical properties	AFLP, RAPD, ISSR, SSR, SNP	50%	2 n 2x = 22	409Mb	Identification of stress- responsive genes	Linkage mapping, Proteomics, Comparative Genomics,	Nil	Lack of reference genome, little integration of modern genomics tools, Lack of common features of nutritional, anti-nutritional compounds, processing characteristics, and health benefits	64,65
Black gram	<i>Vigna mungo</i>	High protein content, adaptability to various cropping systems	AFLP, RAPD, ISSR, SNP	79.2%	2 n = 2x = 22	574Mb	Identification of SNPs associated with seed size, flowering time, and biotic stress resistance	Draft Genome Assembly, Linkage mapping, GWAS, QTL mapping, DEGs	Agrobacterium- mediated transformation	Incomplete reference genome, lack of high yielding and MYMV resistant varieties	66,67
Adzuki bean	<i>Vigna angularis</i>	Nutritious, functional food and medicinal applications	AFLP, ISSR, EST-SSR, SSR, SNP	97.8%	2 n = 2x = 22	542Mb	Identification of SNPs associated with seed size, flowering time, and disease resistance	Draft Genome Assembly, Linkage mapping, GWAS, QTL mapping, DEGs, MAS	Agrobacterium- mediated transformation	Little knowledge on utilization. Little understanding of the anti-obesity mechanism and the specific bioactive components involved	68–70
Mung bean	<i>Vigna radiata</i>	Nutritious, nutraceutical properties, drought tolerance, disease resistance, climate-resilient	AFLP, RAPD, ISSR, SSR, SNP	96.9%	2 n = 2x = 22	543Mb	Identification of SNPs associated with seed size, flowering time, and disease resistance	Draft Genome Assembly, Linkage mapping, GWAS, QTL mapping, DEGs, Comparative Genomics, MAS	Agrobacterium- mediated transformation	Little knowledge on the unraveling of the main functional components relevant to health benefits	71,72
Fonio Millet	<i>Digitaria exilis</i>	Fast maturing, climate-resilient, nutritious, nutraceutical properties, highly adaptable to poor soils and drought conditions	AFLP, RAPD, SSR, SNP	99%	2 n = 4x = 36	761Mb	Identification of drought resistance traits	GWAS, DEGs, Comparative Genomics	Nil	Improvement and domestication is lacking	73

desired traits among thousands of field-grown plants within a short period of time.⁷⁵ The development of core collections is another strategy for accelerating improvement in orphan crops as it serves the objective of supplying data required to enhance the utilization of genetic resources in any crop improvement program.⁷⁶ It eliminates the time it takes breeders to estimate genetic variability, evaluate germplasm, and select parents for crop improvement, and also the development of a core collection allows for target allele mining.⁷⁷ Exploring the genomics of these orphan crops via conventional breeding, Genome-Wide Association Studies (GWAS), modern biotechnology, and computational technology will also hasten orphan crop improvement for wide acceptability and utilization.⁷⁴

Several newly developed technologies and breeding strategies that enable the swift identification and selection of genes underlying desirable traits thereby shortening the time for selection can be applied to fast-track the improvement of orphan crops.⁷⁸ Modern technologies in genomics and gene editing like the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR/Cas system), Transcription Activator-Like Effector Nucleases (TALENs) and Zinc-Finger Nucleases (ZFNs) can be used to enhance the productivity of orphan crops. However, these techniques rely on the sequenced information of the crop. Sequencing the genomes of different orphan crops with tools such as Genotype by Sequencing (GBS) and Single Nucleotide Polymorphism (SNP) will provide the information needed to use these modern technologies to hasten crop improvement. Genes identified from sequencing can then be designed for enhancement using these modern technologies.⁷⁹ Domestication of orphan crops is another method for hastening their improvement. This can lead to the faster improvement and utilization of the crops. Overall, the use of all of these methods in a well-structured breeding program for orphan crops can contribute to their rapid improvement.

High-throughput phenotyping

Over the years a variety of high-throughput phenomics methods have been used for phenotyping trait-specific characters including growth,

phenology, physiology, disease incidence, insect damage, and drought tolerance in major crops, this has accelerated the period between breeding cycles in these crops.⁸⁰ This can also be replicated in orphan crops to provide the same advantage⁸¹ since it is evident that orphan crops will need more efficient phenotyping to dissect important traits they possess. Not only does high-throughput phenotyping hasten the breeding cycle it also enables the fast and accurate measurements of many important traits in model and non-model plant species. For example, the use of high-throughput phenotyping of field-grown cassava in the ongoing ‘cassava source-sink project’ will hopefully overcome some of the limitations of single-trait engineering which will lead to the rapid enhancement of cassava as an orphan crop.⁸² In addition, images of more than one thousand sorghum (*Sorghum bicolor*) panicles from 272 genotypes comprising a subset of the Sorghum Association Panel were used to create a phenotyping pipeline that extracted unidimensional and multidimensional features from the images. This high-throughput phenotyping tool can be used to collect phenotypic data from large orphan cereal populations, causing a transformation in their genetic improvement.⁸³ More so Großkinsky et al.,⁸⁴ in combining multi-omics and advanced phenotyping discussed how these techniques can facilitate the generation of climate-smart *Camelina sativa* (camelina, gold-of-pleasure, false flax) – an orphan oilseed crop.

Zhang et al.⁸⁵ demonstrated that under active field conditions images extracted from multispectral cameras to estimate canopy area, percentage of canopy area, and vegetation indices and images from a thermal camera used to estimate mean canopy temperature can be used for monitoring *Ascochyta* blight disease severity in chickpea. They concluded that real-time information about traits acquired from high-throughput phenotyping techniques can assist efficient, accurate, and timely decision-making for crop improvement. In addition, a high-throughput phenotyping protocol to screen lentil accessions for salt tolerance was developed by Dissanayake et al.⁸⁶ This protocol can be used to screen a large number of lentil accessions in field conditions for salt tolerance. The use of spectroscopic technique FT-MIR coupled with attenuated total internal reflectance sampling interface to

develop multivariate models for total protein concentration in chickpea (*Cicer arietinum* L.), dry pea (*Pisum sativum* L.), and lentil [*Lens culinaris* Medik] was demonstrated by Madurapperumage et al.⁸⁷ They found out that FT-MIR spectroscopy can quantify protein traits quickly and easily in orphan pulse crops. Since the use of techniques such as Marker-Assisted Selection and genome-wide association mapping depends on accurate phenotypic data, the use of high-throughput phenotypic techniques on orphan crops can lead to the accurate detection of markers underlying phenotypic traits.

Marker assisted breeding

This method of breeding is extensively utilized in staple crops and has begun to be employed in some of the orphan crops including barley,⁸⁸ cassava,⁸⁹ pearl millets,⁹⁰ peanuts,⁹¹ and some perennial plants.⁹² The development of molecular markers was once a time-consuming and labor-intensive process. However, the advent of next-generation sequencing (NGS) has enabled the development of large-scale molecular markers, including microsatellite or simple sequence repeat (SSR), insertion-deletions (InDels), and single nucleotide polymorphisms (SNP), this has also made the turnaround time for crop improvement faster.⁹² The identification of molecular markers underpinning phenotypic traits through studies such as GWAS, and bi-parental QTL explains the genetic basis of such traits making the manipulation of the trait faster and easier thereby enabling the development of new varieties via marker-assisted breeding.⁹³

Whole genome sequencing

Next-generation sequencing (NGS), which allows for the sequencing of the whole genome of many crops and their wild relatives, is an efficient way to facilitate the domestication of desired genes in orphan crops, thereby hastening their improvement.⁷⁸ Over the years, as scientific research has shifted focus to orphan crops, whole genome sequences of some orphan crops have been carried out. Genome sequencing has enabled the identification of upstream regulatory elements of genes and the fine-tuning of the expression of target genes, and all these are possible due to the

advent of NGS approaches. These approaches have made it possible to quickly identify target genes and manipulate such genes to bring about new improved crop varieties in a shorter period. A number of orphan crops' whole genome has been sequenced (Table 1). Zhang et al.⁹⁴ sequenced the genome of foxtail millet and reported that around 1500 genes are unique to this crop, where about 580 genes were marked as 'response to water.' Reannotation of these genes provided insights into their classification, wherein a few stress-responsive genes were characterized at a genome-wide level.⁶⁵ developed a de novo genome assembly of *Vigna aconitifolia* using PacBio High-Fidelity reads and Hi-C sequencing data, with a total size of 409 Mb and contig N50 of more than 30Mb. The genome was also annotated for repeat sequences and they found out that the moth bean genome comprises about 54% of repetitive sequences, and predicted 36950 protein-coding genes. The identification of these genes can lead to the rapid genetic improvement of this crop.

TILLING (Targeting induced local lesions in genomes) and Eco-TILLING

These are effective methods for hastening orphan crop improvement since the techniques do not require biosafety regulations as they are free of transgenes. TILLING is a reverse genetic technique that uses traditional mutagenesis followed by high-throughput mutation detection. It is applied to the induced mutagenized population while Eco-TILLING is applied to the natural population.⁹⁵ Eco-TILLING was used to identify single nucleotide polymorphisms (SNPs) and small insertions/deletions (INDELS) in a collection of mung bean accessions. A total of 157 DNA polymorphisms in the collection were discovered in the collection of limited diversity.⁹⁶ Desi and Kabuli chickpea accessions are known to have low genetic polymorphism. However, employing eco-TILLING found approximately 31% phenotypic variation for 100 seed weights.⁹⁷ TILLING and Eco-TILLING have been applied to very few orphan crops to access their diversity but are yet to be used on several orphan crops in inducing mutagenized populations for their improvement.

Genome-wide association studies (GWAS)

Genome-wide association studies (GWAS) are a crucial marker-trait association (MTA) study for accelerating crop improvement.⁹⁸ This method identifies Quantitative Trait Loci (QTLs) from high-density SNP maps that are linked to phenotypic traits in crops. These SNPs can be used to identify the genetic basis of adaptive traits in orphan crops and can be designed and used for Marker Assisted Breeding. Candidate genes of desired traits obtained from orphan crops using GWAS can be used to improve the crop using a genetic modification-type approach.² While thousands of these methods have been reported for staple crops, GWAS of orphan crops is still in its early stages.² For instance, there is little or no record of Genome-Wide Association studies for winged bean. However, it has been carried out on some orphan crops for some traits. By employing DArTseq SNP for a Genome-Wide Association Study, Quantitative Trait Loci (QTL) that could be useful for the improvement of the protein, oil, and starch contents of African Yam Bean were identified by Oluwole et al. and Olomitutu et al.^{36,37}

In addition, in mung bean, Genotype-by-Sequencing GWAS identified 116 SNPs in 61 protein-coding genes. Sixteen of these protein-coding genes have been found to enhance phosphorous uptake and utilization efficiency. Six of these genes showed high expression in the root, shoot apical meristem and leaf. The SNPs in three of these genes have been validated using a Sanger sequencing approach.⁹⁹ Also, on mungbean, Xu et al.¹⁰⁰ identified 19 QTLs containing 32 SNPs that were significantly associated with alkali tolerance on nine chromosomes at the germination stage. Using GWAS, Uba et al.⁹⁸ identified a total of 27 significant marker-trait associations (MTAs) for seed color, days to flowering, days to maturity, terminal leaf length, terminal leaf width, number of seed per pod, pod width in Bambara groundnut. A total of 17 candidate genes were identified, varying in number for different traits for the above-mentioned traits. Marker-trait association analysis in moth bean revealed 29 potential genomic regions for the trait days to 50% flowering.¹⁰¹

Speed breeding

The timing of the release of genotypes to farmers has a considerable impact on breeding. In conventional breeding, the breeding cycle takes roughly three to seven years, while the yield, disease, and quality tests take about four years, and the variety release takes an additional one to three years. Long-term improvements are made to a single gene or variety. As a result, a technique known as “speed breeding” has been devised, which involves altering day-light and duration in order to abbreviate the life cycle.¹⁰² It also enables rapid generation advancement by growing plant populations under controlled photoperiod and temperature regimes to hasten their growth and development. It can play a role in the rapid development of improved crop varieties supporting the cultivation, production, and utilization of orphan crops at a large scale. Using this technology, there was a significant reduction in the time taken for anthesis to occur in spring wheat (*Triticum aestivum*), durum wheat (*Triticum durum*), barley (*Hordeum vulgare*), Chickpea (*Cicer arietinum*), and canola (*Brassica napus*) planted in a temperature-controlled glasshouse fitted with high-pressure sodium lamps. This significantly increased the number of generations grown per year of these crops.¹⁰³

Samineni et al.¹⁰⁴ developed a protocol for increasing the number of generation cycles per year in chickpeas using speed breeding. Their results showed encouraging implications for breeding programs as they were able to produce 7, 6.2, and 6 generations per year in early-, medium-, and late-maturing accessions. This makes for rapid progression toward homozygosity, development of mapping populations, and reduction in time, space, and resources in cultivar development. This technology is important for methods like genomic selection as it reduces the time it takes to generate one breeding cycle.⁷⁸ Plant breeders and plant molecular geneticists can use the speed breeding technique to quicken the genetic variety present in wild relatives of these orphan legumes, introducing top variants that will be widely accepted and cultivated by farmers.

CRISPR/Cas

Clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated proteins (Cas) is the most straightforward, adaptable, and precise strategy for genetic manipulation in plants. Genetic manipulation such as gene knockout, promoter editing, gene knock-in, base editing, and prime editing using the CRISPR/Cas9-assisted gene editing technology has been applied to major crops with success rates some of which include *Medicago truncatula* and soybean,¹⁰⁵ cowpea,¹⁰⁶ rice,¹⁰⁷ cassava,¹⁰⁸ wheat,¹⁰⁹ tomatoes,¹¹⁰ and alfalfa.¹¹¹ CRISPR/Cas9-assisted gene editing technology has also been applied to some orphan crops with a success rate. Phytoene desaturase (PDS) knockout has been achieved in the first application of CRISPR in foxtail millet (*Setaria italica*) protoplasts. This indicates that the technology can be used to improve millet.¹¹²

The CRISPR/Cas9 technology is also the only Site-Specific Nuclease (SSN) to allow efficient multiplexing – a method for simultaneously targeting multiple genes/alleles by multiple using gRNAs. Multiplexing with CRISPR/Cas has been demonstrated in major crops such as soybean¹¹³ and maize¹¹⁴ as well as in some orphan crops such as Eggplant,¹¹⁵ foxtail millet¹¹⁶ and Chickpea.¹¹⁷ In addition, by utilizing CRISPR/Cas9 single- and multi-gene knockout systems to target SiALS and SiACC genes in foxtail millet protoplasts,¹¹⁶ developed a homozygous herbicide-tolerant mutant plant using the Cytosine Based Editor to target SiALS gene. Furthermore, Badhan et al.¹¹⁷ demonstrated the knockout of 4-coumarate ligase (4CL) and Reveille 7 (RVE7) genes in the chickpea protoplast using DNA-free CRISPR/Cas9 editing. High-efficiency editing was achieved for the RVE7 gene in vivo compared to the 4CL gene. This reveals that CRISPR/Cas9 can be used to target agronomically important traits in chickpea.

The success of this technology in these crops shows promise for its application in other orphan crops to target traits beneficial to farmers and consumers. However, in-depth bioinformatic, genomic, and transcriptomic information, and optimization methods for the transformation and regeneration of orphan crops are important for their improvement as the technology relies on

characterized functional genes and efficient transformation and regeneration protocols.¹¹⁸ Therefore, information from studies such as whole genome sequencing, QTL, GWAS, marker-assisted selection, genetic transformation, and regeneration in orphan crops is crucial.⁷⁴ Advantageously, the genome of some orphan crops such as African yam bean and Adzuki bean is being sequenced, and that finger millet assembled by the AOCCC¹¹⁹ and the genome of pigeon pea has been sequenced by Varshney et al.⁶² and white fonio millet by Wang et al.⁷³ Information obtained from these sequences can be used to acquire genomic targets for designing gRNAs for CRISPR/Cas gene editing in these crops. As demonstrated in major crops and some orphan crops, improvement of orphan crops using the CRISPR/Cas technology is achievable.¹¹⁸

Developmental strategies for improvement

Market development

There is growing global interest in new foods and products that can enhance health and nutrition. This trend presents an opportunity to develop markets for non-staple crops, potentially benefiting impoverished communities.¹²⁰ Market, commercialization, and demand limitations are key aspects in promoting any orphan crop. These limitations are often due to the stigma of food of the poor that often accompanies these traditional crops in any country. Promoting the nutritional benefits of orphan crops through consumer education, organizing cooking demonstrations and workshops to showcase their versatility, and developing clear labeling and certification standards can build consumer trust and increase preference for these crops, thereby boosting their production.¹²¹ Popularizing consumption and enhancing market image through partnerships with food companies can address these challenges, as demonstrated by Andean grains. For example, a partnership with the Bolivian coffee shop chain “Alexander Coffee” promoted these grains through marketing campaigns and innovative food recipes, directly linking farmers to the chain for raw material supply.¹²² New food products incorporating Andean grains were developed, and their nutritional benefits were

promoted to increase consumption and inclusion in government programs.¹²³

Strengthening all stages of the value chain from production to consumption and ensuring efficient processing, marketing, and distribution are important to place orphan crop products on supermarket shelves. Value addition is another strategy that can be employed to enhance the acceptability of orphan crops. This process involves economically enhancing the value of a product by altering its characteristics to align with marketplace preferences.¹²² In India, adding value to millet nearly tripled farmer incomes and generated new employment opportunities, particularly for women.¹²⁰ Establishing robust market linkages between producers and various markets, including local, regional, and international ones, is crucial for commercializing orphan crops. This involves conducting market studies to identify potential markets and consumer preferences for orphan crop products and establishing efficient supply chains to connect farmers with these markets and ensure timely product delivery.⁷

Policy and institutional support

Agricultural policies and institutions play a crucial role in crop development by providing support, guidance, and resources to farmers and agribusinesses. These policies and institutions help promote sustainable agricultural practices, enhancing research and development, and ensuring the availability of necessary resources for crop production.¹²⁴ For instance, national agricultural research systems in the developing world have been instrumental in the development and diffusion of modern crop varieties, contributing significantly to the Green Revolutions observed across various food crops such as wheat, rice, maize, and others.¹²⁵ The United Nations General Assembly (UNGA) conventions have identified several developmental strategies to transform production systems, including: increasing research investments to explore the climate resilience and nutritional characteristics of underused and orphan crop species; providing greater support for their inclusion in food security policies and programs; encouraging their use to diversify farming systems and create more

biodiverse landscapes and healthier ecosystems; and upgrading their value chains and markets to ensure their sustainable use.^{8,126}

Various national and international research, funding agencies, and policy institutions, such as Consultative Group for International Agricultural Research (CGIAR), which comprises of institutes like the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), International Center for Tropical Agriculture (CIAT), International Institute of Tropical Agriculture (IITA), International Maize and Wheat Improvement Center (CIMMYT), International Food Policy Research Institute (IFPRI) and International Potatoes Center (CIP), Biodiversity International, African Orphan Crops Consortium (AOCC), Global Crop Diversity Trust, Svalbard Global Seed Vault, Crops for the Future (CFF), Food and Agriculture Organization (FAO), and the National Agricultural Research Systems (NARS) such as the Indian Council of Agricultural Research (ICAR), Kenya Agricultural and Livestock Research Organization (KALRO), Ethiopian Institute of Agricultural Research (EIAR) and National Root Crops Research Institute (NRCRI), Bill & Melinda Gates Foundation, McKnight Foundation, and Biotechnology and Biological Sciences Research and International Fund for Agricultural Development (IFAD) are actively working to identify best management practices and provide financial support for orphan crops.⁵

Despite these players, orphan crops still lack sufficient policy support, breeding programs, and funding. Crops like millet, sorghum, and teff often lack national policies promoting their cultivation and consumption despite their nutritional benefits and resilience to climate change.¹²⁷ In Africa, funding and research focus heavily on maize and rice, while indigenous crops like fonio and bambara groundnut receive minimal attention.¹²⁷ In countries like Nigeria, while cassava has received significant attention, other nutrient-rich orphan crops like African yam bean and moringa are often left out of major agricultural development programs. The implementation of policies, funding, and support that incentivize orphan crop production and processing could hasten their commercialization.

Capacity building

Intensive capacity-building efforts should be implemented to train farmers on the nutritional benefits, best cultivation practices, and marketing of orphan crops. This includes producing quality seeds, managing pests and diseases, and improving harvest and post-harvest methods. Additionally, these efforts should enhance farmers' skills in novel food preparations, transformation processes, nutrition, food safety, and marketing.¹²² Training farmers in storage technologies to minimize post-harvest loss, as well as in processing technologies to convert orphan crops into value-added products, can enhance their marketability and shelf life. This, in turn, can accelerate the integration of orphan crops into the food system.¹²³ To support orphan crop development, it is essential to enhance the capacity of local research institutions through training, funding, and partnerships with international research organizations. Facilitating knowledge exchange among stakeholders through conferences, workshops, and publications, along with investing in research facilities, laboratories, and processing plants, will further strengthen infrastructure and support the overall development of orphan crops.⁸

Collaborative efforts

This involves the sharing of knowledge, resources, and technologies between countries, international organizations, governments, research institutions, and the private sector to tackle common challenges in crop improvement. Models such as Participatory Plant Breeding (PPB) could be utilized to facilitate the smooth collaboration between stakeholders. This breeding model involves farmers, government, private companies, research institutes, consumers, and other stakeholders in breeding improved crop varieties and ensuring that new varieties meet the needs and preferences of all those involved.¹²⁸ This comprises sharing knowledge, making decisions, and pooling resources throughout the entire process of breeding crops, from initial planning to product launch. By understanding the needs and preferences of these groups, developers can create crop varieties that meet market demands with high adoption rates, improve

farmers' livelihoods, and contribute to food security.¹²⁹ The PPB approach integrates biological, psychological, and social dimensions, proving effective in promoting food sovereignty.¹³⁰

In the late 1990s, the International Center for Agricultural Research in the Dry Areas (ICARDA) developed the first participatory action research projects for plant breeding in Morocco, Syria, and Tunisia. These projects were initiated due to the low yield of staple crops, high malnutrition, and famine risk in these regions, where conventional breeding methods failed to address farmers' needs. Decentralized and participatory plant breeding (PPB) proved effective by involving farmers from the beginning, ensuring crops suited to local contexts and farmers' knowledge.¹²⁸ Farmers' involvement in selection hastened the adoption of new varieties.¹³¹

PPB method has been especially useful for maize growers in the USA and Portugal and farmers' input was central to the success of the program. The US project was an equal partnership between farmers and researchers from the start, while the Portuguese project began with researchers who later sought farmer collaboration. In the US, the 'Who gets kissed?' project was initiated by an organic vegetable grower and a scientist from a nonprofit research institute, later joined by a public sector university plant breeder. The project aimed to develop an open-pollinated sweet maize variety under organic systems. Farmers and researchers collaboratively evaluated quality, making the breeding process more social than traditional methods. They completed five cycles of selection and, in 2014, released the variety 'Who Gets Kissed?' allowing regional breeding projects to adapt it to local conditions.¹³²

Bread wheat (*Triticum aestivum*) has numerous participatory breeding (PPB) projects, often stemming from farmers' needs for organic and artisanal bread-making varieties. Key motivations include unmet farmer needs, genotype-by-environment interactions, and logistics. PPB projects involve decentralized selection and addressing issues like Fusarium and pre-harvest sprouting, with farmers and researchers collaborating. Successful projects show that farmer-developed varieties can yield equivalent to modern varieties with added desirable traits and more excellent stability. Market acceptance

is crucial for farmers, who often focus on value-added production through local mills and bakeries.¹³²

In the Netherlands, farmer-breeders worked closely with commercial breeding companies for collaborative potato breeding. The model was successful and contributed significantly to developing a diverse portfolio of potato varieties for the national and international markets.¹³³

PPB has also been implemented in developing countries where farmers with limited resources grow their crops in marginal lands of remote regions. It is also implemented in areas where the technology transfer or adoption of modern cultivars is low (as farmers are not comfortable with taking the risk of replacing their well-known and reliable traditional varieties with new varieties) or where modern cultivars are not available, this is the case for *orphan crops*.¹³⁴

Participatory Plant Breeding (PPB) was implemented for Pearl millet (*Pennisetum glaucum*) and sorghum (*Sorghum bicolor*), both considered orphan crops, by ICRISAT in Mali, Niger, and Burkina Faso to develop new varieties through farmer participation. Participatory variety evaluation trials allowed farmers to test and select promising varieties, leading to better yield performance and early maturity. Furthermore,

seed production and commercialization were facilitated through collaboration with farmer organizations, seed fairs, and emerging private seed enterprises, ensuring the availability of improved crop varieties in the market.¹²³

In Peru and Bolivia, IFAD funded a project to enhance the use of orphan crops, focusing on the case of Andean grains (quinoa, cañahua, and amaranth). Improved varieties of quinoa, cañahua, and amaranth were developed and disseminated using methods, including the PPB method. The project had a positive impact on the production, conservation, and income generation of Andean grains.¹²³

Linking orphan crop breeding to market and value chain development offers considerable potential for their development, and PPB programs could prove useful for hastening the improvement and commercialization of orphan crops.¹³⁴ A flow chart summarizing research and developmental strategies for hastening orphan crop improvement is presented in Fig. 1.

Role of the genebanks

Approximately 1% of accessions conserved in different global germplasm repositories have been

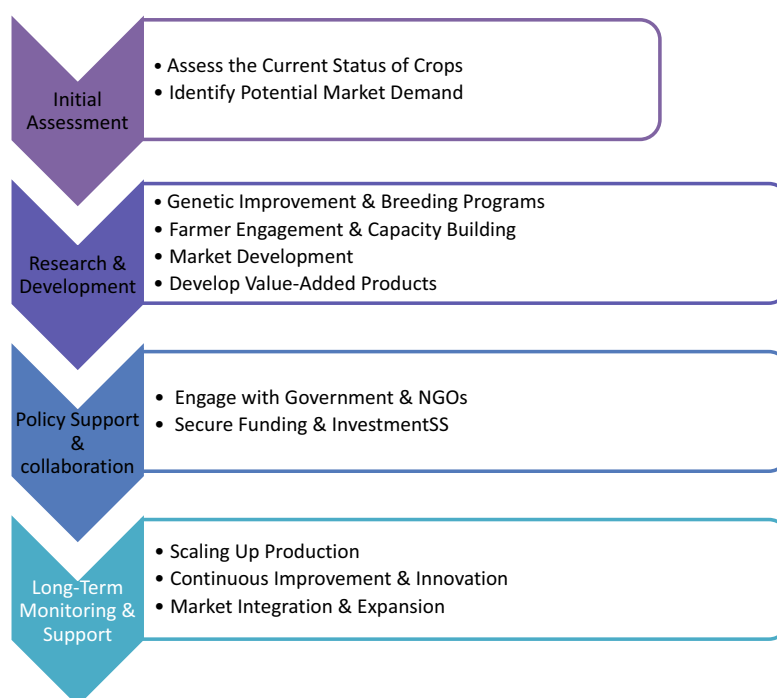


Figure 1. Transforming Orphan crops to a major crop.

exploited for crop improvements. The use of plant genetic resources for developing new varieties has not changed much since 2006, according to reports from the FAO.¹³⁵ Few success stories have been reported regarding the use of alleles from traditional landraces in elite breeding programs,¹³⁶ likely due to the lack of knowledge regarding the potential usefulness of conserved germplasm and the capacity to identify and transfer useful alleles to improved varieties.¹³⁷

The cultivation and conservation of orphan crops contribute significantly to biodiversity maintenance, food and nutritional security, and the livelihoods of small-scale farmers by offering diverse income opportunities.⁷⁹ Genebanks conserve plant genetic resources, including wild relatives or landraces of orphan crop species that possess wide genetic diversity and are reservoirs of useful genes.⁸¹ These genes have occasionally been instrumental in improving elite species. For instance, dwarfing genes from East Asian rice and wheat landraces were successfully introgressed into elite rice and wheat during the Green Revolution. Additionally, Ethiopian landrace barley contains *mlo* alleles, conferring broad-spectrum resistance to powdery mildew, which have been introgressed into elite barley.¹³⁶

Most genebanks conserve a large proportion of minor, neglected, and orphan crops that lack sufficient genomic resources but are repositories of valuable traits for breeders.^{137,138} The initial step for genebanks to hasten orphan crop improvement involves comprehensive and precise genotype-to-phenotype mapping for each accession.^{136,139} This genetic characterization provides insights into traits such as tolerance to biotic and abiotic stresses, disease resistance, yield potential, improved nutritional profiles, and unique phytochemical compounds, enabling informed decisions in breeding programs (FAO, 2015). Multi-location trials are essential to assess accession performance across diverse environmental conditions. This enables genebanks to identify superior genotypes with desirable agronomic and quality traits, informing the selection of parental breeding lines and the development of pre-breeding populations.⁷⁷

Genebanks should aim to provide comprehensive knowledge of germplasm accessions, their relationships, descriptive characters, and optimal evaluation methods. They should adopt

genotypic-based plant identification to establish well-resolved phylogenetic relationships between cultivated species and their Crop Wild Relatives, aiding gene discovery and defining strategies for crop improvement.¹³⁷ Additionally, core collections based on genetic variation and specific traits should be developed for orphan crops to enhance their use in improvement programs. High-throughput phenotyping combined with genotyping should be employed to study functional genetic variation and discover markers for economically important traits efficiently.¹³⁸ Allele mining, including methods like eGWAS, should be applied to all orphan crops to uncover alleles for climate resilience, prioritizing their conservation and use in breeding resilient crops. This information from genebanks serves as a foundation for breeders to expedite orphan crop improvement efforts.¹³⁷

Case studies and success stories of orphan crop improvement

Finger Millet (Eleusine Coracana)

Finger millet, a staple food in East Africa and South Asia, exemplifies successful efforts in improving and commercializing orphan crops.¹²⁰ It is known for its climate resilience against drought and is valued for its nutritional properties and health benefits. Despite these advantages, the cultivation area of minor millets like finger millet declined globally, with an annual production hovering around 3 million tonnes due to challenges such as pests, diseases, striga weed, poor soil quality, sub-optimal agronomic practices, and inadequate product development strategies.^{120,140}

Breeding programs of finger millet prioritized enhancing yield potential, disease resistance, and market appeal¹⁴¹ and through targeted breeding and genomic tools integration, improved finger millet varieties have been developed to meet yield and dietary requirements, resist diseases, and attract commercial interest in gluten-free and functional food markets.¹⁴² Interspecific hybridization involving Indian and African germplasm has further enhanced yield and disease resistance while transgenic varieties have been developed for resistance against leaf blast disease, drought, and salinity stress.¹⁴³

Recent collaborative efforts among international and national research institutions in India, several African countries, Nepal, and Sri Lanka – such as ICAR, KALRO, NaSARRI, EIAR, ICRISAT, and ICARDA – have focused on developing new and improved finger millet cultivars. This global collaboration has resulted in the registration of 143 advanced cultivars by ICRISAT, which now benefits farmers in Kenya and India, with reported yields of up to 10 tons per hectare. These advancements are not just improving farmer incomes and health but also contribute to the shared mission of sustainable agriculture.¹⁴⁴ The recent completion of finger millet genome sequencing is a significant milestone in enhancing future breeding and improvement efforts.¹⁴⁵

Quinoa (*Chenopodium Quinoa*)

Once regarded as a traditional ‘peasant food,’ quinoa has remarkably evolved into a globally traded commodity. This transformation is mainly due to its status as a ‘superfood,’ celebrated for its exceptional nutritional content and adaptability to diverse growing conditions. Its superior nutritional qualities and the growing demand for healthy, gluten-free foods have been key drivers of its worldwide popularity. However, local quinoa varieties typically have low yields and are prone to lodging, shattering, and pest infestations.¹⁴⁶ In response to the high demand for quinoa, research initiatives have aimed at enhancing yield, disease resistance, and processing characteristics, leading to the release of improved varieties.¹⁴⁷ Furthermore, the commercialization of quinoa has been greatly influenced by genetic advancements, market development strategies, and the establishment of international supply chains. For example, the United Nations’ declaration of 2013 as the “International Year of Quinoa” significantly raised global awareness about the crop’s nutritional and cultural importance. This initiative, along with marketing campaigns, improved agronomic practices, and international trade agreements, facilitated quinoa’s entry into global markets.¹⁴⁸ Moreover, the commercialization of quinoa has had notable socioeconomic impacts both in the Andean region and globally. For smallholder farmers in the Andes,

the increased demand for quinoa has resulted in higher incomes and improved livelihoods.¹⁴⁹

Chickpea (*Cicer Arietinum L.*)

Before its genetic and genomic resources were available in 2005, chickpea – currently ranked as the second most significant legume in the world – was considered an orphan crop.^{150,151} Chickpeas are generally grown by rural farmers in dry and semi-arid regions. However, due to their nutritional benefits, socioeconomic importance, and ability to adapt to a variety of climatic conditions, chickpea popularity has increased.¹⁵² Furthermore, through scientific research, production techniques, marketing tactics, value addition, and international collaboration, this native crop has developed into a global crop.¹⁵³ In recent times, scientific research has made it possible for chickpeas to undergo substantial genetic advancements, which have led to improvements in their nutritional quality, disease resistance, and productivity.¹⁵⁴ Organizations such as the ICRISAT, ICARDA, and National Agricultural Research Centers, with funding from organizations such as the FAO, IFAD, and Bill and Melinda Gates Foundation, managed breeding programs that led to the development of improved varieties, which aided its commercialization.¹⁵⁰

Presently, there are over 200 improved varieties of chickpea¹⁵¹ and the adoption of these improved varieties has significantly increased the income of chickpea farmers thereby reducing household poverty.¹⁵⁵ The availability of draft genome assemblies, comprehensive genetic and physical maps, a vast number of SSR and SNP markers, millions of SNPs, and various high-throughput and low-cost marker genotyping platforms of chickpea has led to the development of superior lines. These lines exhibit enhanced drought tolerance, and resistance to Fusarium wilt and Ascochyta blight, making their way to both farmers’ fields and markets.¹⁵¹ Chickpea is now being cultivated in over 57 countries with India, Australia, Canada, Turkey, and Mexico being the top producers and exporters.¹⁵⁶ Consumers increasing demand for plant-based proteins, awareness of the nutritional benefits of chickpea and the utilization of chickpea protein to produce several chickpea-based products such as

hummus, chickpea flour, milk, butter, and snacks have also significantly influenced the extent of its market reach.¹⁵⁷ The advancement of chickpeas from local staple food to a widely cultivated crop through breeding initiatives, product diversification, and consumer awareness offers vital insights for improving and commercialization of other orphan crops.¹⁵⁸

Bambara Groundnut (*Vigna Subterranea*)

Bambara groundnut, native to sub-Saharan Africa, has gained recognition for its nutritional value, drought tolerance, ability to improve soil fertility through nitrogen fixation, and potential for sustainable agriculture.^{159,160} Though an orphan crop, through collaborative efforts, bambara groundnut has experienced a remarkable transformation over the years.¹⁵⁹ The success of Bambara groundnut improvement can be attributed to the establishment of the International Bambara Groundnut Network (BAMNET), a global consortium of researchers, breeders, and development organizations.¹⁶¹ BAMNET has played a crucial role in the genetic characterization, evaluation, and improvement of Bambara groundnut germplasm, leading to the development of enhanced yield potential, pod characteristics, and drought-tolerant, and nutritionally superior varieties making them more suitable for mechanized harvesting and processing.¹⁶² Commercialization efforts have focused on promoting its nutritious attributes in both local and international markets, contributing to enhanced food security and income generation for smallholder farmers.¹⁶³

Furthermore, the promotion of Bambara groundnut's nutritional profile, which includes high protein, fiber, and micronutrient content, has driven increased consumer demand and commercialization efforts. Local and regional value chains have been developed, providing smallholder farmers with better market access and income opportunities.¹⁶⁰

Cassava (*Manihot Esculenta*)

Cassava is widely cultivated for its starchy, tuberous roots, and to a lesser extent, leaves.¹⁶⁴ It has been a basic food for smallholder farmers in sub-Saharan Africa since the 1950s. In the 1970s,

breeding programs for cassava started, and cassava has moved from being a basic foodstuff to a cash crop.¹⁶⁵ The improvement and commercialization of cassava can be attributed to the development and dissemination of improved varieties through initiatives like the Cassava: Adding Value for Africa (CAVA) project and the work of IITA, International Center for Tropical Agriculture (CIAT) and national agricultural research institutes like National Root Crops Research Institute (NRCRI).¹⁶⁶ They developed the first wave of cassava mosaic virus disease (CMD) and cassava bacterial blight-resistant (CBB-resistant) Tropical Manihot Selection (TMS) varieties.¹⁶⁷ Although conventional breeding was first used to improve cassava the development of improved varieties for disease resistance, enhanced nutritional value (provitamin A-rich cassava), improved yield, and stress tolerance (drought resistance) was sped up by the use of advanced biotechnology tools like genetic engineering, gene editing, and marker-assisted selection.¹⁶⁸ Cassava, being a household staple food and the high demand for industrial starch products increased its awareness and commercialization.¹⁶⁹ In the highest cassava-producing nation, Nigeria, cassava commercialization and market promotion programs were implemented between 2002 and 2008.¹⁷⁰ This program, backed up with government policies saw to the development and distribution of cassava varieties resistant to cassava mosaic disease (CMD), promoting investment into cassava micro-processing and supporting small and large-scale processing industries. Value-added products such as High-Quality Cassava Flour (HQCF), starch, glucose syrup, and ethanol were produced by small and micro-scale processors increasing the production of cassava by 10 million tonnes in the six years of implementation.¹⁶⁵

The genomic scientific community shifted its focus to cassava, and in 2009, the cassava reference genome was made public. Cassava was one of the first "orphan" crop genomes to be sequenced. Multiple cassava genome assemblies have been generated, and Single Nucleotide Polymorphism (SNP) has been used to generate a genetic map for cassava. Several transcriptomic data have also been generated and used for gene discovery, trait mapping, and genome editing.¹⁷¹ Advanced

genomic tools like CRISPR/Cas9 have been completed to increase the yield of cassava, including disease resistance, herbicide tolerance, rapid flowering, and reduced cyanide content leaves and roots.⁷⁸

Sweet Potatoes (*Ipomoea Batatas*)

The journey of sweet potatoes from being an orphan crop to a staple crop is a remarkable success story, especially in regions like Africa and Asia. Initially regarded as a poor farmer's crop, orange-fleshed sweet potatoes (OFSP) have gained recognition for their nutritional benefits, particularly in combating Vitamin A deficiency.¹⁷² While their strong flavor and high sweetness levels initially posed challenges to their popularity, concerted efforts in breeding, agronomy, and nutritional advocacy have played a significant role in overcoming these challenges.¹⁷³ Breeding efforts focusing on enhancing β -carotene, dry matter, and sugar content may have enhanced the transformation of sweet potatoes into a staple crop.¹⁷⁴ Additionally, the development of value-added food products and the realization of sweet potatoes' health benefits, such as low glycemic index and suitability for diabetics, have further solidified sweet potato's position as a staple crop with significant importance and potential for diverse applications.¹⁷⁵ Furthermore, efforts to increase awareness, investment in crop improvement, improve postharvest management, and expand market demand for sweet potato products have also been instrumental in promoting their adoption as a commercial crop.¹⁷⁶

In terms of genomics, a genome sequencing initiative was officially launched in 2012. By 2015, the initial reference genome for the wild diploid sweet potato relative, *Ipomoea trifida*, was published, followed by the release of the sweet potato reference genome in 2017.¹⁷⁷ Over the past few decades, traditional breeding and molecular breeding approaches have been widely applied to sweet potatoes and have resulted in the development of many new cultivars with improved yield, nutrient content, pest resistance, and other quality factors.¹⁷⁸ Molecular breeding strategies, including marker-assisted selection and genomic selection, are being explored for sweet potato improvement. Numerous

quantitative trait loci (QTLs) using biparental^{179,180} and GWAS^{181,182} have been identified for agronomic trait, quality traits, and biotic resistance in sweet potato. Moreover, advanced genomic methods like CRISPR-Cas9 (clustered regularly interspaced short palindromic repeats-CRISPR-associated protein 9)-mediated mutagenesis via genome editing has also been used to develop improved varieties on starch quality.¹⁸³ Methods like genomic selection (GS) have also been applied to accelerate genetic gains in sweet potatoes.¹⁸⁴ New bioinformatics tools and pipelines have been developed to facilitate genetic and genomic research in the complex hexaploid sweet potato.¹⁸⁵ The *Ipomoea batatas* genome browser, the Ipomoea Genome Hub, and the Sweet potato GARDEN are databases that provide access to the sweet potato genome, RNA-seq data, and other genomic resources.¹⁷⁷

Lesson learned from successful intervention

The successful transformation of some *orphan crops* into commercially viable and widely cultivated staples provides valuable lessons that can guide the future commercialization of other potential *orphan crops*.¹⁸⁶ These lessons emphasize the importance of leveraging targeted research for consumer/framer preference, climate resilience, fostering collaborative efforts, developing markets, recognizing socio-economic impacts, enacting supportive government policies, and integrating genomic research and breeding efforts.¹⁸⁷ Climate resilience and nutritional value are critical factors in the success of *orphan crops*. Highlighting these attributes can significantly enhance the adoption and cultivation of such crops.¹⁸⁸ For instance, crops with inherent drought resistance and high nutritional value have a better chance of being integrated into farming systems and diets. Promoting these benefits can drive consumer interest and farmer adoption, providing a strong foundation for further development and commercialization.

Targeted efforts on improving yield, disease resistance, and market appeal are crucial for the success of these crops.¹⁸⁹ The use of advanced breeding techniques, such as marker-assisted selection, molecular breeding, and interspecific hybridization could be used to develop superior varieties that can overcome obstacles like pests, diseases,

poor soil quality, and suboptimal agronomic practices, which often hinder the productivity and appeal of *orphan crops*. These advancements have accelerated breeding efforts and improved crop performance, making these crops more competitive in the market.¹⁹⁰

Collaborative efforts among international and national research institutions for the development and improvement of orphan crops are instrumental. Such collaborations facilitate the sharing of knowledge, resources, and technologies, resulting in significant advancements in crop improvement.¹⁹¹ These partnerships are vital for conducting comprehensive research, developing superior germplasm, and ensuring that improved varieties reach farmers. Market development strategies are crucial for the commercial success of *orphan crops*. Developing market-specific traits, such as gluten-free properties or enhanced nutritional content, can open new commercial opportunities and increase the value of these crops.¹⁸ International recognition and marketing campaigns can elevate the status of these crops, facilitating their entry into global markets. Additionally, creating local and regional value chains can enhance market access and income opportunities for smallholder farmers.⁹² Supportive government policies and investments play a crucial role in the commercialization and market development of *orphan crops*. Government-backed programs that promote these crops as cash crops and support processing industries can significantly boost production and farmer incomes.¹⁹² Policies that encourage investment in agricultural research and development are also essential for the sustained growth of these crops.¹⁸⁸

Conclusions

The successful transformation of *orphan crops* into valuable staples points to the importance of targeted breeding programs, international collaboration, market development strategies, supportive government policies, and genomic research. Fast-tracking the improvement of orphan crops to improve desirable traits is more important than ever before. With the advent of new technologies and strategies, the hastening of orphan crop improvement should be possible and feasible. Modern technologies such as speed breeding and CRISPR/Cas9 in an integrative

approach with genomic selection and other high-throughput methods could accelerate the breeding cycle of orphan crops. This will enable the development of new varieties with novel traits with more than one cultivation cycle per year. Still, with the various efforts being made worldwide, our expectation is that these crops will contribute immensely to the food and nutritional security of most households and may likely become staple crops for the world in the not-so-distant future.

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