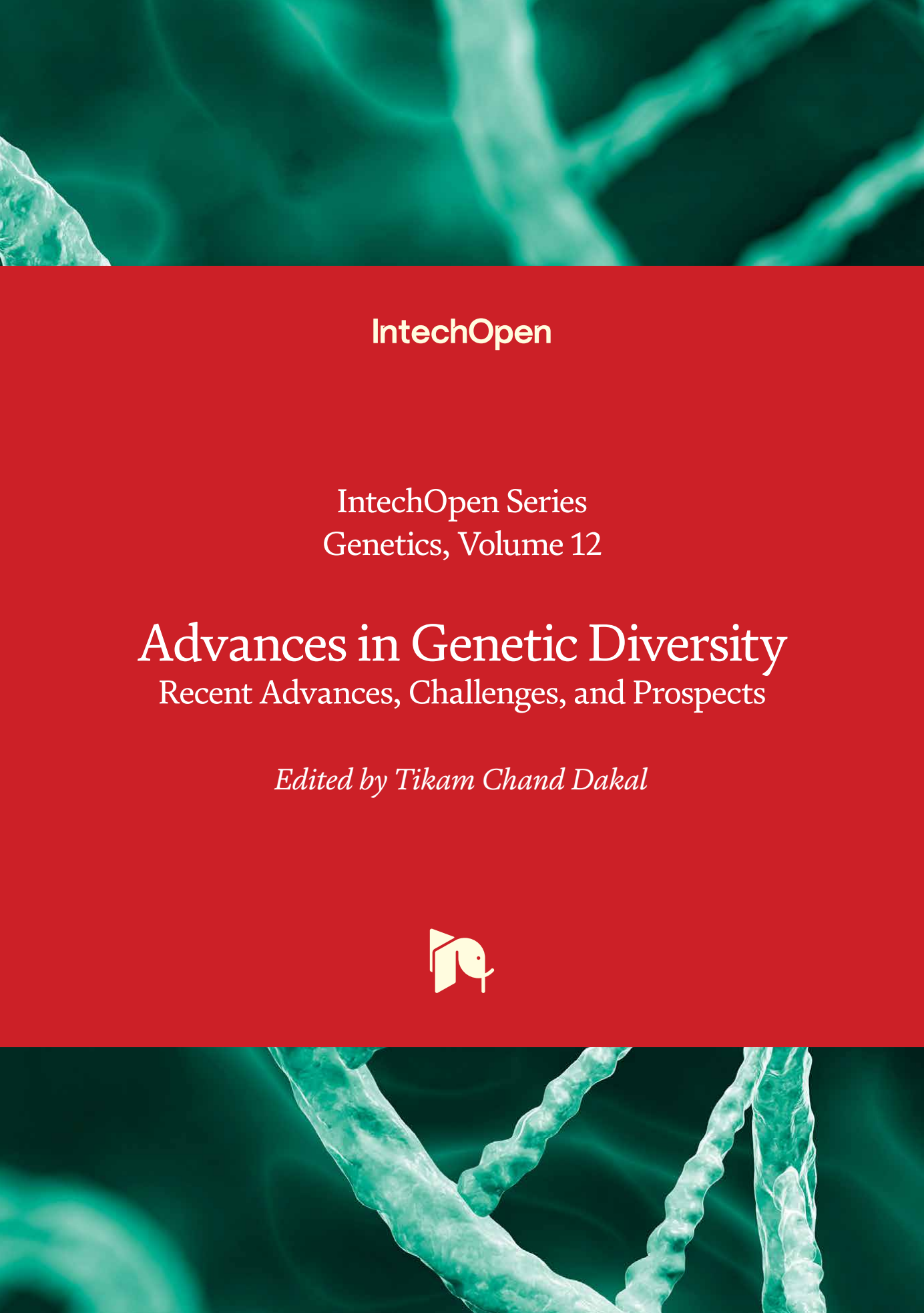




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Genetics, Volume 12

Advances in Genetic Diversity

Recent Advances, Challenges, and Prospects

Edited by Tikam Chand Dakal



Advances in Genetic Diversity – Recent Advances, Challenges, and Prospects

Edited by Tikam Chand Dakal

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IntechOpen Book Series

Genetics

Volume 12

Aims and Scope of the Series

“Genetics,” which has been proud of its tradition since Mendel presented his research results in 1865, initially progressed quite slowly due to simple observational approaches of individuals and groups. However, the discovery of double-stranded DNA by Watson and Crick about 70 years ago triggered rapid progress in life sciences, including genetics, which was primarily conducted using *Escherichia coli* and bacteriophages infecting *E. coli*. Subsequently, genetics has achieved remarkable developments, such as understanding genetic disorders, including cancers, through research on the biogenesis and differentiation of plants and animals. The two topics of this book series - Human Genetics, and Genomics - will address important areas of advancement in genetics.

Human Genetics: After fundamental genetics, initially studied with the main goal of revealing the functions of individual genes and proteins, genetics expanded from understanding the genetic system itself to understanding many infectious diseases caused by bacteria and viruses. Consequently, human beings are now overcoming infectious diseases by developing medicinal chemicals, including antibiotics and vaccines. However, genetic disorders remain challenging to cure up to now. Nevertheless, even the cure for them, including various cancers, is coming closer to reality due to the rapid progress of human genetics. In this way, the welfare of human life continues to improve, and even longevity, which was once a dream, has been achieved to some extent in recent years.

Genomics: On the other hand, the understanding of the comprehensive interrelationship of whole genes or whole proteins functioning in one organism has become possible now, as research has entered the era of genomics, owing to the rapid progress of base sequence analysis and bioinformatics. The development of genomics has further made it possible to understand the evolutionary processes of organisms through comparative studies among the genomes of many organisms.

This book series will discuss the findings obtained during the advancement of human genetics and genomics. It is also expected that this series will trigger the formation of a better world composed of human beings and all other organisms on Earth through discussions of research results obtained under the development of general genetics.

Meet the Series Editor



Kenji Ikehara graduated from the Department of Industrial Chemistry, Faculty of Engineering, Kyoto University in 1968. He received his B. Eng. (1968) and subsequently earned M. Eng. (1970) and D. Eng. (1976) degrees from Kyoto University. He began his career as a research associate in the Faculty of Science at the University of Tokyo before moving on to become an associate professor in the Faculty of Science at Nara Women's University. He was later promoted to professor and subsequently served as the dean of the Faculty of Science at Nara Women's University. Additionally, he held the position of director at the Nara Study Center of the Open University of Japan. For approximately 15 years, he focused his research on sporulation initiation of *Bacillus subtilis*. Later, he shifted his focus to the origins and evolutionary processes of microbial genes, the genetic code, proteins, and life. He has proposed several hypotheses, including the GC-NSF(a) hypothesis on the origin of genes, the GNC-SNS hypothesis on the genetic code, the protein 0th-order structure hypothesis on the origin of proteins, and the [GADV]-protein world hypothesis (GADV hypothesis) on the origin of life. Furthermore, he served as the local chair of the International Conference, Origin 2014, held in Nara in 2014.

Meet the Volume Editor



Dr. Tikam Chand Dakal is a renowned biotechnologist, academician, and scientist. Dr. Dakal is currently working as an Assistant Professor at Mohanlal Sukhadia University, India. Dr. Dakal has earned his Ph.D. degree from Italy and has work experience from Canada, France, and the United States. Dr. Dakal is also the State President of MBSI. He has published over 100 research/review papers in reputable international journals, focusing on microbial genetic diversity, molecular biology, and computational biology. His work emphasizes the role of genetic variation in health, agriculture, and the environment. Dr. Dakal has been actively involved in teaching, mentoring, and advancing interdisciplinary research. This volume reflects his vision of integrating genetic diversity research with sustainable solutions for global challenges.

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Preface

Genetic diversity forms the very foundation of life, shaping the adaptability, resilience, and long-term survival of species. It drives evolutionary processes, underpins agricultural innovation, and safeguards ecological stability. In the 21st century, where humanity faces the dual challenges of climate change and global food insecurity, the study of genetic diversity is not merely an academic pursuit but a critical necessity.

This book, *Advances in Genetic Diversity – Recent Advances, Challenges, and Prospects*, offers a timely exploration of how genetic variation can be harnessed, protected, and applied to address pressing global needs. The chapters included span theoretical insights, applied research, and case studies, collectively underscoring the pivotal role of genetic diversity in conservation biology, crop improvement, biotechnology, and sustainable development.

The introductory chapter, *Genetic Diversity in the Modern World – A Foundation for Conservation, Innovation, and Resilience*, sets the conceptual groundwork by highlighting the interconnectedness of biodiversity conservation, agricultural productivity, and biotechnological innovation.

Following this, Chapter 2, *Role of Genetic Diversity in Crop Improvement Programmes*, details how genetic variability enhances resilience and yield in food crops. Chapter 3, *Domestication History and Genetic Resources of Wild Rice Essential for Food and Nutrition Security*, illuminates the importance of wild germplasm in ensuring future food and nutritional security.

From global tools to regional applications, Chapter 4, *Phenotypic Variation and Clustering of Rice Landraces in South Sulawesi Using Multivariate Analysis*, showcases how local landraces preserve unique traits crucial for adaptation. Broadening the perspective, Chapter 5, *Leafless Vanilla Species from Madagascar as Potential Models to Study Bioclimatic Adaptation*, emphasizes how non-traditional crops provide valuable insights into resilience under environmental change.

Together, these chapters capture the essence of both recent advancements and the enduring challenges in studying and applying genetic diversity. By linking staple crops like rice with underexplored species such as vanilla, the book underscores the importance of widening our genetic resource base to foster resilience, adaptability, and sustainability.

We envision this volume as a resource for researchers, educators, policymakers, and students engaged in genetics, agriculture, conservation, and biotechnology. It aims to stimulate new directions of inquiry, strengthen interdisciplinary dialogue, and contribute to global strategies for safeguarding the irreplaceable wealth of genetic diversity.

I extend heartfelt gratitude to the contributing authors for their scholarly dedication, to the reviewers for their constructive insights, and to the publishing team for their unwavering support in bringing this work to fruition.

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Introductory Chapter: Genetic Diversity in the Modern World – A Foundation for Conservation, Innovation, and Resilience

Tikam Chand Dakal

1. Introduction

Genetic diversity forms the foundation of all biological variation and is vital for the resilience, adaptability, and evolution of species across ecosystems. It underpins agricultural productivity, ecological stability, and the capacity of organisms to respond to environmental challenges such as climate change, disease outbreaks, and habitat loss. This chapter explores the broad significance of genetic diversity in natural and managed systems, highlighting its role in conservation, sustainable development, and biotechnological innovation. The chapter outlines the key drivers of genetic erosion, including industrial agriculture, habitat fragmentation, and climate change, and presents recent technological advances that are transforming how genetic diversity is assessed and preserved. These include next-generation sequencing, pangenomics, CRISPR-Cas gene editing, artificial intelligence in breeding programs, and metagenomics for exploring microbial diversity. Conservation strategies, both *in situ* and *ex situ*, are examined, along with emerging frameworks such as synthetic biology, digital genebanks, and climate-resilient conservation planning. Future directions emphasize the integration of multi-omics, precision phenotyping, and blockchain-enabled biodiversity data management, offering new opportunities to safeguard genetic resources. The chapter also addresses ethical, legal, and social considerations essential to ensuring responsible and equitable use of these technologies. Ultimately, this introductory chapter positions genetic diversity not just as a subject of scientific interest but as a strategic asset for addressing some of the most pressing challenges of our time, from food and health security to environmental sustainability and global equity.

2. Understanding genetic diversity: The core of biological variation

2.1 Defining genetic diversity

Genetic diversity refers to the total number of genetic characteristics in the genetic makeup of a species. It includes variation within species (intraspecific), between species (interspecific), and within populations of the same species.

This variation forms the raw material for evolutionary adaptation and enables populations to adjust to changing environmental conditions, resist diseases, and sustain long-term viability [1].

2.2 Dimensions of genetic diversity

Genetic diversity can be studied at three biological levels:

- Molecular level—variation in DNA sequences such as single-nucleotide polymorphisms (SNPs), insertions, and deletions [2].
- Individual level—differences among individuals in traits like disease resistance or reproductive fitness [3].
- Population level—allele frequencies and heterozygosity that determine the genetic structure of a population [4].

Each level contributes to the adaptability and sustainability of species and ecosystems over time [1].

2.3 The ecological and societal relevance of genetic diversity

2.3.1 A pillar of ecosystem resilience

Genetic diversity ensures the resilience of ecosystems by enabling species to cope with the environmental changes, including temperature shifts, habitat disturbances, and novel pathogens [5]. Populations with high genetic variation tend to show greater adaptability and ecological stability under stress.

2.3.2 Contributions to agriculture and food security

Genetic resources are the cornerstone of crop and livestock improvement. Landraces and wild relatives of domesticated species provide traits such as drought tolerance, pest resistance, and improved nutrient profiles [6]. The erosion of these resources through monocultures and habitat loss threatens food security, especially under climate stress.

2.3.3 Relevance in public health and biotechnology

Genetic variation is central to personalized medicine, vaccine development, and epidemiology. Additionally, microbial diversity offers critical applications in biotechnology, such as the development of antibiotics, fermentation processes, and environmental remediation [5].

2.4 Drivers and consequences of genetic erosion

2.4.1 Anthropogenic pressures

Modern civilization exerts multiple pressures on genetic diversity, including the following:

- Industrial agriculture with the limited crop varieties
- Urban expansion and habitat fragmentation
- Pollution and overharvesting of biological resources
- Accelerated climate change

These drivers lead to genetic bottlenecks and inbreeding, reducing species' evolutionary potential [1].

2.4.2 Case examples of genetic loss

Historical and contemporary examples illustrate the dangers of genetic uniformity:

- The Irish Potato Famine resulted from the cultivation of genetically similar potato varieties susceptible to *Phytophthora infestans*.
- The Cavendish banana faces extinction threats due to its genetic homogeneity and susceptibility to Fusarium wilt.
- An estimated 28% of livestock breeds are at risk of extinction globally due to the dominance of a few commercial breeds [5].

2.5 Recent technological advances in genetic diversity assessment and management

2.5.1 Next-generation sequencing (NGS)

NGS technologies have enabled population-scale genome sequencing, offering insights into genome-wide variation, structural mutations, and adaptation mechanisms [6]. Techniques like Genotyping-by-Sequencing (GBS) and RNA-Seq are instrumental in genetic diversity analysis across taxa.

2.5.2 Pan-genomics and graph-based genomes

Pan-genome assemblies include core and dispensable genes across multiple individuals, capturing the full scope of genetic variation. Graph-based genome models are revolutionizing the way genetic variation is represented, particularly in crops like rice, maize, and soybean [6].

2.5.3 CRISPR-Cas and precision breeding

Genome editing *via* CRISPR-Cas9 allows for targeted insertion, deletion, or alteration of genes in plants and animals. This tool facilitates the enhancement of stress tolerance, yield, and disease resistance without introducing foreign DNA [7]. Emerging methods like base editing and prime editing further improve precision and reduce off-target effects.

2.5.4 AI, machine learning, and genomic prediction

Artificial intelligence (AI) and machine learning (ML) are transforming the interpretation of genomic data. These tools enable the prediction of phenotypic traits based on genotype, optimize breeding strategies, and identify favorable alleles for selection [8].

2.5.5 Metagenomics and microbiome diversity

Metagenomic sequencing of environmental samples has uncovered vast microbial diversity, including unculturable organisms. These microbial communities play essential roles in soil fertility, human health, and ecosystem functioning [5].

2.6 Conserving and enhancing genetic diversity

2.6.1 In situ conservation

In situ strategies preserve species within their natural habitats, allowing continued evolution and local adaptation. Protected areas, biosphere reserves, and community-based conservation are a key to this approach [1].

2.6.2 Ex situ conservation

Seed banks, cryopreservation of genetic material, and DNA libraries are examples of *ex situ* strategies. Facilities like the Svalbard Global Seed Vault act as insurance against catastrophic loss of plant genetic resources [5].

2.6.3 Emerging approaches: Synthetic biology and de-extinction

Synthetic biology offers opportunities to restore lost functions or species using synthetic genes or genomes. Projects aimed at reviving extinct species like the woolly mammoth or enhancing disease resistance in threatened populations demonstrate the frontier of applied genetic science [9].

2.7 Future directions: Toward a technology-driven genetic conservation paradigm

2.7.1 Integrative multi-omics approaches

Integrating genomics, transcriptomics, metabolomics, and proteomics can provide a systems-level understanding of how genetic diversity shapes phenotypes and ecological outcomes. Combined with precision phenotyping and environmental modeling, this approach will drive future conservation and breeding strategies [6].

2.7.2 Digital genebanks and blockchain technology

Digital platforms and blockchain-based traceability systems can enhance transparency in genetic resource sharing and ensure equitable benefit-sharing under frameworks like the Nagoya Protocol [10].

2.7.3 Conservation genomics under climate uncertainty

Climate-responsive conservation genetics involves identifying climate-resilient genotypes and supporting gene flow across landscapes to foster adaptive potential [9]. Assisted migration and targeted restoration using genomic insights will become more prevalent.

2.7.4 Ethical, legal, and social considerations (ELSI)

With the increasing power to modify genomes, ethical governance is essential. It includes ensuring biosafety, protecting Indigenous rights, and balancing innovation with precautionary principles [7].

3. Conclusion

Genetic diversity is not only the basis for biological evolution but also a strategic resource for addressing critical challenges in agriculture, health, and environmental sustainability. Modern tools such as CRISPR, pan-genomics, AI, and synthetic biology are revolutionizing how we study and utilize genetic variation. As we advance further into a data-driven and technology-enabled future, the integration of high-throughput genomics, machine learning, and global digital infrastructures will redefine how we manage and conserve genetic resources. However, these technological possibilities must be pursued with foresight, inclusivity, and responsibility. A global, collaborative effort involving scientists, Indigenous communities, policymakers, and the public is essential to ensure that genetic diversity remains a living legacy, supporting both the natural world and human societies for generations to come.

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Chapter

Role of Genetic Diversity in Crop Improvement

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Ernest Baafi, Philip Ghanney, Jacinta Adoma Opoku,
Augustine Boakye Boateng and Harrison Kwame Dapaah*

Abstract

The existence of genetic diversity among organisms is crucial for maintaining the ecosystem, coping with the fast-changing climate, and enhancing biodiversity. Genetic diversity promotes genetic resource conservation and utilization, which are prerequisites contributor to the attainment of global food security. Genetic diversity aids in detecting and developing sustainable pest and disease management strategies while contributing to the development of cultivars preferred by producers, consumers, and the industries. The chapter presents the importance and sources of genetic diversity in crop improvement. The role of genetic diversity, conservation, and utilization of plant genetic resources is also explored to examine its contribution to crop improvement programmes. In addition, interventions employed in increasing genetic diversity and its application in crop improvement programmes for end-user preferred traits, such as yield stability, tolerance to biotic and abiotic stressors, and climate-change-resilient development, are discussed.

Keywords: genetic diversity, crop improvement, plant genetic resources, germplasm, stress, yield stability

1. Introduction

Crop plant evolution is primarily determined by the genetic diversity present in the population. Diversity is the degree to which species differ from one another. Genetic diversity measures the genetic differences that occur within a population. Crop variation can be due to either environmental factors or genetic differences [1]. Genetic variability refers to the occurrence of variation between individuals caused by differences in genetic composition [2]. Genetic diversity is the extent to which members of a population or variety within a species differ genetically. Thus, it is the primary driver of population adaptability and evolution. The genetic material found in the reproducing individuals of the population determines the diversity found in plant populations. The alleles of a gene that are present in the population, their distribution, and their effects can be used to summarize genetic diversity. The foundation of all crop development initiatives is the existence of intra- and interspecific differences.

There will not be an improvement in the performance of plants if all individuals in the species are identical. The group of individuals in a species must, therefore, represent the biggest gene pool under natural conditions. A healthy population depends on useful genetic variation because it preserves many genes that could confer resistance to diseases, pests, or other stressors. Genetic variety allows different crop kinds to adapt to changing climatic conditions and ensures their survival [3].

In the agricultural landscape, genetic variation among crops is the most crucial element for secure and environmentally conscious agriculture. Hence, several efforts are geared towards having diverse genetic materials in the farming systems for the fear of genetic erosion [4, 5]. Thus, effective for diversifying the output in markets and households and for enhancing agroecological services [6, 7]. Crop genetic variety is seen to be crucial for the security of food, nutrition, business, health, and the environment. The most important component of any variety creation effort is the existence of genetic variation. Genetic diversity among crop germplasm facilitates the effective selection of superior genotypes as improved cultivars or as candidate parents in a breeder's crossing scheme.

There are concerns about the decline in genetic diversity and the narrow genetic base among crop plant species. Diverse breeding lines are essential for generating innovative types and rectifying flaws in commercial varieties. The fundamental objectives of any crop development programme are to identify diverse lines, generate variety, and subsequently utilize them. The prime goal of this chapter is to highlight the need for genetic diversity and the various approaches for generating genetic diversity in crops for breeding programmes. Also, the chapter reveals how plant genetic resources (PGRs) could be conserved and utilized for crop development programmes. Furthermore, the essential functions of gene variation in crop breeding programmes, along with the related problems, are examined comprehensively.

2. Importance of genetic diversity in crop improvement

For plant breeders, the primary concern is to develop crops that are resilient and able to withstand the increasing effects of climate change, including drought and other climate-related stresses on crops [8, 9]. Consequently, genetic diversity is crucial for effective crop improvement programmes as it provides the raw material for selection and breeding, enabling plant breeders to find and combine desirable traits to produce new and improved varieties [3]. Breeders can address challenges such as drought, pest resistance, stress tolerance and yield improvement by capitalizing on natural variation within and between crop species. For example, genetic diversity within and between plant species allows plant breeders to select superior genotypes that can then be used to generate genetic material for hybridisation programmes or to release a crop variety [1]. Genetic diversity enables PGRs to adapt to a variety of environmental situations [10, 11].

Plant genetic resources (PGR) are all alleles of different genes that occur in a plant species and its wild relatives. They are an important resource that people rely on to improve the resilience and profitability of agriculture. As a result, the demand for genetic resources will increase in step with global population growth. To ensure long-term food security, it is necessary to maintain and preserve the genetic diversity of these rich resources. Some valuable genetic resources have already become extinct due to environmental changes and genetic degradation. The most valuable PGRs include landraces, wild relatives, wild species, genetic material, improved breeding material, and modern cultivars. These

numerous resources have contributed to the promotion of biodiversity. These resources have facilitated the production of new plant varieties with desirable characteristics. Biotechnological techniques are used to introduce new genes/alleles associated with the desired trait into commercially produced crop varieties. Diversity should be preserved as a genetic resource to ensure the long-term development of new crop varieties.

Crop improvement relies on genetic diversity [1]. Diverse PGRs allow plant breeders to create or improve plant varieties with desirable traits. Farmers' preferences, such as high-yielding varieties, quality, and tolerance to diseases and pests, must be taken into account when creating new varieties. In ancient times, people selected acceptable genotypes based on the natural genetic variability in the population [10]. Selection for the development of new plant species fluctuates over time as the environment changes. Plant breeders create climate-resilient varieties that exhibit all desirable traits, including tolerance to various biotic and abiotic stress factors.

Genetic variety, such as mutant lines, wild species, and breeding stocks, is employed to improve and develop modern crop types [1]. To produce climate-resilient varieties, unique genes that are tolerant to biotic and abiotic stress factors need to be conserved for future use in breeding programmes. In addition, plant genotypes containing genes for quality traits and esthetic characteristics should be maintained in the available germplasm. Genetic diversity within and between plant species allows plant breeders to identify superior genotypes that can then be used to produce genetic stock for hybridisation projects or to release a plant variety [1]. Genetic diversity allows PGRs to adapt to a wide range of environmental conditions [10, 11]. In addition, greater genetic diversity can help to reduce the harmful effects of inbreeding in communities. Higher levels of genetic diversity in PGRs promote resilience to unfavorable environmental change, community integrity, community structure, and ecosystem function [12, 13]. In addition, it enables plant breeders to use genetically diverse parents in a breeding programme to increase the production of agricultural and horticultural plant varieties (**Figure 1**) [14].

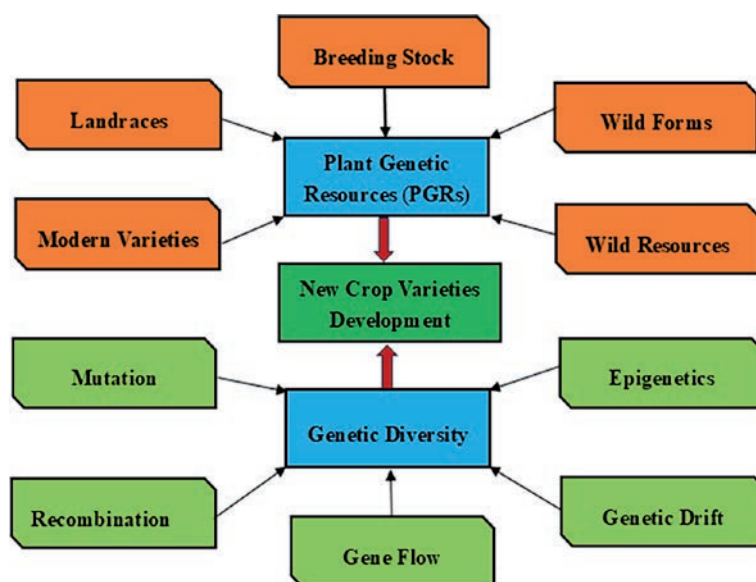


Figure 1.
 Various sources of genetic diversity and their possible application in the creation of new crop varieties.

Genetic diversity in plant species is determined by heritable variation within and between populations. It results from genetic variation in the nucleotide sequence of DNA, chromosomal mutations, and recombination during sexual reproduction [15]. Plant species reproduce sexually by crossing two or more different parents to produce the first filial generation (F1) and higher generations. The offspring of two genetically diverse parents exhibit genetic variants due to recombination during meiosis. As a result, the offspring of the parents are genetically different. However, it is the genetic material of the individuals that accounts for the diversity both within and between species [16].

3. Sources and types of genetic diversity in crops

Genetic diversity within or between crop species, consisting of wild relatives, landraces and cultivars, is critical for crop improvement and food security [17]. The sources of this genetic variation serve as the foundation for plant breeding and enable the creation of superior varieties with traits such as higher yield, resistance to biotic stress factors, and abiotic stress tolerance [2]. According to Smýkal et al. [18], the sources of crop diversity come from various sources such as mutations, domestication from wild relatives, gene flow, and other sources. Activities of humans, including conventional land management and innovative breeding, have led to a good genetic composition of crops [19]. The types of genetic diversity are broadly categorized into inter- or intraspecific diversity as well as DNA levels of molecular diversity [16, 20]. Utilization of varied genetic resources amidst modern breeding genotypes, landraces and wild relatives is of utmost importance for the improvement of crops such as high-yielding, climate-resilient, resistant, and tolerant crop varieties that can withstand the harsh climatic conditions for global food security [21].

3.1 Wild relatives, landraces and elite cultivars in crop improvement

Wild relatives, landraces and elite cultivars are important for crop improvement programmes as they provide a variety of genetic resources that can be used to improve crop species (**Figure 2**). Wild relatives frequently have desirable traits that are not found in modern varieties, such as disease resistance, tolerance to abiotic stress factors, or improved nutrient content [22]. Landraces are adapted varieties, have unique genetic diversity, and can be useful for adapting crops to specific locations and conditions [23]. Elite varieties, on the other hand, epitomize the pinnacle of modern breeding efforts and lay the foundation for future advances.

Wild crop species are an essential source of genetic resources for the improvement of agricultural production and the conservation of agroecosystems [21]. Their diverse and valuable traits can be introduced into cultivated plants through hybridisation. Wild species differ from cultivated plants in a number of essential traits that have significant implications for collection, conservation, and utilization techniques. Repeated rounds of selection have led to the production of crops that feed the world today; however, they have reduced genetic variation, resulting in lower allele bandwidth [24]. This is sometimes referred to as the ‘domestication bottleneck’.

According to Castañeda-Álvarez et al. [25], wild species are plants that appear to occur in their habitat without human intervention or domestication, while wild relatives are wild plant species that have genetic similarities to crops. Wild relatives are a subset of wild species that play a vital role in plant breeding and genetic

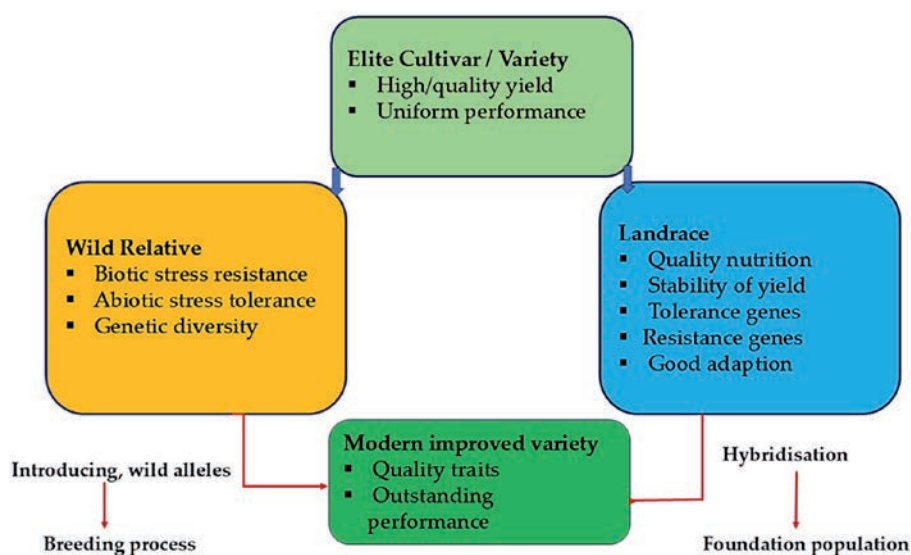


Figure 2.
 Contributions of wild relatives, landraces, and elite cultivars in the crop improvement programme.

diversity. They often contain genes for traits, such as disease resistance, abiotic stress tolerance (drought, salinity, heat, cold, etc.), and specific nutritional traits that can be introduced into crops *via* breeding [26]. The wild relatives of crops are both the raw material for breeding and an important source of biodiversity. This diversity can be used to introduce unique alleles for disease resistance and other quality traits into improved germplasm [2], so that the wild relatives of crop plants can be preserved and used for breeding. Therefore, these wild populations are important for understanding how selection for agricultural traits has altered the genomes of crop species during domestication and improvement [27]. One of the major obstacles in the study of wild relatives is the lack of germplasm and genetic data for many crop species [27].

Landraces are plant varieties that have developed in specific regions and have been passed down through generations of farmers [28]. They often show a high degree of adaptation to the conditions of the local environment and can be useful sources of genes for traits such as disease resistance and drought tolerance. Agricultural species that have been regionally adapted are crucial for maintaining agricultural diversity and improving crop sustainability [29]. They are essential genetic resources that help to ensure the long-term stability of traditional agroecosystems and food and nutrition security [30]. Landraces serve to maintain the genetic diversity of crops, which is necessary to respond to changing environmental conditions and to combat threats such as pests and diseases. Azeez et al. [28] explained that landraces are characterized as dynamic populations of a crop with historical origins, distinct identity, genetic diversity, and local adaptation, and are associated with a range of farmer seed selections and field management practises and a farmer knowledge base. Dwivedi et al. [23] defined landraces as plant varieties that represent diverse local adaptations of domesticated species and provide genetic resources to cope with current and future problems in agriculture under harsh conditions. These local ecotypes can have diverse phenology and low to moderate edible yields, although they are often highly nutritious [23]. Landraces have made an important contribution to plant breeding by introducing traits for more effective nutrient uptake and utilization as well as valuable

genes for adaptability to unfavorable conditions such as high temperatures, salinity, and water stress [28, 30]. Rigorous evaluation of landraces can help identify alleles that improve yield and adaptability to abiotic stress, thus increasing the production and stability of staple crops in sensitive areas [23]. It can also be described as a classical variety with a high tolerance to biotic and abiotic stress factors, resulting in high yield stability and medium yield levels in a low-input agricultural system.

Elite cultivars are selected for outstanding traits and characteristics that make them suitable for commercial or agricultural use [31]. These cultivars are often the result of intensive selection programmes aimed at improving certain traits such as yield, disease resistance, or nutritional quality. A cultivar is a bred variety, that is, a plant that has been bred or selected by humans specifically for certain traits. In terms of cultivars, 'elite' means that the cultivar has been selected for its superior presentation and characteristics compared to other cultivars of the same species [32]. These are cultivars that are known to be favorable and are used as a starting point for further breeding or as the main planting stock in agriculture. In agriculture, elite varieties of wheat or rice can be bred for high yields, disease resistance, or particular grain quality [33]. These are the current varieties that have been developed through plant breeding. They are characterized by high quality in terms of yield, nutrients, and disease resistance [33]. They can serve as a basis for future breeding programmes using wild relatives and landraces to introduce additional valuable genes. In summary, effective crop development usually requires the collection and characterization of genetic resources. Using these resources to breed new and improved crop types means blending favorable genes from many sources to produce plants with higher yields, better quality, and better adaptability to specific locations [2]. In this way, they can benefit from advances in crop enhancement while contributing to food security and sustainability.

3.2 Intraspecific and interspecific diversity

Both intraspecific and interspecific diversity play a crucial role in crop improvement. Intraspecific diversity refers to variation within a single species, while interspecific diversity refers to variation between different species [34]. Utilizing both types of diversity can lead to more robust and resilient crop systems.

Intraspecific diversity within crop species has a long history in agricultural research, and crop breeding has led to the development of increasingly specialized plant varieties [2, 24]. Plant breeding selects for desirable traits and characteristics to increase yields and for traits that limit productivity or are incompatible with agricultural management practises (e.g., mechanical harvesting) or consumer expectations. So, while a limited number of crop species dominate food production worldwide, there are many cultivars of these species that differ functionally. The domestic apple, for example, has over 7500 cultivars. While most have been selected for their flavor and other characteristics of palatability, disease resistance, and climate sensitivity also vary greatly [35]. Even with a primarily vegetatively propagated crop such as the potato, there is a diversity of several thousand cultivars and landraces [36]. Despite this diversity, it was the use of a single varietal clone that was responsible for the late blight epidemic and subsequent famine in nineteenth century Ireland, an extreme example of the consequences of low diversity [37]. For example, the widely used variety 'IR64' was bred by combining traits with different intraspecific varieties to achieve high yields and resistance to pathogens [38]. Intraspecific diversity in maize is enormous due to outcrossing and different geographical production. Maize varieties from Latin America have traits such as drought tolerance and resistance to pests

(armyworm) that are important for commercial maize breeding programmes to ensure food security in Africa [39].

Interspecific diversity refers to the genetic differences that occur between different species within the same genus [39]. This diversity is very important when specific values of long-lived traits are limited in cultivated species. The wild ancestors of crop plants are an important basis for interspecific diversity and therefore often harbor resistance or tolerance genes, stress-adaptive traits, or unique alleles that could be introduced into crop varieties [40, 41]. A typical example is the introduction of (Lr genes), a resistance gene found in the leaf rust of wild wheat (*Triticum aestivum*) [42]. Similar examples of resistance genes to root knotweed and virus-induced diseases in tomato (*Solanum lycopersicum*) have been transmitted from wild ancestors such as *Solanum peruvianum* and *Solanum chilense* [43]. The wild relatives of legumes such as *Arachis duranensis* and *Arachis ipaensis*, which have resistance to late blotch disease and are drought-tolerant, have been introduced into many elite peanut cultivars [44].

According to Kashyap et al. [45], despite the potential of interspecific diversity, it is difficult to transfer traits from wild ancestors into commercial varieties due to barriers to reproduction, resistance to linkage, and undesirable traits. Nevertheless, newer breeding techniques such as marker-assisted selection, genome selection, and pre-breeding techniques help to remove the obstacles by ensuring accurate and efficient gene transfer or introgression [46]. In conclusion, both inter- and intra-specific diversity offer precise potential for improving the genetic basis of plant varieties [47]. Utilizing these approaches can pave the way for the development of better plant varieties with maximized yield, high nutritional quality, and good adaptation to different environmental zones.

3.2.1 Interspecific diversity

Interspecific diversity is the genetic variation that occurs between different species within the same genus [39]. This diversity is particularly valuable when desirable traits are lacking or limited in cultivated species. Wild relatives of crop plants (CWR) are an important source of interspecific diversity and often harbor resistant genes, stress-adaptive traits, or new alleles that can be introduced into cultivated species [40, 41]. A classic example is the introduction of Lr genes for leaf rust resistance from wild wheat relatives such as *Aegilops tauschii* and *Triticum dicoccoides* into commercial bread wheat (*Triticum aestivum*) [42]. Similarly, in tomato (*Solanum lycopersicum*), genes for resistance to root-knot nematodes and viral diseases have been transferred from wild species such as *Solanum peruvianum* and *S. chilense* [43]. Among the legumes, *Arachis duranensis* and *Arachis ipaensis* are the wild ancestors of the cultivated peanut (*Arachis hypogaea*) [44], which have been used to introduce resistance to late leaf spot disease and drought tolerance, which are lacking in many commercial varieties. Despite the potential of interspecific diversity, the transfer of traits from wild species into cultivated lines can be challenging due to reproductive barriers, linkage resistance, and undesirable traits [45]. However, modern breeding tools such as marker-assisted selection, genomic selection, and pre-breeding techniques help to overcome these barriers by enabling more precise and efficient gene introgression [46].

3.3 Other sources

Other sources of genetic variation include mutation, recombination, gene flow, hybridization, polyploidy, and introgression. These can be leveraged to build climate-resilient cropping systems to sustain long-term productivity.

3.3.1 Mutation

Mutation breeding is a powerful tool in crop improvement, particularly for enhancing stress tolerance and stabilizing yields under changing climatic conditions. Mutations, whether spontaneous or artificially induced, serve as a significant source of genetic variation, which is a prerequisite for selection and improvement in breeding programmes [48]. While natural mutations occur at low frequencies, their induction through physical mutagens (X-rays, gamma rays, UV light) or chemical agents (EMS, sodium azide) allowed breeders to accelerate the development of desirable traits [49]. Induced mutations have been found to improve tolerance to various abiotic stresses by modifying genes involved in physiological and biochemical stress responses [50]. Mutation can enhance the expression of genes associated with antioxidant defense, osmolyte accumulation, and stress-responsive transcription factors, thereby improving a plant's capacity to withstand adverse conditions [51, 52]. These alterations can also affect root architecture, flowering time, or stomatal regulation, leading to improved water-use efficiency and stress adaptation [53, 54]. In addition, mutation breeding contributes to yield stability by introducing alleles that ensure consistent performance across different environmental contexts [55]. This is particularly valuable when traditional breeding methods offer limited progress due to narrow genetic bases in elite cultivars. By integrating mutations into existing germplasm, breeders can enhance traits without disrupting other agronomically important characteristics [56, 57].

3.3.2 Genetic recombination

Genetic recombination is a key biological mechanism that promotes genetic variability in sexually reproducing plants and forms the basis of natural evolution and modern crop improvement strategies [58]. During meiosis, exchange of genetic material (DNA) between homologous chromosomes occurs, leading to new allelic combinations that drive phenotypic variation and adaptation [59]. The process is initiated by the formation of programmed DNA double-strand breaks (DSBs), catalyzed by the conserved topoisomerase-like enzyme SPO11 and its associated protein complex [60, 61]. These DSBs are primarily repaired *via* homologous recombination (HR) to serve as a high-fidelity mechanism that utilizes a homologous DNA strand as a repair template [62]. The result is either a crossover (CO), which is a reciprocal exchange of chromosomal segments, or a non-crossover (NCO), where gene conversion occurs without segment exchange [63]. COs are further classified as interference-sensitive (Type I) or interference-insensitive (Type II), reflecting their regulation along chromosomal axes [64]. The distribution of COs across plant genomes is non-uniform, varying at both macro- and micro-genomic scales [65]. This uneven distribution influences linkage disequilibrium (LD) and has direct consequences for genetic mapping, allele introgression, and quantitative trait loci (QTL) resolution in breeding. Understanding recombination landscapes allows breeders to efficiently break undesirable linkages and assemble favorable trait combinations [66, 67]. Beyond meiosis, HR also operates during mitosis, playing a central role in repairing DSBs caused by environmental and endogenous factors, thus maintaining genome stability [68]. However, in plant transformation, nonhomologous end joining (NHEJ) is often the predominant pathway for integrating foreign DNA, leading to random insertions and potential gene disruption [69]. In crop breeding, recombination enables the exploitation of heterosis and transgressive segregation and supports the incorporation of

favourable alleles from diverse genetic backgrounds [70]. It allows breeders to harness variation from wild relatives, landraces, and mutant populations to develop cultivars with enhanced yield, stress tolerance, and climate resilience.

3.3.3 Gene flow

The transfer of genetic material (gene flow) among populations is a fundamental evolutionary process with wide-ranging implications in agriculture, biodiversity, and conservation. In crop production, gene flow occurs both intentionally (breeding and wide crosses) and unintentionally (pollen contamination) to influence crop improvement and genetic purity [71–73]. The advent of transgenic crops has heightened concerns over gene flow to wild relatives and landraces, with implications for ecological stability and food security. For gene flow to occur, spatial proximity, flowering synchrony, cross-compatibility, and hybrid viability must align [74]. When transgenes escape into wild or weedy populations, they may enhance fitness, resulting in invasive traits. Such cases underscore the economic and ecological risks of unmanaged gene flow from genetically modified organisms. Gene transfer technologies have expanded breeding capabilities, allowing for the incorporation of traits like insect resistance (Bt genes), stress tolerance, and viral protection [75, 76]. However, these advances also demand stringent biosafety protocols to prevent unintended consequences, including outcrossing and the creation of superweeds. Gene flow also plays a critical role in conservation genetics [77]. While it can facilitate genetic rescue by increasing diversity and fitness in small populations, unregulated gene flow may disrupt local adaptation and lead to outbreeding depression or genetic swamping.

3.3.4 Hybridization

Hybridization is a foundational technique in plant breeding that involves the crossing of two genetically distinct individuals to produce offspring with desired traits [78]. It is an important phenomenon in genetic enhancement, crop improvement, and the development of new varieties with superior characteristics [79, 80]. Hybridization is defined as the natural or artificial crossing of two individuals from different populations, varieties, species, or genera. The offspring, known as hybrids, may exhibit novel combinations of parental traits or entirely new characteristics resulting from recombination. The process of sexual hybridization in plants involves several stages, including pollination, pollen germination and tube growth, fertilization, embryo and endosperm development, and seed formation and maturation [81, 82]. However, hybridization may be constrained by biological barriers such as sexual incompatibility, differences in flowering times, polyembryony, and male sterility [83]. These challenges can be overcome using advanced biotechnological tools like embryo rescue and somatic hybridization. Hybridization can be classified based on taxonomic relationships as intervarietal (crossing different varieties of the same species), interspecific (crossing different species), and intergeneric (crossing different genera) [84, 85]. Recombinants from hybridization can be used to develop pure lines in self-pollinating crops through selection and inbreeding, as well as to produce heterotic hybrids that express hybrid vigor or heterosis [86]. The degree of heterosis often increases with the genetic distance between parental lines [87]. However, in advanced segregating generations, recombination may disrupt favourable gene combinations, potentially leading to reduced fitness unless effectively managed by selection.

Hybridization introduces novel alleles into populations, increasing heterozygosity and reducing the risk of inbreeding depression [88]. In both wild and cultivated plants, hybridization promotes adaptation to new environments, tolerance to abiotic and biotic stressors, and rescue of endangered or low-fitness populations through evolutionary rescue mechanisms [89]. Natural selection typically favors hybrids with higher fitness, stabilizing populations over time. Hybridization faces several limitations, including reproductive incompatibility between species or genera, hybrid sterility or weakness in distant crosses, and genetic drag from undesirable traits [90]. These limitations can be mitigated through embryo rescue for abortive hybrids and the use of biotechnology tools.

3.3.5 Polyploidy

Polyploid species are widespread across plant lineages and are common in many families. Some species show variation in ploidy levels even within the same species, though odd-numbered ploidies like triploids are relatively rare. Polyploidy is generally classified into autopolyploidy and allopolyploidy, though ancient events are often difficult to categorize [91, 92]. Advances in genomics have revealed that polyploidy induces genetic changes such as gene duplication, differential gene retention, and the evolution of novel gene functions [93]. These changes play critical roles in plant speciation, adaptation, and broader ecological processes. Polyploidy has been linked to shifts in stress tolerance, trait diversification, metabolite production, and interactions with herbivores and microbes [94]. These insights underscore the ecological complexity and evolutionary importance of genome duplication. Polyploid plants often differ functionally from their diploid relatives, showing altered stress responses and ecological performance [95]. Whole-genome duplication can lead to substantial phenotypic shifts, yet the direction and magnitude of trait changes remain inconsistent across lineages. Understanding these lineage-specific outcomes is essential to grasping the full impact of polyploidy on plant adaptation, evolution, and ecosystem dynamics.

3.3.6 Introgression

Introgression plays a critical role in modern plant breeding by enabling the transfer of beneficial traits from wild relatives or less-adapted species into cultivated crops. This approach expands genetic diversity and introduces novel alleles that can enhance yield, stress tolerance, disease resistance, and quality traits [96]. However, the process often faces challenges such as linkage drag, where desirable genes are inherited alongside deleterious traits due to close proximity on the chromosome [97, 98]. This can hinder breeding progress, especially in crops with complex, heterozygous genomes like potato and apple. To overcome these limitations, strategies like Breeding by Selective Introgression (BBSI) have been developed [99]. BBSI combines backcrossing with marker-assisted selection and genome-wide tracking of donor segments, allowing breeders to retain favourable alleles while minimizing unwanted genetic material [99, 100]. Elite introgression lines (ILs) derived through this process are evaluated across environments, and top-performing lines are used for cultivar release or QTL pyramiding. From an evolutionary perspective, introgression is a form of gene flow that can drive adaptation [101]. Adaptive introgression occurs when transferred alleles provide a fitness advantage, such as enhanced abiotic stress tolerance or disease [98].

4. Conservation of genetic diversity

The conservation of genetic diversity is of fundamental importance for sustainable agriculture and long-term food security [102]. Gene banks and other conservation strategies play a crucial role in preserving PGRs, which serve as a reservoir for breeding traits that are important for crop improvement [15]. Two main approaches are used to protect this diversity, and these are *ex situ* and *in situ* conservation.

4.1 *Ex situ* conservation

Ex-situ conservation: *Ex-situ* conservation is the preservation of certain genetic resources outside their natural environment. It includes the conservation of seed gene banks, plant tissue culture, cryopreservation, greenhouses, and so on. It is the process of protecting endangered and overexploited genetic resources outside their natural habitat, which would otherwise be destroyed and degraded, leading to the extinction of any PGR. Consequently, *ex situ* conservation is an alternative strategy for conserving rich genetic resources [16]. This approach protects PGRs from extinction due to natural disasters, human intervention, climate change and overexploitation. To avoid duplication, collected genetic resources should be thoroughly assessed and defined, documented, and conserved under artificial conditions to protect them from external threats [103]. Among the various approaches to *ex situ* conservation, seed storage is the most convenient and easiest method for long-term seed preservation [103, 104]. Orthodox seeds of food crops are used for storage because they can withstand low temperatures and severe desiccation. In *ex situ* conservation, seeds of cereal crops such as rice, wheat, maize, oats, triticale, rye, sorghum, and barley account for about 45% of stored accessions, followed by food legumes (15%), forage crops (9%), and vegetables (7%).

Long-term storage. In this situation, the seed samples are stored at 18–20 degrees celsius to maximize the viability of the seeds [105]. Depending on the species, the moisture content of the seed to be stored should be between 3% and 7% when collected using the basic method. During active collection, seed samples are stored for immediate use. Seed samples are stored for 10–20 years and should be at least 65% viable. The moisture content in the active collection method varies depending on the species and ranges from 7 to 11% for good storable seeds and 3–8% for poor storable seeds. It also depends on the temperature at which the seed samples are stored [106]. However, depending on the storage period, these are categorized into three main types. (i) long-term storage: when the seed samples are stored in basic collection centres and kept at 18–20 degrees celsius; (ii) medium-term storage: when the storage period is not more than 5 years and the seed samples are kept at a temperature between 0 and 10 degrees celsius and a relative humidity of 20–30%; and (iii) short-term storage: when the seed samples are stored for 1 year to 18 months. In the latter case, the temperature should be between 20 and 22°C, with a relative humidity of 45–50%. The seeds can be stored for up to two years without losing their viability [106]. Seed storage is the most cost-effective and widely used method of long-term *ex situ* conservation. The seed is dried and stored at low temperatures. However, unlike conventional seeds, refractory seeds and vegetatively propagated plant species do not survive at low temperatures. This strategy is important for the conservation of forests and tree species. Even unique PGRs could be stored in the home garden for later use in breeding. The *ex-situ* conservation strategy preserves innovative genes/alleles and ensures their long-term application in plant development. *Ex situ* conservation of

PGRs began in the mid-twentieth century as a way to slow the rapid loss of biodiversity from new, high-yielding crops. Farmers replaced their conventional varieties with better varieties [105]. This strategy is also useful for the protection and conservation of wild relatives [107]. Several institutes have applied *ex situ* conservation approaches to protect important PGRs [108].

4.2 *In situ* conservation

In situ conservation: *In situ* conservation involves preserving genetic resources in their natural habitat and maintaining species in their original location. Plant species are conserved where they are discovered and kept in their original habitat [109]. *In situ* conservation allows evolution to occur spontaneously with minimal human interference. This method protects many wild plant species, especially forest and wild fruit plants. *In-situ* conservation allows plant species to evolve, which promotes genetic diversity. Two methods are used in this process: (i) on-farm/field conservation; (ii) conservation in genetic reserves. Although both are concerned with the protection and conservation of genetic diversity, on-farm conservation focuses on traditional plant varieties or cropping systems and off-farm conservation on wild species in the natural environment [103, 104]. In genetic reserve conservation, the area is described as a place where genetic diversity must be preserved through active and long-term conservation, such as a forest reserve. On-farm conservation is about the sustainable management of locally developed landraces. Growers also protect wild relatives and weedy forms within the current cropping system. Farmers select favorable plants for future cultivation, leading to a constant evolutionary process. The *in-situ* conservation technique allows open pollination of different genotypes, and the resulting population of genotypes has multiple alleles. However, to minimize natural disasters and the negative effects of climate change, both *in situ* and *ex situ* conservation should be carried out simultaneously [103, 104].

5. Approaches for increasing genetic diversity

Genetic diversity varies over time due to several factors. Genetic diversity can be increased through a variety of approaches. Some of the approaches include selection of desirable traits, hybridization, line breeding, gene editing, mutation breeding, genetic engineering, germplasm exchange, etc. The selection of superior genotypes by both natural and artificial selection has a major impact on the population's gene and genotypic frequencies [110]. The amount of genetic variability in the population and the type of relationship between various components determine how much a genotype has improved genetically [15]. Genetic diversity resulting from mutations can affect a plant species' many traits in neutral, positive, and negative ways. In addition to selection and genetic drift, genetic differences brought about by DNA mutations are the main factor influencing changes in allele frequencies in a population. Also, in hybridisation programmes, the selection of genotypes as parents affects the genetic diversity. The level of genetic variation in a population also affects how well genotypes are selected for hybridization programmes. The breeding of new hybrid species by hybridization may aid in genetic diversity. However, the introduction of a few loci may encourage adaptive divergence and enable diversity [111]. Germplasm exchange is also a valuable approach to genetic diversity. Germplasm exchange introduces new alleles, genes or traits from one population to another, increasing genetic diversity.

It also expands the genetic pool, providing a broader range of genetic variation. Germplasm exchange provides breeders with access to diverse genetic resources, enabling them to develop new varieties with desirable traits and can also accelerate breeding programmes by the introduction of valuable genetic variation [15].

6. Exploitation of genetic diversity in crop improvement

The degree to which individuals of a variation or population within a species differ genetically is known as genetic diversity [15]. It results from mutations, gene flow, genetic drift, and the recombination of genetic material (DNA) throughout the inheritance process. It promotes alterations to morphological characteristics, physiological characteristics, protein structure or isoenzymes, epigenetic profiles, and DNA sequence. The genetic material found in the breeding individuals of a population determines the diversity found in plant and animal populations [112]. Population selection and evolution are primarily driven by genetic variety. Understanding a crop's genetic variability enables more effective and economical use of resources in crop development initiatives. Genetic progress through breeding is based on the availability and utilization of genetic variation. PGRs are all of a crop species' genetic information, including all of the different gene alleles [113]. Landraces, newly improved cultivars, breeding lines, wild types, weedy forms, wild varieties of domesticated crops, newly developed varieties, cultivated crop varieties, inbred lines, elite lines, mutants and extinct genotypes are all considered PGRs [15]. These serve as the foundation for crops' genetic development. They are very crucial in cultivar development programmes for improved varieties.

To keep up with the world's growing population, there will be a greater need for these PGRs in the future. Furthermore, the overexploitation of PGRs brought on by the previous global population growth has caused the genetic erosion of significant germplasm from ecosystems [15]. The situation is made worse by the biotic and abiotic stresses that occur often, which cause a significant loss of PGRs. It is necessary to use these precious resources wisely and prevent genetic degradation to avoid this disastrous scenario. PGRs must be investigated, gathered, preserved, and used responsibly to address present and future world issues. To ensure future food security, PGR conservation is crucial. Conservation and subsequent sustainable use of genetic resources are essential to meet the demand for future food security. Conservation is also crucial to preventing genetic erosion, since habitat loss has already put many species in danger. To create climate-resilient cultivars, genes that can withstand biotic and abiotic stressors must be preserved for use in breeding initiatives in the future [114]. Furthermore, the plant genotypes with genes of desirable characteristics and superior qualities must be maintained in the germplasm. PGRs can be conserved by *in situ* conservation, *ex situ* conservation, and by a biotechnology approach [103].

7. Roles of genetic diversity in crop improvement programmes

Genetic variability is the basis for crop survival, improvement, adaptation, and trait development. The phenomenon refers to differences in gene alleles or DNA/RNA sequences within the gene pool of a species or population. This diversity spanning both intra- and interspecific variation enables the emergence of new traits and is essential for sustained crop improvement. Since the inception of systematic plant

breeding, identifying and harnessing natural genetic variability has been central to developing high-performing varieties. Diverse alleles allow breeders to select for desirable traits such as yield, quality, and stress tolerance. Moreover, genetic variability drives key heterosis (hybrid vigor) and transgressive segregation, resulting in significant genetic gains. In the face of climate change and dynamic agricultural challenges, conserving and expanding genetic diversity is increasingly vital. It provides the raw materials to address evolving threats from pests, diseases, temperature extremes, and environmental pollutants. Valuable alleles sourced from wild relatives, landraces, breeding lines, and mutants are critical for developing climate-resilient varieties. Preserving the genetic resources of cultivated and underutilized crops ensures a reservoir of traits for future breeding. This diversity enables the selection of superior genotypes for the development of new varieties with improved performance in stress tolerance and yield.

7.1 Enhancing stress tolerance and yield stability through genetic diversity

Plant growth is frequently threatened by biotic (viruses, bacteria, nematodes, insects) and abiotic (heat, drought, salinity, heavy metals) stresses, causing crop losses of 20–70% [115–117]. These stressors pose a major threat to global food security [118, 119]. Plants counter stress through complex morphological, physiological, and molecular defense mechanisms governed by intricate genetic networks, including gene regulation, transcription factors, and signaling pathways. Enhancing these traits through breeding has become essential to developing stress-resilient crops without compromising yield. Traditional breeding methods are now enhanced by modern tools such as marker-assisted selection, genomic selection, and genome editing technologies. Notably, CRISPR/Cas9 offers precise, inheritable, and non-transgenic modifications, enabling rapid development of stress-tolerant traits with minimal regulatory concerns [116]. Genetic diversity forms the backbone of breeding resilient and high-yielding crop varieties. Exploiting the wide genetic base found in wild relatives, landraces, and elite cultivars enables the development of genotypes with improved adaptability and yield stability [120, 121]. This diversity also supports the creation of heterotic combinations suited to variable environments. Particularly in fruit and seed crops, reproductive traits such as flowering time, pollen viability, stigma receptivity, and seed filling are vital for maintaining yield under stress conditions. These traits must be identified through careful phenotyping across multiple environments to ensure stability and adaptability.

7.2 Breeding for resistance to biotic and abiotic stresses

Crop productivity is increasingly constrained by a range of biotic stresses such as pests and pathogens, as well as abiotic stresses including drought, salinity, extreme temperatures, and nutrient deficiencies [122, 123]. These challenges are further exacerbated by climate change, making the development of stress-resilient crop varieties a key strategy for ensuring sustainable agriculture and food security [124, 125]. While conventional breeding has made significant contributions, its progress is often limited by the complexity and polygenic nature of stress-related traits [126].

Modern plant breeding integrates traditional methods with advanced molecular tools such as marker-assisted selection (MAS), quantitative trait loci (QTL) mapping, and gene pyramiding to enhance resistance [127, 128]. These techniques enable the precise identification and stacking of genes associated with important traits like

water-use efficiency, root architecture, and stomatal regulation [129]. The development and use of functional markers and genome editing tools such as CRISPR/Cas9 have further allowed for targeted modification of regulatory and stress-responsive genes, resulting in improved crop tolerance under drought, heat, and salinity conditions [130]. However, translating these genetic gains from controlled environments to field conditions remains challenging due to the dynamic and multifactorial nature of natural stresses [131].

Phenotyping, in particular, is a major bottleneck in breeding programmes [132], as accurate and consistent measurement of complex traits across diverse environments is laborious and resource-intensive. To overcome this, high-throughput plant phenotyping (HTPP) platforms employing non-invasive imaging technologies (red-green-blue (RGB), thermal, hyperspectral) are increasingly used to assess physiological and structural traits at scale [133]. These platforms improve the accuracy of trait selection and enhance the power of QTL mapping and genomic selection [134]. When combined with high-throughput genotyping, they accelerate the identification and validation of stress-resilience genes [134]. Such integration has proven effective for both abiotic and biotic stress breeding, enabling early detection of stress responses and facilitating faster breeding cycles. Additionally, global initiatives and collaborative networks are helping to standardize phenotyping systems and support breeding efforts, particularly in climate-vulnerable regions. The incorporation of multi-omics data, root system analysis, and soil microbiome interactions further strengthens the understanding of plant responses under field conditions [135]. Collectively, these approaches provide a robust framework for developing resilient crop varieties that can thrive in diverse and challenging environments, supporting long-term food production and ecosystem stability.

7.3 Climate-resilient crops and their role in food security

With the global population projected to exceed nine billion by 2050, food demand is expected to increase by 70–85%, placing immense pressure on agricultural systems already threatened by climate change [136, 137]. Rising temperatures, altered rainfall patterns, salinity, drought, and extreme weather events driven largely by human-induced greenhouse gas emissions pose serious threats to global food security [138]. These climate-induced stresses disrupt crop production, degrade natural resources, and increase the vulnerability of farming communities, particularly in developing countries with limited adaptive capacity [139, 140]. Crop production, which forms the basis of global food security and economic stability, must undergo a transformation to become more resilient and adaptive. Climate-resilient crops capable of withstanding biotic and abiotic stresses offer a critical pathway to achieving this goal [141]. Advances in plant science have uncovered mechanisms that enhance stress tolerance. For instance, transgenic crops incorporating genes for drought, salinity, and heat resistance have demonstrated improved yield stability [142]. In rice, the manipulation of cytokinin metabolism has shown promise in maintaining productivity under stress conditions [143, 144], while ice-binding proteins are being explored to develop cold-tolerant varieties [145].

Biotechnological innovations such as QTL mapping, transgenic approaches, and genome editing have accelerated the development of crops with enhanced tolerance to environmental stresses [146]. Key stress-response genes like dehydration responsive element binding (DREB) and C-repeat binding factor (CBF) have been introduced into crops to improve drought and cold resilience [147, 148]. Genetic

switches, photorespiratory bypasses, and stress-related proteins have been engineered to enhance heat tolerance [149]. Despite public concerns about genetically modified organism (GMOs), these technologies represent vital tools in the pursuit of global food security [150, 151]. Soil contamination and salinity are major challenges exacerbated by poor irrigation and climate shifts [152]. Over 10 million hectares of land are lost annually to salinization, and this figure could reach 50% of arable land by 2050 [153]. Phytoremediation, which involves the use of plants to detoxify polluted soils, is gaining traction as a sustainable solution [154]. Genomics and proteomics have further contributed to identifying salt-tolerant genes [155], which are crucial in rice production across flood-prone deltas in Asia. Similarly, crops like pearl millet are being bred for heat tolerance [156], and maize, wheat, and soybean varieties are being enhanced for resilience to drought and temperature extremes [157]. Climate variability also impacts soil moisture, nutrient cycling, and pest dynamics, affecting overall crop productivity [158]. Therefore, sustainable management practices are essential complements to genetic solutions [159].

Conservation agriculture, crop diversification, precision farming, and improved water-use efficiency form the cornerstone of climate-resilient agriculture [160, 161]. Technologies such as drip irrigation, fertigation, and soil moisture sensors optimize water use. Rainwater harvesting and alternate wetting and drying (AWD) techniques help reduce water stress while maintaining yields [162, 163]. In addition, agroforestry systems, including alley cropping and silvopastoral models, not only improve biodiversity and soil health but also provide carbon sequestration and alternative income sources [164, 165]. A significant concern is the over-reliance on a narrow base of staple crops. Of the approximately 50,000 edible plant species, fewer than 50 are widely cultivated, with wheat, rice, and maize alone accounting for 60% of the global food supply [166]. This limited diversity increases the vulnerability of food systems to climate shocks. To address this, it is essential to conserve and utilize crop wild relatives (CWRs), which harbor genetic traits for resistance to multiple stresses. Unfortunately, many of these CWRs are under threat due to habitat loss and climate change [167, 168]. Preserving them through *in situ* conservation and improved gene bank strategies is crucial for future breeding efforts [169]. Historical events, such as polyploidy during past climatic shifts, suggest that plants can evolve to survive extreme conditions [170], but contemporary plant populations often lack the genetic diversity or the time to adapt rapidly [171]. As such, integrating traditional knowledge with modern genomics, large-scale breeding trials, and climate-sensitive modeling offers a powerful strategy for accelerating crop improvement. Evolutionary breeding, global germplasm sharing, and biodiversity mapping must be prioritized in global adaptation strategies. Weather forecasting and data-driven decision-making are additional tools that support farmers in mitigating climate risks. Accurate short- and long-term forecasts help with timely planting, irrigation, and harvesting [172].

Precision agriculture, powered by GPS, drones, sensors, and artificial intelligence, enables targeted resource application, enhances productivity, and minimizes losses [172]. Climate-smart agriculture promotes integrated approaches such as site-specific nutrient management, nano fertilizers, integrated pest and livestock systems, and low-emission practices [173]. These strategies reduce greenhouse gas emissions, enhance resilience, and promote ecological sustainability. Equally important are policies that support research, innovation, and the implementation of adaptive measures, particularly in vulnerable regions. Developing and adopting climate-resilient crops is not just a scientific endeavour but also a socio-economic imperative. Climate-resilient crops stabilize food production, support rural livelihoods, and reduce vulnerability to

climate-related disruptions [174]. By preserving genetic diversity, investing in innovative technologies, and implementing sustainable practices, agriculture can continue to provide food, income, and ecological services in a rapidly changing world.

7.4 Genetic diversity facilitates sustainable agriculture

Genetic diversity facilitates the resilience, productivity, and adaptability of crop systems [175]. The phenomenon encompasses variation within and among crop species, including landraces, wild relatives, and modern cultivars, providing a vital pool of traits for breeding programmes, ecosystem stability, and food security [15]. In modern agriculture, the widespread adoption of genetically uniform, high-yielding varieties leads to a decline in crop genetic diversity [176]. Genetically diverse cropping systems enhance yield stability and reduce production risks by enabling crops to respond variably and adaptively to environmental fluctuations [176, 177]. Genetic diversity improves resilience through several ecological mechanisms. Mixed-genotype fields dilute the presence of susceptible hosts, slow the spread of pathogens, and create microenvironments that disrupt pest lifecycles [178]. These systems also support beneficial biodiversity, including natural enemies of pests, soil microbes, and pollinators, reducing the need for chemical inputs and promoting ecological balance [179]. In addition, diversity within plant populations strengthens plant-plant interactions, encourages resource-use efficiency, and supports niche complementarity [180]. These interactions enhance ecosystem services such as nutrient cycling and water regulation. From a breeding perspective, genetic diversity enables the development of improved crop varieties with traits such as stress tolerance, disease resistance, high nutritional quality, and suitability for diverse agro-climatic zones [15]. Traditional and modern breeding efforts rely on this variability, whether sourced from wild relatives, landraces, or induced mutations, to respond to emerging challenges like climate change and new pest outbreaks [181]. Maintaining high genetic diversity also helps avoid inbreeding depression and supports continued genetic gains over successive breeding cycles [2]. *Ex situ* (gene banks) and *in situ* (on-farm conservation) approaches play important roles in conservation agriculture. However, these efforts face challenges such as inadequate funding, infrastructure limitations, geopolitical instability, and the erosion of traditional knowledge. Strengthening these systems requires global cooperation, investment in research infrastructure, and training in genetics, ecology, and data management. Farmers are crucial custodians of crop diversity [182]. Through seed saving, intercropping, and selective cultivation, they preserve and evolve plant PGRs. Reviving and supporting these traditional practices, especially in regions undergoing agricultural modernization, can help reverse genetic erosion and build more resilient and sustainable food systems.

8. Challenges and opportunities in utilizing genetic diversity

8.1 Genetic erosion and its implications on breeding programmes

Genetic erosion, which refers to the loss of genetic diversity within and among plant species, poses severe challenges to plant breeding programmes globally. One of the most immediate consequences is the disappearance of valuable traits found in landraces, wild relatives, and traditional varieties. These genetic materials often harbor unique alleles that confer resistance to pests and diseases, and tolerance

to abiotic stresses such as drought, salinity, or extreme temperatures. Their loss significantly narrows the genetic base necessary for breeding climate-resilient and high-yielding crops [183, 184]. As the genetic pool available to breeders' contracts, so does the range of options for crossing and selection. This limited variability hampers the potential to introduce novel genetic combinations, ultimately restricting the development of improved cultivars with adaptive advantages. Furthermore, reduced genetic diversity increases the vulnerability of crops to new pest and disease outbreaks and reduces their resilience to fluctuating climatic conditions [176, 185]. A historical example of this vulnerability is the Irish potato famine, where heavy reliance on a genetically uniform potato variety led to devastating crop failure caused by *Phytophthora infestans* [186]. Such genetic uniformity in modern agriculture continues to present similar risks, particularly in large-scale monoculture systems. The long-term sustainability of breeding programmes is also at stake. Breeding strategies grounded in rich genetic diversity contribute to ecological balance and reduced reliance on agrochemicals. In contrast, genetic erosion often forces breeders to compensate with increased chemical inputs or advanced technologies, which may not be economically viable in the long-term [187]. The economic burden of replacing lost genetic traits using biotechnological tools such as gene editing or marker-assisted selection increases the cost and complexity of breeding efforts, particularly for public sector programmes or those in developing countries [188]. Ultimately, the cumulative effect of genetic erosion threatens global food security. With a growing global population and increasing pressure on agricultural systems, the loss of genetic diversity weakens our collective ability to produce food sustainably. Crop improvement depends on access to a broad range of genetic traits to adapt to emerging challenges such as climate change, soil degradation, and shifting pest dynamics. Therefore, safeguarding genetic resources through integrated *in situ* and *ex situ* conservation strategies is of global imperative.

8.2 Policy and regulatory considerations in genetic resource utilization

The effective utilization of genetic resources is intricately linked to policy and regulatory frameworks at both national and international levels. The Convention Biological Diversity (CBD) [189] and its supplementary agreement, and the Nagoya Protocol, establish legal frameworks for access to genetic resources and the fair and equitable sharing of benefits arising from their utilization [189]. These instruments affirm the sovereign rights of countries over their genetic resources and mandate Prior Informed Consent (PIC) and Mutually Agreed Terms (MAT) before access is granted for research or commercial purposes [189]. Complementing this is the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA), which established a Multilateral System (MLS) that facilitates access to key food and forage crops [190]. The treaty supports the open exchange of germplasm while ensuring benefits from their use are shared equitably. It also promotes Farmers' Rights, recognizing the role of traditional custodians in conserving and developing plant genetic diversity [176].

Another important consideration is the management of intellectual property rights (IPRs), such as plant variety protection (PVP) and patents. These rights are intended to incentivize innovation, yet they may inadvertently restrict access to genetic materials, particularly for farmers and public researchers in developing countries. Balancing IPRs with access and benefit-sharing objectives remains a persistent policy challenge [191]. The emergence of Digital Sequence Information (DSI)

and synthetic biology exchange, and traditional access and benefit-sharing (ABS) agreements. This has sparked global debates on how to regulate DSI to maintain fair benefit-sharing without hindering scientific progress [192]. National legislation plays a critical role in operationalizing these international agreements. Countries enact laws that define ownership, set access conditions, establish the benefit-sharing frameworks, and impose sanctions for unauthorized use or biopiracy. Such laws are also essential in protecting indigenous knowledge systems and ensuring that the local community benefits from the use of their genetic resources. Moreover, biosafety and bioethics regulations are increasingly necessary to guide the safe and ethical application of technologies such as genetic modification and genome editing. These regulations typically include risk assessments, public consultation, and regulatory approval to ensure environmental and health safety [193]. Together, these policies and legal instruments form a complex but essential foundation for the ethical, equitable, and sustainable use of PGRs in global breeding efforts.

8.3 Emerging technologies for enhanced exploitation of genetic diversity

Emerging technologies have revolutionized the exploitation of genetic diversity in plant breeding, enabling greater precision, speed, and efficiency in developing improved crop varieties. Genomic selection (GS) has become a powerful tool that utilizes whole-genome markers to predict the breeding value of plants without the need for full phenotypic evaluation, thus significantly shortening breeding cycles and improving the selection of complex traits like yield and stress tolerance [194]. Similarly, CRISPR-Cas9 and other genome editing technologies allow for the precise and targeted modification of genes, facilitating the improvement of traits such as disease resistance and drought tolerance without introducing foreign DNA, which may reduce regulatory concerns in certain jurisdictions [195, 196]. Another widely used tool is marker-assisted selection (MAS), which employs molecular markers linked to specific traits to enable early and accurate selection. MAS is particularly valuable for traits that are otherwise difficult to measure, such as root system architecture or resistance to latent pathogens [128, 197].

Complementing these genomic tools is high-throughput phenotyping, which integrates technologies such as drones, sensors, and imaging platforms to collect large-scale, real-time phenotypic data. This approach allows researchers to assess thousands of plants for multiple traits simultaneously, improving the understanding of genotype-to-phenotype relations [198–200]. To manage and analyse the massive datasets generated from sequencing and phenotyping, bioinformatics and big data analytics, which include machine learning and artificial intelligence, are now essential in identifying gen-trait associations and optimizing breeding decisions [188]. Furthermore, pan genomics has emerged as an innovative approach that moves beyond a single reference genome by analysing the full range of gene variants within a species. This broader perspective uncovers rare and structural variants that can be critical for expanding the genetic base used in breeding programmes [201]. Finally, speed breeding techniques, which involve manipulating environmental factors like light and temperature, enable the production of up to six plant generations per year. When combined with genomic tools, speed breeding greatly accelerates the development and testing of new crop varieties [202, 203]. Collectively, these technologies represent a new frontier in crop improvement, offering unparalleled opportunities to harness genetic diversity for sustainable agriculture and food security.

9. Conclusion and future perspective

Plant breeders utilize genetic resource diversity to create novel and enhanced crop cultivars to tackle global issues impacting nutrition, sustainability, and climate change adaptation. Diversity in PGR offers plant breeders the ability to create new and enhanced cultivars with attractive qualities favored by both farmers and breeders. Genetic diversity is essential in plant breeding as it supplies the fundamental resources for creating enhanced crop types. It enables breeders to select and incorporate preferred attributes, resulting in enhanced yields, superior quality, and improved immunity to diseases and pests. PGRs serve as the cornerstone for sustainable and resilient agriculture, facilitating plant adaptation to changes in climate. The prospects for cultivar development will heavily rely on preserving and employing genetic diversity in crops. Notwithstanding significant advancements in genetic diversity, restrictions and deficiencies persist. Current research is primarily confined to specific plant groupings (e.g., underutilized crops) or designated places (e.g., biodiversity hotspots). We recommend that further genetic diversity studies focus on establishing a long-term tracking system for risk evaluation and guiding *in situ* and *ex situ* conservation strategies by synthesizing knowledge on genetic variability and population patterns.

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Domestication History and Genetic Resources of Wild Rice Essential for Food and Nutrition Security

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Abstract

Rice (*Oryza sativa* L.) is an important staple food grain because half of the world population (>3.5 billion) depends on it for their daily 40-70% calorie intake. During the course of domestication of cultivated rice from wild relatives (*Oryza rufipogon*), there was a significant loss of genetic diversity because of only selection of few desirable agronomic traits by the ancient farmers, and other trait-related genes/QTLs (biotic and abiotic stresses) are not selected during domestication and cultivation. Unlike cultivated rice, which has undergone severe genetic bottlenecks during domestication, wild *Oryza* species (*O. rufipogon*, *O. nivara*, *O. longistaminata*, *O. coarctata*, and others) retain genes/QTLs that confer resilience to abiotic stresses (drought, salinity, submergence, extreme temperatures, nutrient deficiencies), biotic stresses (pests, diseases), and other traits that enhance yield stability and adaptability. Therefore, rice landraces and wild *Oryza* species are considered as a reservoir of agronomically important genes/QTLs and is a critical asset for global food security. Rice landraces and wild relatives like FR13A (*Sub1*), Pokkali (*Saltol*), Kasalath (*Pstol*), Nagina22 (heat/drought QTLs), *O. longistaminata* (blight resistance Xa21), *O. rufipogon* (DRO1, qDTY1.1), *O. coarctata* (PcINO1), *O. minuta* (Pi9), *O. nivara* and *O. minuta* (Bph14), *O. rufipogon* (spikelets QTLs), and *O. glaberrima* (*Pup1*) have been pivotal in developing abiotic and biotic stress-tolerant varieties. Alien introgression of important traits related to biotic and abiotic stress-tolerant genes/QTLs from distant wild *Oryza* species into the cultivars is challenging and time consuming due to linkage drag. These difficulties can be mitigated using modern breeding methods *viz.*, wide hybridization, pre-breeding, bridge cross, and MABC for sustainable global food security.

Keywords: wild rice *Oryza rufipogon*, domestication history, QTLs/genes biotic and abiotic stresses, wide hybridization, *Pstol Sub1 Saltol*, Kala4 gene, climate resilient varieties and food security

1. Introduction

Rice (*Oryza sativa* L.) is an important staple food grain because half of the world population (>3.5 Billion) depends on it for their daily 40-70% calorie intake [1, 2] and

considered as model crop plant under the genus *Oryza* and family poaceae (~430 Mb genome size). Based on genetics, morpho-agronomic characteristics, and geographic distribution, cultivated rice (*O. sativa*) is classified into two subspecies *viz.*, japonica and indica [3]. Subsequent investigators suggested that the Asian cultivated rice can be classified into five subgroups (subpopulations): temperate japonica, tropical japonica, indica, aus, and aromatic, using SSR markers [4], SNPs, and genomic sequence data [5–7]. Instead of “aromatic” the name “*basmati*” is more appropriate because it includes both the fragrant and non-fragrant types of rice varieties [8]. Cultivated rice (*O. sativa*) was originated around 10,000 years ago from the common Asian wild rice *O. rufipogon* through domestication event and artificial/natural selection [6, 9]. Therefore, wild rice *O. rufipogon* Griff. is considered to be the immediate ancestral progenitor of cultivated rice *O. sativa* L. [10, 11]. It is needed to produce double amount of rice by 2050 to feed more than 9.6 billion people in this world in spite of diminishing acreage, deteriorating soil health and environmental stresses induced by global climate change [12]. Thus, developed varieties must be high-yielder and tolerance to biotic and abiotic stresses including adaptability to climate change [13] and should have low input efficiency. The intensive selection and breeding efforts targeted toward the improvement of yield in the green-revolution era (in the last 40 years) inadvertently resulted in the significant reduction in genetic diversity due to limited utilization of genetic resources and consequently narrow genetic base of the improved varieties has resulted in yield stagnation [14–16]. Moreover, genetic bottleneck occurred during the event of domestication of cultivated rice causes significant loss of genetic diversity in the well-adapted cultivars because of only selection of few desirable agronomic traits, and other trait-related alleles are not included during domestication and selection. Many desirable traits *viz.*, resistance to diseases and pests, and adaptation to unfavorable environments were lost, severely decreasing genetic diversity [14, 15]. The allelic diversity in the cultivated rice has been reduced at least by 50–60% compared to wild rice *O. rufipogon* leading to loss of genetic variability with yield potentiality [14]. Wild rice species carry huge genetic diversity compared to cultivated rice. It has been demonstrated that cultivated species only carry 10–20% diversity of the wild rice species [17]. When compared to *O. rufipogon*, the diversity of the entire *O. sativa* population has been reduced by only ~10% of its ancestors [1, 18]. The narrow genetic base in the improved varieties is going to be a main bottleneck for crop improvement program, which not only shield the yield increase but also accountable for the increased vulnerability of rice crop to unpredictable climate change, insect pests, and new pathotypes [9, 19]. In spite of the high genetic diversity that prevails in rice germplasm, the yield-enhancing capacity of the crop has reached a plateau conditions. Therefore, it is important to discover these useful genes and to apply their use in rice-breeding programs to widen the genetic base and maximize the genetic buffer to make them tolerant to unpredictable climate change and more durable to new pathotypes and insect pests [19]. The maximum diversity exists in the wild rice species because they have not undergone rigorous human selection, which is the reservoir of many important genes of agronomic interest (*e.g.*, wide adaptability, resistance to insects, diseases and abiotic stresses, cytoplasmic male sterility, photosynthetic efficiency, and better quality) and that has been accumulated over a period of time though natural process is yet to be exploited fully by plant breeders for varietal improvement [20–22]. Wild species have some hidden genes essential for yield related trait improvement in rice [1, 15]. Yield plateaus can be surmounting through genetic gain by combining the yield-related genes/QTLs from different genetic resources of rice germplasm from both local landraces (CLR) and crop wild

relatives (CWR) [23–25]. Wild species of *Oryza* are the reservoirs of genes for important agronomic traits, *viz.*, yield, quality and nutritional characteristics, resistance to biotic (blight, blast), and abiotic stresses (drought, salinity, submergence, aluminum toxicity) and can be utilized in the pre-breeding program for broadening the genetic base of released varieties to break the yield plateaus [19, 22, 26–31]. The genetic resources of the primary gene pool AA genome (*O. rufipogon*, *O. nivara*, *O. glaberrima*, *O. barthii*) will most easily provide transferable beneficial genes for the further improvement of cultivated rice varieties [22]. The wild rice *O. rufipogon*, the ancestor of *O. sativa* reveals possible locally adaptive genes, yield-regulating QTLs that may provide opportunities for breeding novel rice varieties with climate change-resilient phenotypes [22, 32, 33]. Breeder could introgress these agronomically important genes/QTLs using knowledge of molecular breeding techniques, *viz.*, marker-assisted backcross breeding (MABC) including marker-assisted selection (MAS) to widen the genetic base for the improvement of yield potentiality as well as quality [20, 34–36]. Increasing rice yield and productivity under changing climatic conditions is imperative for sustainable food security, given rice is a major staple crop around the world [37]. Moreover, the usage of wild rice is not streamlined in rice improvement programs due to genetic and genomic constraints. Therefore, emphasis should be given for the utilization of wild rice species that can be exploited for combining yield increases with climate resilience in rice improvement programs [37].

2. Genetic and genome diversity in wild *Oryza* species

Rice belongs to the *Oryza* genus and is highly variable, which is composed of 24 species. By cytogenetic analysis, *Oryza* species can be classified into 11 genome types, 6 of which are diploid ($2n = 2x = 24$: AA, BB, CC, EE, FF, and GG), and 5 of which are allotetraploid ($2n = 4x = 48$: BBCC, CCDD, HHJJ, HHKK, and KKLL) [17]. These wild rice relatives are weedy grasses that have inferior morpho-physiological characteristics, poor grain attributes, and low seed set compared to cultivated rice [38]. The 22 wild species have native distributions in tropical and subtropical regions of Africa, South-East Asia, Australasia, and Central and South America covering diverse ecosystems, from wetlands to saline coasts and drought-prone uplands. Wild relatives of rice are grouped into three gene pools (primary, secondary, and tertiary) based on their ease of hybridization with the cultivated rice and phylogenetic relationships. The primary gene pool comprises the *O. sativa* complex (AA genome) with close relatives of cross compatible rice and a secondary gene pool consisting of *O. officinalis* complex (BB to FF genomes) with less closely related species and a tertiary gene pool constituted with *O. meyeriana* complex, *O. ridleyi* complex, and *O. schlechteria* complex (GG to KKLL genomes) with more distant relatives of rice, necessitating embryo rescue, chromosome doubling, or bridging species to facilitate gene transfer [39]. The primary gene pool consisting of cultivated rice species (*O. sativa* and *O. glaberrima*) and wild rice species (*Oryza nivara*, *O. rufipogon*, *O. barthii*, *Oryza longistaminata*, *Oryza meridionalis*, and *Oryza glumaepatula*) are analyzed for detecting tolerant wild accessions in the limited research investigations. Out of 24 species, two cultivated species, *Oryza sativa* (Asian rice) and *Oryza glaberrima* (African rice). These two cultivated species having been independently domesticated as rice: *Oryza sativa* in Asia ~10,000 years ago and *Oryza glaberrima* in Africa ~3000 years ago [17]. Asian-cultivated rice (*O. sativa* L.), which was domesticated from the wild rice species *O. rufipogon* Griff., is widely planted worldwide. African rice (*Oryza glaberrima* Steud.)

has been originated from different wild progenitor, *Oryza barthii* A. Chev, grown in Saharan region of West Africa only. Both the cultivated rice species are belonging to AA genome category, and these are the primary gene pool for rice improvement [40]. To exploit these distantly related species of cultivated rice as genetic resources needs a better understanding of genomic constitution similarities and differences for breeding and selection [40]. Unlike Asian-cultivated rice (*O. sativa*), which underwent severe genetic bottlenecks during domestication in the Yangtze river Valley in China and *O. glaberrima* in the Inland Delta of the Upper Niger River (in what is today Mali), wild species retain alleles shaped by millions of years of natural selection. Among the wild rices, six species share the same AA genome type as the cultivated rice: *O. rufipogon*, *O. nivara*, *O. barthii*, *O. glumaepatula*, *O. longistaminata*, and *O. meridionalis* and these are critical asset for global food security because they harbor a vast reservoir of genetic diversity that has been shaped by millennia of adaptation to diverse and often harsh environments. Compared with Asian rice, African rice (*O. glaberrima*) has low yield but high resistance to drought, heat, salt, iron toxicity, green leafhopper, weed competition, and bacterial blight. African rice has lower genetic diversity than its ancestor *O. barthii* and is less differentiated than Asian rice. The extensive genetic diversity between Asian and African rice provides rich genetic resources for rice improvement *via* genetic exchange between them. For example, a new hybrid of *O. sativa* and *O. glaberrima*, called NERICA, combining the stress resistance of African rice with the yield advantage of Asian rice, has great potential in Africa to reduce food imports and alleviate hunger. Wild rice *O. coarctata*, earlier known as *Porteresia coarctata*, is an allotetraploid wild rice of halophytic in nature with KKLL genome ($2n = 4x = 48$), which is the only distant rice which could withstand extreme salinity (500 to 650 mM NaCl) [41]. It is a unique wild rice that grows in mangroves along coastal belts. It exhibits multiple defense mechanisms of tolerance and mainly adopts a salt excretion strategy to reduce the high salt load in photosynthetic tissues, thereby retaining a high photosynthetic rate [41].

3. Unraveling the domestication history of cultivated rice

Common Asian wild rice (*Oryza rufipogon* Griff.) is considered as a progenitor of cultivated rice (*Oryza sativa* L.) and estimated that about many thousands of years ago it has been diverged from the progenitor [7]. Asian-cultivated rice is composed of two major subspecies, *O. sativa* ssp. *geng/japonica* and *xian/indica* [32], and can be divided into five subpopulations/groups based on genetics and culinary properties that are as follows: tropical japonica, temperate japonica, indica, aus, and aromatic/sadri [4, 42]. Two different models were proposed for the domestication of cultivated rice (*O. sativa*). One model proposed single domestication that *O. sativa* japonica type was initially originated from the progenitor *O. rufipogon* and acquired the domestication phenotypes then introgressed to other predomesticated populations giving indica and aus varieties (common origins) [43–45]. Other model proposed multiple domestication that japonica, indica, and aus type domesticated independently from the ancestral progenitor *O. rufipogon/O. nivara* [46–48]. Genomic studies suggested that the aromatic/basmati subgroup of rice is a result of the hybridization between japonica and aus in early evolution stage [18, 42, 46, 49, 50]. Some evidence supports the models (independent origins) in which japonica, indica, and aus were domesticated independently [7, 51]. Rc gene, selected for esthetic preferences, replaced red pericarp in domesticated rice, with independent fixation in japonica and indica [52].

Based on genome and QTL mapping, it was proposed single origin model with multiple introgressions that *japonica* rice was domesticated from *O. rufipogon* in Southern China first and then, the *japonica* was crossed with *O. rufipogon* in Southeast Asia, which ultimately gives *indica* rice [1, 49, 53]. The *sh4* gene, which controls non-shattering, is fixed in both *japonica* and *indica*, suggesting a shared domestication event. Recently, it was found that limited japonica-to-indica gene flow (e.g., *sh4*) occurred post-domestication, not as a primary mechanism for indica's origin [2, 54]. Subspecies japonica was first domesticated in the Yangtze River Basin (valley) of China at least ~7000-9000 years ago based on archeobotanical evidences of paddy seeds [1, 49, 55], whereas indica was domesticated later, ~4000 years ago in the Ganges plains of India [55, 56]. The archeobotanical data support the occurrence of rice in the Gangetic plains as early as circa 6000 B.C. [48, 52, 55, 56]. Distinct allele frequencies and phylogenetic trees separate japonica and indica, with indica's genetic base primarily from *O. nivara* [43, 46]. In northern India, sites like Lahuradewa (Gangetic plains) show wild rice (*O. nivara*, an annual form of *O. rufipogon*) cultivation around 7000–6000 years ago, with domesticated indica emerging by ~4000 years ago [48, 56]. Essentially, rice plants that appear wild today and closely resemble *O. sativa* may actually be descendants of cultivated rice that escaped into the wild, rather than true representatives of the original wild ancestors [48]. Reproductive barriers between japonica and indica rice show that they have resulted from independent domestication process or a single domestication history with multiple origins [49, 57, 58]. However, the origin of Asian-cultivated rice is still a relatively complex and contentious issue [42, 55]. However, recent studies [32, 59, 60] support multiple independent domestications of Asian rice. Recent genomic studies [46–48] reinforce the dual domestication model, with japonica originating in the Yangtze River Basin China (~10,000–9000 years ago) and indica in South Asia (~6000–4000 years ago), often involving hybridization with wild species like *O. nivara*. The transition from wild to domesticated rice involved the “domestication syndrome,” a suite of traits selected by humans to enhance yield and manageability. Key traits include transition from prostrate to erect growth (PROG1, TAC1, TIG1), reduced seed dormancy (OsG1 and Sdr4), compact panicle architecture (OsLG1), black hull (Bh4) to straw white, seed shattering (*sh4*), larger grains (qSW5), grain color (Rc/rc gene), and awn (LABA1) [44, 52, 54]. It was revealed that among 17 domestication-related rice QTLs with clear origins, the alleles selected at 11 of the 17 QTLs (65%) are loss-of-function mutations, 4 (23%) are cis-regulatory mutations, and 2 (12%) involve both loss-of-function mutations and cis-regulatory mutations. These reports suggest that loss-of-function mutations have played a more critical role than cis-regulatory mutations in rice domestication [53]. The precise origins of rice domestication in Asia are difficult to pinpoint due to extensive gene flow between cultivated rice and wild populations in areas where rice has been grown for a long time [49]. African-cultivated rice (*Oryza glaberrima* Steud.) was domesticated from its wild progenitor *O. barthii* A. Chev. about 3000 years ago [61]. Although it has been proposed that African rice domestication occurred in the Inner Niger Delta, recent studies [62] have suggested that it was multiregional. Thus, the origin of African rice is still debated [60].

However, domesticated plants and animals occasionally reacquire a portion of their wild-like traits during evolution. This phenomenon, which is called *de-domestication* or *feralization*, has been observed in both livestock species and crops, including rice *Oryza sativa* [63]. Weedy rice (*Oryza sativa* f. *spontanea*), which is also called “red rice,” is a typical and convergent weed of cultivated rice developed *via* de-domestication. In addition to its weedy traits, weedy rice possesses additional novel mutations that are the result of natural selection [64].

4. CRISPR/Cas9 genome editing and neo-domestication

Although MAS and MABC have been routinely used in rice salinity-tolerance breeding, the limitation known as “linkage drag” still exist. Transgenic approach is another potential way of achieving crop improvement using modern biotechnological tools without linkage drag. The emerging CRISPR/Cas9-based genome editing technology, which includes knockout, base editing, allele exchange, is an alternative approach for accelerating crop breeding [65, 66]. CRISPR/Cas9 uses a guide RNA (gRNA) to direct the Cas9 nuclease to a target DNA sequence, inducing double-strand breaks. These breaks are repaired *via* non-homologous end joining (NHEJ) or homology-directed repair (HDR), leading to gene knockouts or precise edits. In rice, CRISPR/Cas9 targets structural genes (directly conferring tolerance) or regulatory genes (controlling stress-response pathways) to improve abiotic stress tolerance. CRISPR/Cas9 offers precision, speed, and the ability to create transgene-free rice, bypassing GMO regulations in some regions. During domestication, breeding rice for maximum productivity under optimal growth conditions reduced genetic diversity, eliminating variants for stress tolerance and grain nutrients. However, wild rice species have rich genetic diversity, including variants for disease resistance, stress tolerance, and grain nutritional quality. Advances in precision gene editing have enabled the rapid domestication of wild crop relatives, a process known as neo-domestication, used for crop improvement purpose [66]. Multiplex editing allows simultaneous targeting of multiple genes, addressing complex quantitative traits like abiotic stress tolerance. CRISPR/Cas9 has been used to knock out the OsbHLH024 transcription factor, enhancing the expression of ion transporter genes (OsHKT1;3, OsHAK7, OsSOS1) leading to enhance salt tolerance [67–70]. This increased salt tolerance at the seedling stage without affecting agronomic traits. It significantly upregulates expression of the ion transporter genes (OsHKT1;3, OsHAK7, and OsSOS1) in the shoot when exposed to salt stress. These findings imply that the OsbHLH024 might play the role of a negative regulator of salt stress, which will help to understand better the molecular basis of rice production improvement under salt stress. OsRR22, a gene regulating salt stress responses, targeted with CRISPR/Cas9 [65]. The advanced technique, CRISPR-Cas has been applied to African-cultivated rice (*Oryza glaberrima*), landrace Kabre, which is known for its environmental stress tolerance but suffers from lower yield and susceptibility to lodging [66]. Targeting domestication loci *viz.*, HIGH TILLER DWARF 1 (HTD1) for plant height and GRAIN SIZE (GS3), GRAIN WIDTH (GW2), and GRAIN NUMBER (Gn1a) for grain quality resulted in considerable improvements in grain yield and reduced lodging [70, 71]. Mutants showed improved salinity tolerance at the seedling stage, maintaining yield and other traits. Knock out of OsmiR535 *via* CRISPR/Cas9 knockout system in rice enhanced the tolerance to salinity, ABA, and dehydration stresses. A further critical advantage of genome editing technology is the possibility to modify several sites simultaneously. For example, three grain weight-related genes (GW2, GW5, and TGW6) were simultaneously mutated in rice *via* the CRISPR/Cas9-mediated multiplex genome editing system demonstrating that trait/gene pyramiding could be rapidly generated. Expanding this approach of CRISPR/Cas9 editing method to polyploid systems that offer advantages like genome buffering and environmental resilience, studies in the perennial allotetraploid wild rice *O. alta* (CCDD genome) targeted six domestication-related traits, including seed shattering (OsqSH1), awn length (OsAN-1), plant height (OsSD1), seed size (OsGS3), and long heading date (OsDTH7 and OsGhd7). Edited lines exhibited reduced shattering, shorter awns, earlier flowering, reduced plant

height, and higher yield [72]. These studies demonstrate a potential path forward for creating stress-resistant rice by combining genomics knowledge of cultivated crops and rapid genetic change *via* genome editing [72]. OsNAC3 is a nuclear protein with self-activation activities and expresses in root cells. Disruption of OsNAC3 by CRISPR/Cas9 reduced rice sensitivity to ABA but increased sensitivity to salt stress, while OsNAC3 overexpression did the opposite. This indicates a significant role of rice OsNAC3 in ABA response and salt tolerance [73]. CRISPR/Cas9 editing of OsNAC3 enhanced salinity tolerance in rice.

An *O. alta* accession has been successfully *de novo* domesticated (neo-domestication) by altering several agronomic traits: seed shattering, awn length, plant height, grain size, stem thickness, and heading date. The successful editing of important traits in tetraploid wild rice *O. alta* laid a solid foundation for future generation of a polyploid rice crop with superior agronomic traits. Series of genes were edited (qSH1, An-1, SD1, GS5, IPA1, and OaGhd7/OaDTH7) using genome editing tool (CRISPR-Cas9) to understand the domestication process. This achievement offers promise of a tetraploid cultivated rice with superior yield, environmental adaptability or resilience, and stress resistance. Population genomic analysis showed higher genetic diversity present in wild rice CCDD populations than in cultivated rice, which offers great potential for future improvement of the domesticated *O. alta*. A recent study established a route for *de novo* domestication and improvement of the tetraploid wild rice *O. alta* (CCDD) showing the feasibility of “creating” new cultivated rice species and opening a new era of rice domestication and improvement. Along with the rapid development of genome editing technology and gradual increase in knowledge about rice domestication and improvement, “creating” new cultivated rice species by *de novo* domestication of wild *Oryza* species with other genome types would expand human food resources [72]. In addition, precise base editing and nanoparticle-mediated delivery of small-interfering RNAs (siRNA) have been demonstrated successful in improving agronomic traits, including reduced seed shattering, awn removal, improved heading, and ideal panicle architecture in wild rice species.

5. Challenges in utilizing underutilized wild *Oryza* species in breeding

There have been landmark introgressions of agronomically useful genes from wild rice into cultivars, but such examples are rare, *for example*, grassy stunt virus, bacterial leaf blight resistance gene Xa-21, blast resistance genes Pi-9, Pi-40(t), BPH resistance, and L-myo-inositol 1-phosphate synthase gene for salt tolerance [20]. The cross-incompatibility between species is a major hindrance to their effective utilization in rice improvement program [34]. Owing to tall plant stature, photosensitivity, poor grain type, low seed set, high grain shattering, and low yield potential, natural wild accessions are regarded as poor agronomic performers [26] and these are not suitable for direct use in agricultural production [73]. But the recovery of widely adaptable cultivars to diverse challenging environments with high yield potentiality would be higher when wild relatives of rice are used in the crossing program [74, 75]. Sexually compatible donor wild rice species can be used in conventional breeding process otherwise transgenic technique is to be employed to introgress the desired gene (s) from CWR to cultivars. Despite its potential (genes and QTL for improving crop performance), challenges remain, to use wild germplasm for crop improvement program [22, 23]. Therefore, the vast majority of these genes remain untapped to date because it is often difficult to transfer these genes into cultivated rice (*Oryza sativa* L.) [76]. Reproductive barriers

and low crossability is a major bottleneck in using wild accessions in rice breeding programs [22, 77, 78]. Pre- and post-fertilization barriers, abnormal development of a hybrid embryo and endosperm, sterile pollen grains, linkage drag, and cytoplasmic male sterility related to cross incompatibility between cultivated and wild rice pose serious complication to transfer valuable genes from wild rice species [22, 37, 77, 79]. These challenges like linkage drag, genetic barrier, or reproductive barriers must be overcome for successful utilization of wild species in breeding. Due to linkage drag, some unwanted poor qualities traits (e.g., seed shattering, low-quality grain) can be introgressed from the wild rice and as a result complication arises in the varietal development. Still breeders are trying to identify and transfer of these valuable gene/QTLs from wild *Oryza* species to improve varieties through wide hybridization and pre-breeding. These are two distinct but complementary breeding strategies (wide hybridization and pre-breeding) are used to introduce genetic diversity, particularly from wild *Oryza* species or distantly related germplasm, into cultivated rice (*Oryza sativa* and *Oryza glaberrima*). These approaches are critical for enhancing traits such as abiotic and biotic stress tolerance, yield potential, and adaptability. The process of crossing cultivated rice (*O. sativa* or *O. glaberrima*, typically AA genome) with distantly related wild *Oryza* species or other genera that have different genomes (e.g., BB, CC, KKLL) or significant genetic divergence, to transfer desirable traits is known as wide hybridization. It is essential for non-AA genome species (*O. minuta*, *O. officinalis*, *O. australiensis*) due to reproductive barriers. The pre-breeding is a process of interspecific (or inter-subspecific) hybridization and back crossing to develop intermediate lines from wild crosses where undesirable traits from wild species are minimized, making alleles accessible for conventional breeding [12]. Pre-breeding process is expedited by using marker-assisted backcross breeding (MABC) to quickly eliminate the linkage drag with a minimum number of generations using DNA-based molecular markers in marker-assisted selection (MAS) [17]. The MABC breeding requires some kinds of mapping populations (ILs, CSSLs, NILs, or BILs) to map the gene/QTLs under consideration [40, 76]. Concentrations has been focused on creating “bridge” materials (e.g., introgression lines) that combine desirable traits from wild or unadapted sources with acceptable agronomic traits, facilitating their use in the cultivar development. Developing introgression lines from *O. rufipogon* x *O. sativa* crosses with drought tolerance QTLs, used as donors in breeding programs. Identified landraces (e.g., local aus rice, Kasalath for *Pup1* gene), or other unadapted materials with valuable traits (e.g., drought tolerance, blast resistance) are used as donor parent in pre-breeding method. Introgression of drought tolerance QTL DRO1 from *O. rufipogon* into IR64 background and submergence tolerance Sub1 gene from FR13A in Swarna variety (Swarna Sub1) are the successful application of pre-breeding method giving emphasis on marker-assisted selection and phenotypic screening.

6. Breeding for biotic stress tolerance genes from *Oryza* species

Biotic stresses, bacterial, fungal, and viral diseases, as well as insect pests, significantly limit rice (*Oryza sativa* L.) productivity, causing yield losses of up to 30–60% under severe conditions [80]. Developing rice varieties with durable resistance to these stresses is a priority for global food security. Wild rice species (*Oryza* spp.), the progenitors of cultivated rice, harbor a rich reservoir of resistance genes against biotic stresses, which have been eroded in domesticated varieties due to selective breeding for yield and quality [81–85]. Wild rice species, including *Oryza rufipogon*,

O. nivara, *O. longistaminata*, *O. minuta*, and *O. glaberrima*, are valuable sources of novel resistance genes for biotic stresses [14]. These species have evolved under diverse environmental pressures, resulting in genetic adaptations to diseases like bacterial leaf blight (BLB), blast, sheath blight, and pests (BPH-brown planthopper). Resistance to bacterial blight was found in wild rice *O. rufipogon*, *O. nivara*, and *O. longistaminata*; resistance to blast in *O. minuta*, *O. rhizomatis*, *O. longiglumis*, *O. ridleyi*, and *O. australiensis*; and resistance to brown planthopper in *O. punctata*, *O. officinalis*, and *O. australiensis*. Several resistance genes originating in wild rice have been cloned, including those against rice blast such as Pi9 from *O. minuta*, Pi3-A4 and OsCERK1DY from *O. rufipogon*, Pi54rh from *O. rhizomatis* and Pi54of from *O. officinalis*, and those for bacterial blight resistance such as Xa21 from *O. longistaminata*, Xa23 from *O. rufipogon*, and Xa27 from *O. minuta* [59]. Recently, *O. nivara* derived BB resistance gene Xa38 was incorporated into popular basmati variety “Pusa Basmati 1121” using a modified marker-assisted breeding program [86]. Wild species *O. barthii* (2n = 24, AA) is a part of the primary gene pool of cultivated rice and presumed progenitor of African-cultivated rice *O. glaberrima*. This species is a potential donor of genes imparting resistance to biotic stresses, viz., rice tungro virus, stem borer, sheath blight, blast, and BB [78]. *O. glaberrima* (2n = 24, AA) evolved and domesticated in West Africa, which is highly resilient against various biotic and abiotic stresses, and responsive under low input agriculture. By crossing *O. glaberrima* with *O. sativa* has resulted in the development of New Rice for Africa, that is, NERICA rice. NERICA lines well-adapted to African conditions had the combination of higher yield potential from *O. sativa* and adaptability to various biotic and abiotic stresses, response to low input condition and weed competitiveness from *O. glaberrima* accessions [78]. Three R genes, Pi9, Pi-40 t, and Pirf21(t), identified from *O. minuta*, *O. australiensis*, and *O. rufipogon* respectively, and have been found to confer broad-spectrum resistance against blast disease caused by *Magnaporthe oryzae* [75, 87]. The wild rice *Oryza nivara* was used as a source of resistance gene against grassy stunt virus and introduced into IR28, IR29, and IR30. Tungro virus-resistant gene introgressed into the cultivar from wild rice *O. rufipogon*. The wild rice *O. longistaminata* was used as a source for bacterial blight resistance gene Xa21 and introduced into cultivar IR24 [77, 79]. For example, the Xa21 gene, conferring broad-spectrum resistance to BLB, was identified in *O. longistaminata* [88], while Bph14 and Bph15 for BPH resistance were sourced from *O. officinalis* [89, 90]. Xa21 is a dominant resistance gene derived from *Oryza longistaminata*, conferring broad-spectrum resistance to bacterial leaf blight (BLB) caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo), a serious disease of rice. Fungal blast is also a devastating disease for rice crop caused by *Magnaporthe oryzae*. The gene Xa21 is located on chromosome 11 and encodes a receptor kinase involved in recognizing bacterial signals and triggering plant defense. The challenge lies in transferring these genes into cultivated rice linked to linkage drag, which can be minimized using MABC and MAS. Two complementary methods of molecular breeding technique, namely marker-assisted backcrossing (MABC) and marker-assisted selection (MAS), have revolutionized the introgression of these resistance genes from wild relatives into elite rice cultivars with precision and efficiency without linkage drag [86, 91–95]. Principles and methods of these two systems are described to understand their efficiency in alien gene transfer. Marker-assisted backcrossing (MABC) is a molecular breeding technique used to introduce (introgress) a specific gene or QTL from a donor parent into an elite or recurrent parent background while minimizing the donor genome background. Marker-assisted backcross (MABC) breeding has been widely used to introgress the Xa21

gene, which confers broad-spectrum resistance to bacterial leaf blight (BLB) caused by *Xanthomonas oryzae* pv. *oryzae* (Xoo), into rice varieties. Details are as follows: IRBB21 and IRBB60 are commonly used as donor parents for Xa21 introgression, as they carry this dominant gene originally derived from *Oryza longistaminata*. Popular high-yielding variety (e.g., Swarna, IR64, Pusa Basmati 1) is used as recurrent parent. Developing an IRBB21 introgression line from *Oryza longistaminata* for the Xa21 gene, which confers broad-spectrum resistance to bacterial leaf blight (BLB), involves a systematic marker-assisted backcrossing (MABC) approach in the genetic background of the elite rice cultivar IR24 (high yield, good grain quality but lacks BLB resistance) [88, 96, 97]. The process involves interspecific hybridization between *O. longistaminata* (donor) and IR24 (recurrent parent). Due to reproductive barriers (sterility in interspecific cross), embryo rescue technique is to be performed to obtain viable F1 hybrid. After 10-14 days' post-pollination, embryo was excised and cultured on Murashige and Skoog (MS) medium supplemented with 2 mg/L 2, 4-D, and 0.5 mg/L kinetin under sterile conditions for viable F1 plant development. F1 hybrid plant was verified for Xa21 gene introgression using Xa21-specific STS marker (pTA248) in PCR, and morphological traits analysis was conducted for intermediate traits between parents. F1 plant (heterozygous for Xa21) was back crossed with IR24 to develop BC1F1 progeny to be used in MAS. Foreground selection is to be performed of the BC1F1 progeny using marker pTA248 to select plants carrying the target gene Xa21 allele. Foreground selection marker is tightly linked to the Xa21 gene on chromosome 11 (<1 cM linkage distance). Background selections are employed using genome-wide markers (e.g., SSRs, SNPs) to select progeny with the highest proportion of the recurrent parent genome recovery, minimizing donor genome segments. Polymorphic SSR markers (~100 markers) or single-nucleotide polymorphism (SNP) markers distributed across the rice genome (evenly spaced across 12 chromosomes) are used as background selection markers to differentiate between *O. longistaminata* and IR24. These markers ensure recovery of the recurrent parent genome (e.g., IR24) of the backcrossed progeny lines with minimum linkage drag. SSR markers, viz., RM21, RM144 (chromosome 11, near Xa21), and genome-wide markers such as RM1, RM5, RM17, used for background selection. Repeated backcrossing is performed with IR24, selecting for Xa21 in each generation using pTA248 markers to identify homozygous Xa21 plants and continued background selection to recover ~87.5% (BC2F1) and ~93.75% (BC3F1) of the IR24 genome and eliminating linkage drag from *O. longistaminata* segments. Selfing has to be performed for generating homozygous lines (e.g., BC3F2 or BC3F3) for evaluation and release including phenotypic evaluation and disease resistance validation.

7. Breeding strategies for abiotic stress tolerance traits

Developing rice varieties with tolerance to abiotic stresses (e.g., submergence, salinity, drought, extreme temperatures, nutrient deficiencies like phosphorus deficiency) is critical for ensuring yield stability in challenging environments, particularly in the context of climate change and food security. Basic breeding methods for abiotic stress tolerance in rice (*Oryza sativa* and *Oryza glaberrima*) leverage genetic diversity from landraces, wild *Oryza* species (e.g., *O. rufipogon*, *O. nivara*), and modern cultivars to introgress or enhance stress tolerance traits. Same technique of molecular breeding (MABC and MAS) is also used in this abiotic stress tolerance improvement, which has been discussed elaborately in the previous topic.

These methods are critical for complex, polygenic traits and have been pivotal for introgressing QTLs such as SUB1, Saltol, DRO1, and Pstol-Pup1.

Marker-assisted selection (MAS): Utilization of DNA markers linked to stress tolerance genes/QTLs to select plants carrying the desired alleles, reducing reliance on phenotypic screening. Target QTL/gene can be identified using specific markers associated with the vital traits, for example, marker K461 for Pup1, and RM8094 for SUB1 are used in MAS. Cross a donor (e.g., FR13A for SUB1) with a recurrent parent IR64/Swarna. Screening has to be followed in F1–F3 progeny using markers to select individuals with the desired tolerance allele. For advanced selected lines, combining marker screening with phenotypic evaluation for yield and quality is to be performed. In this way, submergence tolerant varieties can be developed. SUB1A-1 from FR13A was introgressed into Swarna and IR64 using MAS, producing Swarna-Sub1 and IR64-Sub1, which tolerates 14–17 days of submergence [98]. Saltol from Pokkali was transferred to Pusa Basmati 1121 using MAS, improving seedling-stage salinity tolerance [99]. P deficiency gene, Pup1 from Kasalath was introgressed into IR64 and NERICA lines using markers like OsPupK202, increasing yields by 20–50% in low-P soils [100].

Marker-assisted backcrossing (MABC): A specialized form of MAS that combines backcrossing with marker selection to transfer specific QTLs/genes while recovering the recurrent parent's genome. Cross a donor (e.g., Kasalath for Pup1 in Pstol QTL) with a recurrent parent (e.g., IR64). Foreground markers are to be used to select the target QTL (e.g., Pup1) in BC1F1–BC3F1 generations. And also use background markers to recover the recurrent parent's genome (e.g., 95–98% recovery of IR64 genome by BC3). Self-pollinate to fix the QTL and evaluate for agronomic performance. This advanced technique of MABC has been successfully applied to transfer Pup1 (Pstol) into IR64, improving P deficiency tolerance with minimal Kasalath-derived linkage drag [100]; MABC introgressed SUB1 from FR13A into Swarna, retaining Swarna's yield and quality [101]; salt tolerance QTL *Saltol* from Pokkali was introgressed into BR11, enhancing salinity tolerance in Bangladesh [99]. The SUB1 region (approximately 100–200 kb) was introgressed with minimal linkage drag, preserving the agronomic and grain quality traits of recipient varieties. Swarna-Sub1, Samba Mahsuri-Sub1, CR1009-Sub1, and IR64-Sub1 released in India (2009). Advantages of MABC are its high precision, recover elite traits, and reduce breeding time, effective for major QTLs introgression. Early introgression efforts faced issues with linkage drag, as the SUB1 region from FR13A carried undesirable traits (e.g., low yield, poor grain quality). Fine-mapping and backcrossing resolved these issues. The SUB1A-1 allele is rare, found in only a few landraces (e.g., FR13A, Kurkaruppan), limiting donor diversity. Screening wild rice (*O. rufipogon*) revealed additional SUB1A-like alleles, but these are less characterized. MABC is used to transfer specific QTLs (e.g., SUB1A-1, Saltol, DRO1) from wild species into elite cultivars with minimal linkage drag, as seen in Swarna-Sub1 and salt-tolerant Pusa Basmati 1121.

QTL Pyramiding: Combines multiple stress tolerance QTLs/genes into a single variety to confer tolerance to multiple stresses or enhance trait expression. Identify donors with different QTLs (e.g., FR13A for SUB1, Pokkali for Saltol, Kasalath for Pstol Pup1). Cross donors with a recurrent parent or intercross lines carrying individual QTLs. Use MAS to select progeny with all target QTLs. Evaluate pyramided lines for stress tolerance, yield, and stability. Using this QTL pyramiding IR64-Sub1-Pup1 variety has been developed by combining SUB1 QTL (submergence) and Pup1 in Pstol QTL (P deficiency) for flood-prone, and low-P lowlands regions [102]. Swarna-Sub1-Pup1-DRO1 has been developed through pyramiding SUB1, Pup1 (Pstol),

and DRO1 (drought) for rainfed systems with variable stresses, improving yield by 25–40% under combined stresses. NERICA-L-20-Pup1-Saltol has been developed by introgressing Pup1 and Saltol in NERICA lines for African soils with P deficiency and salinity stress. Major QTLs such as SUB1 (submergence), Saltol (salinity), DRO1 (drought), and Pstol-Pup1 (P deficiency) from wild species (*O. rufipogon*, *O. nivara*, *O. coarctata*) and landraces (e.g., FR13A, Pokkali, Kasalath) have been transferred into elite cultivars IR64 (IR64-Sub1-Pup1-DRO1) to make tolerates for multiple stresses, increasing yields by 25–40% [102].

7.1 Submergence tolerance using QTL Sub1

The successful introgression of the SUB1 QTL from FR13A into high-yielding rice varieties relied on marker-assisted backcross breeding (MABC), which allowed precise transfer of the SUB1A-1 allele while minimizing undesirable traits from the low-yielding FR13A landrace [85]. Below is a detailed overview of the breeding techniques used for the development of submergence tolerant rice varieties [103–110].

Principle: MABC uses molecular markers to track the SUB1 QTL during backcrossing, ensuring its introgression into elite varieties while recovering the recipient's genetic background. The goal is to transfer the SUB1A-1 allele (a 100–200 kb region) without linkage drag (e.g., FR13A's low yield, poor grain quality). Process: Donor and Recipient Selection: FR13A was the donor for SUB1A-1, while high-yielding indica varieties such as Swarna, IR64, and Samba Mahsuri were recipients. Initial Cross: FR13A was crossed with the recipient variety to produce F1 hybrids heterozygous for SUB1. Backcrossing: F1 plants were backcrossed with the recipient parent for 2–4 generations (BC1–BC4), selecting for SUB1A-1 using tightly linked markers (e.g., RM464A, RM219). Foreground selection: Markers specific to the SUB1 region (e.g., SSR markers RM464A, RM23877) confirmed the presence of SUB1A-1 in each generation. Background selection: Genome-wide markers (e.g., 50–100 SSRs) ensured recovery of the recipient's genetic background, minimizing FR13A-derived segments outside SUB1. Selfing and stabilization: After backcrossing, plants homozygous for SUB1A-1 were self-pollinated to produce stable lines (e.g., BC3F2), which were tested for submergence tolerance and agronomic performance. Outcomes: MABC-produced varieties such as Swarna-Sub1, IR64-Sub1, and Samba Mahsuri-Sub1, which retained the recipient's yield, grain quality, and disease resistance while gaining submergence tolerance. The process took 2–3 years, significantly faster than conventional breeding (5–10 years). Fine-Mapping and Marker Development: Fine-Mapping: The SUB1 locus was initially mapped to a 6-cM region on chromosome 9 [111]. Subsequent fine-mapping reduced it to a 0.06-cM region, identifying SUB1A as the key gene [112]. High-resolution mapping using recombinant inbred lines (RILs) and near-isogenic lines (NILs) pinpointed tightly linked markers, enabling precise selection [101, 113]. Molecular markers: Simple sequence repeat (SSR) markers (e.g., RM464A, RM219, RM23877) were developed for foreground selection, with RM464A being closest to SUB1A. Single-nucleotide polymorphism (SNP) markers were later used for higher precision, especially in diverse genetic backgrounds. Functional markers targeting SUB1A-1-specific polymorphisms (e.g., a 45-bp insertion in the promoter) improved selection accuracy. Genomic selection: Genomic selection, using genome-wide SNP markers, has been explored to accelerate SUB1 introgression into diverse genetic backgrounds, predicting performance across environments. This approach is particularly useful for stacking SUB1 with other QTLs (e.g., Saltol, DRO1) [114]. Molecular insights: Many studies elucidated *SUB1A*'s regulatory network, showing it

interacts with ethylene, gibberellin, and abscisic acid pathways to orchestrate submergence responses [115]. Comparative genomics revealed *SUB1A* homologs in wild rice (*O. rufipogon*, *O. nivara*) and African rice (*O. glaberrima*), suggesting evolutionary conservation of submergence tolerance [116]. Additional submergence-tolerance QTLs (e.g., *qSUB8.1* from *O. rufipogon*) are being explored to complement *SUB1*, particularly for deeper or longer floods. Evolutionary conservation: Comparative genomics revealed *SUB1A* homologs in wild rice (*Oryza rufipogon*, *O. nivara*) and African rice (*Oryza glaberrima*), suggesting an ancient origin of submergence tolerance. The *SUB1A-1* allele likely evolved in flood-prone environments, as evidenced by its presence in landraces from eastern India and Sri Lanka [116].

MABC and genomic selection facilitate stacking, ensuring the compatibility of stacked traits. IR64-Sub1 has been further bred to incorporate Xa21 and Saltol, targeting complex flood-saline environments in the Philippines [117]. Integrating *SUB1* with QTLs for anaerobic germination (e.g., *TPP7*) and deep water adaptation (*SNORKEL1/2*) is creating versatile varieties. Multi-omics (genomics, transcriptomics, metabolomics) is guiding trait stacking by predicting gene interactions [118]. The *SUB1A-1* allele is rare, limiting donor diversity. Screening wild rice (*O. rufipogon*, *O. nivara*) has identified additional alleles, but their efficacy is less studied. *SUB1A-1*'s effectiveness diminishes in deepwater or prolonged floods (>20 days), requiring complementary traits (e.g., elongation genes like *SNORKEL1/2*) [119]. The molecular pathways of *SUB1A-1*-mediated submergence tolerance involve a sophisticated interplay of ethylene signaling (activation), GA suppression (quiescence), ABA (abscisic acid) crosstalk (stress balance), enhancing anaerobic metabolism (energy production), carbohydrate conservation, antioxidant defense (oxidative protection), and recovery mechanisms (regrowth). *SUB1A-1* acts as a central regulator, binding GCC-box motifs to orchestrate gene expression, ensuring rice survives 10–20 days of submergence and recovers with minimal yield loss [103–110].

7.2 Phosphorus deficiency tolerance using QTL *Pstol*

Phosphorus (P) is an essential macronutrient for plant growth, critical for energy transfer, photosynthesis, and root development. However, P is often unavailable in soils due to fixation (e.g., in acidic or alkaline soils), affecting approximately 50% of rice-growing areas globally, especially in Africa, South Asia, and Latin America. Low P availability reduces root growth, tillering, and grain yield. To mitigate the P-deficiency difficulties for rice production, a novel QTL *Pup1* was first identified in a mapping population derived from a cross between the P-deficiency-tolerant aus landrace Kasalath (from Assam, India) and a P-deficiency-sensitive japonica cultivar, Nipponbare, and pinpointed *Pup1* on chromosome 12 as a major QTL explaining significant variation in P uptake and grain yield under low-P conditions [120]. *Pup1* spans a ~ 150–170 kb region on chromosome 12 (approximate position, 24.1–24.3 Mb in the rice genome) and contains multiple genes, with *Pstol1* (LOC_Os12g40850) identified as a key gene within the locus. *Pstol1* encodes a serine/threonine kinase (a protein kinase-like gene) that enhances early root growth and P acquisition under P-limited conditions [121]. The tolerant allele (*Pup1*-Kas) is present in Kasalath and some aus and indica landraces but absent or non-functional in most modern high-yielding varieties (e.g., IR64, Nipponbare). The Kasalath allele is characterized by specific insertions/deletions (InDels) and single-nucleotide polymorphisms (SNPs). In field trials, *Pup1* introgression lines show 20–50% higher grain yield under low-P conditions compared to non-*Pup1* lines, with minimal yield penalty in P-sufficient

soils [102]. Pup1 is effective across diverse environments (e.g., acidic soils in Asia, alkaline soils in Africa), making it a versatile target for breeding. SNP and InDel markers tightly linked to Pup1 (e.g., K46-1, K29, OsPupK20-2) have been developed for precise selection of the tolerant allele. These markers enable rapid introgression without extensive phenotyping. Kasalath is the primary donor, but other landraces (e.g., Dular, black Gora, Horkuch) with Pup1-like alleles are also used and expanding the donor pool. *Pup1/Pstol1* has been widely utilized in rice breeding programs to develop P-deficiency-tolerant varieties, primarily through marker-assisted breeding [122–127]. African *O. glaberrima* landraces (e.g., Djimoron) also show P deficiency tolerance, potentially due to Pup1 homologs. Wild *Oryza* species (*O. rufipogon*, *O. nivara*) are being explored for novel P-efficiency alleles, though Pup1 itself is unique to certain cultivated landraces. Intermediate lines with Pup1 are developed through pre-breeding to facilitate its transfer into diverse genetic backgrounds, reducing linkage drag and improving agronomic traits, and consequently, Swarna-Pup1 and IR64-Pup1 were developed. Its discovery in the aus landrace Kasalath and subsequent introgression into elite cultivars *via* MABC demonstrate the power of landrace diversity in addressing global agricultural challenges. With ongoing advances in genomics, gene editing, and multi-stress breeding, *Pup1* will continue to play a pivotal role in ensuring food security and resilience in rice production systems worldwide.

7.3 Salinity tolerance in rice using QTL Saltol

Under excess salt conditions, rice plants face osmotic stress and ionic imbalance, ultimately impacting plant growth. Salt stress includes reduced photosynthesis and photosynthetic translocation, stimulation of photorespiration, degradation of chlorophylls, stomatal closure, and a change in chloroplastic pH. High salinity may also cause cell wall damage, accumulation of electron-dense proteinaceous particles, plasmolysis, cytoplasmic lysis, and damage to endoplasmic reticulum. Rice cultivars grown in flood-prone areas are particularly affected by salinity. Salinity affects the rice production at least 20% mainly irrigated land areas throughout the world. To overcome from this salinity stress, salt-tolerant improved rice cultivar development which is utmost needed. But major bottleneck is that salt tolerance traits are governed by many complex genetic attributes moreover dependent on environmental influences. It is associated with many genes or QTLs. An increase in the concentration of Na^+ and Cl^- invariably affects enzyme activities. The grain yield shows inversely proportional to Na^+ and Na^+/K^+ ratio, and directly proportional to K^+ levels. A few QTL (qSNC7 and qSKC1) responsible for sodium uptake, potassium uptake, and regulation of the Na^+/K^+ ratio is independent of vegetative growth mapped from a F2 population of Nona Bokra x Koshihikari [128] on chromosomes 4, 6, and 9. These QTLs explained 40–48.5% total phenotypic variation in the genotypes. Nona-Bokra is the salt tolerant indica rice cultivar. Hybrids of *O. rufipogon* × *O. sativa* were found to contain nine quantitative trait loci (QTL) and candidate genes (e.g., HKT1;5, HAK6 and some transcriptional factors) controlling the salt tolerance at the seedling stage [29], and 13 of 15 QTLs for salinity tolerance found were from *O. rufipogon*. Recombinant inbred lines (RILs) also derived from a cross of *O. rufipogon* × *O. sativa* showed superior performance with respect to salinity stress [29]. The cultivated varieties, BRRI Dhan 55, in Bangladesh and DRR Dhan 40, Jaraya, and Chinsurah Nona 2 in India, have been released after interspecific hybridization with *O. rufipogon*. Most recently, two seawater adapted rice landraces, Changmaogu [64] and Sea Rice 86 [129], discovered from coastal areas in China, have drawn wide attention.

Changmaogu showed stronger tolerance to salinity than Pokkali at the germination stage. Salinity stress tolerance was present in wild rice relatives but has been lost during domestication [39]. Recent research from an extreme halophyte species of wild rice *Oryza coarctata* (*Porteresia coarctata*), with the KKLL genome (48 chromosomes) appears to be more promising [130]. Wild *Oryza* species *Oryza coarctata* is an Asian halophyte naturally occurring in coastal environments have high salinity and submergence tolerance activity [87]. *Porteresia coarctata*, a wild rice, survives in submergence with extremely saline water, suggesting this could be the potential genetic resource for salinity tolerance, in addition to submergence tolerance [41, 131–133]. High salinity abiotic stress tolerance trait can be transferred to cultivars either using bridge-crossing process or through advance genetic technology. Understanding the molecular and physiological mechanisms of its superior tolerance to salt may open the potential to introduce some key traits into breeding programs. For instance, some allele mining studies have shown that a single base addition resulting in the frame shift for 37 amino acids in the L-myo-inositol 1-phosphate synthase (MIPS) protein is capable of increasing salinity tolerance in rice, a unique example of molecular adaptations contributing to salinity tolerance [41]. Two major QTLs, *qSNTQ-7* for shoot Na⁺ concentration (SNC) and *qSKC-1* for shoot K⁺ concentration (SKC), were identified from a cross between salt-tolerant Nona Bokra and salt-susceptible Koshihikari. The *qSKC-1* on chromosome 1 explained 40.1% of total phenotypic variation and was further fine mapped and isolated. The original functional analysis revealed that the *SKC1* gene encodes an HKT-type transporter (*OsHKT1;5*), which is preferentially expressed in the parenchyma cells surrounding the xylem vessels in rice and regulates K⁺/Na⁺ homeostasis under salt stress. Another notable QTL *Saltol* associated with the shoot Na⁺/K⁺ ratio at the seedling stage was identified from a salt-tolerant landrace Pokkali. The *SKC1* gene (*OsHKT1;5*) was suggested to be the functional gene underlying the *Saltol* segment [134]. In rice, histone gene binding protein (*OsHBP1b*) and zinc-finger transcription factor (*OsGATA8*), both located in the *Saltol* QTL region, also play an important role in seedling salt tolerance by regulating the expression of several genes related to chlorophyll biosynthesis, ion homeostasis, reactive oxygen species (ROS) scavenging, and stress tolerance. Considering its importance and role in seedling level salinity tolerance, attempts have been made to introgress *Saltol* to a high yielding but salinity-sensitive rice Pusa Basmati 1121 [36]. The QTL qST1.1 for seedling salinity tolerance identified from Sea Rice 86 was located within the *Saltol* region with the amino acid sequence of *SKC1* (*OsHKT1;5*) of Sea Rice 86 being the same as that in Nona Bokra. A Chinese landrace Jiuciqing and indica rice variety CSR11 were found to function as a salinity-tolerant. The *Saltol* QTL derived from Pokkali, which is responsible for shoot Na⁺/K⁺ homeostasis, has been successfully introgressed into commercial varieties via MAS and MABC using two polymorphic SSR markers, RM3412 and RM493, which were tightly linked to the *Saltol* region. QTL-based marker-assisted selection (MAS) and marker-assisted backcrossing (MABC) have been proven to be successful in crop molecular breeding. Similarly, the introgression of the *OsRR22* gene identified from the salinity-tolerant mutant *hst1* to the elite cultivar Hitomebore and a high-yielding cultivar Yukinko-mai has improved salinity tolerance at both seedling and reproductive stages [130]. The *Saltol* QTL on chromosome 1 was identified in Pokkali, regulating Na⁺/K⁺ homeostasis [135]. MAS was used to transfer *Saltol* into varieties like Pusa Basmati 1121. Other varieties also developed CSR27 and Luna Sankhi for saline coastal regions. The *Saltol* QTL from *O. rufipogon* enhances seedling-stage salinity tolerance [134] and introgressed into indica cultivars like IR64, which improves

survival in coastal saline regions. Among the different cultivars Pokkali, Nona Bokra, and FL478 are the most salt-tolerant rice genotypes [136]. Many new improved salinity-tolerant rice varieties are developed by extensively using these salt-tolerant rice varieties through breeding program [134, 137]. Salt-tolerant varieties have the more efficiency to compartmentalization of Na^+ in the vacuole [138–141], which maintain the optimum functioning condition in the plant tissues in presence of high Na^+ and Cl^- ions. Sequestration of Na^+ and Cl^- ions has been achieved in the plant tissues through compartmentalization of Na^+ at the cellular and intracellular regions to avoid toxic concentrations within the cytoplasm, mainly in the mesophyll cells of leaf. Due to sequestration, now plants can be capable to maintain a low K^+/Na^+ ratio in the leaf tissues that mechanism ultimately provides salinity stress tolerance to the plant. Besides this mechanism, plants use compatible solutes and different enzymes to catalyze the detoxification reaction of reactive oxygen species (ROS) produced during salt stress [138–141]. Among the wild rice species, *Oryza coarctata* is the highest salt-tolerant rice species, available in the coastal region of India, Pakistan, Bangladesh, and other countries. Salt secretion mechanism is a unique characteristic trait for halophytic grasses [41, 133]. The secretion mechanism allows maintaining the low Na^+ ion concentration in leaf tissues through the extrusion of Na^+ ion from the leaf surface [138–141]. Salinity tolerance involves ion homeostasis, particularly reducing Na^+ accumulation and maintaining K^+/Na^+ ratios. The Saltol QTL, derived from tolerant landraces like Pokkali, regulates Na^+/K^+ transport. Other salt-tolerant rice varieties: Nona Bokra, Cheriviruppu, Kala Rata, Kutipatnai, Getu, and Horkuch have also been used in breeding programs to develop salt-tolerant improved rice varieties. Genes such as OsHKT1;5 (a Na^+ transporter) and bHLH transcription factors (OrbHLH001 and OrbHLH2 from *O. rufipogon*) regulate K^+ homeostasis and stress-responsive pathways. Salt-tolerant varieties such as Jarava and Chinsura Nona 2, developed using *O. rufipogon* and *O. nivara*, show the improved yields in saline soils. The PcINO1 gene, encoding L-myo-inositol 1-phosphate synthase from *O. coarctata*, was transgenically introduced into Pusa Basmati-1, conferring enhanced salt tolerance by improving osmotic adjustment. Varieties such as Pusa Basmati 1121 (with Saltol) and transgenic lines with PcINO1 from *O. coarctata* show improved performance in saline soils, critical for coastal and inland saline regions.

8. Breeding for nutritional pigmented rice

Pigmented rice accumulates various types of secondary metabolites and phytonutrients, for example, phytosterols, polyphenol, flavonoids, anthocyanins, proanthocyanidins, vitamins, and micronutrients [142–144] that are recognized to have high nutritional value and medicinal properties with antioxidant, anti-mutagenic, anticancer, anti-viral, anti-diabetic, anti-inflammatory, and anti-aging protection potentialities [144–148]. The nutritive value of pigmented rice is greatly influenced by genetics, genotypic variation, and environmental factors [149], along with several external influences, soil fertility status, the degree of milling, and the method of preparation before consumption [148]. Black rice has been advocated to be consumed as staple food to substitute white rice due to its outstanding health-promoting effects. Nearly 200 black rice varieties are grown globally and phylogenetically divided into four varietal groups, namely Geng-japonica, Xian-indica, circum-Aus, and

circum-Basmati based on PacBio whole-genome sequencing report [150]. In India, different varieties of black rice are locally grown in different states, specifically Chakhao landraces (Chakhao means delicious) in Manipur (North-Eastern state of India), Kavuni in South India, Njavara in Kerala, and Kalabhat in West Bengal [146, 151, 152]. Despite having nutritional importance (rich source of phytonutrients), pigmented rice is usually low yielding, prone to lodging, susceptible to diseases, and late-maturing [150, 151, 153]. Pigmented rice varieties (black/red/brown) are gaining popularity among consumers due to nutritional health benefits and market demands are expected to rise [154–156]. Looking forward, there is a remarkable opportunity for breeding programs to develop nutritionally enriched (phytonutrients) productive pigmented rice varieties. Pigmented rice cultivars have long been favored by consumers for nutritional benefits and breeders have tried to improve their agronomic traits and quality [152, 156, 157]. A number of black rice lines developed through crossing between black rice “Okunomurasaki” and white rice Koshihikari [157, 158]. The eating quality of the black rice NIL (near-isogenic lines), especially the overall value and glossiness, was superior to that of another check black rice cultivar Okunomurasaki when crossed was made between black Hong Xie Nuo with white Koshihikari [158]. Nutrition-enriched breeding lines were developed from crosses between white and black lines with the high amount of phenolic content and anthocyanin content than the parental black rice, supporting the prospect of developing new rice cultivars with high antioxidant capacity and high yield. Riceberry is newly developed black rice by crossing between aromatic Jasmine rice and local non-glutinous purple variety. Transgressive segregant lines were selected from the cross between black rice Chakhao Poreiton and Sahbhagi dhan (white rice) with colored pericarp, high anthocyanin content, aroma, blast resistance, and increased yield compared to their parental lines [146].

9. Conclusion and future perspectives

In the face of escalating climate change and global food insecurity, the exploitation of wild *Oryza* species germplasm offers a powerful strategy for enhancing abiotic and biotic stress tolerance in cultivated rice. Wild rice species, with their vast genetic diversity, harbor valuable alleles/QTLs that has been harnessed to improve resilience against drought, salinity, flooding, pests, and diseases—threats that increasingly compromise rice yields worldwide. Through modern breeding approaches such as marker-assisted selection (MAS), marker-assisted backcrossing (MABC), genomic selection, transgenic, and genome editing, these traits has been introgressed into high-yielding varieties with greater precision and efficiency than ever before. Stress tolerance breeding leveraging on wild rice relatives (WRR) is not merely a scientific endeavor—it is a critical pathway toward securing global food systems in a rapidly changing world. Recent advances in the successful introgression of resistance genes from wild species into elite cultivars have demonstrated promising outcomes, emphasizing the strategic importance of wild rice germplasm in breeding programs. MAS and MABC breeding has been utilized to alleviate the difficulties of pre-breeding/wide hybridization, and challenges such as linkage drag and reproductive barriers are minimized. Looking ahead, the integration of cutting-edge technologies like CRISPR/Cas-based genome editing, pangenomics, *de novo* domestication of allotetraploid species, transcriptomics, miRNA technology, high-throughput phenotyping, and

genomic selection holds great promise for accelerating the utilization of wild rice in stress tolerance breeding with high-yield potentiality. The development of pre-breeding/wide hybridization populations and core introgression lines (ILs, BILs, CSSLs, NILs) will further facilitate the identification and transfer of valuable traits from wild germplasm. Sustainable and resilient rice production—crucial for feeding a growing global population—depends on a strategic shift toward biodiversity-based breeding approaches that embrace the untapped wealth of wild *Oryza* species.

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Phenotypic Variation and Clustering of Rice Landraces in South Sulawesi Using Multivariate Analysis

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Abstract

Studies on genetic variety and agro-morphological similarities revealed the promising usage of landraces. Research showing the genetic diversity or similarity of rice genotypes (varieties, germplasm accessions) on morphological, physiological, and molecular level features has made extensive use of cluster analysis. This study aims to investigate the morphological variation of 22 rice landraces of South Sulawesi and measure their distance of similarity using the Gower Method. The study was conducted between September 2018 and September 2019. The study examined 22 varieties of rice landraces from four regencies in South Sulawesi. Observations were made of 22 characters based on the UPOV descriptor key. Principal component analysis yielded five main components with a cumulative diversity proportion of 75.19%, and then used as the basis for cluster analysis. The main component analysis and cluster analysis results revealed that local rice varieties in South Sulawesi tend to form six small groups and have high phenotypic similarities with similar regions of origin, except for the sixth cluster, which consisted of several local rice varieties with diverse regional origins.

Keywords: agromorphology, cluster analysis, germplasm, rice landrace, local paddy

1. Introduction

Rice (*Oryza sativa* L.) is a primary staple food for over half of the global population [1–2]. While modern rice varieties produce excellent yields, local landraces

(traditional, non-commercial varieties) are nevertheless important for global food security [3], particularly in regions like Indonesia, where different ecosystems pose agricultural challenges.

Despite their lower yields, landraces are better adapted to local conditions and hold significant symbolic, social, and economic value [4]. In addition, rice landraces serve as a reservoir of genetic potential and contain numerous resistant genes for biotic and abiotic stress [5]. These landraces are more suited to local environments, increasing their likelihood of survival and reproduction, thus enabling them to pass on their traits to subsequent generations [3, 6].

Despite their significance, landrace diversity is rapidly declining due to the widespread adoption of modern varieties [7, 8]. This narrowing genetic base poses a significant threat to future food security.

Rice genetic diversity or similarity of morphological, physiological, and molecular levels has been widely carried out using cluster analysis [9–11]. Multivariate analyses like principal component analysis (PCA) and cluster analysis have proven invaluable in understanding rice populations' genetic makeup and diversity. PCA minimizes information loss, increases interpretability, and reduces dimensionality [12]. Additionally, PCA helps simplify complex datasets by revealing underlying patterns and reducing redundancy [13]. Cluster analysis is a fundamental tool in plant breeding, aiding in selecting superior parent lines for hybridization by grouping similar varieties [2].

Studies on genetic variability and agro-morphological similarity have been conducted and revealed the promising use of landraces in India [14], the Philippines [15], West Bengal [16], and Indonesia [17]. Characterization of Indonesian rice landrace diversity has been reported in some studies, including from Jambi and Riau of Sumatera Island [18], Java island [19], East Nusa Tenggara [20], also South Kalimantan [21]. However, a comprehensive understanding of South Sulawesi's unique rice landraces remains limited, as most indigenous rice is naturally found in the upland or remote areas.

South Sulawesi's agroecology and rice diversity are unique as part of Wallacea, a biogeographic region known for its fascinating evolutionary history. Three distinctive seasonal patterns of wet and dry months and 13 Oldman-climate types shaped the diverse climate and agroecology types of South Sulawesi [22]. This diversity also likely led to the development of landraces adapted to specific conditions like drought tolerance in drier areas or flood resistance in low-lying fields.

The agro-morphological variability of South Sulawesi's rice landraces has been studied, but the similarity distance has not been reported [23]. Indonesia's vast archipelago encompasses diverse agroecological zones, highlighting the need for localized research to capture the specific adaptations and potential of landraces in each region.

This study addresses this gap by investigating the morphological variation of 22 rice landraces specific to South Sulawesi. We employ cluster analysis to assess the similarity between these landraces based on their morphological characteristics. This approach provides valuable insights into the relationships between these landraces and their potential for breeding programs. Conserving these indigenous landraces is imperative as they face the risk of extinction. The findings of this study will aid germplasm managers in strategizing future acquisitions for the region and also contribute crucial information to the global effort to conserve and utilize rice landraces.

2. Materials and method

2.1 Timing and study materials

The study was conducted from September 2018 to September 2019. The research survey observed 22 types of rice landraces at four regencies, four subdistricts, and five villages in South Sulawesi, Indonesia (**Table 1**). Observations were made within two consecutive planting seasons on qualitative and quantitative characters based on the Rice Test Implementation Guide [24] adopted from the UPOV descriptor key (International Union for the Protection of New Varieties of Plants) [25, 26]. The observed parameters of the study include 12 parameters of quantitative traits (**Table 2**) and 15 parameters of qualitative traits (**Table 3**). Experimental data was collected from 10 randomly selected rice plants from each landrace in the field.

No	Code	Local rice	Location of origin			Elevation (m asl)
			Regency	Subdistrict	Village	
1	PN	Puruan	Sidrap	Pitu Riase	Batu	195
2	CW	Calla Wangi	Sidrap	Pitu Riase	Batu	195
3	CM	Calla Malunra	Sidrap	Pitu Riase	Batu	195
4	PK	Pare Kate	Enrekang	Curio	Parombean	983.6
5	PL	Pare Lambau	Enrekang	Curio	Sanglepongan	702.2
6	PP	Pare Pinjan	Enrekang	Curio	Sanglepongan	655.1
7	PS	Pare Solo	Enrekang	Curio	Sanglepongan	650.8
8	PM	Pare Mansur	Enrekang	Curio	Sanglepongan	687.2
9	BE	Bolong Enrekang	Enrekang	Curio	Sanglepongan	682.2
10	LG	Lagading	Pinrang	Lembang	Letta'	981.1
11	PT	Pare Taupadang	Pinrang	Lembang	Letta'	1009
12	PJ	Pare Jagung	Pinrang	Lembang	Letta'	986
13	BP	Bolong Pinrang	Pinrang	Lembang	Letta'	996
14	IL	Ikko Lia	North Toraja	Bangkelekila	To'yasa Akung	1426
15	VM	Varietas Mandi	North Toraja	Bangkelekila	To'yasa Akung	1428
16	PTAN	Pare Tanduk	North Toraja	Bangkelekila	To'yasa Akung	1468
17	BL	Barri Lendong	North Toraja	Bangkelekila	To'yasa Akung	1435
18	BR	Birrang	North Toraja	Bangkelekila	To'yasa Akung	1456
19	BS	Barri Seko	North Toraja	Bangkelekila	To'yasa Akung	1432
20	URE	Kandaure	North Toraja	Bangkelekila	To'yasa Akung	1437
21	BBU	Barri Busa	North Toraja	Bangkelekila	To'yasa Akung	1425
22	BRK	Baruku	North Toraja	Bangkelekila	To'yasa Akung	1463

Table 1.
Rice materials and their origin location.

Trait	Local rice										
	PR	CW	CM	PK	PL	PP	PS	PM	BE	LG	PJ
Plant height (cm)	102.0	123.2	129.0	89.2	160.0	153.6	178.2	158.8	153.6	97.0	171.0
Productive tiller	16	15	18	31	18	21	22	18	17	22	10
Plant age (days)	120	120	120	150	180	180	180	180	180	120	185
Culm: habit (*)	30	30	30	30	45	45	20	30	30	45	45
Culm diameter (cm)	4.0	5.0	5.0	9.0	11.7	11.7	14.0	26.6	12.0	7.0	8.0
Leaf length (cm)	51.5	42.0	60.2	31.3	56.8	56.8	62.7	44.8	51.8	55.0	71.0
Leaf width (cm)	1.0	1.0	0.9	1.2	1.5	1.5	1.7	1.1	1.9	1.3	1.7
Lingule length (cm)	1.5	1.8	2.1	1.5	2.0	2.0	2.0	2.5	2.4	1.9	1.8
Panicle length (cm)	31.6	25.6	29.9	22.0	58.2	30.4	33.4	40.0	41.2	28.5	23.0
Grain length (mm)	6.8	5.9	5.7	8.7	9.7	7.9	10	8.7	9.7	9.5	7.0
Yield (t/ha)	5	5	5	4	5	4	4	4	4	5	3
Potential yield (t/ha)	7	7	7	6	7	5	5	5	5	7	4

Trait	Local rice										
	BP	PT	IL	VM	PT	BL	BR	BS	URE	BBU	BRK
Plant height (cm)	168.0	165.0	120.0	125.2	165.3	120.8	148.6	151.6	134.0	128.8	178.0
Productive tiller	10	10	12	10	12	11	27	33	18	20	12
Plant age (days)	210	185	120	120	120	120	120	150	150	120	120
Culm: habit (*)	45	45	30	30	30	30	30	30	30	45	45
Culm diameter (cm)	7.0	8.0	5.0	6.0	11.1	7.3	12.1	5.4	7.0	5.0	3.8
Leaf length (cm)	72.0	60.0	36.7	39.5	53.0	47.8	47.8	47.5	45.8	45.8	48.9
Leaf width (cm)	1.3	1.5	1.1	0.8	1.5	1.4	1.4	0.9	0.8	0.9	1.2
Lingule length (cm)	1.9	1.9	1.5	1.1	1.0	1.1	1.1	2.7	4.0	2.5	1.0
Panicle length (cm)	44.0	44.0	24.8	26.3	31.4	28.4	28.4	26.1	24.5	22.8	33.4
Grain length (mm)	9.5	9.5	7.6	7.6	8.2	11.9	11.9	8.4	7.4	7.6	8.0
Yield (t/ha)	3	3	3	3	3	3	3	4	3	3	4
Potential yield (t/ha)	4	4	4	4	4	4	4	5	4	4	5

Table 2.
Quantitative traits.

Trait	PR	CW	CM	PK	PL	PP	PS
Culm: habit	erect	erect	erect	erect	erect	erect	erect
Culm: underlying internode coloration	145 A (Strong Yellow Green)	N 144 C (Strong Yellow Green)	145 A (Strong Yellow Green)	137 C (Grayish Olive Green)	147 B (Moderate Yellow Green)	138 B (Moderate Yellow Green)	143 C (Strong Yellow Green)
Leaf blade: pubescence	intermediate	intermediate	intermediate	intermediate	pubescent	pubescent	pubescent
Flag leaf: attitude	moderate	moderate	moderate	moderate	moderate	moderate	erect
Basal leaf color	138 A (Moderate Yellow Green)	137 C (Moderate Yellow Green)	141 C (Strong Yellowish Green)	137 A (Moderate Olive Green)	147 B (Moderate Yellow Green)	138 A (Moderate Yellowish Green)	144 A (Strong Yellow Green)
Ligule color	150 D (Light Yellow Green)	150 D (Light Yellow Green)	150 D (Light Yellow Green)	155 B (Yellowish White)	N155 A (Bluish White)	N155 A (Bluish White)	158 A (Pale Yellow)
Ligule shape	2-cleft	2-cleft	2-cleft	2-cleft	acute acuminate	acute acuminate	2-cleft
Trait	PR	CW	CM	PK	PL	PP	PS
Panicle: attitude of branches	compact	compact	compact	compact	compact	spreading (open panicle)	spreading (open panicle)
Panicle: secondary branching	little	a lot	moderate	a lot	a lot	a lot	a lot
Panicle: attitude of the main axis	drooping	drooping	drooping	Drooping	drooping	drooping	drooping
Awn: presence	hairless	long hair	long hair	hairless	long hair	long hair	long hair
Awn: color		164 C (Moderate Orange Yellow)	163 D (Light Yellow)		161 C (Pale Yellow)	18 A (Light Yellow)	163 A (Deep Orange Yellow)
Threshability	hard	moderate	easy	easy	moderate	moderate	moderate
Grain color	red	aromatic red	red	White	white	white	white
Cooked rice texture	tough	tough	fluffier	Fluffier	fluffier	fluffier	fluffier

Trait	PM	BE	LG	PJ	BP	PT	IL
Culm: habit	erect	erect	erect	erect	erect	erect	erect
Culm: underlying internode coloration	144 B (Strong Yellow Green)	61 A (Moderate Yellow)	Green	Green	Green	Green	N 144 A (Strong Yellowish Green)
Leaf blade: pubescence	pubescent	pubescent	intermediate	pubescent	intermediate	intermediate	intermediate
Flag leaf: attitude	erect	erect	erect	erect	moderate	erect	erect
Basal leaf color	137 D (Moderate Yellowish Green)	137 C (Moderate Yellow Green)	137 A (Moderate Olive Green)	143 A (Strong Yellow Green)	Green	137 A (Moderate Olive Green)	144 A (Strong Yellow Green)
Ligule color	60 D (Pale Yellow)	158 A (Pale Yellow)	White	150 D (Brilliant Yellow Green)	White	White	White
Ligule shape	2-cleft	acute acuminate	2-cleft	2-cleft	acute acuminate	acute acuminate	2-cleft
Panicle: attitude of branches	spreading (open panicle)	compact	compact	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)
Panicle: secondary branching	a lot	a lot	a lot	a lot	little	little	little
Panicle: attitude of the main axis	drooping	drooping	drooping	drooping	drooping	drooping	drooping
Awn: presence	hairless	long hair	hairless	long hair	short hair	long hair	long hair
Awn: color		155 C (Greenish White)		gold yellow	gold yellow	purple	yellow
Threshability	moderate	hard	easy	hard	hard	hard	hard
Grain color	White	Black	White	Red	Black	White	White
Cooked rice texture	fluffier	fluffier	a bit fluffier	a bit tough	fluffier	fluffier	a bit tough

Trait	VM	PTAN	BL	BR	BS	URE	BBU	BRK
Culm: habit	erect	erect	erect	erect	semi-open	erect	erect	erect
Culm: underlying internode coloration	144 B (Strong Yellow Green)	Purple	144 B (Strong Yellow Green)	143 C (Strong Yellow Green)	144 B (Strong Yellow Green)	144 B (Strong Yellow Green)	N 144 C (Strong Yellow Green)	143 C (Strong Yellow Green)
Leaf blade: pubescence	intermediate	pubescent	intermediate	pubescent	intermediate	intermediate	pubescent	pubescent
Flag leaf: attitude	erect	erect	erect	erect	erect	erect	erect	erect
Basal leaf color	143 A (Strong Yellow Green)	143 A (Strong Yellow Green)	137 C (Grayish Olive Green)	143 C (Strong Yellow Green)	143 B (Strong YellowGreen)	144 A (Strong Yellow Green)	144 A (Strong Yellow Green)	141 C (Strong Yellowish Green)
Ligule color	white	purple	white	white	White	white	white	white
Ligule shape	2-cleft	acuminate	2-cleft	acuminate	2-cleft	2-cleft	2-cleft	2-cleft
Panicle: attitude of branches	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)	spreading (open panicle)
Trait	VM	PTAN	BL	BR	BS	URE	BBU	BRK
Panicle: secondary branching	not branched	little	not branched	little	little	not branched	little	not branched
Panicle: attitude of the main axis	straight	straight	straight	drooping	straight	straight	drooping	drooping
Awn: presence	short hair	long hair	moderate hair	long hair	short hair	short hair	hairless	long hair
Awn: color	163 B (Strong Orange Yellow)	165 A (Moderate Brown)	yellow	166 A (Greyish Brown)	165 C (Moderate orange Yellow)	yellowish		165 A (Moderate Brown)
Threshability	moderate	moderate	moderate	moderate	moderate	easy	moderate	moderate
Grain color	White	Dark red	White	White	White	156 B (Yellowish Gray)	156 B (Yellowish Gray)	155 B (Yellowish White)
Cooked rice texture	a bit fluffier	tough	a bit tough	tough	a bit fluffier	tough	a bit fluffier	a bit tough

Table 3.
Qualitative traits.

2.2 Data analysis

Two phases of data analysis were performed: principal component analysis and cluster analysis. AKU is a multivariate analysis that is used to extract the main components that can preserve a portion of the original data while reducing the original variables into new variables with smaller dimensions and independence from one another. The principal component analysis aims to generate new variables that encapsulate or contain the majority of the data from the original variables. As a result, there may be fewer new variables than there were in the beginning. There is no correlation (i.e., this new variable is independent of the other new variables). The observational data is normalized before principal component analysis to ensure that variables are independent of one another and do not affect one another.

STAR software (<http://bbi.irri.org/products>) was used in data processing. A multivariate technique called cluster analysis seeks to group similar subjects into one group by classifying a sample of subjects (or objects) according to a set of measured variables into several groups. Euclidean distance is the measure of dissimilarity and the agglomerative method is the clustering technique used. Reduced variables from the principal component analysis results serve as the foundation for the data processing stage. The software used for this data processing is called STAR (<http://bbi.irri.org/products>).

Measurement of distances was calculated between the observed objects Distance Measures Methods using the Gower method [27]. Data was analyzed using R package *cluster* and *factoextra* programs (<https://www.r-project.org>).

3. Results and discussion

The study of 12 local rice genotypes from South Sulawesi included observations of 12 unique quantitative characters and 15 qualitative traits.

3.1 Quantitative trait

Twenty-two local rice was observed in 12 quantitative traits. Plant height ranged from 97.0 to 178.0 cm on LG and BRK cultivars. Plant height criteria include short plants less than 110 cm, medium 110–130 cm, and height more than 130 cm. There are 3 cultivars classified as short, namely Pare Kate (PK), Lagading (LG), and Puruan (PR), and there are 5 cultivars that have medium height, namely Bau Calla (CW), Calla Malunra (CM), Ikko Lea (IL), Mandi varieties (VM), and Barri Lendong (BL), while the other 14 cultivars are classified as high. The shortest cultivar is Pare Kate (KT) with a height of 89.2 Cm, while the highest cultivar is Baruku (BRK) whose average height is 178.0 Cm. Local rice that is relatively short such as PK, LG, and PR is better to develop because it is more resistant to tires compared to tall varieties.

Productive tiller as an essential part of rice was found to be the lowest (10 tillers) in PJ, BP, PT, and VM cultivars, while the highest (33 tillers) was in the BS genotype. Productive saplings of rice plants are grouped into 3 types, namely fewer saplings that are less than 12 saplings per clump, medium tillering types with 13–20 saplings per clump, and many tillering types more than 20 saplings per clump [28]. Of the 22 cultivars observed, there were 8 cultivars classified as less tillering type, and also 8 medium tillering type cultivars and there were 6 many tiller cultivars.

Harvest at the age of 120 days was successfully obtained from 10 local South Sulawesi cultivars, and the oldest (210 days) was in the BP genotype. Farmers often concern the harvest age of a variety to be cultivated, in general farmers like a mature harvest age. The age of rice harvest is classified into 6, namely ultra genjah less than 85 days after seedling (das), super genjah harvest age 85–94 das, and very genjah 95–104 das, of age 105–124 das, medium age 125–150 das, and age in more than 151 das. The results of this activity obtained 11 cultivars classified as 120 HSS age, and there were 3 medium-aged cultivars and 8 deep-aged cultivars. The deepest aged cultivar is BP with an age of 210 HSS.

The rice landrace cultivar collection found that 15 genotypes had an upright culm habit (30°) and 7 genotypes had a slight upright culm habit (45°). Culm diameter is known to mean that the narrowest is 3.8 cm (rice BRK) and the widest is 26.6 cm (rice PM).

Leaves as rice growth characters for 120 days were successfully obtained from 10 local South Sulawesi cultivars; the longest was in BP (72.0 cm). Leaf width is between 0.75 cm (BL) and 1.9 cm (BE). Ligule length ranged from 1.0 cm (PT and BRK genotype) to 4.0 cm (URE genotype).

Panicle length was shown as the shortest by cultivar BL (21.7 cm) and longest by BP (44.0 cm). Grain length observations range from 5.9 mm (CW) to 11.9 cm (BR). The length of rice plant panicles was grouped into three groups, namely short panicles less than 20 cm, medium panicles measuring 20–30 cm, and panicles measuring more than 30 cm long [29].

Results were known to all panicle cultivars classified as medium to long, with no cultivars with short panicles. There are 12 cultivars whose panicle length was medium and 10 were classified as long.

In the study of 22 local landraces, the yields were around 3 t/ha on 10 cultivars and 5 t/ha on 5 cultivars (PR, CW, CM, PL, and LG). Optimistic yield potential is achieved up to 7 t/ha on PR, CW, CM, PL, and LG genotypes (**Table 2**).

The ideotype for local rice variety development encompasses high yield potential, early maturity, prolific tillering, robust and short culms, broad-spectrum resistance to biotic and abiotic stresses, excellent palatability, and physical grain quality [30, 31]. High-yielding local varieties are one of the alternative bases for increasing national rice production [32].

3.2 Qualitative trait

The research also included observations of 15 important qualitative characteristics of rice (**Table 3**). Culm habit mostly erects except for semi-open BS genotype. Internode coloration shows strong yellow-green color in 13 genotypes, that is, PR, CW, CM, PS, PM, IL, VM, BL, BR, BS, URE, BBU, and BRK, and other colors were grayish olive green (genotype PK), moderate yellow-green (PL, PP, BE), Green (LG, PJ, BP, PT), and purple (PTAN). The pubescence leaf blade characters include intermediate in 12 genotypes and pubescent in 10 genotypes. The flag leaf attitude showed the unique trait of the 22 rice cultivars, specifically moderate and erect. Basal leaf color indicated moderate yellow-green, strong yellow-green, grayish olive green, moderate olive green, and green properties.

Ligule colors as a unique character showed light yellow-green, yellowish-white, bluish-white, pale yellow, white, brilliant yellow-green, and purple. Ligule shapes were 2-cleft in 15 genotypes, acute-acuminate in 6 genotypes, and acuminate in 1 genotype. Panicle's attitude of branches was an important character referred to

compactness in 7 cultivars and spreading in 15 cultivars. Panicle secondary branching varies from no branching, few branching, and many branching. The awn presence that is often referred to as the iconic character of local rice varies from no awning, long awning, short awning, and medium awning. One of the unique morphological features of wild rice species is the long awn. Seed dispersal and protection from predators are among the alleged functions of the awn [33].

Awnless features in modern rice may promote easiness in harvesting without the adverse effects on yield [33]. Their findings about the different frequencies of awns on panicles support the hypothesis that several genes influence awn development in rice. Despite its simple shape, we conclude that awn development is controlled by a complex network of interacting genes. Variations in the awn color were very large, and there was moderate orange-yellow, light yellow, pale yellow, deep orange-yellow, greenish-white, yellow gold yellowish, purple, strong orange-yellow, moderate brown, yellow straw, grayish brown, and moderate yellow.

Threshability was an important trait for rice processing. Our study found three groups of treatability levels: easy, medium, and difficult. Modern rice is often associated with easy breathability. The difficult treatability may prevent more losses during the harvesting and handling process/transportation. However, the milling process can be harder. Variation in grain color was also found, including red, white, dark red, and black. Cooked rice texture variation includes hard, a bit hard, soft/fluffy/waxy, and a bit soft.

Quantitative character selection was carried out to identify essential characters that influenced the diversity of clones observed. In general, identification of the genotype kinship is closely related to the nature of the observed character data. There are several data types on a statistical scale, namely binary, nominal, ordinal, and numeric [34]. Qualitative character or categorical data has a scope in discrete binary, nominal, and ordinal data, although some numeric data also contain discrete numerical data [35].

The nature of discrete data will form a graph with a rigid gap [34, 35] and is excellent in the process of differentiating a trait between genotypes. Genetically, discrete characteristics are influenced by only a few significant genes, so their characters are less affected by the dominance of the environment. The fewer groups of characters, the fewer genes that regulate the trait [36], and it is easier for qualitative characters to distinguish between genotypes.

In contrast, quantitative characters are continuous and controlled by many genes [37], and the environment greatly influences the traits of a genotype unless most of the genes in these traits have the same variance response direction (Acquaah, 2012). Based on their genetic characteristics, coffee plants are relatively highly heterozygous because the propagation of coffee plants is mainly done by cloning of high hybrid vigor plants [38] so that their characteristics will be more diverse between genotypes in an environment. Therefore, the quantitative characters in this study need to be filtered first to get the main characters with a large diversity.

The variable should have a variance pattern among the objectives in kinship identification. It could help to know the specific characters that determine the object mapping, especially in the cluster and PCA. So, based on this, plant habit, leaf petiole color, mature leaf color, inflorescence position, anther insertion, and fruit-disc shape were not included in cluster analysis and PCA. In general, cluster analysis is one of the multivariate analyses used to visualize the relationships between objects based on the similarity or dissimilarity distances of various characters [39].

Several studies widely use this analysis to determine the genetic distance between each genotype of a population, using both quantitative characters [40] and qualitative characters [41], metabolomic [42], molecular data [37], and the combination of each character [43].

3.3 Principle component analysis (PCA)

The PCA result explained the genetic diversity of the rice germplasm accession. The top five axes of the PCA cumulative proportion of variance, which is 75.19% (**Table 4**), with an eigenvalue greater than one, suggest that the detected features significantly impacted the population's variability phenotypes.

Only five of the 20 *principle* components (PC) have an eigenvalue larger than one. Similar to the study by Ahmed [44], the first five principal components were identified as significant, accounting for 82.9% of the overall variability among the 31 rice germplasm. These five main components form the basis for determining their characteristics. This approach aligns with Sartono [45], who stated that the attributes with the largest trait vector value are the main character constituents of the component.

PC1 is the most diverse character, with an accumulative diversity proportion of 24.41%. Of the 10 dominant characters in PC1, leaf width has the highest component score and contributes the most to PC1 grouping, followed by panicle length and plant age (**Table 5**). Six out of 10 are quantitative parameters. Among the qualitative parameters in PC 1 are culm coloration, leaf blade pubescent, ligule shape, and panicle type. The traits grouped within different principal components that explain the variability indicate a tendency to cluster together and should be considered when utilizing these traits in breeding programs [46].

PC2 consisted of four qualitative parameters (culm coloration, leaf blade color, ligule color, and panicle type) and four quantitative parameters (height, tiller, leaf length, and yield). In comparison, PC3 consisted of three parameters (culm habit, leaf blade pubescence, and leaf blade color) and five quantitative characters (**Table 5**). PC4 consists of three qualitative characters (plant shape, leaf blade pubescence, and ligule color) and four quantitative characters (tiller, plant age, leaf width, and ligule length). PC5 consists of three qualitative parameters (culm habit, ligule color, and panicle type) and dominated by quantitative parameters related to yield (age, culm diameter, ligule length, panicle length, grain length, yield, potential yield).

The first three PCs explained a total variation of only 58.66%, with almost all characters drawn. This is in line with the statement by Estabrook [47] that the three main

Principle component	Eigenvalues	Proportion of variance (%)	Cumulative proportion (%)
PC1	4.88	24.41	24.41
PC2	3.75	18.75	43.161
PC3	3.10	15.50	58.66
PC4	1.82	9.08	67.73
PC5	1.49	7.46	75.19

Table 4.
The eigenvalue of principle components from local rice varieties.

Trait	PC1	PC2	PC3	PC4	PC5
Height	0.2933	-0.2498	-0.0735	0.0490	-0.1804
Tiller	0.0280	0.2157	0.3703	0.2906	-0.0510
Age	0.3322	-0.1137	-0.1158	0.2527	-0.2428
Culm habit	0.0955	-0.1989	-0.2080	0.1935	0.4300
Culm diameter	0.2928	0.0332	0.1816	-0.1659	-0.3499
Leaf length	0.2462	-0.1295	-0.3435	0.1802	-0.0575
Leaf width	0.3663	-0.0738	-0.0238	-0.797	0.1178
Ligule length	0.0282	0.418	0.0736	0.4909	-0.3541
Panicle length	0.3427	0.0721	-0.3386	0.1115	0.2301
Grain length	0.0588	-0.1262	0.3386	0.0112	0.2431
Yield	0.0558	0.4459	-0.0890	0.1627	0.2022
Potential yield	0.0231	0.0491	-0.1093	0.1291	0.2559
Plant shape	-0.0812	0.0035	0.1774	0.4976	-0.1727
Culm coloration	0.2419	0.3953	-0.0317	-0.1900	-0.1816
Leaf blade pubescence	0.3052	0.0039	0.2018	-0.2458	-0.0298
Flag leaf	0.0540	-0.0209	-0.4750	0.1484	-0.0973
Blade leaf color	-0.1472	-0.4750	-0.4257	-0.0880	-0.1366
Ligule color	0.1717	0.3420	-0.1536	-0.2162	-0.2827
Ligule shape	0.3039	-0.1486	-0.0494	-0.0227	0.1496
Panicle Type	-0.2012	-0.2798	-0.0465	-0.1323	-0.2162

(+/-) Indicates the direction of the vector in the field of view, it does not affect the size of the vector value of the characteristics.

Table 5.
 Characteristics of the first five principle component.

components are thought to be the most present variation among genotypes and traits that affect grouping. The graph of the two main components can provide information on morphological similarity. In the three main components used, three main group combinations are formed. Each combination consists of several varieties grouped or separated based on the character on which the grouping is based.

The biplot analysis aimed to learn more about the relationships between accessions and related features in general. Four sorts of information can be obtained from a biplot analysis: the relative value of accession to character, character correlation, character variability, and relationship among accessions [48]. The distribution and diversity of the varieties are explained by the biplot in **Figure 1**, which displays the clustering of varieties in the PC1 and PC2 fields with a cumulative diversity proportion of 43.16%.

In terms of the link between accessions, the results were quite variable. Accession origins were well split into diverse directions. However, there is a propensity to group them based on the location of origin. For example, variety codes 1–3 from Sidrap, variety codes 6, 7, and 8 from Enrekang, and variety codes 14, 15, 20, and 21 from North Toraja.

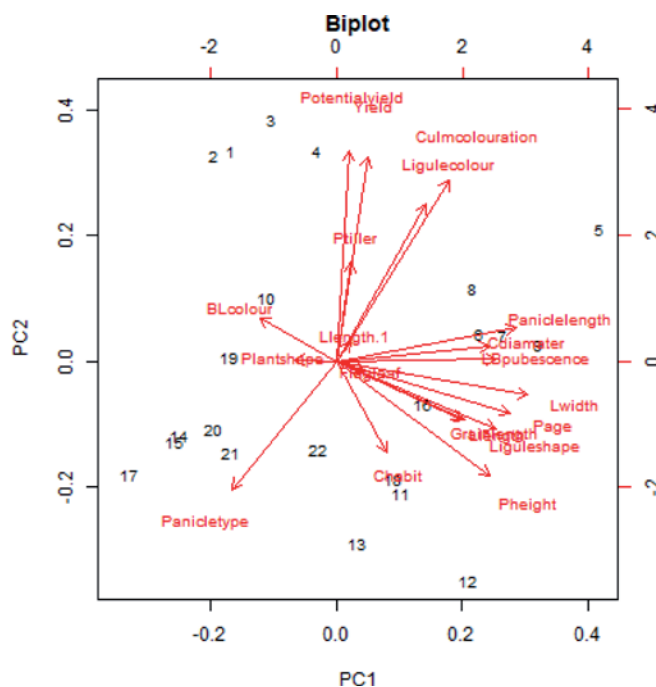


Figure 1.
Grouping of 22 local South Sulawesi rice varieties based on PC1 and PC2.

Parameters with arrows pointing to the right side of PC1 (like panicle length, culm diameter, leaf blade pubescence, leaf width, age, grain length, ligule shape, plant height culm habit) appear influential for varieties grouped on the right side.

Conversely, parameters with arrows pointing to the left side of PC1 (like panicle type and plant shape) might be more pronounced in varieties grouped on the left.

Biplot analysis in **Figure 2** showed the grouping of varieties in the PC1 and PC3 fields with a cumulative diversity proportion of 39.91%, explaining the distribution and diversity. Some varieties/accession clustered in **Figure 1** remain clustered in **Figure 2**, such as varieties 1, 2, 3 from Sidrap and 14, 15, 20, 21 from North Toraja due to their characteristic similarities. Arrows with a narrow angle indicate a correlation between grain length and leaf length culm coloration-ligule color.

For biplot analysis in **Figure 3**, PC2 and PC3 showed varietal clustering with a cumulative proportion of as much as 34.25%, which explains the distribution and diversity. Positive PC2 is shown by some qualitative parameters, such as culm coloration and ligule color, and quantitative parameters, namely yield and potential yield, which are highly correlated, as shown by the narrow angle of both arrows; variety number 5 is included in these criteria. Conversely, negative PC2 was shown by panicle type, plant height, leaf width, and ligule shape (*viz.* varieties number 17, 22).

Positive PC3 is most contributed by quantitative parameters of grain length and tiller number. Variety numbers 18 and 19 seem to be in the same cluster due to their similar character. Some varieties have similar clustering just like in the previous biplot graph; *viz.* 14, 15, 20, 21 remain in the same cluster, and so do variety numbers 11, 12, 13, 7, 8, 9.

From the results of this analysis, it can be concluded that the potential yield of varieties can be improved by utilizing members of different varieties of groups based

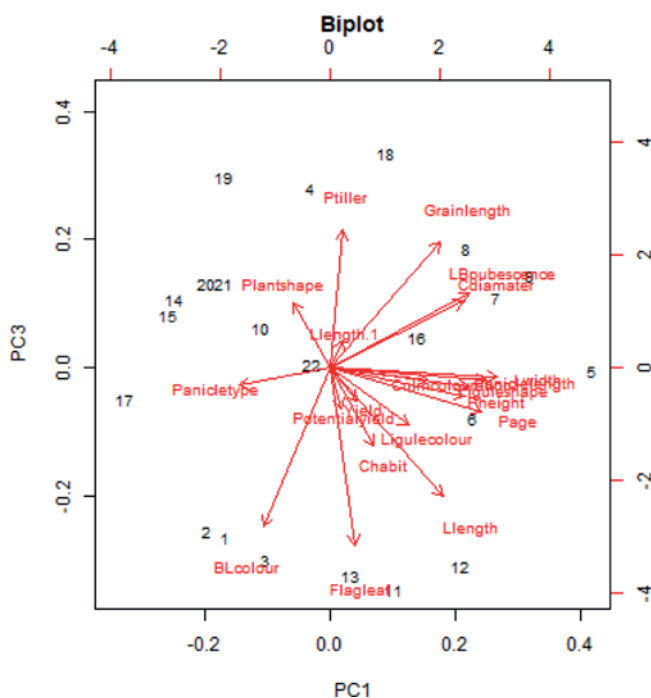


Figure 2.
 Grouping of 22 local South Sulawesi rice varieties based on PC1 and PC3.

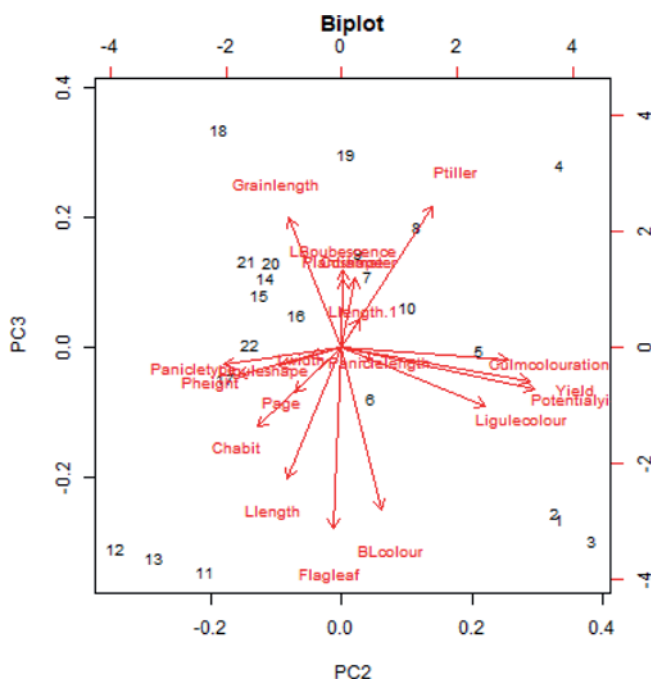


Figure 3.
 Grouping of 22 local Sulawesi rice varieties based on PC2 and PC3.

on the main component as a parental (F1). Varieties with very different characters can also be assumed to have a distant kinship so that, when crossed, they will produce better offspring.

3.4 Cluster analysis

The cluster analysis of the agro-morphological similarity of 22 local rice varieties appears to show two main clusters. The cluster on the left (denoted by negative values on the horizontal axis) appears to contain rice varieties from North Toraja. The cluster on the right (denoted by positive values on the horizontal axis) appears to contain rice varieties from the other three regencies (Sidrap, Enrekang, and Pinrang). The axis represents some sort of overall similarity score based on these factors. Rice varieties closer together on the chart are more similar in their agro-morphology, while rice varieties further apart are more dissimilar.

Further details showed there are six clusters in **Figure 4**. The first cluster consists of three cultivars: Calla Malundra, Puruan, and Calla Wangi from Sidrap Regency. The second cluster includes six genotypes: Pare Kate, Pare Mansur, Pare Solo, Pare Lambau, and Pare Bolong Enrekang. The third cluster contains cultivars from Pinrang Regency: Pare Bolong Pinrang, Pare Jagung, and Pare Taupadang. The fourth cluster comprises Pare Tanduk and Pare Birrang genotypes from North Toraja Regency. The fifth cluster comprises four genotypes: Pare Bau Seko, Pare Barri Lendong, Pare Kandaure, and Pare Mandi from North Toraja Regency. The last cluster is unique, consisting of the cultivar Pare Lagading from Pinrang Regency and Pare Bau Busa and Baruku from North Toraja Regency (**Figure 4**). According to Dhakal [49], if no cluster contained landraces collected exclusively from a single location, suggesting that ecological distribution did not influence genetic divergence. This lack of divergence could be attributed to farmers' free exchange of landraces, the

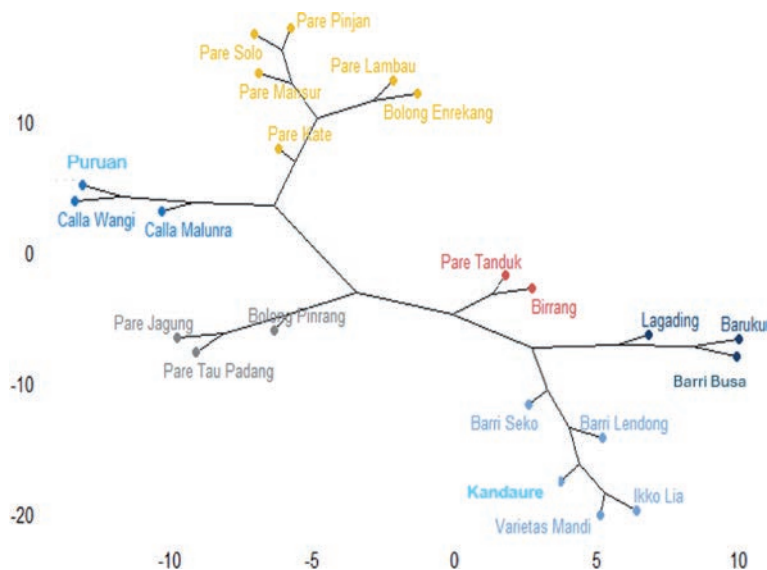


Figure 4.
Rice cluster analysis of 22 rice landraces from South Sulawesi Province.

unidirectional selection of landraces [50], and the proximity and similar geography of the collection sites.

Plant age displayed the most variation among the 22 rice accessions, ranging from 120 to 210 days, with a standard deviation of 31.12 days. Plant height was the second most variable trait, spanning from 89.20 to 178.20 centimeters (**Table 4**). The degree of variation in the paternal lines determines the degree of heterosis, or diversity, in a trait. The admission of distant relatives could be a cross to a remarkably diverse developed population. The establishment of populations with the ability to adapt to hostile settings can be facilitated by genetic variability [51].

This study assisted in identifying ideal local rice varieties for breeding programs focused on developing high-yielding, short-cycle varieties with desirable agronomic traits. Four local rice varieties emerged as promising candidates for parental lines: Pare Kate, Lagading, Puruan, and Baruku. These varieties exhibit a combination of desirable characteristics: (1) Stature: Pare Kate is a short-stature variety; (2) Maturity: Pare Kate has a long to medium harvest age, while Lagading and Puruan mature relatively quickly; (3) Yield: Lagading exhibits medium yield potential, while Puruan and Lagading demonstrate high overall production; (4) Panicle Length: Baruku has the longest panicle among the four varieties; and (5) Tillering: Puruan and Pare Kate exhibit a high number of productive tillers.

A key advantage of these candidate lines is their genetic diversity. Cluster analysis revealed that PK, LG, PR, and BP belong to distinct genetic clusters. According to Nisar [52], parental breeding lines should be chosen from diverse clusters demonstrating high average values for desired characteristics. In other words, superior hybrids or segregates are not yielded by crossing genotypes belonging to the same cluster [53]. This emphasizes that variability is crucial for selecting offspring with the optimal combination of traits for future rice cultivars.

Varietal selection occurs when populations adapt to their agroecological environments and prioritize utility value for farmers. This information is crucial for developing effective conservation methods and determining the best location to maintain genotypes, whether *in situ* or on farms [46]. On-farm conservation of plant genetic resources is the most reasonable in places with high public and private value, such as locations with abundant genetic variety and significant contributions to farmers' livelihoods [54].

While landrace selection for breeding requires a comprehensive evaluation of various factors, this study offers a preliminary framework. The genetic-level analysis should be conducted in subsequent research to gain a deeper understanding.

4. Conclusion

Multivariate analysis, such as clustering patterns and principal component analysis (PCA), can provide valuable insights to breeders regarding the suitability of various rice landraces for future projects. According to component analysis, the diversity was significantly influenced by the following factors: tiller number, leaf width, panicle length, blade leaf color, yield, and flag leaf attitude. The principal component and cluster analysis results revealed that the local rice varieties in South Sulawesi generally formed six distinct groups with high phenotypic similarities to their regions of origin. However, the sixth cluster contained several local rice varieties with diverse regional origins, including Pare Lagading from Pinrang Regency and Pare Bau Busa and Baruku from North Toraja Regency. This study identified four local

rice varieties (Pare Kate, Lagading, Puruan, and Baruku) with favorable traits for breeding programs. These varieties offer a combination of short stature (Pare Kate), fast maturity (Lagading, Puruan), high yield (Puruan, Lagading), and high tillering capacity (Puruan, Pare Kate). Additionally, their genetic diversity (shown through cluster analysis) makes them ideal candidates to generate offspring with a broad range of desirable characteristics for future rice cultivars. The findings indicate that agromorphological traits can be effectively utilized to characterize rice cultivars before documentation. This characterization aids in the on-farm conservation of indigenous rice varieties and their preservation in seed banks.

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Leafless *Vanilla* Species from Madagascar as Potential Models to Study Bioclimatic Adaptation

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Abstract

Within the *Vanilla* genus, leaflessness has evolved as an adaptation to heat and drought conditions. Bioclimatic factors have been shown to be responsible for the ecologically driven speciation of seven leafless *Vanilla* species indigenous to Madagascar. In the present study, we further assessed whether some of these species could be good models for genome-environment associations (GEA) studies at the intraspecific level, in order to later identify genomic signatures of adaptation, which may be useful in vanilla crop breeding for abiotic stress tolerance. For this, we selected two target species in Madagascar, *V. perrieri* and *V. bosseri*, as they are the most widely distributed, spanning over different bioclimatic regions. Principal component analysis (PCA) of 19 environmental variables revealed a bioclimatic structure based on sample collection sites. We also assessed intra-specific genetic variation using previously generated data from seven microsatellite loci. For each species, redundancy analyses demonstrated that environmental variations (temperature, precipitation, and vegetation index) contributed to the genetic structure of the populations through isolation-by-environment (IBE). These results indicate local adaptation of the populations of these two species and suggest that they represent appropriate models for further studying the climatic adaptation of vanilla plants.

Keywords: microsatellite, genome-environment associations, local adaptation, heat and drought adaptation, leafless vanilla

1. Introduction

1.1 Climate change and its effects on agriculture in Madagascar

Climate change has an adverse effect on agriculture. It enhances the outbreak of diseases, increases the frequency and severity of droughts and floods, and increases the likelihood of poor yields and crop failures [1, 2]. Drought alone will reduce global agricultural production by more than 10% in 2050 [3].

The effects of climate change on biodiversity and human activities are more pronounced in tropical, subtropical, and island environments [4, 5]. In Madagascar, for example, temperatures change more rapidly during the dry season than during the rainy season. An increase of more than 2°C is predicted over the next decade [6]. From 1990 to 2015, the degree of increased heat and multiple floods caused agricultural production to drop by more than 50%. The dry season has been extended in recent years in humid climates, and humidity levels have decreased by 10% [6]. Farmers are frequently exposed to pest disease outbreaks and extreme weather events, which lead to significant crop and income losses and worsen food insecurity. Unfortunately, the livelihood of the majority of the rural Malagasy population depends on agriculture [7, 8]. The identification and characterization of new genetic sources of tolerance to abiotic stresses are therefore part of the requirements for dealing with the effects of climate change on agriculture [9–11].

1.2 Vanilla cultivation and climate change

The commercial vanilla species, *Vanilla planifolia* G. Jackson, known as “Mexican” or “Bourbon” vanilla, is native to the rainforests of southeastern Mesoamerica [12]. In the late nineteenth century, *V. planifolia* was introduced into other tropical countries in Asia and Africa from vanilla plants cultivated in Mexico [13]. Madagascar has been one of the world’s leading producers of vanilla since 1960 [14]. Vanilla is among the most important agricultural products for the island’s economy. However, the vanilla crop is considered particularly sensitive to climatic variations [15]. The species has a limited response capacity to disease proliferation, prolonged drought episodes, and heat stress [16]. *V. planifolia* is a hygrosciaphilous species. Indeed, the production of a vanilla plantation depends on the local ecology, particularly light and shade. The tissues of the vanilla plant are very sensitive to sunlight: a lot of shade promotes vegetative growth, to the detriment of flowering. Conversely, an excess of sun and light can cause chlorosis and does not promote growth, and the plant becomes exhausted trying to flower [12]. Immature fruit falling and yellowing occur at high temperatures exceeding 32°C and low relative humidity (below 80%) [17]. Fruit drop can also occur 2 months after pollination after heavy rain. It varies from 15 to 90% depending on the cultivation system [18]. Therefore, it is important to identify strategies to reduce these harmful impacts of climate change.

Various methods are used in agriculture to reduce the effects of climate change on vanilla plants. In Mexico and Latin America, vanilla plants are cultivated in association with coffee, orange, and leguminous trees to provide shade and support [18]. However, this method is not applicable to all regions [19]. Other farmers use artificial shade houses. Irrigation systems can also be installed during the dry season when flowering and pollination occur. However, these strategies are not widely applicable to the majority of small farmers, who have very small plots and unfavorable economic situations. Their application may reduce the production diversification and increase the water usage, which can reduce the resilience to climate variation [7]. A sustainable solution would therefore be to select *V. planifolia* varieties adapted to climate change. To begin with, such an objective requires knowledge of the regions of the genome involved in this trait.

1.3 Leafless vanillas, a model of drought adaptation

The species of the genus *Vanilla* Plumier ex Miller are divided into two large morphological groups: species with leaves (Foliosae section), which include cultivated

vanilla (*V. planifolia*), and species without perennial leaves (Aphyllae section) [12]. Leaflessness was shown to represent an evolutionary convergence, as it appeared at least three times independently in the evolution of the *Vanilla* genus, in America, Asia, and Africa, as an adaptive response to drought conditions, mainly on islands or nearby continental coastal regions [20, 21].

A recent integrative study, based on phylogenetic, genotypic, and morphological data, has allowed the resolution of the taxonomic puzzle [20] represented by the leafless species in the South-West Indian Ocean (SWIO) region [22]. This SWIO monophyletic group, of African descent, has diversified in Madagascar and shows two main lineages corresponding to white versus yellow flower species, regardless of their geographical origin (**Figure 1**). Three independent colonization events from Madagascar have further allowed species diversification in the Seychelles, the Comoros archipelago, and the southeastern coast of Africa (**Figure 1**) [22]. Nine species were discriminated, including seven species present in Madagascar [22].

In Madagascar, five of the seven species (*V. bosseri* L. Allorge, *V. decaryana* H. Perrier, *V. madagascariensis* Rolfe, *V. humblotii* Rchb.f., and *V. perrieri* Schltr) have been observed in the hot dry forests along the west coast (from north to south) and the arid zones in the south, in relation to their adaptation to drought and heat [23]. Two species have been newly described and observed in more humid bioclimatic regions, such as in the east (*V. atsinananensis* Andriamihaja & Paillet) and in a high central elevation area (*V. allorgeae* Andriamihaja & Paillet) (**Figure 1**) [22]. In addition, some leafless species were shown to be resistant to diseases such as *Fusarium* wilt [25, 26]. They are also used in traditional medicine in Madagascar [20].

Although only the species *V. planifolia* is of major economic interest on a global scale, leafless vanilla plants represent a reservoir of important genetic diversity for future varietal selection programs due to their agronomic and pharmacological properties, especially in the context of current climate change.

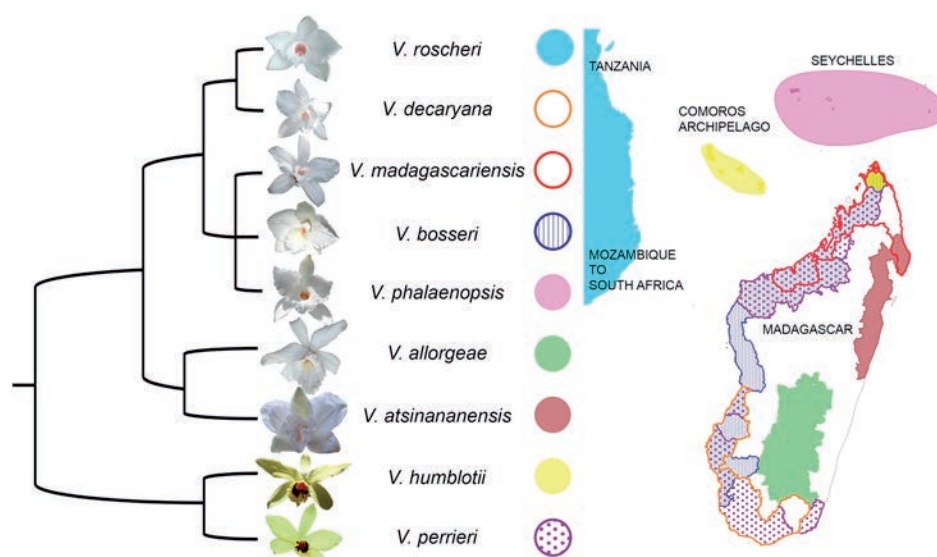


Figure 1.
 The nine leafless *Vanilla* species from the SWIO region: schematic representation of the ITS phylogeny (adapted from Andriamihaja et al., [22]) and their geographical distribution (adapted from Andriamihaja, [23] and Andriamihaja et al. [24]).

1.4 *V. perrieri* and *V. bosseri* as model species for local bioclimatic adaptation studies

Andriamihaja et al. [24] detected the combined effects of geographical distance and environmental distance on the genetic differentiation of the seven Malagasy leafless species. A predominant contribution of abiotic factors (precipitation, temperature, soil pH, and altitude) to their ecological speciation process was demonstrated [23]. These species, therefore, constitute a potential model for studying climate adaptation [20].

Local adaptation occurs when a population of organisms adapts to local conditions and is commonly observed in spatially heterogeneous environments [27]. In the present study, we aimed to verify whether local adaptation was present at the intraspecific level for those leafless species. For this, we selected two species, *V. perrieri* and *V. bosseri*, because they are the two most widely distributed in Madagascar (**Figure 1**), spanning various bioclimatic regions [20]. Local bioclimatic adaptation studies can be conducted using a landscape genetics approach with microsatellite markers combined with the geographical coordinates of individuals and environmental data [28, 29]. This makes it possible to correlate geographical information and the structuring of genetic diversity, for example, to detect the existence of isolation-by-distance (IBD). Genome-environment association analyses [30] also make it possible to determine the existence of phenomena such as isolation-by-environment (IBE) [31, 32]. Such analyses were conducted in the present study as an essential prerequisite for assessing the potential of these two species as models for the future detection of genomic signatures of climate adaptation, to be used in the varietal selection of cultivated vanilla.

2. Material and methods

2.1 Plant material

Seventy-five accessions of *V. perrieri* from nine sites (with 1 to 34 accessions per site) and 192 accessions of *V. bosseri* from nine sites (with 9 to 38 accessions per site) were studied (**Table 1**). The accessions of *V. perrieri* and *V. bosseri* were distributed across three and two geographical zones, respectively, and each spanned three different bioclimatic regions in Madagascar. The species identity of these accessions was verified in previous studies [24].

2.2 Genetic, geographic, and environmental data

The genotyping data of the 267 accessions for seven microsatellite markers previously generated by Andriamihaja et al. [24] were used in our study.

The geographic coordinates and elevation of each sample collection site were collected during sampling. Elevation data was used as an environmental variable. Global climate layers in raster format with a resolution of 1 km², downloadable from the WORLDCLIM online database (<http://www.worldclim.org>), were used to extract 19 bioclimatic variables (mean of 30 years) for each sample using QGIS (v 3.36.2). Eleven variables were related to temperature, and eight were associated with precipitation. The annual mean value of the Normalized Difference Vegetation Index (NDVI) for each sample was extracted from a raster dataset with a resolution of 250 m provided by the GIMMS Global Agricultural Monitoring System [33].

Population	Number of individuals		Geographical zone	Bioclimatic region
	<i>V. perrieri</i>	<i>V. bosseri</i>		
AKF	1	20	W	DF
AKLL	12	15	SW	ST
ATD	1		SW	ST
ATS		23	W	DF
B66	1		SE	LF
BBL	3	19	W	DF
BFD	21		W	DF
BTM	34		W	DF
CMK		9	W	DF
KRD		29	W	SWo
MLT	1		SW	ST
MMD	1		W	DF
MSL		38	W	DF
NMK		23	W	DF
ZVB		16	SW	SWo
Total	75	192		

SE south-east, SW south-west, W west; DF Dry Deciduous Forest, LF Lowland Forest, ST Spiny Thickets, SWo Succulent Woodland.

Table 1.
Geographical zone, bioclimatic region, and the number of accessions of the populations studied.

2.3 Intraspecific genetic structuring

To examine the genetic structure of the populations for both *V. perrieri* and *V. bosseri*, a Bayesian clustering analysis was conducted using the STRUCTURE software using the genetic data from seven microsatellites [34]. The number of K tested in this study varied between 1 and 12 for each of the two species. No prior assumptions were made about the geographical origin of the samples. For each value of K, 100,000 burn-in periods followed by 1,000,000 MCMC iterations were performed with 10 repetitions. As recommended by Wang [35] and used by Andriamihaja et al. [24] on leafless vanilla, a model with admixture and independent allelic frequencies with a low value of the ancestral prior alternative Alpha (reduced to $1/K = 1/12$ in our study) was chosen to correct the sampling imbalance and accurately assign individuals to clusters. The most probable value of K was determined by the use of the maximum value of DeltaK [36] and of the maximum value of the mean of the log posterior probability of K, $\ln P(X|K)$ [34] with POPHELPER (pophelper.com). The geographical distribution of the K genetic groups across the populations of the two species was made on QGIS (v 3.36.2). An accession was considered to belong to a genetic group (cluster) when at least 80% of its genome was assigned to that genetic group.

2.4 Bioclimatic population structuring

For each species, principal component analysis (PCA) was performed on the environmental variables collected by using the “dudi.pca” function from the R package

“ADE4” [37]. This was done in order to verify the bioclimatic structuration and to identify the variables that most determine the distribution area of each species.

To minimize the multicollinearity of these variables, their variance inflation factor (VIF) values were calculated with the functions “vif” and “vifstep” of the R package “usdm” [38]. Only the variables with a VIF <10 were selected. Subsequently, a Pearson correlation test was conducted between the selected variables using the “cor” function from the R package “stats.” When the Pearson correlation coefficient between two selected variables was greater than $|r| > 0.7$, one of the variables was excluded [38–40]. Only the variables retained after these two steps were used for the PCA.

2.5 Isolation by geographic distance and by environment

To check the effects of geographical and climatic factors on the genetic structure, modeling using the distance-based redundancy analysis (dbRDA) with the randomization method was conducted for each species. The presence of IBD (isolation by geographical distance) and IBE (isolation by environmental distance) was tested using the “dbrda” function from the R package “vegan” [41]. To conduct the analysis, three datasets were necessary: (i) a genetic distance matrix between individuals, (ii) a geographical distance matrix between each individual reflecting their geographical position, and (iii) the environmental data of each individual.

Genetic distances were obtained by calculating Bruvo distances [42] between individuals with their microsatellite data using the “bruvo.dist” function from the R package “poppr” [43]. The geographical coordinates of each accession were used to obtain a geographical distance matrix between them using the “spDists” function from the R package “sp” [44]. This geographical distance matrix was then transformed into a continuous rectangular vector through PCA using the “pcnm” function in the R package “vegan” [41]. For the environmental data, the polar coordinates of the individuals derived from the PCA of the noncollinear variables analyzed for bioclimatic structuring were used.

Three types of dbRDA analyses were done: (i) a global analysis using the two variables (geographical and environmental), (ii) marginal analyses independently evaluating the relationship between the genetic distance matrix and each of the two explanatory variables (geographical or environmental factors), and (iii) a partial dbRDA estimating the relative contribution of one explanatory variable (geographical distance or environmental factors) to genetic differentiation, while controlling for the effect of the other variable. The “varpart” function from the R package “vegan” was used to partition the variance and to obtain the proportion of variance explained by the intersection of IBD and IBE. The adjusted coefficient of determination (R^2_{adj}) was calculated to evaluate the quality of the model. The higher the R^2 of a model, the more robust the model is. The contribution of a variable to a model was considered significant if the p-value was less than 0.05.

3. Results

3.1 Genetic structuring

With the microsatellite data from the 75 accessions of *V. perrieri*, the distribution of DeltaK and Ln P(X|K) values revealed a maximum value at K = 3, indicating that the accessions analyzed were distributed in three genetic clusters (**Figure 2A, C**).

The genetic structuration of the nine populations showed a geographical pattern: the populations assigned to the first cluster were located in the southern part, while most of the populations assigned to the second and third genetic clusters were located in the northwestern part of Madagascar (Figure 2A, C).

The analysis of the 192 *V. bosseri* accessions also showed maximum DeltaK and Ln P(X|K) values for K = 3 (Figure 2B, D). The distribution of the three genetic groups among the nine populations of this species revealed that the three genetic groups were present in the western populations, while the southern populations were mainly composed of two groups (Figure 2B, D).

3.2 Bioclimatic structuring

After checking for collinearity between the initial variables, six specific variables were retained for each species to study the bioclimatic structuration with PCA.

For *V. perrieri*, the first three dimensions of the PCA explained 74.8% of the total variance. PC1 (29.7%) was strongly determined by the variables BIO12 (Annual Precipitation) and BIO18 (Precipitation of Warmest Quarter), suggesting it represents a trend related to precipitation. PC2 (24.1%) was associated with the variables NDVI (Normalized Difference Vegetation Index) and BIO10 (Mean Temperature of Warmest Quarter). PC3 (21%) was dominated by two temperature variables: BIO2 (Mean Diurnal Range) and BIO8 (Mean Temperature of Wettest Quarter).

The distribution of the 75 accessions along the first two axes of the PCA showed a bioclimatic structuration of the nine populations analyzed (Figure 3A). PC1 separated the western sites (BFD, BTM, MMD, and AKF) from the south-west sites (AKLL, ATD, and MLT), revealing that the collection sites in the south-west region have lower precipitation than the others. The site B66 in the south-east was characterized by a low vegetation index (NDVI) and a high temperature on PC2 (Figure 3A).

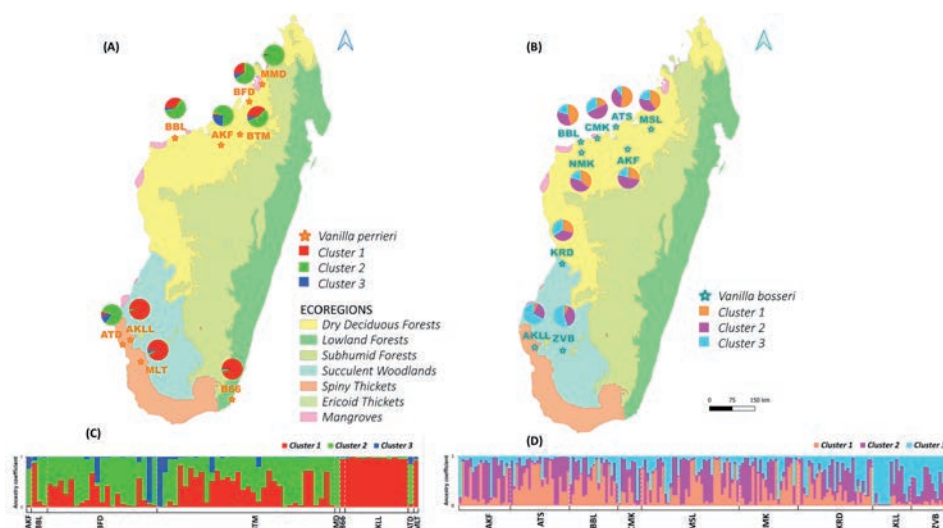


Figure 2. Geographical distribution of the three genetic groups in the nine populations of *V. perrieri* (A) and *V. bosseri* (B); the pie charts indicate the average values of the probability of a population belonging to the three genetic groups. Genetic assignment graph of individuals to the three genetic groups of *V. perrieri* (C) and *V. bosseri* (D): each individual is represented by a vertical bar divided into colored segments representing the probability of an individual belonging to the genetic group of that color.

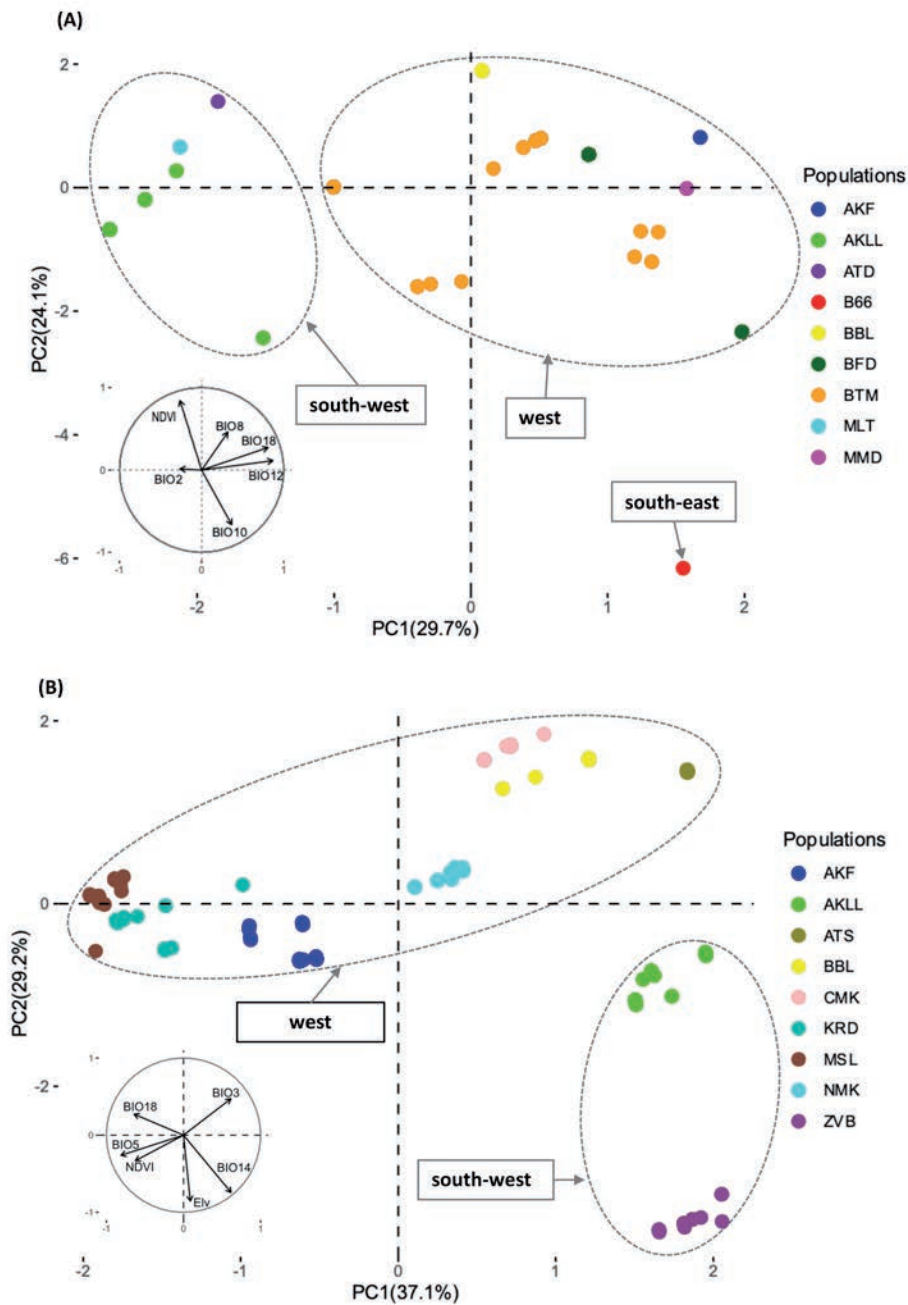


Figure 3. Distribution of the samples of *V. perrieri* (A) and *V. bosseri* (B) on the first two axes (PC1 and PC2) of the PCA of six noncollinear environmental variables. Variables are described in the text.

For *V. bosseri*, the first three dimensions of PCA explained 83.6% of the total variance of the data. PC1 explained 37.1% of the variation and was determined by BIO5 (Maximum Temperature of Warmest Month), BIO18 (Precipitation of Warmest Quarter), NDVI (Normalized Difference Vegetation Index) and BIO3 (Isothermality).

The variables Elevation and BIO14 (Precipitation of Driest Month) formed PC2 (29.2%). PC3 (17.2%) was associated with BIO18 (Precipitation of Warmest Quarter) and NDVI.

Regarding the western populations, the first axis of the PCA allowed for individualizing the sites MSL, AKF, and KRD, located inland, and corresponding to hot and humid areas with vegetation (BIO5, BIO18, and NDVI) (**Figure 3B**). On the other hand, the sites BBL, ATS, and CMK, located closer to the sea, were characterized by a pronounced Isothermality (BIO3). In the south-west zone, AKLL and ZVB were influenced by Precipitation of the Driest Month (BIO14), with AKLL characterized by Isothermality (BIO3) and ZVB distinguished by a higher Elevation (**Figure 3B**).

3.3 Isolation by distance and isolation by environment

The dbrDA analysis allowed the estimation of the amount of the genetic diversity (based on microsatellite data) that can be explained by uncorrelated climatic and geographic factors. The global model revealed an R^2_{adj} of 13.3% for the 75 *V. perrieri* accessions, compared to 7.6% for the 192 accessions of *V. bosseri*. In *V. perrieri*, environmental distance explained slightly more of the genetic structure than geographic distance (IBE: $R^2_{adj} = 11.5\%$; IBD: $R^2_{adj} = 10.2\%$), whereas in *V. bosseri*, the contributions of IBE and IBD were approximately the same (IBE: $R^2_{adj} = 5.2\%$; IBD: $R^2_{adj} = 5.4\%$) (**Table 2**).

Marginal tests indicated significant effects of both IBE and IBD on the genetic structure of the two species. In *V. perrieri*, variance partitioning showed a significant strict contribution of IBE ($R^2_{adj} = 3.1\%$) and a shared effect of IBE $\cap$ IBD accounting for 8.4% of the genetic differentiation (**Figure 4A**). However, the strict contribution of IBD ($R^2_{adj} = 1.8\%$) was not statistically significant ($p = 0.054$). For *V. bosseri*, after removing the shared IBE $\cap$ IBD effects (3.1%), the strict contributions of IBE ($R^2_{adj} = 2.2\%$) and IBD ($R^2_{adj} = 2.3\%$) remained significant in explaining the genetic differentiation of the 192 accessions (**Figure 4B**).

A variance analysis (ANOVA) was performed on the partial redundancy analysis of IBE to determine which environmental factor was mainly involved in the genetic structuration of the species. As a result, five bioclimatic variables (NDVI Normalized Difference Vegetation Index, BIO8 Mean Temperature of Wettest Quarter, BIO12 Annual Precipitation, BIO15 Precipitation Seasonality, and BIO18 Precipitation of Warmest Quarter) were significantly associated with the genetic variation of the

Models	<i>V. perrieri</i>			<i>V. bosseri</i>		
	F-statistic	P-value	R^2_{adj}	F-statistic	P-value	R^2_{adj}
BD ~ GD + ED	2.42	0.001***	0.133	2.31	0.001***	0.076
BD ~ GD	3.80	0.001***	0.102	2.83	0.001***	0.054
BD ~ ED	2.92	0.001***	0.115	2.77	0.001***	0.052
BD ~ GD/ED	1.48	0.054	0.018	1.78	0.001***	0.023
BD ~ ED/GD	1.50	0.029*	0.031	1.72	0.001***	0.022

P-value: * $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Table 2.

Results of modeling and variance partitioning with dbrDA of the effects of environmental distance (ED) and geographical distance (GD) on the Bruvo genetic distance (BD) of the 75 accessions of *V. perrieri* and 192 accessions of *V. bosseri*.

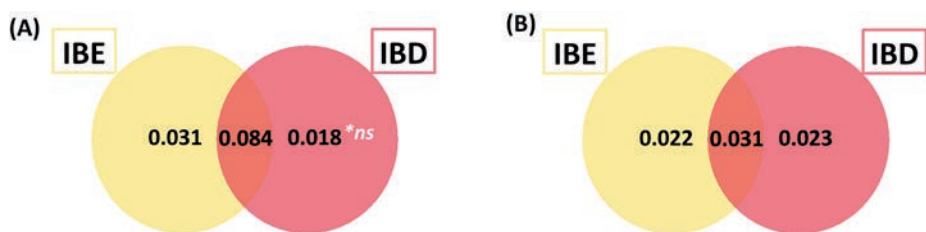


Figure 4. Variance partitioning of the effects of environmental distance (IBE) and geographic distance (IBD) on the genetic differentiation of the accessions of *V. perrieri* (A) and *V. bosseri* (B).

<i>V. perrieri</i>			<i>V. bosseri</i>		
Variables	F-statistic	P-value	Variables	F-statistic	P-value
NDVI	1.96	0.025 *	Elevation	3.16	0.001 ***
BIO2	1.48	0.156	NDVI	1.75	0.023 *
BIO8	3.73	0.001 ***	BIO3	1.14	0.287
BIO12	5.48	0.001 ***	BIO5	2.29	0.002 **
BIO15	2.19	0.014 *	BIO14	0.81	0.686
BIO18	1.81	0.035 *	BIO18	1.18	0.275

P-value: * $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. Variables are described in the text.

Table 3. Results of the ANOVA on the dbRDA model with the relative contributions of environmental variables to the genetic structuration of the two species.

accessions of *V. perrieri* and three bioclimatic variables (Elevation, NDVI Normalized Difference Vegetation Index, and BIO5 Max Temperature of Warmest Month) for *V. bosseri* (Table 3).

4. Discussion

4.1 Genetic structuring and IBD

The intraspecific genetic analysis of the *V. perrieri* and *V. bosseri* accessions showed that they were each represented by three genetic groups, revealing a genetic structuring based on geographical location (western versus southern populations).

The populations of *V. perrieri* from the north-west were more admixed, suggesting the existence of a higher genetic diversity in that region than in populations in the south. Andriamihaja et al. [22] suggested that *V. perrieri* had recently differentiated from *V. humblotii*, and the two species remain very similar morphologically. In Madagascar, *V. humblotii* is a species that is found only in the northern part of the island (Figure 1). *V. perrieri* spreads along the west coast, from north to south, toward much drier ecological niches [45, 46].

Similarly, *V. bosseri* populations showed more admixture in the north-west than in the south-west. *V. bosseri* is part of a phylogenetic group that includes *V. madagascariensis* [22], a species that is restricted to the north of the island (Figure 1). These two species are very similar morphologically, but *V. bosseri* is distinguished by the total

absence of hairs on the labellum. *V. bosseri* has a wider distribution, along the west coast to the south, and may have differentiated very recently from *V. madagascariensis*.

These results are concordant with the reported diversity decrease observed with successive stages of colonization, with populations at the limits of their range distribution area often characterized by a loss of diversity [47–52].

In addition to the genetic structuration of the two species matching their geographical location, the dbRDA analyses showed the existence of IBD with a global contribution of 10.2% for *V. perrieri* and 5.4% for *V. bosseri*. However, in the case of *V. perrieri*, this contribution was only significant in its combined component with IBE (IBE $\cap$ IBD) for 8.4%; the strict contribution of IBD was not significant. For *V. bosseri*, the strict contribution of IBD (2.3%) and IBE $\cap$ IBD (3.1%) was significant. The importance of the IBE $\cap$ IBD factor in both analyses was expected, given the longitudinal geographical pattern of the bioclimatic regions along the west coast of Madagascar, where accessions were sampled.

4.2 Bioclimatic structuring and IBE

The climatic data of the *V. perrieri* and *V. bosseri* accessions analyzed clearly showed a bioclimatic structuring of the collection sites for the two species, in accordance with their localization in various bioclimatic regions in Madagascar (**Figure 2**). The results indicated that both species exhibit a high tolerance to environmental variability (heat and humidity for the two species and thermal stability and altitude specifically for *V. bosseri*). Their occurrence across diverse microclimates, even within the same biogeographic region, highlights their ecological adaptability.

A difference in precipitation was revealed between sites from the northwestern and southern regions of *V. perrieri*. Indeed, the western coast of Madagascar is made up of contrasting ecoregions with an average annual rainfall of between 1000 and 1500 mm in the north and a maximum annual rainfall of 500 mm in the arid zones of the south [20, 53]. In addition, the dbRDA analysis showed the influence of bioclimatic factors (IBE) on the genetic structuring of *V. perrieri* with an overall contribution of 11.5%.

Bioclimatic structuring was observed in the nine *V. bosseri* collection sites based on their proximity to the sea. Among the western populations, inland sites (AKF, KRD, MSL) have a humid and warm climate during the hot season, as well as dense vegetation. Western coastal sites (BBL, CMK, ATS) are marked by less extreme temperature variations (high isothermality) due to the influence of the ocean, which acts as a natural temperature regulator [54, 55]. Conversely, inland areas experience higher temperature variations influenced by the geographical relief [56]. The two southwestern sites are characterized by higher precipitation during the driest month of the year. The gradient of isothermality from the inland to the coastal zones was also observed in the south-west areas. The coastal site AKLL has a more stable temperature, as expected [57, 58], compared to the inland site ZVB, located at a higher elevation. Isothermality may influence the water cycles and contribute to ecological divergences across landscapes [59]. Finally, the dbRDA analysis showed that bioclimatic factors contributed globally to 5.2% of the genetic variation in *V. bosseri*.

The variance partitioning allowed us to demonstrate that, even by controlling the effect of IBD, IBE still remained a significant factor in the genetic structuring of both *V. perrieri* and *V. bosseri* (3.1 and 2.2%, respectively). This strict and significant part of IBE therefore shows that the effect of the environment on the genetic structure of each species is important, even for individuals that are geographically close.

4.3 Prospects

This study showed that *V. perrieri* and *V. bosseri* were suitable model species for a future approach based on genomic scans and genome-environment association (GEA) to identify genomic regions involved in climate adaptation.

Genomic scans are methods applied to the entire genome to detect the genetic structuring expected following local divergent adaptation processes [60, 61]. By genotyping different populations, adapted to contrasting environments, using several thousand single-nucleotide polymorphism (SNP) molecular markers, it becomes possible to identify genomic regions that present selection signatures (such as differences in allele frequencies between environments or reduction in genetic diversity within the same environment). These regions, which potentially control traits under selection [62], correspond to so-called “outlier” loci that deviate from the neutrality hypothesis (detected using F_{ST} or PCA tests) [63, 64]. It is also possible to search for alleles specifically correlated with particular putative selective characteristics of the environment, i.e., genome-environment associations (GEA) with linear modeling [64–67].

A difficulty with this type of approach is that the effect of geography on environmental and genetic variation can confound the interpretation of tests [65], as local adaptation can be hampered by gene flow [68] and can be masked by the effects of genetic drift and demographic history [69]. Indeed, without corrections for the effect of population structure or isolation-by-distance (IBD), tests of associations between loci and environmental variables will be subject to high rates of false positives [61, 70, 71]. However, linear mixed models allow for the potentially confounding effects of demographic history to be controlled by including population structure as a covariate [66, 72]. In view of our results, we will therefore have to use these specific methods to control the effects of genetic structuring and IBD detected in our two species, particularly for *V. bosseri*.

Furthermore, to be suitable for a genome scan/GEA study, the populations studied must be located in environments characterized by contrasting bioclimatic conditions. We demonstrated that this was the case for the two species studied here.

Finally, the plant material studied should show IBE, i.e., a correlation between genetic and bioclimatic distances. The contribution levels of strict IBE revealed in the present intraspecific study (3.1 and 2.2%) are substantially the same as in the previous interspecific study (3.4%) of Andriamihaja et al. [24], suggesting that the sampling of *V. perrieri* and *V. bosseri* encompasses the majority of the genetic variation explained by the environment detected in leafless vanilla plants of Madagascar. Thus, the study of the genomic regions involved in bioclimatic adaptation at the intraspecific level in *V. perrieri* and *V. bosseri* appears entirely feasible. The significant values of R^2_{adj} found for the strict contribution of bioclimatic data to genetic structuring (IBE), although relatively low, appear high enough to develop future research on the genomic signatures of climate adaptation. Indeed, Du et al. [40], in a study of climate adaptation of *Quercus aquifolioides*, used microsatellite data of 587 individuals from 60 sites and found two ancestral populations with STRUCTURE and a strict IBE of 2.45% with dbrDA. With 381 SNPs, they were able to locate 12 candidate genes with the successful use of outlier F_{ST} -based and GEA analyses. Similarly, Pluess et al. [73] revealed a nonsignificant IBD and a marginally significant IBE of 4% on 79 genetically unstructured populations of *Fagus sylvatica*. With GEA analyses, they were able to locate 16 SNPs in 10 genes associated with 1 to 20 environmental variables (temperature and precipitation).

5. Conclusions

For each species, redundancy analyses demonstrated that environmental variations (temperature, precipitation, and vegetation index) contributed to the genetic structure of the populations. Such isolation-by-environment (IBE) indicates local adaptation in the populations of *V. perrieri* and *V. bosseri* and suggests that they represent appropriate model species for further identifying genomic signatures of climatic adaptation of vanilla plants, provided special care will be taken to use appropriate methods to correct for the genetic structuring and IBD confounding effects.

Therefore, SNP markers are now being developed using genotyping-by-sequencing (GBS) [74, 75] to perform genomic scans and GEA analyses in populations of these two species. Ultimately, the candidate loci identified will be useful for the selection of heat- and drought-tolerant vanilla (*V. planifolia*) cultivars.

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Conflict of interest

The authors declare no conflict of interest.

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Advances in Genetic Diversity – Recent Advances, Challenges, and Prospects presents a comprehensive exploration of the role of genetic variation as the foundation of biological resilience, agricultural innovation, and ecological sustainability. Bringing together contemporary research and region-specific case studies, this volume highlights how genetic diversity is central to addressing today's most urgent global challenges, climate change, food insecurity, and biodiversity loss. The book spans from foundational perspectives to applied studies, covering crop improvement programmes, domestication history, and the potential of wild genetic resources. It examines cutting-edge biotechnological interventions to enhance variability, while also showcasing the value of local landraces and lesser-studied species, such as wild rice and leafless vanilla, as models for adaptation. Key themes include:

- The critical role of genetic diversity in crop productivity and food security.
 - Conservation and utilization of wild genetic resources.
- Genomic and biotechnological tools shaping future breeding strategies.
 - Regional studies illustrating unique reservoirs of variability.
- Prospects and challenges in sustaining genetic resources for future generations.

This volume will be an essential reference for researchers, students, and professionals in genetics, agriculture, conservation biology, and biotechnology. It not only surveys recent advancements but also offers a roadmap for leveraging genetic diversity as a driver of resilience, innovation, and sustainable development.

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