



Review on Garlic (*Allium sativum* L.) Breeding Advances and Achievements Globally

Mulat Getaneh Melesse^{1,a,*}

¹Ethiopian Institute of Agricultural Research (EIAR), Fogera National Rice Research and Training Centre, Bahir-Dar, Ethiopia

*Corresponding author

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ABSTRACT

Garlic (*Allium sativum* L., $2n = 16$) is a globally significant edible bulb crop valued for its culinary, nutritional, and medicinal properties. However, its genetic improvement has been constrained by predominant vegetative propagation and widespread sterility, which limit sexual reproduction and narrow genetic base. Consequently, conventional breeding has achieved limited progress in yield, quality, and stress tolerance. This review summarizes global advances in garlic breeding, encompassing traditional approaches such as clonal selection, mutation breeding, and polyploidy induction, alongside modern biotechnological strategies including micropropagation, genetic transformation, and genomic tools. Biotechnological methods have been instrumental in generating genetic diversity through somaclonal variation, mutation induction, and tissue culture-based regeneration, leading to achievements in herbicide tolerance, pest and disease resistance, and the development of improved cultivars. Molecular markers and DNA fingerprinting techniques (RAPD, AFLP, SSR) have further enhanced germplasm characterization, phylogenetic analysis, identification of fertile genotypes, and resistance screening. A major breakthrough has been the discovery of fertile garlic lines and the fertility-restoring gene *AsaNRF1*, which opens opportunities for true seed-based breeding and hybrid development. Despite these advances, optimization of tissue culture and genetic transformation protocols remains essential to improve regeneration efficiency and facilitate genome editing. Future research should focus on expanding fertile germplasm, refining regeneration systems, and integrating genomic selection with phenomics to accelerate genetic gains and ensure sustainable garlic production worldwide.

^a getanehmulat@gmail.com

<https://orcid.org/0009-0009-7091-7192>



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Introduction

Background of Garlic

Garlic (*Allium sativum* L.) is a diploid ($2n = 16$) vegetatively propagated species belonging to the genus *Allium* in the family Amaryllidaceae (Kamenetsky and Rabinowitch, 2001). It has been cultivated for over 5,000 years and is believed to have originated in Central Asia, with secondary diversification in the Mediterranean and Caucasus regions (Vavilov, 1951; Ma, 2023). Archaeological and historical evidence indicates that garlic has been cultivated for more than 5,000 years, with its use documented in ancient civilizations including Egypt, Mesopotamia, India, and China. Today, garlic is grown worldwide, from temperate to tropical regions, and ranks as one of the most widely consumed and traded spices.

Garlic is highly valued for its culinary properties and medicinal benefits, largely due to organosulphur compounds such as allicin, S-allyl cysteine, and diallyl disulphide, which possess antioxidant, antimicrobial, and cardiovascular protective effects (Iciek et al., 2020).

Despite its importance, garlic improvement has been constrained by sterility and vegetative propagation, limiting recombination and genetic diversity (Sun, 2020; Pei, 2022). This has led to a reliance on clonal selection and biotechnological methods for improvement. However, recent advances in genomics and fertility restoration research are transforming garlic breeding, offering new opportunities for genetic improvement and sustainable production.

Garlic is valued globally for its culinary versatility, contributing flavour and aroma as a spice and seasoning in a wide range of dishes (Rana, 2022). Medicinally, garlic has long been used in traditional medicine, and modern pharmacological studies confirm its roles in reducing blood pressure, lowering cholesterol, and exhibiting antimicrobial, antioxidant, and anticancer properties, largely due to its bioactive sulphur compounds such as allicin and S-allyl cysteine (Iciek et al., 2020). Economically, garlic represents a high-value cash crop in

many countries, with global production exceeding 30 million metric tons annually (FAOSTAT, 2022). China is the world's leading producer, while countries such as India, Korea, Spain, and Ethiopia also cultivate garlic for local consumption and export markets (Volkov, 2022).

Despite its global importance, garlic improvement has been limited by its predominant asexual propagation, lack of fertile seeds, and large genome size (~16 Gb), which hinder conventional breeding approaches (Sun, 2020). However, recent advances in genomic tools, molecular markers, and cytogenetics have enabled significant progress in characterizing genetic diversity, identifying trait-associated genes, and developing improved varieties (Ma, 2023). The scope of garlic breeding now encompasses traits such as yield, bulb quality, bolting behavior, disease resistance, and stress tolerance, which are crucial for addressing challenges posed by climate change, pests, and evolving consumer demands. The application of molecular breeding, marker-assisted selection, and genome-wide association studies is expected to accelerate garlic improvement and broaden its genetic base (Pei, 2022). Thus, garlic breeding research holds significant promise for improving the productivity, nutritional value, and adaptability of this ancient yet modern crop.

Breeding Objective

Garlic breeding focuses on improving yield, quality, and stress tolerance. Yield improvement targets larger bulbs, increased clove number, and higher productivity per hectare. Quality enhancement emphasizes better storability, flavour, and nutritional value, particularly organosulphur compounds. Resistance breeding addresses major biotic stresses such as white rot, rust, and nematodes, as well as abiotic stresses including drought, salinity, and temperature extremes.

The main objective is fertility restoration to enable true seed-based breeding and hybrid development. Achieving these goals requires integrated strategies that combine clonal selection, mutation breeding, and modern biotechnological tools.

Review Materials and Methods

This review was conducted through a systematic analysis of published literature on garlic breeding and genetic improvement. Sources included peer-reviewed journal articles, academic books, and relevant electronic resources.

The literature was selected to ensure comprehensive coverage of key thematic areas, including genetic diversity, reproductive biology, conventional breeding methods, fertility restoration, and biotechnological advancements. Emphasis was placed on recent global developments to provide up-to-date insights into genomic tools and breeding innovations.

The review was organized into structured section's introduction, objectives, major literature themes, synthesis of findings, and references to present a clear and coherent overview of global advances and achievements in garlic breeding.

Review

Origin and Genetic Diversity of Garlic

Garlic (*Allium sativum* L.) is one of the oldest cultivated crops, valued worldwide for its culinary, medicinal, and economic importance. The primary center of origin of garlic is widely recognized as Central Asia, particularly the Tien Shan, Pamir, and Kopet Dag mountain ranges, where wild and early cultivated forms are believed to have emerged (Vavilov, 1951; Kazakova, 1981). The Mediterranean basin and the Caucasus are considered secondary centers of diversity, reflecting ancient domestication processes, trade routes, and subsequent diversification (Ma, 2023). Recent genomic studies further support Central Asia as the primary genetic source of garlic, while Mediterranean germplasm exhibits admixture patterns consistent with secondary diversification during historical dispersal (Ma, 2023; Volkov, 2022).

The closest wild relative of cultivated garlic has traditionally been identified as *Allium longicuspis* Regel. However, morphological, cytogenetic, and molecular analyses indicate that *Allium longicuspis* is not consistently distinct from *Allium sativum*, often clustering within cultivated lineages (Ma, 2023; Fritsch and Friesen, 2002). This evidence suggests that *Allium longicuspis* may represent a feral or ancestral form rather than a true wild progenitor (Kamenetsky and Rabinowitch, 2001). Extensive germplasm collections, including 606 accessions from 43 countries characterized by Ma (2023), now provide valuable genetic resources for breeding, conservation, and diversity studies.

At the molecular and cytogenetic levels, garlic is a diploid species ($2n = 16$) with an exceptionally large genome estimated at approximately 16.2–16.9 Gb, of which about 91% consists of repetitive DNA (Sun, 2020; Pei, 2022). The development of a chromosome-level genome assembly has significantly advanced genome-wide diversity analysis, trait mapping, and comparative genomics (Sun, 2020). Population genomic studies based on resequencing and genotyping-by-sequencing have identified distinct subpopulations associated with important agronomic traits such as bolting behavior, bulb yield, and stress tolerance (Ma, 2023; Pei, 2022).

Despite garlic's predominant clonal propagation, molecular marker systems such as SSRs and EST-SSRs reveal moderate levels of polymorphism, with average polymorphism information content (PIC) values of approximately 0.36 (Zhao, 2019). These markers remain valuable tools for germplasm fingerprinting and genetic diversity assessment. Cytogenetic studies consistently report a uniform karyotype ($2n = 16$; six metacentric and two submetacentric chromosome pairs), but variation in heterochromatin distribution (CMA⁺/DAPI⁻ bands) and the number of secondary constrictions distinguishes different accessions (Souza, 2021; Ochoa, 2025).

Overall, garlic genetic diversity reflects the combined effects of domestication bottlenecks and subsequent clonal diversification. Advances in cytogenetics and modern genomics have uncovered substantial allelic variation within global germplasm collections, providing a strong foundation for breeding programmes and long-term conservation strategies.

Reproductive Biology and Breeding Challenges

Sexual and Asexual Reproduction

Garlic is predominantly propagated asexually through vegetative planting of cloves and bulbils. This mode of reproduction ensures high genetic uniformity and stable varietal characteristics; however, it significantly narrows the genetic base and limits meiotic recombination (Kamenetsky, 2021). As a result, genetic improvement through conventional hybridization has historically been constrained.

Although garlic has long been considered a strictly sterile crop, recent breakthroughs have demonstrated that sexual reproduction is possible under controlled conditions. Certain fertile accessions are capable of producing viable pollen and true seeds, challenging the traditional assumption of complete sterility (Shemesh, 2015; Ma, 2023). These findings create new opportunities for true seed-based breeding, which could broaden genetic diversity, facilitate recombination, and enable hybrid development. Nevertheless, natural seed set remains rare and requires carefully optimized environmental conditions, including appropriate photoperiod, temperature regimes, and hormonal treatments (Duangjit, 2020).

Despite these advances, sterility remains widespread in most cultivated garlic. Reproductive failure is commonly associated with male sterility, anther degeneration, and pollen inviability (Shemesh, 2013). Cytoplasmic male sterility (CMS) has been identified as a major factor contributing to low pollen fertility, while fertility restoration is complicated by complex genetic control and the limited availability of fertile germplasm (Jenderek and Hannan, 2021). These constraints continue to limit large-scale sexual breeding efforts.

Based on reproductive behavior and morphological characteristics, garlic cultivars are broadly classified into hard-neck (bolting) and soft-neck (non-bolting) types. Hard-neck types produce a flowering scape and bulbils and may set seeds under favorable conditions, making them particularly important for breeding research. In contrast, soft-neck types rarely bolt, are better adapted to mild climates, and are preferred commercially due to their longer storage life (Kamenetsky, 2015; Huang, 2021). These differences in reproductive biology and adaptation significantly influence breeding strategies, varietal improvement, and resilience to climate change.

Sterility and Fertility Issues

Sterility in garlic has long hindered conventional breeding. The main barriers include male sterility, pollen in viability, and degeneration of ovules (Kamenetsky and Rabinowitch, 2001). Cytoplasmic male sterility (CMS), associated with mitochondrial genome rearrangements, has been identified as a major cause of low pollen fertility (Shemesh, 2013). While several fertile genotypes have been identified in Central Asian germplasm, they remain under-represented in global breeding programmes (Jenderek and Hannan, 2021). Recent genomic studies have started to unravel candidate fertility-restorer genes, but stable fertility restoration in breeding populations is still a challenge (Ma, 2023).

Hard-neck versus Soft-neck Flowering Types

Garlic cultivars are traditionally grouped into two broad categories based on their reproductive behavior: hard-neck (bolting) types and soft-neck (non-bolting) types. Hard-neck

garlic produces a flowering scape and is more likely to set bulbils and, in rare cases, flowers and seeds (Kamenetsky, 2015). Soft-neck garlic, on the other hand, is typically non-bolting, adapted to milder climates, and favored for its storability and higher clove number (Volkov, 2022). The presence or absence of scape development is controlled by genetic and environmental interactions, with bolting types generally found in temperate and continental climates, while non-bolting types dominate in subtropical and Mediterranean regions (Huang, 2021). This classification has important implications for both breeding strategies and adaptation to climate change.

Chromosome Number and Cytogenetics

Garlic is a diploid species ($2n = 16$) with one of the largest known plant genomes, estimated at ~16.2–16.9 Gb, of which ~91% consists of repetitive elements (Sun, 2020; Pei, 2022). Cytogenetic studies confirm a uniform karyotype (6 metacentric + 2 submetacentric pairs), but significant heterochromatin polymorphism has been observed among cultivars, reflecting clonal diversification (Souza, 2021; Ochoa, 2025). Fluorescence in situ hybridization (FISH) and CMA/DAPI banding techniques have revealed variation in secondary constrictions and satellite regions, which may relate to partial fertility differences among accessions (Ochoa, 2025). This cytogenetic knowledge, combined with genomic resources, provides critical insights for overcoming sterility and advancing molecular-assisted breeding.

Conventional Breeding Approaches

Clonal Selection

Garlic is primarily propagated vegetatively through cloves and bulbils, and clonal selection has historically been the dominant breeding approach. Farmers and breeders select superior plants from landraces or introduced germplasm based on desirable traits such as bulb yield, clove size, storability, flavour, and disease resistance (Hannan and Jenderek, 2020). Over time, this continuous selection has resulted in the development of numerous locally adapted cultivars suited to specific agroecological conditions (Volkov, 2022).

While clonal selection is effective for maintaining varietal uniformity and achieving incremental, short-term improvements, it preserves the narrow genetic base inherent in vegetative propagation. Because it does not involve recombination, clonal selection cannot overcome the sterility barrier or generate substantial new genetic variation. Consequently, its potential for broad and long-term genetic progress remains limited.

To address these constraints, clonal selection is increasingly complemented by approaches aimed at expanding genetic variability, including mutation induction, exploitation of somaclonal variation, and the application of biotechnological tools. These strategies provide alternative pathways for generating novel variation in a crop where conventional hybridization has historically been restricted.

Mutation Breeding

Mutation induction has emerged as an important strategy for generating new genetic variability in clonally propagated garlic. Both physical mutagens, such as gamma irradiation and X-rays, and chemical mutagens, including ethyl methanesulfonate (EMS) and colchicine, have been

applied to induce heritable variation within existing germplasm. These treatments create random genetic changes that can be selected for desirable agronomic traits.

Several studies have reported the development of garlic mutants with altered clove number, increased bulb size, early maturity, and improved disease tolerance (Ghafoor, 2021). Such induced variability is particularly valuable in crops like garlic, where limited sexual reproduction restricts natural recombination and genetic diversification.

Mutation breeding therefore provides an effective alternative approach for broadening the genetic base, and selected mutants may serve either as improved cultivars for direct cultivation or as potential parental clones in advanced breeding programmes.

Polyploidy Induction

Polyploidization, particularly tetraploid induction, has been investigated in garlic as a strategy to enhance vigor and expand genetic variability. Chromosome doubling has been successfully achieved using antimitotic agents such as colchicine and oryzalin, which disrupt spindle formation during cell division and lead to polyploid development.

Induced polyploid plants frequently exhibit desirable morphological changes, including increased bulb size, thicker leaves, enhanced vegetative vigor, and modifications in fertility-related traits (Hirakawa, 2021). Such characteristics may contribute to improved yield potential and stress tolerance.

Although polyploid garlic lines remain largely experimental, they represent a promising avenue for overcoming reproductive constraints and introducing novel variation into breeding programmes. When combined with other genetic improvement strategies, polyploidization may contribute to broadening the narrow genetic base characteristic of clonally propagated garlic.

Selection for Yield, Quality, and Stress Tolerance

Conventional selection efforts in garlic have focused on improving key agronomic and quality traits, including bulb yield, clove uniformity, storability, and flavor-related compounds (Block, 2010; Hannan and Jenderek, 2020). In parallel, breeding programmes prioritize tolerance to major biotic stresses such as white rot caused by *Sclerotium cepivorum*, rust (*Puccinia allii*), and plant-parasitic nematodes, which significantly reduce productivity in many garlic-growing regions (Rana, 2022). Adaptation to abiotic stresses including drought, salinity, and temperature extremes has also become increasingly important in the context of climate variability and expanding cultivation zones.

Despite these objectives, conventional breeding in garlic remains constrained by sterility and limited genetic recombination due to predominant vegetative propagation. As a result, genetic progress is often gradual. However, the integration of clonal selection with complementary approaches such as mutation induction and polyploidization offers practical avenues for incremental improvement. Together, these strategies help expand phenotypic variability and enhance adaptation while more reliable sexual breeding systems continue to be developed.

Biotechnological Advances in Garlic Breeding

Micropropagation and Tissue Culture

Micropropagation plays a central role in garlic improvement by enabling rapid clonal multiplication and

the production of high-quality, disease-free planting material. Because garlic is propagated vegetatively, viral pathogens accumulate over successive generations, leading to progressive yield decline and reduced bulb quality. Major viruses affecting garlic include Onion yellow dwarf virus (OYDV), Garlic common latent virus (GCLV), and Shallot latent virus (SLV), all of which significantly impair plant vigor and productivity.

Meristem culture, often combined with thermotherapy and chemotherapy, has proven highly effective in virus elimination. Studies report complete (100%) eradication of SLV and GCLV, and up to 100% efficiency for OYDV depending on genotype and treatment conditions (Gawande, 2023; Lulak, 2023). The use of very small meristems enhances virus elimination efficiency, although regeneration rates may decline. Cryotherapy of shoot tips has also been explored as an advanced technique to improve virus eradication while preserving valuable germplasm (Kumari, 2021).

Beyond sanitation, tissue culture systems based on organogenesis and somatic embryogenesis have been optimized for large-scale propagation and in vitro conservation of garlic germplasm (Rajesh, 2024). These biotechnological tools not only ensure the distribution of virus-free planting material but also support breeding programmes, germplasm exchange, and long-term conservation strategies.

Somaclonal Variation

Somaclonal variation, which arises during in vitro culture, represents both a challenge and an opportunity in garlic improvement. Genetic and epigenetic changes occurring during tissue culture can generate undesirable mutations that compromise clonal uniformity. However, this same phenomenon can also produce novel and potentially valuable variation. In garlic, somaclonal variants have been reported with altered bulb morphology, improved vigor, and enhanced stress tolerance, demonstrating its potential as a supplementary source of variability in a predominantly clonally propagated crop (Kumar, 2023).

Maintaining genetic fidelity is therefore a critical objective in micropropagation systems. Molecular marker analyses using AFLP, ISSR, and SSR techniques have confirmed that carefully optimized protocols can produce true-to-type regenerants with high genetic stability (Singh, 2022). At the same time, identified somaclonal variants can be selectively evaluated and incorporated into breeding programmes as an additional source of variation. Thus, when properly managed, somaclonal variation serves as both a quality-control concern and a complementary tool for garlic genetic improvement.

Genetic Transformation and Genome Editing

Garlic has long been regarded as recalcitrant to genetic transformation, largely due to difficulties in establishing efficient and genotype-independent regeneration systems. The species' strong dependence on vegetative propagation and its limited embryogenic response in tissue culture have constrained the development of stable transformation platforms.

Despite these challenges, both *Agrobacterium*-mediated transformation and particle bombardment (biolistic) approaches have been applied successfully in experimental systems. These methods have enabled the

introduction of antifungal genes such as chitinase and β -glucanase, resulting in enhanced tolerance to fungal pathogens (Lee, 2019). Such studies demonstrate the feasibility of genetic engineering in garlic, although transformation efficiency and reproducibility remain limiting factors.

Genome editing technologies, particularly CRISPR/Cas's systems, hold considerable promise for precise trait improvement. However, their application in garlic is still at the proof-of-concept stage, primarily due to the lack of robust, genotype-independent regeneration and transformation protocols. In related *Allium* crops, such as onion (e.g., targeting the *AcPDS* gene), successful gene editing has been demonstrated, highlighting the potential for similar approaches in garlic once technical barriers are overcome (Zhang, 2023).

Importantly, the availability of a chromosome-level genome assembly (~16.2 Gb) has provided a critical foundation for candidate gene identification, functional genomics, and future genome editing applications (Sun et al., 2020; Pei, 2022). As regeneration systems improve, the integration of transformation and genome editing technologies is expected to play an increasingly important role in garlic breeding and genetic improvement.

Molecular Markers

Molecular markers have played a crucial role in garlic research, particularly in assessing genetic diversity, identifying duplicates within germplasm collections, and developing reliable cultivar fingerprints. Early marker systems such as RAPD and AFLP were widely used to detect clonal variation and assess relationships among accessions. Although effective, these markers often showed limitations in reproducibility and cross-study comparability.

The development of simple sequence repeat (SSR) markers represented a significant advancement due to their higher reproducibility, codominant inheritance, and greater informativeness. Recent SSR panels developed for garlic have demonstrated moderate levels of polymorphism, with polymorphism information content (PIC) values averaging approximately 0.36, confirming their suitability for diversity assessment and germplasm characterization despite the crop's predominant clonal propagation (Zhao, 2019).

The availability of a chromosome-level garlic genome has further accelerated molecular breeding efforts by enabling the discovery of high-density single nucleotide polymorphisms (SNPs). These markers are increasingly applied in population genomics, genome-wide association studies (GWAS), and marker-assisted selection, allowing the identification of loci associated with key agronomic traits (Ma, 2023).

With the ongoing transition from low-throughput marker systems to high-throughput genotyping platforms, SNP-based tools are expected to substantially enhance breeding efficiency, improve germplasm management, and accelerate genetic improvement in garlic.

Achievements in Garlic Breeding

Recent advances in garlic (*Allium sativum* L.) breeding have led to the development of high-yielding cultivars with improved resistance to diseases and pests, as well as progress in herbicide tolerance, fertility restoration, and hybrid development. In Ethiopia, Tadesse et al. (2024)

evaluated 13 garlic genotypes across multiple environments and identified two promising lines, G-020/03 and G-054/03, which outperformed the check cultivar Kuriftu by 25.39% and 18.39%, respectively, while demonstrating stable yields across diverse agroecological conditions. Similarly, in Italy, Caruso et al. (2024) assessed 69 garlic families and reported top-performing families achieving yields of up to 19.8 t/ha, substantially exceeding average commercial yields. These results highlight the value of both genotype selection and family-based breeding approaches in enhancing productivity.

Disease resistance remains a major breeding objective. Wendin et al. (2024) screened garlic cultivars for resistance to key fungal pathogens, including *Stromatinia cepivora* (white rot) and *Fusarium proliferatum*. Cultivar 'Elephant' exhibited complete resistance to both pathogens, while cultivars such as 'Sabagold' and 'Topadrome' showed moderate to partial resistance. Complementary molecular studies identified a resistance gene analogue, AsRGA29, in the resistant line CBT-As153. This NBS-LRR family gene was significantly upregulated during *Fusarium* infection and stress, making it a strong candidate for marker-assisted selection (Zhang et al., 2024).

Pest resistance in garlic has been associated with sulphur-containing compounds. Zhou et al. (2017) found that Chinese cultivars Qixian and Cangshan exhibited high resistance to the root maggot (*Bradysia odoriphaga*), linked to increased thiosulfinate content, which reduced larval survival and prolonged development. Similarly, Wang et al. (2019) reported that clones with higher allicin content showed enhanced resistance to onion maggot (*Delia antiqua*), reinforcing the role of sulphur metabolites in pest defense.

Herbicide tolerance and insect resistance have also been explored through biotechnological approaches. Mughal et al. (2023) reviewed the development of the first transgenic garlic lines via *Agrobacterium*-mediated and biolistic transformation, which exhibited resistance to both herbicides and insect pests such as the beet armyworm, demonstrating the potential of genetic engineering in garlic improvement.

A major breakthrough in garlic breeding has been the restoration of male fertility, historically absent in most commercial cultivars. Li et al. (2024) identified the transcription factor AsaNRF1 in the fertile line G398, which regulates callose degradation during microsporogenesis and enables viable pollen production. Molecular markers linked to AsaNRF1 allow clear distinction between fertile and sterile lines, paving the way for true seed-based hybrid breeding. Supporting this, Sun (2023) published a chromosome-level genome assembly and transcriptomic resources, providing foundational tools for modern garlic breeding programmes.

Kamenetsky (2024) summarized the current landscape of garlic improvement, highlighting three integrated strategies: vegetative propagation, true seed-based hybrid breeding using fertile lines, and molecular biotechnology approaches, including genome editing and transformation. Collectively, these developments illustrate significant progress in combining conventional selection with advanced biotechnological and genomic tools to achieve higher productivity, enhanced stress resistance, and broader genetic improvement in garlic.

Table 1. Major breeding objectives, methods, and achievements

Objective	Method	Key Achievements
Yield improvement	Clonal selection, mutation breeding	High-yielding lines (Tadesse et al., 2024; Caruso et al., 2024)
Disease resistance	Clonal selection, transformation	Resistant cultivars (Wendin et al., 2024; Zhang et al., 2024)
Pest resistance	Selection based on compounds	Resistance linked to allicin/thiosulphinate (Zhou et al., 2017; Wang et al., 2019)
Fertility restoration	Molecular genetics	AsaNRF1 gene discovery (Li et al., 2024; Liu et al., 2024)
Virus-free propagation	Meristem culture	Efficient virus elimination (Gawande, 2023; Lulak, 2023)

Garlic Nutritional and Phytochemical Improvement

Enhancing Organosulfur Compounds

Garlic (*Allium sativum*) is rich in organosulfur compounds (OSCs), which are primarily responsible for its therapeutic effects. Allicin, alliin, diallyl disulphide (DADS), diallyl trisulfide (DATS), and S-allyl cysteine (SAC) are key OSCs found in garlic. These compounds are released or enhanced through mechanical disruption or processing such as ageing and fermentation. Among these, allicin is the most abundant and bioactive, although it is highly unstable and quickly converts into other beneficial sulphur compounds (Ahmad et al., 2019).

Aged garlic extract (AGE) and black garlic are processed forms known to increase the stability and bioavailability of organosulfur compounds (OSCs). AGE is particularly rich in SAC and shows higher antioxidant and anti-inflammatory activity. Black garlic contains up to six times more SAC than raw garlic, and its longer processing enhances antioxidant potential due to higher total polyphenol and flavonoid content (Zhang, 2023). These forms have been shown to be more effective in cardiovascular protection, immunomodulation, and gut microbiota regulation (Muasa et al., 2019).

Furthermore, the enhancement of OSCs through biotechnological methods, such as elicitor application during cultivation or gene expression studies targeting the alliinase pathway, is a growing area of interest (Halder et al., 2019).

Improving Minerals, Vitamins, and Other Bioactive Compounds

Garlic also serves as a good source of micronutrients, including selenium, zinc, iron, manganese, calcium, magnesium, and phosphorus, along with vitamins C, B1 (thiamine), B6 (pyridoxine), and B9 (folate) (Polyakov et al., 2020). The composition varies significantly with soil conditions, cultivar type, and processing method.

Biofortification and organic cultivation practices have been shown to enhance these nutritional properties. For example, selenium-enriched garlic exhibits both higher selenium content and greater antioxidant capacity. The mineral content can also be improved through foliar application of micronutrients or by using mineral-rich substrates during cultivation (Diretto et al., 2017).

Garlic is also rich in phenolic acids (gallic acid, caffeic acid), flavonoids (quercetin, kaempferol), saponins, and polysaccharides, which provide antioxidant, anti-inflammatory, and antidiabetic effects (Lanzotti, 2006). Purple garlic cultivars, in particular, show significantly higher levels of saponins and phenolic compounds than white garlic varieties (Diretto et al., 2017). Ageing processes such as fermentation can enhance these bioactive

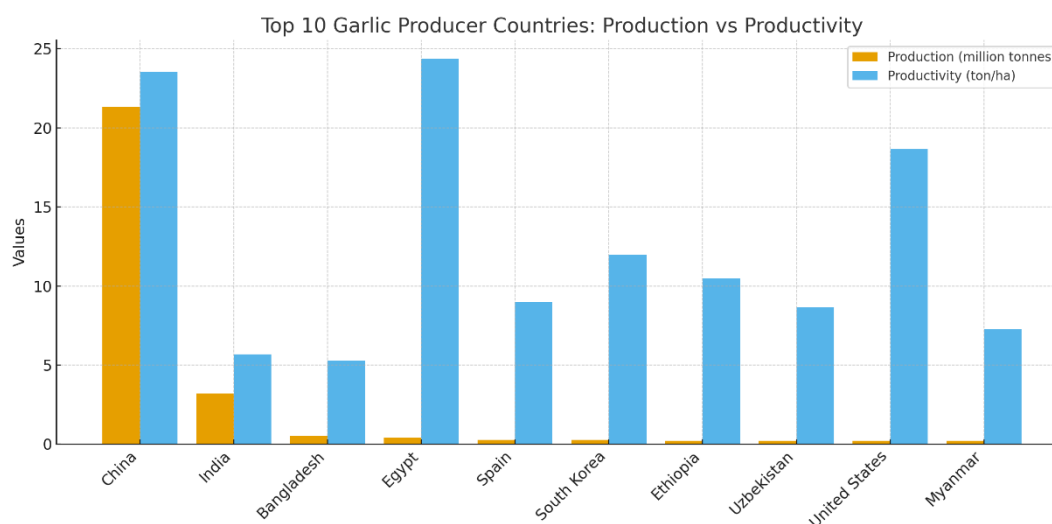
profiles, making the compounds more bioavailable and potent (Zhang, 2023).

Global Production, Adaptation, and Cultivar Development

Globally, garlic (*Allium sativum* L.) production is overwhelmingly dominated by Asia, with China alone contributing approximately 73–80% of total output, exceeding 21 million tonnes annually, establishing it as the undisputed leader in garlic cultivation (Mordor Intelligence, 2025). Other notable producers include India and Bangladesh, although their contributions are comparatively modest. The Asia-Pacific region not only leads in production volume but also in varietal innovation, developing high-yielding cultivars tailored to local agroecologies. In contrast, Africa is an emerging garlic-producing region, with initiatives in Kenya, Egypt, and South Africa aiming to expand production, reduce import dependence, and enhance local food security.

Garlic's adaptability to diverse climates underpins its global cultivation. It thrives in loose, well-drained soils rich in organic matter, prefers full sunlight, and grows optimally in USDA hardiness zones 4–9. Temperature and photoperiod sensitivity are critical: hard-neck varieties require vernalisation and are better suited to cooler, temperate climates, whereas soft-neck types adapt well to milder regions and are valued for their longer shelf life and lower chilling requirements (dmcoffee.blog, 2025; Kamenetsky, 2015). Optimal growth occurs at temperatures between 10 and 21°C and soil pH of 6.0–7.0. Some cultivars demonstrate remarkable resilience, such as the Himalayan "Snow Mountain garlic," capable of surviving sub-zero temperatures, and Ethiopian varieties like Tsedey 92, which exhibit strong adaptation to highland agroecologies with advantages in yield and disease tolerance (Jafar et al., 2021).

Commercially, garlic cultivars are classified into hard-neck (*Allium sativum* var. *ophioscorodon*) and soft-neck (*Allium sativum* var. *sativum*) types, each with distinct morphological and agronomic traits. Soft-neck varieties dominate global production due to their longer shelf life, adaptability to diverse growing conditions, and suitability for large-scale mechanical harvesting. They are particularly prominent in China, which leads global garlic production and export (FAOSTAT, 2023; Kamenetsky and Rabinowitch, 2006). Hard-neck garlic, although less widely produced, is valued for its stronger flavor, larger cloves, and higher concentrations of sulfur-containing compounds such as allicin. It is generally better adapted to cooler climates and is favored in specialty and gourmet markets (Volk and Stern, 2009; Brewster, 2008).



Source: (FAOSTAT. (2023))

A rich diversity of regional and heritage cultivars exists worldwide, reflecting both flavor and storage preferences. For example, Italy's Aglio Rosso di Nubia is known for its intense allicin content and distinctive red hue, while Red Sulmona Garlic enjoys protected status in Abruzzo. Globally, cultivars include Porcelain types (e.g., Georgian Fire, German Extra Hardy), Purple Stripe types (e.g., Chesnok Red), Asiatic, Creole, and other region-specific varieties, each with unique characteristics related to growth habit, storage life, flavor, and stress adaptation (Volkov, 2022).

In summary, garlic production is concentrated in Asia but is expanding globally, with cultivar selection, climate adaptation, and market preferences shaping production patterns. Hard-neck and soft-neck types provide complementary options for different agroecologies, while global and regional cultivar diversity supports both culinary value and breeding programmes.

Challenges and Future Prospects

Garlic faces multiple biological and agronomic challenges that significantly constrain its genetic improvement and long-term sustainability. A primary limitation is its restricted sexual propagation. Most commercial cultivars of *Allium sativum* L. are sterile and are propagated vegetatively through cloves, which severely limits opportunities for controlled hybridization and genetic recombination. As a result, conventional breeding efforts remain constrained, slowing the development of improved cultivars (Shemesh, 2015; Liu et al., 2024).

Vegetative propagation also contributes to progressive pathogen accumulation, particularly viral infections, across successive generations. This leads to yield decline, bulb quality deterioration, and increased production costs. Although techniques such as meristem culture, thermotherapy, and cryotherapy have been developed to eliminate viruses, they require specialized infrastructure and technical expertise, making them costly and less accessible for routine large-scale use (Turner, 2023; Shemesh, 2015).

Another major challenge is the narrow genetic base of cultivated garlic. Centuries of clonal selection, coupled with limited introduction of new genetic material, have resulted in low heterozygosity and restricted genetic variability. This genetic bottleneck reduces adaptive potential and limits breeding progress (Yang et al., 2024; Arizaga et al.,

2017). Population structure analyses using high-throughput genotyping platforms such as SLAF-seq and DArTseq have demonstrated tight clustering and limited genetic differentiation among global garlic accessions, further confirming the narrow genetic background of the crop (Yang et al., 2024; Arizaga et al., 2017).

Despite these constraints, advances in molecular genetics and genomics offer promising opportunities for garlic improvement. The identification of the fertility-restoring gene *AsaNRF1* and the development of its associated molecular marker (*AsaNRF1-M281*) represent a significant milestone toward restoring fertility and enabling true seed-based breeding in garlic (Liu et al., 2024). Moreover, transcriptomic and proteomic studies have identified candidate genes associated with fertility (e.g., *MS2*, *GPAT2*, and *MMD1*) and sterility (e.g., *nad7* and *18S rRNA*), providing valuable targets for marker-assisted selection and functional genomics studies (Shemesh, 2015).

To achieve sustainable garlic production, integrated strategies that combine genetic improvement with sound agronomic management are essential. Agronomic practices such as crop rotation, cover cropping, organic matter enrichment, reduced tillage, and efficient irrigation systems can enhance soil health, water-use efficiency, and disease suppression. When combined with emerging technologies including precision agriculture tools, sensor-based irrigation scheduling, and advanced phenotyping systems these practices can optimize resource use and reduce environmental impact.

In summary, garlic breeding continues to face critical challenges, including sterility, narrow genetic diversity, and pathogen accumulation associated with vegetative propagation (Yang et al., 2024; Arizaga et al., 2017). However, the discovery of fertility-restoring genes such as *AsaNRF1* provides a realistic pathway toward seed-based breeding systems (Liu et al., 2024). Future research should prioritize the expansion of fertile germplasm, refinement of regeneration and transformation protocols for genome editing, and integration of genomic selection with high-throughput phenotyping. Strengthened international collaboration and germplasm exchange will be essential to broaden the genetic base and develop climate-resilient, high-performing garlic cultivars.

Conclusion

Garlic is a globally significant, high-value crop widely recognized for its culinary, medicinal, and economic importance. Originating from Central Asia, garlic has undergone extensive domestication and long-term clonal propagation, resulting in numerous cultivars adapted to diverse agroecological conditions. Despite its global demand and wide cultivation, genetic improvement of garlic has been constrained by its predominant sterility, dependence on vegetative propagation through cloves, and exceptionally large genome (approximately 16–17 Gb), all of which limit genetic recombination and conventional breeding progress.

Traditional garlic improvement has relied primarily on clonal selection, mutation induction, and polyploidy to generate variation and enhance yield, bulb quality, stress tolerance, and adaptability. While these methods have produced useful variability, their impact remains limited because of the narrow genetic base and the plant's reduced ability to reproduce sexually. The absence of regular seed production restricts hybridization and recombination, slowing long-term genetic gain.

Recent advances in molecular biology and genomics have opened new opportunities for garlic breeding. The identification of fertile genotypes and fertility-restoring genes has made it possible to reintroduce sexual reproduction under controlled conditions. This development represents a major milestone toward true seed-based hybrid breeding. Modern breeding tools such as marker-assisted selection, genomic selection, and genome editing hold significant promise for accelerating trait improvement, although efficient and stable transformation and regeneration systems are still under refinement.

Notable achievements in garlic improvement include the development of high-yielding and disease-resistant cultivars suited to different agroecological regions. Screening programs have identified genotypes with tolerance to key pests and pathogens, while advancements in virus-free micropropagation, meristem culture, and cryotherapy have enhanced planting material quality and germplasm conservation. These technologies have significantly reduced pathogen accumulation associated with long-term clonal propagation.

In addition to agronomic traits, efforts have focused on improving garlic's nutritional and phytochemical properties. Garlic is valued for its organosulfur compounds, such as allicin and S-allyl cysteine, which contribute to its recognized health benefits. Processing methods, including the production of aged and black garlic, as well as the use of elicitors and improved agronomic practices, have been explored to enhance bioactive compound content. Biofortification strategies and organic production systems further strengthen garlic's role as a functional food.

Globally, garlic production is concentrated in Asia, particularly in China, though cultivation continues to expand in Africa, Europe, and the Americas. Breeding programs increasingly aim to match climatic adaptation with market preferences, focusing on bulb morphology, clove arrangement, flavor intensity, storability, and the distinction between hard neck and soft neck types.

Despite substantial progress, major challenges remain. Genetic bottlenecks, low natural fertility, and virus accumulation in clonally propagated lines continue to limit breeding efficiency. Addressing these issues requires integrated strategies that combine advanced molecular techniques, sustainable agronomic practices, and international collaboration for germplasm exchange and conservation.

Overall, garlic breeding has evolved from traditional clonal selection toward modern genomic and biotechnological approaches. The emergence of fertile lines and fertility-restoring mechanisms presents transformative opportunities for seed-based breeding systems. Future research should prioritize expanding fertile germplasm, improving regeneration systems for genome editing, applying genomic selection, and strengthening global germplasm networks. These coordinated efforts will accelerate genetic improvement and support sustainable garlic production under changing climatic conditions.

Final Outlook

The future of garlic breeding lies in harnessing sexual reproduction, expanding the genetic base, and utilizing cutting-edge genomic tools. While conventional methods still hold value for local adaptation and incremental improvement, the path forward must prioritise biotechnological innovation, climate resilience, and nutritional enhancement. By integrating genetics, agronomy, and sustainability, garlic can continue evolving from an ancient crop to a modern, high-value food and medicinal plant.

Declarations

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Conflicts of Interest

The author declares that there are no conflicts of interest regarding the publication of this review article.

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