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Genomic Resources and Their Role in *Camellia* Breeding Strategies

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Abstract This study explores genomic resources that can be used for breeding strategies in tea genus, focusing on their importance in improving traits such as quality, yield, and stress resistance, and assesses the state of current genomic tools, including sequencing programs and molecular markers, to facilitate targeted breeding efforts. The results show that the integration of genomic resources has improved selection efficiency and resulted in the development of superior varieties, especially in *Camellia sinensis* and *Camellia oleifera*, and the results highlight the potential of genomic tools to accelerate breeding procedures and address challenges in tea cultivation. Efficient use of genomic resources is essential to advance tea breeding, which will ultimately contribute to sustainable production practices and improved economic efficiency.

Keywords Genomic resources; *Camellia* breeding; Molecular markers; Trait enhancement; Sustainable agriculture

1 Introduction

The genus *Camellia* encompasses approximately 200 species, many of which hold substantial economic, ornamental, and cultural value (Liu, 2024). Notably, *Camellia sinensis* is the primary source of tea, one of the most widely consumed beverages globally, contributing significantly to the economies of many countries (Wu et al., 2022; Gao et al., 2023). Additionally, several *Camellia* species are cultivated for their ornamental flowers, which are highly prized in horticulture for their aesthetic appeal (Gao et al., 2023). Furthermore, *Camellia oleifera* and other oil-tea camellias are vital for producing high-quality edible oils rich in unsaturated fatty acids and beneficial secondary metabolites, making them important for both culinary and health-related applications (Shen et al., 2022; Chen et al., 2023).

Breeding *Camellia* species presents several challenges. One of the primary difficulties is the long breeding cycle, which can span several years due to the perennial nature of these plants (Yan et al., 2018). Additionally, *Camellia* species often face environmental stresses such as drought, cold, and nutrient deficiencies, which can adversely affect their growth and productivity (Dong et al., 2017; Ye et al., 2023). Improving resistance to these stresses is crucial for ensuring stable yields and quality. Another significant challenge is enhancing the quality traits of *Camellia* products, such as the flavor and aroma of tea or the oil content and composition in oil-tea camellias (Xia et al., 2020; Wu et al., 2022). These quality improvements require a deep understanding of the genetic and molecular bases of these traits, which can be complex and multifaceted.

This study will provide a comprehensive review of genomic databases and tools currently used for tea research, analyze the impact on genetic variation and its function, and use these genomic insights to develop new breeding strategies by integrating the latest advances in genomic, transcriptomic, and metabolomic data. Seek to identify key genetic factors that influence economically important traits such as stress resistance, yield, and quality. The aim of this study was to accelerate the breeding process of tea and improve the economic and agronomic performance of tea varieties.

2 *Camellia* Species Diversity and Breeding Goals

2.1 Overview of major *Camellia* species

The genus *Camellia* encompasses over 200 species, many of which hold significant economic, ornamental, and cultural value. Among these, *Camellia sinensis* and *Camellia oleifera* are particularly noteworthy. *Camellia* *sinensis* is primarily cultivated for tea production. It includes two main varieties, *C. sinensis* var. Sinensis and *C. sinensis* var. assamica, which have been independently domesticated and exhibit significant genetic diversity due to extensive intra- and interspecific introgressions (Xia et al., 2020; Zhang et al., 2021). The tea plant is clonally propagated, and its genetic and evolutionary history has been extensively studied to enhance desirable traits such as flavor and stress resistance (Zhang et al., 2021). *Camellia oleifera* is known as the tea-oil camellia, this species is a crucial woody oil crop in southern China and Southeast Asia. It is valued for its high oil content and resistance to environmental stresses such as drought and nutrient deficiency (Dong et al., 2017; Ye et al., 2023). Recent genomic studies have provided insights into its complex genome and identified genes related to economic traits and stress tolerances (Ye et al., 2023).

2.2 Key traits of interest in *Camellia* breeding

Breeding programs for *Camellia* species focus on several key traits to enhance their economic value and adaptability. In *C. oleifera*, high oil content and quality are primary breeding goals. Studies have identified genes involved in oil biosynthesis, such as *acetyl-coenzyme A carboxylase* and diacylglycerol acyltransferase, which are crucial for high oil and oleic acid content (Figure 1) (Gong et al., 2022). For *C. sinensis*, traits related to tea quality, such as catechin and caffeine content, are of paramount importance. Genomic studies have revealed genes associated with these secondary metabolites, which are critical for the flavor and quality of tea (Lubanga et al., 2021; Wu et al., 2022). Resistance to diseases like anthracnose is a significant breeding objective for *C. oleifera*. Transcriptomic and metabolomic analyses have identified key metabolites and genes involved in flavonoid biosynthesis that contribute to disease resistance (Yang et al., 2022). Both *C. sinensis* and *C. oleifera* are bred for enhanced resistance to environmental stresses. For instance, drought tolerance in *C. oleifera* has been linked to genes involved in abscisic acid synthesis and protective enzyme activity (Dong et al., 2017).

2.3 Traditional breeding approaches and their limitations in *Camellia* species

Traditional breeding approaches in *Camellia* species have primarily relied on phenotypic selection and cross-breeding. However, these methods face several limitations. *Camellia* species are perennial plants with long generation times, making traditional breeding time-consuming and labor-intensive (Ye et al., 2023). Many desirable traits, such as tea quality and oil content, are complex and controlled by multiple genes. Traditional breeding methods struggle to effectively select for these traits due to their polygenic nature (Lubanga et al., 2021). The genetic base of cultivated *Camellia* species is often narrow, limiting the potential for improvement through traditional breeding. This is particularly true for clonally propagated species like *C. sinensis* (Zhang et al., 2021). Phenotypic traits can be significantly influenced by environmental conditions, complicating the selection process and reducing the accuracy of traditional breeding methods (Chen et al., 2023).

3 Genomic Resources Available for *Camellia* Breeding

3.1 Genomic sequencing projects in *Camellia*

Genomic sequencing projects have significantly advanced our understanding of *Camellia* species, particularly *Camellia sinensis*, which is crucial for tea production. The draft genome sequence of *Camellia sinensis* var. sinensis has provided insights into the evolution of the tea genome and the biosynthesis of key metabolites such as catechins, theanine, and caffeine. This high-quality genome assembly, which includes 33 932 high-confidence protein-coding genes, has revealed two rounds of whole-genome duplications that have played a critical role in the evolution of these metabolites (Wei et al., 2018). Additionally, the chromosome-level genome of *Camellia lanceoleosa* has been sequenced, offering valuable resources for understanding genome evolution and self-incompatibility mechanisms in *Camellia* species (Gong et al., 2022).

3.2 Transcriptomic, proteomic, and metabolomic data in *Camellia* species

Transcriptomic, proteomic, and metabolomic analyses have been extensively conducted in various *Camellia* species to understand their genetic diversity and metabolic pathways. For instance, a comprehensive transcriptome dataset of *Camellia sinensis* has been generated using high-throughput RNA sequencing, identifying numerous genes involved in primary and secondary metabolic pathways, including those critical for tea quality such as flavonoid, theanine, and caffeine biosynthesis. Comparative transcriptomic analysis of 116 *Camellia* plants has also unveiled the deep phylogeny and secondary metabolite evolution within the genus, highlighting the accumulation of metabolites like catechins and caffeine in specific sections (Wu et al., 2022). Metabolomic studies on diverse *Camellia sinensis* populations have identified signature metabolites associated with different phylogenetic groups, providing insights into the genetic and metabolite diversity useful for breeding programs (Yu et al., 2020).

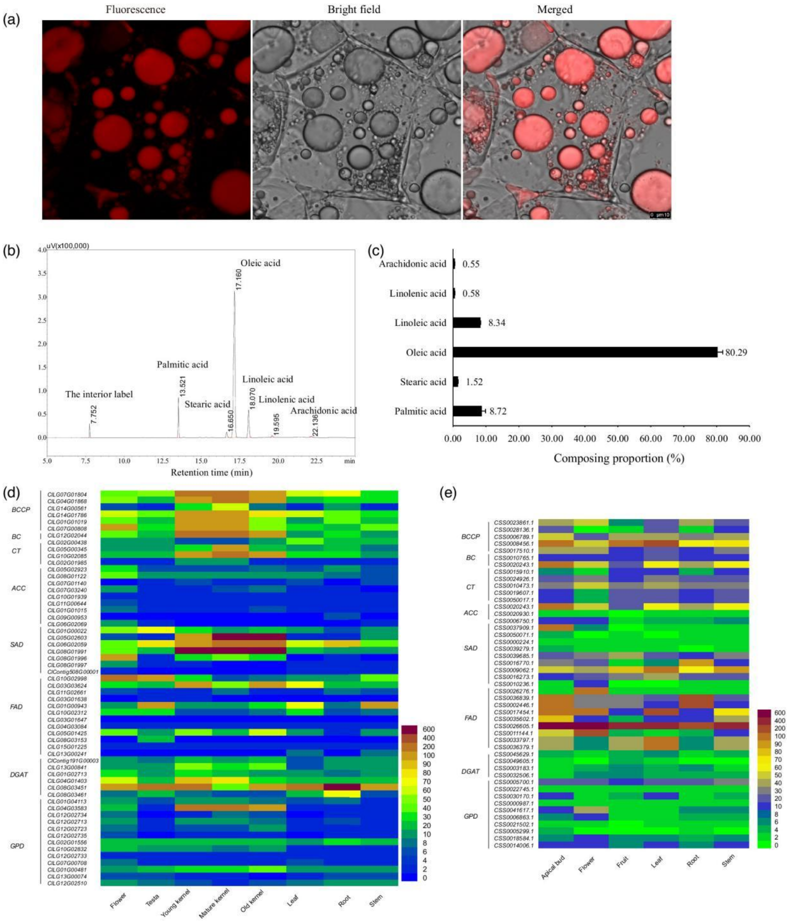

Figure 1 Analyses of oil compositions and oil synthesis-related genes in the seeds of *Camellia lanceoleosa* (Adopted from Gong et al., 2022)

Image caption: (a) Oil body showing red autofluorescence under a 512-nm laser with a confocal microscope. (b) Fatty-acid component analysis with gas chromatography-mass spectrometry. The number next to the peak denotes the retention time. (c) Fatty-acid compositions in mature seeds. %, percentage of all fatty acids detected. Expression patterns of genes encoding homogeneous and heteromeric ACCase, stearoyl-ACP desaturase, omega-6 fatty acid desaturase and omega-3 fatty acid desaturase, diacylglycerol *O*-acyltransferase and glycerol-3-phosphate dehydrogenase in different tissues and developmental seeds of *C. lanceoleosa* (d) and *Camellia sinensis* (e). Three independent measurements were used to calculate the mean and standard deviation values (Adopted from Gong et al., 2022)

3.3 Publicly available databases and resources

Several publicly available databases and resources have been developed to facilitate the conservation and utilization of *Camellia* germplasm. For example, a web-accessible database has been created for efficient retrieval of *Camellia* transcriptomes, which includes data from the pan-transcriptome of 116 *Camellia* plants (Wu et al., 2022). Additionally, unigene derived microsatellite markers (UGMS) identified from publicly available sequence databases have been developed for genetic analysis, gene mapping, and marker-assisted breeding in tea. These resources, along with the extensive transcriptome datasets and genome assemblies, provide a robust platform for genomic, transcriptomic, and functional genomic studies in *Camellia* species, thereby accelerating breeding strategies and improving tea plant varieties (Wei et al., 2018).

4 Molecular Markers and Marker-Assisted Selection (MAS)

4.1 Identification of molecular markers linked to key traits in *Camellia*

The identification of molecular markers linked to key traits in *Camellia* has been a significant advancement in plant breeding. Molecular markers such as single nucleotide polymorphisms (SNPs) and expressed sequence tag-simple sequence repeats (EST-SSRs) have been effectively utilized to identify associations with traits of interest. For instance, a functional molecular marker, EST-SSR073, has been identified for detecting blister blight disease resistance in tea (*Camellia sinensis*), marking a milestone in tea molecular breeding (Karunarathna et al., 2020). The development of these markers involves genotyping populations and performing linkage analysis to associate specific markers with phenotypic traits.

4.2 Application of MAS in improving traits like oil content, tea quality, and stress tolerance

Marker-assisted selection (MAS) has been applied to improve various traits in *Camellia*, including oil content, tea quality, and stress tolerance. MAS allows for the selection of desirable traits at the seedling stage, thus saving time and resources (Devi et al., 2017). For example, MAS has been used to enhance stress tolerance by selecting for traits related to abiotic stress resistance, which is crucial given the challenges posed by climate change. Additionally, MAS has been employed to improve tea quality by selecting for traits such as disease resistance and nutrient efficiency, which directly impact the quality of the final product (Hasan et al., 2021).

4.3 Success stories of MAS in *Camellia* breeding programs

There have been several success stories of MAS in *Camellia* breeding programs. One notable example is the use of the EST-SSR073 marker for breeding blister blight-resistant tea cultivars, which has significantly reduced crop losses due to this fungal disease (Karunarathna et al., 2020). Another success story involves the application of genotyping-by-sequencing (GBS) and amplicon sequencing (AmpSeq) technologies, which have streamlined the process of marker discovery and genotyping, thereby accelerating the breeding of stress-tolerant and high-quality *Camellia* varieties (Yang et al., 2016). These advancements have demonstrated the potential of MAS to revolutionize *Camellia* breeding by increasing the precision and efficiency of selecting superior genotypes.

5 QTL Mapping and Association Studies in *Camellia*

5.1 Overview of quantitative trait loci (QTL) mapping in *Camellia*

Quantitative trait loci (QTL) mapping is a powerful tool used to identify the genetic basis of complex traits in plants. This method involves linking phenotypic data (observable traits) with genotypic data (genetic markers) to locate regions of the genome that contribute to variation in these traits. Traditional QTL mapping relies on biparental populations, which are derived from crossing two genetically distinct parents. This approach has been successfully applied in various crops to identify loci associated with important agronomic traits (Pascual et al., 2016).

5.2 Application of genome-wide association studies (GWAS) to identify loci related to important traits

Genome-wide association studies (GWAS) have emerged as a complementary approach to traditional QTL mapping. Unlike biparental QTL mapping, GWAS utilizes natural populations with diverse genetic backgrounds, leveraging historical recombination events to achieve higher resolution in identifying loci associated with traits of interest. GWAS has been effectively used in crops like tomato, soybean, and rice to identify QTLs for traits such as fruit quality, yield, and stress tolerance (Kim et al., 2021). In *Camellia*, GWAS can be particularly useful for identifying loci related to traits such as flower color, oil content, and disease resistance. By analyzing a diverse collection of *Camellia* accessions, researchers can uncover marker-trait associations that are valuable for breeding programs. For instance, a study on soybean demonstrated the utility of integrating GWAS with genotyping-by-sequencing (GBS) to provide dense genome-wide marker coverage, leading to the identification of significant loci for various agronomic traits.

5.3 Challenges and opportunities in using QTL mapping for *Camellia* improvement

While QTL mapping and GWAS offer significant potential for *Camellia* improvement, several challenges must be addressed. One major challenge is the reproducibility of results across different environments and populations. The transferability of QTLs identified in one population to another can be limited due to differences in genetic backgrounds and environmental interactions (Mohammadi et al., 2020; Chen et al., 2021). Additionally, the detection of rare variants and QTLs with small effects remains difficult, as current methods are more suited to identifying common variants with moderate effects (Mohammadi et al., 2020; Lima et al., 2022).

Despite these challenges, there are numerous opportunities for advancing *Camellia* breeding through QTL mapping and GWAS. The integration of next-generation sequencing technologies and advanced statistical methods can enhance the resolution and accuracy of QTL detection. Moreover, the use of multi-parent populations, such as MAGIC (Multi-parent Advanced Generation Inter-Cross) populations, can increase the precision of QTL mapping by capturing a broader range of genetic diversity (Pascual et al., 2016).

Furthermore, leveraging existing phenotypic data from breeding programs and combining it with genomic data can facilitate the identification of robust QTLs that are stable across different environments. This approach has been successfully demonstrated in long-lived tree species like Norway spruce, where extensive phenotypic data from breeding programs were standardized and used for GWAS, leading to the identification of novel QTLs associated with important traits (Chen et al., 2021).

6 Genomic Selection (GS) in *Camellia* Breeding

6.1 Principles of genomic selection and its benefits for perennial crops like *Camellia*

Genomic selection (GS) is a predictive breeding approach that leverages genome-wide markers to estimate the breeding values of individuals within a population. Unlike traditional marker-assisted selection, which focuses on a few significant loci, GS incorporates all available marker data to predict the performance of genotypes more accurately (Crossa et al., 2017). This comprehensive approach is particularly beneficial for complex traits controlled by many genes with small effects, which are common in perennial crops like *Camellia* (Wang et al., 2018).

The primary advantage of GS in perennial crops is the acceleration of the breeding cycle. By predicting the genetic potential of seedlings before they reach maturity, breeders can make selection decisions earlier, thus reducing the time required to develop new varieties (Figure 2) (Cappetta et al., 2020). Additionally, GS can enhance genetic gain per unit time and cost by improving selection accuracy and intensity (Xu et al., 2019). This is crucial for perennial crops, which typically have long generation intervals and require significant resources for phenotypic evaluation.

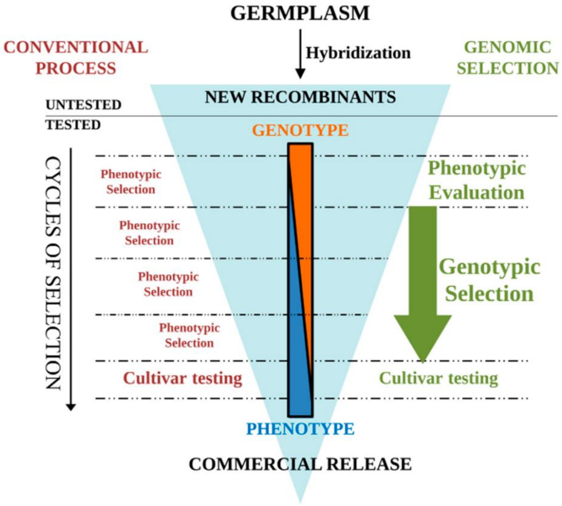

Figure 2 Comparison of genomic selection (GS) and conventional selection in tomato breeding programs (Adopted from Cappetta et al., 2020)

Image caption: Screening of recombinant lines through GS approaches optimizes the genetic gain obtained in each selection cycle. Breeding cycles (horizontal dashed lines) are shortened by removing phenotypic evaluation of lines before training population (TRN) evaluation for the next cycle (Adopted from Cappetta et al., 2020)

6.2 Recent advancements in GS for *Camellia* species

Recent advancements in GS have significantly impacted the breeding of *Camellia* species. The integration of high-throughput genotyping technologies, such as next-generation sequencing (NGS), has enabled the collection of dense marker data at a reduced cost, making GS more feasible and effective. These technologies have improved the accuracy of genomic estimated breeding values (GEBVs) by providing comprehensive marker coverage and reducing ascertainment bias (Wang et al., 2018).

Moreover, the development of sophisticated statistical models and algorithms, including GBLUP, Bayes, and machine learning approaches, has enhanced the prediction accuracy of GS models. These models can account for non-additive genetic effects and genotype-by-environment interactions, which are critical for the reliable selection of *Camellia* genotypes under varying environmental conditions (Wang et al., 2018). In practical applications, GS has been successfully implemented in breeding programs for other perennial crops, such as perennial ryegrass, demonstrating significant genetic gains and reduced breeding cycle times. These successes provide a promising outlook for the application of GS in *Camellia* breeding.

6.3 Incorporating genomic selection into traditional breeding programs for more efficient selection

Incorporating GS into traditional *Camellia* breeding programs requires a strategic approach to optimize the use of genomic and phenotypic data. One effective strategy is to reorganize field designs and training populations to maximize the accuracy of GEBVs (Merrick et al., 2022). By increasing the number of lines evaluated and leveraging data collected across different growing seasons and environments, breeders can improve heritability estimates and selection accuracy (Cappetta et al., 2020; Merrick et al., 2022).

Additionally, integrating GS with high-throughput phenotyping and deep learning approaches can further enhance the efficiency of selection. These technologies enable the rapid and precise measurement of phenotypic traits, which can be used to update prediction models and refine selection decisions (Cappetta et al., 2020; Merrick et al., 2022). To fully realize the benefits of GS, it is essential to develop breeding schemes that combine GS with traditional methods. For instance, GS can be used to pre-select superior genotypes, which can then be subjected to further evaluation and selection through conventional breeding techniques (Xu et al., 2019). This integrated approach can accelerate the development of new *Camellia* varieties with improved traits, such as disease resistance, yield, and quality.

7 Case Study: Genomic Tools for Tea Quality Improvement in *Camellia sinensis*

7.1 Overview of tea quality traits and their significance in the tea industry

Tea quality traits are critical for the tea industry as they directly influence consumer preference and market value. Key quality traits include flavor, aroma, and biochemical composition, such as catechins, theanine, and caffeine. These compounds not only contribute to the sensory attributes of tea but also to its health benefits. For instance, catechins are known for their antioxidant properties, while theanine is associated with relaxation effects. The complexity of these traits, often influenced by both genetic and environmental factors, makes their improvement a challenging task (Wei et al., 2018; Yu et al., 2020; Lubanga et al., 2021).

7.2 Application of genomic resources for improving flavor and quality

The advent of genomic resources such as genome sequencing, transcriptomics, and metabolomics has revolutionized the breeding strategies for tea quality improvement. High-quality genome assemblies of *Camellia sinensis* have facilitated the identification of gene families involved in the biosynthesis of key metabolites. For example, the draft genome sequence of *Camellia sinensis* var. sinensis has highlighted the role of specific gene duplications in the production of catechins and theanine (Wei et al., 2018). Additionally, genomic selection (GS) models have been employed to predict complex quality traits using genome-wide markers, showing promising results in improving traits like theogallin and epicatechin gallate (Lubanga et al., 2021).

Transcriptomic analyses have further elucidated the expression patterns of genes associated with flavor and aroma compounds. For instance, genes involved in terpene biosynthesis, which contribute to tea aroma, have been found to be significantly amplified in the tea plant genome (Xia et al., 2020). Metabolomic studies have also identified signature metabolites in different tea phylogenetic groups, aiding in the selection of varieties with desirable quality traits (Yu et al., 2020).

7.3 Outcomes of using genomics in tea breeding and lessons learned

The application of genomic tools in tea breeding has led to several significant outcomes. The haplotype-resolved genome assembly of an Oolong tea cultivar, Tieguanyin, has provided insights into the genetic diversity and evolutionary history of tea plants, revealing extensive intra- and interspecific introgressions that contribute to modern cultivar diversity (Figure 3) (Zhang et al., 2021). This genetic information is crucial for targeted breeding programs aimed at enhancing specific quality traits.

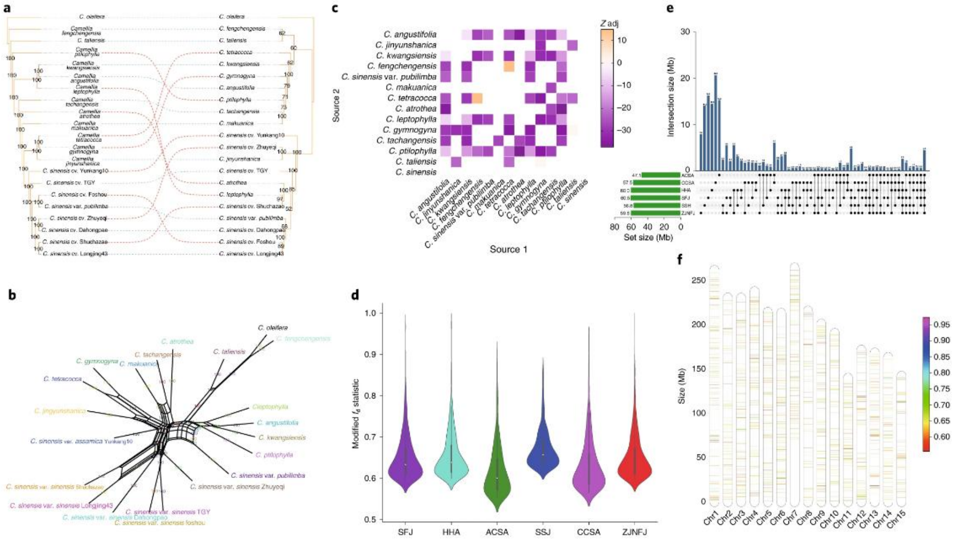

Figure 3 Genome-wide patterns of genetic introgression to modern tea cultivars from their close relatives (Adopted from Zhang et al., 2021)

Image caption: a, Cytonuclear conflicts between nuclear and chloroplast phylogenetic trees among 14 resequenced *Camellia* section *Thea* species with *C. oleifera* included as the outgroup. b, SplitsTree network for *Camellia* accessions from section *Thea*. c, Detection of introgression events between *C. sinensis* and close relatives using the f_3 test. Z scores were adjusted based on a Benjamini-Hochberg false discovery-rate correction method, and significant introgression is indicated with purple if adjusted (adj) Z score < -1.96. d, Distribution of 95th percentile f_d outliers using modified f_d statistics (y axis) in six groups of cultivated tea populations (x axis). The white dot in the center of each violin plot represents the median value, and the bounds of each box indicate first (25%) and third (75%) quartiles. Minima and maxima are present in the lower and upper bounds of the whiskers, respectively, and the width of whiskers are densities of modified f_d statistics. P values were calculated using two-sided Fisher's exact test without multiple comparisons. e, Amount of unique and shared introgressed sequences (in Mb) among six groups of cultivated tea populations. f, Distribution of introgressed loci along chromosomes (chr) 1-15, with the colored bar indicating the maximum of modified f_d statistics in each 100-kb non-overlapping window (Adopted from Zhang et al., 2021)

Genomic selection has demonstrated moderate to high prediction accuracies for various quality traits, suggesting its potential for implementation in breeding programs (Lubanga et al., 2021). The identification of quantitative trait loci (QTLs) related to important agronomic traits, such as the timing of bud flush, has also been achieved, providing markers for selection in breeding (Tan et al., 2022). However, the integration of genomic tools in tea breeding is not without challenges. The complexity of tea quality traits, influenced by multiple genes and environmental interactions, necessitates comprehensive and multi-faceted approaches. Additionally, the high cost and technical expertise required for genomic analyses can be limiting factors for widespread adoption.

8 Biotechnological Advances in *Camellia* Breeding

8.1 Genetic engineering and genome editing tools (e.g., CRISPR-Cas9) for trait improvement

Genetic engineering and genome editing tools, particularly CRISPR-Cas9, have revolutionized the field of plant breeding by enabling precise modifications to the genome. These tools allow for the targeted alteration of genes associated with desirable traits such as increased yield, stress resistance, and improved nutritional content.

CRISPR-Cas9, in particular, has been widely adopted due to its simplicity, efficiency, and versatility. It has been successfully applied to various crops to enhance traits such as abiotic stress tolerance and disease resistance (Jaganathan et al., 2018; Thudi et al., 2020; Nascimento et al., 2023). For instance, CRISPR-Cas9 has been used to edit genes in *Camelina sativa* to alter its fatty acid content, demonstrating the potential of genome editing in modifying complex traits in polyploid plants (Kawall, 2021). The integration of these advanced biotechnological tools in *Camellia* breeding could significantly accelerate the development of improved varieties with enhanced economic and agronomic traits.

8.2 Enhancing stress resistance and yield in *Camellia* through biotechnological approaches

Biotechnological approaches, including genomic selection and genome editing, have shown great promise in enhancing stress resistance and yield in crops. By leveraging genomic resources and high-throughput genotyping, researchers can identify and select for alleles associated with desirable traits such as drought tolerance, heat resistance, and high yield potential (Dwivedi et al., 2017; Thudi et al., 2020). For example, the use of CRISPR-Cas9 has enabled the development of crop varieties with improved tolerance to multiple abiotic stresses, such as salinity and temperature extremes, by targeting specific genes involved in stress response pathways (Jaganathan et al., 2018; Nascimento et al., 2023). In *Camellia*, the application of these biotechnological tools could lead to the identification and manipulation of key genes responsible for stress tolerance and yield, thereby improving the resilience and productivity of *Camellia* species under changing environmental conditions (Yan et al., 2018; Ye et al., 2023).

8.3 Ethical considerations and regulatory challenges in deploying biotechnology in *Camellia* breeding

The deployment of biotechnological tools in plant breeding, including genetic engineering and genome editing, raises several ethical considerations and regulatory challenges. One major concern is the potential unintended effects of genome editing on non-target genes and the broader ecosystem. For instance, alterations in the genome of *Camelina sativa* have been shown to potentially affect the plant's metabolism and its interactions with the environment (Kawall, 2021). Additionally, the regulatory landscape for genetically modified organisms (GMOs) and genome-edited crops varies significantly across different countries, impacting the commercialization and acceptance of these technologies (Marone et al., 2023). Public perception and acceptance of genetically modified crops also play a crucial role in the adoption of these technologies. Therefore, it is essential to address these ethical and regulatory challenges through transparent communication, rigorous safety assessments, and the development of clear regulatory frameworks to ensure the responsible use of biotechnology in *Camellia* breeding (Marone et al., 2023; Ye et al., 2023).

9 Challenges and Limitations in Utilizing Genomic Resources

9.1 Data integration and complexity in genomic data for *Camellia* species

Integrating and managing the vast amounts of genomic data generated for *Camellia* species presents significant challenges. The complexity arises from the need to incorporate extensive genomic information alongside new phenotypic data, which is crucial for understanding genotype-by-environment interactions and improving prediction models for complex traits (Eeuwijk et al., 2019). The development of new genotype-to-phenotype (G2P) models that can handle this integration is essential but remains a significant hurdle (Eeuwijk et al., 2019). Additionally, the uneven distribution of repetitive sequences and genomic rearrangements, as observed in species like *Camellia lanceoleosa*, further complicates data integration efforts (Gong et al., 2022).

9.2 Limited genomic resources for non-model *Camellia* species

While significant progress has been made in sequencing and understanding the genomes of some *Camellia* species, many non-model species still lack comprehensive genomic resources. This limitation hampers the ability to conduct detailed genetic and genomic studies necessary for effective breeding programs. For instance, the genomic resources available for *Camellia oleifera* are still in the early stages, and more extensive sequencing and characterization are needed to fully exploit its breeding potential (Yan et al., 2018; Chen et al., 2023). The lack of genomic data for these non-model species restricts the application of advanced breeding techniques such as genomic selection and marker-assisted selection (Thudi et al., 2020; Merrick et al., 2022).

9.3 Need for better phenotyping and environmental data for precision breeding

Precision breeding in *Camellia* species requires high-quality phenotypic and environmental data to accurately predict and select for desirable traits. However, the collection of phenotypic data is often a limiting factor due to the complexity and inaccessibility of certain traits, such as root characteristics. High-throughput phenotyping platforms have been developed, but their efficiency in increasing genetic gain is still under evaluation. Moreover, the integration of phenotypic data with genomic information is crucial for improving the accuracy of selection models, yet this remains a challenging task (Eeuwijk et al., 2019). Better phenotyping methods and comprehensive environmental data are essential to enhance the precision and effectiveness of breeding strategies (Crossa et al., 2017; Merrick et al., 2022).

10 Future Prospects and Strategies for *Camellia* Breeding

10.1 Emerging trends in genomics and breeding

Recent advancements in genomics and breeding technologies are paving the way for significant improvements in *Camellia* breeding strategies. The integration of multi-omics approaches, including genomics, transcriptomics, proteomics, and metabolomics, is becoming increasingly important. These technologies allow for a comprehensive understanding of the genetic and molecular bases of key traits, such as flower and fruit development and stress tolerance (Yan et al., 2018; Mahmood et al., 2022). High-throughput genotyping and phenotyping technologies are also enabling the screening of large germplasm collections, which helps in identifying novel alleles from diverse sources, thus expanding the genetic variation available for breeding. Additionally, the use of genomic selection (GS) and speed breeding (SB) techniques can accelerate the breeding cycle and enhance genetic gains by allowing for the rapid selection of superior genotypes (Crossa et al., 2017; Jighly et al., 2019).

10.2 Opportunities to accelerate breeding cycles and improve genetic gains through modern tools

Modern breeding tools offer numerous opportunities to accelerate breeding cycles and improve genetic gains in *Camellia*. Genomic selection (GS) and speed breeding (SB) are particularly promising. GS uses genome-wide markers to predict complex phenotypes, which can significantly reduce the time required for breeding cycles and increase selection intensity and accuracy (Grattapaglia et al., 2018). Speed breeding, on the other hand, involves optimizing growth conditions to shorten the generation time, thereby allowing for more breeding cycles per year. The combination of GS and SB, known as SpeedGS, has shown to result in higher genetic gains per year, especially for traits with low heritability (Jighly et al., 2019). Moreover, integrating omics data with phenotypic information can lead to the identification of genes and pathways responsible for important agronomic traits, further enhancing the efficiency of selection and accelerating genetic gains (Mahmood et al., 2022).

10.3 Recommendations for future research and policy support to enhance genomic applications in *Camellia* breeding

To fully harness the potential of genomic applications in *Camellia* breeding, several recommendations for future research and policy support are essential. First, there is a need for comprehensive genomic and phenotypic databases that can be used to identify key genetic markers and candidate genes for important traits (Yan et al., 2018). Second, investment in high-throughput genotyping and phenotyping infrastructure is crucial to enable large-scale screening and selection (Cobb et al., 2019). Third, breeding programs should adopt a culture of continuous optimization and improvement, focusing on reducing breeding cycle times and enhancing selection accuracy (Cobb et al., 2019). Fourth, policies should support collaborative research efforts and data sharing among breeding institutions to maximize the use of available resources and knowledge. Finally, there should be a focus on developing and implementing strategies to mitigate inbreeding and maintain genetic diversity within breeding populations, ensuring long-term sustainability and genetic gains (Grattapaglia et al., 2018; Jighly et al., 2019).

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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