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Genomic selection strategies in crop science for sustainable agriculture in Korea

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Abstract

Genomic selection (GS) is an effective approach to address the growing need for increasing and improving food production and quality, respectively, under challenging environmental conditions. In Korea, GS significantly advanced major crops such as rice and wheat by improving critical agronomic traits. However, minor crops such as mung bean and sesame still require development because of limited resources and breeding infrastructure. These crops, though less prioritized, are vital for their nutritional and functional properties and contribute significantly to agricultural diversity and rural livelihoods. Addressing the research gap in minor crops is essential to prevent the loss of genetic diversity and to enhance their resilience to environmental changes. Unlike traditional selection methods, GS enhances the accuracy of complex trait selection, accelerates breeding cycles, and boosts genetic gain. It leverages genome-wide markers to predict genomic estimated breeding values (GEBVs) with high precision, enabling faster and more effective breeding strategies, especially for traits controlled by multiple genes. Genotyping techniques, such as Genotyping by Sequencing and Whole Genome Resequencing, are integral to GS, each offering specific benefits and limitations. Multispecies single nucleotide polymorphism arrays present a cost-effective solution for improving GS in minor crops by capturing the genetic diversity across species and enabling cross-species data integration. Expanding the GS in minor crops is essential for preserving genetic diversity, improving adaptability, and supporting sustainable agriculture and food security in South Korea. By addressing these challenges, GS can transform breeding programs, ensuring a sustainable and resilient agricultural system for the future.

Keywords: Breeding, Crops, Genomic selection, Genotyping by Sequencing, Single nucleotide polymorphism platform, Sustainable agriculture.

Contents

Contribution of this paper to the literature

This study uniquely focuses on applying genomic selection (GS) to under-researched minor crops in Korea, including mung bean and sesame. By proposing multispecies single nucleotide polymorphism (SNP) arrays as a cost-effective tool, it bridges the gap between major and minor crop research, emphasizing genetic diversity preservation and adaptability.

1. Introduction

Although more food is required for the rapidly growing human population, food quality needs to be improved, particularly with increased nutrient content [\[1\]](#page-5-2). The ability to increase or even sustain crop yield and quality in the face of dynamic environmental and biotic threats is particularly challenging in the face of rapid global environmental changes $[2]$. In response to challenges such as climate change and mechanization, the gradual shrinkage of cultivation areas led to an increased reliance on imports. Concurrently, a demand exists for highquality varieties, including those rich in functional compounds, adaptable to climate change, resistant to pests and diseases, and suitable for mechanization and processing.

Modern crop breeding must prioritize the development of crop varieties with agronomic traits to address the dual demands of increased food production and improved nutritional quality. Particularly in Korea, both major and minor crops are essential not only for food security but also for nutritional quality and economic stability. Major crops, such as rice, wheat, and maize, have seen considerable advancements in breeding, focusing on yield, disease resistance, and environmental adaptability [\[3\]](#page-5-4). Contrastingly, minor crops, which are valuable for their nutritional and functional properties, have lagged in breeding improvements and require significant genetic advancements to meet their full potential.

Genomic Selection (GS) is a transformative tool for genetic improvement that enables breeders to predict the genetic value of crops based on genome-wide markers [\[4\]](#page-5-5). Unlike traditional phenotypic selection, which depends on observable traits that may not be consistently expressed under various environmental conditions, GS allows for the accumulation of minor genetic effects across the genome essential for complex traits, such as yield, disease resistance, and drought tolerance $\begin{bmatrix} 5, 6 \end{bmatrix}$. Many countries extensively adopted GS for major crops, benefiting from faster breeding cycles and greater selection accuracy, particularly for traits controlled by multiple genes [\[4\]](#page-5-5). In Korea, GS have begun to influence major crops, including rice and wheat, showing promise in improving agronomic traits [\[7\]](#page-5-8). However, for minor crops, the adoption of GS faced limitations due to economic challenges, lack of accessible high-throughput genotyping resources, and less-established breeding infrastructure compared to those of staple crops. Consequently, minor crops receive limited breeding resources despite their cultural and nutritional significance, raising concerns regarding the possible loss of valuable genetic diversity. Applying GS to minor crops can safeguard their unique genetic traits and enhance yield stability and environmental adaptability, making them better suited to the climate challenges and agricultural shifts anticipated in Korea.

In this study, we examined the potential of GS in addressing breeding challenges for both major and minor crops in Korea. While GS demonstrated substantial gains in yield, resilience, and disease resistance in major crops such as rice and wheat, minor crops remain underserved due to limited resources and infrastructure. We discuss the critical need to expand GS applications to minor crops to ensure the preservation of genetic diversity and enhance their adaptability to climate and agricultural demands. Furthermore, we highlight that the methodologies explored in this study can be applied to regions with agricultural challenges similar to Korea, thereby providing solutions to enhance food security and economic stability in these contexts.

2. Advantages of GS

Conventional plant breeding methods historically relied on phenotypic selection where observable traits such as plant height, disease resistance, and grain yield are used to select individuals for breeding programs. Although phenotypic selection proved successful for simple traits, it struggles with complex traits due to their polygenic nature and environmental sensitivity. One of the major challenges is the GxE interactions (genotype-byenvironment), in which the same genotype may be expressed differently under varying environmental conditions [\[8\]](#page-6-0). Hence, phenotypic selection is less effective for complex traits controlled by multiple genes and significantly influenced by environmental factors $\lbrack 9 \rbrack$.

To overcome these challenges, marker-assisted selection (MAS), which utilizes Deoxyribo Nucleic Acid (DNA) markers linked to specific traits to guide breeding decisions, was developed. MAS showed particular success for simple Mendelian traits such as disease resistance or other qualitative traits involving one or a few major effect loci [\[10\]](#page-6-2). However, complex traits like grain yield or drought resistance influenced by numerous small-effect genes scattered across the genome, MAS proved to be less effective due to its dependence on a limited number of markers $[11]$

GS represents a major leap forward by enabling the prediction of breeding values based on genome-wide markers without the need to identify individual trait-specific markers [\[12\]](#page-6-4). GS uses statistical models estimating the contribution of each single nucleotide polymorphism (SNP) across the genome to the overall genetic merit of an individual, thereby capturing major and minor allele effects. This allows for the prediction of genomic estimated breeding value (GEBV) an individual with high accuracy, even in the absence of phenotypic data. A key advantage of GS over MAS is its ability to capture the cumulative effects of numerous small effect genes across the genome often missed by MAS [\[13\]](#page-6-5). This comprehensive genomic information enables more accurate selection and improves genetic gains over time.

One of the main benefits of GS is that it reduces breeding cycle time. Traditional breeding methods rely on the phenotypic evaluations of multiple generations, whereas GS allows for selection based on genetic information alone [\[4\]](#page-5-5). Additionally, GS is particularly advantageous for crops with long generation intervals or those grown in environments where phenotyping is difficult or expensive, such as minor crops [\[14\]](#page-6-6). In these crops, GS can potentially accelerate genetic improvement, even in the absence of extensive phenotypic or genomic resources [\[15,](#page-6-7) [16\]](#page-6-8).

In contrast to traditional breeding methods, GS allows breeders to maximize genetic gain per unit of time by focusing on genomic predictions rather than on phenotypic performance alone [\[15,](#page-6-7) [17\]](#page-6-9). As GS evolves with advances in sequencing technologies and reduced genotyping costs, it is set to revolutionize breeding programs for both the animal and crop industries by improving the selection of traits difficult to measure or have low heritability [\[18,](#page-6-10) [19\]](#page-6-11). [Table](#page-2-1) 1 illustrates the characteristics of breeding methods from phenotypic selection to genomic selection.

Table 1. Advancements in selection strategies in crop breeding.

Method	Features	Advantages	Limitations	
Phenotypic selection	Relies on observable traits and phenotype measurements.	Simple	Time-consuming	
		Low-cost	Long breeding cycles	
		Widely applicable	Inefficient for complex traits	
Marker- assisted selection	Uses specific DNA markers linked to traits of interest.	High accuracy for simple traits	Limited for small-effect loci	
		Specific DNA markers	Ineffective for complex traits	
		Effective for major genes	Requires known marker-trait association	
Genomic selection	Utilizes genome-wide markers to predict breeding values.	Genome-wide coverage	High costs with high density platforms	
		Accurate for complex traits	Requires computational resources	
		Shortens breeding cycles	Data-intensive process	

3. Genotyping Techniques for GS in Crop Science

3.1. Genotyping by Sequencing (GBS)

The GBS has been widely adopted in modern crop breeding, particularly for species with complex genomes or limited genomic resources. This innovative technique, which was developed as a cost-effective, high-throughput alternative to traditional genotyping methods, allows for a more efficient exploration of genetic diversity [\[20,](#page-6-12) [21\]](#page-6-13). GBS operates by digesting genomic DNA with restriction enzymes to simplify the genome and simultaneously sequence multiple DNA fragments, effectively capturing a wide range of genetic variations across the genome [\[22\]](#page-6-14).

Another key feature of GBS is its flexibility in handling diverse species and populations, including biparental, multi-parental, and natural populations. This adaptability allows researchers to conduct genome-wide association studies (GWAS), quantitative trait locus (QTL) mapping, and GS in a wide range of species [\[22-25\]](#page-6-14). Furthermore, GBS can generate dense marker sets crucial for capturing recombination events and improving the accuracy of genomic predictions in breeding programs [\[20\]](#page-6-12).

However, despite its cost effectiveness and utility, GBS has some limitations. It focuses only on specific parts of the genome, and certain regions may not be represented or completely missed. Additionally, imputing missing genotypes can be challenging, particularly in species with high heterozygosity or complex structural variation [\[20\]](#page-6-12). To mitigate these issues, GBS data require stringent quality control and thorough bioinformatic processing to ensure reliable downstream analyses [\[26\]](#page-6-15).

As sequencing technologies improve, GBS has advanced with better bioinformatics pipelines, such as Trait Analysis by association, Evolution and Linkage (TASSEL)-GBS, which increase the efficiency of SNP discovery and genotype calling [\[27\]](#page-6-16). These innovations, combined with a reduction in sequencing costs, make GBS an indispensable tool for accelerating genetic gain in crop breeding programs, particularly for minor crops such as mung bean and adzukibean, which are critical for global food security and agricultural sustainability.

3.2. Whole Genome Resequencing (WGR)

The WGR emerged as one of the most powerful tools for unraveling genetic diversity and identifying genetic variation across the entire genome. Unlike targeted sequencing approaches, WGR enable researchers to capture the complete genome sequence of an individual, thereby providing the most comprehensive dataset for genetic studies [\[28\]](#page-6-17). WGR was instrumental in mapping the genetic architecture of complex traits, enabling the identification of SNPs, structural variants, insertion-deletions, and other genomic alterations across both coding and noncoding regions [\[29\]](#page-6-18).

The ability to detect both common and rare variants of WGR is particularly beneficial for crops with complex genomes or limited reference data [\[30\]](#page-6-19). A high depth of coverage of entire genomes can reveal subtle genetic differences that may contribute to important agronomic traits such as disease resistance [\[31\]](#page-6-20). For instance, [Cook,](#page-6-21) et al. [32] reported resistance to soybean cyst nematodes (SCN), and [Maron, et al. \[33\]](#page-6-22) revealed that a higher copy number of the MATE1 gene is linked to superior AI tolerance in maize. This high resolution makes WGR particularly useful for GS and GWAS because it offers specific genomic markers for agronomic traits across the entire genome [\[34\]](#page-6-23).

However, despite its high performance, WGR remains more expensive and data-intensive than those by reduced-representation sequencing (RRS) methods such as GBS and Restriction site-associated (RAD) Seq [\[35\]](#page-6-24). WGR provides much more comprehensive genome coverage than that by RRS but also comes at a higher cost in both sequencing and data processing. RRS methods selectively sequence portions of the genome, which makes them more cost-effective and faster to analyze $\lceil 35 \rceil$.

A major challenge with WGR is managing the depth of coverage necessary for accurate variant calling, particularly when distinguishing rare variants or completing structural variations. For example, in species with large repetitive genomes, aligning sequenced reads to a reference genome can be computationally intensive and prone to errors if coverage is insufficient [\[36\]](#page-6-25). Despite these challenges, as sequencing costs gradually decreased and computational analyses have developed, WGR has become accessible, especially for crops where detailed genomic information is required for selection $[31]$.

3.3. SNP Array

With the development of Next-Generation Sequencing (NGS) technology, large-scale sequencing enabled the discovery of genetic variants. The identification of large numbers of SNPs in crops was accompanied by the

development of high-throughput genotyping tools, such as SNP arrays, which allow for the simultaneous genotyping of thousands to millions of molecular markers [\[37\]](#page-6-26). Currently, more than 40 K SNPs array tools that play a crucial role in accelerating the rate of genetic gains in crop breeding have been developed [\[38-40\]](#page-6-27). The major crops include wheat (35, 90, and 820 K) $[41-43]$ rice (44 and 50 K) $[44, 45]$ $[44, 45]$ maize (50 and 600 K) $[2, 46]$ $[2, 46]$ and cotton (35 and 63 K) [\[47\]](#page-6-32). Such high-throughput and easy to genotyping SNP arrays can cost-effectively and quickly proceed with GWAS, quantitative trait locus (QTL) mapping, and GS $[48-50]$.

In addition to their cost-effectiveness and high-throughput capacity, SNP arrays offer several advantages for crop-breeding programs. They provide excellent reproducibility and consistency across different platforms and studies [Hiraoka, et al. \[51\]](#page-7-0) and [Boichard, et al. \[52\]](#page-7-1) which is critical for large-scale breeding initiatives where data comparability is key. Furthermore, allowing precise and accurate genotyping with a high call rate and low error rate, it is suitable for crops with complex genomes [\[37\]](#page-6-26). Accordingly, SNP arrays for particular species were developed and can be utilized diversely across different populations, studies, and purposes.

The conflict with the prominent functions of SNP arrays and the development of novel SNP arrays associated with agronomic traits can be restricted by the reference population or cost [\[31\]](#page-6-20). Although SNP arrays are effective for detecting known variants, they are designed based on reference populations, which can limit their ability to detect novel or rare alleles in other populations [\[53\]](#page-7-2). If the genetic diversity of a reference population is not representative, SNP arrays may miss important variants in different breeding lines or crops. Consequently, the development of a novel SNP array can be time- and cost-intensive due to the identification of new genetic variants with agronomic traits in other reference populations and validation tests to determine whether they are useful [\[54\]](#page-7-3). [Table 2](#page-3-1) presents the advantages and limitations of various genotyping methods.

4. Limitation of Application in Korea

As described in the 'Advantages of the GS', it has significant advantages over traditional MAS or phenotypic selection, primarily because it enables breeders to capture small genetic effects involved in complex traits or quantitative traits [\[14\]](#page-6-6). GS is now widely adopted in crop breeding programs globally for major crops, such as rice, wheat, and maize. [Cui, et al. \[55\]](#page-7-4) reported the GS for ten agronomic traits, whereas [Huang, et al. \[56\]](#page-7-5) focused on disease resistance in rice. In maize and Wheat, many researchers are working to maximize breeding efficiency through GS by following breeding strategies of the International Maize and Wheat Improvement Center (CIMMYT) [\[18,](#page-6-10) [57-59\]](#page-7-6). In addition to rice, wheat, and maize, other major crops such as soybean and cotton have also seen extensive applications of GS in breeding programs. For example, in soybean, researchers developed highdensity SNP arrays, such as Soy50K and SoySNP arrays, to facilitate the identification of key traits such as seed composition, flooding tolerance, and disease resistance. Advancements in soybean genomics accelerated breeding for improved yield and stress resilience [\[60,](#page-7-7) [61\]](#page-7-8). Similarly, in cotton, genomic resources were employed to improve fiber quality $[62]$.

In Korea, studies increasingly focused on the application of GS in various major crops. [Kang, et al. \[7\]](#page-5-8) conducted a study using the Korean wheat (K-wheat) core collection to optimize the GS for key agricultural traits. Similarly, [Kim, et al. \[63\]](#page-7-10) developed a customized 580 K chip array to enhance GS and GWAS in rice. [Kang, et al.](#page-5-8) [7] and [Kim, et al. \[63\]](#page-7-10) emphasized the importance of tailoring GS tools to local crop varieties and specific traits of interest. In wheat, Kang et al. focused on optimizing GS for traits related to adaptability and yield, whereas Kim et al. addressed key productivity and quality traits in rice. These efforts led to significant advancements in the use of high-throughput genotyping platforms to improve the precision and efficiency of breeding programs for major crops in Korea, ultimately contributing to the development of more resilient and high-yield varieties adapted to local agricultural conditions [\[7,](#page-5-8) [63\]](#page-7-10). Genetic diversity analyses and GS were actively pursued for other major crops in Korea. For example, [Cho, et al. \[64\]](#page-7-11) conducted soybean research focusing on identifying key adaptive traits using whole-genome sequencing data. They analyzed soybean accessions from various countries, including Korea, China, Japan, and the United States, and found that Korean accessions revealed significant genetic diversity.

Minor crops, similar to those of major crops, have significantly high nutritional value and require GS to improve their productivity and adaptability. However, in Korea, research on these crops faces challenges due to their relatively low domestic demand, which makes funding and research initiatives difficult to prioritize. Despite their importance in enhancing agricultural diversity and nutrition, research in Korea traditionally focused on major crops such as rice, wheat, and soybean.

[Ha, et al. \[65\]](#page-7-12) conducted a detailed genomic study on mung bean, providing essential genetic resources by identifying quantitative trait loci (QTLs) associated with important traits, such as drought tolerance and pod maturity. However, even with these foundational genetic resources, GS has not yet been widely applied in mung bean breeding programs. Similarly, [Kim, et al. \[66\]](#page-7-13) reviewed the current genomic resources available for mung

bean, emphasizing the need for further GS development to optimize breeding for traits such as disease resistance and seed quality $[66]$.

Similarly, sesame, another important minor crop, has seen advances in genetic studies, particularly in the identification of key loci associated with complex traits, such as disease resistance. [Asekova, et al. \[67\]](#page-7-14) combined QTL mapping and GWAS to identify candidate genes related to Phytophthora blight resistance in sesame. They identified SNP markers on chromosome 10 associated with resistance to Phytophthora nicotianae. These findings highlighted the potential use of genetic markers to improve disease resistance in sesame through breeding strategies.

However, despite the discovery of numerous QTLs and genetic variants related to various agronomic traits, the application of GS has not progressed in minor crops. The primary challenges are limited domestic demand and high costs associated with GS implementation, which have significantly hindered the development of comprehensive GS programs for these crops [\[14,](#page-6-6) [68\]](#page-7-15). Although the genetic groundwork is in place, including significant progress in marker discovery and the mapping of complex traits, the practical implementation of GS in Korea remains a challenge [\[14\]](#page-6-6).

5. Future Challenges

To overcome the current challenges of GS for minor crops in Korea, cost-effective genotyping methods such as GBS or custom SNP chip arrays offer a viable solution. GBS is a cost-effective, high-throughput method for generating genome-wide markers, making it a popular tool for GS, particularly in species with limited genomic resources [\[20\]](#page-6-12). Customized SNP arrays also offer a targeted approach, allowing breeders to focus on known genetic variants relevant to specific traits $\lceil 69 \rceil$. However, even cost-effective methods face limitations when applied to minor crops because the scale of research and available resources remain insufficient to justify the high cost of customized chip development.

A promising approach to address the various challenges in minor crops, where GS cannot play a critical role, the multi-species SNP array is proposed, where a single chip can be used across multiple species, significantly lowering the costs per species. For example, Silva-[Junior, et al. \[70\]](#page-7-17) developed a flexible multi-species 60 K SNP chip for Eucalyptus, demonstrating its utility across 12 species and its potential to extend multi-species genotyping for practical breeding applications in closely related species. Similarly, a multispecies SNP array was designed for Colossoma macropomum (tambaqui) and Piaractus mesopotamicus (pacu), providing an efficient genomic tool for both species, thereby reducing costs and enhancing genetic research in aquaculture [\[71\]](#page-7-18). Furthermore, multispecies SNP arrays were developed for applications in both plant and aquaculture, covering species such as Rubus spp. (raspberry and blackberry), Leptospermum scoparium (mānuka), Chrysophrys auratus (Australasian snapper), and Pseudocaranx georgianus (silver trevally). These arrays facilitate comparative genetic studies across species, enabling researchers to optimize genetic resources for use in breeding programs and conservation and addressing important economic and ecological goals in both fields [\[72\]](#page-7-19). [Table 3](#page-4-1) presents the criteria used for SNP selection in the development of multi-species SNP arrays for each species, detailing sequencing methods, call rates, minor allele frequencies (MAF), and final SNP counts, along with their references.

Species	Sequencing method	Call rate	MAF	Final SNPs	Reference
Eucalyptus spp.	WGR	$>97.2\%$	> 0.01	60,904	Silva-Junior, et al. $\lceil 70 \rceil$
Rubus spp.	GBS, WGS	96.4	>0.05	12,723	
Manuka	WGR			9,002	Montanari, et al.
Snapper	Illumina Novaseq	98.3		18,489	[73]
Trevally	WGS			20,234	
Tambaqui	$RAD-seq$	$>97\%$	>0.01	23,739	Mastrochirico-
Pacu				23,768	Filho, et al. $[71]$

Table 3. Summary of criterions of SNPs selection for multi-species SNP array.

Multispecies SNP arrays offer several advantages beyond cost-effectiveness for GS in minor crops. First, they enable researchers to capture a broader range of genetic diversity by including polymorphisms conserved across multiple species, allowing for more comprehensive assessments of genetic variation, and aiding in the study of population structure and evolutionary dynamics. This diversity also strengthens genomic prediction models, especially when resources for unique species-specific arrays are limited, making multispecies SNP arrays ideal for minor or underfunded crops [\[73,](#page-7-20) [74\]](#page-7-21).

Furthermore, multispecies SNP arrays support data integration across species, facilitating meta-analyses and improving the statistical power of genetic predictions. This approach is particularly beneficial for breeding programs because it enables researchers to perform cross-species comparisons more effectively, thereby enhancing the understanding of complex traits influenced by environmental interactions [\[75\]](#page-7-22). Additionally, by integrating genomic data across species, multi-species arrays can significantly increase the accuracy and power of predictions for agronomic traits such as disease resistance and yield, as pooling diverse datasets strengthens the reliability of genetic predictions and accelerates breeding cycles [\[72\]](#page-7-19).

Conclusively, multi-species SNP arrays present an optimal approach for implementing GS in minor crops and provide a cost-effective and robust solution. This approach allows the application of a single SNP chip across multiple species, thereby significantly reducing the expenses associated with developing species-specific genotyping platforms. For minor crops, which often face funding and resource constraints, this method is especially practical, as it not only reduces costs, but also captures a wider range of genetic diversity. Such diversity is instrumental in improving the accuracy and statistical power of genetic predictions, enabling a more effective selection of complex traits across diverse environmental conditions. [Figure 1](#page-5-9) illustrates the process of SNP selection for multi-species SNP arrays, while [Figure 2](#page-5-10) presents the overall flowchart for the development and application of these arrays in genomic selection.

Figure 2. Overall flowchart of development and application of Multi-species SNP Array.

6. Conclusions

Summarily, multispecies SNP arrays provide an effective and economical approach for advancing GS in minor crops, enhancing genetic diversity capture, and enabling the robust selection of complex traits, thereby supporting sustainable agricultural productivity and adaptability across diverse environments.

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