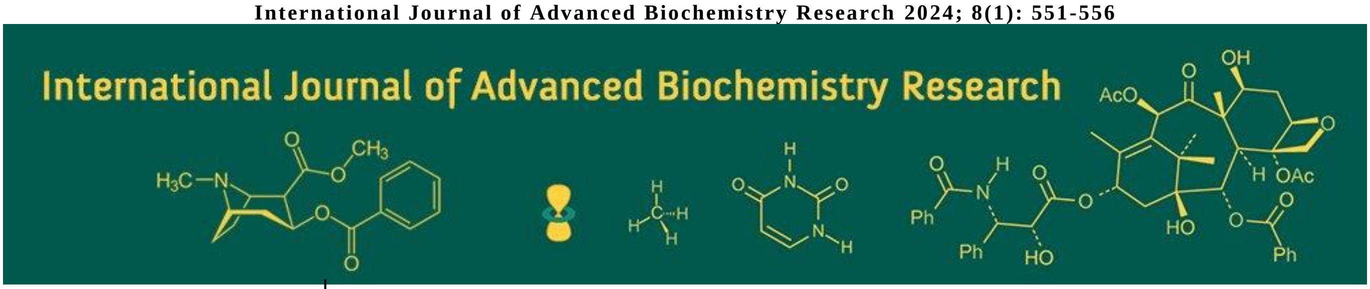

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Accelerating soybean breeding: A comprehensive review of speed breeding

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Abstract

This review explores the pivotal role of soybeans in global agriculture, emphasizing their nutritional richness and multifaceted contributions. Recognizing the challenges faced by traditional breeding practices, including limited genetic diversity and prolonged breeding cycles, the paper underscores the significance of innovative approaches such as speed breeding (SB) in soybean improvement. Speed Breeding, grounded in environmental manipulation, emerges as a revolutionary tool, accelerating plant growth, development, and breeding cycles. Integrating speed breeding with modern breeding technologies, including genomic selection, high-throughput phenotyping, marker-assisted selection, genome editing, and precision phenotyping, offers unparalleled advantages such as accelerated genetic gain and efficient trait improvement. However, challenges in optimizing growth conditions, ensuring phenotypic stability, and addressing economic constraints are discussed. The paper highlights the need for collective efforts to fully harness the benefits of speed breeding in soybean breeding, paving the way for sustainable, resilient, and high-yielding soybean varieties to meet global food security demands.

Keywords: Speed breeding (SB), soybean, genomic selection (GS), high-throughput phenotyping (HTP), marker-assisted selection (MAS), genome editing

Introduction

Due to its multifaceted contributions, soybean (*Glycine max*), a prominent member of the Fabaceae family and the Glycine genus, is a crucial player in global agriculture. With its taproot system, short-day flowering response, and determinate or indeterminate growth habit, soybean produces one to five seeds per pod, characterized by high protein and oil content. Believed to have originated in China around 5000 years ago, the soybean's journey has become a crucial component of worldwide agriculture. Flourishing in various climatic and soil conditions, soybean exhibits resilience to drought, salinity, acidity, and alkalinity while remaining sensitive to frost, waterlogging, and pests. Reducing the dependence on nitrogen fertilizers for sustainability, soybean demonstrates the capability to fix atmospheric nitrogen through symbiosis with rhizobia bacteria. (Pagano & Miransari, 2016) [11]. For 60.5% of total global oilseed production in 2022-23 (FAOSTAT), soybean holds unparalleled importance, finding applications in human food, animal feed, biodiesel, and industrial products. The crop's nutritional richness, boasting high-quality protein, essential fatty acids, phytoestrogens, antioxidants, and dietary fiber, further underscores its significance for human and animal consumption. As the most critical oilseed crop globally, soybean faces challenges ranging from climate change and pests to environmental concerns. Developing new cultivars with desired characteristics through genetic improvement is critical in solving these challenges (Jiang, 2023) [9]. Breeding is a powerful tool to improve soybean traits and meet the growing demand for this crop. However, breeding also faces challenges, such as the limited genetic diversity of cultivated soybeans and the long and complex process of developing new varieties. Therefore, speed breeding (SB) is used to accelerate the breeding process. This review focuses on the limitations of traditional breeding practices, principles, and applications of SB in soybean crops and the integration of SB with modern breeding technologies.

Limitations of traditional breeding practices

Traditional breeding methods involve cross-pollination between two different plants and selecting desired traits in the offspring. While this process has successfully improved crop varieties, it relies heavily on natural pollination processes and is time-consuming. Additionally, traditional breeding often leads to limited genetic variation due to its dependence on naturally available genetic resources. SB is a modern technique that utilizes controlled environments with optimized growth conditions to accelerate plant growth and development. By providing artificial lighting and carefully controlling temperature, humidity, and nutrient levels, scientists can manipulate plant growth cycles to achieve multiple generations within a single year. This allows for rapid trait selection and genetic improvement. SB overcomes several limitations of traditional breeding methods. Firstly, it significantly reduces the time required for generating new varieties compared to traditional methods, which may take several years or even decades. Secondly, it allows researchers to quickly introduce new genes from diverse sources into existing crops, thereby enhancing genetic diversity. (Bhatta *et al*., 2021) [3].

Current challenges in soybean breeding and need for speed breeding

Soybean breeding encounters challenges such as genotype inflexibility and a low transformation frequency, hampering the efficiency of transgenesis and breeding endeavors. Achieving genetic transformation across diverse soybean genotypes has been a formidable task, with an average transformation frequency of less than 5%. (Xu *et al*., 2022 & Fang *et al*., 2021) [18, 4]. Innovative SB methods have been devised to address these challenges, incorporating strategies like off-site generation advancement, fresh seeding, and marker-assisted selection. This integrated approach aims to mitigate the limitations by reducing generation length and facilitating soybean improvement, offering a promising solution to enhance the overall efficiency of soybean breeding efforts. (Fang *et al*., 2021) [4].

Principle of speed breeding

Speed Breeding is a technique that involves the manipulation of environmental conditions to accelerate plant growth, development, flowering, and seed set, reducing the time taken to generate each breeding generation. It allows plant breeders to deliver improved crop varieties more rapidly and integrate with conventional, marker-assisted, and genetic engineering breeding approaches to select elite genotypes and lines with novel traits effectively. The most appropriate selection methods amenable to SB include single seed descent (SSD), single pod descent (SPD), and single plant selection (SPS) methods, which allow for rapid generation advancement and maintenance of genetic diversity (Wanga *et al*., 2021) [16].

SB involves intentionally adjusting and controlling various cultivation conditions, as outlined below: -

A. Lighting Conditions: Speed Breeding employs variations in daily exposure to light and dark regimes, known as photoperiod, to impact plant growth, flowering, and seed set. It encompasses adjustments in the amount and wavelength of light, influencing crucial physiological processes such as photosynthesis, stomatal conductance, and transpiration rate. Furthermore, alterations in light quality and intensity, indicative of diverse light energy levels per unit area, impact the pace of photosynthesis and biomass accumulation. Manipulating these parameters-photoperiod, light quality, and light intensity-can induce early flowering and seed set in the crop, ultimately reducing the time needed to generate each breeding generation (Wanga *et al*., 2021) [16].

B. Temperature: Speed breeding emerges as a technique capable of manipulating temperature to induce early flowering and seed set. Each crop exhibits a distinct optimum temperature range for optimal growth and development, with deviations from this range potentially inducing stress and diminishing yield potential. SB utilizes controlled environments such as growth chambers, greenhouses, or polytunnels to precisely adjust the temperature in alignment with the specific crop requirements, thereby expediting the breeding cycle. The impact of temperature extends across various facets of plant physiology and biochemistry, influencing critical processes such as photosynthesis, respiration, transpiration, enzyme activity, hormone synthesis, gene expression, and flowering time (Wanga *et al*., 2021) [16]. This comprehensive approach to temperature manipulation underscores the versatility and effectiveness of SB in optimizing plant development for improved crop outcomes.

C. Nutrient and Hormone Delivery: Under SB conditions, various plant hormones, including gibberellins, cytokinins, auxins, and ethylene, play pivotal roles in influencing flower induction, seed development, and seed dormancy across different crops. Additionally, diverse nutrient solutions significantly impact the growth rate, flowering time, and seed set of various crops within SB. The interaction between plant hormones and nutrient solutions highlights the intricate mechanisms in optimizing crops' growth and reproductive processes under accelerated breeding conditions.

D. Plant Density: Plant population density, denoting the number of plants per unit area, plays a crucial role in shaping the growth and yield of crops. Specifically, high-density planting has demonstrated its potential to induce early flowering and seed set in select crops like wheat, barley, chickpea, and canola (Wanga *et al*., 2021) [16]. This effect is achieved by intensifying resource competition and creating a microclimate within the canopy (Warnasooriya & Brutnell, 2014). However, it is essential to recognize that the optimal plant density is contingent upon factors such as crop species, genotype, and environmental conditions. Determining the ideal density necessitates experimentation to prevent adverse effects on plant health and quality. In SB, practitioners strategically employ high-density planting alongside other environmental manipulations, including extending the photoperiod, increasing light intensity, adjusting temperature, and managing soil moisture. This synergistic approach accelerates generation cycles and effectively shortens the overall breeding time, exemplifying the versatility of SB techniques.

E. Carbon Dioxide Levels: Elevated carbon dioxide (CO_2) levels can expedite plant growth and facilitate shifting from vegetative to reproductive stages in specific plant species (Jagadish *et al*., 2016) [7]. However, the impact of increased

CO_2 varies across different crop species and genotypes. For example, increased carbon dioxide levels of 400 ppm reduced the days to flowering by two days in soybeans, suggesting that elevated CO_2 concentrations may positively affect the flowering process in soybean plants (Springer & Ward, 2007) [15]. The strategic supplementation of CO_2, coupled with precise light and temperature cycles, has showcased the ability to significantly reduce crop cycles, enabling the generation of multiple crops per year, particularly notable in soybeans. However, the effect on flowering time may not be consistent with increased CO_2 levels. A consistent enhancement in the overall flower count offers advantages for developing numerous crosses (Wanga *et al*., 2021) [16].

Applications of Speed Breeding in Soybean Improvement

Sl. No.	**Cultivation Condition**	**Parameter Focused**	**Experimental Material**	**Results**	**Reference**
1.	Lighting Conditions (Day Length, Light Quality, Light Intensity)	Plant growth and development	Light Emitting Diodes. Day length- Adjusted to 10 hrs. Light Quality- Blue light enriched, Far-red deprived.	1. Short and sturdy soybean plants obtained. The plants flowered 23 DAS and matured within 77 days, allowing up to 5 generations/year. 2. Far-red light negatively affected morphology, elongating the petioles and increasing the chances of lodging. 3. Lower Red: Blue ratio led to short and sturdy plants, but flowering time and plant height were unaffected. 4. Green light improved visual observations but did not affect flowering time and plant height. 5. Light intensity above 1000 $\mu mol/m^2s$ led to 2 days earlier flowering and shorter plant stature.	Jähne, F., Hahn, V., Würschum, T., & Leiser, W. L. (2020) [8]. Speed breeding short-day crops by LED-controlled light schemes. Theoretical and Applied Genetics, 133(8), 2335-2342.
2.	Red and Blue lights (RB) vs. Full Spectrum White Lights (FS)	1. Plant Growth and Development.	Soybean lines and breeding materials.	RB light significantly reduced plant height at the R1 and R7 stages. FS light also reduced plant height but less significantly. No significant impact on vegetative biomass, Leaf Soil Plant Analysis Development values (SPAD), and seed numbers were not significantly affected.	Harrison, D., Da Silva, M., Wu, C., De Oliveira, M., Ravelombola, F., Florez-Palacios, L., & Mozzoni, L. (2021) [5]. Effect of light wavelength on soybean growth and development in a context of speed breeding. Crop Science, 61(2), 917-928.
		2. Days to Critical Reproductive Stages.	Maturity Group 4 (MG4) and Maturity Group 5 (MG5) lines, segregating populations, Mixed Maturity groups	RB light shortened the interval from planting to R7 by 1.5 days compared to FS light. Significant variations were observed based on maturity classes. Generation time was reduced by 56-66 days compared to regular field conditions.	
		3. Seed Production and Quality.	Seed harvested at R7 growth stage.	RB light enabled meeting the minimum of 1 seed/plant. Seeds harvested immature had an average germination rate of 81.7%.To conclude, RB provides a slight advantage in growth acceleration and reduced plant height compared to FS light. Under RB light conditions, soybean breeding programs in the U.S. Mid-south could advance up to 5 generations/year.	
3.	CO_2 supplementation.	1. Growth enhancement.	Compact Growth Chambers with Fluorescent lamps, Elite Japanese Soybean cultivar Enrei.	CO_2 supplementation enhanced total leaf area, plant height, total length of branches, dry leaf weight, dry stem weight, and dry root weight. In the Enrei cultivar, seed yields significantly increased in plants with CO_2 supplementation. Average seed numbers per plant were higher with CO_2 supplementation, and average seed weight significantly increased with CO_2 supplementation, indicating improved seed quality.	Nagatoshi, Y., & Fujita, Y. (2019) [10]. Accelerating soybean breeding in a CO_2-supplemented growth chamber. Plant and Cell Physiology, 60(1), 77-84.
		2. Efficiency in crossing.	Growth chambers with and without CO_2 supplementation, smaller pots (0.4L) for flower production analysis	Number of healthy flowers significantly increased with CO_2 supplementation. Abnormal flowers were less frequent in CO_2-supplemented chambers. In flower production analysis, healthy flowers were observed even in smaller pots with CO_2 supplementation, this indicates potential for accelerated breeding with smaller individual plant spaces. Crossing efficiency was significantly higher	

				in CO_2-supplemented growth chambers. 98.5% of harvested seeds were hybrids, demonstrating the success of the crossing process. Up to 5 generations/year is possible in growth chambers compared to 1-2 generations in a field or greenhouse.	
4.	Off-site Summer Nursery	Generation Turnover	Cost-saving off-site summer nursery pattern, shorter day length, higher temperature	Reduced generation cycles under natural conditions, Successful generation of two soybean cultivars in a shorter time, at least 4 generations/year possible.	Fang, Y., Wang, L., Sapey, E., Fu, S., Wu, T., Zeng, H., & Han, T. (2021) [4]. Speed-breeding system in soybean: integrating off-site generation advancement, fresh seeding, and marker-assisted selection. Frontiers in Plant Science, 12, 717077.
5.	Fresh Seeding Method	Generation Turnover	Harvesting mature pods at R6 or full-seed stage, drying seeds, and immediate sowing	Shortened generation duration by 7-10 days, Quicker turnover of generations for more rapid selection and evaluation of lines.	

Integration of speed breeding with modern breeding technologies

A. Combining Genomic Selection (GS) with SB: Speed genomic selection (Speed GS) is a breeding strategy that combines the principles of genomic selection (GS) with the rapid generation advancement achieved through SB. Genomic selection is a modern breeding approach that uses genomic data to predict the breeding value of individuals, allowing for the selection of superior plants at an early stage of development. In the context of SB, Speed GS aims to leverage the accelerated breeding cycle to enhance the efficiency of genomic selection. By rapidly advancing generations through SB, breeders can perform more intense and frequent selection based on genomic information, leading to higher genetic gain/year. The integration of Speed GS with SB offers several potential advantages:

1. **Accelerated Genetic Gain:** By combining the rapid generation advancement of SB with genomic selection, breeders can achieve faster genetic gain compared to traditional breeding methods.
2. Early Selection: Genomic selection allows for the early identification of superior individuals, and when combined with SB, this early selection can be further amplified due to the shortened breeding cycle.
3. **Efficient Trait Improvement:** Speed GS enables the simultaneous improvement of multiple traits with different genetic architectures, improving crop varieties in a shorter time frame (Singh I. *et al*., 2021) [13].
4. However, implementing Speed GS requires careful consideration of the specific genomic and phenotypic data needed for accurate selection and the development of tailored breeding strategies to leverage the benefits of both speed and genomic selection fully.

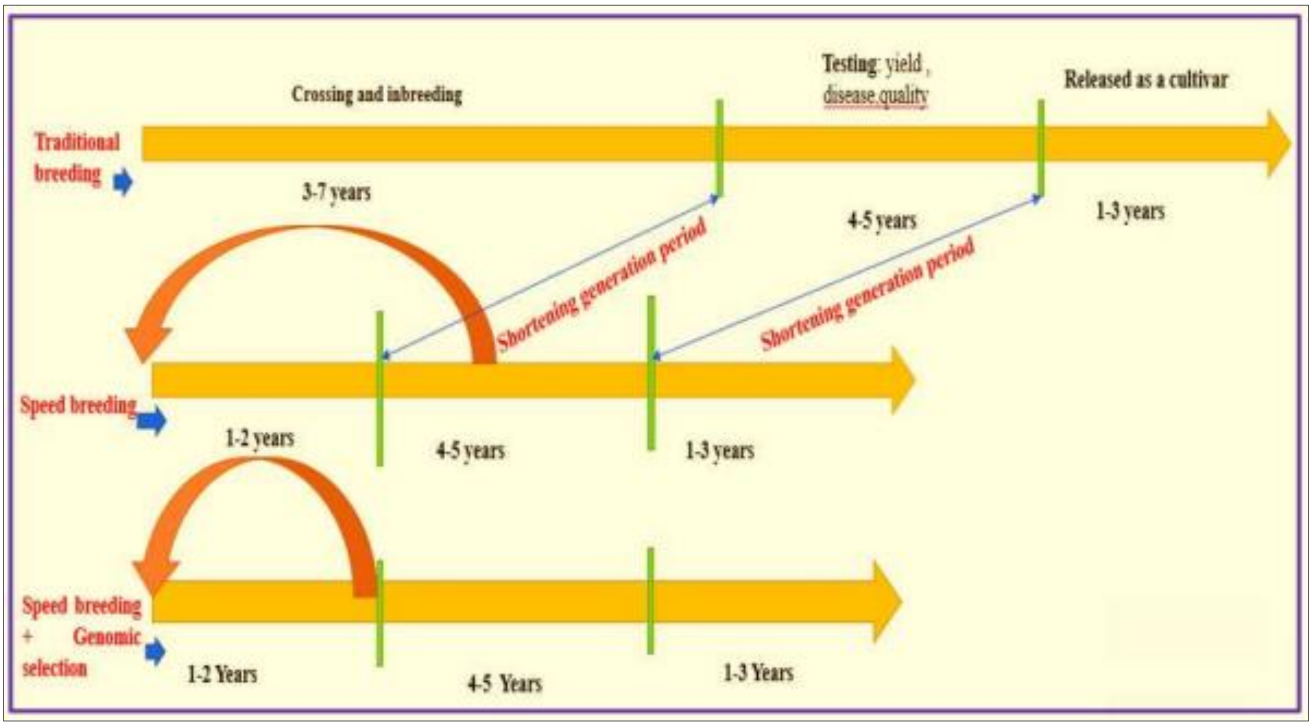

Fig 1: Improving genetic gains through speed breeding and genomic selection approaches. (Singh, S. *et al*., 2021) [13]

B. Combining High-Throughput Phenotyping (HTP) with SB: High-throughput phenotyping (HTP) is a modern breeding technology that uses advanced imaging and sensing technologies to collect large amounts of data on plant traits. This data can be used to identify desirable traits and select plants with those traits for further breeding. When combined with speed breeding, HTP can accelerate gene discovery and characterization, developing new and improved crop varieties. SB allows for the rapid generation advancement of crops, while HTP enables the collection of large amounts of data on plant traits quickly. This combination can significantly reduce the time and resources required for traditional breeding methods. For example, HTP can collect data on plant height, leaf area, other morphological traits, and physiological traits such as photosynthesis rate and water use efficiency. This data can be used to identify and select plants with desirable traits for further breeding. Additionally, HTP can identify plants resistant to pests and diseases, which can be incorporated into breeding programs to develop more resilient crop varieties (Singh I. *et al*., 2021) [13].

C. Combining Marker-Assisted Selection (MAS) with SB: Marker-Assisted Selection (MAS) is a breeding approach that uses molecular markers to identify plants with desirable traits. By combining MAS with SB, breeders can more efficiently identify and select plants with desirable traits, developing improved crop varieties. MAS allows breeders to identify and select plants with specific genetic markers associated with desirable traits, such as disease resistance, improved yield, or enhanced nutritional content. By incorporating MAS into SB programs, breeders can rapidly screen and select plants with the desired molecular markers, thereby accelerating the development of improved crop varieties (Singh I. *et al*., 2021) [13-14].

However, it is essential to note that integrating MAS with SB also presents some limitations. For instance, the availability of validated molecular markers for all desirable traits may be limited, especially in certain crop species. Additionally, the cost and technical expertise required for molecular marker analysis may pose challenges for widespread adoption, particularly in resource-constrained breeding programs.

D. Combining Genome Editing with SB: Genome editing is a modern breeding technology that enables the precise modification of specific genes in a plant's genome. Breeders can more efficiently develop crops with desirable traits by combining genome editing with SB, such as disease resistance or improved yield. The integration of genome editing with SB offers several potential advantages. Firstly, SB allows for the rapid generation advancement of crops, enabling breeders to assess the effects of genome edits across multiple generations quickly. This accelerated breeding cycle facilitates the evaluation of edited traits and the selection of plants with the desired genomic modifications in a shorter time than traditional breeding methods. Furthermore, the precise nature of genome editing techniques, such as CRISPR-Cas9, allows breeders to target specific genes associated with desirable traits. This targeted approach enhances the efficiency of trait modification and enables the development of crop varieties with precise genetic alterations, including disease resistance, improved nutritional content, and enhanced agronomic traits.

While integrating genome editing with SB holds significant promise for crop improvement, ethical and regulatory considerations surrounding using genome-edited crops should be carefully addressed. Additionally, the potential off-target effects of genome editing techniques should be thoroughly evaluated to ensure the safety and stability of edited crop varieties (Singh I. *et al*., 2021) [13-14].

E. Combining Precision Phenotyping with SB: Precision phenotyping involves using advanced imaging and sensing technologies to collect detailed data on plant traits at a high resolution. By combining precision phenotyping with SB, breeders can more accurately identify and select plants with desirable traits, developing improved crop varieties. The integration of precision phenotyping with SB offers several advantages for crop improvement. Advanced imaging and sensing technologies, such as drones, high-resolution cameras, and spectral sensors, enable the non-destructive and high-throughput assessment of plant traits, including morphological, physiological, and biochemical characteristics. By leveraging precision phenotyping in conjunction with SB, breeders can rapidly and accurately evaluate a large number of plants for specific traits, such as disease resistance, drought tolerance, and yield-related attributes. This comprehensive and detailed assessment allows for precisely identifying plants with the most desirable traits, facilitating the selection of superior genotypes for further breeding and variety development.

Furthermore, the high-resolution data obtained through precision phenotyping can provide valuable insights into the genetic and environmental factors influencing trait expression, enabling breeders to understand better the underlying mechanisms governing trait variation. This information has the potential to guide specific breeding approaches and the creation of crop varieties showcasing improved performance across various environmental circumstances. (Singh I. *et al*., 2021) [13-14].

While precision phenotyping offers significant benefits for crop improvement, implementing advanced imaging and sensing technologies may require specialized expertise and infrastructure. Interpreting and integrating large-scale phenotypic data into breeding programs necessitate robust bioinformatics and data analysis capabilities (Singh I. *et al*., 2021) [13-14].

Challenges in speed breeding of soybean

Implementing speed breeding for soybean improvement brings several challenges requiring careful consideration and management. One crucial aspect involves maintaining optimal growth conditions, including precise control of temperature, light intensity, and photoperiod, to ensure the effectiveness of the SB protocol. Additionally, the diverse genetic backgrounds of soybean genotypes pose a challenge, as different cultivars may exhibit varying responses to accelerated breeding conditions. Harvesting seeds at the proper maturity stage guarantees high seed viability and prevents premature germination. The resource-intensive nature of establishing and maintaining SB facilities, especially those equipped with controlled environments like growth chambers, presents economic challenges that may limit widespread adoption, particularly in resource-constrained settings. Ensuring the phenotypic stability of soybean lines developed through SB is another critical challenge, requiring a thorough evaluation to confirm that accelerated breeding does not compromise trait stability across diverse environments (Sharma *et al*., 2022) [12]. Furthermore, the successful integration of SB with modern breeding technologies demands careful coordination to maximize synergies between accelerated breeding and advanced genomic approaches. Addressing these challenges collectively is imperative for harnessing the full potential of

SB in soybean improvement and its seamless integration into mainstream breeding programs.

Conclusion

In summary, soybeans' vital role in global agriculture and their nutritional richness highlight the need for innovative approaches like SB to address challenges in traditional breeding methods. Using environmental manipulation, SB is a revolutionary tool for accelerating plant growth and breeding cycles. Integrating SB with modern breeding technologies, including genomic selection (GS), high-throughput phenotyping (HTP), marker-assisted selection (MAS), genome editing, and precision phenotyping, offers unprecedented benefits such as faster genetic gain and efficient trait improvement. Despite the transformative potential, challenges like optimizing growth conditions and ensuring phenotypic stability must be addressed for successful SB adoption in soybean breeding. Collective efforts are crucial to harness the full advantages of SB, paving the way for sustainable and high-yielding soybean varieties to meet global food security needs.

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