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Review

Revolutionizing Crop Production: The Imperative of Speed Breeding Technology in Modern Crop Improvement

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ABSTRACT

Speed breeding (SB) technology is an innovative solution to shorten the breeding cycle and accelerate crop improvement. The key factors of plant growth and development, including photoperiod, light intensity and quality, temperature, relative humidity, planting density and plant nutrition are manipulated in such a way as to stimulate flowering and seed set under controlled conditions. The development of SB technology may be challenging as crops tend to vary in their response to physiological manipulations. Therefore, crop-specific optimization is highly critical to developing successful SB technology in crops. The SB technology can also be synergistically integrated with cutting edge genomics and marker-assisted selection technologies to enhance genetic gain in crop breeding programmes. In this review, various aspects concerning the science and techniques underpinning SB technology, the successful implementation of SB technology in different crops, the inherent challenges faced, and the potential opportunities to integrate SB technology with cutting-edge genomics technologies towards accelerating crop improvement are discussed.

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INTRODUCTION

The expanding world population is projected to reach 10 billion by 2050, and the expected demand for food will increase significantly [1,2]. Crops, being sessile, get exposed to a variety of environmental challenges like climate change, pests, and diseases that threaten food security [3,4]. It will be necessary to develop new cultivars while minimizing the environmental damage caused to agriculture and sustaining higher yields [5]. Conventional breeding methods have been successful in producing high-yielding cultivars with resistance to pests and diseases and tolerance to abiotic stresses, which involves crossing different parent materials and developing multiple generations for desired traits. The most commonly used conventional breeding methods include mass selection, pure-line selection, hybridization, backcrossing, recurrent selection, etc., depending upon the mode of pollination of the crops [6]. These methods are time consuming for the development of new crop cultivars and decrease crops' genetic gain [7]. Owing to demerits in conventional breeding methods, the plant breeders have been continuously aiming to look for time and cost-effective breeding programs.

Plant breeding programmes require series of field experiments under diverse environmental conditions for testing and advancement of filial generations, which is costly and time-consuming. The method of single-seed descent (SSD) was born out of a need to speed up the breeding programmes by rapidly inbreeding a population prior to beginning individual plant selection and evaluation while reducing a loss of genotypes during the segregating generations [8,9]. Off-season sowing at the same or different locations [10,11] has been used to reduce the time required in plant breeding programs. Doubled haploid (DH) technology, which is capable of creating homozygous lines very rapidly, has been widely used to speed up crop breeding efforts. However, the DH process is very genotype-dependent, time-consuming, and highly skilled in nature [8,12–15]. Plant breeders, using the DH system unintentionally practice selections for many loci, thereby increasing the success rate of this approach. However, this might limit genetic variation in the breeding populations in responsive genome regions [14,16,17].

Recently, speed breeding (SB) has emerged as a successful technology that aims to shorten the breeding cycle (i.e., the time between crossing and the selection of progeny to use as parents for the next cross) and accelerate crop improvement through rapid generation advancement (RGA) [4,14,18,19] (Table 1). This is achieved by creating growing conditions that promote rapid plant growth and hasten flowering in controlled environments. SB enables researchers to develop new cultivars of crops in

a short time frame to achieve rapid genetic gain [20,21] and, thus, has great potential to revolutionise plant breeding and improve crop yields.

Table 1. Brief comparison with traditional breeding methods.

Aspect	Traditional Breeding	Speed Breeding
Breeding Cycle	Slow, taking several years	Accelerated, reducing timeframes
Evaluation	Few generations can be evaluated	Multiple generations in a short period
Trait Introduction	It takes a longer time to introgress new traits	Enables rapid trait incorporation
Adaptation to Climate Change	Limited capacity to develop climate-resilient varieties	Facilitates rapid development of climate-adapted crops
Resource Utilization	Requires large land areas and resources	Optimizes space, energy, and labor
Screening Efficiency	Limited population screening capacity	Allows screening of larger populations in small spaces and quicker time
Innovation Potential	A slower pace of innovation and research	Stimulates innovation and advancements
Genetic Gain	Gradual accumulation of genetic improvement over time	Facilitates faster genetic gain and selection progress by reducing generation time
Application Scope	Broadly applicable to various crops	Applicable to a wide range of crops after protocol optimization
Adoption Challenges	Established practices	Requires infrastructure and technical expertise

Attaining genetic gain, or the enhancement in the mean performance of the progenies over selection cycles, is difficult due to the long generation time. It is influenced by factors such as genetic variability, heritability, selection intensity, and breeding time. The use of advanced molecular and omics tools can help recover the lost genetic variation, and high-throughput genotyping and phenotyping tools can increase the selection intensity [22]. However, reducing the time required for a breeding programme is critical to maximizing genetic gain [23]. SB methods accelerate trait introgression, and the progression of high-priority crosses to achieve homozygosity, provides an opportunity for trait selection in parallel with the fast development of inbred lines, leading to higher genetic gain [24] (Figure 1).

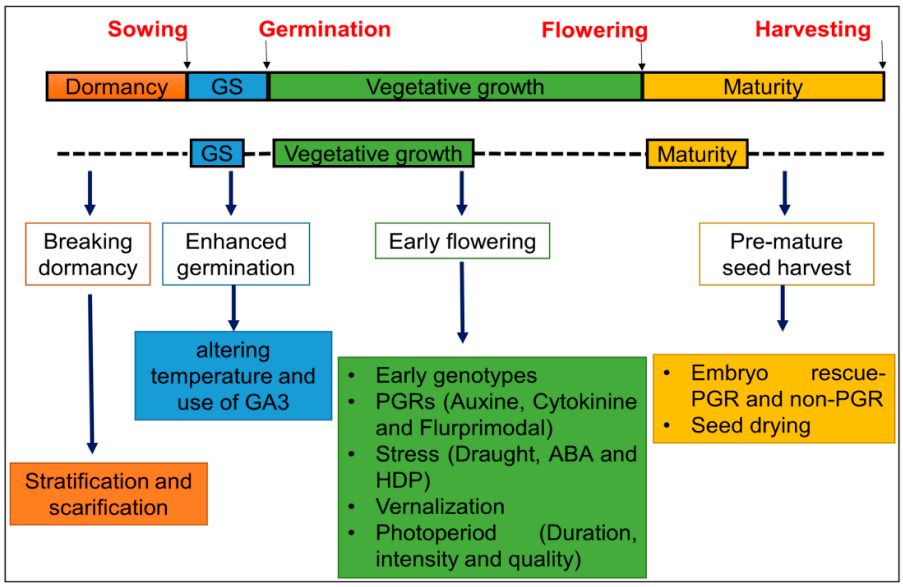

Figure 1. Intervening the key developmental stages of plants to reduce generation time (Source: [24]).

The first-ever SB procedure was developed by University of Queensland scientists in Australia [2,16,19] in crops such as wheat, barley, and chickpea [25,26]. Other research institutions and commercial companies around the world have since adopted the technology.

KEY OBJECTIVES AND BENEFITS OF SPEED BREEDING TECHNOLOGY

The key objectives of SB technology are to expedite the development of new crop cultivars and enhance plant breeding programmes efficiency and effectiveness. By creating growth conditions and manipulating light and temperature regimes, multiple generations of plants can be obtained in a shorter period, allowing breeders to achieve in months what would have previously taken years for line development and fixation. The shortened breeding cycle allows breeders to screen larger populations of crosses and select the most promising individuals quickly. Comparing the economics of RGA and the pedigree method for rice showed that RGA's cost-effectiveness was a part of SB [27]. SB optimises the use of resources such as space, energy, and labor. By manipulating growth conditions, researchers can accurately measure plant responses to different stresses, nutrient availability, or disease pressures. This data helps identify desirable traits and select superior individuals for further breeding work.

Successful implementation of SB technology has the significant potential to accelerate crop improvement, enhance genetic gain, and address global challenges in agriculture quickly. The accelerated breeding process enables the introduction of beneficial traits, such as increased yield [28], improved nutritional content, disease resistance [2,29,30] tolerance to specific stresses [31] and other agronomically important characteristics at a faster rate.

SB facilitates the rapid development of climate-resilient crop cultivars by enabling breeders to test and select desired traits under controlled

conditions that mimic the target environment [27,32]. SB uses the SSD approach to represent all alleles untill the genes are fixed. Practicing selection during SB negates the very purpose. It may be useful to create donor parents for a specific trait. SB can be suitably combined with phenomics, genomics, marker-assisted selection (MAS) and gene editing technologies for accelerating breeding programs. Utilizing high-throughput phenotyping technologies one can assess the performance of plants grown quickly under SB conditions [30,33]. Automated imaging systems can capture data on plant height, leaf area, flowering time, and stress responses among others [34]. Genomic data obtained through high throughput genotyping can be utilized to predict an individual plant's genetic potential for various traits, even at early growth stages.

PRINCIPLES AND CRITICAL COMPONENTS OF SPEED BREEDING TECHNOLOGY

Speed breeding relies on creating highly controlled environments that provide conditions for plant growth, flowering and seed formation. Growth chambers, controlled greenhouses, or specially designed growth rooms are used to maintain precise temperature, humidity, and light regimes. By manipulating these environmental factors, plant breeders can create conditions that stimulate accelerated plant growth and development. One of the fundamental principles of SB is providing plants with the required photoperiod by manipulating light and dark periods based on crop requirements for rapid development. For instance, crops like chickpea and wheat are long-day plants; flowering can be hastened by exposing plants to more extended periods of light [20], typically achieved through the use of supplemental lighting. The duration of the day can be effectively extended beyond the natural day length. This continuous light exposure promotes faster development, biomass production and increases stem digestibility in switchgrass [35]. Extended photoperiod is commonly employed to reduce generation time in several crops apart from accelerating plant phenotyping and gene transformation pipelines [20]. SB of short-day crops has been limited because of their flowering requirements. Nevertheless, recently, Lee [36] and his research team worked on developing protocols for short-day crops like sorghum (*Sorghum bicolor* L. Moench) and pigeonpea (*Cajanus cajan* Millsp.). At the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) under the scheme funded by the Bill and Melinda Gates Foundation and a proposed photoperiod of 13 h: 8 h: 13 h is recommended at vegetative: flowering: pod filling stages of pigeonpea development to hasten the breeding cycle [16,37].

SB also involves achieving multiple overlapping generations of plants within a short period of time. Instead of waiting for one generation to complete its entire life cycle, SB allows for the concurrent growth of multiple generations [38]. This is achieved by staggering the sowing and planting of different generations so that they overlap, allowing breeders

to evaluate and select desired traits more rapidly. The precise timing of sowing and planting is critical to achieveing multiple overlapping generations. The sowing schedule should be carefully planned to ensure continuous plant growth and the overlap of different generations. This allows breeders to evaluate and select plants at different stages of development simultaneously [19]. SB often involves efficient plant propagation techniques to expedite the breeding process. This includes the use of tissue culture, rapid cloning, or other methods to quickly propagate plant material and generate large populations of plants for evaluation [39]. These techniques allow breeders to multiply desired plant lines efficiently and rapidly increase the number of plants available for selection and crossing through high-density planting. They also evaluate large populations, introgress desirable traits and select promising individuals more rapidly than traditional breeding methods [16].

SPEED BREEDING REQUIREMENTS AND STRATEGIES FOR HASTENED PLANT GROWTH

Numerous internal and external cues, in particular, photoperiod [40], light intensity and quality [41], temperature [42], planting density, and plant nutrition regime control the growth and development of plants.

PAR/Light Requirements

The quality of the light is crucial for the growth and development of plants. Through phytochromes, plants sense and react to red and far-red light; through cryptochromes and phytotropins, they perceive and react to blue light. Plant growth and developmental processes, such as shoot and root growth, plant height, flowering, maturity, circadian rhythm, photomorphogenesis, and leaf senescence, are significantly influenced by phytochromes and cryptochromes [43]. Early experiments categorized plants into three groups based on the critical night length that initiates flowering: day-neutral plants (DNPs), long-day plants (LDPs), and short-day plants (SDPs). SDPs require a longer night length than the critical night length, while DNPs are not affected by night length. By giving LDPs and DNPs a shorter night period [44] and SDPs a more extended night period [45], optimization of light quality and light exposure period type and controlled environmental conditions in SB programmes speed up the flowering and breeding process [18].

High-intensity lighting systems are a critical component of SB as they regulate flowering [46], which typically include the use of high-intensity discharge lamps, LED (Light emitting diode) lights, sodium vapour lamps (SVLs) or other specialized lighting technologies [20]. LED as a light source provides linear photon output with the electrical current input, making it amenable for designing light arrays according to plants' needs [27]. Recently, the LED-based SB protocol has been standardized for short-day crops like rice, amaranth and soyabean [45]. These lighting systems provide the necessary light spectrum and intensity to support

photosynthesis, maximize plant growth rates and improve plant yield, as in basil [47]. Croser et al. (2016) [48] developed early- and late-flowering genotypes for peas (*Pisum sativa* L.), chickpeas (*Circer arietinum* L.), faba beans (*Vicia faba* L.), and lupins (*Lupinus albus* L.) under controlled conditions using various parts of the light spectrum (blue and far red-improved LED lights and metal halide). These species showed a positive correlation to the diminishing red: far-red proportion (R:FR).

Temperature and Relative Humidity Requirements

Maintaining temperature and humidity conditions is crucial for a successful SB. The temperature should be set within the optimal range for the specific plant species to promote healthy growth and development. Humidity levels need to be controlled to prevent excessive moisture buildup, which can lead to diseases or fungal infections. Additionally, the use of the vernalization technique, which mimics the cold temperature exposure needed to induce flowering in wheat [1], has been incorporated to speed up the flowering process. Precise nutrient and water management strategies must be employed to promote rapid and healthy growth, and plant development [16]. Furthermore, efficient plant propagation techniques, including tissue culture and rapid cloning, have been applied to increase the number of plants available for evaluation and selection [49].Warmer temperatures often result in faster growth rates, and in the majority of species, vegetative development takes place at a greater optimal temperature than reproductive development. Many crops are vulnerable to high temperatures during the reproductive process, as this can affect meiosis and pollen viability in particular [50]. Higher temperatures may be employed to speed up vegetative growth [51] and lower temperatures may be maintained during reproductive growth in order to optimize SB procedures [50,52,53]. Germination of immature seed generated from wheat and barley embryo culture occurred at temperatures between 20 and 22℃. For accelerated plant growth and early flowering, seedlings were moved to a temperature regime of 25/22℃ after germination, synchronised with a 16/8-hour light/dark photoperiod [54].

SPEED BREEDING STRATEGIES FOR KEY CROPS: SUCCESSES AND CHALLENGES

Successful Implementation of SB in Various Crops

Implementing SB techniques necessitates different approaches and may vary for different crops. In an effort to quickly breed cereal types, researchers have looked at cutting the time it takes to achieve homozygous lines following hybridization (Table 2). The following are some specific instances of methods and adjustments that have been used with particular crops:

Table 2. Generation time of individual crops: a comparison between speed breeding and conventional breeding.

S.No	Crop	Generation Time Conventional Breeding	Generation Time Speed Breeding	Methodology	Reference
1	Rice (*Oryza sativa* L.)	2–3 generations/year	4–5 generations of *indica* and/or *japonica* rice in a year	24 h long day (LD) photoperiod for the initial 15 days of the vegetative phase	[52]
2	Spring wheat (*Triticum aestivum*)	2–3 generations/year	6 generations per year	photoperiod of 22 h light and 2 h dark under PAR of 150–190 μE $m^{-2}s^{-1}$	[19]
3	Durum wheat (*Triticum durum*)	2–3 generations/year	6 generations per year	22 h of extended light using red LED lamps and 2 h of dark	[55]
4	Barley (*Hordeum vulgare*)	2–3 generations/year	6 generations per year	photoperiod of 16/8 h light/dark with a light intensity of 500 μmol/m^2/s	[54]
5	Chickpea (*Cicer arietinum*)	2–3 generations/year	4–6 generations/year	photoperiod length of 12/12 h light/dark using standard incandescent bulb of 60 W with a light intensity of 870 lm	[21]
6	Pea (*Pisum sativum*)	2–3 generations/year	6 generations per year	22 h photoperiod supplied by fluorescent T5 tubes, a temperature of 20 ± 2 °C	[8]
7	Canola (*Brassica napus*)	2–3 generations/year	4 generations/year	Kindly, refer song et al., 2022 at add specifications here	[56]
8	Soyabean (*Glycine max*)	1 generation/year	5 generations/year	10 h photoperiod enriched with blue light and deprived of far-red light	[43]
9	Amaranth (*Amaranthus* spp. L.)	2 generations/ year	8 generations/ year	16 h photoperiod was used to initiate strong vegetative growth, after which plants were transferred to an 8 h photoperiod	[57]
10	Pigeon pea (*cajanus cajan*)	1 generation/year	2–4 generations/year	Photoperiod of 13 h: 8 h: 13 h is recommended at vegetative: flowering: pod filling stages	[16]

Cereal crops

The incorporation of SB protocols in cereal crops was emphasized by many studies [14,19,27,58]. A SB protocol utilizing constant light and temperature *viz*., 22℃ day and 17℃ night temperatures resulted in accelerated plant growth in wheat (*Triticum aestivum* L.). In around three weeks, plants reach the adult growth stage, or stem elongation [59]. This enables breeders to phenotype for rust resistance traits rapidly. Similarly, in oats (*Avena sativa* L.), the breeding cycles were accelerated by exposing plants to a 22 h continuous photoperiod, resulting in a reduction of 11 days (62 *vs.* 51 days on average) for days to flowering [58]. In rice (*Oryza sativa* L.), to breed for salt tolerance, the biotron (growth chamber) based SB technique was employed. In order to shorten the time until seed maturity, an extended day length (14/10 h light/dark) employs a 6400-02B LED light source for the first 30 days to speed up vegetative growth, followed by a shorter day length (10/14 h light/dark) to stimulate reproduction, tiller removal, and embryo rescue. This way, breeders achieved six generations in 17 months [60]. Spring wheat produces four generations annually when grown under a 22 h/2 h (light/dark) photoperiod at 22℃ and 70% humidity [56]. For winter wheat (*Triticum aestivum* L.) a longer day length (22 h day/2 h night; with 25/22℃ day/night temperatures) resulted in rapid generation advancement [1]. Similalry, for spring wheat, a 22 h/2 h (light/dark) photoperiod at 22℃ with a humidity of 70% allowed for high throughtput and rapid generation [56]. In day-neutral crops like maize (*Zea mays* L.), SB integration will open new avenues for accelerating the maize breeding programmes [61].

Pulse crops

The procedure of pulse breeding involves a lot of time. To release an improved cultivar, most traditional breeding programmes require 10 to 15 years. A modified photoperiod was employed to advance the breeding cycles in chickpea. The most prolonged period of flowering was generally found in red to far red (R:FR) ratios greater than 3.5. Light with the maximum intensity in the FR region was the most inductive to flower in situations where the R:FR was less than 3.5 [48]. The photoperiod was prolonged to promote early flowering. In early, medium, and late-maturing accessions of chickpeas, extended artificial light shortened the duration of flowering by 8–19, 7–16, and 11–27 days, respectively, in comparison to the control [20]. Recent studies reported SB protocols in long-durations crops (6–9 months) like pigeonpea which demands 12–13 years employing conventional methods, 7 years by SSD method and 4 years by SB employing photoperiodism. Photoperiod of 13 h: 8 h: 13 h is recommended at the vegetative: flowering: pod filling stages of pigeon pea to hasten the breeding cycle. The production of pods and early vegetative growth were accelerated by broad spectrum light (5700 K LED). Conversely, early blossoming was promoted by far red (735 nm) light

[16,37]. In the case of pea (*Pisum sativum* L.), a photoperiod of 20 h supplied by fluroscent tubes (500 lM m^{-2} s^{-1} light intensity) and a temperature of 20 ± 2°C resulted in a considerable decrease in days to flowering compared with field sown varieties (F = 34.9; $p < 0.001$) [8].

Oilseed crops

Speed breeding activities pertaining to oilseeds were restricted to a few crops like soybean (*Glycine max* L. Merril), groundnut (*Arachis hypogaea* L.) and canola (*Brassica napus* L.). In groundnut, compared to conventional systems, where field-based pedigree breeding procedures are frequently used, the combination of SB techniques with a single seed decent breeding strategy offers the potential to cut the time considerably spent on producing new cultivars. Through this protocol, breeders can produce 4–5 generations of groundnut in a year, which usually takes 3 years [62]. Similarly, continuous photoperiod accelerated the life cycle of the canola, enabling it to raise 4 generations in a year compared to 2 to 3 generations in a normal greenhouse condition (Figure 2) [19,63]. Likewise, the growth of short soybean plants that flowered approximately 23 days after sowing and matured within 77 days was facilitated by adjusting the photoperiod to 10 h and employing a blue-light-enriched LED with a far-red-deprived light spectrum. This allowed breeders to realize up to five generations per year [45].

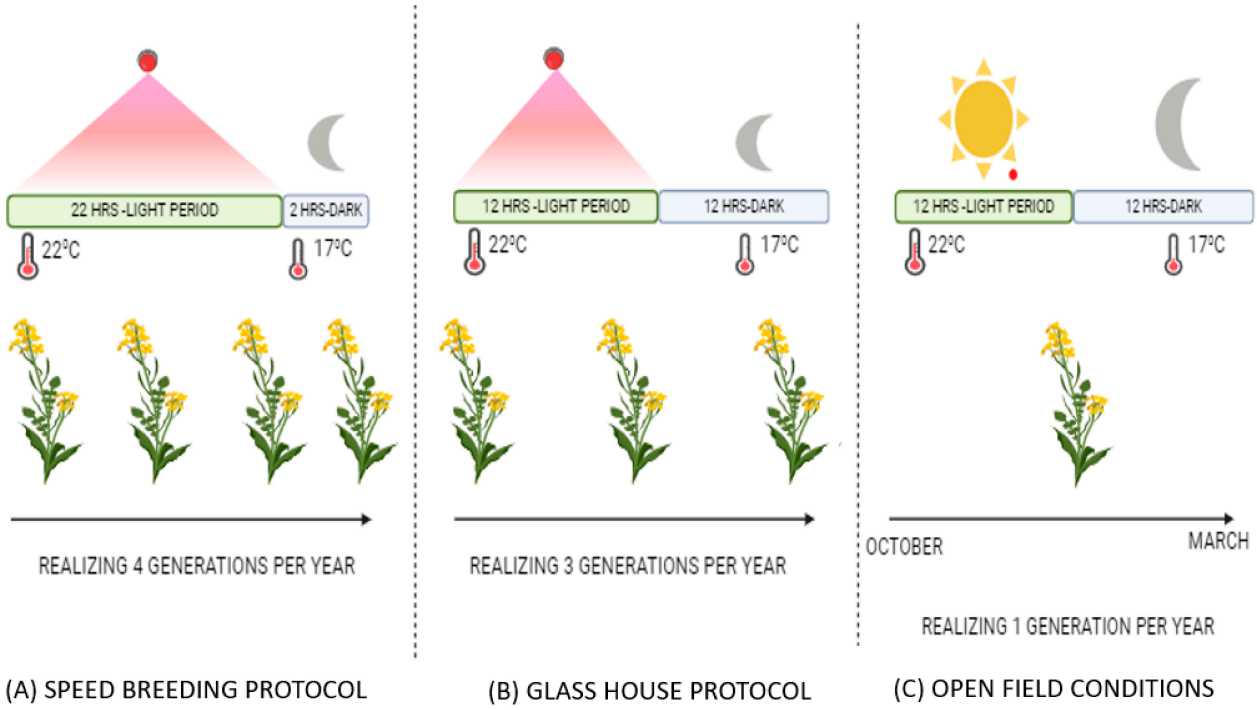

Figure 2. Pictorial representation of (**A**) Speed breeding protocol. (**B**) Glass house protocol. (**C**) Open field conditions.

SB has taken the plant breeding to the next level by allowing 4–6 generations in a year. As compared to glasshouse (12 h sunlight, 12 h dark), SB chamber (22 h artificial light, 2 h dark) produced four generations of canola. While, glasshouse could produce 3 generations and open field only one generation of canola.

Vegetable crops

Vegetables are high value crops and demand more resources for generating materials and testing in breeding programmes. High throughput line development in vegetable breeding would certainly enhance cost-effectiveness and breeding efficiency so that 'time to market' can be substantially reduced. In amaranth, a reduction in generation time, plant height and number of flowers could be achieved by growing plants under short-day conditions (8 h) and at 30℃. The flowering was controlled by the transfer of plants from long day (16 h, 35℃) conditions to short day conditions [57]. In pepper (*Capsicum spp* L.), Liu et al. [13] reported that plants bloomed about 40 days after sowing under a photosynthetic photon flux density (PPFD) of 420 mol m^{-2} s^{-1} and a 12 h photoperiod and haversted seeds after 82 days sowing had an acceptable seed germination rates. The extended photoperiod to 20 h still enhanced early blooming (2−3 days) and further supplementation of far-red light (R:FR = 2.1) enhanced the fruit ripening and seed germination, but this was not recommended due to the high costs involved in providing extended light with marginal gains. Choi et al. [64] established a SB system in (*Capsicum annum* L.) in a greenhouse with a 20 h photoperiod and a 3:8 R:FR ratio, which resulted in a breeding cycle of 110 days from seed to seed. In tomato, Gimeno-Páez et al. [65] demonstrated that agronomic practices such as container size, cold priming and K supplementation, when combined with embryo rescue considerably reduced the generation time and helped to achive one additional generation in a year, thereby four generations can be produced in a year.

INTEGRATING SB WITH OTHER BREEDING METHODS: SYNERGISTIC APPROACHES

The combined use of SB and high-throughput technologies represents a cutting-edge approach to crop research and breeding. It accelerates the development of improved crop varieties by significantly reducing the time required for breeding cycles while maintaining genetic diversity (Figure 3).

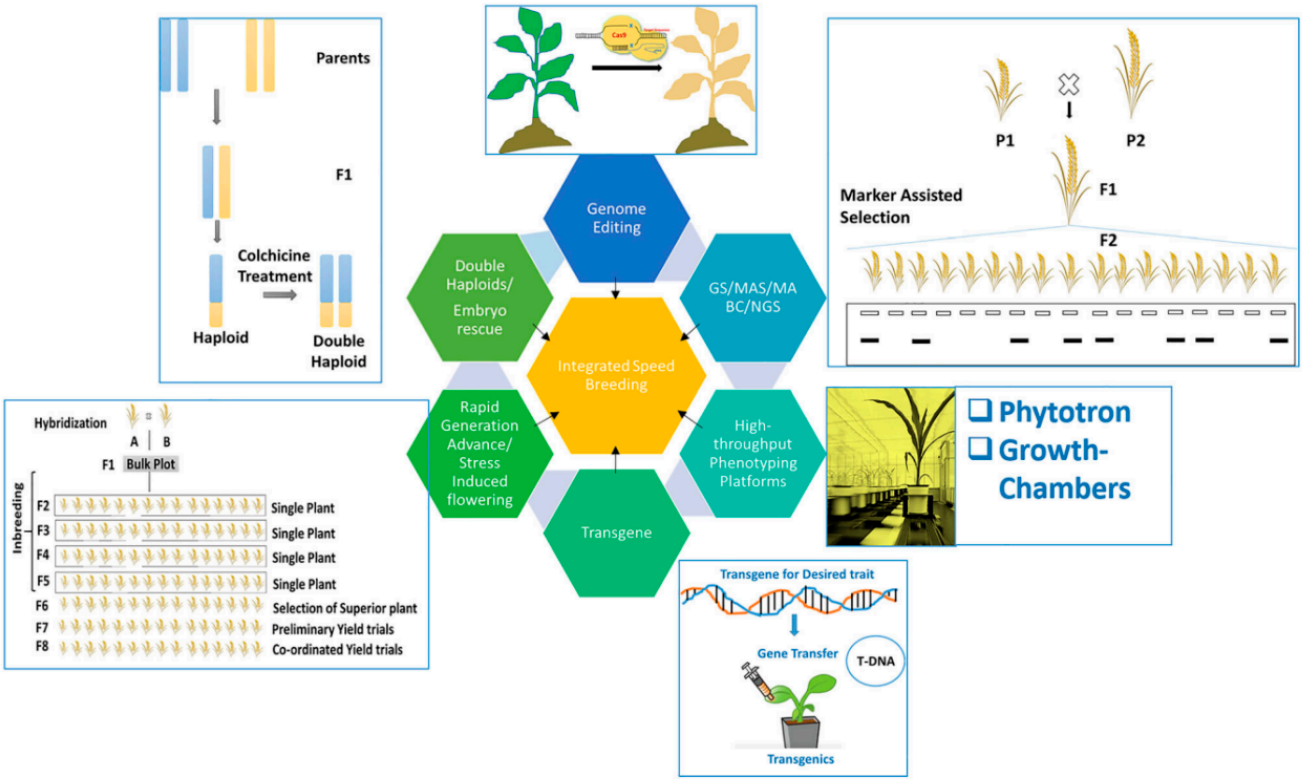

Figure 3. Integration of different techniques with SB platform to enhance the result. GS, genomic selection; MABC, marker assisted backcrossing; MAS, marker-assisted selection; NGS, next-generation sequencing (Source: [66]).

High-throughput genotyping and phenotyping technologies, such as SNP arrays, genotyping-by-sequencing (GBS), and automated imaging systems, allow for rapid and efficient data collection on a large scale. High-throughput genotyping allows breeders to tailor crop varieties to specific regions or growing conditions [67]. SB can be used to rapidly advance generations of crop wild relatives, which often possess valuable traits like drought tolerance or resistance to specific pests [19]. High-throughput genotyping helps transfer these traits to cultivated crops. The combined use of SB and phenotyping technologies enables breeders to focus on improving yield, nutritional content, and quality traits [68]. This leads to higher crop productivity and improved food quality. Data-driven decision-making in crop breeding allows the selection of plants with the desired genetic makeup and performance traits, reducing uncertainty in variety development. SB and precise trait selection minimize the need for extensive field trials and reduce resource usage in the breeding process. However, selection in early generations for a specific trait may lead to the loss of alleles for performance unless markers are available for yield as well.

In an innovative approach called 'ExpressEdit', the integration of SB and genome editing tools has effectively circumvented many of the traditional labour-intensive steps, thereby alleviating the workload in the laboratory and contributing to time-efficient crop generation. ExpressEdit

represents a novel technique that combines marker-assisted selection and preassembled genome editing tools (e.g., CRISPR Cas9 and CRISPR-Cpf1) with SB, streamlining the process of eliminating the delicate callous culturing step [14]. Integrating state-of-the-art technologies such as SB with genetic engineering and genome editing has been employed as a novel approach in several crop breeding programmes to speed up the process of introgression of desired traits and varietal development [19,38,69] (Figure 4).

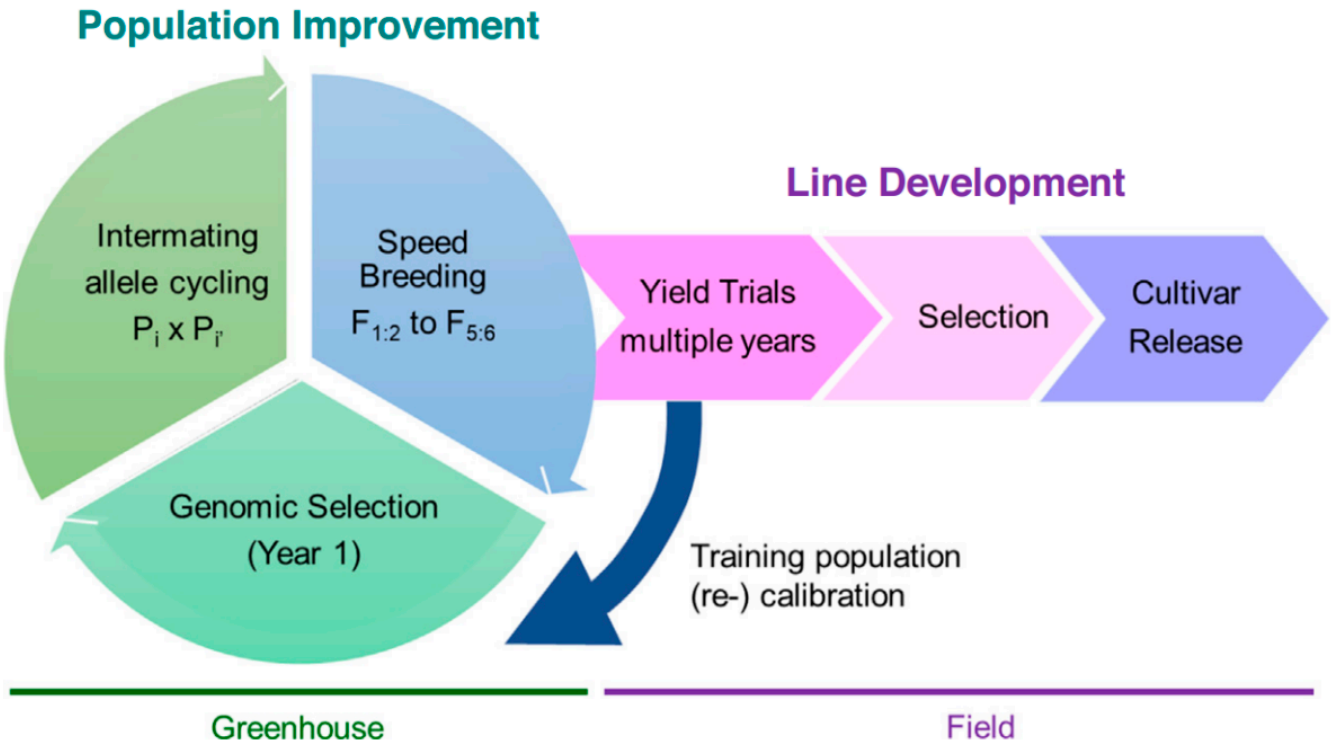

Figure 4. Integration of different techniques with SB platform to enhance the result. GS, genomic selection (Source: [18]).

Another option where SB can be integrated with modern breeding tools is the integration of SB and genomic selection (GS) in a plant breeding program to accelerate genetic gain [27]. In this case, the population improvement component has the goal of increasing the allelic frequencies of favourable alleles in the population. Selection can be conducted at different levels in breeding programmes, but there is no need to wait until lines are completely homozygous to perform the crossing. SB can enable fast cycling in the genomic recurrent selection component. The line development component has the goal of testing inbred lines and selecting fixed lines to release as cultivars or to further use in hybrid production. Field testing is required at this stage [18]. Genomic prediction can further aid in the selection of parents by deploying training populations with extensive field evaluations. The line development program will provide phenotypic information for re-calibrating the models for genomic

selection and should, therefore, be carefully planned for predictive ability. SB can be used to accelerate the inbreeding process [70].

Combining the big data of Omics, GWAS, and advanced breeding techniques like GS and MAS with SB will help narrow down the desired genes and facilitate a rapid selection process to speed up crop improvement programs. Next-generation artificial intelligence (Next-gen AI) and machine learning are revolutionizing modern agriculture by collecting and processing large amounts of data and offering precise insights in identifying specific traits; hence, the integration of SB with Next-gen AI and machine learning tools results in speeding up the crop breeding cycles and reducing laborious processes. However, the adoption of these advanced techniques is hindered by factors like shortage of trained researchers and lack of instruments, infrastructure, and funding sources [71,72].

In summary, the combined use of SB and high throughput phenotyping and genotyping technologies revolutionizes crop breeding by significantly shortening breeding cycles, enhancing precision, and preserving genetic diversity. It is a promising approach to addressing global challenges like food security and climate change, as it enables the rapid development of crop varieties that can thrive under evolving environmental conditions and meet the needs of a growing population [73].

CHALLENGES AND LIMITATIONS ASSOCIATED WITH SPEED BREEDING OF DIFFERENT CROP SPECIES

While SB and high throughput technologies offer tremendous potential in agriculture and genetic research, they also come with several limitations and challenges that need to be addressed for their efficient implementation and applications.

A key limitation is the access to controlled environmental conditions required for the rapid cycling of the target species, for example, temperature and light maintenance, during winter [53]. More than half of the cost of SB systems goes to lighting and temperature-controlled conditions [20]. SB relies on inducing early flowering in photoperiod-responsive crops. However, different plant species behave differently depending on photoperiod requirements and light intensity. So, implementation of SB in a short day and day-neutral plant requires species and variety-specific standardization. The differences between the photoperiodic conditions for a short day and a long day range from minutes to hours, making SB standardization very difficult [27]. SB protocols for LDP and DNPs require continuous light or prolonged photoperiods, which can limit plant growth and may be correlated to photo-oxidation, chlorosis, leaf injury, high starch production, elevated levels of stress hormones and lowered productivity [53,18]. The intensive growth conditions may result in limited seed yield and quality, which can constrain subsequent field evaluations [53]. SB also comprises the early

harvest of immature seeds that could interfere with the germination, phenotyping of some seed traits and generation advancement [27,63].

Phenotyping agronomic traits can be undertaken in conjunction with SB; for instance, in wheat, SB was combined with phenotype screening such as disease resistance against tan spot stripe rust (*Puccinia striiformis*), leaf rust (*Puccinia triticina*) [18] and crown rot (*Fusarium pseudograminearum*) [18,53]; however, care is required as the phenotypic expression can be biased under controlled environment conditions and protocols must be refined to ensure if trait expression is related to the field environment. For example, in the case of plant height and flowering time in oats, there was no consistency due to the cross-over interaction between genotypes and growth systems [18,53]. As a result, the phenotyping of the crops under SB should be validated in the field conditions to certify that trait expression is associated with the field environment.

Comparison of glasshouse-grown crops with SB for different phenotypic traits revealed a lower number of seeds per spikelet, comparable germination, and viability in wheat and barley [19]. Once SB is established, species can show genotypic differences in response to intensive growth conditions [53]. Moreover, in pushing for speed, plants are grown at the edge of their physiological capability, and favourable conditions for fast cycle turnover are often detrimental to the plant's ability to defend itself and, without controlled management, can lead to catastrophic losses of valuable breeding material. The number of crosses and the population sizes in the evaluation process are restricted by the size and cost of an infrastructure facility [74]. While not so problematic in developed countries, routine use of SB for research and breeding programmes remains a constraint in developing and underdeveloped countries due to limited infrastructure, a lack of expertise, and collaborations with international organizations [53].

Addressing these challenges and limitations requires (i) collaborative efforts among scientists of different disciplines (for example breeders, physiologists, geneticists, molecular biologists, plant nutritionists, policymakers and farmers) (ii) Further technological advances, such as high-throughput phenotyping, genomic tools, and gene-editing techniques, are helping to overcome some of these challenges and accelerate crop improvement efforts (iii) Additionally, conservation and utilization of crop genetic diversity, implementing sustainable agricultural practices and improving breeding methodologies are essential.

STRATEGIES FOR OVERCOMING OBSTACLES AND OPTIMIZING SB PROTOCOLS

These strategies aim to enhance SB methods' efficiency, reliability, and scalability. This requires sustainable energy input options such as solar energy, energy-efficient LEDs and inverter-based air conditioning systems [20,27]. In the future, LEDs cost will be lower and could be replaced by laser lights due to their electrical conversion efficiency, which ultimately

cuts down SB's operational cost [27]. These could be efficient outside growth chambers, reducing the cooling cost and creating controlled environments. The difficulty in standardizing SB conditions for short day and long-day plants can be overcome by defining separate photoperiods for vegetative and reproductive phases, as shown in amaranth [57].

Some crop species may be sensitive to controlled environments and need to be acclimatized to the conditions, which requires additional time and mitigation strategies. Mitigation of the damage caused by SB comes from the adaptation of controlled conditions to control photoperiod saturation and temperature limits for each crop species and, in some cases, for genotypes within species. Another challenge is maintaining backup seeds from each individual cross in each generation and providing protection from biotic and abiotic factors [53]. Establishing cost-effective operations and facilities, integration SB into a modern plant breeding programmes, accelerating research, pre-breeding and training the next generation are crucial to optimizing SB protocols [18].

Further, determining the proper integration of SB with other plant breeding programmes could reduce the project's overall cost [27]. The use of next-generation sparse field phenotyping trial designs can assist in overcoming the problem of low seed numbers [53]. Choosing genotypes that are responsive to SB conditions is essential to ensure better outcomes. Some genotypes may not perform well under accelerated growth conditions, reducing quality or reproductive success.

EXPLORATION OF PROSPECTS AND ADVANCEMENTS IN SB TECHNOLOGIES

The prospects and advancements in SB hold great promise for further revolutionizing agriculture, genetic research, and crop improvement. Here are some of the exciting developments we can anticipate:

Advances in functional genomics will allow for the direct manipulation of gene function, facilitating the development of crops with tailored traits, including improved stress tolerance [75], nutritional content, and quality [76]. The use of advanced imaging technologies, including drones, hyperspectral imaging, and 3D scanning, will improve high-resolution phenotyping [77]. These techniques will provide detailed insights into plant growth, health, and responses to environmental conditions.

Integrating next-generation genomics, advanced breeding tools, next-gen AI, machine learning, genetic engineering and genome editing with SB will continue to advance, allowing for precise modifications of crop genomes to introduce desired traits, such as enhanced nutritional content and disease resistance [69]. The development of crop varieties tailored to specific local climates that can adapt to changing weather patterns will help farmers and reduce the environmental impact of agriculture [78,79] (Figure 5).

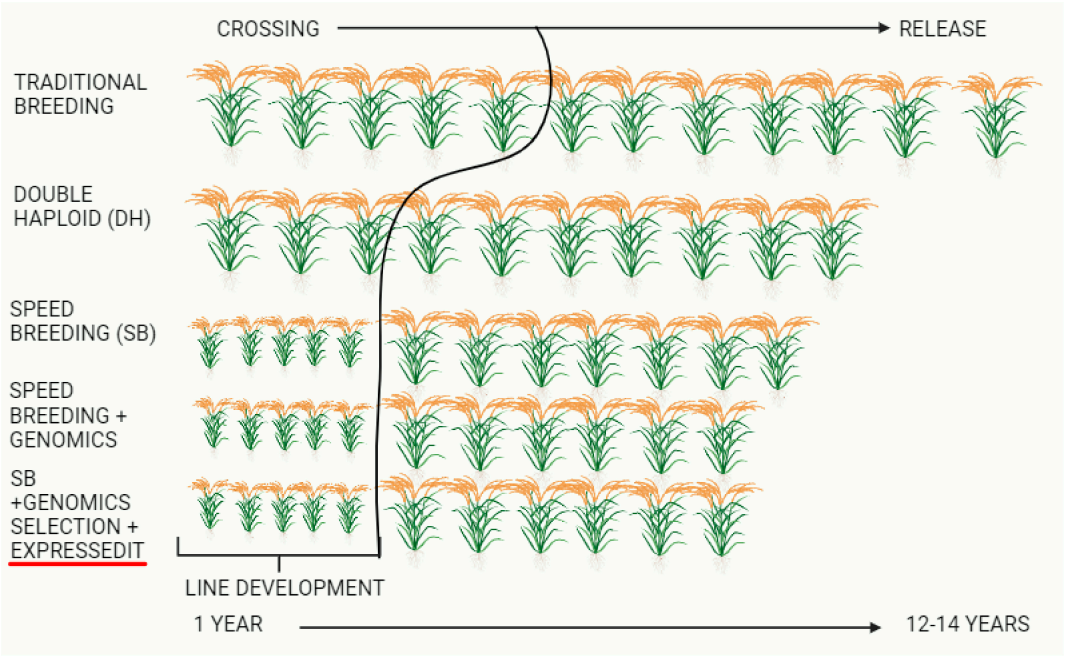

Figure 5. Breeding strategies—visual representation of breeding strategies and comparison of cycle length for traditional breeding versus progressive strategies that exploit doubled haploid (DH), SB (SB), genomic selection (GS) and ExpressEdit.

The future of SB and high throughput technologies is marked by a convergence of various scientific disciplines, cutting-edge technologies, and global collaboration. These advancements hold the potential to greatly enhance our ability to develop crops that are more productive, resilient, and sustainable, ultimately addressing the challenges of food and nutritional security and climate change.

CONCLUSIONS: ACCELERATING CROP IMPROVEMENT FOR A SUSTAINABLE FUTURE

In summary, SB has revolutionized agriculture by accelerating breeding cycles, enhancing precision, and contributing to the development of crop varieties that are more productive, resilient, and sustainable. SB allows for multiple plant generations in a single year, significantly reducing the time required. It also helps develop enhanced resistance to pests and diseases, reducing pesticide usage. Resource-efficient crop varieties developed through these technologies reduce the use of water, fertilizer, and plant protection chemicals, contributing to sustainable agriculture. SB enables the development of high-yielding crop varieties that produce more food per unit of land. This is crucial to meet the growing food demand driven by population growth. Combining SB with high-throughput phenotyping, genotyping and gene editing technologies offers new critical tools for achieving global food security, offering solutions to the challenges posed by increasing population, climate change, limited resources, and the need for more resilient and diverse food systems. By accelerating breeding cycles, improving crop

traits, and reducing the time required, these technologies contribute to a more secure and sustainable food future.

DATA AVAILABILITY

All data generated from the study are available in the manuscript.

AUTHOR CONTRIBUTIONS

RP designed and initiated manuscript preparation. MC, BP, SN and GS worked on manuscript preparation. KP, SS, ARV, MRK and PVVP contributed to manuscript refinement. All authors contributed to the article and approved the submitted version.

CONFLICTS OF INTEREST

The authors declare that there is no conflicts of interest.

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