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REVIEW ARTICLE

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Combining speed breeding with traditional and genomics-assisted breeding for crop improvement

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Abstract

Accelerated crop growth strategy innovations are required as we reach saturation peaks regarding the productivity of major food crops. Speed breeding (SB) is one of the most promising technologies adopted for this purpose. SB hastens crop production by reducing plant growth and development, breeding time and swift generation advancement. Prolonged daily light exposure shortens the life cycle in some long-day or day-neutral plants leading to early seed harvest. This approach is best suited for controlled environment prebreeding/breeding activities and analysed for several crop species. SB can be integrated with different traditional and advanced genomics-assisted breeding technologies like marker-assisted selection (MAS), genomic selection (GS), pollen-based selection (PBS), overexpression/knock-down transgenics and genome editing to achieve more precise and faster results on translational genetic enhancement. This review will discuss the approaches and strategies adopted for the SB and its potential to integrate existing crop improvement technologies to attain more efficient outcomes on major food crops' varietal improvement.

KEYWORDS
genome editing, genomic selection, growth chamber, marker-assisted selection, pollen-based selection, speed breeding (SB)

1 | INTRODUCTION

The burgeoning human population forced the researchers to look for higher yielding varieties and methods to speed up crop production. According to an estimate, by 2050, we need to produce 60–80% more food to sustain 10 billion people (Hickey et al., 2019). The ever-changing climate brings about a severe threat in achieving these goals. Therefore, scientists are prompted to develop efficient methods and strategies to give impetus for future breeding programmes and ultimately increase crop yield and productivity in a short period. This requires innovation in the plant breeding cycle, as presented in Figure 1.

Speed breeding (SB) came into the limelight with NASA's plan to grow crops in space. For this, NASA scientists supplied continuous light to wheat plants enabling them to reproduce early and accelerate their breeding cycle. Australian scientists inspired to speed up crop production by SB confirmed its genetic gain for crop research and breeding (Hickey et al., 2009). As a result, SB could increase wheat crop production by three times utilizing different temperatures and photoperiod regimes in a controlled condition, resulting in six crop generations in a single year. This extra lighting in the glasshouse environment permits rapid generation cycling via the single-seed descent (SSD) method, potentially impacting larger scale improvement in future breeding programmes. SB has generated much interest globally for the technique because its significance has been shown in cutting-edge research of space crop production. Further, adaptation of SB may inspire the generation of plant breeders to innovate agriculture by utilizing novel breeding techniques to generate a new generation of climate-smart crops.

In the current scenario, crop production and productivity are limited by crop generation time and there is pressure for researchers and breeders to fast-track the varietal development. SB could shorten crop duration and breeders can accelerate the number of generations per year with selection for various traits. Collectively, strategies

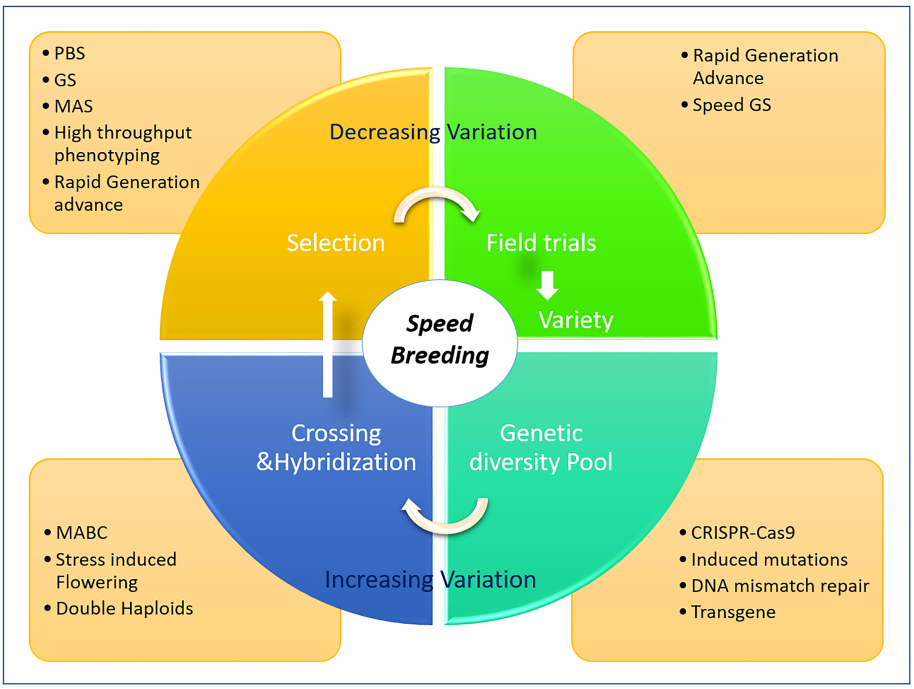

FIGURE 1 Schematic representation of different approaches for rapid generation advancement of crops with speed breeding as integral part of breeding cycle innovation. GS, genomic selection; MABC, marker-assisted backcrossing; MAS, marker-assisted selection; PBS, pollen-based selection [Color figure can be viewed at wileyonlinelibrary.com]

involved in plant breeding and genomics-assisted breeding coupled with SB have encouraged rapid progression towards developing novel crop varieties with superior agronomic performance by minimizing the time, field space and overall resources. SB's technique has generated attention around the breeding community due to its potential application in reducing crop generation time (Table 1). Moreover, integrating SB with other technologies such as transgenic research could help reduce the generation time for plant phenotyping and other traits. SB can be coupled with targeted gene editing, chemically induced mutation and trans-genesis to develop the final product in less than half the time than presently required (Figure 2). Such a mixture of combinatorial approaches will help us transform simple breeding into SB (Ahmar et al., 2020). Nevertheless, its application in crop research has to be substantiated.

2 | POTENTIAL STRATEGIES ADOPTED FOR THE SB PROGRAMME

SB requires novel approaches that reduce the time for flowering, seed set, embryo development and so forth. SB has evolved over the years and could broadly be divided into three categories: The first category is where plants were grown in controlled growth chamber conditions with SB specifications; the second one is where the glasshouse is used with SB specifications; and the third one is a customized homemade growth room designed for low-cost SB programmes (Watson et al., 2018). These SB specifications in common are 22 h photoperiod, 70% humidity, temperature (22°C day and 17°C night) and high light intensity (360 to 650 μmol m^{-2} s^{-1}). These specifications vary according to the vegetative and reproductive plant growth stage. In this section, we will discuss potential approaches utilized to hasten the crop breeding in various crops under various SB categories (Figure 3).

2.1 | Extending light exposure (prolonged photoperiod) through supplementary lighting

Prolonged photoperiod is the most common approach to hasten the crop plant breeding cycle (Ghosh et al., 2018; Sysoeva et al., 2010). It shortens the time to flower by altering the photoperiod. It has been earlier utilized to facilitate plant growth in winter for extending day length. This SB approach required specifications like lighting and temperature control in growth chambers. The light sources used are sodium vapour lamps (SVLs) or a mixture of light-emitting diode (LED) with metal halide lighting (Ghosh et al., 2018). 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. Researchers should optimize lighting conditions according to energy efficiency with the different light spectrum for other crops in a specified area. For example, additional light ranges are used to develop early and late flowering genotypes in chickpea, pea, lupin and faba beans (Croser et al., 2016). Monochromatic (blue or red) and dichromatic (a mixture of blue and red) light treatments with broader spectrum light as control are tested for their effect on einkorn seedlings (Bartucca et al., 2020). Dichromatic light effectively improves biomass production, plant CO_2 assimilation, evapotranspiration, and maintaining carotenoid and chlorophyll contents. Adjusting the light spectrum that matches the plant absorbance spectrum has been proven to promote growth and plant yield in basil (Rihan et al., 2020). This optimization will work for both long-day and day-neutral plants. For example, upon extended light exposure, photoperiod-sensitive

TABLE 1 Examples of SB in different crop plants

Crop	Goal	Generation per year	Approach utilized	Reference
Spring wheat	Resistance to stem rust, stripe rust and yellow spot	4–6	Extending light exposure through supplemental light with SSD	(Ghosh et al., 2018; Riaz et al., 2016)
Durum wheat	Resistance to crown rot	6	SB with multi-trait phenotyping	(Alahmad et al., 2018)
Barley	Resistance to leaf rust	4–6	Extending light exposure through supplemental light with SSD	(Hickey et al., 2017)
Pea	Rapid generation advance	2–3	Extending light exposure through supplemental light with SSD	(O'Connor et al., 2013)
Chickpea	Rapid generation advance	4–6	Rapid generation advance	(Samineni et al., 2019)
Radish	Rapid generation advance	NA	Extending light exposure through supplemental light with SSD	(Ghosh et al., 2018)
Alfalfa	Rapid generation advance	NA	Extending light exposure through supplemental light with SSD	(Ghosh et al., 2018)
Canola	Pod shattering	4–6	Extending light exposure through supplemental light with SSD	(Watson et al., 2018)
Flax	Rapid generation advance	NA	Extending light exposure through supplemental light with SSD	(Watson et al., 2018)
Arabidopsis	Rapid generation advance	NA	Extending light exposure through supplemental light with SSD	(Watson et al., 2018)
Apple	Fire blight resistance	1	Early flowering induction and MAS	(Flachowsky et al., 2011)
Rose	Rapid generation advance	NA	Extending light exposure through supplemental light with SSD	(Ghosh et al., 2018)
Lentil	Rapid generation advance	8	Early flowering induced by phytohormone	(Mobini et al., 2015)
Faba bean	Rapid generation advance	7	Early flowering induced by phytohormone	(Mobini et al., 2015)
Lupin	Rapid generation advance	5	Early flowering and in vitro germination of immature seeds	(Croser et al., 2016)
Clover	Rapid generation advance	2.7–6.1	In vitro-assisted single-seed descent method	(Pazos-Navarro et al., 2017)
Amaranth	Rapid generation advance	6	Extending light exposure through supplemental light up to vegetative growth then short-day exposure for flowering	(Stetter et al., 2016)
Soybean	Rapid generation advance	5	Extending light exposure through supplemental light and LED lighting under SB for short-day plant	(Jähne et al., 2020)

Abbreviations: LED, light-emitting diode; MAS, marker-assisted selection; SB, speed breeding; SSD, single-seed descent.

switchgrass increases stem digestibility and biomass production (Zhao et al., 2017). Apart from the photoperiod, ratio of red and far-red light is also critical and responsible for plant flowering. Adjusting these will help induce the flowering, for example, wheat crop flowered with pink light with the ratio of 1 (Monostori et al., 2018). Experiments performed in *Arabidopsis* in response to laser light showed a reduction in the light and radiation stress-related protein expression (Ooi et al., 2016). So, researchers could utilize these higher energy lights without damaging plants for extending photoperiod. Comparison of extended photoperiod and multisegment light intensity with constant photoperiod (12 h light/12 h dark) has shown the applicability for plant growth in *Lactuca sativa* L. (Mao et al., 2019).

This approach is most commonly used and demonstrated to considerably reduce the generation time for different crops with 22 h of photoperiod (Table 1) (Ghosh et al., 2018). Researchers have found normal plant development, amenability for crossing and higher seed germination rate in these rapidly generated plants. These plants were phenotyped for different traits such as disease resistance (wheat), pod shattering (canola) and glaucousness (barley). It proves the applicability of this method in accelerating plant phenotyping and gene transformation pipelines. Harvesting seeds prematurely with a short drying and chilling treatment is helpful for a uniform generation tested for wheat and barley in this method (Ghosh et al., 2018). The positive effect of extended light duration on growth and development has been shown in watermelon (Wei et al., 2020). Recently, LED-based SB protocol has been standardized for short-day crops like rice, amaranth and soybean (Jähne et al., 2020). LED with blue light-rich and far-red-deprived light spectrum and adjusted photoperiod were used,

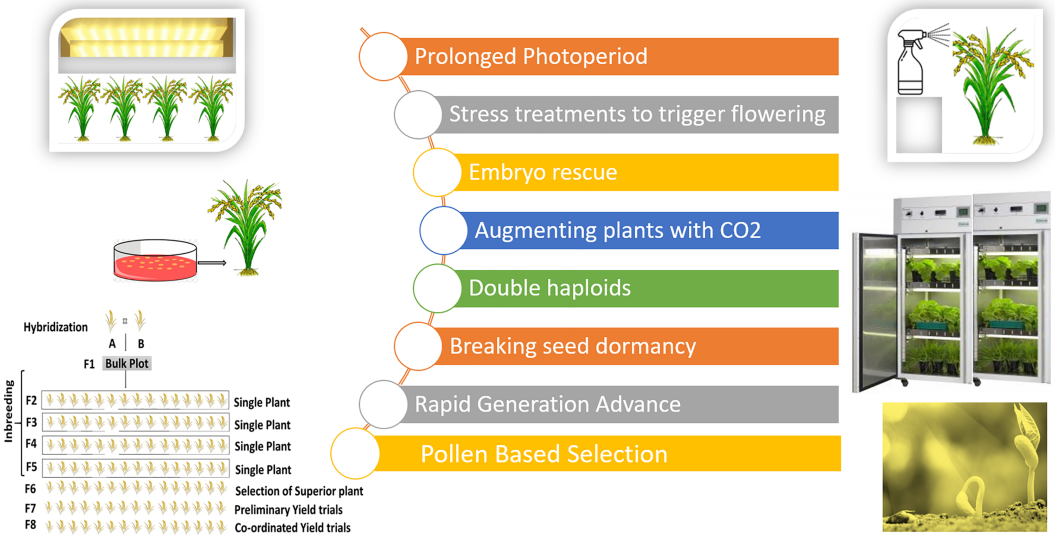

FIGURE 2 Schematic representation of potential strategies adopted for speed breeding programme [Color figure can be viewed at wileyonlinelibrary.com]

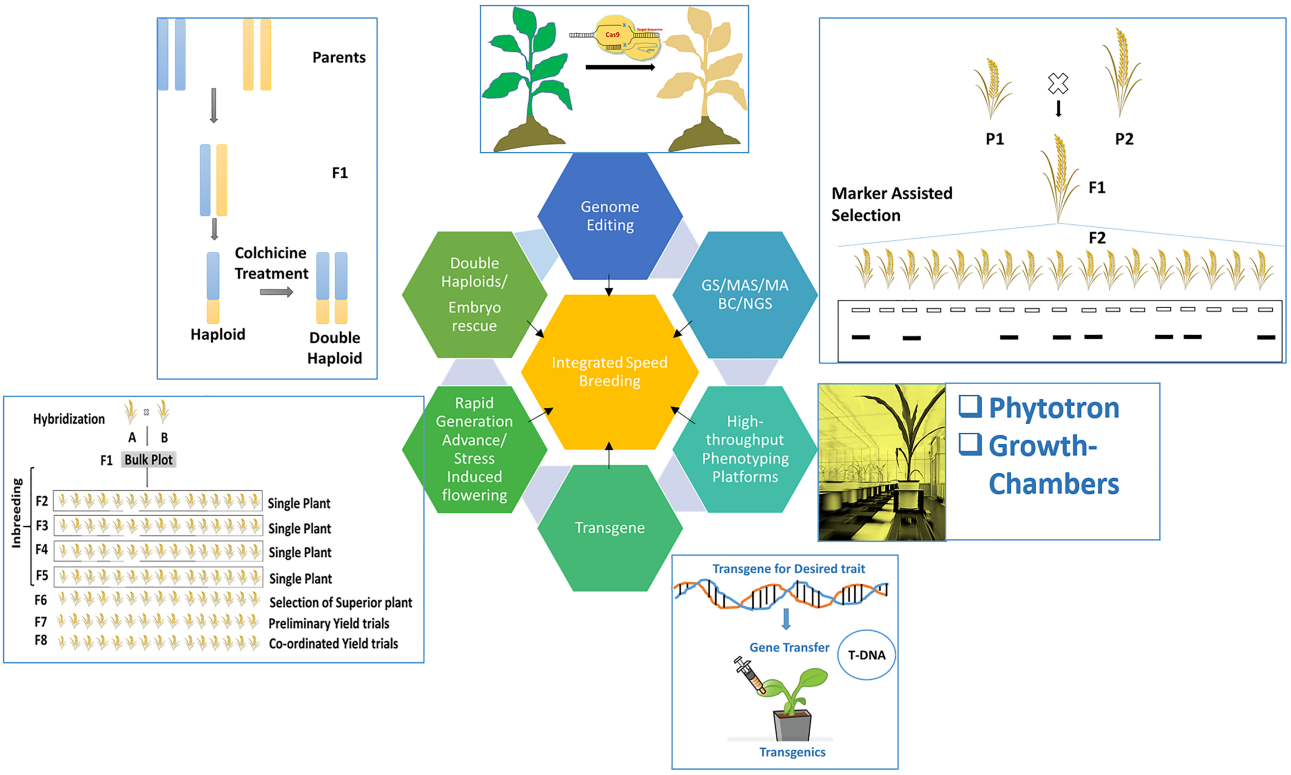

FIGURE 3 Integration of different techniques with speed breeding platform to enhance the result. GS, genomic selection; MABC, marker-assisted backcrossing; MAS, marker-assisted selection; NGS, next-generation sequencing [Color figure can be viewed at wileyonlinelibrary.com]

which reduces the generation time for soybean, rice and amaranth. Authors have checked the effect of far-red light for inducing flowering in these crops and found that only rice and amaranth were responsive in this condition. Therefore, the light spectrum and light quality are vital for standardizing SB protocols. As shown for rose, plant genotypes differ in response to different light quantities and qualities (Crespel et al., 2020). This study signifies the importance of genotype and light quality interaction and should consider SB in many crops.

All these reports support the idea of using this approach for better plant growth in minimum time and optimal resources. The said strategy is the most commonly used method for SB. However, it has limited application due to photoperiod response variation in the crop

species, varieties and cultivars. Therefore, defining and optimizing crop-specific SB protocols are advisable with flexibility in procedures according to research objectives.

2.2 | Stress treatments to trigger flowering for early seed sets

Stress treatments are another approach utilized in SB for early seed sets in plants. Plant response for flowering is generally governed by photoperiod and vernalization. The third type is induced by stresses and is named stress-induced flowering. It has been well documented that physiological stresses can induce flowering (Takeno, 2016). Most plant species are amenable to stress-induced flowering (Wada & Takeno, 2010). These stress treatments could be high or low temperature, nutrient deficiency, water excess or drought, low or high light intensity, crowding, UV treatments and pathogen infection (Takeno, 2016). Induction of drought has promoted flowering in *Arabidopsis* (long-day conditions) and *Citrus* spp. (Garmendia et al., 2019; Riboni et al., 2020). It was reported that drought-induced flowering in the tree *Sapium sebiferum* facilitates a reduction in flowering time that has potential for its breeding (Yang et al., 2015). Apart from drought, UV-C is also said to induce flowering in *Arabidopsis* (Martinez et al., 2004). The stress-affected plant has regular fruit and seed development that could be utilized for SB (Kolar & Senkova, 2008). Recently rice, pea and canola are bred with stress-induced flowering (Collard et al., 2017; Yao et al., 2016). This approach could bypass the seasonal induction of flowering in an SB programme. For instance, a protocol for inducing early flowering in a species-specific manner has already been reported, which can be integrated with the SB for rapid generation advancement (Samineni et al., 2019). Similarly, transiently manipulating the key molecular controller in vernalization, such as '*VERNELISATION 2*', could reduce the flowering transition time in many other crops.

Temperature stress applied at a specific growth stage accelerates plant growth. Generally, high temperature creates water deficit and pollen sterility, whereas permissive water loss at specific elevated temperatures accelerates vegetative growth and senescence, as demonstrated for maize (Hatfield & Prueger, 2015). Determining the temperature-sensitive growth stage will help us apply high temperatures at the appropriate time to achieve accelerated growth, such as bread wheat has temperature sensitivity at meiosis, and a short period of temperature exposure causes a reduction in yield at this stage (Draeger & Moore, 2017). Temperature stress can accelerate the vegetative growth, and lower temperature could be reapplied at the flowering stage in this approach. Geographical locations with mild temperature differences in summer and winter are ideal for this method integration in SB programmes. In contrast, extreme temperature locations require specific arrangements for temperature regimes suitable for rapid generation advances (RGAs). Crops with such genotypes amenable to extreme conditions would be ideal for integrating with SB.

2.3 | Embryo rescue

Embryo rescue is an in vitro tissue culture technique that assists plant embryo development and is utilized for SB. In this method, immature seeds are harvested and germinated in the culture medium with or without the plant growth regulator (PGR). This approach has been successfully applied in lentil and fava bean with PGR for achieving four to eight and six to eight plant generations in a year, respectively (Bermejo et al., 2016; Mobini et al., 2015). Similarly, the PGR application in subterranean clover resulted in three to four generations per year (Castello et al., 2015). This approach has also been used without PGR in wheat—eight (Yao et al., 2017; Zheng et al., 2013), barley—nine (Zheng et al., 2013), pea—6.9 (Ochatt et al., 2002) and soybean—five (Roumet & Morin, 1997) generations per year. In combination with stress treatments, embryo rescue is utilized for shortening the generation time in oat, triticale, pea and canola (Liu et al., 2016; Ribalta et al., 2014; Yao et al., 2016). PGR flurprimidol usually retards plant growth and is used along with embryo rescue to induce early pea maturation to reduce the generation time (Ribalta et al., 2017). The breeding cycle shortens in the mutant sorghum population by using the embryo rescue technique (Rizal et al., 2015). In all these methods, young embryos are chosen to fine-tune the generation time for different crop species in combination with photoperiod variation, light quality alteration, temperature and soil management. Young embryos are critical in this approach due to their differential responsiveness, stage and ability to produce fertile plants according to species. The embryo's size affects the germination rate of an embryo and should be considered during embryo rescue. The nurse endosperm technique augments these embryos for significant germination (Niu et al., 2014).

This SB approach has limited application because of species-specific protocols, recalcitrant seeds, the requirement in terms of handling expertise and infrastructure development (Wang et al., 2011). However, embryo rescue can augment SB's approaches, such as prolonged photoperiod, and help for efficient species-specific protocol generation.

2.4 | Augmenting plants with CO_2

Plants require carbon dioxide (CO_2) for their proper growth. However, increasing the CO_2 concentrations augment plant growth and photosynthetic efficiency as in rice and wheat (C3 plants), resulting in early flowering and higher biomass. Additional CO_2 could also add up the threshold level for other inputs such as extended light, which will augment better growth. We must consider optimum water and nutrient supply to realize actual potential due to CO_2 elevation (Asseng et al., 2004). Here, hydroponics can be utilized for better nutrient and water supply and increased CO_2 concentration. This approach is being used in RGA with canopy thinning, restricted root growth and embryo rescue for reducing time in the rice breeding cycle (Tanaka et al., 2016). Additionally, CO_2-supplemented growth chambers

accelerate soybean breeding (Nagatoshi & Fujita, 2019). These innovations could strengthen the SB for expanding its application across crop species.

2.5 | Double haploid (DH)

DH is another well-developed in vitro tissue culture technique for crops that can be utilized for SB. In this technique, haploid embryos have been rescued and subjected to chromosome doubling for obtaining homozygous lines in two generations compared with six or more taken by conventional breeding (Fuente et al., 2013). Genotypes with high crossability rates tend to form more embryos and be instrumental in SB programmes shown in wheat (Hussain et al., 2012). Application of DH at F_1 generation reduces the breeding time but decreases the genetic gain. However, more breeding cycles will compensate for the genetic gain at a certain period (Li et al., 2013). This approach has been well documented for crop improvements in rice and maize crops (Chaikam et al., 2019; Palanisamy et al., 2019). Integration of maize inducer system and centromere-specific histone CENH3 mutations, where only female haploid plants are left after elimination by the inducer lines, could revolutionize the haploid breeding programme in major cereals. Candidate gene *MATRILINEAL (MTL)* has been identified as a haploid inducer (Kelliher et al., 2017) in maize, and its homologue in rice induces haploid formation (Yao et al., 2018). This gene is conserved among cereals and could be explored for the haploid inducer system in other crops (Kelliher et al., 2017). Similarly, two natural inducer lines were identified in sorghum, which could be used in DH production (Hussain & Franks, 2019). Additionally, we could utilize CENH3 mutations in barley for haploid creations (Karimi-ashtiyani et al., 2015).

This approach has a limitation in genotype dependence, technical knowledge, high cost and labour-intensive populations (Dwivedi et al., 2015). However, DH, along with other approaches, could potentially accelerate the breeding cycle of plants in an SB programme.

2.6 | Breaking seed dormancy

Another critical component in the breeding cycle acceleration is breaking the seed dormancy. Many species force dormancy to seeds during embryogenesis, which delays their germination and, ultimately, generation time. These dormant seeds could be treated with cold stratification, soaking seeds with water or germination-promoting hormones such as gibberellins (Penfield, 2017). For example, wheat and barley seeds are prematurely harvested at 14 days after synthesis and dried for three days, followed by a cold stratification of four days (Watson et al., 2018). These measures enable the breaking of dormancy and reduction in generation time. This approach has also been utilized in lentil to break seed dormancy (Lulsdorf & Banniza, 2018). Combining embryo rescue with the breaking of seed dormancy will save more time in the generation cycle (Zheng et al., 2013).

2.7 | RGA

RGA, popularly known as the SSD method, plays a massive role in each of these approaches. It was firstly utilized for advancing segregating populations derived from a modified cross in soybean (Brim, 1966). The distinction between RGA and SSD is that we operate conditions to enforce early flowering and seed set compared with expected growth conditions. Here, selection starts from the F_2 generation, where a single seed from each F_2 plant is randomly taken, bulked together and advanced to the subsequent generation. This process is repeated up to F_5 and F_6, segregating generations. By integrating embryo rescue techniques, SSD helps obtain eight to nine generations in wheat (Yao et al., 2017; Zheng et al., 2013) and barley (Zheng et al., 2013). This method is implied in two different conditions: first is screen house RGA, and the other is field RGA. In these methods, plants are sown in small trays, transferred to pots and grown until a single panicle with sufficient seeds is produced. The main advantage of RGA method integration with SB is to obtain homozygous lines with many rounds of recombination in minimum time. This method's superiority lies in its speed, less resource requirement, technical simplicity and less expenditure overall. It shortens the breeding cycle by two years in comparison with conventional breeding (Collard et al., 2017).

As SB is an emerging area of plant breeding, more techniques such as high-throughput phenotyping, multi-trait phenotyping, next-generation sequencing, CRISPR-Cas9 and DNA mismatch repair to create genetic diversity can be integrated at a different level of the breeding cycle to hasten the rapid breeding of crop plants (Hickey et al., 2019; Karthika et al., 2020). Faster and better phenotyping with advanced plant phenotyping platforms could reduce the cost with the challenge of data and image processing. The advanced phenotyping technique can be combined with SB for the traits that behave stably in the targeted controlled environment. These platforms could facilitate rapid gene and locus discovery (Al-Tamimi et al., 2016; Awlia et al., 2016).

3 | POLLEN-BASED SELECTION (PBS): POTENTIAL TOOL FOR SB

The anthesis stage is critical for pollen production and a more sensitive stage for stress (Satake & Yoshida, 1978). Minor biotic and abiotic stress exposure during microsporogenesis leads to pollen sterility and causes a significant loss in crop production (Begcy & Dresselhaus, 2018). The primary cause of pollen sterility is a reduction in pollen germination and pollen tube growth during stress (Yang et al., 2013). Consequently, screening at the pollen stage has the potential for sporophytic selection against stress. Applying stress on the composite pollen mixture can also increase pollen grain fitness (Dominguez et al., 2005). Hence, a combined pollen selection and marker-assisted selection (MAS) approach can be utilized to mine our genotype of interest.

The effect of stress exposure during the gamete stage has been reported in several studies and proved successful in increasing the tolerant plants (Clarke et al., 2004; Mohapatra et al., 2020; Singh et al., 2020; Totsky & Lyakh, 2015). An increase in the number of tolerant plants is due to pollen's presence containing tolerant alleles and subsequently fertilizing female gamete, and the selected zygote has those alleles. Therefore, pollen selection exploits the shift in allelic frequency towards the tolerant progeny and achieves homozygosity faster. Various groups have reported the efficiency of pollen selection in tobacco, chickpea and maize (Ravikumar et al., 2007; Singh et al., 2020; Touraev et al., 1995) for simply inherited traits as well as complex traits like heat stress.

Thus, cyclic PBS for desirable traits will lead to homozygosity, reducing the breeding cycle. However, this method needs at least four seasons of crops (Singh et al., 2020). PBS at the F_1 generation increases the tolerant plants in the F_2 generation by channelizing the variation. Further, the F_2 population can be forwarded by SB to produce tolerant genotypes in significantly less time. PBS can also be used as a foreground selection and molecular marker used for background selection and forwarded with the SB platform. So, the combination of PBS, MAS and SB is the potential approach for incorporating desirable alleles in significantly less time, even for the complex polygenic trait. Overall, the pollen-selected progeny was more vigorous and tolerant for adverse conditions (Mohapatra et al., 2020; Singh et al., 2020). Therefore, PBS will overcome the problem in SB, such as less seed set and poor germination which can help future breeding programmes at the field level.

4 | MAJOR APPLICATIONS OF SB

SB is a revolution in plant breeding and has many applications to feed the ever-growing world population with other breeding techniques. The SB's initial application reduces the generation time of crops in controlled conditions (Ghosh et al., 2018). This approach is first utilized for grain dormancy in wheat cultivated under managed temperature and light conditions (Hickey et al., 2009). Key phenotypic traits such as reduced height (Rht) genes could be easily manipulated under SB specifications (Derkx et al., 2012). Further, SB could be utilized for accelerating plant phenotyping, transformation and mutant studies, as demonstrated by Ghosh et al. (2018). Quantitative traits such as plant height, seminal root angle, root number, resistance to leaf rust (Alahmad et al., 2018), root adoption in wheat (Christopher et al., 2015) improve stay-green, and integration of multiple disease-resistance traits in barley (Hickey et al., 2017) is phenotyped efficiently by the help of SB protocols.

Apart from major cereals, SB has excellent potential in breeding other crops such as oilseed. Higher yield should proportionally result in higher oil content and take 10–12 years to reach as variety in the market. For example, soybean has a lifespan of 100–125 days, where their reproductive stage covers a significant portion of their life cycle. (Roumet & Morin, 1997) Find variability among soybean for precocious germination of 22 different genotypes, resulting in plantlets producing viable seeds. Taking a clue from this Nagatoshi and Fujita (2019) standardized the SB protocol in soybean cultivar 'Enrei' and achieved four to five generations in a year instead of one to two. Pod shattering trait in canola is phenotyped and achieved four generations per year by preharvesting the pod (Ghosh et al., 2018). Sunflower is a short-duration crop, but its generation time is prohibited by fresh seed dormancy that persuades from 40 to 70 days. Utilizing the embryo rescue technique, scientists reduced the breeding cycle for sunflower (Dagustu et al., 2012). Therefore, other oilseed crop, such as sesame, has excellent potential to be advanced through SB protocols.

Legumes are the primary plant protein source for animal and human consumption. Legume breeding mainly suffered by their seed's recalcitrant nature for in vitro approaches (Ochatt et al., 2002). In a combination of in vitro and in vivo techniques, RGA is adopted for pea and Bambara groundnut for rapid generation cycling (Ochatt et al., 2002). SB protocols are developed for peanuts, lentils and faba bean (Mobini et al., 2015; O'Connor et al., 2013). In fruit crops, juvenile phases ranged from a few years to 20 or more years (Korbo et al., 2013). Implementation of SB in fruit crops can scale up their production for meeting future demand. SB has been successfully applied in apple (Flachowsky et al., 2011) to develop disease-resistant plants against fire blight. Leafy vegetable crops often suffered from late flowering and the recalcitrant nature of their lines, which SB could overcome. Some of these crops have been standardized under SB protocols, for example, amaranth (Stetter et al., 2016). Clonally propagated crops lacking diversity are often prone to climatic adversities, pests and disease attacks. SB could be applied in these crops to create advantageous traits to produce diversity in lesser time and generate climate-smart new varieties.

It can be integrated with genetic engineering and modern breeding methods with great potential in crop improvement programmes; for example, it is used with CRISPR-Cas9 for gene insertion followed by MAS to develop elite hybrid lines (Wolter et al., 2019). SB's industrial potential has also been highlighted recently. Dow AgroSciences released the 'DS Faraday' variety, possibly solving the preharvest sprouting wheat problem in Australia. Protocols for short-day crops such as sorghum, pigeon pea and millets have also been part of SB project taken up by Lee Hickey in collaboration with the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) (https://geneticliteracyproject.org/2020/03/02/how-speed-breeding-will-help-us-expand-crop-diversity-to-feed-10-billion-people/). This project aims at standardizing the early flowering and crop improvement for these subsistence crops important for Asia and Africa (Chiurugwi et al., 2019). SB protocols having flexibility for light quality, photoperiod and temperature regime based upon location could be implemented for broader applications for the whole spectrum of crop species.

Plant pathogens often evade the resistance of plant varieties over a long period. This needs a continuous generation of varieties for disease-resistant traits. SB is a powerful tool for screening the plants at the early stages of disease development, and this will help to develop new varieties quickly, as demonstrated for spring wheat,

durum wheat and barley (Alahmad et al., 2018; Hickey et al., 2017; Riaz et al., 2016). Phenotyping and scoring of disease-resistance traits such as wheat stripe rust and wheat leaf rust could be quickly done under the SB specifications (Hickey et al., 2009; Riaz et al., 2016). SB with a combination of RNA interacting protein against microbes could provide functional variation for the pathogen resistance (Pandey et al., 2020). All these reports indicate SB as evolutionary technology with a wide array of applications in breeding programmes.

5 | LIMITATIONS AND COST-EFFECTIVENESS OF SB

SB relies on inducing early flowering of photoperiod responsive crops. However, different plant species behave differently with photoperiod requirements and light intensity. So, SB's implementation in a short-day and the day-neutral plant requires species and variety-specific standardization. The differences between the photoperiodic condition for a short day and a long day range from minutes to hours, making SB standardization very difficult (Jackson & Jackson, 2009). This shortcoming of SB can be overcome by defining separate photoperiods for vegetative and reproductive phases, as shown in amaranth (Stetter et al., 2016). Daylight and temperature also vary with geographical locations, adding a new dimension of adjustment for SB protocols. Its application is limited to artificial stimulated conditions. SB also comprises early harvest of immature seeds that could interfere with the germination, phenotyping of some seed traits and generation advancement (Hickey et al., 2009). Comparison of glasshouse grown crop with SB for different phenotypic traits revealed less number of seeds per spikelet, comparable germination, and viability in wheat and barley (Watson et al., 2018).

SB requires an initial investment for growth chamber, lighting and temperature control requirement which is relatively high. However, the initial investment will be compensated by the benefits of more generations per year. This can be done by increasing small grain cereals' densities for inbred developments to reduce costs. Comparing the economics of RGA and the pedigree method for rice shows that RGA's cost-effectiveness is part of SB (Collard et al., 2017). Lighting and temperature control also require higher energy consumption, which increases the project's total cost. This requires sustainable energy input options such as solar energy and energy-efficient LEDs (Yao et al., 2017). In the future, LEDs' costs will be lower and could be replaced by laser lights due to its electrical conversion efficiency, which ultimately cuts down the SB's operational cost (Ooi et al., 2016). These could be efficient outside growth chambers, reducing the cooling cost for creating controlled environments. Further, determining the proper integration of SB with other plant breeding programmes could reduce the project's overall cost, which requires invention in the plant breeding tools and computational tools for simulation of such mixed programmes. SB has its advantage, application and limitations. Therefore, SB's comparison with other breeding approaches for RGA could be helpful (Table 2).

6 | THE WAY FORWARD: SB IN COMBINATION WITH MAS, GS, TRANSGENICS AND GENOME EDITING

Many advanced techniques could be integrated with the SB platform to accelerate the breeding programme (Figure 2). A schematic presentation of such integration has been shown in Table 3. MAS is a tool based on DNA-linked markers for the indirect selection of traits. MAS's principle is the presence of a DNA marker that is tightly linked

TABLE 2 Comparison between different breeding methods and SB

Particulars	SB	RGA	MABC	Genomic selection	Shuttle breeding
Methods involved	Photoperiod and temperature	SSD	MAS with backcrossing	GEBVs	Off-season breeding
Transfer of genes from other sources	Very quick	Quick	Quick	Quick	Quick
Time required for release of new variety (years)	2–3	6–8	6–8	6–8	6–8
Frequency of desirable plants	Less (only desired plants with desired trait continue)	Less (phenotypically selected plant continue)	More	More	Less
Technical skill required	Required to handle the system	Very less	Required	Required	Very less
Expenditure involved	More (higher establishment cost)	Very less	Required	More	Less
Equipment required	Yes (growth chambers/ greenhouses)	No	Required (wet lab establishment)	Required (wet lab establishment)	No
Facilities required	More (growth chambers/ greenhouses for controlled environments)	No	Required (wet lab establishment)	Required (wet lab establishment)	No

Abbreviations: GEBVs, genomic estimated breeding values; MABC, marker-assisted backcrossing; MAS, marker-assisted selection; RGA, rapid generation advance; SB, speed breeding; SSD, single-seed descent.

TABLE 3 Schematic representation of breeding cycle for different methods integrated with speed breeding platform

Methods	Prebreeding	Breeding
PBS	P1 × P2 ——→F1——→F2→ (selection pressure)	4 generations (SB)
GS	P1 × P2——————→	6 generations (SB)
MAS	P1 × P2 ——————→	6 generations (SB)
CRISPR-Cas9	P ——————→	3 generations (SB)
High-throughput phenotyping	P1 × P2——————→	6 generations (SB)

Abbreviations: GS, genomic selection; MAS, marker-assisted selection; P1, P2 and P, parent; PBS, pollen-based selection; SB, speed breeding.

to the gene of interest. MAS follows three types of selection: foreground (gene of interest), background and recombinant selection. MAS's wide application in reducing generation time in many crops is already reported (Das et al., 2017; Prabhu et al., 2009). The DNA marker linked to the gene of interest (foreground) can select the desired plant. Further, the plant with the desired trait can continue by rapid generation (SB) to stabilize them. The use of 'seed chipping' with barcoding can facilitate high-throughput MAS at the individual plant level. Breeding activities such as crossing, mapping population generation and phenotyping for particular traits can be performed by SB (Watson et al., 2018). SB can also be integrated with backcrossing, pyramiding and transgenic pipelines to expedite these processes (Figure 2) (Watson et al., 2018). Therefore, the combination of MAS with SB will accelerate plant breeding and reduce the project's overall cost.

Similarly, genomic selection (GS) deploys dense marker at the genome level to determine genomic estimated breeding values (GEBVs) for the collective effect of all quantitative trait loci (QTL), which explains all the possible genetic variance for any trait (Hayes et al., 2009). Plants with higher GEBV have been advanced to the next generation. GS is predominantly devised to study complex genetic traits such as yield, controlled by many genes. GS has an advantage over other breeding methods in selection speed for variety development, time and resource utilization. Recently, GS application at the industry level has shown in maize breeding for drought tolerance and released for farmers use as 'AQUAmax' hybrids (Cooper et al., 2014; Gaffney et al., 2015). Currently, genome sequencing cost is the primary concern with GS. The GS cost can be reduced by applying it in an alternate generation or used only for selected traits that could pass the threshold value through other breeding methods such as SB (Riaz et al., 2016). Further, knowing the precise location of genetic mutation with new techniques such as ExpressEdit, rapid disease-resistance gene discovery and cloning technologies GS can expedite the editing process (Arora et al., 2019).

Therefore, combining SB and GS could provide additional strength for accurate selection and contribute to more genetic gain per year (Gorjanc et al., 2018; Hickey et al., 2017). In this approach, parents were selected on the basis of GEBVs with reducing time for selection and then selected progenies produced by SB. The process is repeated many times to promote rapid breeding cycling. This combined SB and GS strategy can increase the genetic gain to select parents in each generation further in a breeding programme. This combination reduces the inbreeding problem compared with the phenotypic selection or GS scheme (Jighly et al., 2019). This scheme, combined with multiple traits, could achieve higher gains, such as normalized difference vegetation index and canopy temperature with available high-throughput phenotyping platforms, enabling early-stage selection (Crain et al., 2018). Simulation studies with GS and SB combined for different traits with various genetic architecture and heritability suggested the additional genetic gain and reduction in generation time compared with conventional selection and breeding (Jighly et al., 2019). Examples of this combination, also known as 'Speed GS', have been demonstrated for the wheat crop (Voss-Fels et al., 2019). With genome editing and mutagenesis, SB can develop biofortified foods such as decreasing anti-nutritional components from *Brassica* and *Lathyrus* or increasing vitamins in staple crops such as rice.

In a varietal developmental programme, variability is most important. However, the long domestication process reduced the genetic diversity available for breeding. The CRISPR/Cas system now creates new genetic variability at a fast pace (Shen et al., 2017). CRISPR/Cas system has a multiplexing ability that allows the modification of multiple targets and immediate pyramiding of multiple traits within one generation (Zhou et al., 2019). It also creates diversity by interfering with regulatory elements such as promoters and enhancers. By inhibiting regulatory factors, CRISPR/Cas improved the inflorescence architecture (Soyk et al., 2017) and flower production (Liu et al., 2013). In polyploid crops such as potatoes with more than one copy of gene, it is difficult to alter/delete a single target gene that reduces potato quality through breeding. In that case, the genome editing platform (CRISPR-Cas9 most common) seems to be more efficient, especially in the polyploid plant's genome. It could add/delete/substitute the gene of interest. CRISPR-Cas9-mediated editing depends upon single guide RNA (sgRNA) to direct the Cas9 enzyme to target a particular DNA sequence (Doudna & Charpentier, 2014; Haroon et al., 2019). However, genome editing plants require in vitro tissue culture manipulation, and these edited plants are subjected to transgenic plant regulation. Combining genome editing and SB could decrease the time to produce the variety compared with the traditional process. This integration, technological manipulation/advances related to tissue culture could avoid the regulatory implications of genetically modified products.

For instance, the exogenous application of genome-edited constructs with Cas9 protein can achieve desired allelic modification.

These exogenous DNA applications could utilize clay nanosheets as shown for RNA interference construct delivery for raising virus-resistant plants (Mitter et al., 2017). CRISPR-Cas9 ribonucleoprotein complexes are another advance used for targeted editing in maize, wheat and potato (Andersson et al., 2018; Liang et al., 2017; Svitashev et al., 2016). Here, protoplast or immature embryos are used as ideal target tissue, which implies optimizing germinating seedlings and mature seeds (Hamada et al., 2017). Delivery of such constructs could also be done by utilizing viral vectors (geminivirus group) or particle bombardment *in planta* in shoot apical meristems of mature seeds or through biolistic delivery for tissue-specific editin (Hamada et al., 2017). These delivery methods could introduce edits in different tissues, such as pollen and inflorescence. Genome editing can create variants of our choice to expedite the selection.

7 | CONCLUSION AND FUTURE PERSPECTIVES

General breeding procedures take around four to six generations to develop a stable line for a specific trait. With the increased demand for better agricultural crop production, fast-growing varieties with less generation time could benefit crop research. Further, SB provides the platform for researchers across the globe to explore genome editing technologies and selective breeding in tandem with SB to revolutionize the arena of plant research. SB majorly depends upon extending the photoperiod to hasten the crop generation with a continuous light application, and its potential is not realized for many crops. However, researchers find some genes in light-sensitive crops such as tomato to make them functional for extending photoperiods (Velez-ramirez et al., 2014). These discoveries will lead to more comprehensive applications over time in different crops. As SB application is limited for some crops, implementing more crops will determine its industrial potential. The coupling of other approaches like pollen selection could provide a new dimension to the future of plant breeding. Combining SB with genomic, pollen selection with MAS, genome editing and high-throughput phenotyping could improve its overall competence of breeding for feeding the world population over the next decade.

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CONFLICT OF INTERESTS

No conflicts of interest declared.

AUTHOR CONTRIBUTIONS

S. P. and A. S. wrote the manuscript. S. K. P. revised the manuscript. M. P. conceptualized and outlined the article.

DATA AVAILABILITY STATEMENT

Data availability statement is not applicable to this work.

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