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Enhancing Crop Improvement with Speed Breeding: Applications, Challenges, and Future Prospects

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ABSTRACT

Speed breeding (SB) has emerged as a revolutionary tool in the modern agricultural system. It plays a vital role in accelerating the improvement of crops by shortening the generational cycle of crops. This review explores the principles, methodologies, and applications of SB in enhancing crop improvement. By using SB techniques such as extended photoperiods and optimized temperature regimes, SB enables rapid generation advancement and genetic gain.

The integration of molecular breeding tools, such as marker-assisted selection and genomic selection, further enhances the efficiency and precision of this approach. This review explains different protocols and applications of SB in different crop species, including wheat, rice, barley, oats, and vegetables. Additionally, this review also explains the integration of plant breeding tools such as gene editing and high-throughput phenotyping to further improve breeding efficiency. In the end, the paper explains the major challenges and constraints to SB. Although SB has achieved a significant level of success and improvement in several crop species but still the challenges of high cost, interdisciplinary expertise, and different protocols for each crop species remain major constraints, especially for developing countries.

In conclusion, SB offers an innovative and sustainable solution for accelerating crop improvement and ensuring global food security in the face of climate change and increasing population demands. Future research should focus on expanding its applicability to a wider range of crops and refining protocols to optimize efficiency and accessibility.

Keywords: Speed breeding, Crop improvement, Photoperiod manipulation, Genetic gain, Controlled environment

Introduction

By 2050, the current rate of crop improvement in agriculture is expected to be insufficient to meet the food demands of the growing global population, which is projected to increase by 25% and reach 10 billion.[1] Traditional crop breeding requires significant time, space, and resources for selecting and crossing desirable plants. The length of the seed-to-seed cycle remains a major hurdle in advancing plant research and breeding.[2] In many crop breeding programs, the pace of yield improvement falls short of meeting the rising food demand driven by rapid global population growth. The lengthy growth cycle of crops poses a major challenge in plant breeding, limiting the development of enhanced crop varieties. Since breeding new cultivars requires multiple stages of crossing, selection, and testing, the entire process can take 10–20 years.[3] However, with advancements in technology, breeders have boosted the process of advancement of novel breeding lines and varieties.[4] This approach accelerates growth cycles by efficiently managing light and temperature conditions while utilizing immature seed propagation. As a result, it boosts biomass and seed yield in long-day plants such as lettuce and wheat, along with certain short-day varieties like rice, cotton, and sorghum.[5,6] Speed breeding (SB) enables the integration of advanced techniques like gene editing, genotyping, and phenotyping, hence speeding up crop improvement.[7] SB has been widely utilized for plant phenotyping and trait pyramiding to develop new crop varieties.[2] It has been successfully applied to cereals, pulses, and canola, achieving 4–6 generations annually. With broader crop adaptability and lower labor demands than traditional breeding, SB is a powerful and efficient tool for rapidly developing new plant varieties with notable improvement in vegetable, cereal, and oilseed crops.[7] It has enabled breeders to develop disease resistance, drought, salt tolerance, and crops with high protein content.[7] SB, once integrated with gene editing, genotyping, and genome-wide selection, offers significant potential for SB in the future of crop improvement. However, challenges such as infrastructure limitations, genotypic variations, and stress responses remain obstacles to it.[1]

How SB Works

Since 1940, techniques such as shuttle breeding have been used to manipulate the life cycle of the plant.[8] Recently, the techniques that are used to further truncate the life cycle of the plants by manipulating the environment of the plants are termed SB techniques.[9]

SB has accelerated generation cycles by controlling light and temperature (see Figure 1). Established protocols exist for both short-day and long-day species, and the method integrates well with advanced breeding techniques like genomic selection[10] (see Figure 2). SB techniques can be used to accelerate the outcomes of breeding programs, such as mapping populations, evaluation for traits of agronomic interest, and advancing the generations of crosses for these plants are grown under a controlled environment (CE) where researchers tend to manipulate temperature and photoperiod of the plants consequently reducing the time required for floral initiation, reproductive growth, and seed maturity.[11,12] Especially the extension of photoperiod in long-day species has been used for a very long time to manipulate the flowering time of these crop species.[13] The introduction of advanced LED lighting systems has supported efforts to speed up lifecycle transitions by allowing control over wavelength composition. This enables the activation of light-responsive mechanisms, such as shade avoidance, and accelerates the rapid progression of plants toward

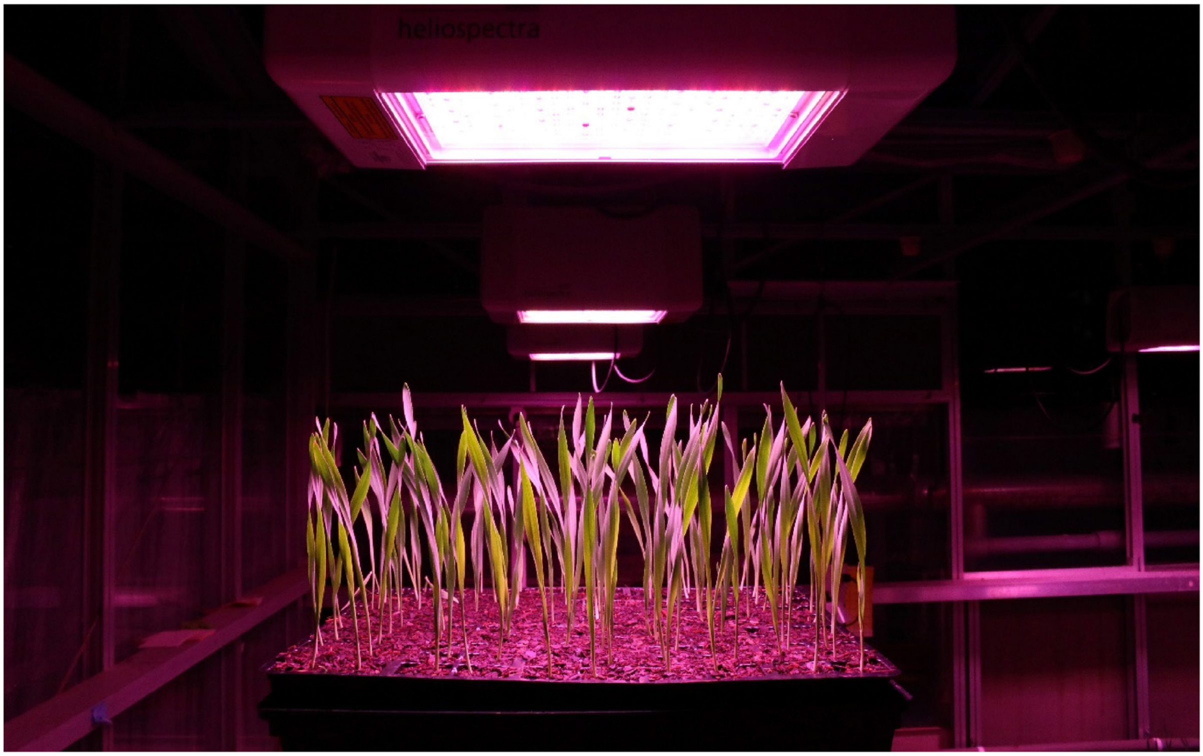

Fig 1 | LED-assisted SB for accelerated plant growth. Attribution: Queensland Alliance for Agriculture and Food

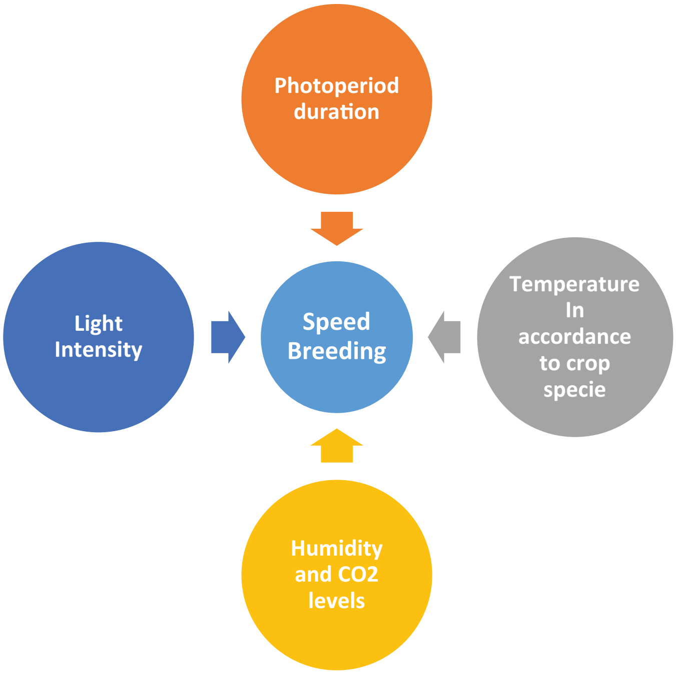

Fig 2 | Key environmental factors that optimize SB for crop improvement

flowering.[14] Additionally, the economic cost of the growth room can also contribute to the versatile role of the SB based on local resources.[15]

Broad Applications of SB for Accelerating Crop Improvement and Genetic Advancement

SB finds its wider application in the genetic mapping of plant populations, enhancing crop allelic diversity, consequently making them more resilient to climate change and trait stacking. The techniques of SB also align well with different breeding methods, such as single-seed and plant descent methods. Additionally, the integration of SB techniques with genomic selection, genotyping, and genome editing shows significant potential in the future.[1] Additionally, the cost of maintaining the inbred lines can also be significantly reduced by increasing the planting densities.[16] SB is also very useful when it comes to tackling challenges when dealing with double haploids, such as issues of germination, plant vigor, and overall growth.[17] The breeding methods, such as single-seed descent integrated with SB, have been shown to increase the generational turnover by 3 times in contrast to the techniques of shuttle breeding.[18] Hence, SB can be an effective technique to reduce breeding cycles resulting in reproduction in a comparatively shorter period than normal. It will help in coping with the problem of future food security, and it can be done by integrating SB techniques with modern tools of plant breeding to cope with this ever-increasing population of humans and issues of food security.[19]

This section of the paper highlights the importance and the application of SB in different crop species and its outcomes in those crops.

Wheat

Being a rich source of nutrients and food and having fewer water-consuming crops, bread wheat (*Triticum aestivum*) and durum wheat (*Triticum durum*) are crucial cereal crops for food security.[20] In wheat (*Triticum aestivum*), increasing the generational turnover is crucial for genetic gains in winter wheat; the vernalization requirement of winter wheat is a hindrance to its improvement, hence delaying progress. A 22-hour photoperiod (22 h light/2 h dark, 25 °C/22 °C) in 50-cell trays accelerated the generational advancement, hence enabling four generations of winter wheat per year by reducing 30 days per cycle.[21] In another study, SB was applied to durum wheat (*Triticum durum*), multiple traits of agronomic importance were selected for the F2 population, and significant results were found for the selection of most of the traits. Hence, this method of multi-trait selection integrated with SB can accelerate the selection cycle by enriching inbred lines with alleles of desired traits in a comparatively shorter period in *Triticum durum*[22] (see Figure 3).

In another study, the effectiveness of selection for Fusarium head blight (FHB) resistance level was evaluated under SB conditions in six wheat genotypes, and a significant correlation was found between FHB and deoxynivalenol across all conditions, hence allowing the phenotyping for FHB) at 14 days rather than at 21 consequently reducing the phenotyping time by 1 week. Therefore, this method can also be used to accelerate the rapid development of FHB-resistant wheat varieties in the future.[23] In another study, four to six generations of wheat were produced by harvesting seeds 15–20 days post-anthesis and subjecting them to hydrogen peroxide (H_2O_2) treatment at a reduced temperature.

Hence, SB can hold great potential for improvement by accelerating generational advancement, overall rapid trait selection, and enhancing disease resistance in wheat.

Rice

Rice is one of the most important cereals worldwide, feeding more people than any other cereal, such as maize, barley, and wheat. Rice breeders continuously improve yield and climate resilience by utilizing their vast genetic diversity. The crop has undergone significant phenotype changes, from traditional varieties to semi-dwarf, hybrid, and super rice types, ensuring food security.[24]

In a study, salt-tolerant rice varieties were developed by integrating marker-assisted selection (MAS) and SB by introgression of the *hst1* gene from one variety into another high-yielding variety by producing a BC3F3 population over a period of six generations in 17 months using SB. It maintained higher yields under salt stress, making it a strong candidate for a new climate-resilient, salt-tolerant rice cultivar.[25] An SB protocol called the speed flower has also been developed by scientists who were able to get 4–5 generations of rice per year under optimized photoperiodic conditions, such as photoperiod. In this study, it was found that a continuous light period followed by a reduced light phase for 15 days reduced the time required for flowering. Additionally, under controlled temperature and humidity conditions, they tested 198 accessions while successfully producing 5–6 generations per year.[26]

For short-day crops such as rice, another SB protocol was developed by using LED lights. It was found that a photoperiod of 10 hours with blue light enriched far blue spectrum induced the flowering in rice at 60 days, and the addition of far-red light in the spectrum reduced the days-to-flowering time by 20 days

Fig 3 | Speed breeding of wheat under optimized LED lighting conditions (Attribution: Queensland Alliance for Agriculture and Food.)

in some species of rice. This protocol can be integrated with genomics to enhance the overall efficiency of the breeding.[12] Another breakthrough in increasing the generation turnover in rice is a breeding protocol termed the biotron breeding system. The system works by regulating temperature, CO_2 levels, and photoperiod, and it is also augmented with embryo rescue techniques.[27] Biotron breeding system (BBS) has been successfully used to reduce the generational interval of 2 months in Nipponbare,[28] and without the embryo rescue, the generational interval was reduced to 3 months.[28] Recent research has been successful in obtaining 4–5 generations of rice per year.[9]

Hence, these modern SB protocols can be utilized to expedite the improvement process in rice, especially once they are integrated with MAS and other modern breeding tools.

Barley

Barley has been cultivated for centuries and remains a widely grown grain across various climates, covering 48 million hectares. It thrives with minimal resources and serves multiple purposes, including livestock nutrition, brewing, and direct consumption. Regional preferences vary between seasonal and ear-type varieties. Advances in breeding techniques are speeding up the development of improved strains, ensuring their continued role as a reliable staple in agriculture.[29]

SB can be utilized to get up to six generations per year in barley, hence accelerating the plant growth and reducing the time required for research.[15] A recent study under two different light conditions—22h under SB and 16h under standard breeding conditions—was able to identify two genes—PPDH-1 and ELF3—responsible for controlling the flowering in barley, and it was found that late flowering was observed in cultivated species of barley and early in wild one under light condition high lighting the importance of the gene in adaptability a practical insight into SB in barley for improvement.[30] Improvement in the barley cultivar named Scarlet has been induced by integrating phenotypic screening and SB protocols. The scientists were able to successfully develop 87 BC1F3:4 introgression lines by using a backcross strategy with four resistant donors within a short span of 2 years, and they were able to develop four high-yielding and disease-resistant lines in barley.[31]

Hence, SB offers great potential for improvement in barley by reducing generation time, enabling faster trait selection, and improving its resilience to climate change.

Oat

Oats are one of the important grain crops in many countries. Its world production averages 1/3 of wheat and 2/5 of rice, with the USA and Canada as major producers and used as major feed for animals. Despite its known nutritional benefits, it is still consumed by <5% for human consumption.[32] Like other crops, it takes 10–15 years to develop a cultivar after crossing oats by using conventional breeding methods. It also requires several generations to properly evaluate the variety before release.[33]

SB, MAS, Quantitative trait loci mapping, and genomic selection are commonly used to identify the genes of agronomic importance, induce climate resilience, and accelerate the overall genetic gain in oats.[34] SB has been successfully integrated into oats (*Avena sativa* L.) by using 22 hours of photoperiod which consequently reduced the days-to-flowering time of plants by 11 days compared to normal. Further, more germination tests showed the viability of the seed 21 days after flowering. This method accelerates breeding cycles, supporting faster cultivar development through single-seed descent integrated with SB.[35] In another study, SB integrated with high-density planting in soils with low fertility reduced the time of generational cycle in oats, and also found that the photoperiod of 22 hours accelerated the flowering, complementing a resource-efficient growth condition, hence making breeding programs more time and cost-efficient.[36]

Legumes

Legumes are essential for human consumption, livestock feed, and soil enrichment through nitrogen fixation. However, conventional pulse breeding is a lengthy process, often requiring over a decade to develop improved varieties. Methods like shuttle breeding and in vitro culture exist but lack efficiency in widespread use. SB overcomes these limitations by optimizing environmental factors such as light, temperature, and photoperiod, accelerating plant growth and flowering while maintaining a non-GMO approach.[37]

Protocols for speeding up generation cycles have been refined across various legume crops, particularly in temperate pulses that thrive under extended daylight due to their adaptable long-day growth patterns.[11] Recent studies have optimized photoperiodic duration in legumes such as lentils, faba beans, and chickpeas in LED-lit growth rooms and found that a photoperiod of 22H promoted flowering, while in contrast, 14H of photoperiod delayed the flowering, the photoperiod of 18H was found to be optimum to reduce the stress and to shorten the vegetative cycle of the legume crops.[38] The optimum ratio of different colors of LEDS has also been optimized as a study evaluated different red-blue light ratios, 5:3, 3:5, respectively, and found that 3:5 improved overall vegetative growth and canopy cover while 5:3 was found to be cost-effective and efficient for SB in a CE.[39] In another study, six chickpea accessions from early, medium, and late-maturing groups were used to study optimum generation cycles under greenhouse conditions. It was found that extended photoperiods reduced flowering time by 8–19, 7–16, and 11–27 days, respectively. Immature seeds germinated 20–23 days post-anthesis, enabling cycles of 43–60, 44–64, and 52–79 days. The late-maturing CDC-Frontier stalled after three cycles due to photoperiod sensitivity. Annual cycles averaged 7 for early, 6.2 for medium, and 6 for late types, demonstrating the potential of accelerated breeding in chickpeas.[40]

The recent advancements in SB have now enabled plant breeders to achieve generational advancement and homozygosity in a comparatively short time, which holds great promise for crop improvement in legumes.

Vegetables

The extension of photoperiod has also shown promising results in reducing the generational cycle of crops such as tomatoes, peppers, and amaranth.[41] In a recent study, the effect of the size of the container on the growth of tomatoes found that the 6L container improved the growth of the tomatoes and reduced the sowing to anthesis and anthesis to fruit ripening. Additionally, it was also found that cold priming also reduced the sowing to anthesis time while treatment with potassium supplement also reduced the anthesis to fruit ripening time, and once both treatments were combined, it reduced the anthesis to ripening time by 2.9–3.9 days and with embryo rescue the generation cycle reduced by 22–23.3 days post-anthesis shortened generation time by 8.7–11.6 days increasing the overall cycle of crops to 3–4 per year.[42] In amaranth, the photoperiodic variation has been shown to improve reproductive synchronization, which, once integrated with modern technologies such as MAS, can lead to the identification of hybrids, thus accelerating the breeding programs.[43] Booting the expression of the flowering genes can also be an effective approach and strategy, as shown by some studies on increasing generational turnover.[44]

Hence, although the protocols of SB are not well developed in vegetable crops, and there is a gap in research about SB in vegetables, it still holds great potential for vegetable breeding in the future.

Challenges

Although SB is a valuable tool for accelerating the process of crop improvement, it also requires proper infrastructure, expertise in the use of technology, phenomics facilities, and constant financial support.[45] Despite its broad application in crop improvement, SB still has many potential challenges to SB usage for crop improvement, such as the unavailability of trained staff, long-term funding, and major changes in breeding programs, which are the major hindrances in SB.[46] A major constraint in SB is the availability of CE conditions optimized for rapid generation turnover in target crops. SB can be costly when advanced CE facilities are lacking, and integrating it with methods like embryo rescue and MAS demands extra resources and expertise. Additional challenges involve ensuring an uninterrupted power supply and maintaining stable temperatures, particularly during winter seasons.[47] Additionally, the availability of specialized equipment for trait selection during early-generation advancement is limited.[48] In developed countries, the application of SB is not a problem. However, in resource-poor nations, it remains a challenge. Limited infrastructure, lack of expertise, and fewer collaborations with international organizations make routine use difficult.[46] The lack of trained active plant breeders and experts can also be a major challenge, especially for developing countries.[49]

When it comes to phenotyping of the characters, such as plant height and flowering, once recorded under the SB setup, it can provide a field-based determination, but at the same time, some characters cannot be phenotype with accuracy due to their interaction with the SB environment.[35]

It is evident that SB has played a very positive role in accelerating the breeding programs of many species, but the scientific community still has to achieve its full potential to meet the pace of crop improvement with the growing human population.

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