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REVIEW ARTICLE

Speed breeding: A technique for early development of plant varieties with high productive capacity and resilience

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Abstract

Speed breeding (SB) has emerged as a technology that helps in developing new, improved crop varieties by dramatically shortening the time period taken for their generation. This is achieved by optimizing environmental parameters such as photoperiod, temperature and soil moisture. This process enables the development of multiple generations per year, thereby speeding up the development of homozygous lines and elite cultivars. Integration with modern molecular tools, including marker-assisted selection (MAS) and genomic selection (GS) with SB, enhances the precision and efficiency of trait selection, leading to faster genetic gain. Despite these advantages, adoption of this technique faces challenges such as infrastructure demands, shortage of skilled personnel, energy requirements and regional disparities in technology access. Addressing these bottlenecks through targeted investment, capacity building and policy support is required to harness SB technique for global food security. This review elucidates the principles, applications and limitations of SB and highlights its pivotal role in modern plant breeding and sustainable agriculture.

Keywords: crop improvement; generation advancement; genetic gain; genomic selection; marker-assisted selection; plant breeding; speed breeding

Introduction

Plant breeding has been crucial to ensuring food security and safety since the early 1900s and had a significant impact on the world's food supply (1). But as the world's population has been expanding quickly, there have been problems with both food quality and quantity in recent years. Additionally, heat and drought stress are being generated by extreme weather changes brought on by global climate change, which causes significant loss of crops for farmers worldwide (2). Global epidemics, such as the Irish potato blight of the 1840s and the Southern maize leaf blight of the 1970s in the United States, killed millions of people as a result of a lack of food (3). The goal of traditional agricultural methods is to increase the nutritional content of different crops. Numerous plant breeding alternatives and novelties have become available as a result of recent scientific developments (4). The existing annual yield enhancement levels in major crop species (ranging from 0.8 %-1.2 %) must be quadrupled to fulfil the rising demand for plant-based goods (5). Nowadays, farmers feed 10 times more people than they did 100 years ago on the same or less land area. Mendelian breeding principles revolutionised the industry. Traditional breeding procedure takes a minimum of 8-10 generations (6) before developing a variety and release takes another 3 generations; therefore changes are required in the ongoing breeding program. Shortening the duration of each generation, we can reduce the total time required for forwarding the segregating generations, thereby accelerating the crop growth time and lowering the generation time for day-neutral long-day crop.

Speed Breeding (SB) is a technique used to accelerate the growth and breeding of plants. This method involves using specialized lighting and temperature systems to create optimal growing conditions for plants, which allows them to complete multiple generations in a shorter time than traditional breeding methods. One of the main benefits of SB is that it allows for faster (early) development of new plant varieties. This can be especially useful for crops that have long breeding cycles, such as cereals like wheat and barley. By using SB techniques, researchers can develop new varieties in a short time as compared to traditional methods. Additionally, SB can also help to create more resilient and productive crops, which can help to address food security issues in the condition of rapid increase in global population. Another advantage of SB is that it can be used to breed plants in controlled environments. This allows researchers to more easily study the genetic makeup of the plants and the impact of environmental factors on the breeding process. Additionally, SB techniques can also be used to create plants that are more resistant to pests, diseases and environmental stressors, which can help to improve crop yields and reduce the need for pesticides and other inputs. For

example, researchers in Kashmir are using SB to rapidly develop rice varieties resistant to diseases such as blast and bakanae, as well as lines able to withstand cold stress (7). Also, the use of SB in millets has resulted in rapid generation of varieties with increased tolerance to environmental stresses such as drought and heat, as shown in recent research in controlled environment agriculture (8).

Despite the potential benefits of SB, there are also a few drawbacks. One of them is the use of artificial lighting and temperature systems can be costly and energy-intensive. Additionally, SB techniques may also increase the risk of genetic homogeneity in crops, which can make them more susceptible to disease and other threats. Overall, SB is a promising technique for improving crop productivity and resilience. However, advanced research in this direction can help us to fully comprehend the long-term impacts of this method and to develop more cost-effective and sustainable techniques for speeding up the breeding of plants.

Speed breeding

Traditional breeding practices have proved useful in developing a large number of plants globally over the past 100 years. conventional breeding procedure takes a long time, around 10 to 15 years—from the hybridization stage till the release of a cultivar (9). Additionally, combining a significant number of polygenic traits is also a difficulty (10). Even though marker-assisted selection (MAS) has served as a helpful technique in crop improvement programmes, it works best when it focuses on one or few major genes. Leaf rust resistance genes such as *Lr23* and stripe rust resistant gene such as *Yr15* in durum (11). It is necessary to identify the specific gene or quantitative trait locus (QTL) that is responsible for the desired characteristic to perform MAS. However, this method becomes less effective when the underlying genetics of a trait are unknown (12). Genomic selection (GS) is a more advanced breeding technique that overcomes the limitations of MAS. It involves estimating breeding values (EBVs) and evaluating the genomic merit of all potential improvements throughout the genome (13). Despite its potential benefits, the high cost of genotyping acts as a hindrance to widespread adaptation of this method. Additionally, GS can be used to simultaneously select for multiple traits, but the time required for crossings and producing stable new selection candidates slows down the rate of progress, as it is often applied to inbred lines (14).

The term "speed breeding" was coined in 2003 by researchers at the University of Queensland to describe a series of methods aimed at accelerating plant breeding. Compared to traditional selection procedures, which only produce 1 to 2 generations annually, SB produces 3 to 9 generations annually (15) (Fig. 1). This approach enables the rapid progression of generations and the production of homozygous and stable plant genotypes, leading to the development of novel cultivars (16). SB technology is complementary to MAS and high-throughput phenotyping (HTP) methods, allowing for the characterization and selection of various traits in early generations of population development. This reduces labor and field-testing expenses, saving time and money for breeding programs. A high-throughput, reliable and robust screening process is necessary to develop new phenotyping techniques and refine existing ones for genetic research and plant breeding. High-throughput, rapid, efficient and repeatable approaches are also required for variable traits in both the field and greenhouse. SB techniques can also increase the diversity of breeding populations and hasten the attainment of breeding objectives by synchronizing the flowering of domesticated and wild crop species. This can be achieved through genetic engineering, grafting, using plant growth regulators and collecting immature seed, among other methods (17).

Components of speed breeding

Manipulation of photoperiod

Light is a determining factor for the speed of growth, development, flowering and seed production in plants (18). Photoperiod affects the rate at which plants grow and mature. However, the ideal light requirements vary for each crop and genotype. Light quality and intensity, as well as the daily ratio of light to darkness, have a direct impact on various aspects of plant growth, including net photosynthetic rate, stomatal conductance, intercellular carbon dioxide (CO_2) and transpiration rate (19). To promote efficient growth and development, SB utilizes light sources that emit photosynthetic active radiation (PAR) with a wavelength of 400-700 nm and an intensity of 360-650 µmol m^{-2} s^{-1} in crops such as wheat, peanut, chickpea, pea, barley and canola (15, 16, 20). The use of these light sources allows for year-round sustained photosynthesis,

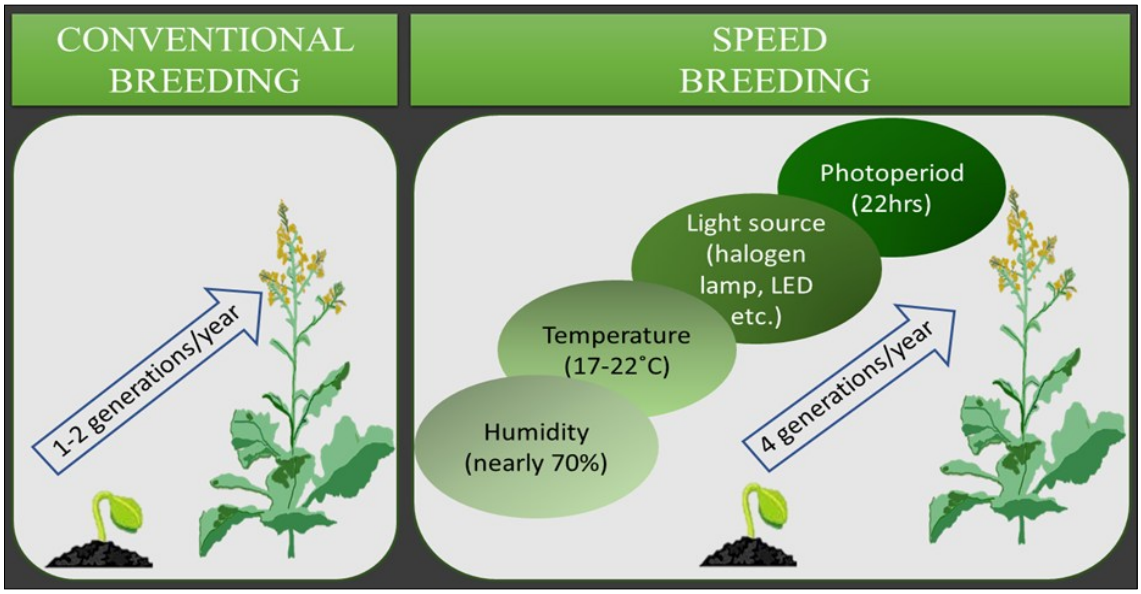

Fig. 1. Comparison of the number of generations obtained per year through conventional breeding and speed breeding method in canola crop by controlling the humidity, temperature, light source and photoperiod.

leading to faster growth and maturation (21). For example, a study conducted earlier (22) in wheat showed that a photoperiod of 22 hr of light and 150-190 µE m^{-2} s^{-1} PAR value reduces the number of days to flowering as compared to wheat grown with a 12/12 hr light/dark cycle.

Studies have been conducted on several wheat genotypes, including Paragon, Watkins landrace W352 and a late flowering Paragon x W352 F6 recombinant inbred line, to assess the effect of photoperiod on flowering. Results showed that flowering initiated in 35-39 days with the use of a 22/2 hr light/dark photoperiod, while the plants grown with a 12/12 hr photoperiod were in the stem elongation phase. In a separate study, it was determined that short day (SD) conditions (8/16 hr light/dark) followed by long day (LD) conditions (16/8 hr light/dark) could induce flowering without the need for vernalization. This was demonstrated in the winter wheat genotype G3116 (AY485969) grown under SD-LD conditions with a light intensity of 200-270 mol m^{-2} s^{-1}. The results showed that days to flower in non-vernalized genotypes were comparable to genotypes that had undergone vernalization for 6 weeks. Similar results were observed in barley genotypes exposed to a photoperiod of 16/8 hr light/dark and a light intensity of 500 µmol m^{-2} s^{-1} (23).

A combination of factors such as changes in length of photoperiod, immature seed germination, moisture control and nutrient management leads to acceleration of wheat and barley generations by 6 to 8 and 7 to 9 respectively. Chickpea has also shown early flowering when exposed to a photoperiod of 12 hr light and 12 hr dark with a 60 W incandescent bulb, causing blooming in early-, medium- and late-maturing genotypes in 37 to 65 days (24). Amaranth was able to flower in 4 weeks by alternating 2 weeks of long-day conditions with a light intensity of 150 mmol and short-day conditions (25). Similarly, groundnut was able to flower in 25 to 27 days after germination when exposed to continuous light using a 450 W PAR lamp (20). The use of low-energy LED lighting, powered by a solar-based battery inverter system, proved as a cost-effective photoperiod source and a viable option for nations with unstable electrical supplies. The optimized growth parameters (photoperiod, light intensity, temperature and plant density) for SB in major crops that can be referred to for designing specific protocols for other plants have been summarized in Table 1.

Manipulation of the temperature

Temperature fluctuations in the soil and air have a significant effect on seed germination and plant development. Optimal temperatures for most crops are typically between 12 ℃-30 ℃. The ideal range for growth, flowering and seed production lies between 25 ℃ -30 ℃ (26). In a study using chickpeas, temperature conditions of 25 ± 1 ℃ and 12/12 hr of light/dark were used to get direct sowing of immature chickpea (24). However, extreme temperatures can alter the pace of plant development and lead to a transition from the vegetative to reproductive stage (26, 27). For example, low temperatures are necessary to trigger the transition of the growth phase in winter wheat (22, 28), while high temperatures can decrease pollen viability, leading to male infertility in crops like rice, sorghum and soybean (26, 29, 30). Temperature regimes can be controlled and synchronized with light conditions, such as a 16/8 hr light/dark photoperiod, to optimize the speed of seed germination and plant growth (20). The reactions of different crops to temperature regimes that influence the physiological changes leading the plant into the reproductive growth phase can vary. Some crops may require different temperature and light conditions for early flowering (31). The use of solar or battery-powered AC systems could provide a cost-effective and stable technology, especially for indoor cultivation in developing nations. However, its scalability is currently limited by the initial capital investment, ongoing maintenance requirements and the availability of reliable power sources. These factors may restrict widespread adoption in large-scale breeding programs, particularly in resource-limited settings. Therefore, alternative low-cost cooling or ventilation methods may also be necessary to ensure broader applicability (6).

Management of soil moisture

Soil moisture stress can affect plant growth significantly, leading to changes in plant height, days to flowering, seed production and seed maturity (32, 33). Most SB protocols do not intentionally employ soil moisture stress; rather, they focus on manipulating photoperiod, temperature and planting density to accelerate crop development, while maintaining optimal or near-optimal soil moisture for healthy plant growth. However, soil moisture stress (such as controlled drought or reduced irrigation) can be selectively applied in specific protocols when early flowering and maturity are reliably induced under such conditions for certain crops (6, 34).

Drought stress is a commonly used strategy in crops such as wheat, barley and pearl millet (35). While drought-induced early flowering in pearl millet may act as an "escape mechanism" for the next generation (36). It can also cause sterility in some genotypes or delay flowering in others (37). A study with cowpeas showed that exposure to drought stress resulted in early blooming about 12 days earlier than those grown in well-watered conditions (38, 39). Conversely, watering wilted wheat and barley plants can stimulate growth and development and combining watering regimes with other techniques like embryo rescue, modified photoperiods and altered temperatures can result in faster generation turnover (8 and 9 generations per year in wheat and barley respectively) (23). However, reducing soil moisture levels gradually after flowering might speed up grain filling and maturation (40). This highlights the potential of SB technique to optimize water management for efficient turnover. Water management strategies can impact the growth and development of crops, including the timing of flowering and maturation. An

Table 1. Optimized growth parameters for speed breeding technique in some crop plant

Crop	Photoperiod	Light source and intensity	Temperature	Plant density	References
Wheat	22 hr light / 2 hr dark	LED or PAR lamp; 150–190 µmol m^{-2} s^{-1}	22 °C –28 °C	300–400 plants m^{-2}	(15, 16, 22)
Barley	16 hr light / 8 hr dark	LED; 500 µmol m^{-2} s^{-1}	22 °C –28 °C	300–350 plants m^{-2}	(16, 23)
Chickpea	12 hr light / 12 hr dark	Incandescent or LED; ~360 µmol m^{-2} s^{-1}	25 ± 1 °C	200 plants m^{-2}	(24)
Groundnut	24 hr continuous light	PAR lamp; 450 W	25 °C –28 °C	250 plants m^{-2}	(20)
Grain Amaranth	Alternating 14 days LD/14 days SD	LED; 150 µmol m^{-2} s^{-1}	25 °C –30 °C	150 plants m^{-2}	(25)
Peanut	22 hr light / 2 hr dark	LED; 360–650 µmol m^{-2} s^{-1}	25 °C –30 °C	200 plants m^{-2}	(15)
Canola	22 hr light / 2 hr dark	LED; 360–650 µmol m^{-2} s^{-1}	20 °C –25 °C	150–200 plants m^{-2}	(15, 21)

earlier study showed that reducing watering frequency from daily to twice weekly 4-6 weeks after flowering and a week without watering before harvest, could accelerate the breeding process for crops such as wheat, barley, canola and chickpea (16). These techniques can be applied in both outdoor and indoor growing conditions.

Plant population density

Growing plants at a higher density than the typical yield-maximizing number is known as high-density planting. This method results in increased competition for light, causing taller plants and an accelerated transition into the reproductive growth stages (41). This can lead to an increased number of generation cycles per year. In one study, rice grown at a high density of 400 plants m^{-2}, rather than the normal 25 plants m^{-2}, allowed for up to 4 generations per year (42). High-density planting can reduce the crop duration in rice by 15-40 days; however, this effect is dependent on both the genotype and environmental conditions. Genetic differences among rice varieties influence their response to planting density, while environmental factors such as soil fertility and moisture availability further modulate this interaction, resulting in variable impacts on crop duration across different growing conditions. Also, results have varied in different crops, with some studies indicating that high-density planting does not affect flowering and grain yield (43, 44). For example, the sorghum plant growth and grain yield were not affected by plant density (45), while in cotton, high-density planting shortened flowering time by a few days (46, 47). It is important to note that the influence of high-density planting on flowering and maturity is dependent on the genetic variation of the crops. To optimize the use of high-density planting for SB, the specific requirements of a particular genotype must be established through testing. Table 2 provides an overview of how different plant densities influence plant growth, flowering time and yield under SB conditions. Nevertheless, high-density planting remains a low-cost method for producing generations quickly while maintaining a large population size for advanced selection.

Alteration in CO_2 levels

Higher levels of CO_2 can accelerate plant growth in the vegetative stage, leading to an accelerated reproductive growth phase (51). However, the response towards elevated levels of CO_2 varies even within a crop species. For instance, reduced exposure to increased CO_2 levels of 400/700, 350/700 and 350/650/100 ppm reduced the days to blooming in soybeans, rice and cowpea by 2, 7 and 12 days respectively (52). Conversely, CO_2 sustained at 20 ppm postponed soybean flowering by 11 days (53). When the CO_2 level in pigeonpea was raised to 550 mol mol^{2}, it caused the short-duration cultivar ICPL 15011 to flower 9 days later (54). The crop growth cycle of soybean (cv "Enrei") was shortened from 102-132 days under field conditions to 70 days using a combination of a 14 hr light (30 °C)/10 hr dark (25 °C) cycle with CO_2 supplementation > 400 ppm in growth chambers (55). This permitted up to 5 generations per year, as against 1-2 generations per year in the field. According to the same study, higher CO_2 levels did not significantly affect flowering time but did result in more flowers, which is beneficial for creating more crosses. In the rice varieties Nipponbare and Yamadawa, increased CO_2 (600 ppm) under growth chamber conditions decreased the days to heading from 51 to 52 and 80 to 88 days, to 48 to 49 and 70 to 74 days respectively (56). SB that modifies CO_2 levels relies on the right equipment, including growth chambers, CO_2 cylinders and regulators, as well as operational expenditures. Additionally, when handling and utilizing CO_2 cylinders and valves, it's important to follow safety and health regulations.

Utilization of plant growth regulators, nutrition and micropropagation

Plant growth regulators (PGRs) have been used to accelerate plant development, enhance anthesis and grain filling, it also facilitate *in vitro* germination of immature seeds (57). In controlled environments where photoperiod and temperature are regulated, the effects of PGRs are often dose-dependent and crop-specific, with outcomes that can be either positive or negative based on the type of PGR, concentration applied and plant species involved. For instance, the combination of auxin and cytokinin hormones flurprimidol (0.3 µM), indole-3-acetic acid (5.7 µM) and zeatin (2.3 µM) induced 100 % *in vitro* flowering and 90 % seed set in faba bean plants (55). Additionally, the exogenous application of 6-benzylaminopurine (10^{-5} M BAP) given 4 days after blooming in faba beans increased seed set (58, 59). It was observed that blooming and seed set were increased 90 % and 80 % in lentils when the combined treatment of fluprimidol (0.9 µM) and 4-chloroindole-3-acetic acid (0.05 µM) was given respectively (52).

The researchers also altered the photoperiod (18/6 hr light/dark), temperature (22/18 °C light/dark), applied PGR and did embryo rescue to reduce the generation cycle of faba beans and lentils from 102 and 107 days to 54 and 45 days respectively. This strategy allowed for up to 8 generations per year. Furthermore, the researchers employed an *in vivo* method involving embryonic seed culture in a hydroponic system with a vermiculite substrate, timed fertilizer application and a light intensity of 500 M m^{-2} s^{-1} (using fluorescent light bulbs) under a 20 hr light (21 °C)/4 hr (16 °C) dark regime. When flurprimidol (0.6 µM) was applied to treated and untreated pea plants, both had 100 % flowering and 98 % seed set in 33 and 68 days respectively. The use of hormones and plant nutrition has been shown to accelerate plant growth, promote blooming and seed set and *in vitro* germination of immature seeds in controlled environments such as greenhouses

Table 2. Effect of plant density in speed breeding on growth, flowering and yield of plants

Plant sensity	Effects on plant growth	Effects on flowering and generation time	Effects on yield	Notes	Reference
Low	Vigorous vegetative growth, higher nutrient availability	Delayed flowering, longer generation time	Potentially higher per-plant yield but lower overall population yield	Lower plant stress, used for detailed phenotyping	(6, 48, 49)
Medium	Balanced growth and resource allocation	Optimal flowering timing, moderate generation time	Optimal yield balance between plants and population	Preferred for many speed breeding protocols	(6, 50)
High	Increased competition for light, water and nutrients; stress may occur	Early flowering, faster generation turnover	Variable yield; may increase population yield but reduce per-plant yield	Low-cost strategy to accelerate breeding generations; risk of stress	(6, 34)

and growth chambers (57).

Researchers have found that by combining the right balance of hormones such as auxins and cytokinins, they can induce *in vitro* anthesis, fertilization and grain filling in crops like faba beans and lentils (58, 60). The number of generations grown annually was increased by the researchers by shortening the generation cycles of faba beans and lentils and modifying variables like photoperiod, temperature, PGRs and utilizing an *in vivo* methodology (59). Additionally, the use of immature embryos for lentil embryo culture on MS culture media and adjusting the environment for wheat and barley seed germination are effective in increasing generation cycles and achieving high rates of flowering and seed set (16, 57, 61). Quick germination rates can also be achieved through the harvesting of immature seed and creating ideal germination conditions (62).

Practice of other breeding and genetic techniques to improve the efficacy of speed breeding

The rising demand for food cannot be fulfilled by traditional breeding techniques for cereal crops as the development of a variety requires a minimum of 8-10 seasons. Urbanization, climate change, harsh weather, the need to reduce the environmental impact of agricultural activities and conflicting demands for food, feed and fuel make the task of guaranteeing global food and nutrition security more difficult (26, 63, 64). To achieve increased crop yields in less time, breeding procedures must be improved. Breeder and researchers can advance more quickly by reducing the number of breeding cycles required to develop new cultivars as well as the period between crossing and choosing offspring to utilize as parents for the following cross. A variety of conventional and molecular breeding strategies are applied to get enhanced agricultural productivity and quality.

Use of molecular genetics in speed breeding

Molecular scientists have created transgene-free genome editing technologies like clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9 (CRISPR/Cas9), clustered regularly interspaced short palindromic repeats / CRISPR from Prevotella and Francisella (CRISPR/Cpf1), prime editing, base editing, dead Cas9 (dcas9) epigenetic modification and many others. These genome editing tools speed up the process of improving crops by adding desired features. Recent advancements in breeding methods, such as genetic engineering, GS and doubled-haploid (DH) technology, have shortened breeding cycles and improved genetic gain rates in crops like wheat, rice and maize (9). These advancements can have a greater impact when used in conjunction with SB techniques, which permit generation advancement quickly by preserving plant populations under photoperiod and temperature regimes that are not ideal for their growth and development (16).

Modern genetics has significantly altered crop development during the past 150 years (65). Numerous methods have been used to reduce plant reproductive cycles. Utilizing the new techniques created in the previous 10 years, such as GS, HTP, and modern SB, plant breeding is accelerated. Genetic engineering and molecular technology have also been utilized to develop crops with desired traits through gene transformation (66). Other approaches, such as high-throughput molecular markers, quick gene isolation, large-scale sequencing and genomics, have all been proposed as ways to enhance the breeding of commercially significant crop species, including cisgenesis, intragenesis, polyploidy breeding and mutant breeding (67).

For the goal of generating new plant varieties using conventional breeding techniques, plant genome improvement is inadequate. To overcome this obstacle in plant breeding techniques, molecular markers have been used since the 1990s to identify superior hybrid lines (68). To improve plant phenotype for a particular desirable trait, the plant breeder must artificially choose and breed this provided attribute. Breeders typically concentrate on diploid or diploid-like features (such as those in tomatoes and maize) rather than polyploidy traits (such as those in potatoes and alfalfa), which have more complicated genetics. Breeders prefer to use crops with shorter reproductive cycles that allow the production of numerous generations in a single year, as opposed to perennial plants that only sporadically reproduce or crops that only reproduce once a year. Faster artificial breeding of desired phenotypes results from this (25).

SB is frequently used for generation progression without phenotypic selection. But it is possible to successfully incorporate contemporary technology (such as high-throughput genotyping approaches, MAS, etc.) for the selection of target qualities. SB differs from MAS and GS mainly in its purpose and mechanism. SB focuses on accelerating the number of generations produced per year by manipulating environmental conditions such as light and temperature, thereby shortening the breeding cycle and rapidly advancing generations. In contrast, MAS and GS are genetic selection methods that use molecular markers—MAS targets specific known genes or QTLs, while GS uses genome-wide markers to predict breeding values for complex traits. While MAS and GS improve the precision and efficiency of selecting desirable traits, they do not inherently reduce generation time. Combining SB with MAS or GS can maximize genetic gain per unit time by both accelerating breeding cycles and enhancing selection accuracy. Thus, SB is a physical acceleration technique, whereas MAS and GS are genomic tools for targeted genetic improvement. The maintenance of a healthy breeding population and genetic variety, as well as the generation of the highest yields, should be possible with the help of SB and efficient selection techniques. Choosing genotypes with the highest yields often requires a stable plant population, which is achieved through traditional selection techniques such as bulk, mass, recurrent, pedigree and pure line selection. However, these methods involve prolonged inbreeding and selection cycles, making them less efficient for fast breeding. Alternative methods such as single seed descent (SSD), single pod descent (SPD) and single plant selection (SPS) can be used in conjunction with SB and are discussed in brief below.

Single seed descent method

SSD is a method of breeding that builds on the principles of bulk breeding. The goal of SSD is to create homozygous populations by continually inbreeding individuals from segregating populations, selecting only one seed from each F_2 plant to carry forward to the next generation. This allows for tracing each inbred line back to its origin in an F_2 plant (69). Like the DH method, SSD takes a similar amount of time to produce inbred lines (61), but requires less labour in the early stages, as it allows for compact nurseries, growth chambers or greenhouses with dense plantings (70, 71). However, it is important to note that SSD may result in lower seed yields compared to other breeding methods, such as pure line,

pedigree and recurrent selection (72). In order to move forward to the F_3-F_4 generations using SSD, a large number of F_1 plants (50-100) are needed to produce 2000-3000 F_2 plants (73). For the best results, plants should be grown at the F_5 generation under optimal field conditions and spacing, allowing for the selection of superior F_6 genotypes and their advancement using a head-to-row technique SSD has shown varied outcomes across crops, including soybean, durum wheat and rice. SSD-derived lines often exhibit comparable or higher yields than those from bulk or pedigree methods, though results can vary with environmental conditions. SSD also facilitates rapid breeding cycles, enabling 3-4 generations per year in controlled environments like greenhouses. In terms of genetic stability, SSD generally maintains moderate to high heritability for key traits, but some studies note occasional variation in genetic diversity and variance between SSD and bulk populations. Overall, SSD provides faster generation advancement and consistent genetic improvement, although outcomes depend on the crop and context (56, 74-76). In general, SSD is considered an efficient method for fast breeding, suitable for both indoor and outdoor cultivation.

Single pod descent approach

The SPD method in plant breeding involves selecting 1 entire pod from each F_2 to F_4 plant instead of a single seed. This method increases the likelihood of preserving each plant in subsequent generations because many legume species produce multiple seeds per pod. Relying on only 1 seed per plant increases the risk of losing genetic diversity due to seed germination failure or plant loss. By advancing the whole pod, breeders ensure that progeny from every plant are better represented, thus maintaining broader genetic variation within the breeding population. Studies have shown that using SPD can also lead to early pod selection and smaller population sizes (71). For lines improved or created using the SSD, SPD and bulk approaches, the scientists discovered no changes in selection effectiveness that was statistically significant. Another benefit of SPD is that it enables early pod selection, which advances a smaller population. Research on soybean plants has shown that the SPD method can lead to higher yields than other methods such as SSD or bulk selection (77). To ascertain the efficacy of SPD for a particular crop and trait under SB conditions, preliminary trials must be carried out.

Single plant selection method

The SPS approach involves gathering all of the seeds from a chosen plant and using them to develop the next generation. By using a modified backcross technique, this method has been used to create introgression lines (ILs) in barley within 2 years (9). For example, researchers used the SPS method to create lines of barley that were resistant to leaf rust, net blotch and spot blotch by crossing the European barley cv. "Scarlett" with other parents. They used a SB method, selecting 87 $BC_1F_{3:4}$ generation plants from 5000 BC_1F_2 plants (78), which resulted in a yield much greater than that of cv. "Scarlett." Early plant selection using the SPS method is based on a reduced population size, as opposed to other techniques like SSD and SPD. SPS was used in bread wheat breeding to improve traits such as foliar disease resistance, grain dormancy, seminal root angle, seminal root number, crown rot tolerance, leaf rust resistance and plant height. The SPS-selected lines showed better trait performance than unselected F_3 seedlings, demonstrating the method's effectiveness for early-generation improvement in wheat. (79).

Among the breeding techniques of SSD, SPD and SPS, SSD is considered the most compatible and widely integrated method alongside SB protocols, particularly for self-pollinated crops like wheat, barley, rice, pea and soybean (6, 64). Because it allows 4-6 generations per year, supports the advancement of large populations with minimal resources and rapidly achieves homozygosity. In practice, integrating SSD with SB has enabled breeders to develop pure lines of crops like wheat, barley, chickpea and pea in as little as 1-2 years, greatly reducing the time and cost needed for variety development.

Applications of speed breeding

The urgent demand to rapidly develop superior crop lines and shorten breeding cycles has driven breeders to adopt speed breeding across a broad array of crop improvement programs. Over the past decade, its applications have expanded significantly, integrating with advanced techniques such as MAS, GS, DH technology, genome editing and HTP. Table 3 provides a concise overview of strategies where SB is combined with modern breeding technologies to get maximum benefit and desired varieties. Major

Table 3. A concise overview of practical integration of other techniques and strategies, their advantages and outcomes, serving as a guide for designing combined speed breeding programs

Integration approach	Description	Benefits	Example outcomes
Speed breeding + Marker-assisted selection	Use molecular markers to select for major genes in early generations advanced by speed breeding.	Early fixation of target alleles; reduced field screening costs	Accelerated introgression of disease-resistance genes in barley within 2 years (9)
Speed breeding + Genomic selection	Apply genomic estimated breeding values to populations cycled rapidly via speed breeding.	Increased selection accuracy for complex traits; higher genetic gain per year	Theoretical ~18-fold increase in genetic gain rate compared to conventional methods
Speed breeding + Doubled-haploid technology	Immediately fix haploid lines produced via doubled-haploid under speed breeding conditions for multiple generations.	Instant homozygosity; rapid line development	Production of homozygous wheat lines within six months instead of 2 -3 years.
Speed breeding + CRISPR/Cas genome editing	Generate targeted edits in early generations and advance edited lines rapidly through speed breeding.	Precise trait modification; multiplex editing; fast trait validation	Rapid development of gene-edited tomato lines in under 1 year.
Speed breeding + High-throughput phenotyping	Integrate automated phenotyping platforms in controlled environments to evaluate speed-bred populations.	Detailed trait assessment; improved selection of quantitative traits	Advancement of over 1000 recombinant inbred wheat lines through 3 generations in 18 months with root phenotyping (80).
Speed breeding + Single seed/ pod descent	Combine single-seed or single-pod advance schemes within speed breeding cycles for rapid inbreeding.	Reduced labour; small footprint; near-homozygous lines by F_5- F_6	Near-homozygous durum wheat lines were developed in 2 years.
Speed breeding + Single plant selection	Early phenotypic selection on whole plants cycled rapidly under speed breeding.	High selection intensity; trait-targeted early-generation advance	Development of leaf rust resistant barley introgression lines in 2 years.

Table 4. Improvement in different crops using the speed breeding technique

Crop	Days to flowering	Number of generations per year	Selection method	Reference(s)
Amaranth	28	6	SSD	(25)
Arabidopsis	20-26	10	-	(81)
Barley	24-36	9	SSD[i]	(23)
Barley	-	4-6		(16)
Canola	73	4	SSD[i]	(16)
Chickpea	33	7	SPD	(24)
Faba bean	29-32	7	SPD[ii]	(58)
Groundnut	25-27	3	SPD[ii]	(20)
Lentil	31-33	8	SPD[ii]	(47)
Pea	33	5	-	(60)
Pigeon pea	50-56	4	SPD[ii]	(82)
Rice	75-85	4	SPD[ii]	(83)
Sorghum	40-50	6	SSD[i]	(84)
Soybean	23	5		(85)
Wheat	28-41	7.6	SSD[i]	(23)
Spring wheat	-	4-6	-	(16)
Peanut	-	2-3	-	(20)

i: Single Seed Descent; ii: Single Pod Descent.

applications and achievements of SB across different crops have been given in Table 4. Some of these applications and successes are discussed in detail below.

Speed breeding assisted domestication

Plant domestication is the intentional process of transforming wild plant species into crop plants. Early hybridization in this process is followed by a selective breeding approach. Polyploid crops present unique challenges and opportunities in plant breeding. Being a time -consuming approach, it has been used with SB to reduce the length of time and the number of generations of that crop that have been produced. Polyploid plants, such as bananas, peanuts, have been domesticated using rapid breeding (20). The time taken to create several generations is shorter as compared to the conventional breeding phase (86).

Simultaneous phenotyping under speed breeding

Phenotyping is the first step in any breeding selection technique. On the other hand, modern plant phenotyping assesses complex characteristics associated with growth, yield and stress adaptation with better precision and accuracy at a wide range of organizational sizes, from organs to canopies (87). A more recent and comprehensive definition of plant phenotyping includes the evaluation of complex plant traits such as growth, development, tolerance, resistance, architecture, physiology, ecology and yield, as well as the crucial measurement of individual quantitative parameters that serve as the basis for complex trait evaluation (88). The dynamic and local interactions of phenotypes with the above- and below-ground environment contribute to plant phenotype.

Moreover, traits related to plant biomass (89), root structure and function (90), leaf characteristics (91) and fruit traits are examples of structural and functional aspects that can be directly quantified. The evaluation of complex plant traits related to growth, development and all other characteristics that provide the basis for complex trait assessment is known as phenotyping. Temperature variation is noted throughout the year all around the world. This has an effect on crop production, which causes human misery due to a shortage of food resources. Realizing that there was evidence of a persistent increase in temperature and a decline in rainfall in that region (92). An experiment was conducted to test the effectiveness of combining phenotyping and SB to encourage root adaptation to changing environmental conditions and water scarcity. A combined approach integrating phenotyping with SB was used to accelerate yield improvement. In this strategy, a large population of more than 1000 wheat recombinant inbred lines was advanced through several generations within just 18 months, demonstrating the efficiency of simultaneous population development and trait assessment under SB conditions.

The analysis thus offers a strong basis for incorporating genetic advancements for improved adaptation to water-limited environments (92). In order to increase crop output quality and respond more effectively to climatic change and the emergence of new diseases, plant breeders are experimenting with various new strategies. In a study, the 2-row barley cultivar Scarlett, together with novel techniques for rapid trait introgression (9). Using 4 donor lines with multiple disease resistance and a modified backcross strategy that incorporated phenotypic multi-trait screens and quick generation advanced technology, SB, they created 87 $BC_1F_{3:4}$ Scarlett ILs over two years (79).

Development of homozygous line rapidly

After initial crosses of chosen parents with complementary features, SB procedures have been applied on a variety of crops to quickly create homozygous lines. These techniques have been used to accelerate seed germination and early flowering, shortening the time needed to produce each breeding generation (Table 1). Breeding generations (3-9) can be produced using this procedure each year. This is ideal for population evaluation and faster breeding in the target production contexts using several selection techniques like SSD, SPD and SPS (93). The careful modification of diverse growing circumstances, as explained here, is the foundation of SB.

Gene editing in combination with speed breeding

While traditional plant breeding methods have been successful in creating superior crop varieties, recent domestication techniques and ongoing selection have led to a decline in genetic quality, which is a significant obstacle in improving crop quality. However, genome editing technology offers a solution to this problem. By using the technique of gene editing, the genes of a crop species can be modified to enhance crop production. In a study CRISPR/Cas9 was used to create genomic variations at various locations, opening new opportunities to enhance genetic diversity (94). The technology also allows for multiple changes to be made at once, known as

multiplexing. To solve this problem and produce several generations in a single year, genome editing and fast breeding may be used (94). While this technique is labour-intensive and time-consuming, it offers a viable solution for producing high-yielding crop varieties.

Accelerating genetic gain and genomic selection via speed breeding

Reducing the number of breeding cycles and the interval between crossing and offspring selection can be advantageous for breeding and research efficiency. Shorter breeding cycles and greater genetic gain have been achieved in crops like wheat, rice and maize with the use of contemporary breeding techniques, including genetic engineering, GS and DH technology (9). These advancements can be amplified when combined with SB methods, which involve maintaining plants under accelerated growth and development conditions. This can be achieved by manipulating the photoperiod and temperature regimes. The genetic gain rate can be represented by an equation, as shown in eqn. 1 (94).

$$R = \frac{(\delta g)ir}{L} \qquad \text{(Eqn. 1)}$$

Where R = change in the trait mean per year

δ_g = the amount of genetic variation

I = selection intensity

r = selection accuracy and

L = length of breeding cycle

Based on this formula, genetic gain can be enhanced by increasing the number of plant generations per year using SB techniques. Before field testing, this is especially helpful for crossing and development of a line. To increase the genetic benefit, SB and GS are applied. It is reported that GS and SB can enhance genetic benefits in a range of crops. The concept of GS was first put forth earlier (95). The primary advantage of GS is that it accelerates the breeding generation, produces higher-quality plant varieties more quickly and increases genetic gain. Researchers have shown that crop quality can be increased even more successfully by combining GS with other modern breeding techniques. The recent development of SB techniques offers the potential to greatly speed up breeding efforts for many crops by increasing generations in a shorter amount of time (96).

Bottlenecks in speed breeding

Utilizing SB methods is an effective approach for accelerating traditional breeding programs. But the technology needs knowledge, efficient facilities for plant phenomics, suitable infrastructure and ongoing financial support for research and development. SB techniques should be recognized as integral to traditional breeding, MAS and genetic engineering to justify allocation of necessary resources. The comprehensive toolkit also needs long-term finance, government policy backing skills and knowledge in biotechnology and plant breeding. In Sub-Saharan Africa (SSA), for instance, the majority of public plant breeding programs employ conventional plant breeding techniques. Technical, economic and institutional challenges constrain the adoption of modern breeding technologies in the public sector. For example, stringent regulatory requirements for genetically modified organisms (GMOs) limit the capacity of public breeders to deploy advanced gene-editing tools, delaying variety release and increasing costs. Additionally, funding shortages and limited infrastructure in many public research institutions restrict their ability to invest in and maintain cutting-edge breeding platforms, resulting in slower development of improved crop varieties compared to the private sector (97). The introduction of conventional and genetically modified crop cultivars in SSA could be sped up by using SB techniques. Access to appropriate facilities, having trained personnel, making significant modifications to the breeding program, proper design and management and long-term finance requirements are among the most prevalent obstacles to accelerating breeding adoption. Major bottlenecks in SB, their impact and their mitigation strategies are given in Table 5.

Scarcity of technical skills and skilled personnel

The scarcity or lack of skilled and engaged plant breeders and plant breeding technicians in developing nations is a significant obstacle that could prevent the public sector from implementing SB (98). The public sector breeding programs suffer as regular workers move to private seed companies and training institutions that provide better compensation than government service. Furthermore, few scientists specialize in plant breeding, as limited universities in developing nations offer postgraduate degrees in this field. In certain nations, the framework for managing plant breeders' rights and seed regulation has not been built to promote plant breeding for the value chain's benefit from farmers to consumers (99). Developing nations must change their policies and practices surrounding investments in plant breeding education, research and personnel retention in order to preserve the viability of long-term crop improvement programs and the adoption of scientific innovations like SB.

Infrastructure hurdle and high initial investment

Advanced infrastructure is required to implement these breeding techniques and to regulate key environmental variables such as soil moisture, temperature and photoperiod. However, insufficient funding for public plant breeding initiatives in many resource-limited countries makes it challenging to apply

Table 5. Summary of key bottlenecks in speed breeding, their impacts and recommended mitigation strategies

Sl. No.	Bottleneck	Impact	Mitigation strategy
1	Scarcity of skilled personnel	Limits effective protocol implementation; high risk of program failure	Invest in training programs; improve retention through incentives; develop university curricula in plant breeding
2	High infrastructure costs	Restricts adoption, especially in resource-poor settings	Adopt low-cost infrastructure like repurposed containers; promote regional facility sharing; secure long-term funding
3	Energy and water dependency	Unreliable supply disrupts environmental control; increases costs	Use renewable energy (solar) with battery backup; optimize water-use efficiency; explore alternative energy sources
4	Data management challenges	Limits the integration of high-throughput phenotyping and genotyping	Develop bioinformatics capacity; use cloud-based data platforms; standardize data workflows
5	Crop-specific limitations	Protocols may not suit all crops; they hamper universal adoption	Tailor protocols to specific crops; conduct crop-specific optimization studies
6	Regulatory and germplasm access barriers	Delays innovation and access to diverse genetics	Advocate for flexible policies; promote germplasm exchange agreements; collaborate internationally

contemporary breeding methods and technologies. Additionally, there is a scarcity of specialized equipment necessary for early-stage trait selection (100). Furthermore, a lack of coordination between regional breeding programs and a "donor mindset" can lead to duplicated efforts and increased resource expenditure. To address these issues, there is a need for resource and information sharing, as well as active collaboration between national and regional organizations during the infrastructure development process. One potential solution to reduce infrastructure costs is the use of repurposed shipping containers equipped with solar-powered lighting and temperature controls, along with locally developed technology (101).

Energy availability

In indoor growing facilities, a dependable source of water and energy is required for the regulation of environmental variables such as moisture, temperature and photoperiod. SB facilities need energy that is reliable, affordable and sustainable for lighting, heating and cooling. For example, in Queensland and Australia, the cost of regulating temperature during the winter can account for a significant portion of the overall cost of managing plants. Unreliable electricity sources can greatly impede the regulation of temperature and photoperiod in public plant breeding programs. In addition, traditional agronomic practices such as land preparation, fertilization and irrigation are necessary for growing crops in the field and can be costly, requiring significant infrastructure investments. To address these challenges in developing nations, it may be necessary to explore creative approaches for providing water and electricity, such as utilizing renewable solar energy. One potential solution is to develop compact indoor SB systems powered by solar energy with battery backup, providing energy for LED lights and temperature controls.

Conclusion

SB highlights its transformative impact on crop plants. It enables rapid development of a breeding population through multiple generations within a specified timeframe and accelerates genetic gain. It also enhances resource and energy use efficiency, optimizing land, water and time. Integration of SB with different breeding approaches, such as MAS and GS, further strengthens selection accuracy and breeding outcomes. Addressing the challenges outlined, ranging from infrastructure training, policy and funding, is essential to exploit the potential of this technology. Strategic investment in facility development, capacity building and sustained support from both governmental and scientific stakeholders can prove useful in mainstreaming SB. A coordinated and pragmatic approach is necessary to make SB a viable, scalable and impactful solution for meeting the increasing global demands for food security and sustainable agriculture.

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Authors' contributions

SKS and SP were involved in the conceptualization, supervision, review and editing the final paper. ES, JU and GM participated in literature collection and formatting. SKS and MS prepared the cover image and visual content. All authors contributed equally to revising the manuscript and approved the final draft.

Compliance with ethical standards

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