Indian Journal of Agricultural Sciences **91** (9): 1267–73, September 2021/Review Article
https://doi.org/10.56093/ijas.v91i9.116059

Speed breeding in maize (*Zea mays*) *vis-à-vis* in other crops: Status and prospects

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Received: 18 January 2021; Accepted: 22 February 2021

ABSTRACT

The prevailing global climate change and population explosion have threatened global food security by mounting the demand of more quantity and better quality food. Crop breeding attempts to meet this increasing demand but having a major limitation of long breeding cycle required for developing any suitable cultivar. Therefore, shortening the crop duration in every generation of a breeding cycle has been a long dream of breeders. In the past, many efforts have been made to fasten crop generation time by implementing several techniques like shuttle breeding, embryo rescue, and doubled haploid. In this direction, recently, speed breeding (SB) has emerged as a novel technology to shorten the crop breeding cycle and fasten the crop improvement through rapid generation advancement. Growing crops in the customized growth chambers of SB helps to speed up research on crops with adult plant phenotyping, crossing, mutant studies, and transformation. Till now many crop-specific protocols have been developed in wheat, rice, barley, canola, etc. for SB in growth chambers or glasshouses with controlled environmental conditions. But, still, SB protocol for maize (*Zea mays* L.), one of the three major staple foods worldwide has not been developed yet. Considering the multiple uses and economic importance of maize, there is a need to accelerate its production to meet future demands. Deploying the SB technique in maize could be beneficial in achieving the same. Thus, despite being challenging, we need to explore the possibilities of using SB in the maize breeding programme. The present review throws light on the current status of SB and future perspectives to make SB successful in maize. The adoption of SB along with other breeding methodologies can be an effective and efficient tool to develop suitable maize hybrids in a short time frame for meeting global demands.

Keywords: Food security, Maize, Rapid generation advancement, Speed breeding

Developing, testing and release of improved cultivars in crops like maize is a time taking process, i.e. generally 8-10 years, even after the use of the off-season facilities. To fasten the same, researchers are always looking for alternative technologies for accelerated crop improvement (Kumar *et al*. 2020a, Kumar *et al*. 2021). In this direction, recently, a new technique named 'Speed Breeding' (SB) was developed, wherein we can shorten the breeding cycle and accelerate crop research through rapid generation advancement. The SB can be carried out in numerous ways, one of which involves extending the duration of the plant's daily exposure to light combined with early seed harvest, thereby reducing the generation time. This technique has been successfully demonstrated by Australian scientists to develop a pre-harvest sprouting resistant wheat variety, DS Faraday (Hickey *et al.* 2019).

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The basic principle behind SB involves modulating the optimum light (quality/intensity) to extend crop photoperiod using supplementary lighting with sodium vapor lamps (SVL) or metal halide and light-emitting diode (LED) lighting. These are useful in controlling temperature to accelerate the crop plant photosynthesis and flowering coupled with early seed harvesting to fasten the plant life cycle. By adopting this methodology, generation times have been substantially reduced for many crops such as spring bread wheat (*Triticum aestivum*), durum wheat (*T. durum*), barley (*Hordeum vulgare*), chickpea (*Cicer arietinum*), pea (*Pisum sativum*), canola (*Brassica napus*), the model grass, *B. distachyon*, and the model legume, *Medicago truncatula* (Ghosh *et al.* 2018). Globally, maize (*Zea mays* L.) is the third most important cereal crop after wheat and rice. It has multifarious uses so there is a huge demand for it in the poultry, livestock, food, and starch industry, etc. (Rakshit and Karjagi 2018). Considering its high demand, global maize production has to increase significantly in near future. Therefore, there is an urgent need of developing high-yielding maize hybrids in a very short period.The maize hybrid breeding program is highly time–consuming as it

has various components (Kumar *et al*. 2020b) and hence, can be potentially accelerated by using the SB approach. To date, there is no report available on the use of SB in maize.

Comparison with other breeding methods

For generation advancements, many breeding methodologies such as shuttle breeding, embryo rescue and doubled haploid are already available in various crops. In the series, shuttle breeding paves a way to access two or more generations per year by growing crop material in alternative suitable locations. It was first applied in wheat breeding at CIMMYT in the 1950s and since then it has been used in many crops. But it is a lengthy, costly and laborious process with generally two generations advancements per year. For many crop species, there is no alternative location, so shuttle breeding is not a viable option. In past, many efforts have been made to harness plant growth by creating stresses like increasing plant density, nutrient and water stress (Wada and Takeno 2010) or using variable light intensity to induce early flowering and seed setting. Such experiments have been practiced in rice (Collard *et al.* 2017), pea, and canola (Yao *et al.* 2016). Under embryo rescue, the immature seed is harvested and induced to germinate on a culture medium with or without using plant growth regulators (PGRs) to rapidly mature the seed. This process is species-specific and has a sensitive protocol with extensive testing procedures. This method with PGRs has been used in lentil and faba bean to achieve 4 and 6.8 generations annually, respectively (Mobini *et al.* 2015, Bermejo *et al.* 2016). Without PGRs application it has been applied in wheat, barley, pea, and soybean that resulted in 8, 9, 6.9, and 5 generations per year, respectively (Ochatt *et al*. 2002, Zheng *et al*. 2013, Yao *et al.* 2017). Embryo rescue is useful only if required infrastructure is available, mainly for recalcitrant species by manipulating temperature and photoperiod.

Doubled-haploid (DH) enables 3-4 generations per year but it has a variable success rate depending on genotype and restricts recombination to a single round of meiosis. DH technology is used in many crops especially in maize to develop homozygous lines (De La Fuente *et al.* 2013) but this requires special skills and labor for large populations. In comparison to all the previously available methods, SB enables to achieve 4-6 generations per year and is less labor-intensive especially with large populations. Its procedure is more accessible to crops together with embedding phenotyping. It has the potential to further accelerate the production of DH lines by speeding up crossing, plant regeneration, and seed multiplication steps. Unlike DH, it increases recombination during line development and also enables selection in early generations for some traits. Further DH, where haploid embryos are produced and after doubling of chromosome homozygous lines are developed (Laurie and Bennett 1988), SB is applicable to diverse germplasm without the need of any special lab facility for *in-vitro* culturing. It is a very efficient technique for small grain cereals to save space and cost by growing a large number of inbred lines at high densities (Ghosh *et al.* 2018). Field level testing is also needed in SB but this method is accessible for diversified crops including cereals, pulses, and legumes.

Current status of speed breeding in crop plants

As we all know, breeding is a time-consuming and cost-intensive activity. In crops, even after practicing off-season cultivation, it takes at least 5-6 years to develop a new variety. So, SB is in limelight to accelerate the inbred and variety development. In many crop plants such as cereals, legumes, and oilseeds (Zheng *et al.* 2013, Watson *et al.* 2018, Ghosh *et al.* 2018) already SB has been practiced. Utilizing different variants of the SB approach, in chickpea, three generations have been achieved in a year (Gaur *et al.* 2007) by growing in the field and rainout shelters. In faba bean and lentil 7 and 8 generations, respectively, can be achieved per year by applying hormones and early seed harvesting (Mobini *et al.* 2015). In field pea also by altering growth conditions and applying growth regulators, 5 generations have been achieved in a year (Mobini and Warkentin 2016). In peanut (*Arachis hypogaea* L.) also SB protocol has been applied by controlling temperature and continuously supplying light in a single seed descent (SSD) program to accelerate plant growth (O'Connor *et al.* 2013). Under controlled conditions, plants show normal development with a good germination rate and crosses can also be easily attempted (wheat and barley). Various traits for phenotyping of adult plants such as plant height, disease reactions, and flowering time in wheat, glaucousness in barley, and pod shattering traits in barley can be measured under SB conditions (Watson *et al.* 2018).

For most of the important crops, SB protocols have been developed to harness the rapid generation advancement (Table 1) (Hickey *et al.* 2019). This approach reduces the generation time by 5 and 2.5 in comparison to field and glasshouse conditions, respectively (Snedecor 2020). For crops like wheat, rice, soybean, barley, sorghum, rapeseed, millets, peanut, sugarcane, potato, and tomato, generation time has been shortened rapidly by manipulating light intensity, day length, and temperature, etc. In comparison to a glasshouse with a natural photoperiod, where only 2-3 generations of wheat, barley, chickpea, and canola can be achieved per year, SB enables 4-6 generations of these crops to be grown in a year (Watson *et al.* 2018). Early harvesting and then drying in an oven/dehydrator (~3 days) also further fasten seed cycling compared to the normal seed ripening process, which takes about 15 days. Although it lowers the grain weight but seed viability remains unaffected (Hickey *et al.* 2019). Various protocols have been modified for phenotyping several diseases and disorders such as pod shattering, pre-harvest sprouting, wheat rust, crown rot, etc. under SB methodology (Ghosh *et al.* 2018). In short-day species as *Amaranths* spp., this protocol has been developed to synchronize flowering among diverse germplasm to attempt hybridization (Stetter *et al.* 2016).

In maize, so far there is no report regarding the utilization of the SB method. Since the maize hybrid

Table 1 Summarized speed breeding protocol in major crops (Adopted and modified from Hackey *et al.* 2019)

Crop	Field or green-house generation time (days)	Photoperiod response	Rapid cycling generation time (days)	Protocol
Wheat (*Triticum aestivum*)	113	LD	66	22 h light, 22°C day/17 °C night, high-intensity PAR , early seed harvest
Rice (*Oryza sativa*)	113	SD	95–105 78–85	Field-based rapid generation advance with CO2 (560–800 ppm) supplementation, 10 h light, 2°C day/25°C night, 260 cm^3 soil/plant
Barley (*Hordeum vulgare*)	110	LD	63	22 h light, 22°C day/17°C night, high-intensity PAR, early seed harvest
Sorghum (*Sorghum bicolor*)	119	SD	88	Split culm to produce both self- and cross-pollinated seeds in uniculm sorghum; embryo rescue
Rapeseed (*Brassica napus*)	123	LD	113	22 h light, 22°C day/17°C night, high-intensity PAR, early seed harvest
Millets (*Echinocloa frumentacea, Eleusine coracana, Eragrostis abyssinica, Panicum miliaceum, Paspalum scrobiculatum, Setaria italica, Pennisetum glaucum*)	85-90	Facultative or obligate SD		Increased growth rate of pearl millet at 38°C compared to 31°C
Groundnut (*Arachis hypogaea*)	140	SD	89	Continuous light, 28°C maximum/17°C minimum, high-intensity PAR
Sugarcane (*Saccharum officinarum*)	>365	LD (12–13 h photoperiod required for flowering)		SD and continuous application of fertilizer to induce synchronous flowering
Potato (*Solanum tuberosum*)	138	LD or SD		Speed breeding with extended photoperiod in development
Tomato (*Solanum lycopersicum*)	80	SD		Introgression of light tolerance gene CAB-13 to increase productivity under continuous light
Soybean (*Glycine max*)	102-132	SD	70	14 h light, 30°C day/25°C night, CO_2 supplementation (400–600 ppm), increased crossing efficiency

LD- Long day, SD- short day, PAR- photosynthetic active radiation

breeding program is highly time-consuming so there is great potential to accelerate maize breeding by deploying this novel approach. It offers a possibility to exploit rapid generation advancement and the SSD method in maize breeding. But to combat challenges, more research and standardization are needed to make this approach suitable and efficient for maize breeding. Besides the advantages of SB, there are certain constraints in its application in maize breeding. As maize is the most diversified crop so growing with the SSD method there is a possibility to lose major useful genetic diversity.

Conditions for speed breeding

The basic motto of SB is to shorten the breeding cycle by promoting the vegetative and flowering stages. The key altering factors are light, day length by extending photoperiod, temperature, and humidity (Fig 1). Alteration of light intensity, quality, and duration can promote rapid vegetative growth, thus reducing the time to induce flowering in many crops like wheat, barley, chickpea, canola, etc. Temperature greatly influences the rate of plant development so generation time may be further reduced by elevating the temperature to accumulate desired growing degree days (GDD). However, it may induce stress and affect plant performance. So a higher temperature can be applied at appropriate growth stages. The maize crop is sensitive to a higher temperature as large losses were observed in yield when the minimum temperature was high at night time. Thus, Hickey *et al.* (2019) suggested to apply a high temperature during vegetative growth and a low temperature during reproductive stages to sustain proper grain development. Another important factor is synchronous flowering across genotypes which is desirable for attempting crosses.

Different crop plants vary in their response to light duration, temperature and humidity hence crop plants are divided into short-day, long-day, or day-neutral based on

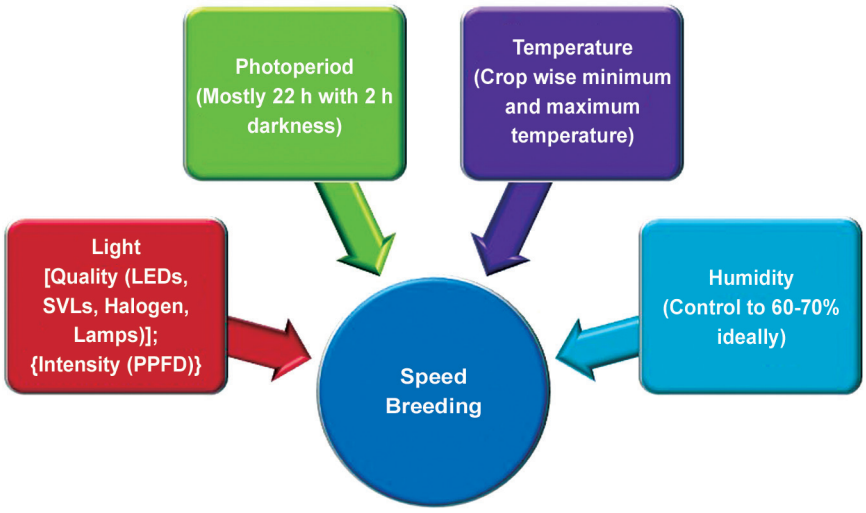

Fig 1 Key altering factor in speed breeding. *Light:* An appropriate spectral range (400-700 nm) can be achieved through light-emitting diodes (LEDs) or other lighting sources as halogen lamps or sodium vapor lamps (SVLs). In addition to controlling light quality, light intensity should also be taken care of, so the recommended photosynthetic photon flux density (PPFD) of ~450–500 µmol/m^2/s. *Photoperiod:* Normally recommended photoperiod of 22 h with 2 h of darkness in a 24-h diurnal cycle. *Temperature:* The optimal temperature regime (maximum and minimum temperatures) should be applied for each crop. *Humidity:* A reasonable range of 60–70% is ideal and for crops adopted in drier conditions, can apply a lower level.

their response. A single protocol is not feasible for all crop plants. Thus, a lot of work has been undertaken and undergoing to build up a low-cost SB cabinet with light and temperature-controlled conditions. It has a flexible procedure that can be applied to many crop species with a few modifications. A large population can be tested under SB by increasing plant density in the SSD method that also is one of the factors to increase plant growth. This has been practically demonstrated in wheat and barley by growing at different plant densities. Analyzing morphological, physiological and yield parameters show that the SB approach is very efficient to save resources and time too (Ghosh *et al.* 2018). The original approach was first described and implemented for wheat and peanut (*Arachis hypogaea*) (O'Connor *et al.* 2013). Variations of this approach have been demonstrated to be an efficient system for rapid screening of wheat germplasm for adult plant resistance to various diseases (Dinglasan *et al.* 2016, Riaz *et al.* 2016, Alahmad *et al.* 2018) and also for pyramiding multiple disease resistance in barley (Hickey *et al.* 2017). The approach has also been adapted for high-density plant production systems for SSD programs.

Speed breeding capsules (SBC)

Developing SB protocols for crops is expensive as it needs a lot of investment to develop infrastructure. However, the cost of building such controlled environments can be brought down by using refrigerated shipping containers fitted with LED lights. The artist's impression of an SBC was made from a disused refrigerated shipping container fitted with temperature and light controls, irrigation systems, and greenhouse benches (Chiurugwi *et al.* 2019).

One technology alone is not enough, so need all the tools under a single shed

SB enables to ease so many objectives within a short period like to accurately score adult plant resistance (APR), adult plant or multi-trait phenotyping, to evaluate the effect of loss-of-function of any transformed lines, to develop disease-resistant lines using marker-assisted backcross breeding (MABB), and to accelerate gene pyramiding by transferring desirable genes. To fulfill all these objectives, integrations of SB with other breeding methodologies can be a real boon for breeders in changing the time game to get any variety or product by accelerating breeding procedures (Fig 2). It possesses great potential for integrating with other modern crop breeding technologies like high-throughput genotyping, precision phenotyping, marker-assisted selection (MAS), genomic selection (GS), and genome editing (Kumar *et al*. 2021). It is ideally suited to a backcrossing breeding strategy, where the major objective is to incorporate a relatively simple inherited trait into a new variety. Breeding populations segregating for the desired trait can now be rapidly and non-destructively screened using high-throughput phenotyping techniques. SB coupled with seed chipping technologies and barcoding for suitable desired plant selection can facilitate speedy MAS. Many activities such as crossing, development of mapping populations, and adult plant phenotyping can be performed using the speed breeding process (Watson *et al.* 2018). It can also speed up the backcrossing and pyramiding for any trait of interest (Hickey *et al.* 2017) as well as the development of new transgenic (Watson *et al.* 2018). It could also help in discovering new genes and allelic diversity in landraces. SB facilities can be established on a small scale also by designing low-cost speed breeding units (Ghosh *et al.* 2018). SB in integration with high-throughput phenotyping (Al-Tamimi *et al.* 2016) can also accelerate gene discovery and characterization. GS is a demonstrated method to improve selection efficiency for maize and many other crop plants. It reduces the breeding cycle length (i.e. allowing a selection of superior plants at the seedling developmental stage), which improves genetic gain per unit of time. Combining GS with SB will allow more intense and frequent selection that will help in higher genetic gain per year hence this process is named 'Speed GS'. Both GS and SB strategies into crop breeding programs can improve multiple traits at a time with different genetic architectures. First, the parent for crosses should be selected based on their genomic estimated

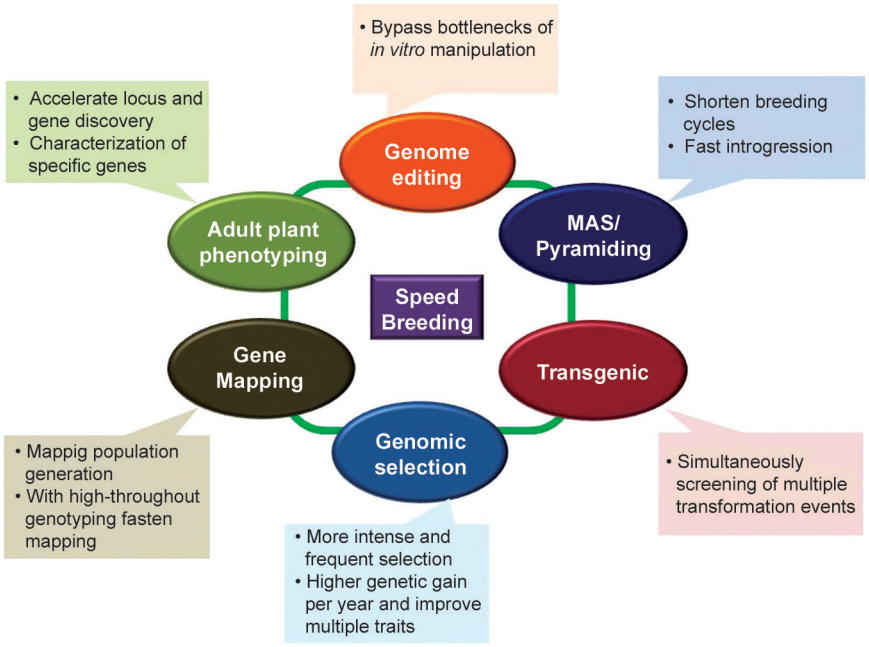

Fig 2 Speed breeding coupled with other breeding methodologies.

breeding values (GEBVs), and then their progeny should be generated through SB and the process will be repeated multiple times in a year.

Limitations of speed breeding

As the name suggests it is not a simple procedure. Different crop plants vary in their response to different physiological conditions so need to develop and standardize a different protocol for all crops. In long-day and day-neutral crops, it is easy to modulate photoperiod duration for flowering as they do not require vernalization but in short-day plants, it is a bit challenging as these crops require photoperiod less than the critical day length (Thomas and Daphne 1996). But still, some facultative species show exceptions by flowering in a particular photoperiod. Speed breeding has been performed in controlled growth chambers. Hence, many traits, particularly quality-related traits will significantly differ from the field conditions so eventually for seed production crops should be preferred to grow in the field only. Although studies show there is no negative impact on yield and other activities but traits that reflect particular environmental conditions should be tested at the field level. Early harvesting of pre-mature seeds in SB will also be constraint to study true seed type traits and causes seed shrinkage that will alter further seed germination or seed quality.

To construct a growth chamber with appropriate lighting and a temperature-controlled system is the basic requirement for speed breeding so it will outweigh the initial cost of any project to set up such a facility. It has been analyzed that for the long term SB is cost-effective in comparison to conventional breeding methods as shown in rice (Collard *et al.* 2017) and for further simplification already established glasshouses can also be converted into SB chambers with minimized costs. To integrate SB with other methodologies, re-designing, and restructuring of the overall procedure is required with careful consideration. To evaluate the efficiency of SB with other breeding methods, performing computer simulations should be a great step to find reliability before implementing such changes.

Challenges and opportunities for developing protocols for speed breeding in maize

Maize is a photo-insensitive plant, in which flowering is primarily under the control of accumulated growing degree days (GDD)/heat units (HUs). GDD in maize for heat accumulation ranges from 800-2700 (Bell *et al.* 2013). Therefore, precise maximum and minimum temperatures needed to be standardized for optimum plant growth. Further, maize being a heavy feeder and a tall crop requires more space and bigger controlled growth chambers for its development. Maize has a taller canopy with a height from 1.0 to 2.5 m. The temperature thresholds for optimum maize growth are, 10°C (minimum) to 30°C (maximum). But still, maize has a huge opportunity to work in the directions of implementation of SB for generation advancement. Maize has a high radiation use efficiency (RUE, defined as the micromoles of dry matter produced per mole of photosynthetically active photons absorbed by green canopy components), i.e.~4.0 g dry matter/MJ and can tolerate high light intensity (PAR 1500 or more) (Banjara *et al.* 2021). Moreover, maize photosynthesis rate may be enhanced at elevated CO_2 levels (>500 ppm). Maize growth is not adversely affected if the minimum temperature is not ≥ 25°C and the maximum temperature is ≤ 35°C.

Conclusion

In the present era of climate change and rapid population growth, crop researchers have a major responsibility to make availability of sufficient quantity and quality of food to fulfill global demand in a short time frame. For achieving the same, the SB technique - involving a set of improved methods to hasten crop breeding - can be a potential tool. This technique utilizes optimal light quality and intensity, day length, temperature, and humidity control to accelerate photosynthesis and flowering. SB integration in maize breeding will open up new avenues to attain the new heights of maize production. It can accelerate the inbred development and crossing programmes. SB will be useful in developing various RILs mapping populations, mapping genomic regions for target traits and MABB in maize. It will help in shortening the time of seed to seed cycle which, in turn, will accelerate the selection of maize

genotypes for kernels quality traits. This will be very much useful in the maize mutation breeding programme. Further, it will strengthen and short down the inbred development programme through doubled haploid. It can be useful in phenotyping and genomic selection programme.

Simulating breeding methods with other technologies like GS will be a nice strategy to efficiently optimize maize breeding in a cost-effective manner (Hickey *et al.* 2019). Re-sequencing of different maize germplasm accessions densely covering the whole genotypes will also provide the opportunity to amalgamate GS with SB in maize. The discovery of genes/markers associated with photo-insensitivity in maize will be utilized to advance medium and late maturity maize germplasm through rapid generation advancement. Proper care should be taken during standardizing the SB protocol in maize. To standardize, the experiment should be conducted parallel in field conditions also. All the phenotypic parameters of plants grown under the SB should be more or less comparable with field expression, then only we can select the desired phenotype. For example, under SB, we should have the proper grain filling in terms of normal endospermic development. This would be useful to have the normal germination and plant growth in the next stage. All these issues need to be addressed carefully while standardizing SB protocol in maize.

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