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Customized speed breeding as a potential tool to advance generation in wheat

V. K. Vikas*, M. Sivasamy, P. Jayaprakash, K. K. Vinod[1], M. Geetha, R. Nisha, P. Shajitha and John Peter

ICAR-Indian Agricultural Research Institute (IARI), Regional Station, Wellington 643 231, The Nilgiris; [1]Division of Genetics, ICAR-IARI, New Delhi 110 012

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Abstract

In the context of the growing human population and climatic change, the current pace of wheat improvement is slow to meet future demand. This downturn partly owes to long generation time which demands technologies such as speed breeding (SB) that can accelerate plant growth and generation turnover. In field crops like wheat, SB is particularly contextual, because annual crop cycle is limited to one to two generations per year. To enable rapid generation advancement, SB uses extended photoperiod with supplementary lighting and temperature control to accelerate the development rate. However, if a part of these conditions is naturally available, such as temperature and humidity, SB can be launched with photoperiod manipulations alone. To test this hypothesis, we have conducted a study involving ten wheat cultivars, of which six were of *Triticum aestivum* and two each were of *T. durum* and *T. dicoccum*. The cultivars were subjected to 22 hours of extended light using red LED lamps and 2 hours of dark in a polyhouse, under natural temperature range of 17-22°C and relative humidity of 75-80%. In all the cultivars, except HD 2967, plants reached heading in 36-42 days and physiological maturity in 67-73 days. In contrast, the same cultivars took 53-72 days for heading and 105-132 days for physiological maturity under field conditions. With SB, we could obtain five generations per year as against two generations under field conditions. Our results suggest that the customized SB has the potential for accelerated breeding as well as for integration with modern wheat improvement technologies.

Key words: Speed breeding, wheat, rapid generation turnover, extended photoperiod and genetic gain

Introduction

Wheat provides 20% of the dietary calories and protein worldwide (Shiferaw et al. 2013). In India, wheat is one of the vital cereal crops, providing food security. During the green revolution period, a significant gain in wheat productivity was witnessed, but in past two decades, wheat yield gain was tending to plateau in India, as being witnessed in many wheat-growing countries (Ray et al. 2012). The current rate of wheat improvement is @ 0.9% per year which is far less than the required rate of 2.4% per year to double global food production by 2050 (Ray et al. 2013). This slump in growth rate is attributed partly to the long generation time (Watson et al. 2018) and the genetic diversity erosion in wheat (Voss-Fels et al. 2015). Moreover, vagaries of climate change in the form of rising temperature are estimated to deter wheat yield by 6% for every 1°C of increase in temperature (Asseng et al. 2014). Thus, the current scenario demands fast-track research on varietal development and trait discovery to improve the productivity of the wheat crop.

Often limited to 1-2 generations per year, wheat breeding is slow due to the long generation time (Watson et al. 2018). In the classical scenario, it takes several years for the development of new and improved cultivars in wheat. After crossing of selected parental lines, a minimum of 5-6 generations of inbreeding is required to make a genetically stable line (Ghosh et al. 2018). After stabilization, at least another 3-4 years are required for cultivar evaluation and subsequent release. Similarly, for the trait discovery, generation of homozygous lines with fixed trait takes quite a long period. All these necessitate the development of technologies that shrink phenological stages and accelerate plant growth leading to rapid generation

*Corresponding author's e-mail: vkvikaswtn@gmail.com
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turnover. One such technology is speed breeding (SB), which uses extended photoperiod under controlled temperature to accelerate plant development stages to reduce generation time (Hickey et al. 2019). Speed breeding has been established to reduce the generation time in wheat significantly.

Studies on the effect of artificial lights on plant growth had been reported since the 1860s. National Aeronautics and Space Administration (NASA) and Utah State University explored growing of wheat in space station under constant light to reduce the generation time, for rapid cycling. Result of this study concluded in the development and release of two dwarf wheat lines in 1996, USU-Apogee (Bugbee and Koerner 1997) and USU-Perigee (Li et al. 2017). Similar effects of continuous light from different sources, in hastening the reproductive phase in the majority of the long-day plants (LDP) has been reported, such as spring wheat (Zhukov and Romanovskaja 1980), barley and radish (Moshkov 1987), pea (Berry and Aitken 1979) and chickpea (Sethi et al. 1981). Among the different lights used under artificial lighting, red and blue lights regulate the majority of the plant developmental stages. Further research on different light sources revealed that use of light-emitting diode (LED) for artificial lighting gave better results due to its wavelength specificity, longevity and low energy consumption (Goins et al. 1997; Monostori et al. 2018).

Wheat being an LDP, requires more than the critical duration of photoperiod to flower. Under artificial lighting, the majority of the light sources produce a spectrum that reasonably encompasses the photosynthetically active radiation (PAR) ranging within 400-700 nm. However, the blue and red region of the light spectra supports the vegetative and reproductive growth respectively. In wheat, under controlled conditions, red LED light alone is found sufficient to complete its life cycle, however, combined with blue light resulted in better growth and production of larger amount of seeds (Goins et al. 1997). Although blue light delayed flowering time in wheat, the combination of red and blue light was found to shorten the flowering time significantly (Monostori et al. 2018).

Besides optimal light intensity with extended duration, SB uses optimum temperature to accelerate flowering and early seed harvest to recover higher generation turnover in a short period (Hickey et al. 2019). Using this technique, 'DS Faraday' is the first spring wheat variety released in Australia during 2017. In the making of DS Faraday, grain dormancy was manipulated through introgression of genes, while SB was used to forward the generation (Hickey et al. 2019). Usually, the whole SB process was carried out in a glasshouse or growth chamber lit with high-pressure sodium vapour lamps or LEDs with artificially controlled temperature regime. This makes the SB technically challenging, with specifically designed growth chambers, that become very expensive when scaled for handling larger breeding materials. However, if some of the conditions are naturally available such as temperature and humidity, SB infrastructure can be designed with lesser technicality, except for the lighting control. Following this, the protocol performed in the present study used artificial lighting coupled with naturally prevailing temperature regime without any external control.

Wellington, located in the Nilgiris mountain ranges of Western Ghats of Southern India (11^{o}22' N; 76^{o}46' E; altitude-1850m MSL) has a tropical montane wet and sub-humid climate. With a mean annual temperature of 17°C and mean annual rainfall of 1800 mm, Wellington has a mean summer temperature of 20°C and winter mean temperature of 14°C. The mean annual relative humidity (RH) is 75% and receive mean daylight of 12 hours. Weather parameters such as temperature range and RH at Wellington is highly conducive for SB, particularly for wheat, but not the day length. Therefore, we have attempted to investigate the response of wheat to SB in a polyhouse only under controlled lighting, involving cultivated wheat species, *Triticum aestivum*, *T. durum* and *T. dicoccum* and a mapping population.

Materials and methods

Ten popular cultivars of wheat, including six *Triticum aestivum* L. genotypes such as HD3086, HD2967, DBW17, PBW550, GW322 and RAJ 4079, along with two genotypes each of *T. durum* Desf. (HI8737 and MACS3949) and *T. dicoccum* (HW1098 and DDK1025) were used in the study. These cultivars were released for cultivation in different wheat growing zones of India (Table 1). Mapping population for the identification of stem rust resistance genes involving Malvi Local (Susceptible) X NP201 (Resistant) was included to advance the generation. For the SB setup, cultivars were soil sown in a polyhouse on a 3 m row and replicated thrice in randomized block design. Hill sowing was adopted for mapping population (183 lines). The polyhouse used was a normal one fitted with sprinklers for irrigation and fans for providing air circulation. No temperature control was available in

Table 1. Details of the cultivars used in the study

S.No.	Variety	Species	Pedigree	Areas of adoption*	Duration (days)	Average yield (t/ha)
1	HD3086	*Triticum aestivum*	DBW14/HD2733//HUW468	NWPZ, TS & IR	145	5.46
2	HD2967	*Triticum aestivum*	ALD/COC//URES/HD2160M/ HD2278	NWPZ, NEPZ, TS & IR	143	5.04
3	DBW17	*Triticum aestivum*	CMH79A.95/3*CNO 79// RAJ3777	NWPZ, TS & IR	135	4.84
4	PBW550	*Triticum aestivum*	WH 594/RAJ 3856//W 485	NWPZ, TS & IR	145	4.77
5	GW322	*Triticum aestivum*	GW 173/GW196	CZ, TS & IR	115	4.47
6	RAJ4079	*Triticum aestivum*	UP 2363/WH 595	Rajasthan, TS & IR	110	4.37
7	HI8737	*Triticum durum*	HI 8177/HI 8158//HI 8498	CZ, TS & IR	118	5.34
8	MACS3949	*Triticum durum*	STOT//ALTAR84/ALD/3/ THB/CEP7780//2*MUSK4	PZ, TS & IR	115	4.40
9	HW1098	*Triticum dicoccum*	Mutant of NP 201	PZ, TS & IR	106	4.55
10	DDK1025	*Triticum dicoccum*	DDK 1013/DDK 1001//278-13	PZ, TS & IR	110	3.80

*NWPZ-North West Plain Zone; NEPZ- North East Plain Zone; CZ-Central Zone; PZ-Peninsular Zone; TS-Timely Sown; LS-Late Sown; IR-Irrigated; RF-Rainfed

the polyhouse, but the fans helped maintain the temperature and humidity uniform within and the same as that of the ambient.

In this study, for lighting control, red LEDs were used as a primary source of light (Figure 1). Moreover, LED lighting consumes relatively less energy and produce low heat compared to other lighting sources. A photosynthetic photon flux density (PPFD) of ~450-500 $\mu mol/m^2/s$ was maintained to maintain the light quality (PPFD is a measure of the number of photons in the PAR spectrum that fall on a square meter of target area per second). In a 24-hour diurnal cycle, a photoperiod regime of 22 hours of light with 2 hours of dark was followed. Plants were subjected to 12 hour temperature cycling regime of 22±2/17±2°C with 2 hour of darkness occurring within 12 hour of 17±2°C. The same set of cultivars were raised in the field under natural condition. Recommended agronomic practices for a good crop were followed.

Crop growth and developmental stages *viz.,* days to heading, seed development duration and days to maturity were measured based on Zadoks decimal code for the growth stages (GS) (Zadoks et al. 1974). Days to heading (HD) was determined from sowing to emergence of 75% of spikes/ears in a row, coinciding between the stages GS65-GS68. Days to maturity (MD) refers to physiological maturity representing the maximum dry weight of the kernel and the end of dry weight accumulation and seed filling period (GS90 - GS92). Seed development duration (SDD) was determined in days as the interval between days to heading and days to maturity. Data on days to heading, seed development duration, and days to maturity were subjected to statistical analyses under 'R' statistical environment.

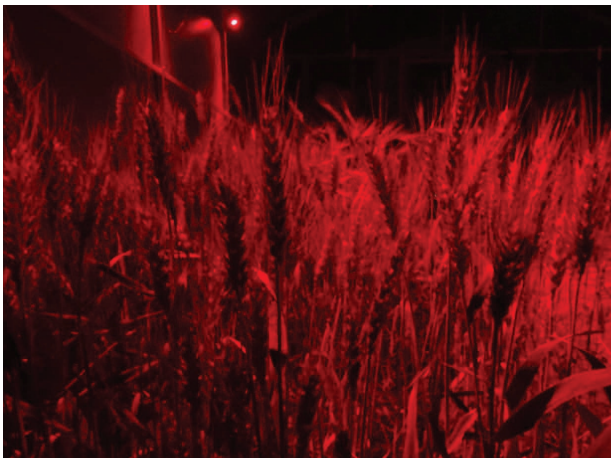

Fig. 1. Wheat plants exposed to extended photoperiod using red LED light source

Results and discussion

Rapid generation advancement in crop breeding

provides opportunities for quick cultivar development which can aid in the quick replacement of extant cultivars as well as in trait discovery. Moreover, it offers to screen of a large number of progenies, targeted for specific trait improvement. Rapid generation turnover has another advantage in crop breeding. Generally, genetic gain (ΔG) on breeding is determined by the breeder's equation, $\Delta G = ih\sigma_A/L$, where *i* is the selection intensity, *h* is the square root of the narrow sense heritability, σ_A is the square root of the additive genetic variance and L is the length of the breeding cycle or generation time (Eberhart 1970). Since the length of the breeding cycle in the contemporary terms extends into several years per cycle, it significantly influences the gain in selection due to the denominator effect. This makes achieving linear progress of >2% genetic gain from the current rate of 0.9%, a huge challenge. The challenge further becomes formidable in a situation where yields have plateaued as observed in wheat. Therefore, the targeted genetic gain of 2.5% per annum could possibly be achieved at a faster rate by shortening the breeding cycle or generation time rather than selection intensity and heritability which are highly trait and environment-dependent. In this context, SB can contribute significantly to the genetic gain in wheat by reducing the generation time.

Recently, SB is perfected in wheat (Watson et al. 2018) and is being tried in other frontline crops. However, SB uses highly customised infrastructure, that aids specific control of crop growing environments. To make this technique into wider use, local customisation of the protocols and infrastructure is imperative. A maiden attempt was made in present study to customise SB in wheat, integrating local environment and controlled exposure to extended light period, at a tropical hill station where ambient temperature and humidity shows little annual fluctuation than other places such as plains. It was found that wheat plants falling across three species and ten cultivars remained healthy and normal under SB as under field condition. Irrespective of the species, cultivars responded almost uniformly to extended photoperiod. Analysis of variance revealed significant variation among almost all the sources such as cultivars, species, growth conditions and interactions, for all the traits except a few (Table 2). A significant reduction in days to heading, seed development duration and days to maturity was observed in all the cultivars in SB compared to field condition (Tables 3 to 5). For days to heading, SB had an average of 43.6 days, as against 60.9 days required under field-grown situations (Table 3).

All the cultivars of *T. aestivum* attained heading in a range of 36-41 days except HD 2967 which took 61days in SB as compared to 57-72 days and 54-70 days in winter and summer season respectively under field condition. Among the cultivars, PBW 550 took a

Table 2. Analysis of variance, showing the variance components for the traits used for assessing the efficiency of speed breeding

Source		df	HD	MD	SDD
Treatment		69	353.29**	1214.91**	288.85**
Lines		9	733.62**	1302.62**	97.96**
	Species	2	161.21**	340.76**	49.72**
	T. aestivum	5	1235.91**	2197.70**	148.19**
	T. durum	1	14.88**	42.00**	6.88^{ns}
	T. dicoccum	1	85.71**	11.52**	34.38**
Breeding		6	2810.22**	11842.55**	3129.23**
	Type	1	16626.80**	70586.01^{ns}	18696.55**
	Speed breeding	4	7.29**	1.12**	6.64^{ns}
	Field Breeding	1	205.35**	464.82**	52.27**
Lines x Breeding		54	16.91**	19.45**	5.06^{ns}
Residual		138	1.35	2.25	3.74
Total		209	117.60	402.71	97.84

Df = Degrees of freedom; HD = Days to heading; MD = Days to maturity; SDD = Seed development duration

**significant at 5% level; ns, not significant

minimum of 36 days to reach heading, while HD2967 needed 61 days to reach heading. Poor response of HD 2967 to SB could be due to the presence of winter adaptation obtained through its pedigree. Whereas under field conditions, the cultivars, GW322 and HD 2967 took respectively minimum and maximum time to reach heading in both winter (57 and 72 days) and summer (54 and 70 days) season. The truncation of heading time observed in PBW550 under SB could be attributed to its early flowering. However, the cultivar GW322 which had the shortest heading time under field conditions came second after PBW550 in SB. Similarly, in *T. durum* and *T. dicoccum* cultivars, days to heading occurred in 40 days and 39-42 days respectively under SB. Both the *T. durum* cultivars (HI8737 and MACS3949) headed in 40 days, while *T. dicoccum* cultivars, HW 1098 took 39 days and DDK1025 needed 42 days to flower. Under field condition, however, *T. durum* cultivars reached heading between 55-64 days, while the *T. dicoccum* cultivars took 60-67 days to flower. Relative earliness of *T. durum* and *T. dicoccum* cultivars *vis-a-vis T. aestivum* for heading observed in SB could be attributed to less number of genotypes tested under these species, as well as to the short duration of the cultivars. Lines in the mapping population headed in a range of 39 to 43 days. Notwithstanding, synchronous flowering was observed among all the species, under SB than field conditions, which is highly desirable for hybridization.

We have noticed that, under SB, reduction in days to heading led to a reduction in the days to maturity among all the cultivars (Table 4). On average, maturity occurred under SB in 75 days, in contrast to 115 days required for maturity in the field. This indicated that SB required only 65.5% time of field maturity in all the cultivars. In *T. aestivum,* most of the cultivars matured in 67-73 days except HD 2967 which took 98 days to mature. As that of heading, PBW 550 matured in a short period of 67 days followed by DBW17 that matured in 73 days. Rest of the genotypes matured in 71 days. Under the field-grown condition, maturity in *T. aestivum* cultivars ranged between108 and 132 days in winter, while it ranged between 105 and 124 days under summer season. The lowest days to maturity was recorded in GW322 (106-109 days) in the field. In a parallel pattern, both *T. durum* and *T. dicoccum* matured in 71-72 days under SB, which was extended upto 109 to 118 days in field conditions. Lines in the mapping population matured in a range of 70 to 73 days.

Seed development duration (SDD), the interval between days to heading and maturity is a crucial parameter, that determines the advantage of SB over field condition. We have found that SDD reduced significantly under SB conditions relative to field condition (Table 5). Among the *T. aestivum* cultivars, SDD ranged from 30 to 37 days, with a shorter duration

Table 3. Days to heading (HD) of the cultivars subjected to speed breeding (SB) and under field condition (FC)

Genotypes	SB1 (days)	SB2 (days)	SB3 (days)	SB4 (days)	SB5 (days)	FC-WIN (days)	FC-SUM (days)
Triticum aestivum							
HD3086	41.0^{bc}	40.7^{bc}	41.3^{bc}	41.3^{b}	40.7^{b}	66.3^{23}	61.3^{2}
HD2967	61.3^{a}	61.0^{a}	61.3^{a}	61.7^{a}	62.7^{a}	72.0^{1}	69.7^{1}
DBW17	39.3^{bc}	40.3^{bc}	41.0^{bc}	42.3^{b}	41.3^{b}	65.0^{234}	60.7^{2}
PBW550	35.7^{d}	36.0^{d}	36.3^{d}	35.7^{c}	36.3^{c}	61.3^{56}	59.7^{2}
GW322	39.7^{bc}	39.7^{bc}	41.7^{bc}	42.0^{b}	40.0^{b}	57.3^{7}	53.7^{3}
RAJ4079	40.7^{bc}	41.0^{bc}	41.7^{bc}	42.3^{b}	41.3^{b}	62.3^{456}	61.0^{2}
Triticum durum							
HI8737	39.0^{c}	40.0^{bc}	40.7^{bc}	40.3^{b}	41.7^{b}	63.7^{345}	60.3^{2}
MACS3949	39.7^{bc}	41.3^{bc}	40.0^{bc}	41.0^{b}	40.3^{b}	59.7^{67}	55.3^{3}
Triticum dicoccum							
HW1098	38.7^{cd}	39.3^{c}	39.0^{cd}	40.7^{b}	39.3^{bc}	64.7^{234}	59.7^{2}
DDK1025	42.3^{b}	42.7^{b}	42.7^{b}	43.3^{b}	41.7^{b}	67.3^{2}	61.3^{2}

Means of genotypes with the same letter (superscript) and number (superscript) are not significantly different by Tukeys's Honest Significant Difference (HSD) Test. SB1-SB5= Speed breeding cycles 1 to 5 per year; FC-WIN= Field condition in Winter (*Rabi*) and FC-SUM= Field condition in Summer (*Kharif)*

Table 4. Days to maturity (MD) of the cultivars subjected to speed breeding (SB) and under field condition (FC)

Genotypes	SB1 (days)	SB2 (days)	SB3 (days)	SB4 (days)	SB5 (days)	FC-WIN (days)	FC-SUM (days)
Triticum aestivum							
HD3086	72.3^{bc}	71.7^{bc}	70.3^{bc}	72.0^{b}	71.7^{b}	121.7^{2}	114.7^{2}
HD2967	98.3^{a}	97.7^{a}	99.3^{a}	99.0^{a}	100.0^{a}	132.3^{1}	124.7^{1}
DBW17	73.3^{b}	72.7^{b}	73.3^{b}	73.3^{b}	73.0^{b}	119.7^{23}	114.7^{2}
PBW550	68.3^{d}	67.7^{d}	66.7^{c}	65.7^{c}	66.3^{c}	113.7^{56}	107.3^{456}
GW322	69.3^{cd}	68.7^{cd}	71.7^{b}	72.3^{b}	73.3^{b}	108.7^{7}	105.7^{6}
RAJ4079	71.3^{bcd}	72.7^{b}	71.0^{b}	70.7^{b}	71.0^{b}	115.3^{456}	110.7^{34}
Triticum durum							
HI8737	70.7^{bcd}	72.3^{bc}	70.7^{b}	71.3^{b}	72.3^{b}	118.0^{234}	113.0^{23}
MACS3949	70.3^{bcd}	71.0^{bcd}	71.3^{b}	71.7^{b}	71.0^{b}	112.3^{67}	106.7^{56}
Triticum dicoccum							
HW1098	71.0^{bcd}	71.7^{bc}	71.3^{b}	71.3^{b}	71.7^{b}	114.3^{456}	110.3^{345}
DDK1025	73.0^{bc}	73.3^{b}	71.7^{b}	72.3^{b}	72.0^{b}	117.0^{345}	109.7^{345}

Means of genotypes with the same letter (superscript) and number (superscript) are not significantly different by Tukeys's Honest Significant Difference (HSD) Test. SB1-SB5= Speed breeding cycles 1 to 5 per year; FC-WIN= Field condition in Winter (*Rabi*) and FC-SUM= Field condition in Summer (*Kharif)*

Table 5. Seed development duration (SDD) of the cultivars subjected to speed breeding (SB) and under field condition (FC)

Genotypes	SB1 (days)	SB2 (days)	SB3 (days)	SB4 (days)	SB5 (days)	FC-WIN (days)	FC-SUM (days)
Triticum aestivum							
HD3086	31.3^{bc}	31.0^{bc}	29.0^{bc}	30.7^{bc}	31.0^{bc}	55.3^{23}	53.3^{23}
HD2967	37.0^{a}	36.7^{a}	38.0^{a}	37.3^{a}	37.3^{a}	60.3^{1}	55.0^{1}
DBW17	34.0^{b}	32.3^{b}	32.3^{b}	31.0^{b}	31.7^{b}	54.7^{2}	54.0^{2}
PBW550	32.7^{cd}	31.7^{cd}	30.3^{cd}	30.0^{cd}	30.0^{cd}	52.3^{34}	47.7^{34}
GW322	29.7^{cd}	29.0^{cd}	30.0^{cd}	30.3^{cd}	33.3^{cd}	51.3^{34}	52.0^{34}
RAJ4079	30.7^{cd}	31.7^{cd}	29.3^{cd}	28.3^{cd}	29.7^{cd}	53.0^{34}	49.7^{34}
Triticum durum							
HI8737	31.7^{bc}	32.3^{bc}	30.0^{bc}	31.0^{bc}	30.7^{bc}	54.3^{23}	52.7^{23}
MACS3949	30.7^{bcd}	29.7^{bcd}	31.3^{bcd}	30.7^{bcd}	30.7^{bcd}	52.7^{234}	51.3^{234}
Triticum dicoccum							
HW1098	32.3^{bcd}	32.3^{bcd}	32.3^{bcd}	30.7^{bcd}	32.3^{bcd}	49.7^{234}	50.7^{234}
DDK1025	30.7^{d}	30.7^{d}	29.0^{d}	29.0^{d}	30.3^{d}	49.7^{4}	48.3^{4}

Means of genotypes with the same letter (superscript) and number (superscript) are not significantly different by Tukeys's Honest Significant Difference (HSD) Test. SB1-SB5, Speed breeding cycles 1 to 5 per year; FC-WIN, Field condition in Winter (*Rabi*); FC-SUM, Field condition in Summer (*Kharif)*

recorded in RAJ4079 (30 days) and a longer duration in HD2967 (37 days) under SB. Whereas, the same set cultivars in field condition had an SDD ranged between 51 (GW322) and 60 (HD2967) days during winter and 48 (PBW550) and 55 days (HD2967) during summer. A similar SDD pattern was recorded among *T. durum* and *T. dicoccum* cultivars, wherein 31 days of seed development occurred under SB, as against

the duration of 48-54 days under field-grown conditions. Seeds obtained from each generation was used to forward the next generation. On average, the seed maturity under SB took only 58.6% time required for the same under field-grown conditions. Under SB, average SDD was 31 days while 51 days were required for seed maturity under field conditions. Interestingly, under both conditions, germination percentage of the harvested seeds remained at >95%, irrespective of species, and seasons. Both these parameters, low SDD and high seed fertility gave a clear advantage to SB over field condition, suggesting that this method can be further exploited in regular wheat breeding programmes.

To resolve the overall variability in response of ten cultivars in the study, the data were subjected to principal component (PC) analysis, which resolved the overall variability into two major sets, one represented by the SB and other by the field condition (Fig. 2). The

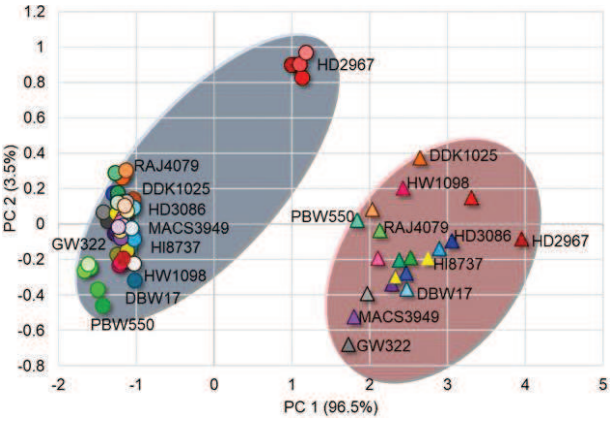

Fig. 2. Principal component analysis of ten wheat cultivars belonging to *T. aestivum*, *T. durum* and *T. dicoccum* groups subjected to generation advancements through speed breeding (○) and field condition (△) indicated by different shades

primary orthogonal axes, PC1 and PC2 accounted for a cumulative variation of 100%, with the former accounting for 96.5% and the later 3.5%. This implied that, the maximum variation among the cultivars could be attributed to growing conditions alone, and represented by the PC1, while the remaining variation between the cultivars was attributable to duration. Additionally, PC plot showed congregation of cultivars across different generations indicating that within cultivars, variation was almost negligible. However, genotype variation within SB, indicated contrasts between two genotypes HD2967 and PBW550, as observed with their distinct positioning. The remaining cultivars were intermediate, but more proximal to earliness. Further, within the field grown generations, the distinct pattern between the genotypes were largely absent. Although, HD2967 and PBW550 showed same behaviour, late and early respectively, the dispersion pattern of these cultivars with respect to the remaining ones were not distinct.

By adopting the SB protocol, five generations per year could be obtained in our experiment, as compared to two generations per year in the field. As far as mapping population is concerned, it is possible to advance F3 to F7 generation in a year i.e. five generations. Rapid development of recombinant inbred lines (RILs) will expedite the trait discovery. We have noticed that yield attributing traits such as productive tillers per plant and spike length remained unaffected and showed the same response both under SB and field conditions. However, seeds per spike and thousand-grain weight decreased significantly (but not always) under SB (data not shown). This could be attributed to the faster growth occurred in a short period, but, with a lesser penalty on vital parameters such as seed viability.

Watson et al. (2018) reported SB protocols for bread wheat (*T. aestivum*) and durum wheat (*T. durum*), in which genotypes were subjected to extended light exposure using high-pressure sodium lamps in a temperature-controlled glasshouse. The photoperiod exposure was fixed to 22 hour using sodium lamps under SB, while a 12-hour day-neutral photoperiod was maintained under control treatment in the glasshouses. Both the conditions used the same temperature regime (22/17°C). They reported a significant reduction in time to anthesis under SB (37-45 days) relative to control condition (54-75 days) depending on the cultivars, which almost overlapped the results obtained in the present study. Moreover, seed harvested before maturity in SB i.e. 14 days post-anthesis followed by four days cold treatment didn't affect the viability of the seed, providing a further reduction in generation time.

In most of the cultivar development and trait discovery research, single seed descent (SSD) is frequently used to develop homozygous lines following a cross (Chahal and Gosal 2002). Six to seven generations of selfing are required to develop lines with >99% homozygosity. With a generation turnover rate of 1-2 generations per year, 3-6 years are required to complete the development process of homozygous

lines (Ghosh et al. 2018). Usually, one seed per plant is required to advance each generation in SSD. In this study, mapping population from the cross involving Malvi Local (Susceptible) X NP201 (Resistant) were forwarded using SSD method from F3 generation using SB protocol. In a year mapping population reached F7 generation. Therefore, SB can be well utilized to advance generation using SSD method, which can help in achieving the homozygosity in one year, if five generations are covered annually as obtained in this study. Integrating SB with SSD can significantly shorten the generation time to achieve a faster genetic gain. In wheat, shuttle breeding is one of the most important generation advancement procedures followed wherein genotypes are shuttled from one location to the other as quickly as possible after each crop season, enabling two generations per year. Shuttle breeding requires the movement of research materials, resources, other logistics etc. which is cumbersome compared to *in situ* breeding. SB allows *in situ* generation outturn without shuttling between locations, reducing the breeding burden.

Yet another rapid technique used in the production of homozygotes is doubled haploidy (DH). DH lines are obtained either through androgenesis (microspore/anther culture) or gynogenesis (ovary/ovule culture) or by wide hybridization (Santra et al. 2012). Two important steps involved in DH production, haploid induction and chromosome doubling are highly dependent on several factors such as genotype, physiology, pre-treatment, media composition, regeneration environment, and chromosome doubling (Forster and Thomas 2005). However, despite the rapidity, DH development has got serious limitations such as specialised skills, genotype specificity, cost involvement in establishing tissue culture and growth facilities and restricted recombination etc. (Dwivedi et al. 2015). Remarkably, SB can achieve five generations per year without special skills and tissue culture, such as required for DH development. Compared to such technically demanding protocols, SB is simple, versatile, cost-effective and less labour intensive. In addition to generation advancement, SB systems have been put into use for evaluating adult plant traits. Also, rapid phenotyping of wheat diseases such as leaf rust (Riaz et al. 2016), tan spot (Dinglasan et al. 2016), stem rust (Riaz and Hickey 2017) and *Fusarium* head blight (Watson et al. 2018) within 10 weeks period is reported using SB. Moreover, phenotyping can be conducted throughout the year and can be made resource-efficient.

Scaling to newer heights, it is proposed that potential of speed breeding can be harvested by inclusion in technologies such as marker-assisted selection (MAS), genomic selection (GS), genome/gene editing etc. Rapid generation advancements can help in developing mapping populations within the limited time for efficient mapping of genes/QTLs. Further, the time required for the development of improved cultivars and near-isogenic lines through MAS and population improvement through marker-assisted recurrent selection (MARS) can be significantly reduced using SB. Besides, SB can be particularly useful in a selection where significant genotype-environment interaction (GEI) plays a masking role rendering selection inefficient. However, shuttling the generations between the target environment/field and speed breeding could be an option to improve selection efficiency. Although, the initial investment to develop a SB facility, i.e., glass/polyhouse house with appropriate lighting and temperature control or growth chamber is substantial, selecting appropriate locations for installing such facility where natural environment can supplement some of the critical requirements could help in reducing the establishment cost. In this study, we could use the natural environment prevailing in Wellington to modify an existing polyhouse to a SB facility. In case if the initial cost is high, depending on the objective(s) and budget, a detailed cost-benefit analyses need to be performed to assess the long-term benefit of an SB facility. In rice, a comparison was made between rapid generation and pedigree-based breeding method and concluded that rapid generation method could be more economical and would take only one year to reap the benefits (Collard et al. 2017).

Wheat research has a wide range of technological options from traditional to advanced methods for cultivar development, high throughput genotyping and phenotyping, trait discovery, MAS, genomic selection, genome editing etc. Despite such technological advancements, slow generation turnover continues to impose hurdles. Integration of such technologies with SB will boost up the research leading to an acceleration in wheat improvement which is vital in the present context of changing climate and ever-increasing human population.

Author's contribution

Conceptualization of research (VKV); Designing of the experiments (VKV, MS, JP); Contribution of experimental materials (VKV, MS, JP); Execution of

field/lab experiments and data collection (VKV, MG, RN, PS, PJ); Analysis of data and interpretation (VKV, KKV); Preparation of the manuscript (VKV, KKV).

Declaration

The authors declare no conflict of interest.

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