Plant Methods

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Acceleration of wheat breeding: enhancing efficiency and practical application of the speed breeding system

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Abstract

Background Crop breeding should be accelerated to address global warming and climate change. Wheat (*Triticum aestivum* L.) is a major food crop. Speed breeding (SB) and speed vernalization (SV) techniques for spring and winter wheat have recently been established. However, there are few practical examples of these strategies being used economically and efficiently in breeding programs. We aimed to establish and evaluate the performance of a breeder-friendly and energy-saving generation acceleration system by modifying the SV + SB system.

Results In this study, a four-generation advancement system for wheat (regardless of its growth habits) was established and evaluated using an energy-efficient extended photoperiod treatment. A glasshouse with a 22-hour photoperiod that used 10 h of natural sunlight and 12 h of LED lights, and minimized temperature control during the winter season, was successful in accelerating generation. Even with one or two field tests, modified speed breeding (mSB) combined with a speed vernalization system (SV + mSB) reduced breeding time by more than half compared to traditional field-based methods. When compared to the existing SV + SB system, the SV + mSB system reduced energy use by 80% to maintain a 22-hour photoperiod. Significant correlations were found between the SV + mSB and field conditions in the number of days to heading (DTH) and culm length (CL). Genetic resources, recombinant inbred lines, and breeding materials that exhibited shorter DTH and CL values under SV + mSB conditions showed the same pattern in the field.

Conclusions The results of our SV + mSB model, as well as its practical application in wheat breeding programs, are expected to help breeders worldwide incorporate generation acceleration systems into their conventional breeding programs.

Keywords Breeding, Generation acceleration, Speed breeding, Speed vernalization, Wheat

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Background

Wheat (*Triticum aestivum* L.) is a major global food crop that accounts for 20% of the calories and proteins in the human diet [1]. Wheat yield, stability, and disease resistance have gradually improved as a result of breeding progress [2]. Breeding initiatives have also successfully addressed global food security concerns, resulting in a doubling of wheat production within 20 years [3]. However, the ongoing effects of global climate change necessitate the development of crop varieties that can adapt to the changing environmental conditions [4]. The generation time of new cultivars is a crucial limiting factor in their rapid development [5]. Traditional breeding methods often take one to two decades to develop a new cultivar, involving processes such as crossing, selection, and field-based testing [6, 7], as well as a substantial amount of field space and manpower.

To address this issue, a speed breeding (SB) system with an extended photoperiod (22 h) was developed, allowing for up to six generations of spring wheat and spring barley per year [8]. An advanced speed vernalization (SV) system was also developed [9]. When the SV system is combined with the SB system (SV+SB), up to five generations of winter wheat and winter barley can be grown per year at relatively higher vernalization temperatures. The SV+SB system is particularly useful for shortening generation times in crosses between spring and winter wheat cultivars while effectively satisfying the vernalization requirements across diverse genetic resources. The SV+SB system has enabled the use of genetic resources with varied genetic backgrounds in generation-acceleration systems for breeding, removing growth-habit restrictions.

The SV+SB system contributed to a reduction in breeding time. However, to optimize breeding efficiency, adequate phenotypic and genotypic selection must be carried out during breeding cycles. Under SB conditions, resistance to multiple diseases, including tan spots, stripe rust, leaf rust, and crown rot, can be evaluated 4–6 times using a large numbers of plant materials, whereas in field conditions, it can only be conducted once a year [10–13]. The SB and SV+SB systems can also be used in conjunction with marker-assisted selection (MAS) and genomic selection (GS) to stack key target genes or traits [13]. Nonetheless, certain agronomic traits need to be evaluated more effectively and economically using direct phenotypic screening methods [14]. For example, flowering time and plant height can be visually evaluated by breeders at the time of harvesting [15]. This effectively decreases the size of breeding material while reducing the time and cost of genotyping breeding lines over generations.

Wanga et al. [16] emphasized that certain key aspects must be addressed for the SB system to be effectively used by plant breeders worldwide. First, experts were proficient in using the SB system for breeding purposes. Second, sophisticated facilities capable of regulating temperature and light conditions must be set up. Finally, the facilities must have a dependable supply of water and electricity to operate. Two growth rooms capable of controlling temperature and light conditions were required for plant growth in the SV+SB system. One is the vernalization room, which is kept at 8–10 °C with a photoperiod of 22 h of light [9]. These vernalization conditions must be maintained to meet the vernalization requirements of varied genetic resources within breeding programs. In contrast, the SB room, which is set at 22 °C during the day (22 h) and 17 °C at night (2 h) [17], can be modified to take advantage of natural environmental conditions to save energy and money on the installation and management of the controlled indoor growth room. Cha et al. [7, 18] reported a significant reduction in the days to heading (DTH) for spring wheat and triticale using a 22-h photoperiod with 10 h of natural sunlight and 12 h of artificial lighting.

By adapting the SV+SB system, we established and tested the efficacy of a breeder-friendly and energy-saving generation acceleration system that enables four generations of spring and winter wheat per year. A large amount of breeding material was used to test the modified SB (mSB) system combined with SV (SV+mSB), which uses a glasshouse and natural sunlight, to ensure that this system can be applied to breeding routines. To ascertain whether intuitive phenotypic selection could be carried out under the SV+mSB settings, phenotypic correlations between the field and SV+mSB conditions were also assessed.

Results and discussion

Glasshouse with minimized artificial control enables speed breeding in wheat

The photoperiod for mSB conditions was 22 h per day, consisting of 10 h of natural sunlight and 12 h of LED light (Fig. 1a). Compared to prior research that used LED lamps or high-pressure sodium vapor lights throughout a 22-h photoperiod (Fig. 1b) [8, 9], the mSB technique substantially reduced dependency on artificial lighting by harnessing natural sunlight. The mSB facility in the glasshouse, equipped with 60 LED lamps, accommodated 144 trays, whereas the conventional SB growth room accommodated 120 trays with 210 LED lights (Fig. 1c and d, Table S1). As a result, despite its ability to accommodate a larger number of trays, the mSB condition used 80% less energy for LED lighting than the SB condition. During the day, the photosynthetic photon flux density (PPFD) from the shelf to the lights was 200 μmol/m^2/s (Fig. 1e), while at night it was 65 μmol/m^2/s (Fig. 1f). Although this light intensity was lower than that of SB

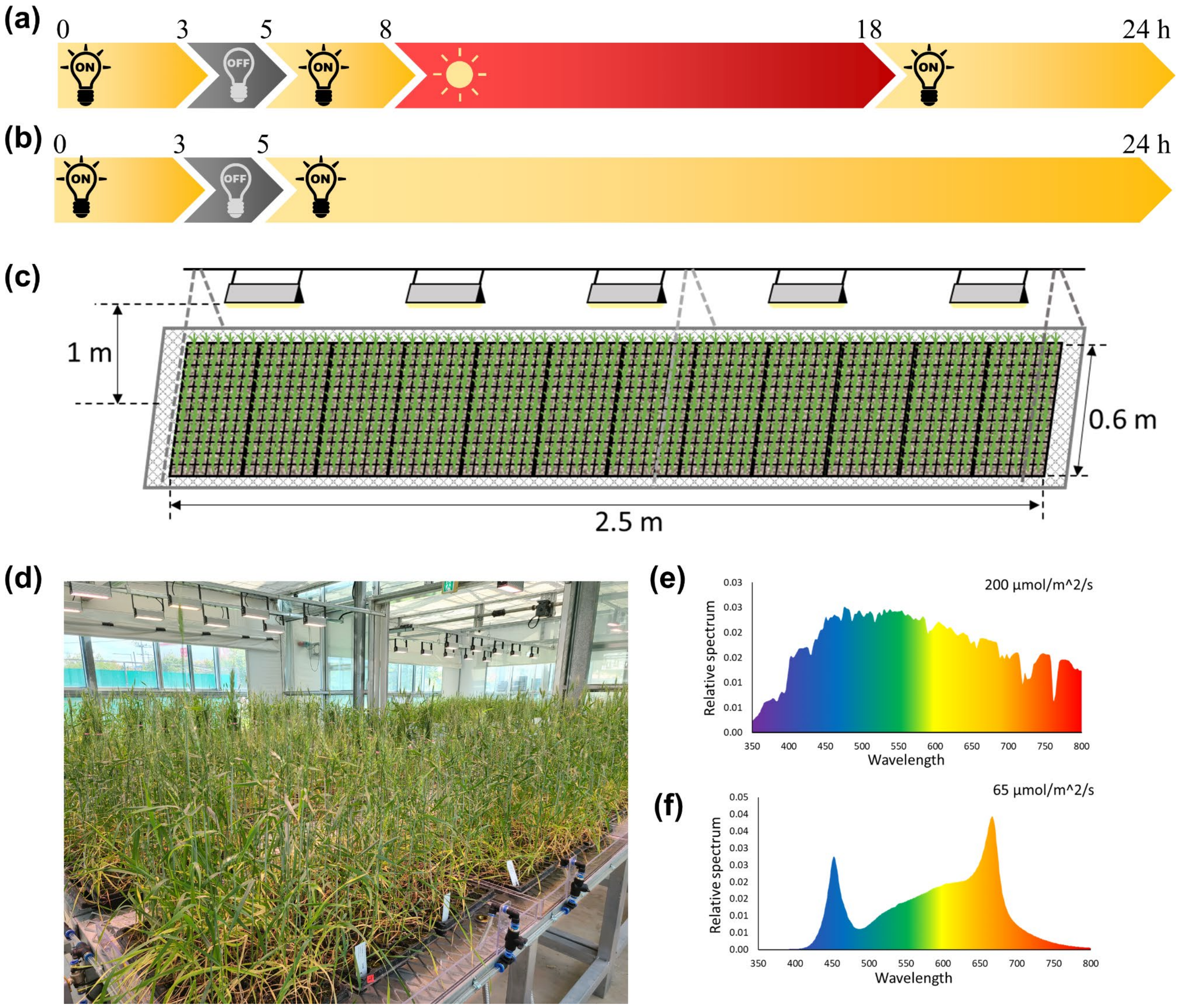
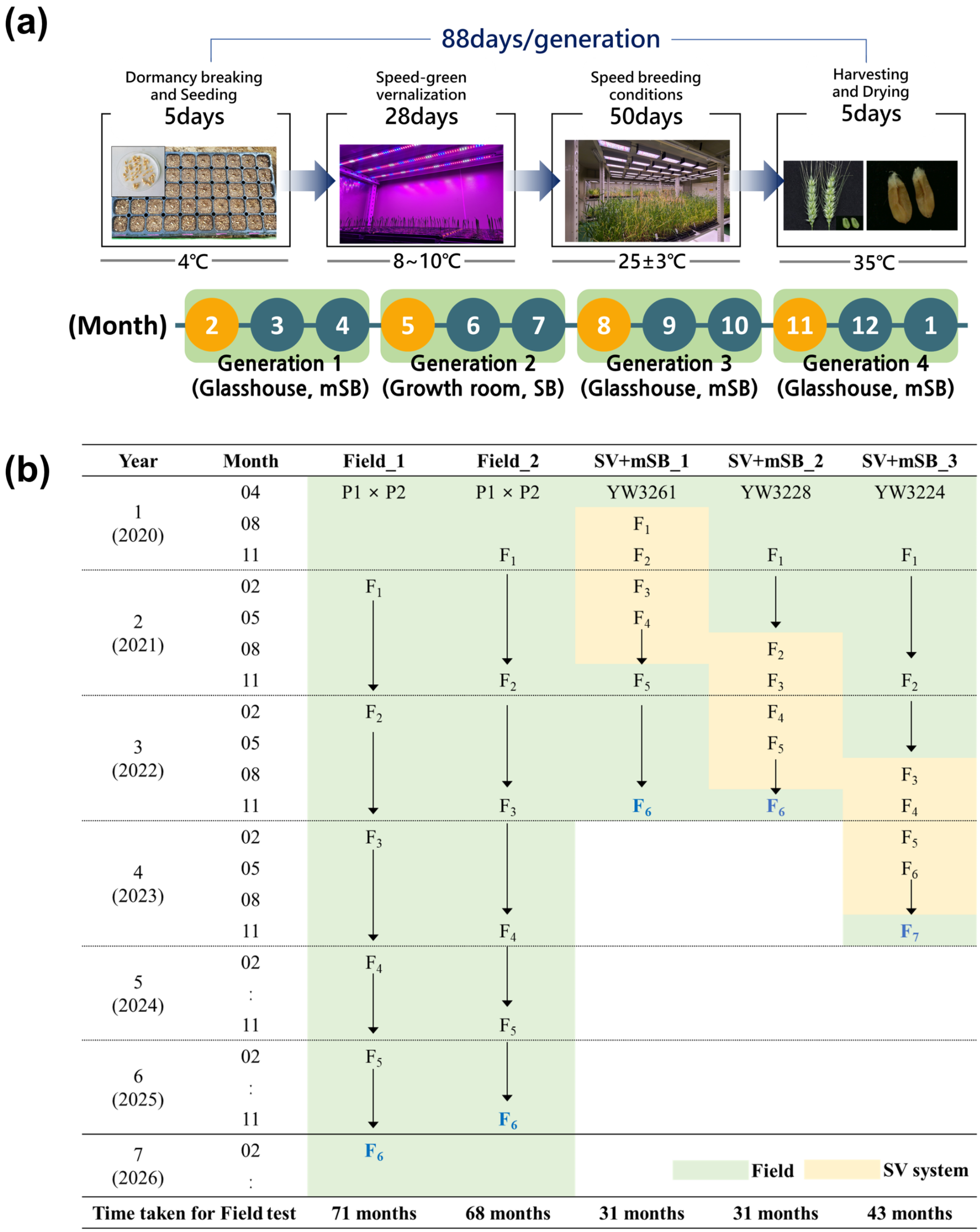


Fig. 1 Modified speed breeding (mSB) condition using natural sunlight Comparison of light conditions between (a) mSB in a glasshouse, and (b) original speed breeding in growth room. Schematic (c) and photograph (d) of light installations in a glasshouse. Light intensity and quality in the glasshouse in the day (e) and at night (f)

rooms in previous studies, which ranged from 350 to 500 µmol/m²/s [8, 9, 19, 20], no significant differences in days to heading (DTH) or grain number per spike (GN) were observed between the SV+mSB and SV+SB conditions (Fig. S1a and b). This may be because plant growth is influenced by various conditions, including light intensity, light spectrum, temperature, and CO_2 concentration [13, 17, 21–23]. Bhatta et al. [13] reported that higher plant height and GN were observed in a glasshouse than in a speed-breeding room, although this was the result of delayed DTH in a glasshouse with a natural photoperiod. Because a short DTH and sufficient GN are the main factors for accelerating wheat generation, the mSB condition is considered suitable for decreasing the generation time while maintaining minimal plant growth and enough grains.

Four-generation advancement system for wheat breeding program

Figure 2a describes the four-generation advancement system using the SV+mSB conditions. The glasshouse has been used for three generations of advancement, with only one cycle requiring a controlled growth room. The timeline was altered to start in February, instead of January, to reduce the duration of wheat growing in the glasshouse during the summer season. Because the temperature in Korea is highest from June to August (Table S2), it was preferable to execute the second cycle (May–July) in the growth room. The third cycle



Year	Month	Field_1	Field_2	SV+mSB_1	SV+mSB_2	SV+mSB_3
1 (2020)	04	P1 × P2	P1 × P2	YW3261	YW3228	YW3224
	08			F_1		
	11		F_1	F_2	F_1	F_1
2 (2021)	02	F_1		F_3		
	05			F_4	↓	
	08		↓	↓	F_2	↓
	11	↓	F_2	F_5	F_3	F_2
3 (2022)	02	F_2			F_4	
	05				F_5	↓
	08		↓	↓	↓	F_3
	11	↓	F_3	**F_6**	**F_6**	F_4
4 (2023)	02	F_3				F_5
	05					F_6
	08		↓			↓
	11	↓	F_4			**F_7**
5 (2024)	02	F_4				
	:		↓			
	11	↓	F_5			
6 (2025)	02	F_5				
	:		↓			
	11	↓	**F_6**			
7 (2026)	02	**F_6**				
	:					
Time taken for Field test		71 months	68 months	31 months	31 months	43 months

🟩 Field 🟨 SV system

Fig. 2 (See legend on next page.)

(See figure on previous page.)

Fig. 2 Modified speed breeding condition combined with speed vernalization (SV+mSB) system enables four generations per year for rapid development of new wheat lines (a) Diagram of SV+mSB conditions. The months marked with yellow indicate one week of speed vernalization (SV) treatment, while blue indicates speed breeding (SB) or modified speed breeding (mSB) conditions. (b) Schematic representation for comparing the generation advancement in traditional field and three SV+mSB conditions. The blue bold generation applies to observed yield trials. Field_1 and 2 represent spring and winter wheat, respectively. The numbers followed by SV+mSB indicate each model using the SV+mSB system starting from different generations. YW3261: Jokyoung/Joongmo2008//Baekkang/m Joongmo2008, YW3228: Milyang46/Garnet, and YW3224: Keumgang/Joongmo2008. Jokyoung, Baekkang and Garnet are spring cultivars, and the others are winter cultivars

(August–October) includes the hottest month of the year, August, yet four weeks of SV treatment can limit plant growth in the glasshouse at this time. Although the second cycle can be conducted in a glasshouse, as a result of high temperatures in the heading and flowering stages, GN and plant fertility significantly decreased compared with the other cycles (Fig. S1, Table S3 and S4). The time schedule can be adjusted according to the climate conditions in each country and region, and entire cycles can be conducted under glasshouse conditions if the temperature is relatively low throughout the summer. According to Chat et al. [9], five generations of spring × winter wheat population can be developed in 12 months. However, four generations can be accelerated in some winter wheat cultivars. As numerous genetic resources with varying development behaviors are used in breeding programs, this four-generation advancement system can be optimized for wheat breeders to use on a regular basis.

In observed yield trials (OYT), the SV+mSB reduced the time from artificial crossing to sowing wheat grains in the field by more than half when compared to conventional field breeding systems (Fig. 2b). Under field conditions, because one generation of spring and winter wheat can be developed per year, the F_6 generation typically takes 68–71 months to develop. When large breeding materials from various cross combinations were developed using the SV+mSB system, four generations could be stably advanced in one year, with additional time for sufficient seed maturity before evaluating them in the field (Fig. 2b, Table S5). The breeding time in the SV+mSB_1 and SV+mSB_2 models, which accelerated generation from F_1 and F_2, respectively, was shorter than in the SV+SB _3 model, which originated from F_3 (see the schematic for each model in Fig. 2b). However, to maintain sufficient segregation of the F_2 population size and achieve targeted gene-recombinant lines [24, 25], the SV+mSB_3 model would be suitable for field breeding programs. Because wheat grown in pots yields more grains than wheat grown in trays under SB conditions [7], pots would be more efficient for developing the last generation to be sown in the field as lines.

Phenotypic selection in the SV+mSB system

Agronomic traits, such as DTH, plant height, and spike length (SPL) are highly heritable under a variety of field conditions [26–28]. Spring wheat grown in the SB condition also showed high heritability for such agronomic traits [29]. We investigated the correlation between SV+mSB and field conditions for several agronomic traits to enable phenotypic selection in SV+mSB conditions for breeding materials obtained from both spring and winter wheat cultivars. When the data from SV+mSB and field conditions were compared with 609 genetic resources and 184 Jokyoung × Joongmo2008 recombinant inbred lines (RILs), high correlations between DTH (r=0.691***) and culm length (CL) (r=0.854***) were found (Fig. 3a). RILs had a weaker correlation in both DTH and CL than the genetic resources because of their lower phenotypic diversity and narrower distribution. SPL also showed a significant correlation with SV+mSB and field conditions, whereas awn length (AL) and spikelet number per spike (SPN) showed no significant correlation between these two conditions (Fig. S2).

Based on these findings, visual phenotypic selection for DTH and CL was applied on the Joongmo2008*/Tapdong (winter-type × winter-type) BC_1F_4 lines under the SV+mSB conditions (Fig. 3b, Fig. S3). Lines with early heading and short CLs were harvested and sown for the next generation. Under field conditions, all BC_1F_5 lines had earlier DTH than Tapdong (late heading and short culm length), and shorter CL than Joongmo2008 (early heading and long CL) (Fig. 3c and d). This result indicates that efficient phenotypic selection can be conducted under the SV+mSB conditions to reduce the population size and labor required for evaluating breeding lines in the field.

However, generation acceleration and phenotypic selection in the SV+mSB conditions remain limited owing to indoor testing across multiple generations. The annual evaluation of breeding lines in local fields allows better-adapted cultivars to be selected [30–32]. Borlaug's shuttle breeding method allows for generation acceleration and natural selection through cultivation in diverse environments [33, 34]. Furthermore, the selection of major yield-related agronomic traits, such as tiller number, number of grains per spike, and thousand grain weight, cannot be conducted under the SV+mSB conditions. As a result, although the SV+mSB system can substantially reduce breeding time and input energy on its own, it still requires the use of modern breeding technologies such as MAS and GS. Because numerous markers have been developed for selecting breeding targets, including major yield-related traits, MAS and GS would helpmaximize genetic gain and enable the selection of

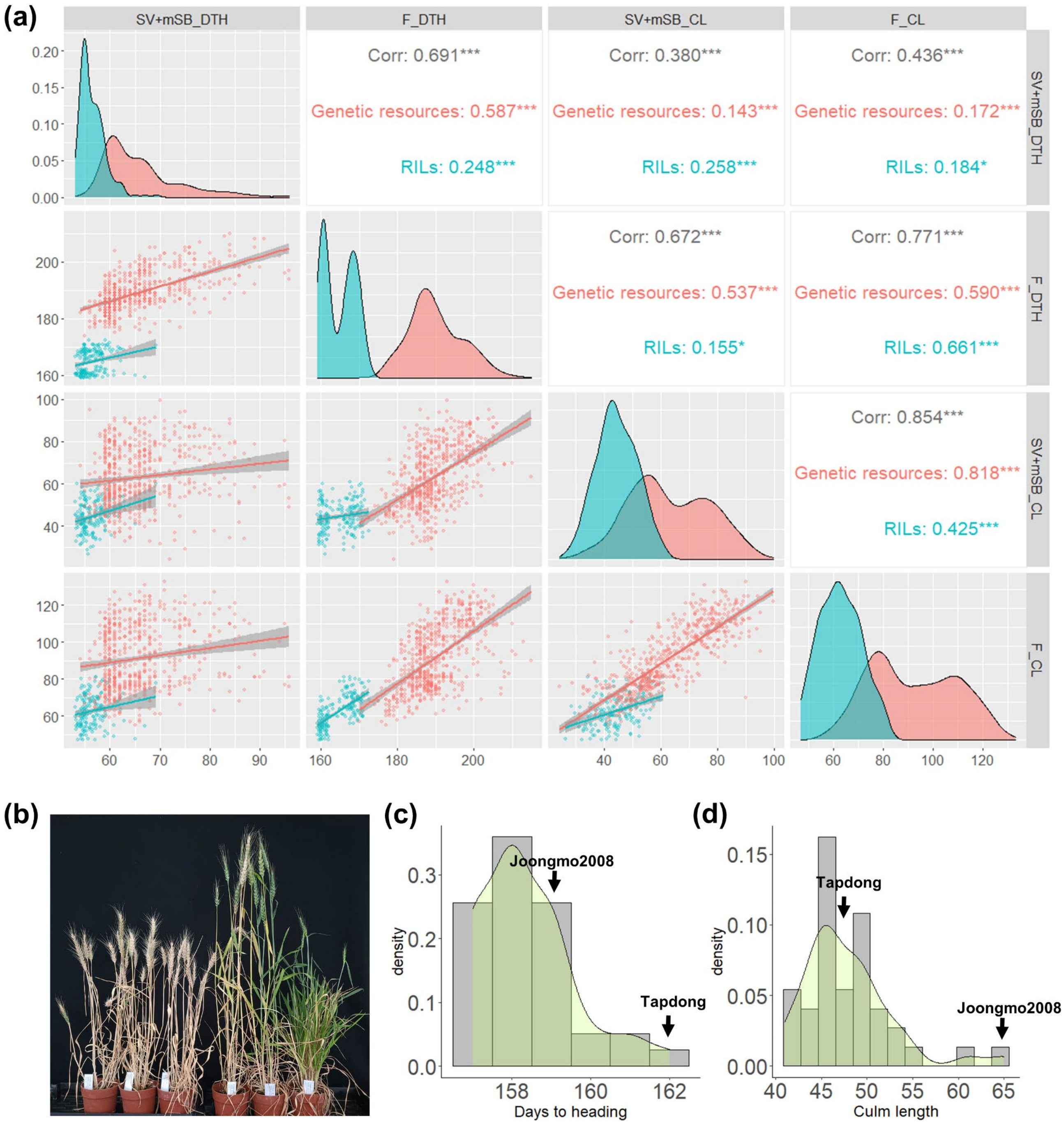


Fig. 3 Phenotypic selections can be conducted under the modified speed breeding combined with the speed vernalization condition (SV + mSB). (a) Correlations of days to heading (DTH) and culm length (CL) between the SV + mSB and field conditions. Genetic resources: a total of 609 wheat cultivars collected worldwide; RILs: Jokyoung×Joongmo2008 derived 184 recombinant inbred lines. (b) The phenotypic difference in Joongmo2008*2/Tapdong BC_1F_4 lines under the SV + mSB condition. The left three individuals represent selected lines with early heading and short CL, while the right three lines were eliminated due to their delayed DTH and long CL. The distribution of DTH (c) and CL (d) in Joongmo2008*2/Tapdong BC_1F_5 37 lines evaluated in field

lines that are adaptable to each cultivation environment [17, 35, 36].

Conclusion

We modified SB conditions in this study to create a breeder-friendly and energy-saving generation acceleration system. The SV+mSB system uses 10 h of natural sunlight and 12 h of LED light, resulting in an 80% reduction in energy consumption compared to the conventional SV+SB system. Four generations of wheat can be developed using the SV+mSB system as standard procedure in breeding programs, enabling the production of a sizable amount of breeding material. When the SV+mSB system was combined with field tests, the breeding time was reduced by more than half compared to the traditional field-based breeding method. Visual phenotypic selection was effective in the SV+mSB condition. Genetic resources, RILs, and breeding lines that had shorter DTH and CL under SV+mSB conditions also had shorter DTH and CL under field conditions. The findings of this study, which involved the successful use of phenotypic selection while accelerating the development of four generations of bulk breeding materials, are expected to serve as a model for breeders worldwide. However, it is still difficult to evaluate major yield-related traits under SV+mSB conditions. Therefore, developing and utilizing gene-specific markers that match the genotype and phenotype in each field condition would enhance both speed and efficiency for wheat breeding.

Materials and methods

Modified speed breeding condition set up in a glasshouse

A glasshouse with shelving for plant trays was used for the testing of mSB conditions. LED lights (Full Spectrum LED PLANT 50WB_SPOT_Full; Yunlighting Co., Namyangju, Korea) were mounted at a height of one meter from the shelves where the plants were placed, with five LED lights per 1.5 m^2 in the modified speed breeding (mSB) glasshouse (Fig. 1c, d). The light composition and intensity were measured using an RS-3500 field portable spectroradiometer (Spectral Evolution Inc., Haverhill, MA, USA) and an LI-250 light meter (LI-COR Biosciences, Lincoln, NE, USA), respectively. Each shelf held twelve 72-cell trays, and the glasshouse had 12 shelves altogether. The total area of the glasshouse was 115.5 m^2 (Table S1). The glasshouse is located at the National Institute of Crop Science (NICS), Rural Development Administration (RDA), Miryang, Republic of Korea (35°29′32.9′′N, 128°44′33.4′′).

The temperature inside the glasshouse was adjusted by opening and closing the windows, without a cooling system, and a heating system was used for 192 days per year, when the mean minimum temperature was less than 10 °C (late October to March). A Testo 174 H logger (Testo Industrial Services GmbH, Kirchzarten, Germany) was used to record the temperature inside the glasshouse. The weather data supplied by the Korea Meteorological Administration Open MET Data Portal (https://data.kma.go.kr/) was used to collect outdoor temperature data.

Seeding and vernalization treatment

Using the SV method developed by Cha et al. [9], the vernalization room was set to 8 °C to meet the vernalization requirements of all wheat cultivars, genetic resources, and breeding materials included in this study. All the seeds were moistend and chilled at 4 °C for 3 to 4 days, then moved to the vernalization room shortly after sowing. The 72-cell trays (W 27 cm, L 58 cm) were used for generation advancement with the single-seed descent method, whereas 250 ml pots were used for artificial crossing and generation advancement of F_1 plants. The trays and pots were filled with a mixture of commercial paddy rice soil (Punong Co. Ltd., Gyeongju, Korea) and horticultural soil (Seoul-Bio Co. Ltd., Eumseong, Korea) in a 2:1 ratio. All plants were moved to the SB or mSB conditions after four weeks of vernalization. The SB condition was the same as that used by Cha et al. [9], which maintains the 22 °C during the 22 h of day, and 17 °C during the 2 h of night.

Plant materials and growth evaluation

To compare the growth characteristics under SV+SB and SV+mSB conditions with different seeding dates, ten wheat cultivars, including both spring- and winter-type, were evaluated using five plants per cultivar (Table S4).

To evaluate the correlation between agronomic traits in SV+mSB and field conditions, 609 worldwide wheat genetic resources reported by Min et al. [37] and 184 RILs derived from a cross between Jokyoung (spring-type) and Joongmo2008 (winter-type) were sown in 72-cell trays with six plants per cultivar. The detailed information of the worldwide wheat accession is reported by Kang et al. [38]. Field data on genetic resources were collected over three years (2018–2020), whereas RILs were evaluated over two years (2021–2022). Tottman et al. [39] detailed the recording of the heading stage date (GS59). The culm length, spike length, awn length, and spikelet number per spike were determined using the RDA Standard Evaluation Manual for Agricultural Experiments and Research [40].

To assess the impact of phenotypic selection under SV+mSB conditions, 37 Joongmo2008*2/Tapdong BC_1F_5 lines were developed, as shown in Fig. S3. Visual selection under SV+mSB conditions was conducted in the BC_1F_5 generation. Phenotypic evaluation in the field was carried out in 2022.

Statistical anaylsis

RStudio (version 1.4.1717; RStudio, PBC, Boston, MA, USA) was used for all statistical analyses. Correlation analysis, analysis of variance, and Duncan's multiple tests were conducted using ggplot2, agricolae, and GGally packages.

Abbreviations

AL	awn length
CL	culm length
DTH	days to heading
GN	grain number per spike
GS	genomic selection
MAS	marker-assisted selection
mSB	modified speed breeding
OYT	observed yield trials
PPFD	photosynthetic photon flux density
RILs	recombinant inbred lines
SB	speed breeding
SPL	spike length
SPN	spikelet number per spike
SV	speed vernalization

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13007-023-01083-1.

Supplementary Material 1

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Not applicable.

Authors' contributions

J.-H.L. conceived the study. J.-H.L., K.-W.O., and J.-M.K. supervised this project. J.-H.L., J.-K.C., and S.-W.K. designed the experiments. J.-K.C., H.P., Y.K., and S.-M.L. developed and investigated breeding materials. J.-K.C., C.C., and H.P. investigated the genetic resources. J.-K.C., Y.K., and S.-M.L. analyzed the data. J.-K.C. and J.-H.L. prepared the manuscript. All the authors have discussed and agreed to participate in the manuscript.

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Data availability

The datasets used and/or analyzed in the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

1. Erenstein O, Jaleta M, Mottaleb KA, Sonder K, Donovan J, Braun H-J. Global trends in wheat production, consumption and trade. In: Reynolds MP, Braun HJ, editors. Wheat improvement: food security in a changing climate. Cham: Springer International Publishing; 2022. pp. 47–66.
2. Kiszonas AM, Morris CF. Wheat breeding for quality: a historical review. Cereal Chem. 2018;95:17–34.
3. Curtis T, Halford N. Food security: the challenge of increasing wheat yield and the importance of not compromising food safety. Ann Appl Biol. 2014;164:354–72.
4. Lopes MS, El-Basyoni I, Baenziger PS, Singh S, Royo C, Ozbek K, et al. Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. J Exp Bot. 2015;66:3477–86.
5. Ghosh S, Watson A, Gonzalez-Navarro OE, Ramirez-Gonzalez RH, Yanes L, Mendoza-Suárez M, et al. Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. Nat Protoc. 2018;13:2944–63.
6. Ahmar S, Gill RA, Jung K-H, Faheem A, Qasim MU, Mubeen M, et al. Conventional and molecular techniques from simple breeding to speed breeding in crop plants: recent advances and future outlook. Int J Mol Sci. 2020;21:2590.
7. Cha J-K, Lee J-H, Lee S-M, Ko J-M, Shin D. Heading date and growth character of korean wheat cultivars by controlling photoperiod for rapid generation advancement. Korean J Breed Sci. 2020;52:20–4.
8. Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey M-D, et al. Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants. 2018;4:23–9.
9. Cha J-K, O'Connor K, Alahmad S, Lee J-H, Dinglasan E, Park H, et al. Speed vernalization to accelerate generation advance in winter cereal crops. Mol Plant. 2022;15:1300–9.
10. Hickey LT, Wilkinson PM, Knight CR, Godwin ID, Kravchuk OY, Aitken EA, et al. Rapid phenotyping for adult-plant resistance to stripe rust in wheat. Plant Breed. 2012;131:54–61.
11. Dinglasan E, Godwin ID, Mortlock MY, Hickey LT. Resistance to yellow spot in wheat grown under accelerated growth conditions. Euphytica. 2016;209:693–707.
12. Riaz A, Periyannan S, Aitken E, Hickey L. A rapid phenotyping method for adult plant resistance to leaf rust in wheat. Plant Methods. 2016;12:1–10.
13. Bhatta M, Sandro P, Smith MR, Delaney O, Voss-Fels KP, Gutierrez L, et al. Need for speed: manipulating plant growth to accelerate breeding cycles. Curr Opin Plant. 2021;60:101986.
14. William H, Trethowan R, Crosby-Galvan E. Wheat breeding assisted by markers: CIMMYT's experience. Euphytica. 2007;157:307–19.
15. Fischer R, Rebetzke G. Indirect selection for potential yield in early-generation, spaced plantings of wheat and other small-grain cereals: a review. Crop Pasture Sci. 2018;69:439–59.
16. Wanga MA, Shimelis H, Mashilo J, Laing MD. Opportunities and challenges of speed breeding: a review. Plant Breed. 2021;140:185–94.
17. Hickey LT, Hafeez N, Robinson A, Jackson H, Leal-Bertioli SA, Tester SC. Breeding crops to feed 10 billion. Nat Biotechnol. 2019;37:744–54.
18. Cha J-K, Park M-R, Shin D, Kwon Y, Lee S-M, Ko J-M, et al. Growth characteristics of triticale under long-day photoperiod for rapid generation advancement. Korean J Breed Sci. 2021;53:200–5.
19. Vikas V, Sivasamy M, Jayaprakash P, Vinod K, Geetha M, Nisha R, et al. Customized speed breeding as a potential tool to advance generation in wheat. Indian J Genet Plant Breed. 2021;81:199–207.
20. Schoen A, Wallace S, Holbert MF, Brown-Guidera G, Harrison S, Murphy P, et al. Reducing the generation time in winter wheat cultivars using speed breeding. Crop Sci. 2023;63:2079–90.
21. Rickman R, Klepper B, Peterson CM. Wheat seedling growth and developmental response to incident photosynthetically active radiation 1. J Agron. 1985;77:283–7.
22. Tamaki M, Imai K, Moss DN. Effects of water supply and light intensity on the growth of spring wheat. Environ Control Biol. 2001;39:103–9.
23. Dong C, Fu Y, Liu G, Liu H. Growth, photosynthetic characteristics, antioxidant capacity and biomass yield and quality of wheat (*Triticum aestivum* L.) exposed to LED light sources with different spectra combinations. J Agron Crop Sci. 2014;200:219–30.
24. Wricke G, Weber E. Quantitative genetics and selection in plant breeding. Berlin; Walter de Gruyter; 2010.
25. Poehlman JM. Breeding field crops. Springer Science & Business Media; 2013.

26. Laghari KA, Sial MA, Arain MA, Mirbahar AA, Pirzada A, Dahot M, et al. Heritability studies of yield and yield associated traits in bread wheat. Pak J Bot. 2010;42:111–5.
27. Fellahi Z, Hannachi A, Guendouz A, Bouzerzour H, Boutekrabt A. Genetic variability, heritability and association studies in bread wheat (*Triticum aestivum* L.) genotypes. Electron J Plant Breed. 2013;4:1161–6.
28. Khan SA, Hassan G. Heritability and correlation studies of yield and yield related traits in bread wheat. Sarhad J Agric. 2017;33:103–7.
29. Watson A, Hickey LT, Christopher J, Rutkoski J, Poland J, Hayes BJ. Multivariate genomic selection and potential of rapid indirect selection with speed breeding in spring wheat. Crop Sci. 2019;59:1945–59.
30. Döring TF, Annicchiarico P, Clarke S, Haigh Z, Jones HE, Pearce H, et al. Comparative analysis of performance and stability among composite cross populations, variety mixtures and pure lines of winter wheat in organic and conventional cropping systems. Field Crops Res. 2015;183:235–45.
31. Knapp S, Döring TF, Jones HE, Snape J, Wingen LU, Wolfe MS, et al. Natural selection towards wild-type in composite cross populations of winter wheat. Front Plant Sci. 2020;10:1757.
32. Henry RJ, Nevo E. Exploring natural selection to guide breeding for agriculture. Plant Biotechnol J. 2014;12:655–62.
33. Borlaug NE. Sixty-two years of fighting hunger: personal recollections. Euphytica. 2007;157:287–97.
34. Ortiz R, Trethowan R, Ferrara GO, Iwanaga M, Dodds JH, Crouch JH, et al. High yield potential, shuttle breeding, genetic diversity, and a new international wheat improvement strategy. Euphytica. 2007;157:365–84.
35. Cha J-K, Park H, Kwon Y, Lee S-M, Oh K-W, Lee J-H. Genotyping the high protein content gene *NAM-B1* in wheat (*Triticum aestivum* L.) and the development of a KASP marker to identify a functional haplotype. Agronomy. 2023;13:1977.
36. Rasheed A, Wen W, Gao F, Zhai S, Jin H, Liu J, et al. Development and validation of KASP assays for genes underpinning key economic traits in bread wheat. Theor Appl Ganet. 2016;129:1843–60.
37. Min K, Na Kang Y, Kim C, Choi C, Kim A. Genetic diversity and population structure of korean common wheat (*Triticum aestivum*). Korean J Breed Sci. 2021;53:277–88.
38. Tottman D. The decimal code for the growth stages of cereals, with illustrations. Ann Appl Biol. 1987;110:441–54.
39. RDA. Manual for standard evaluation method in agricultural experiment and research. Suwon: RDA Press; 2012.

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