



Integrating speed breeding with artificial intelligence for developing climate-smart crops

Krishna Kumar Rai¹

Received: 21 January 2022 / Accepted: 5 July 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract

Introduction In climate change, breeding crop plants with improved productivity, sustainability, and adaptability has become a daunting challenge to ensure global food security for the ever-growing global population. Correspondingly, climate-smart crops are also the need to regulate biomass production, which is imperative for the maintenance of ecosystem services worldwide. Since conventional breeding technologies for crop improvement are limited, time-consuming, and involve laborious selection processes to foster new and improved crop varieties. An urgent need is to accelerate the plant breeding cycle using artificial intelligence (AI) to depict plant responses to environmental perturbations in real-time.

Materials and methods The review is a collection of authorized information from various sources such as journals, books, book chapters, technical bulletins, conference papers, and verified online contents.

Conclusions Speed breeding has emerged as an essential strategy for accelerating the breeding cycles of crop plants by growing them under artificial light and temperature conditions. Furthermore, speed breeding can also integrate marker-assisted selection and cutting-edged gene-editing tools for early selection and manipulation of essential crops with superior agronomic traits. Scientists have recently applied next-generation AI to delve deeper into the complex biological and molecular mechanisms that govern plant functions under environmental cues. In addition, AIs can integrate, assimilate, and analyze complex OMICS data sets, an essential prerequisite for successful speed breeding protocol implementation to breed crop plants with superior yield and adaptability.

Keywords Speed breeding · Artificial intelligence · Crop breeding · Yield · Stress

Introduction

Global climate changes have severely impacted agricultural productivity worldwide. The severe repercussions of climate change range from extreme temperatures (high and low), excess sunlight, and elevated CO₂ altering rainfall's geographical nature, making crops more prone to disease [1]. Several researchers have well-advocated climate change has become a prime aspect that tremendously affects plant growth, development, and productivity by provoking biotic and abiotic stresses [1, 2]. Conversely, decreased agricultural yield will hamper food security, leading to micronutrient

deficiencies and chronic hunger for the ever-growing global populations [2, 3]. Additionally, in the pandemic era, such as severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), food security has further deteriorated as agricultural scientists have recorded a steep increase in hunger index by 2020 [4]. The predicament becomes more complex as food security depends on economic growth, markedly influenced by global climate change [3, 4]. Therefore, it has become imperative to exploit next-generation plant breeding technologies to foster climate-smart crops with enhanced nutritional properties [5, 6].

The conventional plant breeding approach has been the savior for ensuring food and nutritional security worldwide. It does it by strengthening genetic diversity and unraveling novel genes [7]. The gain in genetic diversity and identification of novel genes through classical breeding is a time-consuming process involving hybridization/intercrossing of elite/wild cultivars with common landraces [8]. The new crop varieties developed through the classical

✉ Krishna Kumar Rai
raikrishna16@gmail.com; krishna.raia4@bhu.ac.in

¹ Centre of Advanced Study in Botany, Department of Botany, Institute of Science, Banaras Hindu University (BHU), 221005 Varanasi, Uttar Pradesh, India

breeding approach possess superior agronomic traits that help increase their yield potential and stress resilience [7, 8]. However, the length of the breeding cycle required to complete the breeding program is the major bottleneck for developing desired cultivars/varieties [9]. For instance, it takes approx. 6–7 years to build genetically homozygous/stable lines/cultivars in a multistep process, from parent selection, hybridization/crossing to data recording, analysis, and field evolution of individual traits [8, 9]. Additionally, researchers have corroborated that this period dramatically influences the subsequent breeding cycle, affecting net genetic gain in the newly developed cultivars and their release to farmer's fields [8]. Therefore, to accelerate the rate of gene gain and breeding cycles, next-generation breeding technologies such as speed breeding powered by artificial intelligence (AI) are now being extensively used for crop improvement programs [10].

Speed breeding technology has emerged as a versatile suite for manipulating the growing environment of crop plants to accelerate their breeding generation by enhancing the rate of flowering and seed set under the influence of AI [10, 11]. In addition, speed breeding instigates rapid generation advancement via reducing breeding time and resources by accelerating essential cellular and metabolic processes [5, 6]. Speed breeding mainly works by modifying the light, intensity, and duration, which, upon subsequent perception by photoreceptors, triggers rapid reproductive development in plants [6]. These photoreceptors, upon perceiving light, regulate the natural circadian rhythm, which is the first and rapid responder to changing environmental conditions [12]. The researchers have devised speed breeding protocols by categorizing plants into three groups' viz. short-day plants (SDP), long-day plants (LDP), and day-neutral plants (DNP) [6]. The speed breeding instigates rapid generation advancement in SDP and DNP by providing light for more extended and LDP for a shorter duration [6, 13]. The main objective of any plant breeders is to increase the yield and resistance of crop plants by predicting which line/cultivars will produce the best hybrids upon their subsequent hybridization.

Furthermore, integrating classical breeding with OMICS techniques such as phenomics, genomics, transcriptomics, proteomics, and metabolomics has remarkably influenced the quality and quantity of data that has helped breeders perform unprecedented improvements in their breeding programs [14]. However, handling multi-omics data is a big challenge. They are a humungous, complex web of data that could hamper predicting and selecting the best lines/cultivars for breeding programs [14, 15]. Therefore, AI in agriculture represents a state-of-the-art technique that can quickly process big multi-omics data and relate them with underlying biological processes under varying environmental conditions [15]. Speed breeding and AI can tremendously

accelerate breeding programs by efficiently handling the problem posed by big OMICS data resulting in the generation of stress-resistant/tolerant cultivars with higher genetic gains and yield to the farmer's field.

Therefore, the present review aims to provide an in-depth understanding of concepts and procedures of how speed breeding can overcome the limitations of classical breeding techniques. Furthermore, how AI can be integrated with speed breeding protocol or design and revolutionize the processing of big OMICS data to take a step toward digital agriculture. Finally, we provide comprehensive knowledge about the possible role of these next-generation breeding technologies and how they will expedite crop improvement programs for food and nutritional security.

Traditional breeding: the liberator

Initially, ancient farmers practiced plant breeding to increase the domestication of plants within their surroundings. Its subsequent evolution has become one of the acclaimed approaches for improving yield and disease susceptibility in crop plants [7]. The foremost step in plant breeding involved selecting wild cultivars with desired agronomic traits and then crossing or hybridizing them with local cultivars to incorporate superior characteristics. It followed rigorous selection for 5–6 generations [8, 16]. The variations among different progenies with ideal agronomic traits were identified based on morphological characteristics or markers such as plant height, branch number, yield/plant, and then analyzed using a statistical program [17]. Later, plant breeders started exploiting molecular/genetic markers that allow robust and quick assessment of genetic variation among the progenies [17]. In addition, molecular markers also serve as an indispensable tool for underpinning genetic variation and structure more efficiently than the morphological and biochemical markers, which help in accelerating breeding programs and greatly facilitate their efficient conservation [8, 17]. Furthermore, an amalgamation of molecular techniques with classical breeding helps to untapped the hidden genetic potential of common landraces, wild relatives, and varieties by expediting the identification of quantitative trait loci (QTLs), thereby identifying new alleles/genes that may be absent in the local cultivars [17].

These novel genes/alleles can be integrated into elite cultivars/varieties via the gene pyramiding/accumulation approach to increase the scope of genetic variation for given agronomic traits [18]. Various genetic/linkage/QTL maps have been made for multiple agriculturally essential crops that have helped plant breeders unlock favorable genetic variations in crop species by using a specific set of molecular markers [17]. Researchers have also performed

whole-genome sequencing or RNA sequencing to decipher genome-wide interpretation by identifying single nucleotide polymorphisms, solely dependent upon sample size [17, 18]. Adequate sample size and robust molecular markers are essential for constructing high-resolution QTL mapping with fewer genomic gaps [18]. More significant genomic gaps within the genetic/QTL map indicate partial genotyping and coverage which could be due to (i) loss of marker-trait association for the observed phenotype, (ii) loss of target gene during subsequent generation of mapping, (iii) non-significant genome-wide association studies and (iv) in-efficient population structure, linkage disequilibrium and marker-assisted selection [19]. Nonetheless, integrating these molecular approaches has led to the precise construction of a genetic/linkage map and paved the way to explore the hidden genetic potential of landraces, elite cultivars, wild relatives, and inbred lines.

Conventional breeding has been most prominently used to develop and breed new perennial crops by domesticating wild/superior cultivars from one place to another or mediating its crossing or hybridization with cultivated genotypes [20]. Conversely, domestication of any line/variety involves its establishment at the desired place, followed by rigorous phenotyping for selecting superior cultivars with desired traits [7]. In contrast, hybridization is more realistic and practical than domestication because if the hybridization of two contrasting cultivars is successful, it can develop hybrids having superior agronomical traits [20]. Several perennial crops have been improved using a comprehensive hybridization approach, such as sorghum (*Sorghum bicolor* × *S. halepense*), wheat (*Triticum* spp. × *Thinopyrum* spp.), rice (*Oryza sativa* × *O. longistaminata*) and buckwheat (*Fagopyrum* spp. × *Fagopyrum* spp.) [20]. However, both the conventional techniques are time-consuming and often involve robust data collection; researchers have now incorporated various molecular breeding techniques that have significantly expedited the traditional breeding approaches to develop and breed improved cultivars, which have been comprehensively discussed in the following section.

Advancements in molecular breeding techniques

Genomics-assisted tools have provided plant breeders with an excellent opportunity to improve plant growth and productivity under changing environmental conditions by using DNA-based markers to successfully select the best crossbreeds via marker-aided selection [8]. Furthermore, in conjunction with classical breeding, plant genomics has provided an in-depth understanding of diversity among the hybrids at the phenotypic and gene-level that have

accelerated crop improvement programs [7]. Successful application of genomic assisted breeding involves the selection of cultivar/wild species for the concerned biotic/abiotic stress-tolerant or agronomic traits, then linking the phenotype by performing genotyping with a specific set of markers followed rigorous selection to foster climate-ready crops [21]. DNA fingerprinting using high-density DNA markers of economically essential crops could also help relate crop physiology with plant phenology, identifying the best ideotypes with special characters [17]. In addition, researchers have also well confirmed that the rigorous genotyping followed by phenotyping followed by appropriate biometrical analysis could reveal valuable information that can lead to the identification of QTLs. Several researchers have constructed a high-density linkage/genetic map using biparental of double haploids mapping population. They have successfully identified QTLs controlling disease resistance and agronomic traits in cereals and legume crops [22–24].

With the advent of next-generation sequencing techniques, researchers have been able to identify and link QTLs for biotic/abiotic stresses and other yield-related traits. Next-generation sequencing technologies have expedited the development of robust/specific genetic markers such as SNP and InDels, which have greatly facilitated the identification of novel genes/alleles via exploiting in genotyping by sequencing approaches (GBS) or by incorporating them with genome-wide association studies (GWAS) [22, 23]. Several studies have corroborated that using GWAS with next-generation sequencing technology can significantly improve the mapping resolution, identifying the precise location, and statistically validated QTLs/genes/alleles [23, 24]. For instance, GWAS reveals 90 novel marker-trait associations related to abiotic stress, grain yield, and other agronomic traits in drought-stressed synthetic hexaploid wheat [25]. Furthermore, association mapping with MAS has tremendously aided the selection of the most responsive QTLs, which has accelerated the genomic selection of the best cultivars for their subsequent utilization in breeding programs [26].

Furthermore, GWAS has facilitated the identification of a marker-trait association between markers and several agronomic traits such as fruit size, stone size, and fruit cracking in *Ziziphus jujube* plants. This study identified 21 potential candidate genes that can be exploited for the breeding programs and genetic selection of improved *Ziziphus jujube* plants [27]. GWAS was conducted to identify a study's salt tolerance-related QTLs/genes in cotton cultivars. They performed a GBS of 217 cotton cultivars and identified 12 candidate salt-tolerant genes that can be used in the breeding program for cotton improvement [28].

Moreover, genomic-assisted breeding (GAB) has also tremendously expedited the characterization/improvements

of crop plants more precisely and rapidly by deciphering the allelic variations underlying agronomically essential traits [29]. Recent years have witnessed the progress of more than 100 agriculturally vital crop plants through GAB approaches that have improved their yield/productivity and tremendously accelerated their survival under extreme environments [30]. Various plant breeders have extensively exploited GAB techniques to identify prominent QTLs for different disease resistance traits such as bacterial blight (*Xanthomonas oryzae* pv. *Oryzae*), blast diseases (*Magnaporthe oryzae*), barley yellow mosaic viruses, and powdery mildew (*Blumeria graminis* f. sp. *hordei*) [30]. Unlike cereals, GAB has also led to the identification of QTLs in underutilized legume crops such as cyst nematode (*Heterodera glycines*) in *Glycine max* and rust resistance (*Puccinia arachidis*) in *Arachis hypogaea* [29, 31]. In addition, GAB has also been used to unravel QTLs associated with abiotic stress tolerance in plants and QTLs related to nutritional quality traits [32]. GAB has successfully identified QTLs associated with salt stress and drought stress in plants which has been exploited in the breeding programs for developing new and improved cultivars [32]. QTLs associated with grain protein content, amylose content, and oleic acid content have also been identified using GAB approaches in wheat, rice, and ground nut [30]. Since GAB exploits breeding by a design approach that includes selecting two contrasting cultivars, allele mining and extensive crossing to obtain the desired genotype are time-consuming and involve rigorous phenotyping [30]. Plant scientists have developed GAB version 2.0, an expansion of GAB 1.0 that will significantly impact breeding for stress tolerance cultivars with high nutritional value in a time and cost-effective way [29]. GAB 2.0 combines MAS, GWAS, and genome editing (CRISPR-Cas9 system); in combination with speed breeding that can fast-track manipulation of the target region in the genome to create a novel allelic variation for crop improvements [29].

Mutation breeding has also been extensively used to create genetic variations to accelerate the breeding of agriculturally important crops [33]. Mutation breeding employs chemicals and high-energy radiation to induce mutation at a specific region in the genome that exaggerates allelic/genetic variations in the crop plants [34]. Target-induced local lesions in the genome (TILLING) is one of the primary techniques which is used to introduce mutation in a precise and efficient manner as compared to chemical mutagens such as ethyl-methane sulfonate (EMS) and methyl-methane sulfonate (MMS). TILLING approach has been used in various crop plants to identify novel allelic variations for nutritional and stress-tolerant traits [33]. Researchers have exploited mutation breeding to improve crop plants' growth and stress tolerance, particularly wheat, rice, tomato, and legumes. However, they have found mutation breeding an

extensively labor-intensive and time-consuming approach to identifying genotypes with desired traits [34, 35]. Furthermore, both conventional and mutation breeding require extensive crossing and rigorous phenotyping, selecting a superior cultivar with the desired features. Its subsequent integration into the breeding program requires more extended time and backcrossing [36].

Recently Meta-QTL (MQTL) analyses are being used to accelerate the process of QTL identification and their subsequent position by exploiting mapping data reported from various studies and analyzing it with a suitable computer program [37]. For example, MQTL analysis using the BioMercator program was successfully used to dissect the genetic basis of complex abiotic/biotic stress traits in durum wheat. Researchers identified and mapped the precise location of candidate genes for quality and disease-resistant characteristics [38]. Similarly, Khahani et al. [37] performed GWAS to identify Meta-QTLs, ortho-MQTLs, and other candidate genes responsible for controlling yield and related traits in rice. Their study identified 1052 QTLs and 144 MQTLs in 122 rice populations and successfully linked them with important agronomic traits that can be later used in the breeding program to foster new and improved rice cultivars. All the techniques mentioned above have allowed breeders to shuffle/reshuffle alleles/genes to generate potential combinations required to develop improved cultivars. Nonetheless, limitations exist for all the classical breeding techniques involving GBS, GWAS, and MQTL analysis are often associated with genetic drag, gene erosion, hybridization incompatibility, and laborious selection process. Therefore, functional genomic tools were later incorporated with gene cloning techniques to generate genetically modified crops aided with all the essential genes to fulfill the demand of ever-growing global populations.

Genetically modified (GM) crops

The conventional breeding strategies used in the early 90s would take 10–15 years to develop a crop variety for the farmer's field. Later GBS, GWAS, and MAS revamped the conventional breeding techniques by using genetic markers to construct high-resolution genetic/linkage maps, and take around 6–7 years to develop a variety. Correspondingly, advancements in modern breeding technology allowed plant scientists to genetically engineer crop plants [13]. Genetically modified (GM) crops exhibit superior agronomic, yield, and disease-resistant traits by efficiently overcoming the potential barrier of conventional breeding techniques [8, 13]. Genetic engineering mainly involves the insertion/deletion of a gene or gene segment in a concerned organism using biotechnology and offers diverse advantages over classical

breeding approaches. First, it allows quick and easy ways to introduce, remove, or modify specific genes of interest without altering crop plants' basic genetic structure of crop plants thus facilitating the early development of crops with improved traits. Second, genetic engineering is a robust tool that can significantly ease the integration of genes from different sources, whether plant or animal origin, without impairing GM plants' essential physiological and metabolic processes. Third, genetic engineering is restricted to rooted plants and can successfully modify vegetatively propagated plants like banana and cassava, making it a powerful tool that efficiently uses genetic material across the genus/species [7]. Traditionally, genetic engineering is an exaggerated version of the plant tissue culture technique that combines traditional transgenic approaches that involve isolation and integration of the desired gene at a random location with advanced gene-editing technologies that allow integration/deletion of a gene at a precise location [39]. The former approach tailors crop plants using foreign DNA, whereas the latter enables accurate addition and deletion of foreign and plant origin (Cis-genic or Intra-genic plants). The cis-genic approach involves modifying recipient plants using a perfect natural copy of a gene from the same plant species or sexually compatible donor plants [39]. In comparison, the intra-genic method requires modification of recipient plants by using genetic elements isolated from the same plant species or sexually compatible donor plants, rearranging them in-vitro, and then integrating them into recipient plants [40].

Since transgenic plants are subjected to rigorous screening and selection procedures/policies before their commercial application and are often restricted to specific geographical cultivation [40], however, various countries like Brazil, Argentina, and the USA have developed genetically modified crops by using genes from plant species (Cis-genic or Intra-genic) and are approved for their commercial application by genetic engineering regulatory bodies [40]. Several lines of literature have well corroborated that transgenic plant over-expressing genes from a pathogen or virus origin successfully induced the plant's innate immune response against insect/pathogen attack [39, 40]. Later, the researchers identified that RNA interference (RNAi) led to the ectopic expression of defense responsive genes that have boosted their innate immunity against biotrophic attackers [41]. At the beginning of the 20th century, RNAi emerged as a promising tool for genetically tailoring crop plants against biotic stresses, particularly viral disease, as most plant viruses have a single-stranded RNA genome and their transgenic overexpression often leads to them the formation of double-stranded RNA (dsRNA), thus activating RNAi [41]. In the USA, several transgenic plants have been developed using the RNAi approach, such as transgenic tomato, tobacco, squash, and papaya, commercialized

and grown for more than 20 years [41]. RNAi functions via three pathways (i) small interfering RNA pathway (siRNA), (ii) micro-RNA (miRNA) pathway, and (iii) piwi-interacting RNA (piRNA) pathway. All three pathways stimulate defense response either by regulating the transposable elements, gene expression, or suppressing the expression of the germ-line transposon, thereby silencing the target gene [42]. The most notable breakthrough of RNAi technology was the development of GM maize resistance to western corn rootworm (*Diabrotica virgifera*) by over-expressing *vATPaseA dsRNA* leading to larval stunting and mortality [43]. Likewise, GM cotton was also developed using the RNAi approach by stimulating the expression of the cytochrome P450 gene, which enabled various enzymatic and non-enzymatic antioxidants, thereby conferring resistance against cotton bollworm (*Helicoverpa armigera*) [44].

Similarly, GM cotton overexpressing hairpin RNA (hpRNA) differentially regulated the expression of *CYP6AE14* in cotton bollworms, which leads to a significant reduction in larval growth [42]. Recently, transgenic cotton was developed by employing the RNAi approach by overexpressing *CYP392A4 dsRNA*, which significantly reduced the *Tetranychus cinnabarinus* pest's reproducibility [45]. Han et al. [46] developed transgenic cotton plants using RNAi technology that conferred resistance against cotton bollworm by overexpressing the *HaHR3* gene, which is a molt regulating transcription factor and induces a high level of larval mortality. Additionally, the RNAi technique has also been used to create transgenic wheat by overexpressing the *chitin synthase 1 (CHS1)* gene, thereby conferring resistance against aphids [45]. Likewise, Hou et al. [47] also used RNAi technology to silence the olfactory-related *Gqα* gene in transgenic wheat plants, increasing their resistance to aphids. Furthermore, the exploitation of dsRNA for juvenile hormone and acid methyltransferase in conjunction with RNAi technology efficiently stimulated the resistance of transgenic potato plants against *Leptinotarsa decemlineata* [48].

CRISPR-Cas system

Clustered regularly interspaced short palindromic repeats (CRISPR)-CRISPR-associated protein 9 (Cas 9) technologies have revolutionized the way the genome is being edited in the present era [49]. Being derived from bacteria that stimulate antiviral defense systems, the application of CRISPR-Cas has also extended to the eukaryotic system for engineering crop plants against abiotic and biotic stresses [49]. CRISPR-Cas system involves Cas9, a nuclease protein, and single-guide RNA of 100 nucleotides long to cleave specific target sites, leading to the degradation of

viral DNA or RNA via forming complementary base pairing between CRISPR RNA and target RNA/DNA [49]. Various Cas proteins have been identified in plants displaying sequence-specific nuclease activity to minimize the impediment and increase the specificity of the CRISPR-Cas system for their effective exploitation [50]. The classes of Cas proteins involve six main types; classes I, III, and IV include Cas3, Cas10, and Csf1, showing high affinity to multiple effector proteins. Class II includes Cas9, whereas Class V involves Cas12a, Cpf1, and class VI includes Cas13a, c-d, which are linked to single effector proteins and are most readily used for genome editing [50].

The Cas 9 system was initially identified in *Streptococcus pyogenes*, consisting of CRISPR RNA (crRNA), trans-activating crRNA (tracrRNA), guide RNA, and Cas9 proteins. The mechanism by which the CRISPR Cas system functions in bacteria is that the bacterial genome contains a large amount of CRISPR locus. Around that CRISPR locus, several short DNA sequences known as spacer sequences are present [49]. These spacer sequences come in repetitive contact with invading nucleic acids, converting them into crRNA. When these crRNA contact invading nucleic acids, they are transcribed into tracrRNA. When these crRNA and tracrRNA bind with each other, they activate and guide Cas9 protein to the target DNA sequence to be cleaved [50]. However, an important question arises how does Cas9 protein recognize the target sequence? It recognizes due to the presence of the NGG motif around the target sequence or protospacer sequence, also called the adjacent protospacer motif (PAM) sequence [49].

Nonetheless, the Cas9 system has its limitation due to its high level of toxicity in the target organism. The toxicity could be due to the over-expression of Cas9 protein or the unavailability of homologous DNA [49, 50]. Therefore, scientists have developed a more sophisticated CRISPR-Cas system known as CRISPR from *Prevotella* and *Francisella* 1 (Cpf1), which shows up to 90% more efficiency than the Cas9 system [50, 51].

CRISPR-Cpf1 offers the following advantages over the Cas9 system (i) the Cpf-1 system generates cohesive ends whereas Cas9 generates blunt ends; therefore, the integration of new DNA segment is easier in Cpf-1 (ii) Cpf- generate shorter crRNA than Cas9. Therefore, off-targets low and (iii) Cpf-1 contain RNAase III activity for preprocessing crRNA, whereas Cas9 does not have this activity [51]. Much progress has been made in tailoring crop plants using the CRISPR-Cas system for increasing growth, yield, and survival under extreme environmental conditions [50, 51]. For instance, Kim et al. [52] used the CRISPR-Cas9 system for target editing of genes involved in abiotic stress tolerance in wheat, such as ethylene-responsive factor 3 (ERF3) and dehydration responsive element-binding

protein 2 (DREB2). Likewise, Zhang et al. [53] exploited the CRISPR-Cas9 system to improve salt stress tolerance in rice seedlings by mutating the expression of the OsRR22 gene. Their results indicated that T2 homozygous mutant lines exhibited enhanced salinity tolerance to wild-type plants.

Similarly, CRISPR-Cas9 mediated mutagenesis of the *SINPR1* gene differentially regulated the drought stress tolerance in tomato plants by positively modulating the activities of enzymatic and non-enzymatic antioxidants [50]. CRISPR-Cas9 system was used to generate mutation in the ITPK1 gene responsible for regulating inositol triphosphate synthesis in barley plants. They reported that mutant plants showed a higher level of salt tolerance than wild-type plants [54]. Recently, the CRISPR-Cas9 system was used to decipher soybean phospholipases' structural and functional properties under multiple abiotic stresses. The researchers knocked out two essential genes, viz., GmPLA-II ϵ and GmPLA-II ζ of the phospholipase pathway, and observed that few of the mutant lines showed enhanced tolerance to flooding and drought stress, and few mutants performed well under Fe limiting conditions [55]. Correspondingly, technological advancements in the CRISPR Cas system have opened a new realm for plant breeding research to overcome the limitation of conventional plant breeding technology. If used strategically, it could improve various agronomic and yield-related attributes in crop plants.

Speed breeding: the redemption

Speed breeding is the most recent and fascinating breeding technology that significantly accelerates the pace of plant growth, development, and commercialization [5, 6, 31]. It decisively improves yield potential, nutritional content, and tolerance of crop plants exposed to abiotic and biotic stresses. Speed breeding offers a compelling advantage over conventional plant breeding technology as the former symbolically reduces the crop cycle by 1 to 2 months to expedite the breeding program [5]. NASA scientists inspire the development of a speed breeding protocol for earthly plants to grow wheat plants under artificial lights [5]. For agronomic improvements, the speed breeding experimental suit has been developed for various other crop species [6]. Comprehendingly, speed breeding imitates natural day and night conditions where crop plants are subjected to artificial lights of different combinations/wavelengths and temperature conditions for 22 h [6, 7]. The extended light source and controlled temperature momentarily enhance crop photosynthetic activities and other physiological and metabolic processes, stimulating early flowering fruiting and seed development [7]. Increasing literature has contemplated

Table 1 Successful implementation of speed breeding techniques for rapid generation advancement in different crops

Crops	Speed breeding technique	Days to flowering	Generation achieved/year	Selection method	Trait enhanced	References
<i>Glycine max L.</i>	Photoperiod (incandescent lights) and temperature	21	5	Single pod descent	Production of recombinant inbred lines	[56]
<i>Arabidopsis thaliana L.</i>	Photoperiod (LED light) and temperature, growth regulators	20–26	10	-	Shortening of the generation time	[57]
<i>Arachis hypogaea L.</i>	Photoperiod (PAR light), gas heating	25	4	Single seed descent	Advancement of early generation breeding material	[58]
<i>Triticum aestivum L.</i> , <i>Hordeum vulgare L.</i>	Photoperiod (LED light) and temperature, growth regulators, embryo rescue	24–36	9	Single seed descent	Rapid production of segregating populations and pure lines	[59]
<i>Sorghum</i>	Photoperiod (LED light), temperature and immature seed germination	40–50	6	Single seed descent	Rapid development of high yielding variety	[60]
<i>Vicia Faba L.</i> , <i>Lens culinaris L.</i>	Photoperiod (LED light) and temperature, growth regulators	29–32, 31–33	7,8	Single pod descent	Early flowering and seed development	[61]
<i>Amaranthus. spp</i>	Photoperiod (LED light) and temperature	28	6	Single seed descent	Rapid production of segregating populations	[62]
<i>Pisum sativum L.</i>	Photoperiod (LED light) and growth regulators	33	5		Development of recombinant inbred lines	[63]
<i>Oryza sativa L.</i>	Photoperiod (LED light), temperature	75–85	4	Single seed descent	Rapid development of high yielding variety	[64]
<i>Trifolium subterraneum L.</i>	Photoperiod (incandescent lights) and temperature, growth regulators	32–35	6	Single seed descent	Rapid development of biparental and multi-parental populations	[65]
<i>Triticum aestivum L.</i>	Photoperiod (incandescent lights) and temperature, embryo culture	20–25	8	Single seed descent	Production of recombinant inbred lines	[66]
<i>Brassica napus L.</i>	Photoperiod (LED light) and temperature	73	4	Single seed descent	Pod shattering resistance	[5]
<i>Cajanus cajan L.</i>	Photoperiod (LED light), temperature and immature seed germination	50–56	4	Single pod descent	Development of photoperiod insensitive lines	[67]
<i>Pisum sativum L.</i>	Photoperiod (LED light), temperature, growth regulators and micro-nutrients	18–26	5	Single seed descent	Production of recombinant inbred lines	[68, 69]
<i>Triticum aestivum L.</i> , <i>Triticum durum L.</i> , <i>Hordeum vulgare L.</i> and <i>Cicer arietinum L.</i>	Photoperiod (LED light) and temperature	37	6–7	Single seed descent	Biotic stress tolerance and development of pure lines	[5, 6, 70]
<i>Glycine max L.</i>	Photoperiod (LED light)	23	5	Single seed descent	Effect of light intensity on germination rate	[71]
<i>Avena sativa L.</i>	Photoperiod (LED light), temperature and micro-nutrients	21	5	Single seed descent	Shortening of the generation time and early panicle harvest	[72]

the exemplary role of speed breeding in transforming the present-day agricultural system around the globe by shortening the duration of imperative breeding processes such as crossing, backcrossing, gene pyramiding, MAS, and developing GM crops [5–7]. Correspondingly, researchers have successfully achieved 4 to 6 generations of crop plants such as *B. napus*, *P. sativum*, *T. aestivum*, *H. vulgare*, and *C. arietinum* in one year as compared to conventional plant breeding techniques, which usually achieve two generations per year (Table 1).

Furthermore, several lines of literature have also corroborated that speed breeding can be easily blended with the MAS/GWAS program, which helped breeders develop and

select homozygous/stable genotypes for accelerating the development and release of new, improved cultivars [6, 71]. Both intensity and quality of light are the critical parameters for developing an effective speed breeding protocol. High light intensity, elevated CO₂, and adequate temperature control can tremendously enhance the photosynthesis rate, which reduces the days to flower in plants. Nonetheless, setting up a speed breeding experiment requires practical considerations of light intensities and the financial costs associated with energy utilization in the facility [71]. Additionally, temperature fluctuation also affects morphological developments in plants and thus also needs necessary adjustment for optimizing SB protocols [5, 6]. The technological

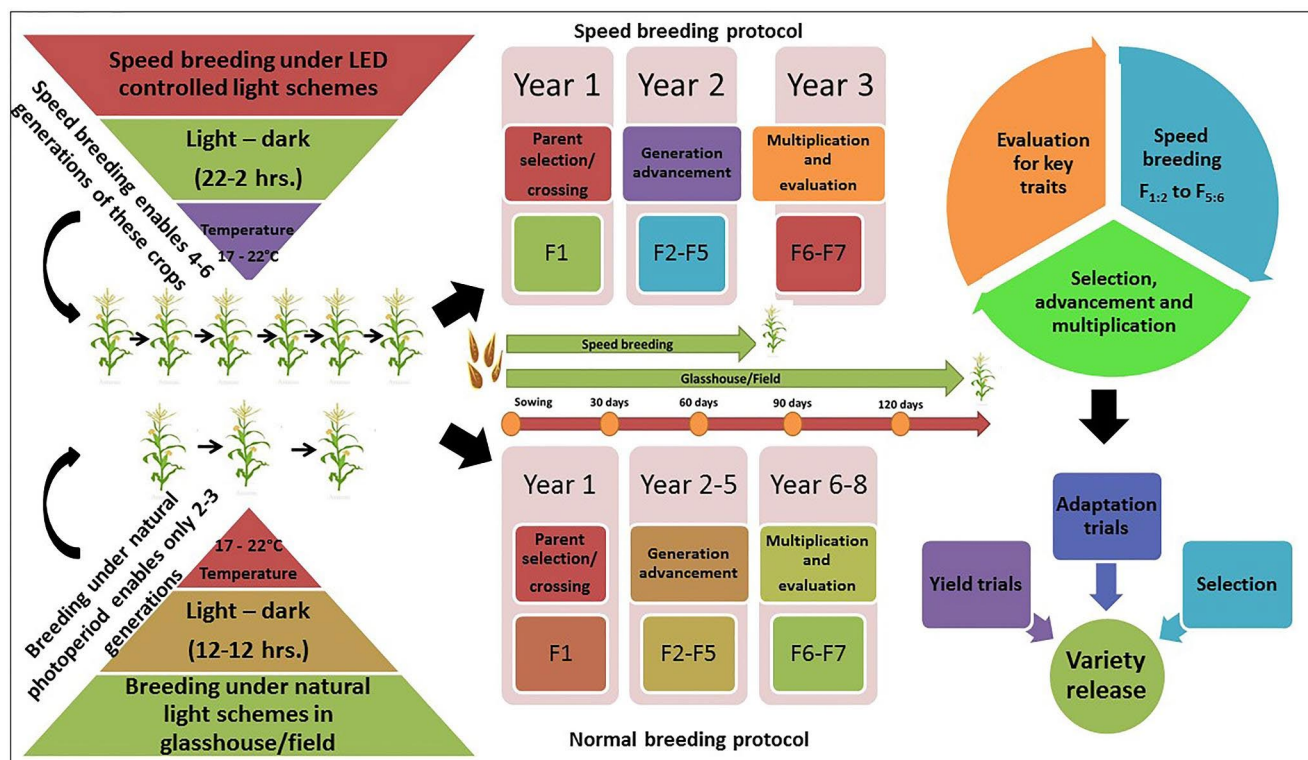


Fig. 1 An outline of speed breeding protocol and its implication for accelerating breeding cycles for improving growth and yield as compared to the conventional breeding approach under regular photoperiod

advancements have significantly impacted the implementation of speed breeding experiments by providing light systems/sensors that are automatically adjusted as per need/protocol devised at low cost [71]. The new LED lighting systems have offered plant scientists to precisely regulate the duration and intensity of light to effectively manipulate photosynthesis, growth, and development of crop plants [71, 73]. This new LED, technology-based speed breeding protocol has effectively optimized flowering and suppressed lupin and soybean plants [71, 73].

Additionally, researchers have also well confirmed that harnessing the light of a specific wavelength can dynamically regulate phytohormone activity; for example, the light of far-red wavelengths promotes early flowering, whereas light of blue wavelength suppresses stem elongation and plant height, as observed in rice plants grown under speed breeding facility [74]. Likewise, the actual implementation of appropriate light intensity successfully regulated the activity of plant growth regulators in pea plants grown under the speed breeding protocol [74]. However, increasing light intensities for a prolonged period have significantly affected plant growth and immunity trade-off. Therefore, consistent efforts are required to improve the efficiency of speed breeding protocols by including more plant species in the speed breeding operations. An illustration of establishing a speed breeding facility for crop improvement is depicted in Fig. 1.

Establishing speed breeding protocols: a case study

Speed breeding programs have been extensively developed to accelerate genetic gains in various crops cultivated under glasshouse/indoor conditions retrofitted with sophisticated soil moisture, temperature, and photoperiod analytical devices [45, 46]. Initially, Hickey et al. [75] used controlled environmental conditions to improve seed dormancy in fixed wheat lines grown in extended photoperiods described by NASA scientists [58]. They observed that extended photoperiod (low-pressure sodium lamps) and controlled temperature accelerated wheat plants' seed germination rate to maturity. They further concluded that the controlled environmental conditions could be effectively used in the breeding program for selecting superior genotypes in off-season conditions for developing stress-tolerant cultivars [75]. O'Connor et al. [58] exploited speed breeding technology to accelerate the peanut breeding program a few years later. They used photosynthetically active region (PAR) lamps to expedite the growth of peanut plants by growing them under extended photoperiod for 24 h under controlled temperature conditions. Their study also confirmed the reliability of speed breeding technology over conventional breeding to quickly develop improved cultivars. Concomitantly, Watson et al. [5] developed a speed breeding protocol to accelerate

several crop generation times. They used LED lights of PAR under controlled environmental conditions. They obtained six generations/year for wheat, barley, pea, and chickpea and four generations/year for canola plants which can be further exploited in the crop improvement programs for developing disease-resistant/high-yielding crops.

In their study, Ghosh et al. [6] developed and standardized speed breeding protocol for wheat, barley, oat pea, chickpea, and various Brassica species plants. Their study has provided an in-depth understanding of practicing speed breeding experimental suits under glasshouse conditions to generate large populations using a single seed descent method. They demonstrated their speed breeding experiment using bench-top-cabinet and under LED supplemented glasshouses. They accelerated the generations of the crops as mentioned above by 4–6 generations/year under controlled conditions of both soil moisture and temperature [6, 70]. Jahne et al. [71] developed a speed breeding protocol for short-day crops like *Glycine max*, *Oryza sativa*, and *Amaranthus* spp. They exploited LED lights of different wavelength-specific for each crop for developing a large number of cultivars with a high rate of leaf appearances and low leaf numbers by adjusting photoperiod to 10 h and obtaining five generations/year. Likewise, Cazzola et al. [68] tested three different methods to identify the best rapid generation technologies for commercial varieties of pea plants. Their study cultivated pea plants under in-vitro conditions that ultimately failed to accelerate the generation time—a combination of an in-vitro-in-vivo system that shortened the generation cycle of crops at a low rate and intermediate efficiency. However, a successful result was obtained when they cultivated the plants under a hydroponic system with 22-h photoperiod using T5 fluorescent tubes under controlled temperature conditions. They cost-effectively get five generations/year [68]. Researchers have also confirmed that speed breeding protocol can accelerate panicle harvest in oat plants if practiced sophisticatedly. Their study evaluated eight genetically divergent oat genotypes under speed breeding conditions (22 h photoperiod). They observed a compelling reduction in germination and flowering time in oat plants compatible with the single seed descent method [72]. All the studies mentioned above have firmly concluded that practical and systematic application of speed breeding protocol can have tremendously accelerated leaf appearance, anthesis, and maturity leading to increase grain yield and seed number without compromising plant health.

An asset at low expense: opportunity and challenges

Speed breeding techniques are extensively used to accelerate conventional plant breeding programs. Nonetheless, the technology can negatively impact the growth and productivity of crops and requires expertise for its successful implementation [5]. Furthermore, several researchers have confirmed that the SB protocols developed for various crop plants often require prolonged photoperiod, which, if not adequately controlled concerning temperature, moisture, and nutrients, results in chlorosis, necrosis, stunted growth, and yield loss [58, 68, 71]. Moreover, studies have also indicated that a decrease in growth and productivity of certain crop plants under continuous light conditions could be due to the enhanced production of starch, abscisic acid, and ethylene which ultimately lead to photooxidative damage [71]. One of the significant constraints for the successful implementation of speed breeding protocol in the public sector is the lack of adequate training and state-of-the-art facility for the regular farmers/plant breeder, especially in developing countries [5].

Additionally, the public sector plant breeders are also negatively affected by the un-even government policies/programs that do not provide sufficient facilities to conduct speed breeding. As a result, several plant breeding researchers migrate to private seed companies to give better remuneration [72]. Besides, the development of speed breeding platforms requires automated infrastructure equipped with essential tools to carry streamline operations such as regulating temperature/light, soil moisture level, and water and electric supplies [68].

Due to the lack of sufficient funding from the government, it is not economically feasible for many of the public sectors to develop such a state-of-art facility for commercializing speed breeding technology for farmers [6, 71]. Furthermore, environmental factors in indoor growing facilities, especially temperature and light, require a continuous flow of water and electricity, which is another problem associated with the successful speed breeding protocol [5, 6]. Several researchers have corroborated that efficient regulation of temperature, moisture, and light requires consistent and reliable electricity and water supply source that significantly affects public sector breeding programs [68, 70]. Recent data have corroborated that the total cost incurred for regulating the continuous supply of electricity and water flow is more than the actual cost required for establishing a speed breeding facility [72]. Correspondingly, the cost of electricity in speed breeding facilities may rise exponentially during extreme winter or in scorching summer, which may impose additional weight on the total cost of running speed breeding facilities smoothly.

Nonetheless, efforts are to minimize the input cost by developing specialized equipment that can use sustainable solar power to supply a continuous flow of water and electricity to the facility. Conversely, researchers have built a speed breeding infrastructure with a fully automated system for land preparation, fertilization, and irrigation based on solar power [71]. They have also developed a speed breeding ‘toolkit’ that can establish a small indoor facility retrofitted with LED light and temperature controls powered by the solar system and equipped with backup batteries to provide an uninterrupted power supply at night [71]. In addition, several private sector organizations are now collaborating with public sector breeders to develop efficient speed breeding protocols for various crops by providing necessary facilities that are cost-efficient and knowledgeable in terms of learning [44, 49]. Therefore, the development of efficient speed breeding protocols and infrastructure is of utmost importance for avoiding the negative effect of prolonged photoperiod on the growth and development of plants.

Assimilating traditional breeding with speed breeding: the future

Integration of speed breeding with the classical approach requires extensive planning and a good selection of candidate cultivars with higher genetic gain to accelerate the breeding program for generating high-yielding/tolerant cultivars [71]. The choice of cultivars/inbred lines with higher genetic growth will allow the breeder to accelerate crop improvement programs and enable the early selection of cultivars with the superior phenotype [5, 6]. Further, the genomic selection can also predict prominent individuals by incorporating the MAS and GWAS approach to accelerate the inbreeding process and subsequent commercialization in the farmer field [73, 74]. Until the 90s, phenotyping followed by genotyping was extremely expensive and low throughput, which has intimidated the crop improvement program to a greater extent. Later, the next-generation sequencing technology transformed the genomic selection process. Its potential application in plant breeding programs opened a new door for improving cultivar crop improvement by empowering MAS at a low cost [76]. This NGS-based cost-efficient approach significantly enhanced the genomic selection process, which led to the identification of several essential QTLs/genes by generating a QTL/linkage map through the forward breeding approach [72, 76]. However, despite these technological breakthroughs, time is still a major constraint for their successful implementation to generate superior allelic combinations through hybridization experiments and genetic recombination for subsequent selection, varietal development, and commercialization

[77]. Therefore, to overcome this limitation, researchers have diverted their attention to complementing NGS/molecular breeding approach with speed breeding technology to rapidly accelerate the crop generations to hasten the varietal developmental process [76, 77].

Present-day speed breeding technology enables plant breeders to accelerate crop improvement programs precisely and straightforwardly, thereby generating plants faster and cheaper [77]. Single seed descent is a powerful way of implementing speed breeding protocol to any crop plant to generate a fixed population at a more incredible speed that is much cheaper than generating double haploids [78]. Furthermore, the generated SSD populations will offer higher genetic gain, which will ultimately lead to the development of improved cultivars upon their subsequent utilization in the breeding program [6, 7]. Researchers have corroborated that the speed breeding protocol is beneficial for rapid introgression of the gene of interest into superior cultivars by implementing MAS and GWAS approaches [72, 76]. A large body of literature has also confirmed that practicing speed breeding protocol with classical breeding approaches will rapidly generate recombinant inbred lines (RILs) or near-isogenic lines (NILs) to accelerate the identification of QTLs for a specific trait [77, 78].

Conversely, the speed breeding suit can also revamp the accuracy and efficiency of genome editing technology by rapidly accelerating the generation cycle after the successful transfer of Cas9 construct in plants [79]. Integration of speed breeding with classical breeding approaches has been tested and confirmed in various crop plants like chickpea, pea, lentils, faba bean, and pigeon pea [67, 68, 70, 80, 81]. These researchers, in their study, used a speed breeding facility to reduce the generation cycle of plants by growing them under extended (20–22 h) photoperiod and adequate temperature conditions. They achieved 5–6 generations/year of the individual plants, which were subsequently analyzed by their respective high yielding/disease-resistant traits through a breeding program. Nonetheless, successful integration of both approaches requires hands-on training, pre-breeding research, an appropriate breeding approach, and the, most important diverse germplasm for the respective trait.

Artificial intelligence (AI) in plant breeding: accelerating the speed

Technological advancements in plant “OMICS” research have led to the excessive production of complex datasets. Deciphering the exact meaning of these complex datasets is of paramount importance for characterizing crop plants for a specific trait [10]. Concurrently, NGS technology has

significantly accelerated the availability of the complete genome sequence of desired plant species, leading to the production of large datasets [13]. Furthermore, in conjunction with transcriptomics and proteomics analysis, MAS and GWAS approach also comprehensively study plant genotypes and phenotypes. Therefore, this section offers significant insight into machine learning/artificial intelligence in plant breeding and improvement. In addition, the review also highlights recent progress made in the implementation of AI in crop breeding programs to analyze different phenotypic, biochemical, and yield-related traits resulting in the identification of superior genotypes.

How plant breeding can benefit from AI

The application of Next-Gen AI in plant breeding requires intelligent and efficient mining of breeding datasets by employing relevant models and definitive algorithms [10]. Researchers are constantly working to innovate and improve the efficiency of AI to enable high definition image recognition for analyzing complex data sets and therefore has become a prime target for accelerating the crop improvement process [10, 13]. AI, such as neural networks (NN) and deep learning (DL), are currently being exploited to improve the efficiency and accuracy of multi-omics data [82]. The mechanisms by which these two AI functions are often opaque involve multiple nonlinear hierarchical methods to build nodes for easy classification of datasets mimicking brain neurons [82, 83]. Conversely, plant breeders are conceptualizing a Next-Gen AI that will analyze breeding values and provide a comprehensive analysis of complex traits under changing environmental conditions [83]. Furthermore, AI will also be learned and improved iteratively to improve data mining accuracy and efficiency to predict better the factors underlying disease resistance/agronomic traits, thereby accelerating breeding programs. Extensive hybridization and rigorous selection parameters have significantly altered the phenotypic plasticity of crop plants [82]. In addition, phenotypic plasticity of economically important traits is also substantially reduced upon genotypic variation occurring among the genotypes as a direct consequence of their interaction with the environment [83]. Therefore, current breeding programs aim extensively to improve the abiotic stress tolerance of crop plants by bridging the genotype-phenotype gap that has occurred due to alteration in the phenotype plasticity [83, 84].

Researchers are now integrating genotypic and environmental data and the observed phenotype to strengthen the agronomic abiotic stress breeding program to identify the best genotype with critical agronomic traits [84]. As these are complex traits governed by more than genes, a

sophisticated monitoring system should record tiny changes/alterations occurring in the plants (Table 2). To overcome this hurdle, scientists have devised an AI-based physiological gravimetric system that can measure the slightest change occurring in plants concerning soil and atmosphere called the soil-plant-atmosphere continuum (SPAC) [10, 13]. This system offers plant scientists ease of phenotyping the slightest variations among the complex traits at different plant growth and development [10, 84]. In addition, constant and rigorous monitoring of these phenotypic data and their subsequent analysis by employing the Next-Gen AI approach can facilitate the identification of stress-responsive QTLs or QTLs related to important agronomic traits [82, 83]. A field phenomics suite has also been devised to accelerate breeding programs by providing high-resolution images for easy discrimination of better-performing genotypes in large populations [83]. The field phenomics suite incorporates a machine learning approach to capture high-throughput phenotypic data relevant to breeding programs using unmanned aerial vehicles (UAV) and ground-based equipment. This UAV and ground-based equipment are fitted with high-resolution cameras and sensors to generate comprehensive data from thousands of field-grown plants [84]. The data generated are then analyzed by the AI or specific software that enables breeders to identify superior genotypes displaying the best agronomic/disease-resistant traits (Fig. 2). This advanced phenotypic tool can be combined with MAS and GWAS approaches to dissect plants at the molecular level to identify novel genes/QTLs [84, 85].

Significant progress has been made in field phenomics implemented recently in *Glycine max* to study stress-responsive traits [10]. However, the barrier still exists to linking phenomic data generated with the help of AI to the genotype, leading to identifying genotype with higher genetic gain. Furthermore, harnessing complex traits and their subsequent correlation with the environmental variables is of utmost requirement to remove the above barrier is also a significant challenge. Therefore, future research directed at the generation of next-gen AI is an essential prerequisite to bridging the phenotype-genotype gap to facilitate crop improvement programs. An overview of how AI and speed breeding can lead to improved cultivar development within a short period is depicted in Fig. 2.

Studying biochemical phenotype through AI

Technological advancements have made recording genotypic and phenotypic variation in plants more sophisticated and precise, leading to easy extraction of valuable information within the complex datasets [84, 85, 104]. Concurrently, researchers are also on the verge of using AI to analyze

Table 2 Successful implementation of artificial intelligence/machine learning models in plant breeding studies

Crops	Machine learning technique	Algorithm used	Trait studied	Predictable function	References
<i>Glycine max L.</i>	Best linear unbiased prediction (BLUP), Neural networks (NNs), Kernel methods	Multilayer perceptron (MLP), support vector machine (SVM), ensemble-stacking (E-S) and random forest (RF), Stochastic gradient descent (SGD)	Pre-harvest, Yield performance	Selection of high yielding cultivars	[86, 87]
<i>Glycine max L.</i>	Convolutional Neural Networks (CNNs)	Batch Normalization (BN)	Seed per pod estimation	Prediction of seed characters under changing environment	[88]
<i>Phaseolus vulgaris L.</i>	Artificial neural networks (ANNs)	Mean square deviation (MSD) and mean square of residue (MSR)	Average yield	High adaptability and phenotypic stability under stress conditions	[89]
<i>Zea mays L., Triticum aestivum L.</i>	Neural networks (NNs), Deep NNs, CNNs	Generalized matrix factorization (GMF). MLP, SVM	Yield performance, salt stress tolerance	Identification of best performing parental populations, enhanced genomic selection for stress resistance	[90–94]
<i>Brassica rapa L.</i>	Artificial neural networks (ANNs)	MLP	Yield performance	Prediction of seed setting	[94]
<i>Abelmoschus esculentus L.</i>	Deep neural networks (DNNs)	Image processing (IP)	Yield performance under salt stress	Tolerance to salt stress	[95]
<i>Carum copticum L., Trachyspermum ammi (L.) Sprague</i>	Artificial neural networks (ANNs)	Multiple regression analysis	Oil content, physical properties of callus	Prediction of secondary metabolite production and somatic embryos	[96, 97]
<i>Oryza sativa L.</i>	Deep CNNs	Video detection metrics	Pest and disease resistance	Tolerance to biotic stress	[98]
<i>Lycopersicon esculentum L.</i>	Artificial neural networks (ANNs)	IP, SVM	Callus regeneration and late blight infection	Induction of callus and disease resistance	[97]
<i>Arabidopsis thaliana</i>	Deep learning	SVM, Naive Bayes	Stress tolerance	Prediction of miRNA expression for enhancing stress tolerance	[99]
<i>Daucus carota L.</i>	Random forest	-	Yield potential	Precision agriculture for yield enhancement	[100]
<i>Solanum tuberosum L.</i>	Artificial neural networks (ANNs)	IP	Agronomic traits	Identification of superior genotypes	[101]
<i>Carthamus tinctorius L., Sesamum indicum L.</i>	Artificial neural networks (ANNs)	Multiple regression analysis	Seed yield, oil content	Identification of superior genotypes	[102]
<i>Pennisetum glaucum</i>	Deep CNNs	IP, SVM	Disease identification	Identification of disease resistant genotypes	[103]

complex biochemical pathway data sets to help them decipher the real-time changes occurring at the molecular level under abiotic stress conditions [85]. Several biochemical/metabolic changes are governed by discrete changes occurring at the genomics (gene expression), proteomics (protein distribution), metabolomics (expression of metabolites), and epigenomics (DNA/histone modification) level. However, technological advancements have developed sophisticated technology/instruments that have greatly facilitated the measurements of critical metabolic traits at the OMICS level [82, 83]. The data generated by these instruments, such as Next Generation Sequencing (NGS), Chromatin Immunoprecipitation (ChIP), Matrix-assisted laser desorption and ionization-Time of Flight-Mass Spectrophotometry (MALDI-TOF-MS), etc. are so vast and complex that it

would take a lot of time and effort to decipher and conclude the final results [84]. Therefore, researchers have started exploiting AI to analyze large/complex datasets due to a lack of technological knowledge and understanding to analyze complex data sets for accurate interpretation of given biochemical traits [84].

Many studies have shown the potential application of AI to interpret biochemical data to enhance the understanding of plant stress biology. For example, the application of AI successfully predicted genomic crossovers occurring in the maternal and parental maize plants and helped predict probable genomic regions displaying high mutation rates [105]. Likewise, researchers used AI to classify and characterize genomic regions by analyzing the DNA methylation pattern of maize plants grown under stress conditions into

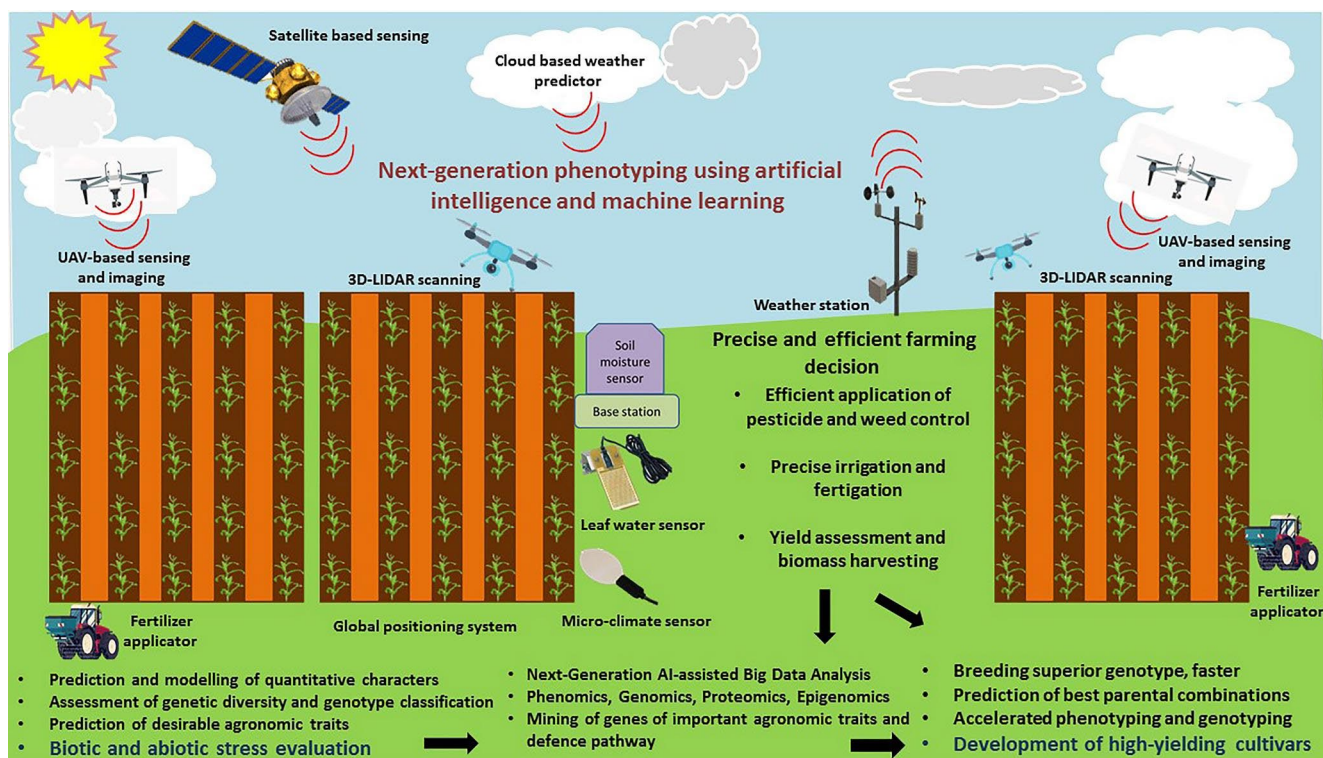


Fig. 2 An overview of the potential application of artificial intelligence in augmenting plant breeding technology for easy, precise, and early prediction of genotypes/parental combinations for varietal development

functional genes and pseudogenes [14]. Similarly, Uygun et al. [106] also employed AI to predict gene promoters and cis-regulatory elements in Arabidopsis and maize plants by studying the expression pattern of essential genes. Several studies have also affirmed the usefulness of AI in learning plant metabolic regulatory networks by deciphering tissue-specific changes occurring in the biosynthetic genes, such as nitrogen use efficiency, starch biosynthesis, and other secondary metabolites in Arabidopsis and rice [98, 107]. Correspondingly, Meena et al. [108] also exploited AI to stimulate the production of biofuels by enhancing biomass production using plant species and algal bloom, thus highlighting the vital contribution of AI for managing bioenergy production.

A large body of literature has well indicated the versatile application of AI in studying single-cell RNA sequencing, DNA methylation, and post-translational modifications, which can provide testable insight into a specific region of the genome or candidate gene governing secondary metabolite production under stress conditions [14]. Conversely, researchers have begun testing AI to predict complex genomic traits such as photosynthesis, hormonal changes, and yield [15]. In addition, the application of AI in breeding programs could also help identify QTLs by analyzing a complex region of the genome associated with a specific trait via facilitating MAS and GWAS [17]. Furthermore, AI in breeding could provide an in-depth understanding of

genetic architecture, revealing the position/localization of essential genes governing economically crucial traits. The exploitation of AI could also integrate genomics, transcriptomics, proteomics, and metabolomics data to analyze macroscopic biochemical features controlling plant growth and development in response to environmental stimuli.

Integrating phenomics with genomics for smart breeding

One of the significant limitations of the classical breeding approach is its inability to provide substantial insight into the genomic architecture of plant species due to the lack of correlation between genotype and phenotype [84]. Speed breeding coupled with Next-Gen AI can significantly facilitate understanding of genomic architecture by linking phenotype with genome by generating genomic selection models for the particular crop species. These genomic selection models are prediction-based models developed by estimating marker-trait association via genetic markers followed by extensive phenotyping of test populations [83]. These models often reflect important genomic regions or loci present in a given haplotype and regulate the trait of interest. Most current breeding programs focused on developing climate-smart crops exploit genomic selection models to analyze

genetic components such as SNPs and InDels associated with specific characteristics [84]. The models developed by analyzing SNP and InDels are exploited as potential tools for a breeding population that helps plant breeders predict their phenotype before reaching maturity [82].

Furthermore, the data generated by these models are then analyzed by AI to predict heritable components accurately, decreasing the breeding cycle and increasing plant yield [109]. Most genomic selection models are based on the correlation between genotype and phenotype data generated by genetic/linkage disequilibrium mapping development, which is challenging and prone to error [109, 110]. Therefore, scientists developed neural networks amalgamating various AI-based algorithms to improve the accuracy of data interpretation of genomic selection models [82, 83]. These neural networks are computational models displaying output as neuron-like nodes linking and analyzing information by communicating with refined production [84].

These neural networks have emerged as a successor for genomic selection models. Still, for most plant species, it has failed to analyze complex data sets and, concomitantly, has been unable to improve the accuracy [88]. The fall of neural networks helped realize that the plant scientists' fully automated AI is insufficient to analyze big data; humans' involvement is also critical to improving AI-based models' accuracy [88, 110]. The human touch is essential because, from the breeder's perspective, they can manipulate the complex sets of OMICS data as per the goal of a breeding program in a much better way than AI alone [88, 91]. Therefore, researchers from the plant science community are developing and testing various AI-based algorithms capable of analyzing a large variety of data that can demarcate specific features as per the need of the experimental program. Several transfer learning approaches circumventing published data into machine learning format have shown promising results [91].

Additionally, a new deep transfer learning approach called ARIGAN (Arabidopsis rosette image generator AN) has been successfully used to generate synthetic rose-shaped plants by integrating in-silico data with field-based data using generative adversarial networks [111]. Furthermore, ARIGAN was also exploited to analyze complex multi-omics data, which successfully rendered extensive gene expression data to provide a glimpse of transcriptional regulation in a predictive model [111, 112]. However, research is still lagging regarding the black-box nature of AI models and their potential application in plant breeding to develop climate-smart crops. Therefore, efforts are required to create a more sophisticated Next-Gen AI-based system capable of screening a sizeable multi-omics data set that will open a new realm for plant breeders, enabling them to envision a hunger-free world.

Conclusion and future directions

In recent decades, plant breeders have stumbled to develop and breed high-yielding cultivars that can withstand abiotic and biotic stresses. Noteworthy, speed breeding has emerged as a potential alternative for reducing time, space, and cost to develop, release, and commercialize new/improved cultivars with improved accuracy and predictability. Plant growth and developmental conditions are the critical factors that govern plant performance under changing environmental conditions; speed breeding protocol technically mimics the natural environment artificially (light and temperature) to accelerate plant growth. Furthermore, molecular breeding techniques like MAS and GWAS can also be successfully integrated with speed breeding protocol to identify genes/QTLs underlying biotic/abiotic stress tolerance, nutritional qualities, and high yield. Application of Next-Gen AI has opened a new realm for speed breeding and agriculture that will enable decision making and handling of big OMICS data with great precision, which will help get novel insight into plant functions under climate extremes. However, its application in developing countries is still lagging due to a lack of trained plant breeders, infrastructure facilities, and government support at the financial level to sustain speed breeding protocol for crop improvements. Implementation of speed breeding requires extensive planning and a continuous supply of electricity and water to maintain adequate light and temperature in the facility. Therefore, efforts should be diverted toward developing public and private ventures to facilitate capacity building, technology transfer, and finance speed breeding coupled with AI-driven research to facilitate crop improvement programs. These public-private partnerships will also help create a framework for successfully implementing AI-augmented plant breeding research and innovation for the betterment of humans, animals, and the environment.

Authors' contribution KKR conceived the idea, wrote the manuscript, prepared all figures, and edited and prepared the final draft of the manuscript.

Funding and acknowledgement The author declares that no funds, grants, or other support were received during the preparation of this manuscript.

Data Availability All data generated or analyzed during this study are included in this published article.

Declarations

Competing interests There is no conflict of interest.

Ethical approval: Not applicable.

Informed consent: Not applicable.

References

- Wang J, Vanga SK, Saxena R, Orsat V, Raghavan V (2018) Effect of climate change on the yield of cereal crops: a review. *Climate* 6(2):41. <https://doi.org/10.3390/cli6020041>
- Hasegawa T, Fujimori S, Havlik P, Valin H, Bodirsky BL, Doelman JC, Fellmann T, Kyle P, Koopman JF, Lotze-Campen H, Mason, Croz D (2018) Risk of increased food insecurity under stringent global climate change mitigation policy. *Nat Clim Change* 8(8):699–703. <https://doi.org/10.1038/s41558-018-0230-x>
- Ray DK, West PC, Clark M, Gerber JS, Prishchepov AV, Chatterjee S (2019) Climate change has likely already affected global food production. *PLoS ONE* 14(5):e0217148. <https://doi.org/10.1371/journal.pone.0217148>
- Ukhurebor KE, Singh KR, Nayak V, Gladys UE (2021) Influence of the SARS-CoV-2 pandemic: a review from the climate change perspective. *Environ Sci Process Imp.* <https://doi.org/10.1039/D1EM00154J>
- Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey MD, Hatta MAM, Hinchliffe A, Steed A, Reynolds D, Adamski NM (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. *Nat Plants* 4(1):23–29. <https://doi.org/10.1038/s41477-017-0083-8>
- Ghosh S, Watson A, Gonzalez-Navarro OE et al (2018) Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. *Nat Protoc* 13(12):2944–2963. <https://doi.org/10.1038/s41596-018-0072-z>
- Ahmar S, Gill RA, Jung KH, Faheem A, Qasim MU, Mubeen M, Zhou W (2020) Conventional and molecular techniques from simple breeding to speed breeding in crop plants: recent advances and future outlook. *Int J Mol Sci* 21(7):2590. <https://doi.org/10.3390/ijms21072590>
- Al-Khayri JM, Jain SM, Johnson DV (2015) Advances in plant breeding strategies: breeding, biotechnology and molecular tools. Springer Int Publishing. <https://doi.org/10.1007/978-3-319-22521-0>
- Qaim M (2020) Role of new plant breeding technologies for food security and sustainable agricultural development. *Appl Econ Perspect Policy* 42(2):129–150. <https://doi.org/10.1002/aep.13044>
- Harfouche AL, Jacobson DA, Kainer D, Romero JC, Harfouche AH, Mugnozza GS, Moshelion M, Tuskan GA, Keurentjes JJ, Altman A (2019) Accelerating climate resilient plant breeding by applying next-generation artificial intelligence. *Trends Biotechnol* 37(11):1217–1235. <https://doi.org/10.1016/j.tibtech.2019.05.007>
- Razzaq A, Kaur P, Akhter N, Wani SH, Saleem F (2021) Next-generation breeding strategies for climate-ready crops. *Front Plant Sci* 12. <https://doi.org/10.3389/fpls.2021.620420>
- Leal Filho W, Wall T, Mucova SAR, Nagy GJ, Balogun AL, Luetz JM, Ng AW, Kovaleva M, Azam FMS, Alves F, Guevara Z (2022) Deploying artificial intelligence for climate change adaptation. *Technol Forecast Soc Change* 180:121662. <https://doi.org/10.1016/j.techfore.2022.121662>
- Godwin ID, Rutkoski J, Varshney RK, Hickey LT (2019) Technological perspectives for plant breeding. *Theor Appl Genet* 132(3):555–557. <https://doi.org/10.1007/s00122-019-03321-4>
- Sartor RC, Noshay J, Springer NM, Briggs SP (2019) Identification of the expressome by machine learning on omics data. *Proc Natl Acad Sci USA* 116(36):18119–18125. <https://doi.org/10.1073/pnas.1813645116>
- Rajasundaram D, Selbig J (2016) More effort—more results: recent advances in integrative ‘omics’ data analysis. *Curr Opin Plant Biol* 30:57–61. <https://doi.org/10.1016/j.pbi.2015.12.010>
- Thudi M, Palakurthi R, Schnable JC, Chitkineni A, Dreisigacker S, Mace E, Srivastava RK, Satyavathi CT, Odeny D, Tiwari VK, Lam HM (2021) Genomic resources in plant breeding for sustainable agriculture. *J Plant Physiol* 257:153351. <https://doi.org/10.1016/j.jplph.2020.153351>
- Gupta PK, Kumar J, Mir RR, Kumar A (2010) Marker-assisted selection as a component of conventional plant breeding. *Plant Breed Rev* 33:145. <https://doi.org/10.1002/9780470535486.ch4>
- Rana M, Sood A, Hussain W, Kaldate R, Sharma TR, Gill RK, Kumar S, Singh S (2019) Gene pyramiding and multiple character breeding. In: *Lentils*, Academic Press, pp 83–124 <https://doi.org/10.1016/B978-0-12-818299-4.00006-3>
- Dormatey R, Sun C, Ali K, Coulter JA, Bi Z, Bai J (2020) Gene pyramiding for sustainable Crop improvement against biotic and abiotic stresses. *Agronomy* 10(9):1255. <https://doi.org/10.3390/agronomy10091255>
- Crews TE, Cattani DJ (2018) Strategies, advances, and challenges in breeding perennial grain crops. *Sustainability* 10(7):2192. <https://doi.org/10.3390/su10072192>
- Ashkani S, Rafii MY, Shabanimofrad M, Miah G, Sahebi M, Azizi P, Tanweer FA, Akhtar MS, Nasehi A (2015) Molecular breeding strategy and challenges towards improvement of blast disease resistance in rice crop. *Front Plant Sci* 6:886. <https://doi.org/10.3389/fpls.2015.00886>
- Wang Y, Xu J, Deng D, Ding H, Bian Y, Yin Z, Wu Y, Zhou B, Zhao Y (2016) A comprehensive meta-analysis of plant morphology, yield, stay-green, and virus disease resistance QTL in maize (*Zea mays* L.). *Planta* 243(2):459–471. <https://doi.org/10.1007/s00425-015-2419-9>
- Bhadauria V, Ramsay L, Bett KE, Banniza S (2017) QTL mapping reveals genetic determinants of fungal disease resistance in the wild lentil species *Lens ervoides*. *Sci Rep* 7(1):1–9. <https://doi.org/10.1038/s41598-017-03463-9>
- Nzuki I, Katari MS, Bredeson JV, Masumba E, Kapinga F, Salum K, Mkamilo GS, Shah T, Lyons JB, Rokhsar DS, Rounsley S (2017) QTL mapping for pest and disease resistance in cassava and coincidence of some QTL with introgression regions derived from *Manihot glaziovii*. *Front Plant Sci* 8:1168. <https://doi.org/10.3389/fpls.2017.01168>
- Bhatta M, Morgounov A, Belamkar V, Baenziger PS (2018) Genome-wide association study reveals novel genomic regions for grain yield and yield-related traits in drought-stressed synthetic hexaploid wheat. *Int J Mol Sci* 19(10):3011. <https://doi.org/10.3390/ijms19103011>
- Gupta PK, Kulwal PL, Jaiswal V (2019) Association mapping in plants in the post-GWAS genomics era. *Adv Genet* 104:75–154. <https://doi.org/10.1016/bs.adgen.2018.12.001>
- Hou L, Chen W, Zhang Z, Pang X, Li Y (2020) Genome-wide association studies of fruit quality traits in jujube germplasm collections using genotyping-by-sequencing. *Plant Genome* 13(3):e20036. <https://doi.org/10.1002/tpg2.20036>
- Xu P, Guo Q, Meng S, Zhang X, Xu Z, Guo W, Shen X (2021) Genome-wide association analysis reveals genetic variations and candidate genes associated with salt tolerance related traits in *Gossypium hirsutum*. *BMC Genom* 22(1):1–14. <https://doi.org/10.1186/s12864-020-07321-3>
- Varshney RK, Bohra A, Yu J, Graner A, Zhang Q, Sorrells ME (2021) Designing future crops: genomics-assisted breeding comes of age. *Trends Plant Sci* 26(6):631–649. <https://doi.org/10.1016/j.tplants.2021.03.010>
- Hickey LT, Hafeez N, Robinson A, Jackson H, Leal-Bertioli SA, Tester S, Gao M, Godwin C, Hayes ID, Wulff BJ BB (2019)

- Breeding crops to feed 10 billion. *Nat Biotechnol* 37(7):744–754. <https://doi.org/10.1038/s41587-019-0152-9>
31. Varshney RK, Bohra A, Roorkiwal M, Barmukh R, Cowling WA, Chitkineni A, Lam HM, Hickey LT, Croser JS, Bayer PE, Edwards D (2021) Fast-forward breeding for a food-secure world. *Trends Genet* 37(12):1124–1136. <https://doi.org/10.1016/j.tig.2021.08.002>
 32. Adlak T, Tiwari S, Tripathi MK, Gupta N, Sahu VK, Bhawar P, Kandalkar VS (2019) Biotechnology: An advanced tool for crop improvement. *Curr J Appl Sci Technol* 33(1):1–11. <https://doi.org/10.9734/CJAST/2019/v33i130081>
 33. Raina A, Laskar RA, Khurshed S, Amin R, Tantray YR, Parveen K, Khan S (2016) Role of mutation breeding in crop improvement-past, present and future. *Asian J Agric Res* 2(2):1–13. <https://doi.org/10.9734/ARJA/2016/29334>
 34. Chaudhary J, Alisha A, Bhatt V, Chandanshive S, Kumar N, Mir Z, Kumar A, Yadav SK, Shivaraj SM, Sonah H, Deshmukh R (2019) Mutation breeding in tomato: advances, applicability and challenges. *Plants* 8(5):128. <https://doi.org/10.3390/plants8050128>
 35. Bado S, Forster BP, Nielsen S, Ali AM, Lagoda PJ, Till BJ, Laimer M (2015) Plant mutation breeding: current progress and future assessment. *Plant Breed Rev* 39:23–88
 36. Jayakodi M, Padmarasu S, Haberer G, Bonthala VS, Gundlach H, Monat C, Lux T, Kamal N, Lang D, Himmelbach A, Ens J (2020) The barley pan-genome reveals the hidden legacy of mutation breeding. *Nature* 588(7837):284–289. <https://doi.org/10.1038/s41586-020-2947-8>
 37. Khahani B, Tavakol E, Shariati V, Rossini L (2021) Meta-QTL and ortho-MQTL analyses identified genomic regions controlling rice yield, yield-related traits and root architecture under water deficit conditions. *Sci Rep* 11(1):1–18. <https://doi.org/10.1038/s41598-021-86259-2>
 38. Soriano JM, Colasuonno P, Marcotuli I, Gadaleta A (2021) Meta-QTL analysis and identification of candidate genes for quality, abiotic and biotic stress in durum wheat. *Sci Rep* 11(1):1–15. <https://doi.org/10.1038/s41598-021-91446-2>
 39. Dias MI, Sousa MJ, Alves RC, Ferreira IC (2016) Exploring plant tissue culture to improve the production of phenolic compounds: A review. *Ind Crops Prod* 82:9–22. <https://doi.org/10.1016/j.indcrop.2015.12.016>
 40. Cardi T (2016) Cisgenesis and genome editing: Combining concepts and efforts for a smarter use of genetic resources in crop breeding. *Plant Breed* 135(2):139–147. <https://doi.org/10.1111/pbr.12345>
 41. Rosa C, Kuo YW, Wuriyangan H, Falk BW (2018) RNA interference mechanisms and applications in plant pathology. *Annu Rev Phytopathol* 56:581–610. <https://doi.org/10.1146/annurev-phyto-080417-050044>
 42. Zhu KY, Palli SR (2020) Mechanisms, applications, and challenges of insect RNA interference. *Annu Rev Entomol* 65:293–311. <https://doi.org/10.1146/annurev-ento-011019-025224>
 43. Niu X, Kassa A, Hu X, Robeson J, McMahon M, Richtman NM, Steimel JP, Kernodle BM, Crane VC, Sandahl G, Ritland JL (2017) Control of western corn rootworm (*Diabrotica virgifera virgifera*) reproduction through plant-mediated RNA interference. *Sci Rep* 7(1):1–13. <https://doi.org/10.1038/s41598-017-12638-3>
 44. Reddy KRK, Rajam MV (2016) Targeting chitinase gene of *Helicoverpa armigera* by host-induced RNA interference confers insect resistance in tobacco and tomato. *Plant Mol Biol* 90(3):281–292. <https://doi.org/10.1007/s11103-015-0414-y>
 45. Shi L, Zhang J, Shen G, Xu Z, Xu Q, He L (2016) Collaborative contribution of six cytochrome P450 monooxygenase genes to fenpropathrin resistance in *Tetranychus cinnabarinus* (Boisduval). *Insect Mol Biol* 25(5):653–665. <https://doi.org/10.1111/imb.12251>
 46. Han Q, Wang Z, He Y, Xiong Y, Lv S, Li S, Zhang Z, Qiu D, Zeng H (2017) Transgenic cotton plants expressing the HaHR3 gene conferred enhanced resistance to *Helicoverpa armigera* and improved cotton yield. *Int J Mol Sci* 18(9):1874. <https://doi.org/10.3390/ijms18091874>
 47. Hou Q, Xu L, Liu G, Pang X, Wang X, Zhang Y, You M, Ni Z, Zhao Z, Liang R (2019) Plant-mediated gene silencing of an essential olfactory-related Gqα gene enhances resistance to grain aphid in common wheat in greenhouse and field. *Pest Manag Sci* 75(6):1718–1725. <https://doi.org/10.1002/ps.5292>
 48. Guo W, Bai C, Wang Z, Wang P, Fan Q, Mi X, Wang L, He J, Pang J, Luo X, Fu W (2018) Double-stranded RNAs high-efficiently protect transgenic potato from *Leptinotarsa decemlineata* by disrupting juvenile hormone biosynthesis. *J Agric Food Chem* 66(45):11990–11999. <https://doi.org/10.1021/acs.jafc.8b03914>
 49. Kumar V, Jain M (2015) The CRISPR–Cas system for plant genome editing: advances and opportunities. *J Exp Bot* 66(1):47–57. <https://doi.org/10.1093/jxb/eru429>
 50. Manghwar H, Lindsey K, Zhang X, Jin S (2019) CRISPR/Cas system: recent advances and future prospects for genome editing. *Trends Plant Sci* 24(12):1102–1125. <https://doi.org/10.1016/j.tplants.2019.09.006>
 51. Puchta H (2017) Applying CRISPR/Cas for genome engineering in plants: the best is yet to come. *Curr Opin Plant Biol* 36:1–8. <https://doi.org/10.1016/j.tplants.2019.09.006>
 52. Kim D, Alptekin B, Budak H (2018) CRISPR/Cas9 genome editing in wheat. *Funct Integr Genomic* 18(1):31–41. <https://doi.org/10.1007/s10142-017-0572-x>
 53. Zhang A, Liu Y, Wang F, Li T, Chen Z, Kong D, Bi J, Zhang F, Luo X, Wang J, Tang J (2019) Enhanced rice salinity tolerance via CRISPR/Cas9-targeted mutagenesis of the OsRR22 gene. *Mol Breed* 39(3):1–10. <https://doi.org/10.1007/s11032-019-0954-y>
 54. Vlěko T, Ohnoutkova L (2020) Allelic Variants of CRISPR/Cas9 induced mutation in an inositol trisphosphate 5/6 kinase gene manifest different phenotypes in barley. *Plants* 9(2):195. <https://doi.org/10.3390/plants9020195>
 55. Xiao Y, Karikari B, Wang L, Chang F, Zhao T (2021) Structure characterization and potential role of soybean phospholipase A multigene family in response to multiple abiotic stress uncovered by CRISPR/Cas9 technology. *Environ Exp Bot* 188:104521. <https://doi.org/10.1016/j.envexpbot.2021.104521>
 56. Roumet P, Morin F (1997) Germination of immature soybean seeds to shorten reproductive cycle duration. *Crop Sci* 37(2):521–525. <https://doi.org/10.2135/cropsci1997.0011183X003700020035x>
 57. Ochatt SJ, Sangwan RS (2008) In vitro shortening of generation time in *Arabidopsis thaliana*. *Plant Cell Tissue Organ Cult* 93(2):133–137. <https://doi.org/10.1007/s11240-008-9351-7>
 58. O'Connor DJ, Wright GC, Dieters MJ, George DL, Hunter MN, Tatnell JR, Fleischfresser DB (2013) Development and application of speed breeding technologies in a commercial peanut breeding program. *Peanut Sci* 40(2):107–114. <https://doi.org/10.3146/PS12-12.1>
 59. Zheng Z, Wang HB, Chen GD, Yan GJ, Liu CJ (2013) A procedure allowing up to eight generations of wheat and nine generations of barley per annum. *Euphytica* 191(2):311–316. <https://doi.org/10.1007/s10681-013-0909-z>
 60. Forster BP, Till BJ, Ghanim AMA, Huynh HOA, Burstmayr H, Caligari PDS (2014) Accelerated plant breeding. *CAB Rev Perspect Agric Vet Sci Nutr Nat Resour* 9:20149043. <https://doi.org/10.1079/PAVSNNR20149043>
 61. Mobini SH, Lulsdorf M, Warkentin TD, Vandenberg A (2015) Plant growth regulators improve in vitro flowering and rapid generation advancement in lentil and faba bean. *In vitro Cell Dev Biol-Plant* 51(1):71–79. <https://doi.org/10.1007/s11627-014-9647-8>

62. Stetter MG, Zeitler L, Steinhaus A, Kroener K, Biljecki M, Schmid KJ (2016) Crossing methods and cultivation conditions for rapid production of segregating populations in three grain amaranth species. *Front Plant Sci* 7:816. <https://doi.org/10.3389/fpls.2016.00816>
63. Mobini SH, Warkentin TD (2016) A simple and efficient method of in vivo rapid generation technology in pea (*Pisum sativum* L.). *In vitro Cell Dev Biol-Plant* 52(5):530–536. <https://doi.org/10.1007/s11627-016-9772-7>
64. Collard BCY, Beredo JC, Lenaerts B, Mendoza R, Santelices R, Lopena V, Verdeprado H, Raghavan C, Gregorio GB, Vial L et al (2017) Revisiting rice breeding methods—evaluating the use of rapid generation advance (RGA) for routine rice breeding. *Plant Prod Sci* 20(4):337–352. <https://doi.org/10.1080/1343943X.2017.1391705>
65. Pazos-Navarro M, Castello M, Bennett RG, Nichols P, Croser J (2017) In vitro-assisted single-seed descent for breeding-cycle compression in subterranean clover (*Trifolium subterraneum* L.). *Crop Pasture Sci* 68(11):958–966. <https://doi.org/10.1071/CP17067>
66. Yao Y, Zhang P, Liu H, Lu Z, Yan G (2016) A fully in vitro protocol towards large scale production of recombinant inbred lines in wheat (*Triticum aestivum* L.). *Plant Cell. Tissue Organ Cult* 128:655–661. <https://doi.org/10.1007/s11240-016-1145-8>
67. Saxena KB, Saxena RK, Hickey LT, Varshney RK (2019) Can a speed breeding approach accelerate genetic gain in pigeonpea? *Euphytica* 215(12):1–7. <https://doi.org/10.1007/s10681-019-2520-4>
68. Cazzola F, Bermejo CJ, Guindon MF, Cointy E (2020) Speed breeding in pea (*Pisum sativum* L.), an efficient and simple system to accelerate breeding programs. *Euphytica* 216(11):1–11. <https://doi.org/10.1007/s10681-020-02715-6>
69. Ribalta FM, Pazos-Navarro M, Nelson K, Edwards K, Ross JJ, Bennett RG, Munday C, Erskine W, Ochatt SJ, Croser JS (2017) Precocious floral initiation and identification of exact timing of embryo physiological maturity facilitate germination of immature seeds to truncate the lifecycle of pea. *Plant Growth Regul* 81(2):345–353. <https://doi.org/10.1007/s10725-016-0211-x>
70. Samineni S, Sen M, Sajja SB, Gaur PM (2020) Rapid generation advance (RGA) in chickpea to produce up to seven generations per year and enable speed breeding. *Crop J* 8(1):164–169. <https://doi.org/10.1016/j.cj.2019.08.003>
71. Jähne F, Hahn V, Würschum T, Leiser WL (2020) Speed breeding short-day crops by LED-controlled light schemes. *Theor Appl Genet* 133(8):2335–2342. <https://doi.org/10.1007/s00122-020-03601-4>
72. González-Barrios P, Bhatta M, Halley M, Sandro P, Gutiérrez L (2021) Speed breeding and early panicle harvest accelerates oat (*Avena sativa* L.) breeding cycles. *Crop Sci* 61(1):320–330. <https://doi.org/10.1002/csc2.20269>
73. Chiurugwi T, Kemp S, Powell W, Hickey LT (2019) Speed breeding orphan crops. *Theor Appl Genet* 132(3):607–616. <https://doi.org/10.1007/s00122-018-3202-7>
74. Rana MM, Takamatsu T, Baslam M, Kaneko K, Itoh K, Harada N, Sugiyama T, Ohnishi T, Kinoshita T, Takagi H, Mitsui T (2019) Salt tolerance improvement in rice through efficient SNP marker-assisted selection coupled with speed-breeding. *Int J Mol Sci* 20(10):2585. <https://doi.org/10.3390/ijms20102585>
75. Hickey LT, Dieters MJ, DeLacy IH, Kravchuk OY, Mares DJ, Banks PM (2009) Grain dormancy in fixed lines of white-grained wheat (*Triticum aestivum* L.) grown under controlled environmental conditions. *Euphytica* 168(3):303–310. <https://doi.org/10.1007/s10681-009-9929-0>
76. Bhat JA, Ali S, Salgotra RK, Mir ZA, Dutta S, Jadon V, Tyagi A, Mushtaq M, Jain N, Singh PK, Singh GP (2016) Genomic selection in the era of next generation sequencing for complex traits in plant breeding. *Front Genet* 7:221. <https://doi.org/10.3389/fgene.2016.00221>
77. Barabaschi D, Tondelli A, Desiderio F, Volante A, Vaccino P, Valè G, Cattivelli L (2016) Next generation breeding. *Plant Sci* 242:3–13. <https://doi.org/10.1016/j.plantsci.2015.07.010>
78. Varshney RK, Pandey MK, Bohra A, Singh VK, Thudi M, Saxena RK (2019) Toward the sequence-based breeding in legumes in the post-genome sequencing era. *Theor Appl Genet* 132(3):797–816. <https://doi.org/10.1007/s00122-018-3252-x>
79. Wolter F, Schindele P, Puchta H (2019) Plant breeding at the speed of light: the power of CRISPR/Cas to generate directed genetic diversity at multiple sites. *BMC Plant Biol* 19(1):1–8. <https://doi.org/10.1186/s12870-019-1775-1>
80. Idrissi O (2020) Application of extended photoperiod in lentil: Towards accelerated genetic gain in breeding for rapid improved variety development. *Mor J Agri Sci* 1(1):14–19
81. Mobini S, Khazaei H, Warkentin TD, Vandenberg A (2020) Shortening the generation cycle in faba bean (*Vicia faba*) by application of cytokinin and cold stress to assist speed breeding. *Plant Breed* 139(6):1181–1189. <https://doi.org/10.1111/pbr.1286>
82. Parmley KA, Higgins RH, Ganapathysubramanian B, Sarkar S, Singh AK (2019) Machine learning approach for prescriptive plant breeding. *Sci Rep* 9(1):1–12. <https://doi.org/10.1038/s41598-019-53451-4>
83. Niaziyan M, Niedbała G (2020) Machine learning for plant breeding and biotechnology. *Agriculture* 10(10):436. <https://doi.org/10.3390/agriculture10100436>
84. van Dijk ADJ, Kootstra G, Kruijer W, de Ridder D (2021) Machine learning in plant science and plant breeding. *iScience* 24(1):101890. <https://doi.org/10.1016/j.isci.2020.101890>
85. Esposito S, Carputo D, Cardi T, Tripodi P (2020) Applications and trends of machine learning in genomics and phenomics for next-generation breeding. *Plants* 9(1):34. <https://doi.org/10.3390/plants9010034>
86. Yoosofzadeh-Najafabadi M, Earl HJ, Tulpan D, Sulik J, Eskandari M (2021) Application of machine learning algorithms in plant breeding: predicting yield from hyperspectral reflectance in soybean. *Front Plant Sci* 11:2169. <https://doi.org/10.3389/fpls.2020.624273>
87. Xavier A (2021) Technical nuances of machine learning: implementation and validation of supervised methods for genomic prediction in plant breeding. *Crop Breed Appl Biotechnol* 21. <https://doi.org/10.1590/1984-70332021v21Sa15>
88. Uzal LC, Grinblat GL, Namiás R, Larese MG, Bianchi JS, Morandi EN, Granitto PM (2018) Seed-per-pod estimation for plant breeding using deep learning. *Comput Electron Agric* 150:196–204. <https://doi.org/10.1016/j.compag.2018.04.024>
89. Corrêa AM, Teodoro PE, Gonçalves MC, Barroso LMA, Nascimento M, Santos A, Torres FE (2016) Artificial intelligence in the selection of common bean genotypes with high phenotypic stability. <https://locus.ufv.br/handle/123456789/12869>
90. Altuntaş Y, Cömert Z, Kocamaz AF (2019) Identification of haploid and diploid maize seeds using convolutional neural networks and a transfer learning approach. *Comput Electron Agric* 163:104874. <https://doi.org/10.1016/j.compag.2019.104874>
91. Montesinos-López OA, Martín-Vallejo J, Crossa J, Gianola D, Hernández-Suárez CM, Montesinos-López A, Juliana P, Singh R (2019) A benchmarking between deep learning, support vector machine and Bayesian threshold best linear unbiased prediction for predicting ordinal traits in plant breeding. *G3. Genes Genomes Genetics* 9(2):601–618. <https://doi.org/10.1534/g3.118.200998>
92. Khaki S, Khalilzadeh Z, Wang L (2020) Predicting yield performance of parents in plant breeding: A neural collaborative filtering approach. *PLoS ONE* 15(5):e0233382. <https://doi.org/10.1371/journal.pone.0233382>

93. Ravari SZ, Dehghani H, Naghavi H (2016) Assessment of salinity indices to identify Iranian wheat varieties using an artificial neural network. *Ann Appl Biol* 168:185–194. <https://doi.org/10.1111/aab.12254>
94. Niedbała G, Piekutowska M, Weres J, Korzeniewicz R, Witaszek K, Adamski M, Pilarski K, Czechowska-Kosacka A, Krysztofiak-Kaniewska A (2019) Application of artificial neural networks for yield modeling of winter rapeseed based on combined quantitative and qualitative data. *Agronomy* 9(12):781. <https://doi.org/10.3390/agronomy9120781>
95. Feng X, Zhan Y, Wang Q, Yang X, Yu C, Wang H, Tang Z, Jiang D, Peng C, He Y (2020) Hyperspectral imaging combined with machine learning as a tool to obtain high-throughput plant salt-stress phenotyping. *Plant J* 101(6):1448–1461. <https://doi.org/10.1111/tpj.14597>
96. Niaziyan M, Sadat-Noori SA, Abdipour M (2018) Artificial neural network and multiple regression analysis models to predict essential oil content of ajowan (*Carum copticum* L.). *J Appl Res Med Aromat Plants* 9:124–131. <https://doi.org/10.1016/j.jarmap.2018.04.001>
97. Niaziyan M, Sadat-Noori SA, Abdipour M, Tohidfar M, Mortazavian SMM (2018) Image processing and artificial neural network-based models to measure and predict physical properties of embryogenic callus and number of somatic embryos in ajowan (*Trachyspermum ammi* (L.) Sprague). *Vitr Cell Dev Biol Plant* 54:54–68. <https://doi.org/10.1007/s11627-017-9877-7>
98. Li D, Wang R, Xie C, Liu L, Zhang J, Li R, Wang F, Zhou M, Liu W (2020) A recognition method for rice plant diseases and pests video detection based on deep convolutional neural network. *Sensors* 20(3):578. <https://doi.org/10.3390/s20030578>
99. Vakilian KA (2020) Machine learning improves our knowledge about miRNA functions towards plant abiotic stresses. *Sci Rep* 10(1):1–10. <https://doi.org/10.1038/s41598-020-59981-6>
100. Wei MCF, Maldaner LF, Ottoni PMN, Molin JP (2020) Carrot yield mapping: A precision agriculture approach based on machine learning. *AI* 1(2):229–241. <https://doi.org/10.3390/ai1020015>
101. Azizi A, Abbaspour-Gilande Y, Nooshyar M, Afkari-Sayah A (2016) Identifying potato varieties using machine vision and artificial neural networks. *Int J Food Prop* 19(3):618–635. <https://doi.org/10.1080/10942912.2015.1038834>
102. Abdipour M, Younessi-Hmazekhanlu M, Ramazani SHR (2019) Artificial neural networks and multiple linear regression as potential methods for modeling seed yield of safflower (*Carthamus tinctorius* L.). *Ind Crops Prod* 127:185–194. <https://doi.org/10.1016/j.indcrop.2018.10.050>
103. Coulibaly S, Kamsu-Foguem B, Kamissoko D, Traore D (2019) Deep neural networks with transfer learning in millet crop images. *Comput Ind* 108:115–120. <https://doi.org/10.1016/j.compind.2019.02.003>
104. Jung J, Maeda M, Chang A, Bhandari M, Ashapure A, Landivar-Bowles J (2021) The potential of remote sensing and artificial intelligence as tools to improve the resilience of agriculture production systems. *Curr Opin Biotechnol* 70:15–22. <https://doi.org/10.1016/j.copbio.2020.09.003>
105. Demirci M, Gozde H, Taplamacioglu MC (2021) Comparative Dissolved Gas Analysis with Machine Learning and Traditional Methods. In: 2021 3rd International Congress on Human-Computer Interaction, Optimization and Robotic Applications (HORA) IEEE. pp 1–6. <https://doi.org/10.1109/HORA52670.2021.9461371>
106. Uygun S, Azodi CB, Shiu SH (2019) Cis-regulatory code for predicting plant cell-type transcriptional response to high salinity. *Plant Physiol* 181(4):1739–1751. <https://doi.org/10.1104/pp.19.00653>
107. Varala K, Marshall-Colón A, Cirrone J, Brooks MD, Pasquino AV, Léran S, Mittal S, Rock TM, Edwards MB, Kim GJ, Ruffel S (2018) Temporal transcriptional logic of dynamic regulatory networks underlying nitrogen signaling and use in plants. *Proc Nat Acad Sci USA* 115(25):6494–6499. <https://doi.org/10.1073/pnas.1721487115>
108. Meena M, Shubham S, Paritosh K, Pareek N, Vivekanand V (2021) Production of biofuels from biomass: Predicting the energy employing artificial intelligence modelling. *Bioresour Technol* 340:125642. <https://doi.org/10.1016/j.biortech.2021.125642>
109. Nabwire S, Suh HK, Kim MS, Baek I, Cho BK (2021) Application of artificial intelligence in phenomics. *Sensors* 21(13):4363. <https://doi.org/10.3390/s21134363>
110. Shen Y, Zhou G, Liang C, Tian Z (2022) Omics-based interdisciplinarity is accelerating plant breeding. *Curr Opin Plant Biol* 66:102167. <https://doi.org/10.1016/j.pbi.2021.102167>
111. Valerio Giuffrida M, Scharr H, Tsaftaris SA (2017) Arigan: Synthetic arabidopsis plants using generative adversarial network. In: Proceedings of the IEEE International Conference on Computer Vision Workshops, pp 2064–2071
112. Ubbens J, Cieslak M, Prusinkiewicz P, Stavness I (2018) The use of plant models in deep learning: an application to leaf counting in rosette plants. *Plant Methods* 14(1):1–10. <https://doi.org/10.1186/s13007-018-0273-z>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.