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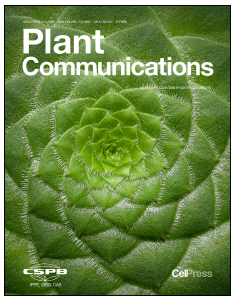

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Integrating genome editing with omics, artificial intelligence and advanced farming technologies to increase crop productivity

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Abstract

Celebrated for boosting agricultural productivity and enhancing food security worldwide, the green revolution constituted some of the most significant advances in crop production within the 20th century. Many recent studies, however, have identified occurrences of crop yield stagnation in certain areas of the world, with worries that global yield gains are no longer sufficient to feed an exponentially growing world population. Here, we review the current issues facing global crop production and discuss the role of genome editing technologies in overcoming yield stagnation and current legislative bottlenecks in the use of genome editing on crops. We explore strategies to integrate genome editing with omics, artificial intelligence, robotics and advanced farming technologies for major advancements in crop performance. To achieve real-world yield improvements, agricultural practices must also evolve. This review discusses how precision farming approaches, combining satellite technology, AI-driven decision support and real-time monitoring, can support climate-adaptive and sustainable farming. Going forward, it will be essential to address issues throughout the pipeline to fully integrate fast-developing genome editing technologies with other advanced technologies in global agriculture, so the industry can keep up with the changing environment and ensure future food security.

Short summary: In the face of growing global population and yield stagnation, technologies such as robotics, artificial intelligence and high throughput omics and phenomics must be strategically integrated across the agricultural pipeline to inform and implement advances in crop genetic improvement. Key bottlenecks in the production of new crop lines and the barriers limiting their tangible yield improvements in the field are examined. In an era of rapid technological advancement, increasing climate pressures and shifting global policies, strategies outlined in this review are critical to future food security

Keywords: Genome editing, Robotics, Artificial Intelligence, Farming, CRISPR, Phenomics

Introduction

From 1960 to 2000, agricultural productivity tripled with the development and adoption of improved germplasms, alongside important advancements in infrastructure and energy inputs (Briggs, 2009; Evenson and Gollin, 2003; Pingali, 2012). While the new techniques have been recognised for increasing food security and preventing projected food shortages in many parts of the world, it is generally understood that these techniques have been unable to boost yields

in all countries, and in all crops, equally (**Figure 1**) (Evenson and Gollin, 2003; Liu et al., 2020b; Pimentel and Pimentel, 1990; Pingali, 2012). Conventional breeding is slow, often taking decades to generate new crop varieties, making it challenging to address urgent food security and environmental issues. Advanced techniques like TILLING and CRISPR/Cas-based mutagenesis enable precise genetic modifications, significantly accelerating the development of improved crop varieties. These innovations enhance breeding efficiency, offering new solutions to create resilient and high-yield crops more effectively than traditional methods. Nevertheless, some bottlenecks persist which limit the applications of genome editing for food production. This review will give an overview on the current challenges in crop production, discuss limitations and prospects of traditional crop breeding and outline how genome editing technologies could overcome yield stagnation. Additionally, it evaluates current regulations on genome editing in crops and provides a viewpoint on strategies for integrating genome editing with other advanced technologies to enhance the whole pipeline of crop production to overcome yield stagnation.

1. Current challenges in crop production

Crop genetic improvement and the use of pesticides, fertilizers and water application have been an important aspect of yield gain but have led to some unintended consequences on the environment and the long term food production system that require careful examination. It is estimated that global pesticide production has increased by 850% over the past 50 years (Briggs, 2009; Grigg, 2001, McKenzie and Williams, 2015; Pimentel and Pimentel, 1990; Pingali, 2012). However, pesticide use is remarkably inefficient with only about 1% of total pesticide application effectively controlling target pests while the rest is released into the environment via a combination of leaching, adsorption, spray drift and run-off, causing detrimental effects on the environment (**Figure 2**) (Aktar et al., 2009; European Environment Agency, 2023; Tudi et al., 2021). The effects of climate change will only aggravate the negative effects of chemical pollution caused by high pesticide and fertilizer use. Increasing temperature enhances soil erosion and soil cracking, increasing the movement of water and chemical runoff deep into soil, risking surface and ground water contamination (**Figure 2**) (Tudi et al., 2021). Moreover, increased irrigation to support high yield has led to increased soil salinization in areas where water cannot be drained off the land properly, which can lead to salt accumulation in the root zones of crops. This can result in ion toxicity, nutritional imbalances and reduced germination (**Figure 2)** (Briggs, 2009; Khamidov et al., 2022). As climate change alters temperatures and precipitation patterns, soil salinization is expected to worsen in some areas, further reducing yield (Briggs, 2009; Jaggard et al., 2010; Skendžic et al., 2021; Tarmizi, 2019; Turin et al., 2023).

The introduction of monocropping practices replaced traditional intercropping practices that helped maintain rural biodiversity and encouraged greater resistance to pests (Briggs, 2009). The growth of a single cultivar at high densities enhances transmission of disease between plants of high genetic homogeneity (**Figure 2**). This is exemplified by the breakdown of resistance of wheat to stripe rust (Yr17) in England and Denmark, where cultivars containing a single resistance gene were grown over an extensive area from 1994 to 1998, leading to 100% virulence (de Vallavieille-Pope, 2004). Moreover, a high level of fertilizer input is associated with an increase in plant nutritional content and soil minerals, which can increase the risk of disease and make crops more attractive to phytophagous pests (Grigg, 2001; Pimentel and Pimentel, 1990). Additionally, climate change allows the establishment of pest populations in regions where they were previously absent (Skendžic et al., 2021). It is estimated that crop pests and diseases cause global yield losses of 21.5%, 30.3% and 22.6% in wheat, rice and maize, respectively, with plant pathogens costing the global economy an estimated $220 billion annually (He and Creasey Krainer, 2020; Ristaino et al., 2021).

At present time, many areas in the world are experiencing stagnating yield growth, with many developing countries predicted to fail to meet projected food demands due to insufficient yield increases (**Figure 1**) (Ray et al., 2013). Global average yields in maize, rice, wheat and soybean are increasing at a rate of 1.6%, 1.0%, 0.9% and 1.3% each year, respectively, falling far below the annual 2.4% increases required to meet projected future demand (Ray *et al.*, 2013). For example, in India, yield growth has stalled in some significant areas of crop production, with yield stagnation occurring in 76% of wheat, 47% of rice, and 18% of maize producing regions (George, 2014; Madhukar et al., 2020). This trend is particularly concerning considering that the number of undernourished people in the world has been rising in recent years and it is vital that trends in declining yield growth are reversed in order to ensure sufficient food production in the coming years (World Health Organisation, 2024).

2. Limitations and prospects of traditional crop breeding

Crop breeding has been used to enhance the productivity of cultivated species through a variety of methods including pure line selection, hybrid breeding, population breeding, pedigree breeding and double haploids. Despite its utility, breeding is becoming increasingly difficult as cultivated varieties are experiencing dwindling genetic heterogeneity, known as genetic erosion (Khoury et al., 2022; Salgotra and Chauhan, 2023). It is estimated that 75% of plant genetic diversity has been lost in the last century (FAO, 2004). These losses can be attributed to changing land use, climate change, and the replacement of local landraces with high-yielding varieties (Khoury *et al.*, 2022*;* Salgotra and Chauhan, 2023). As plant genetic resources are important reservoirs for disease and climate resilience genes, natural genetic variation must be conserved for use in breeding programs (Bohra et al., 2022; Salgotra and Chauhan, 2023; Tanksley and McCouch, 1997). Gene banks represent the most widely used method of conservation with around 1,750 gene banks containing roughly 7 million samples worldwide (FAO, 2010). Crop wild relatives are of particular conservation interest; lacking the intense genetic bottleneck that domestication has imposed on related cultivated varieties, and representing an important source of genetic diversity for trait improvement. However, they account for only 16% of total genebanks worldwide. Furthermore, while the introgression of genes from crop wild relatives has an estimated added value to the world economy of $186 billion annually, breeding efforts are often focused on members of the primary gene pool (close relatives), despite crosses between more distantly related species resulting in higher benefits (Bohra *et al.*, 2022; Tanksley and McCouch, 1997; Tyack et al., 2020).

The introgression of improved traits into crop varieties may not always be possible. Reproductive barriers between domesticated strains and their wild relatives can hamper the transfer of genes between wild and cultivated varieties, or even confer poor quality and yield related traits, limiting the capacity for improvement (Bohra *et al.*, 2022). In addition, desirable alleles can be transferred to progeny along with deleterious alleles, a phenomenon called linkage drag whereby two loci that are in proximity remain genetically linked in the offspring population. These alleles are said to be “linked” as they are inherited together throughout generations. Linkage drag presents an important challenge for conventional breeding methods as deleterious alleles are unlikely to be removed through crossing (Bohra *et al.*, 2022). One potential solution to break linkage drag is to engineer meiotic recombination. This can be done by increasing the total number of recombination events and to change the location of these events in germ cells. Recombination events occur during meiosis and can be modulated by changing temperature and epigenetic factors or through overexpression and inactivation of genes involved in the regulation of meiotic recombination (Fayos et al., 2022; Kuo et al., 2021). Considering the current limitations on conventional breeding and that the average breeding pipeline takes approximately 7-12 years to generate a new line, conventional methods, although important, are unlikely to facilitate germplasm improvement swiftly enough to keep pace with a rapidly changing climate and an exponentially growing global population.

3. Development of genome editing techniques

Since the first evidence of induced plant mutagenesis in 1928, using radiation in maize and barley (Stadler, 1928a; b), scientists have used various approaches to create novel genetic variation and improve traits in plants, with the first varieties appearing in the late 1950s/early 1960s like Golden promise barley and Canola varieties of oilseed rape (**Figure 3**) (Shelake et al., 2019). In 2000, Targeting Induced Local Lesion IN Genomes (TILLING) emerged as a technique that combines traditional cross breeding, chemical mutagenesis and DNA-analysis methods to establish desired mutations and generate new lines (**Figure 3**) (McCallum et al., 2000). The original TILLING protocol was a relatively short-lived method of screening mutant populations, now superseded to a great extent by genomic methods to widen its application such as EcoTILLING (Comai et al., 2004) , iTILLING (Bush and Krysan, 2010), De-TILLING (Li et al., 2001), and PolyTILLING (Wang et al., 2012). These methods can create and identify new alleles in coding as well as non-coding regions and can tackle large genomes, creating mutant populations that can be directly used in breeding programs (Singh et al., 2024). Successful applications of TILLING-based approaches for crop improvement include the development of oilseed rape with higher oil quality (Lee et al., 2018; Wang et al., 2008) and tomato with *Potato virus Y* and *Pepper mottle virus* resistance (Piron et al., 2010).

Despite these successes, the randomness of DNA mutation leads to high levels of unwanted background mutations that need to be removed through several rounds of backcrossing and chemical and radiation mutagenesis cannot be used for rapidly engineering changes in the genome. This led to the development of targeted mutagenesis systems based on the use of endonucleases that induce a DSB at a specific site. The DSB is subject to repair by an endogenous mechanism; normally error-prone non-homologous end joining (NHEJ) which introduces deletions and insertions of nucleotides at the site of repair (**Figure 4**). Sometimes Homologous Recombination (HR) is employed, which can introduce precise editing via DNA repair donors with homology arms (**Figure 4**). However, HR is less frequently used as it is only active during somatic S-phase and in meiosis, whereas NHEJ is active throughout most of the somatic cell cycle (Symington and Gautier, 2011). The first targeted mutagenesis system to be developed was zinc finger nucleases (ZFNs), which comprises the fusion of a DNA binding domain from a zinc finger class of transcription factors with the non-specific DNA cleavage domain of Fok I, a Type II(S) restriction enzymes (**Figure 3**). A major limitation in this technique is the difficulties to predict the DNA binding sites of the zinc finger domains (Khalil, 2020) and it took 9 years from the discovery of ZFNs to produce the first ZFN plant genome editing technology (Townsend et al., 2009). In 2009, the discovery of transcription activator-like effectors (TALEs) in the phytopathogen *Xanthomonas oryzae* led to the development of a new technique based on the fusion of TALEs with a nuclease to form a complex (TALEN), which can generate a DSB like ZFNs (**Figures 3-4**). TALEs are simpler to design as each module recognises just one base, making their binding sites significantly more predicable than ZFNs, and therefore TALENs exhibit fewer off target effects. However, the cloning of TALEs can be labour intensive (**Table S1**) (reviewed in Khalil, 2020; Zhang et al., 2018).

In 2012, the discovery of the Clustered Regularly Interspaced Short Palindromic Repeats CRISPR-Cas system revolutionized genetic engineering, offering new possibilities for precise and efficient genome editing (**Figure 3**). Initially discovered as a viral defence mechanism in bacteria, CRISPR-Cas9 technology uses a single guide RNA (sgRNA) that combines pre-CRISPR RNA (crRNA) and tracrRNA, directing the Cas9 nuclease to a target DNA sequence. This enables efficient, precise gene editing by matching the 5' crRNA complementary base pair component to the target sequence (**Figure 4**) (reviewed in Gao, 2021). Over the past few years, it has dominated the genome-editing field, significantly advancing plant research and holding great potential for crop improvement (Li et al., 2021b). CRISPR-Cas9 is a versatile, simple, and inexpensive tool for sequence-specific DNA modifications, including gene knockout, single-base substitution, gene/allele replacement and multiplex genome

engineering (Li et al., 2021b; Cong et al., 2013; Mali et al., 2013) (**Table S1**). Using multiple sgRNAs to engineer multiple DSBs, it is possible to cause chromosomal deletions, gene inversions, chromosomal translocations and target multiple genes simultaneously (Beying et al., 2020; Lu et al., 2021; Rönspies et al., 2022; Sedeek et al., 2019). Many novel Cas orthologues have been found with advantages over Cas9, such as Cas12j that has a smaller size for delivery (Sun et al., 2024), Cas12a with a different PAM recognition (Zhang et al., 2023) or Cas13 that can target RNA viruses (Hak et al., 2014; Kavuri et al., 2022). Engineering of Cas proteins represents a novel avenue to expand the range of genome editing tools available. For example, Cas-SF01 is an Artificial Intelligence (AI)-guided genetically engineered derivative of the natural Cas12i3 but with improved gene editing activity in animals and plants (Duan et al., 2024).

The applications of genome editing technologies in breeding are rapidly expanding (**Table 1**) (reviewed in Zhu et al., 2020). Base editing was developed in 2016 that enables the direct conversion of one target DNA base into another without requiring DSB formation or a donor template (Gaudelli et al., 2017; Komor et al., 2016; Nishida et al., 2016; reviewed in Li et al., 2021b and Molla et al., 2021). This method involves the fusion of a cytidine deaminase enzyme with an engineered CRISPR-Cas9 that lacks the ability to induce DSB (CRISPR-dCas9) but can still be brought to a target sequence with a guide RNA (**Figure 5A**). The first successful applications in crops were demonstrated in wheat, rice, tomato and maize (Lu et al., 2017; Li et al., 2017; Ren et al., 2017; Shimatani et al., 2017; Zong et al., 2017). As base editing is limited to specific nucleotide changes, new methods with wider editing properties were explored. Prime editing was described in 2019 as a "search-and-replace" genome editing technology that can achieve targeted insertion or deletion in all 12 types of base-to-base conversion (Anzalone et al., 2019; reviewed in Li et al., 2021b and Molla et al., 2021). Prime editing consists of a reverse transcriptase fused to an RNA-programmable nickase and a prime editing guide RNA (pegRNA). The genetic information is directly copied from the pegRNA into the target genomic locus, offering high versatility and precision in genome editing beyond the capabilities of base editing alone (Anzalone et al., 2019). Prime editing technology has low editing efficiency in plants but improved prime editing systems were developed to overcome these limitations (Jin et al., 2023; Li et al., 2022a; Ni et al., 2023). Prime editors were successfully used to insert a 30-bp long cis-regulatory element into the promoter of the *R* gene *Xa23* to engineer resistance to bacterial blight in rice (Gupta et al., 2023). Although prime editing can be used to achieve targeted insertion of a short cis-regulatory element, it is limited in the length of element that can be inserted and multiplexing is difficult. Lu et al (2020) developed an efficient method for inserting long as well as short elements at target sites in the plant genome. This method involves particle bombardment of callus cells with CRISPR-Cas constructs to generate DSBs at target sites and double stranded donor DNA fragments that are chemically modified to have 5'-phosphorylation and two phosphorothioate linkages at the 5'- and 3'-ends of both DNA strands. The modified donor DNA is stable in cells and can be inserted efficiently at the DSB sites. For example, insertion of four TALE binding elements into the promoter of rice Executor gene Xa10 or Xa23 generated rice plants resistant to all *Xanthomonas oryzae pv. oryzae (Xoo)* strains tested (Zhang et al., 2024b).

Mitochondrial and chloroplast genome editing has high potential in breeding as it can improve respiration and photosynthesis pathways but requires specific modifications of genome editing technologies currently used for nuclear genome editing (Dorogova and Sidorchuk, 2023). The main challenge is the apparent lack of the NHEJ pathway for repair. The HR pathway instead prevails, retained from their prokaryotic ancestors, which limits the introduction of mutations after DSB induction (Maliga, 2022). Moreover, there are difficulties with using CRISPR-Cas9 because sgRNA is difficult to transport across the mitochondrial membrane. However, this difficulty with transportation to target organelle genomes is not seen with TAL effectors (**Table**

S1). The first application of this approach was the use of TALENs fused with N-terminal mitochondrial localisation signals (mitoTALENs) to successfully knockout genes for cytoplasmic male sterility (CMS) in rice and rapeseed (Kazama et al., 2019). Base-editing methods by fusion of TALEs with nucleotide deaminases (TALEDs) have been used to introduce point mutations in mitochondrial and chloroplast genomes. DddAtox-derived base editors (DdCBEs) are highly effective TALEDs synthesised by the fusion of TALEs and a cytidine deaminase domain ($DddA_{tox}$) (Li et al., 2021a). DdCBEs were first implemented in mitochondria and have recently been adapted for use in chloroplasts (Kim and Chen, 2024; Zhang et al., 2024a). This approach has been effective in engineering herbicide resistance in lettuce and creating a stop codon in the chloroplast gene *psaA* in rice (Li et al., 2021a; Mok et al., 2022).

Epigenome editing represents another avenue for crop improvement. CRISPR-dCas9 can methylate or demethylate cytosine at a target site and change the level of gene expression (Qi et al., 2023). CRISPR-dCas9 methylation was recently developed in plants using a variant of the bacterial CG-specific DNA methyltransferase, MQ1 (**Figure 5B**). MQ1 has reduced activity but high specificity, accurately targeting de novo DNA methylation in Arabidopsis (Ghoshal et al., 2021). Targeted DNA methylation in CG context produces phenotypic changes in plants that can be maintained in mitosis and meiosis without mutating the genome. When fused with the catalytic domain of the human demethylase TEN-ELEVEN TRANSLOCATION1 (TET1cd), CRISPR-dCas9 was able to target DNA for demethylation in Arabidopsis (Li et al., 2020b). The dCas9-SunTag transcriptional activator system has also been adapted for site-specific DNA methylation editing in plants. The catalytic domain of the human demethylase TEN-ELEVEN TRANSLOCATION1 (TET1cd) fused to the dCas9-SunTag system was able to target demethylation and activate gene expression of the well-characterised epiallele *FWA* in Arabidopsis (**Figure 5B**) (Gallego-Bartolomé et al., 2018). This approach was successfully used to change DNA methylation and gene expression and to create epialleles that are heritable to the next generation in rice (Tang et al., 2022). In another study, the tobacco methyltransferase catalytic domain NtDRMcd was used in the SunTag system which successfully methylated the *FWA* promoter and caused early flowering (Papikian *et al.*, 2019). Epigenome editing was also efficient at increasing bacterial blight resistance in cassava (Veley et al., 2023). Since epigenome editing has shown high potential, this technology should be explored further in crop breeding.

Overall, genome engineering techniques such as TILLING and CRISPR-Cas-based systems enable precise modifications, unlocking valuable genetic traits that might otherwise remain inaccessible. These tools enhance genetic diversity, providing breeders with new opportunities to develop resilient and high-yielding crops.

4. Bottlenecks in the delivery of genome editing components into plant

Since the advent of CRISPR-Cas9 genome editing, efforts have been made to refine and eliminate bottlenecks in the process to aid global implementation of the technology to support food systems. Nevertheless, a main bottleneck that limits the full potential of genome editing in crop breeding is the delivery of genome editing reagents as Cas proteins are large and delivery mechanisms must be species specific (Atia et al., 2024). In vegetatively propagated crops such as potato, targeted gene mutations have been achieved by transiently expressing CRISPR-Cas9 ribonucleoproteins in protoplasts (Andersson et al., 2017, Tuncel et al., 2019). Similarly, the delivery of pre-assembled CRISPR/Cas9 ribonucleoproteins to lettuce protoplasts generated transgene-free mutant plants (Woo et al., 2015). However, the regeneration of plants from cultured protoplasts remains very challenging in most monocotyledons, particularly in major cereal crops. Tissue culture-free strategies such as RNA virus-mediated transformation, nanoparticles and polyethylene glycol (PEG)-mediated delivery have also been used but face their own challenges such as cell damage, cargo size

and low effectiveness in plant cells (**Figure 4**) (Cardi et al., 2023; Hwarari et al., 2024; Wang et al., 2022b).

One of the most widely used methods to transfer the genetic material to plants is *Agrobacterium*-mediated transformation, which involves infection of the plant with an engineered *Agrobacterium tumefaciens* strain. sgRNA and Cas can be expressed transiently or from a transgene integrated in the plant genome as part of a T-DNA (Zhang et al., 2016). This method poses some challenges as they can have low efficiency and not all plant species can be infected by *Agrobacterium tumefaciens*. To improve these methods, T-DNA vectors are increasingly being designed to include developmental regulator genes (DRs) to induce embryogenesis or organogenesis from somatic cells in tissue culture and stimulate growth of transformed plants (Nasti and Voytas, 2021). The expression of DRs is particularly advantageous for plant species that are recalcitrant to regeneration or have a long regeneration period (Laforest and Nadakuduti, 2022). DRs such as PGA37/MYB118 (Wang et al., 2009), WUS2, BBM (Lowe et al., 2016), STM (Maher et al., 2020), and WOX5 (Wang et al., 2022a) have demonstrated regeneration-promoting effects in plant transformation. However, the constitutive expression of these regulators can lead to negative pleiotropic effects and infertility, necessitating their removal from transgenic plants and limiting their practical application. Alternatively, the expression of Growth Regulating Factor (GRF) and GRF-interacting Factor (GIF) as a GRF4-GIF chimera has been shown to increase the speed and efficiency of plant regeneration (Debernardi et al., 2020). Co-delivery of the GRF4-GIF chimera along with CRISPR-Cas9 on the same T-DNA vector enhances regeneration efficiency in both monocotyledonous and dicotyledonous species, resulting in fertile edited plants (Debernardi et al., 2020). An important way forward for tackling the bottleneck of plant regeneration is to integrate rapid genome editing directly into speed breeding systems which use optimal light intensity, temperature and daytime length control, combined with an early harvest of seeds to reduce the generation time (Hussain et al., 2023; Watson et al., 2018). In approaches such as ExpressEDIT, Cas9 and sgRNA sequences are directly applied to plants and rapid trait selection identifies plants that lack Cas9 but carry the new trait and segregate them from plants that retain Cas9 which can be subjected to more cycles of editing for different targets (Hickey et al., 2019).

5. Global policies on genome edited crops

The emergence of new genome engineering technologies provides opportunities for the development of crops with improved agricultural values. Given the potential of using genome engineering tools, it is surprising that out of 195 United Nations recognised countries, 166 countries prohibit Genetically Modified organisms (GMOs). It is often observed that countries in surrounding areas have similar stands on the use of genome edited crops and GMOs with Americas and Asia having less stringent regulations for genome edited crops when compared to Africa and Europe. The adoption of genome editing has the potential to increase yield gains. Given this and considering that about 1 in 11 people globally suffer from hunger, the prohibitory stance towards the use of genome editing in plants needs exploring further. Africa's population is expected to reach 2.5 billion by 2050 and food production will need to increase in the region to prevent exacerbating pre-existing food insecurity in this area (United Nations Department of Economic and Social Affairs (UNDESA), 2017). For many major crops grown in Africa, realised yields are falling well below potential yields. This can be seen with maize, a staple crop in sub-Saharan Africa, where the average grain yields in Africa is 2.1 tons/ha/year, which is much lower than the worldwide maize grain yield average of 5.8 tons/ha/year (Woomer et al., 2024). This yield gap is largely underpinned by abiotic and biotic stresses. Although genome editing can create opportunities to close the yield gaps of several staple African crops, only four African countries have regulatory policies that allow for genome edited crops. This is despite the African Union Agenda stating in 2023 that one of their aims was to improve productivity and crop disease resistance through the utilization of genome editing (Buchholzer

and Frommer, 2023). In 2020, Nigeria became the first country in Africa to implement new guidelines that allow for genome edited crops (Report of the House Committee on Environment and Habitat, 2019). This was followed by Kenya (2022), Malawi (2022), and Ghana (2023) (Ledford, 2024). Several other African countries are currently considering developing regulatory policies for genome editing. These countries include Burkina Faso, South Africa, Ethiopia, Sudan, Eswatini, and Zimbabwe (Tripathi et al., 2022).

The international regulatory environment surrounding genetic technologies is evolving rapidly and a growing number of countries are revising their policies to exclude genome edited crops from pre-existing GMO regulations. Argentina was the first country to make this change in 2015 when they implemented what is now known as the “Argentina model”. This model exempts plants produced by genome editing, containing no permanent insertion of foreign DNA from GMO regulations and decisions are made on a case-by-case basis (Whelan & Lema, 2015). Following the regulatory change in Argentina several other countries passed similar legislation. These countries include Chile (2017), Brazil (2018), Colombia (2018), and the USA (2018) (Buchholzer and Frommer, 2023; Zarate et al., 2023). The USA, like Argentina, regulates GMOs based on the genetic material of a plant rather than the method used to engineer the plant, while the EU’s Court of Justice ruled in 2018 that organisms produced using New Genomic Techniques (NGTs), including genome edited crops, are still subjected to stringent GMO regulations. However, the EU has drafted new regulations to change the way that NGT plants are risk assessed (Watson and Hayta, 2024). Countries like Japan, Canada, the USA and Argentina, have adopted a proportionate regulatory system for precision breeding that approve targeted genetic changes, which could have arisen naturally or through traditional breeding. In China, genome edited crops containing no foreign DNA are still subjected to risk assessment before regulatory approval, albeit the assessment is less stringent than that used for GMOs (Zhu, 2022). After leaving the EU in 2020, the UK reconsidered its stance on genome edited crops and the UK Government introduced a new Statutory Instrument applied to the existing GM regulations in 2022. The 2023 Act was a new legislation on genome edited crops but only applies in England, with the devolved governments of the UK all rejecting it so far. Under the Genetic Technology (Precision Breeding) Act passed into law in 2023, plants and animals developed using precision breeding technologies will no longer be under the regulatory requirements of GMOs and will be subject to more proportionate and less strict regulations. In the near future, it is likely that more countries will re-examine their regulatory system on the use of genome edited crops as the population is becoming more informed on genome editing technologies and the impact of climate change on crop yield is becoming harder to mitigate.

6. Combining genomics with phenomics to underpin genome engineering strategies

With the availability of affordable and efficient genome editing tools and the less stringent regulations on genome edited crops, the focus is now moving towards knowing what genes to target with genome editing technology. For instance, yield is a highly complex, polygenic trait which is hard to noticeably increase by targeting one gene (Cao et al., 2020). Moreover, breeders are constantly trying to improve yield and stress resistance in plants, traits that are often antagonistic to each other. A 20-year project by Corteva Agriscience determined the effects of 1671 genes on yield, nitrogen use efficiency, and drought tolerance in maize and identified 22 genes that confer physiological functions (Simmons et al., 2021). Genetic redundancy in polyploid species like wheat, represents another challenge as it can often obscure novel phenotypes with improved agronomic traits. In view of these challenges, a holistic approach that combines genetics, metabolomics, genomics, phenomics and environmental data is required to identify genes and regulatory pathways underlying complex traits and to predict crop performance under variable climate conditions (**Figure 6**). This approach is highly impactful to provide a wealth of knowledge to design precise strategies for

crop improvement. This is evidenced by the recent multi-omics approach that sequenced the genome of 1,035 wheat varieties, comprising Watkins landraces and modern cultivars, and that collected 717,000 phenotypic observations for 137 traits and identified 8,253 genetic effects, which include 15 new loci conferring resistance to yellow rust (Cheng et al., 2024).

A high-quality reference genome is an essential resource for omics approaches and the study of gene functions (Adamski et al., 2020; Yao et al., 2025). The genomes of rice, maize, soybean and wheat were sequenced, and their annotations released in 2005, 2009, 2010 and 2018, respectively (**Figure 3**) (International Rice Genome Sequencing Project and Sasaki, 2005; Schmutz et al., 2010; Schnable et al., 2009; International Wheat Genome Sequencing Consortium et al., 2018). Although the reference genomes provide essential resources for scientists and breeders, they contain gaps, which are regions of unknown sequences, and sequences that cannot be assigned to a particular chromosome because of lack of continuity in sequences. Long-read DNA sequencing is a powerful technique to fill the gaps in genome assembly (Aury et al., 2022; Chen et al., 2023; Liu et al., 2020a). As technology improves, long-read DNA sequencing has recently been used to explore natural genetic and structural variations across large sets of accessions to generate a large amount of genomic information that can be used to identify loci of agricultural relevance and guide future breeding programmes (Li et al., 2020a; Shang et al., 2022; Zhang et al., 2022).

Plant phenomics is not a new concept as Furbank (2009) described the plant phenomics approaches to provide the quantitative phenotyping needed to elucidate the genetic bases for agricultural traits as well as to screen germplasm for genetic variation. Many countries have been investing in plant phenomics platforms for canopy and rooting traits under controlled and field conditions. Platforms could be ground-based or aerial-based (manned and unmanned aerial vehicles-drones) and can be manually driven, vehicle carried or robotic. Several institutes and universities have invested heavily in generating phenotyping platforms, some for controlled environment (Sadok et al,2007) and others for field (Virlet et al, 2016). Phenotypic data are collected by drones in field trials that are equipped with RGB cameras (to capture crop growth rates) and/or thermal cameras for creating field maps and monitoring for biotic (pest and diseases) and abiotic (drought) stresses. Many institutions have constructed data integration and storage systems for crop phenotypic data. Two well-known systems are firstly, the Internet of Things (IoT) technology, which was used to develop CropSight, an open-source information management system for automated data acquisition by sensors and phenotyping platforms. Secondly, the Phenotyping Hybrid Information System of the French National Institute of Agricultural Sciences (Institut Nationale de la Recherche Agronomique, INRA) integrates and manages phenotypic data from multiple experiments and platforms using an ontology-driven architecture. These platforms are a minefield of data that lead to gene discovery from traits.

A huge amount of data is generated which needs to be processed. Robotics and autonomous systems now emerge as next horizon technologies with considerable potential to transform agricultural activities (Pearson et al., 2022). The phenomics approach is promising for taking gene discovery to farmgate (Furbank, 2009), but the “big data” problem of how to process the incredibly large amount of data generated by various sensors on phenotyping platforms was a major bottleneck. The use of artificial intelligence (AI) is emerging as an essential tool for addressing this problem to sustain and boost agricultural output. AI is gaining traction in almost all spheres of life. AI can collect, manage and process large quantities of datasets from multiple omics experiments and climatic information to precisely link complex phenotypes with genotypes and predict gene function and crop performance (**Figure 6**) (Khan et al., 2022). Crop traits such as plant height and leaf area can be detected with high accuracy by AI-driven sensors and imaging systems for rapid screening of lines in breeding programmes (Benos et al., 2021). Machine Learning and Deep Learning approaches have shown great potential in extracting image-based phenotypic information (Khan et al., 2022; Poorter et al., 2023). Other promising AI models include DeepBind and DeepSEA to analyse genetic features, DeepBSA

for mapping genetic regions that influence phenotypic variations (Quantitative Trait Loci), and AlphaFold which uses a deep learning technique to predict protein structures (Alipanahi et al., 2015; Jumper et al., 2021; Li et al., 2022b; Zhou and Troyanskaya, 2015). These open the door for a myriad of possibilities that can help the field of 'omics' into finding genes of interest faster for crop breeding.

7. Use of robotics and AI to maximise agricultural output from genome edited crops

Maximising the agronomic benefits of genome edited crops requires precision farming (also referred to as smart farming) approaches that leverage robotics, AI, and IoT to improve sustainability and maximise yields (**Figure 6**) (Sharma et al., 2023). This approach relies on farmers receiving real-time information on the crop and soil health to evaluate the specific needs of the field and make informed decisions on the level of irrigation and use of pesticides and fertilisers to maximise agricultural outputs (**Figure 6**). With uncertain weather conditions it is very hard to predict the performance of our crops. The IoT network connects sensors, drones and data-processing systems to monitor climate, soil conditions and crop health. IoT sensors placed in fields collect data on soil moisture, acidity and nutrient levels, which combined with aerial imagery and environmental parameters, allow AI models to predict stress factors and optimise irrigation, fertilisation, and pesticide application (Sharma et al., 2023). AI-driven thermal imaging can rapidly detect nutrient deficiencies, enabling farmers to take swift corrective action before yield loss occurs.

AI-powered decision support systems and mobile applications are further transforming farm management (**Figure 6**). These tools provide real-time updates on pest outbreaks, disease progression, and weather patterns, helping farmers respond proactively. Mobile phone based applications have proven especially useful in bridging knowledge gaps, particularly in regions with limited access to other Information and Communication Technologies, such as computers (Ayim et al., 2022). Recent developments include deep-learning models for early disease detection, such as mango leaf disease identification, and integrated platforms that combine real-time crop diagnostics with e-commerce, weather information and government market updates (Aslam et al., 2024; Puranik et al., 2024). Such technologies empower smallholder farmers and reduce global yield gaps by making important insights for precision farming widely accessible.

A recent advancement in agricultural monitoring is the NASA-ISRO Synthetic Aperture Radar (NISAR) satellite, set to launch in 2025. NISAR's dual-frequency radar can penetrate clouds and crop canopies, providing high-resolution, uninterrupted global crop monitoring twice every 12 days (ICO SSR, 2025). This will allow farmers and policymakers to track crop growth, soil moisture, and biomass levels in real-time, optimise planting schedules, irrigations and resource allocation and enhance global crop forecasting and food security planning. Making this data publicly accessible and integrating it with AI-driven decision support systems and mobile applications, could further transform farm management, particularly in regions with limited access to monitoring technologies such as sensors and drones (ICO SSR, 2025).

Precision and smart farming also integrates AI with unmanned ground vehicles (UGVs) and robotic systems for automated planting, monitoring and harvesting (**Figure 6**). As climate change drives agriculture into new terrain and genome edited crops that are resilient to more extreme environments emerge, robotics will be crucial in enabling farming and management of these crops in regions other than traditional flat fields (Botta et al., 2022). Platforms like Agri. Q address challenges posed by uneven terrain, tight spaces and poor Global Positioning System (GPS) reception (Botta & Cavallone, 2021). Collaborative UGVs and drones equipped with multispectral sensors can map fields, monitor crop growth and optimise resource

allocation. Autonomous weeding robots, from companies such as ecoRobotix, use AI to identify weeds and selectively treat with herbicides with an application precision of 6x6cm, reducing herbicide use (Bykov, 2023). Similarly, robotic harvesters improve efficiency for labour-intensive crops, like strawberries (Chang and Huang, 2024) and tomatoes (Kim et al., 2022), minimising post-harvest losses. Integrating these robotic systems with genome edited crops can further enhance productivity, ensuring that agricultural practices keep up with advances in plant science in order to produce crops for a growing population in the face of climate change. Adoption of precision and smart farming practises with genome editing technology could not only alleviate yield stagnation, but also enhance product quality and reduce environmental footprint, delivering significant social, economic and environmental benefits.

Concluding remarks and perspectives

Genome editing technologies represent a powerful tool to confer new traits to crops and improve agricultural productivity. The applications of these technologies are rapidly expanding with editing of single bases to long nucleotide sequences, and their scope is ever-increasing as new Cas orthologues are developed with varying PAM specificity. The target site of genome editing is no longer restricted to the nuclear genome, and mitochondrial and chloroplast genome editing techniques have unlocked the genetic potential of previously inaccessible genes involved in photosynthesis and respiration. With new epigenome editing techniques, improvements can be engineered without mutating the genome, and transcriptional regulation can be controlled to induce nuanced changes in gene expression levels. This less permanent editing approach could be under less stringent legislative regulations and has the potential to be more widely implemented.

To maximise impact on crop production, genome editing technology should be integrated with other innovations, like speed breeding, phenomics, AI, robotics and satellite technology (**Figure 6**). While regulatory restrictions on the commercialisation of genome edited crops remains a challenge, there is a growing trend of countries exempting genome editing from these regulations, paving the way for broader adoption in agriculture. This period of decreasing regulation and new advancements in technology has the potential to aid in the development of crop varieties to combat challenges caused by climate change. Achieving meaningful progress requires not only technological advancements but also a cohesive pipeline with collaboration between biotechnologists, agronomists, engineers, plant breeders, farmers, agribusinesses and policy makers. Greater communication between these sectors will be essential to ensuring that the advancements in genome editing and AI-driven technologies translate into real-world agricultural solutions that address global yield stagnation, food security and climate resilience.

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Figure legends

Figure 1. Yearly yield average in tonnes per hectare per continent for wheat, rice, maize and soybean between 2000 and 2022.
(A) maize yield, (B) rice yield, (C) soybean yield, (D) wheat yield (Yield data are from Ritchie et al., 2022).

Figure 2. Impacts of climate change on crops and the environment.
The increase in temperature and growth of single cultivar at high density accelerate disease transmission (1), pest damage (2) and soil pathogens (5). The spray of chemicals (purple circles) in the field, like fertilisers and pesticides, leads to chemical release into the environment (3). Global climate change causes soil cracking and increases chemical movement into soil (4). Hot and dry climates increase soil salinization (white crystals represent salt) (6). Figure created with BioRender.

Figure 3. Timeline of the milestones in crop genetic improvement.
Light green indicates mutagenesis advancements, purple indicates plant genome sequencing, yellow indicates ZFN discoveries, red indicates CRISPR/Cas discoveries, orange indicates TALEN discoveries and light blue indicates expanding precision breeding techniques. All genome editing technologies have dark blue lines. Figure created with BioRender.

Figure 4. General genome editing pathway.
Schematic representation showing the procedures for genome editing. These include design and cloning, plant transformation, DSB formation, DSB repair pathways, screening of the transformed plants. For Design and Cloning, a representation of a plasmid is shown containing a developmental regulator gene (DR), Cas9 and sgRNA. Calli (green) are transformed with Agrobacterium (red), or protoplasts (green) are transformed via biolistic (grey gene gun) or polyethylene glycol (PEG)-meditated delivery. NGTs are shown in the blue box as mechanisms to engineer DSBs in a target site. ZFN comprises of a pair of zinc finger proteins, each with 4 binding domains (blue boxes), and a C-terminal Fok I nuclease (red) joined by a spacer (black line). TALEN consists of 2 transcription activator-like effector (TALE) proteins with effectors. Each effector has a repeat variable di-residue (RVD) that binds to a specific nucleotide (shown in the light blue box). Each TALE protein is attached to a C-terminal Fok I nuclease (red) by a spacer. Diagram of CRISPR/Cas9 shows single guide RNA (sgRNA, purple) bound to target site in DNA (dark blue) next to the PAM motif "NGG". Cas9 (cyan) RuvC and HNH domains then cut the DNA at the 2 cleavage sites (red triangles), which are opposite to each other. Diagram of CRISPR/Cas12a shows guide RNA only consists of crRNA (not tracrRNA). Note that PAM sequence is "TTN" and is at 5' end of the DNA. Cleavage sites (red triangles) are not aligned, therefore a staggered DSB is made. All DSBs can then be repaired by NHEJ or HR pathway, which can introduce small insertions and deletions, or DNA insertions, respectively. Figure created with BioRender.

Figure 5. Expanding genome editing technologies.
(A) Schematic representation of a cytosine base editing system (CBE) which uses nCas9 (cyan) fused with a cytidine deaminase (purple) to catalyse the conversion of cytosine (red circle) to uridine. Uracil glycosylase inhibitor (UGI) inhibits U:G mismatch from being resolved back to C:G so that U has to change to T. The single-guide RNA (sgRNA) is made up of CRISPR RNA (crRNA) and trans-activating CRISPR RNA (tracrRNA) and guides nCas9 (cyan) to the target site. Once the PAM motif "NGG" is recognised, nCas9 nicks a single strand of the DNA (SSB, red triangle), which is processed by the base editor. (B) Schematic representation of an epigenome editor with dCas9 (cyan) fused to TET1 or MQ1 epieffector domains. TET1 catalyses the demethylation of DNA while MQ1 catalyses the methylation of DNA. sgRNA and PAM sequence ensure dCas9 is located at target site. (C) Schematic representation of a CRISPR activation (CRISPRa) system where dCas9 is fused to transcription activator VP64. "TSS" represents the transcription start site. (D) Schematic representation of a CRISPR interference (CRISPRi) system where dCas9 is fused to transcription repressor SRDX. Figure created with BioRender.

Figure 6. Integration of genome editing and advanced technologies to increase crop productivity
Overview of how advanced technologies can be integrated from research to real-world agricultural application. Phenomics and genomics enable the identification of target genes, which inform genome editing strategies for developing new resilient and high-yield crop varieties. In the field, precision farming approaches involving use of robotics, AI, IoT network and satellite imagery, optimise resource use, reduce yield gaps, and expand productivity into less arable regions. Figure created with BioRender.

1194 **Table 1. Applications of the genome editing toolkits for crop improvement.**
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Crops	Target gene	Genome editing	Trait improvement
Strawberry	*FaPG1*	Mutagenesis (CRISPR-Cas9)	Improved fruit firmness (Lopez-Casado et al., 2023)
Soybean	*AIP2a, AIP2b*	Mutagenesis (CRISPR-Cas9)	Increased protein content (Shen et al., 2022)
Wheat	*TaGW2*	Mutagenesis (CRISPR-Cas9)	Increased yield (Wang et al., 2018)
Tomato	*SlWUS, SlCLV3, SlWOX9, SlTFL1*	Mutagenesis (CRISPR-Cas9)	Variations in fruit size, inflorescence branching and plant architecture (Rodriguez-Leal et al. 2017)
Maize	*ARGOS8*	Mutagenesis (CRISPR-Cas9)	Increased drought tolerance (Shi et al., 2017)
Soybean	*FAD2-1A, FAD2-1B, FAD3A*	Mutagenesis (TALEN)	High oleic acid content (Demorest et al., 2016)
Rice	*Os11N3*	Mutagenesis (TALEN)	Increase bacterial blight resistance (Li et al., 2012)
Maize	*IPK1*	Mutagenesis (ZFNs)	Herbicide tolerance and reduced phytate level (Shukla et al., 2009)
Wheat	*ALS*	Base editing (CRISPR-based method)	Herbicide resistance (Zhang et al., 2019)
Strawberry	*FvebZIPs1.1*	Base editing (CRISPR-based method)	Fine tuning sugar content (Xing et al., 2020)
Maize	*ZmALS1, ZmALS2*	Base editing (CRISPR-based method)	Herbicide resistance (Li et al., 2020c)
Rice	*Xa5, Xa23*	Prime editing	Increase bacterial blight resistance (Gupta et al., 2023)
Rice and rapeseed	*ORF79, ORF125*	Mitochondrial gene mutagenesis (mito TALENs)	Cytoplasmic male sterility (Kazama et al., 2019)
Lettuce	*psaA, psbA, rrn16*	Base editing on chloroplast genome	Herbicide resistance (Mok et al., 2022)
Cassava	*MeSWEET10α*	Epigenome editing	Increased bacterial blight resistance (Veley et al., 2023)

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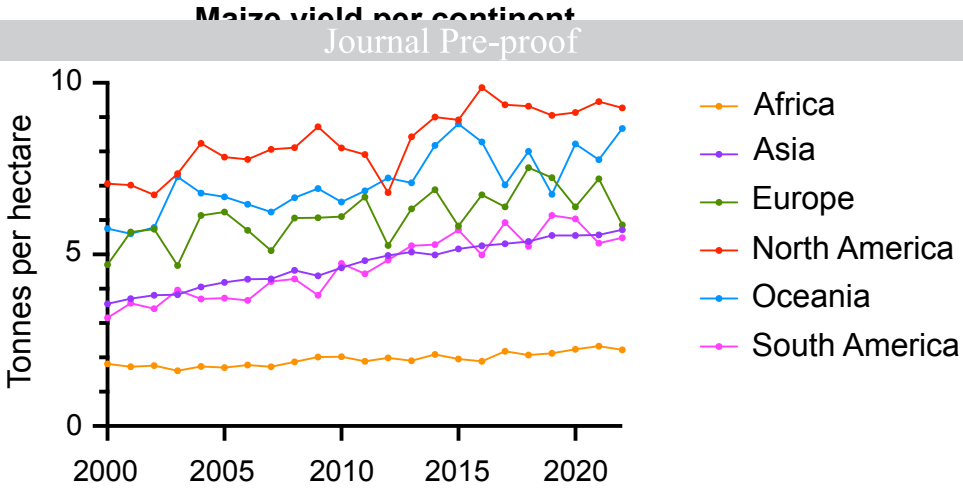
A



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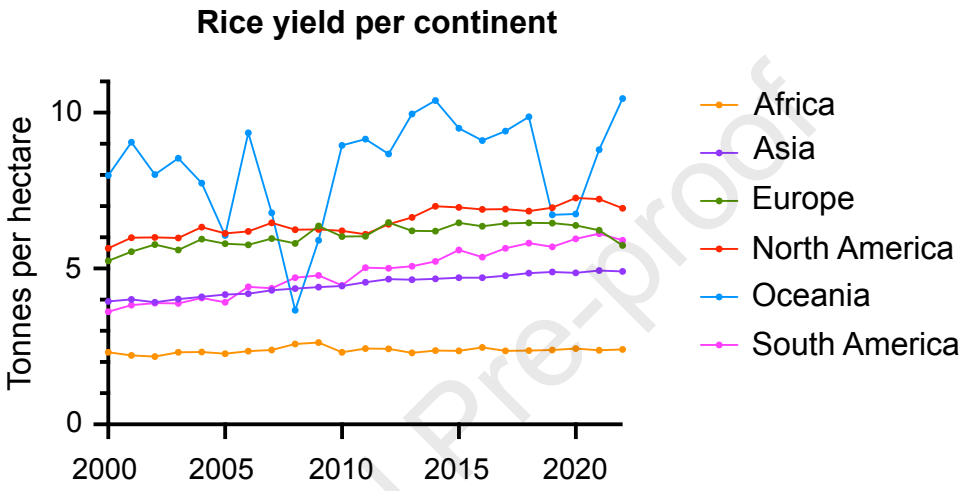

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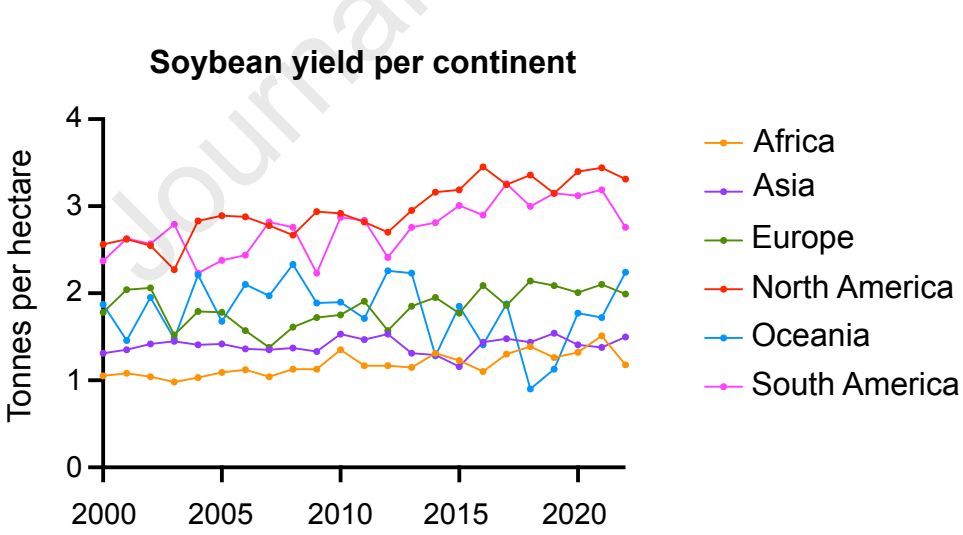

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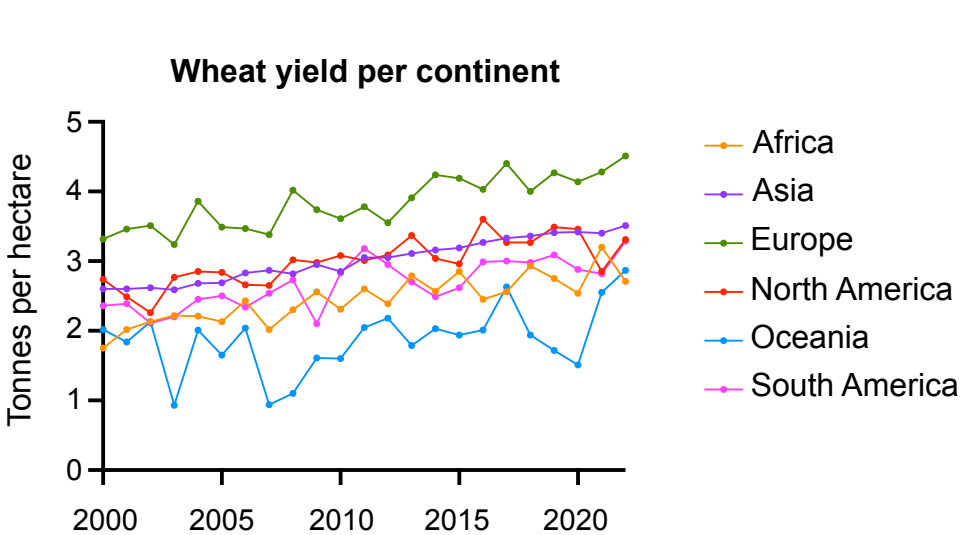
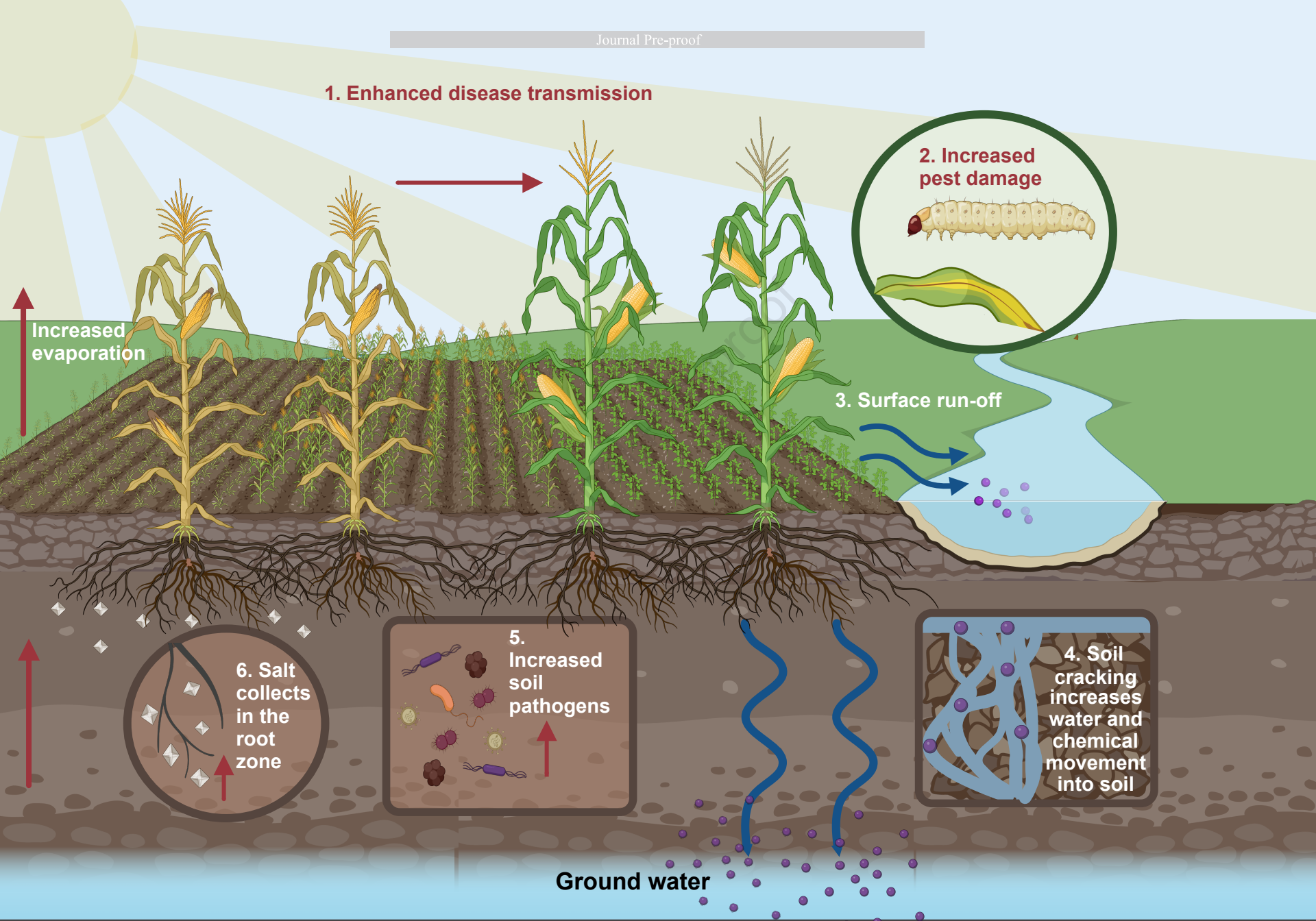




1928 **Radiation mutagenesis**
Induced mutagenesis using radiation in maize and barley (Stadler, 1928a,b)

1960s **Green revolution**

2000 **Arabidopsis genome sequenced** (The Arabidopsis Genome Initiative, 2000)

2000 **TILLING** (McCallum et al., 2000)

2007 **Discovery of CRISPR/Cas bacterial immune system** (Barrangou et al., 2007)

2009 **Maize genome sequenced** (Schnable et al., 2009)

2012 **CRISPR/Cas is an RNA-guided endonuclease** (Jinek et al., 2012)

2014 **Epigenome editing** (Johnson et al., 2014)

2016 **Base editing** (Komor et al., 2016)

2019 **Prime editing** (Anzalone et al., 2019)

2019 **Mitochondrial genome editing in plants**
Curing CMS in rice and rapeseed with mitoTALENS (Kazama et al., 2019)

1944 **Chemical mutagenesis** (Auerbach and Robson, 1944)

1994 **First commercial GM crop**
Flavr-Savr tomato (Kramer and Redenbaugh, 1994)

2002 **ZFNs developed** (Bibikova et al., 2002)

2005 **Rice genome sequenced** (International Rice Genome Sequencing Project and Sasaki, 2005)

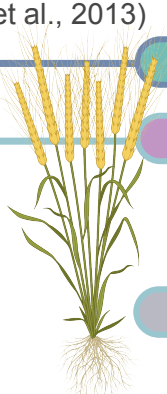
2010 **Soybean genome sequenced** (Schmutz et al., 2010)

2011 **TALENs developed** (Mahfouz et al., 2011)

2013 **CRISPR/Cas first used in eukaryotes** (Jinek et al., 2013), (Cho et al., 2013)

2013 **CRISPRa and CRISPRi** (Bikard et al., 2013)

2018 **Wheat genome sequenced** (The International Wheat Genome Sequencing Consortium et al., 2018)

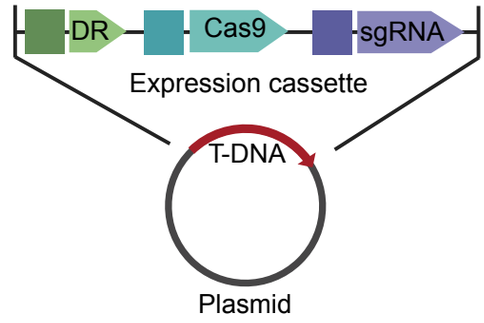


2018 **Speed breeding** (Watson et al., 2018)

Selection of genomic target (20 bp sequence followed by PAM)

Design and selection of targeting sgRNA

Cloning of construct in suitable plant vector

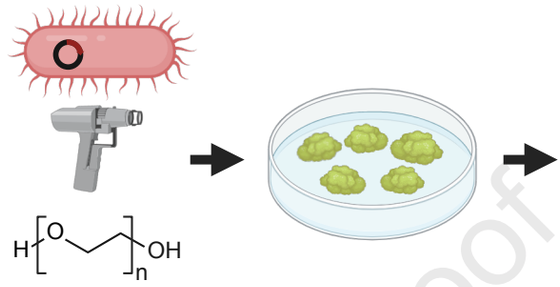


Design & Cloning

Rapidly proliferating calli incubated with agrobacterium

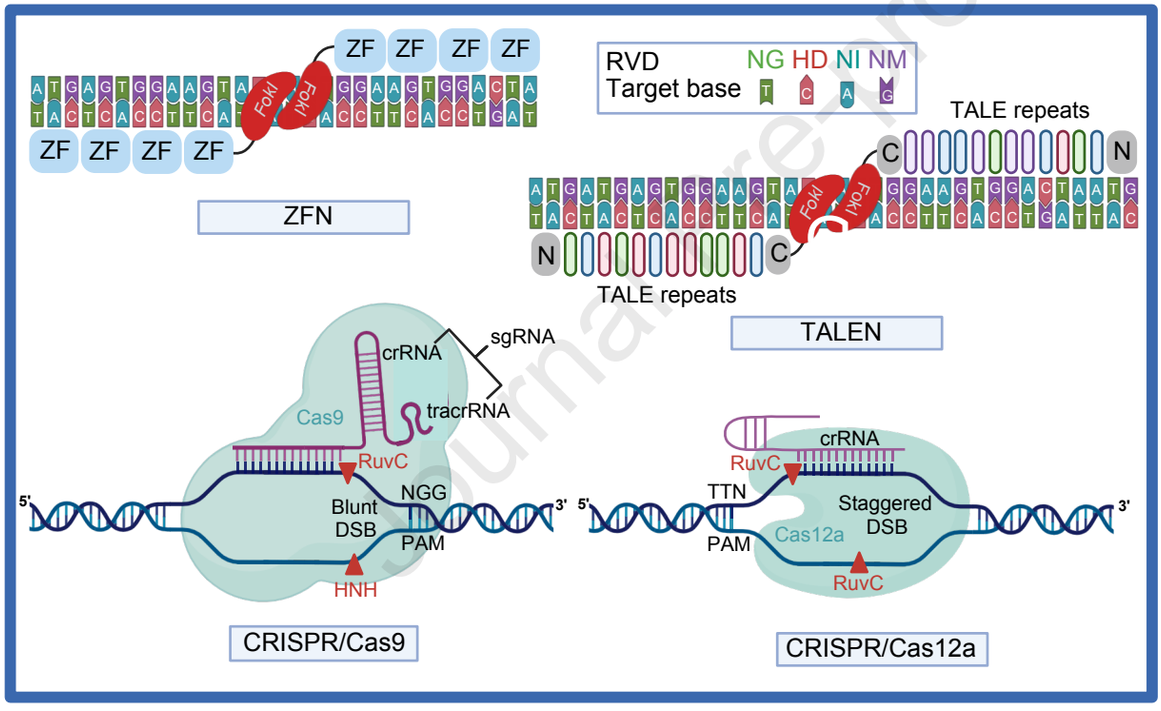
or biolistic delivery

or polyethylene glycol (PEG)-mediated delivery



Regeneration of transgenic plants

Transformation



Create a DSB

G1 and G2 phase

NHEJ

HR

S phase

DSB

Small insertions and deletions

Template DNA

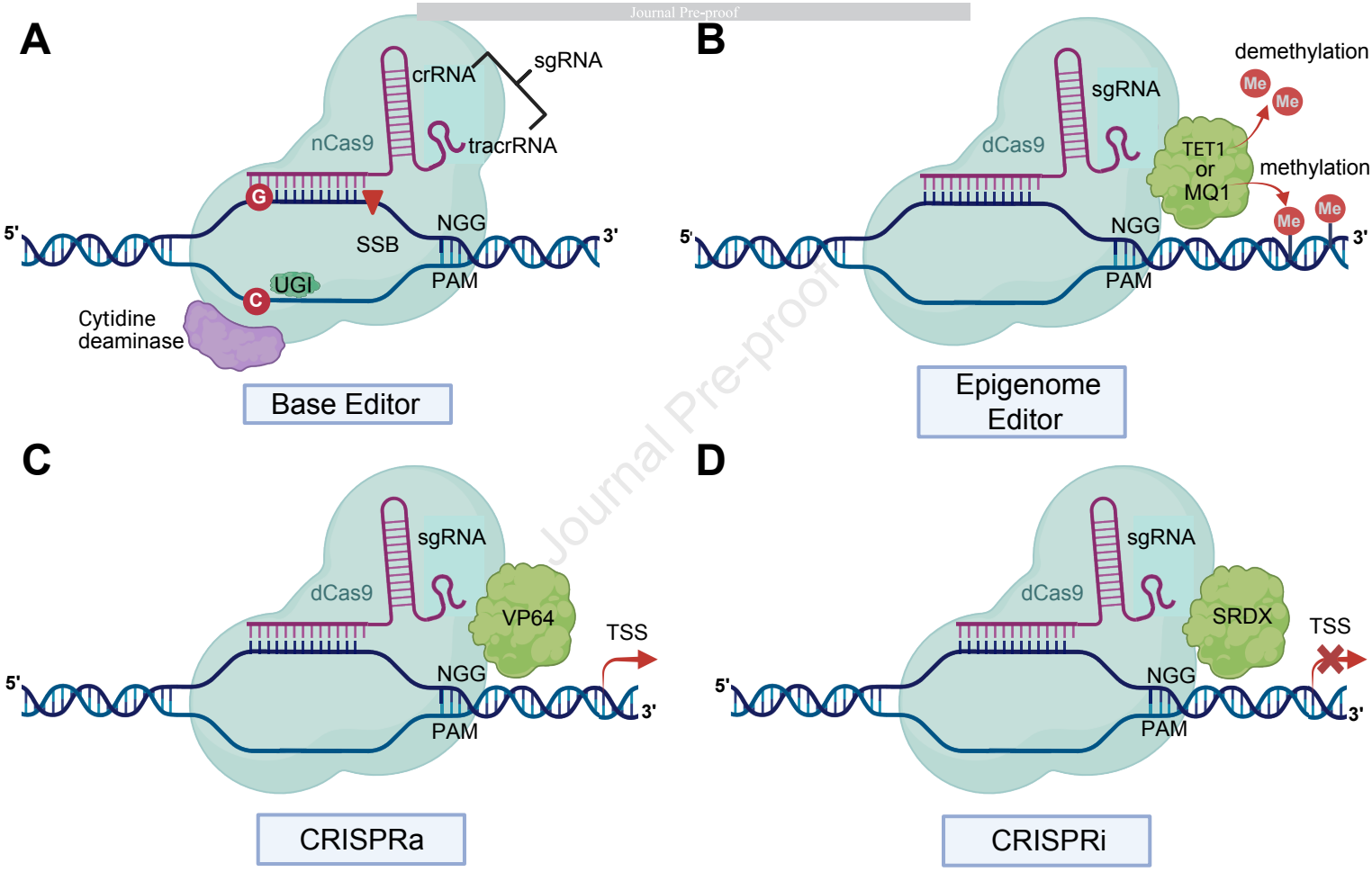
DNA insertion

DNA repair enzymes mistakenly cause indels

Repair

Identification of edited lines for screening by Sanger sequencing

Screening



AI & data processing

Linking complex phenotypes to genotypes and predicting gene function

Genome Editing

Targeted editing and tuning expression of identified genes for resilience and productivity

Precision farming with GE crops

Satellite data for global crop forecasting

AI-powered mobile apps for decision support for farmers

Real-time imaging and mapping

Collaborative UGVs

Robotics & automation for optimisation and sustainability

IoT sensors

IoT sensors

Monitoring growth and biotic and abiotic stress

Phenomics

Plant trait data

Genomics

Sequence and analyse genomes

Research → **Application**