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Novel Strategies for Designing Climate-Smart Crops to Ensure Sustainable Agriculture and Future Food Security

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ABSTRACT

To fulfil food and nutritional demand for nine billion people by the mid-21st century, global food production must increase by 60% regardless of challenges such as environmental pollution, water scarcity and land degradation. Climate change exacerbates the frequency and intensity of biotic and abiotic stresses, which, in turn, severely compromise global crop yields, jeopardize food supply, deteriorate sustainable development goals for achieving global food safety, and limit sustainable climate-smart crop production. Current food production and consumption practices negatively influence the environment, posing a major threat to the global ecosystem and human health. Addressing these critical issues to achieve sustainable agriculture necessitates designing future crops employing cutting-edge breeding strategies for enhanced productivity with minimal environmental footprints. This endeavour requires a comprehensive understanding of plant stress adaptation, signalling pathways and mitigation mechanisms. In this review, we first explain the diverse impacts of ongoing climate change events on crop production. Subsequently, we outline various strategies to tackle climate change, including agronomic practices, and advanced technologies for understanding the physiological and molecular mechanisms of plant stress tolerance. We also discuss breeding and engineering crops with superior stress tolerance and disease resistance and nurturing healthy microbial partnerships between plants and soil to ensure food and nutrition security for current and future populations amidst mounting environmental challenges.

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1 | Introduction: Future Need of Climate-Smart Crops

Climate change threatens global food and nutritional security, sustainable development and efforts to combat deficiencies (e.g., protein, vitamins, iron, zinc and other micronutrients) (<https://www.un.org/en/climatechange/science/causes-effects-climate-change>; Zandalinas et al. 2021; Yang et al. 2024). The rising frequency and intensity of climatic (e.g., extreme temperatures, flood, drought and UV), biotic (e.g., bacteria, viruses, insects and fungi), soil-related (e.g., soil salinity, nutrient deficiency, microbiome dysbiosis and pH imbalance) and anthropogenic (e.g., heavy metals, organic pollutants, microplastic, elevated CO₂ and herbicides) stresses are impacting agricultural production and notably threatening the entire food system globally (Figure 1; <https://openknowledge.fao.org/items/e5a5771a-6127-4e4a-ae1c-9f26fe8aa770>).

These stresses, individually or in combination, significantly affect morphological, physiological, biochemical, molecular and metabolic mechanisms, thereby hampering growth, productivity and harvest quality (Rivero et al. 2022; Cooper and Messina 2023; Raza, Bashir, et al. 2024; Raza, Salehi, et al. 2024; Zandalinas et al. 2021, 2024). It is worth noting that agriculture sustains the livelihoods of more than 2.5 billion people globally (<https://openknowledge.fao.org/items/e5a5771a-6127-4e4a-ae1c-9f26fe8aa770>). Considering the critical reliance of agriculture on natural sources and its dynamic roles in national socio-economic development, decisive and urgent actions are imperative to build and design more climate-smart agricultural systems (<https://openknowledge.fao.org/items/e5a5771a-6127-4e4a-ae1c-9f26fe8aa770>).

The world's population is predicted to reach 9.7 billion by 2050 and 10.4 billion by the mid-2080s, with the maximum expansion

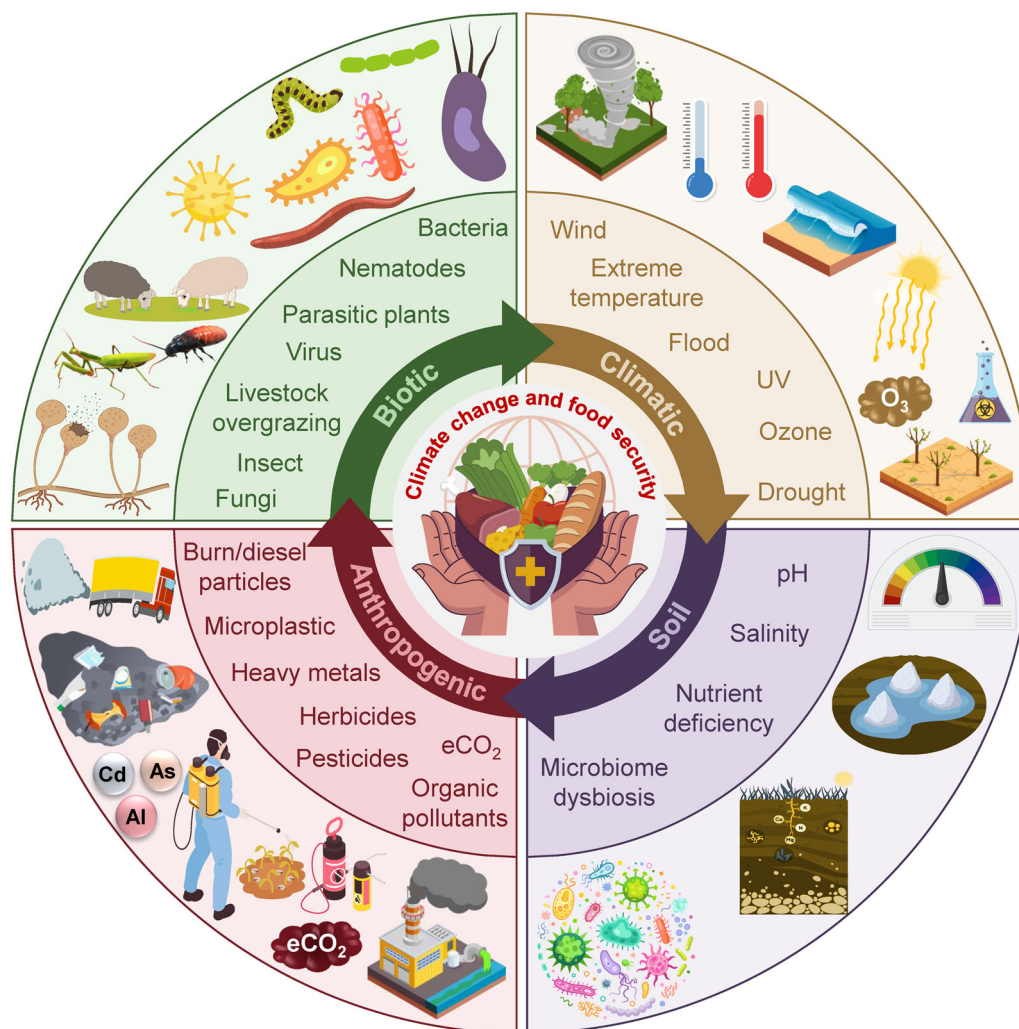


FIGURE 1 | Diverse stress sources affect crop yield and food security. Individual or combined stresses from different sources, such as biotic, climatic events, soil-related and anthropogenic, could adversely affect yield and trigger food, feed and fibre deficiencies. Climatic stresses describe climate-related environmental factors that impose stress on crops. These climatic events can disrupt growth, damage plant tissues, and decrease crop yields. Biotic stresses include various living organisms that can harm crops. These stresses can lead to diseases, infestations and other detrimental effects on plant health. Soil-related stresses can hinder plant growth, nutrient uptake and global productivity. Anthropogenic stresses focus on human-induced stress factors and these pollutants can contaminate the soil and water, triggering long-term damage to ecosystems and world food security. The central part of the figure features the interconnection of these stresses and their combined impact on climate change and food security. The circular arrows indicate the interaction between different types of stress and their combined effect on agricultural productivity. The idea of stress types were obtained from Zandalinas et al. (2021) under CCBY 4.0 license.

in developing countries (<https://www.un.org/en/global-issues/population>). The growing demand for food and animal feed requires a 60% increase in agricultural production by 2050, driven mainly by population increase, shifting diets and economic changes in many regions. Furthermore, future food demand will also depend on factors such as income levels and consumption models, which may change by region (<https://www.iaea.org/topics/food-security-and-climate-change>). Nonetheless, future climate change events will continue to impact global agricultural production, making it even more difficult to meet the growing demands. In 2023, 713–757 million people confronted hunger, and ~2.4 billion underwent moderate to severe food insecurity (<https://www.fao.org/interactive/state-of-food-security-nutrition/en/>; <https://www.fao.org/newsroom/detail/world-must-look-to-south-america-success-in-reducing-hunger-fao-chief-economist/en>). Food insecurity is anticipated to deteriorate as the global population expands and climate change events (mainly drought, heat, floods, soil salinity, etc.) become more frequent. Achieving food security and the ‘zero hunger’ UN Sustainable Development Goal for the anticipated population requires a substantial agricultural revolution (<https://www.un.org/sustainabledevelopment/hunger/>). This necessitates designing climate-smart, stress- and disease-tolerant agricultural systems capable of advancing food and nutrition security for current and future generations, notwithstanding mounting threats.

Diverse stress factors are already affecting crop and livestock production globally (Figure 2). When combined, these factors have

the potential to trigger catastrophic crop production losses (Rivero et al. 2022; Zandalinas et al. 2021, 2024). For example, climate change has disrupted the global yields of 10 major crops, that is, rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), sorghum (*Sorghum bicolor* L.), barley (*Hordeum vulgare* L.), cassava (*Manihot esculenta* L.), oil palm (*Elaeis oleifera* L.), rapeseed (*Brassica napus* L.), soybean (*Glycine max* L.), and sugarcane (*Saccharum officinarum* L.), reducing overall consumable food calories by about 1% (Schleussner et al. 2018; Ray et al. 2019). Agriculture is also confronted by the dual challenges of reducing emissions while dealing with the devastating consequences of extreme climatic events, which erode productivity and inflict significant nutritional deficiencies (<https://www.fao.org/interactive/state-of-food-security-nutrition/en/>).

The predicted future climate scenarios require a dramatic change in cropping patterns and the implementation of mitigation systems to adapt to new crop/land suitability. Current agricultural systems are changing with more specific use of technologies and inputs, driven by climate change and the progressive requirements of the global food system (<https://www.worldbank.org/en/topic/climate-smart-agriculture>). Therefore, novel strategies are required to assess the influence of climate change and adjust to its effects, enhancing agriculture and strengthening food invention systems. Sustainable production and mitigation technologies can safeguard food security and nutrition, advance food quality and safety, support livelihoods of farmers, shield the environment and biodiversity and assist safe trade and financial growth,

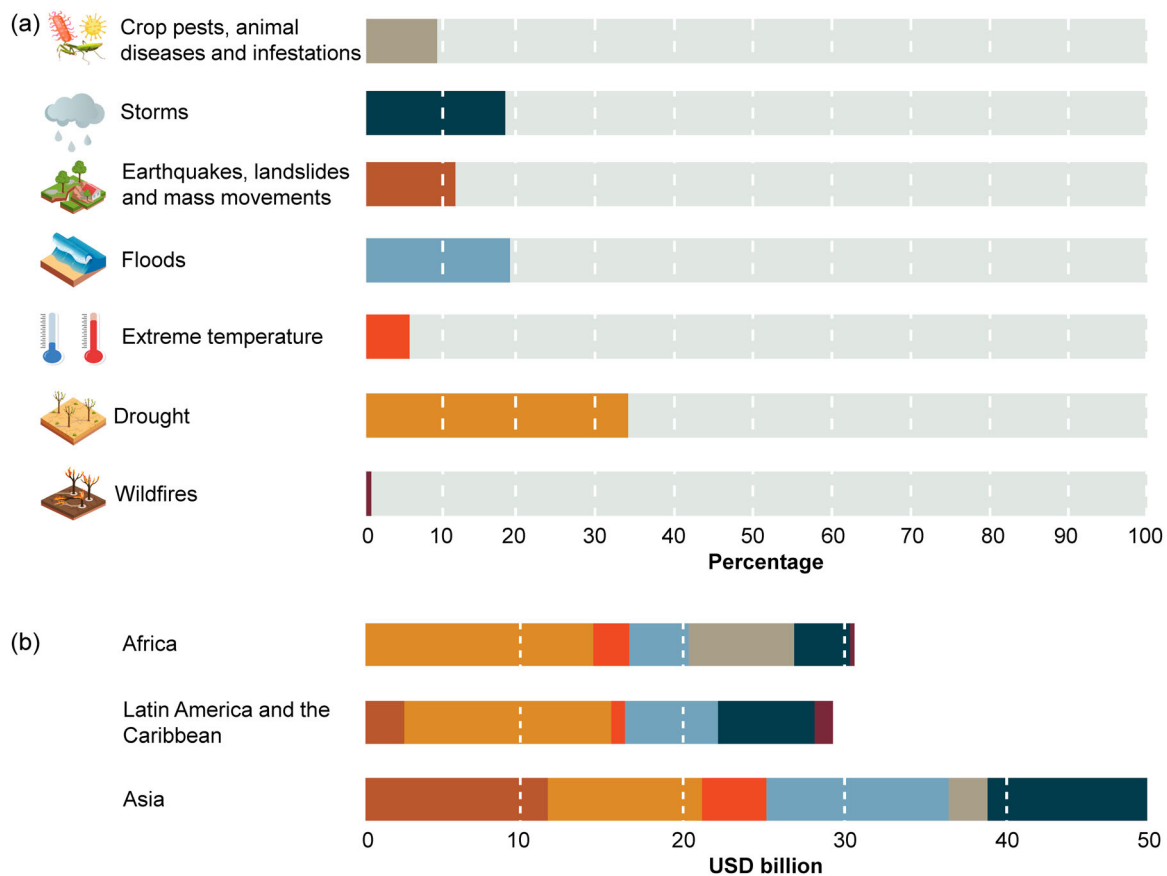


FIGURE 2 | Production losses caused by climate change events. (a) Total crop and livestock production loss per stress type, and (b) loss by region per stress. Colour represents the stress type, as shown in part (a). Adapted from FAO (<https://openknowledge.fao.org/handle/20.500.14283/cb3673en>) under CC BY-NC-SA 3.0 IGO license.

mainly in developing countries (<https://www.fao.org/plant-production-protection/about/en>). To achieve this goal and mitigate the impact of climate change on crop yield and productivity, it is essential to understand the adaptation and tolerance mechanisms of plants, as well as various adaptation and mitigation strategies, including agronomic, physiological, biotechnological and microbiome approaches for designing climate-smart crops for the future.

2 | The Interplay of Climate Change and Agricultural Production: How Does Climate Impact Yield and Productivity?

2.1 | CO₂ Is One of the Major Drivers for Climate Change

It is anticipated that future interplay of climate change events will continue to affect agricultural production globally (Figure 3a). This impact is mainly associated with the reduction/impairment of cropland due to the negative impact of climate change on croplands that significantly affect productivity (Figure 3b). As climate change increases, various environmental stresses pose significant challenges to crop yield and quality (Yang et al. 2024). Of these, carbon dioxide (CO₂) has long been deemed a fundamental driver of climate change, with concentrations surging from 280 mmol mol⁻¹ (pre-industrial) to 420 mmol mol⁻¹ in a mere 150 years (Figure 4) (https://earth.org/data_visualization/a-brief-history-of-co2/). Elevated CO₂ concentrations, coupled with emissions of other greenhouse gases (e.g., methane, nitrous oxide and fluorinated) into the atmosphere, contribute to the entrapment of planetary heat and pose a profound challenge to global warming (Zandalinas et al. 2021; Yang et al. 2024). Despite the International Panel on Climate Change's (IPCC's) final warning to restrict global temperature increases to 1.5°C, numerous countries have already surpassed this critical threshold (<https://www.climate.gov/news-features/features/whats-number-meaning-15-c-climate-threshold>; <https://www.ipcc.ch/sr15/>).

2.2 | Elevated CO₂: Friend or Foe to C₄ and C₃ Plant Growth

Intriguingly, CO₂ also acts as an atmospheric fertilizer, improving plant growth, based on nutrient and water availability, species, and environmental conditions (De Kauwe et al. 2021). Nonetheless, C₄ plant species, including major crops such as maize and sorghum, demonstrate a less pronounced response to elevated CO₂ due to the localization of ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) in bundle sheath cells. Within these cells, CO₂ becomes concentrated to levels three to six times higher than atmospheric concentrations, leading to RuBisCO saturation. Theoretically, this saturation impedes any further increase in CO₂ uptake despite rising atmospheric CO₂ concentrations (Long et al. 2006; Sales et al. 2021). In contrast, C₃ crops such as rice and wheat exhibit heightened responsiveness to elevated CO₂ because of their augmented CO₂ saturation threshold for photosynthesis, with intercellular CO₂ levels reaching approximately 600 mmol mol⁻¹. This response is complicatedly governed by the dynamic interplay between RuBisCO carboxylation rates and the inhibition of RuBisCO oxygenation

rates (Figure 4) (Dingkuhn et al. 2020; Eckardt et al. 2023). Notably, experimental findings indicated that elevated CO₂ (550–590 mmol mol⁻¹) results in a substantial increase of approximately 17% in wheat and rice yields relative to ambient concentrations (Ainsworth and Long 2005; Hu et al. 2021). Hence, it can be postulated that C₃ crops present a distinctive opportunity to efficiently capture more carbon from a CO₂-enriched environment (with anticipated CO₂ levels reaching 550–600 mmol mol⁻¹ by 2050) and convert it into biomass and yield (Ainsworth and Long 2021). Nonetheless, one of the forthcoming research efforts should concentrate on enhancing the carbon sink capability of C₃ crops to optimize carbon assimilation rates (Dingkuhn et al. 2020).

2.3 | Elevated CO₂ Intensifies Climate Change Drivers and Subsequently Impacts Plant Performance

The entrapment of planetary heat and the resulting global warming have led to a rise in atmospheric temperature, which are intricately associated with other climate-change induced drivers, collectively exerting pernicious impacts on crops. The elevated temperature alone consistently exerts detrimental impacts on plant growth and development, encompassing but not limited to (i) disruption of photosynthetic efficiency, leading to a shortened life cycle and diminished yields; (ii) decline in respiratory enzyme activities, resulting in energy deficiency; (iii) heat-induced movement of biomolecules disturbing plasma membrane homeostasis, altering permeability and fluidity, leading to ion and amino acid leakage; (iv) a surge in reactive oxygen species (ROS) causing irreversible oxidative damage, particularly in photosystems I and II; and (v) alterations in plant phenotypes including growth retardation and wilted plant architecture in the vegetative stage, and reduced pollen viability, abnormal fertilization, and compromised grain filling in the reproductive stage (Figure 4) (Zhao et al. 2017; Raza, Bashir, et al. 2024). Furthermore, the recent escalation in night temperatures exceeding optimal thresholds presents a novel threat, adversely impacting various crops, including rice, wheat and cotton (*Gossypium hirsutum* L.), through heightened night respiration rates and reduced starch accumulation in developing organs (Khan, Min, et al. 2020; Eckardt et al. 2023). Projections anticipate a 1°C temperature rise detrimentally impacting growth of pivotal crops such as rice, maize and wheat, resulting in respective yield declines of 2.8%, 2.6% and 2.4%. Interestingly, positive responses are anticipated for the yields of potato (*Solanum tuberosum* L.), sorghum and soybean, with projected increases of 1.5%, 1.9% and 2.2%, respectively, in response to the equivalent temperature increment (Agnolucci et al. 2020). It was also reported that 1.5°C and 2°C warming above pre-industrial levels and different CO₂ levels has been affecting the yield of wheat, rice, soybean and maize, and increasing CO₂ will have a more potent effect than 0.5°C increase on crop yield reduction in the future (Schleussner et al. 2018).

Nonetheless, the escalation of temperatures raises the vapour pressure deficit, potentially intensifying daily crop water demand and exacerbating drought stress without adequate soil water supply (Sadok and Jagadish 2020). Unfortunately, projections indicate a potential doubling of water demand for agriculture by

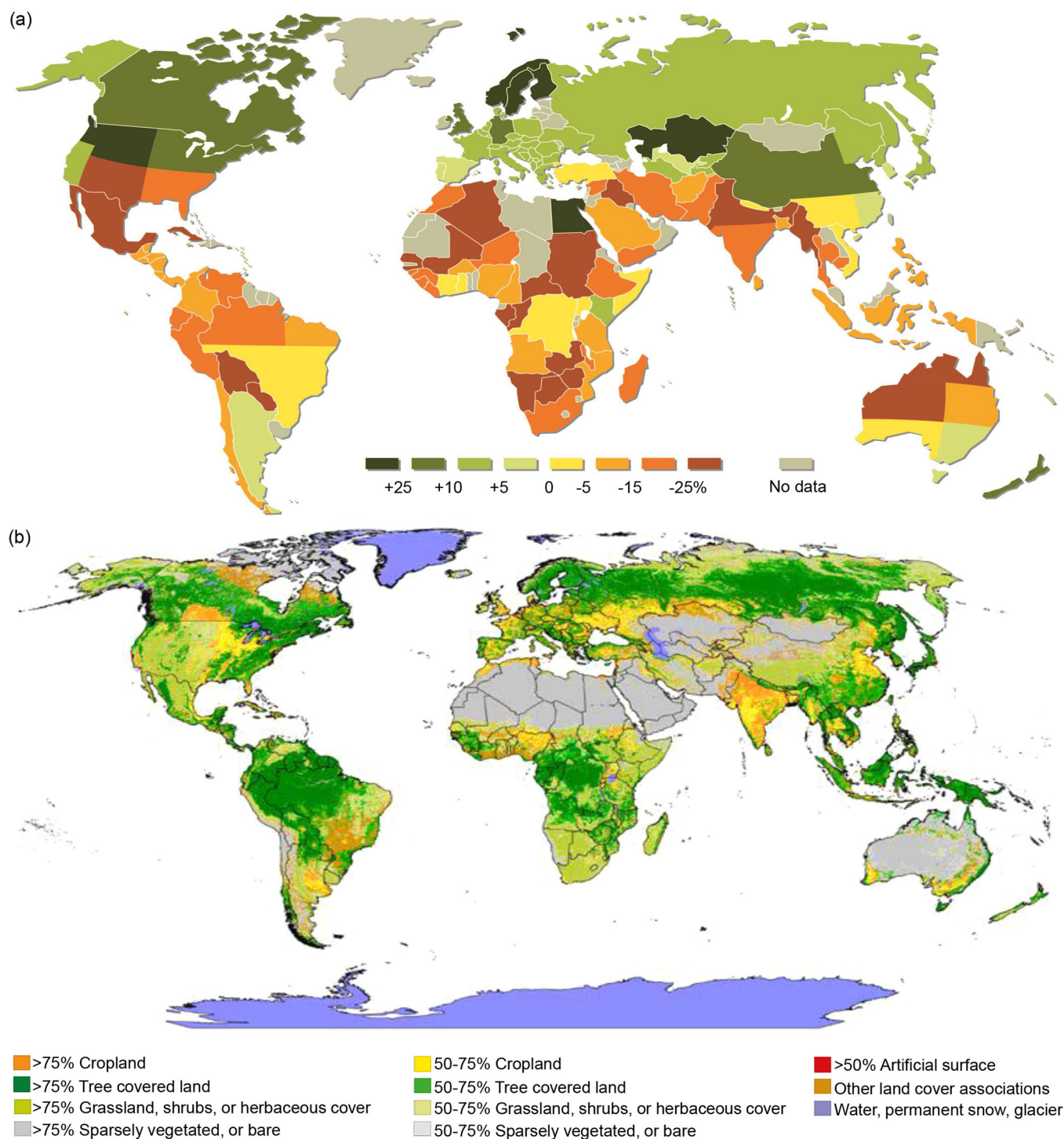


FIGURE 3 | The interplay of changing climate and agricultural production worldwide. (a) Predicted impact of climate change incidents on agricultural production by the 2080s, compared to 2003 levels. This map describes the anticipated effects of climate change on crop production, highlighting the urgent need to increase agricultural production in the face of the climate crisis and threatening food scarcity. Adapted from EEA (<https://www.eea.europa.eu/en>). (b) Agricultural land use and climate. Quick growth in urban areas has shifted all types of agricultural land use. Adapted from FAO (<https://openknowledge.fao.org/items/55def12b-2a81-41e5-91dc-ac6c42f1cd0f>) under CC BY-NC-SA 3.0 IGO license.

2050, coupled with a predicted 50% reduction in freshwater availability due to climate change. Consequently, drought has been deemed the single most significant cause of agricultural production loss, amounting to approximately \$37 billion in the past decade (<https://www.fao.org/interactive/disasters-in-agriculture/en/>). In addition, the rapid onset of flash droughts within a short period, in contrast to the traditionally long and

slowly developing drought, has become an emerging threat, impacting approximately 74% of global regions over the past 6 decades (Yuan et al. 2023). The deleterious impacts of drought commence with hindrances to seed germination, extending to subsequent reductions in leaf area, thereby limiting light interception area and, ultimately photosynthesis (Raza, Charagh, Salehi, et al. 2023; Raza, Mubarik, et al. 2023; Cooper and

Messina 2023). Furthermore, drought-driven stomatal closure may elevate overall crop temperatures, causing detrimental impacts on the photosynthetic apparatus and reducing RuBisCO activity and thylakoid membrane stability. This, in turn, accelerates development and intensifies leaf senescence rates, resulting in yield penalties (Leakey et al. 2019; Moore et al. 2021; Cooper and Messina 2023). Drought stress also catalyzes nutrient

stress, as the decrease in soil moisture results in a lowered rate of nutrient diffusion from the soil matrix to the absorbing root surface and disrupts the translocation of nutrients to the leaves (Cooper and Messina 2023).

Rising temperatures elevate the atmosphere's capacity to hold moisture, resulting in increased humidity. This warming also

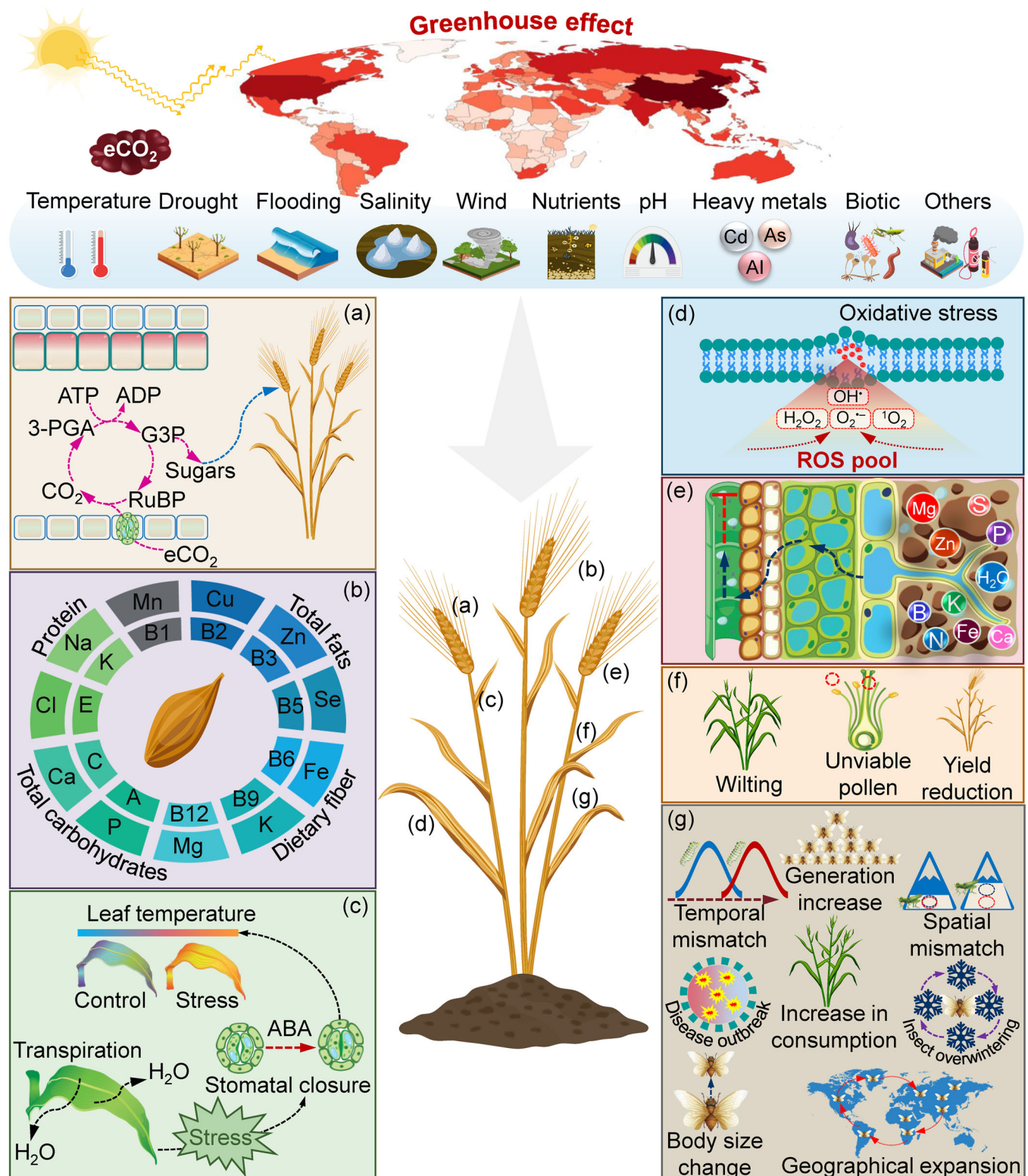


FIGURE 4 | Legend on next page.

accelerates the melting of polar ice sheets and glaciers, contributing to the heightened risk of flooding, which is ranked as the second gravest disaster (<https://www.fao.org/interactive/disasters-in-agriculture/en/>). While droughts may take weeks to manifest in the field, flooding can swiftly ensue within hours to days after a sudden downpour, particularly in areas with poor soil drainage. Globally, approximately 27% of cultivated lands experience annual flooding and the annual costs of flood damage over the last half-century have reached a significant value of US\$ 21 billion (<https://www.fao.org/interactive/disasters-in-agriculture/en/>). Climate models predict an escalation in yield penalties due to waterlogging, rising from historically observed levels of 3%–11% to an anticipated range of 10%–20% by 2080. These penalties underscore a trade-off intricately tied to the duration and timing of waterlogging relative to the crop growth stage (Liu et al. 2023). With notable exceptions such as rice, the complete submergence of plants induces a diminished oxygen supply to the roots, inhibiting aerobic respiration, leading to rapid depletion of starch reserves and the generation of harmful by-products such as alcohols, aldehydes and ROS (Voesenek and Bailey-Serres 2015). During waterlogging, there is an overall shift of the plant energy allocation from growth to survival, resulting in reductions in growth, height and yield, ultimately posing a potential threat to plant viability (Langan et al. 2022). Escalated temperatures-induced rising sea levels and persistent drought have given rise to an additional silent threat, soil salinity, that results in a projected annual loss of US\$ 31 in agricultural productivity, declaring up to 1.5 Mha of cropland unproductive each year and reducing the production capacity of up to 46 Mha annually (<https://www.fao.org/global-soil-partnership/areas-of-work/soil-salinity/en/>). A distinctive aspect of salinity stress lies in its ability to concurrently induce ionic toxicity, osmotic stress and oxidative stress, directly influencing plant growth and development, ultimately leading to yield penalty of crops (Raza, Tabassum, et al. 2023; Raza, Charagh, Salehi, et al. 2023).

2.4 | Elevated CO₂-Induced Climate Change Drivers Intensifying Biotic Stress and Subsequently Impacts Plant Performance

The complicated interplay of climate change drivers, encompassing elevated CO₂, increasing temperatures, impulsive precipitation and humid conditions, prompts outbreaks of plant diseases, resulting in an annual economic toll of approximately

US\$220 billion globally (<https://www.fao.org/newsroom/detail/New-standards-to-curb-the-global-spread-of-plant-pests-and-diseases/en>). Global crop yield losses due to pests and diseases are substantial, with mean losses of 21.5% in wheat, 30.3% in rice, 22.6% in maize, 17.2% in potato and 21.4% in soybean (Savary et al. 2019). As the climate shifts, the natural timing of insect life cycles is thrown into disarray, causing a cascade of mismatches between crops and the environmental conditions they depend on (Figure 4). Consequently, farmers grapple with crops that no longer align with the seasons or agricultural schedules, making it harder to cultivate and harvest at the right time. Meanwhile, pests and pathogens are rapidly adapting to the warmer climate. Their accelerated life cycles result in more frequent and severe outbreaks, posing a significant threat to crop yields. This quickening pace is further complicated by the shifting geographical ranges of both crops and their adversaries (Figure 4). As the climate changes, pests, diseases and invasive species spread into new territories, presenting fresh challenges for agricultural management and food security. Warmer winters, once a period of relief, now allow more pests to survive the cold months of the year (Figure 4). Consequently, their populations surge, intensifying the damage they inflict on crops.

A warmer climate has the potential to intensify the metabolic rate of individual insects, leading to a subsequent increase in the rate of their food consumption (Figure 4). Additionally, rising temperatures shorten the incubation period of pathogens, contributing to an elevated abundance of pathogens throughout a growing season (Deutsch et al. 2018). Notably, elevated temperatures can give rise to the emergence of new strains of pathogens that exhibit enhanced adaptation and increased virulence (Cohen and Leach 2020). For instance, *Fusarium culmorum*, which thrives in cool and wet conditions, may be outcompeted by the more aggressive *F. graminearum*, which prefers warm and humid conditions (Parikka et al. 2012). Elevated CO₂, on the other hand, influences the outcomes of plant–pathogen interactions, intensifying the powdery mildew of cucurbits (Khan and Rizvi 2020) and head blight and blotch of wheat (Váry et al. 2015), while reducing susceptibility in soybeans towards the downy mildew (Eastburn et al. 2010), highlighting the need for a comprehensive framework to better understand and predict these effects and consequences. Elevated humidity and soil moisture exacerbate infection rates of *Sclerotinia sclerotiorum* in lettuce (*Lactuca sativa*) (Mamo et al. 2021) and *Phytophthora sojae* in soybean (Tada et al. 2021), while low moisture conditions increase pathogen

FIGURE 4 | Impact of climate change on crop productivity. (a) Increased atmospheric CO₂ benefits C3 plants by boosting intercellular CO₂ concentration and leaf area, ultimately enhancing crop growth and yields. (b) Increased CO₂ boosts C3 plant growth but diminishes essential nutrient concentrations in different organs due to increased biomass and carbon content dilution. Elevated levels of CO₂, along with other greenhouse gas emissions, result in heat retention in the atmosphere, presenting a significant challenge in the form of global warming. (c) This heightened heat triggers various abiotic stresses such as drought, salinity and waterlogging, reducing transpiration rate as plants conserve water by utilizing abscisic acid. This reduction, in turn, increases leaf temperature and disrupts photosynthetic efficiency. (d) Consequently, reactive oxygen species rises, causing irreversible oxidative damage, especially in photosystems I and II. (e) Notably, these stresses also diminish the rate of essential nutrient acquisition by disrupting root hydraulic conductivity. (f) All these ultimately lead to growth retardation and a wilted appearance during the vegetative stage. In the reproductive stage, there is a reduction in pollen viability, abnormal fertilization, and compromised grain filling, resulting in a significant yield penalty. (g) The complex interaction of climate change drivers, including elevated CO₂, rising temperatures, erratic precipitation and increased humidity, triggers the emergence of plant diseases. These factors collectively contribute to temporal shifts in pathogen activity, population growth, spatial changes, overcoming winter periods, altered geographical distribution, reduced body size, heightened consumption and ultimately, the onset of disease outbreaks.

numbers for *Magnaporthe oryzae*, the causal agent of rice blast (Bidzinski et al. 2016), and *Streptomyces* spp., responsible for bacterial scab in potatoes (Johansen et al. 2015). Nonetheless, the unpredictability of climate change will induce many uncertain shifts in insect and pathogen biology, host specificity and environmental favorability, posing challenges to accurate predictions.

3 | Novel Strategies for Designing Future Climate-Smart Crops

3.1 | Agronomic Practices: Nurturing the Soil and the Soul of Agriculture to Adapt to Changing Climate

Healthy soils ensure food and nutritional security, water quality, climate change mitigation/adaptation, and human health and help to establish healthy ecosystems and societies (<https://news.un.org/en/story/2015/04/496462>). Soil health management is of significant importance to meet global food demands as it dictates crop yield outcomes (Grassini et al. 2013). The theory underlying the relationship between agricultural production and soil health is primarily predicated on the idea that better soil health will mitigate changing climate that restricts crop development (such as improved availability of nutrients or water and increased disease resistance), ultimately leading to higher yields (<https://www.fao.org/plant-production-protection/about/en>).

Diversification is emphasized in ecologically oriented agricultural practices by utilizing locally adapted seeds, spreading green manure, combining crops and intercropping, and employing biological pest management. These methods specifically concentrate on plant health, water balance and soil texture for sustainable agricultural production in the face of a changing climate (<https://www.fao.org/family-farming/practices-techniques/en/>). In this context, it is vital to highlight the role of locally adapted seeds and crop diversification in enhancing tolerance against stressful conditions. Applying such practices can improve nutrient cycling, pest suppression and water-use-efficiency, which are necessary for climate adaptation.

To preserve and enhance the competitiveness and sustainability of crops exposed to diverse stressors, diverse agronomic strategies need to be implemented. For instance, coping with adverse environmental conditions requires the implementation of potential adaptations for cropping systems (Brito et al. 2019). Notably, a significant proportion of the crops grown in organic farming today were initially chosen for conventional farming that count on heavily on high-input methods (Gamage et al. 2023). However, this presents an opportunity for researchers and farmers to focus on developing new varieties that are better suited to organic farming practices. In this way, we can continue to improve the sustainability and overall success of organic farming (Gamage et al. 2023). Thus, we argue that future research efforts should focus on agronomic programmes that prioritize traits such as biotic resistance, abiotic stress tolerance and nutrient use efficiency, specifically designed for low-input and organic systems.

One of the major barriers to agricultural productivity is low soil fertility. Adding legumes to cropping systems has improved soil

fertility and its physical, chemical and biological characteristics. Compared with sole cropping, legume-based intercropping has been shown to augment crop productivity under stressed environments (Chamkhi et al. 2022). For example, overall yield was observed to be intensified under low water supply when pearl millet (*Pennisetum glaucum*) and cowpea (*Vigna unguiculata*) were intercropped (Nelson et al. 2022). Similarly, arbuscular mycorrhizal fungi (AMF) application in thyme (*Thymus vulgaris* L.) plants intercropped with soybean improved their macro- and micro-nutrients and essential oil percentage under water deficit conditions (Amani Machiani et al. 2021). Escalation in the environmental use efficiency via different root distributions could be the major reason for this intercropping-mediated increase in nutrient content. Root exudation of enzymes, higher symbiotic nitrogen fixation by legumes, and decline in soil acidity by H⁺ release are also responsible for the increase in nutrient content in intercropping systems (Duchene et al. 2017). Intercropping of Kochia (*Kochia scoparia*), Guar (*Cyamopsis tetragonoloba*) and Sesbania (*Sesbania aculeata*) resulted in improved yield of these plant species under salinity stress (Ghaffarian et al. 2020). These highlight the importance of integrating legumes and other compatible crops into intercropping systems to boost soil health and crop tolerance to climate change-related stresses. These fruitful advances offer hope for farmers battling to maintain crop yields in the face of challenging climates. Nevertheless, future studies should explore the long-term benefits and potential trade-offs of such practices for sustainable agriculture.

By estimating the diversity of AMF species in agricultural soils, we can stabilize or improve plant productivity by employing efficient agricultural management strategies with a population of host plants. Consequently, we need to increase our understanding of the complex interactions that exist within the AMF community regarding the identification and colonization of a single host plant (Verzeaux et al. 2017). An in-depth understanding of these symbiotic relationships can lead to more successful exploitation of AMF in crop production, improving nutrient uptake and stress tolerance. Legume-based cropping is a proven and renewable nitrogen source for improving soil health and crop productivity. These systems effectively achieve a favourable nitrogen balance in nutrient-poor soils, making them an essential tool for sustainable agriculture, which was reviewed elsewhere (Stagnari et al. 2017). As discussed above, recognizing the potential benefits of intercropping legumes in diversifying crops and promoting sustainable agricultural practices is stimulating. Through the symbiotic relationship between legumes and rhizobia, these systems offer a renewable source of nitrogen that can enrich soil and improve soil quality. This represents a valuable opportunity for farmers to enhance their cropping systems' productivity and sustainability, while promoting greater soil health and organic carbon accumulation.

The global interest in organic farming as one of the sustainable agricultural solutions is rising rapidly, as it has been shown to improve various ecosystem functions, such as the quality of groundwater, soil nutrient mineralization, abundance, diversity and activity of microorganisms. Additionally, it has been demonstrated to enhance soil health, yield, and product quality in different crops (Schrama et al. 2018; M. Tahat et al. 2020; Yang et al. 2024). Soil fertility and depletion erosion have long been

significant concerns for farmers and the general public worldwide (Montgomery and Bickel 2021). Both the abundance and diversity of micro-organisms are increased by performing organic practices despite using tillage for weed control. For instance, healthier soils with higher soil organic matter content were found when a national comparison of farms across the United States was conducted with conventional farming practices (Ghabbour et al. 2017). Likewise, Lori et al. (2017) compared the conventional and organically farmed fields with the same type of soil over an average of 16-years by analyzing 56 studies worldwide. They reported higher biomass, activity and diversity of microbes in organically farmed soils than in conventionally farmed soils. Using compost and manure is crucial for maintaining soil fertility in organic farming. However, it is important to note that these amendments can vary significantly in their nutrient content. Therefore, they are increasingly being utilized as a fundamental carbon source to improve overall and long-term soil health (Ghabbour et al. 2017; Stockdale et al. 2002). It should be noted that the root's growth, distribution and function are the primary aspects that are initially affected by agronomic practices, followed by the aboveground parts and yield (Guan et al. 2014; Liu et al. 2017). Understanding the root-soil interactions and their response to different agronomic practices is critical for advancing more resilient cropping systems. In this context, advanced imaging and modelling techniques can deliver new insights into these dynamics.

Plant stress tolerance never ceases to amaze us, especially when we learn about the potential of plant growth-promoting rhizobacteria (PGPRs) to help them endure even the most challenging conditions. By tapping into remarkable stress tolerance of these bacteria, adaptation and response mechanisms, we can open new ways to engineer climate-smart crop plants. PGPR protects plants from biotic and abiotic stress factors by inducing different mechanisms, such as the production of metabolites, antibiotics, enzymes and induced systemic resistance to influence different physiological activities of the plant (Majeed et al. 2018; Li, Wang, et al. 2022). For instance, PGPR inoculation to perennial ryegrass (*Lolium perenne*) significantly mitigated the copper (Cu) and cadmium (Cd) stress by reducing the uptake and translocation of metals, emphasizing that PGPR can enhance phyto-stabilization efficiency of Cu and Cd in heavily polluted soils, making it a promising solution for soil pollution challenges (Ke et al. 2021). Emphasizing the use of plant growth-promoting bacteria (PGPB) is well-known in agronomic fields for increasing soil quality, agricultural sustainability and climate change adaptation (Majeed et al. 2018; Cao, Narayanan, et al. 2023). Several strains of PGPB improved the immunity potential of crop plants to biotic stress by producing antagonistic metabolites and by suppressing diverse plant pathogens present in the rhizosphere and above ground (Majeed et al. 2018; Bakker et al. 2018). The inoculation of PGPB remarkably mitigated the red rot disease symptoms in sugarcane plants by inducing systemic resistance, improving plant growth, increasing proline content and boosting activities of antioxidative enzymes (Amna et al. 2020). By improving soil properties and increasing plant stress tolerance, PGPB can make a significant difference in ensuring more sustainable practices so that we can continue to feed our growing population in the face of changing climate.

As sessile organisms, plants cannot avoid stressful environments; therefore, they modify their endogenous defence mechanisms to improve overall growth and productivity. In this context, exogenous application of various chemical molecules such as phytohormones, gasotransmitters, osmoprotectants and neurotransmitters were proved to be significant in improving stress tolerance in plants (Mukherjee and Corpas 2020; Sabagh et al. 2021; Raza, Charagh, et al. 2022; Raza, Salehi, et al. 2022; Raza, Charagh, Najafi-Kakavand, et al. 2023; Raza, Bhardwaj, Rahman, et al. 2024b). Phytohormones coordinate differential signal transduction pathways and many internal and external stimuli to regulate stress responses in plants, and for a better tolerant phenotype, these multifunctional molecules alter the metabolic fluxes within the plant cell (Sabagh et al. 2021; Raza, Salehi, et al. 2022; Raza, Charagh, Najafi-Kakavand, et al. 2023). For example, the exogenous application of silicon (Si) along with indole-3-acetic acid and cytokinin significantly alleviated chromium-induced toxicity in wheat roots by improving overall plant productivity (Kandhol et al. 2024). Similarly, gasotransmitters such as nitric oxide, hydrogen sulphide and methane with signalling functions help to enhance stress tolerance in plants by regulating cellular activities, maintenance of ion balance, antioxidant enzyme activity and lipid peroxidation (Mukherjee and Corpas 2020; Sabagh et al. 2021). The mineral content of the soil can be improved by increasing the number of soil microbes that perform immobilization and mineralization, ultimately helping to augment crop yield (Kalita et al. 2018). Under different stress conditions, distinct functions in plant defence mechanisms are mediated by the high accumulation of cellular osmoprotectants such as proline, trehalose, glycine betaine, polyamines, raffinose, sorbitol, amino acids, mannitol, gamma amino butyric acid and carbohydrate sugars (Sabagh et al. 2021; Raza, Bhardwaj, Rahman, et al. 2024a; Raza, Charagh, Abbas, et al. 2023). Furthermore, osmoprotectants are harmless to intracellular metabolism in plants under unfavourable environmental conditions, even when present in high concentrations (Zulfiqar et al. 2020). Neurotransmitters such as serotonin, melatonin, dopamine and acetylcholine play an important role in plant development, adaptation and tolerance against stress conditions (Sabagh et al. 2021; Raza, Charagh, et al. 2022; Raza, Salehi, et al. 2022; Raza, Bhardwaj, Rahman, et al. 2024b). For example, the overall development of rapeseed seedlings was improved in serotonin-treated seedlings under cold stress (He et al. 2021). By strengthening the cell walls and having antioxidant qualities, serotonin also protects against biotic stressors, such as pathogens and herbivores (Ramakrishna et al. 2011). However, more in-depth research efforts are required to investigate the synergistic effects of these exogenously applied molecules on plant stress tolerance and crop productivity.

In addition to the above-mentioned molecules, biostimulants are a sustainable solution to mitigate and adapt to diverse stresses, but they often have poor stability. However, micro- and nano-based formulations that encapsulate plant growth regulators and microorganisms are promising to boost plant protection against climate change (Campos et al. 2023). Nanoparticles play an important role in plant defence against various environmental stresses by mimicking the activities of antioxidant enzymes. Their effectiveness in mitigating salinity and drought are reviewed by Raza, Charagh, Salehi, et al.

(2023). Applying bio-selenium nanoparticles have improved the germination and development of rapeseed seedlings under salinity stress (El-Badri et al. 2022). Similarly, the use of biogenic Si nanoparticles and calcium nanoparticles improved the growth of rapeseed under cadmium and drought stress (Ahmed et al. 2023; Ayyaz et al. 2022). It is critical to examine the long-term environmental influences and likely risks accompanying the use of nanoparticles in agriculture. Therefore, we suggest that upcoming efforts should focus on developing safe and effective nano-formulations designed for specific crop needs and stress conditions.

Improving soil health and crop yield via environmentally friendly and non-toxic agricultural practices is essential for designing sustainable climate-smart crop plants. Since plants encounter multiple stresses simultaneously, future strategies should highlight an integrated approach that combines traditional knowledge with modern technologies to boost productivity and stress tolerance in the face of climate change.

3.2 | Stress Physiology: Understanding Plants Adaptation and Tolerance to Climate Change

Understanding the physiological mechanisms underlying plant adaptation and tolerance to climate change is essential for developing strategies to design climate-smart crops. Plants are adaptable across diverse ecosystems, as demonstrated by seagrasses flourishing in marine environments and resurrection plants adapted to extreme heat and dryness (Dolferus 2014). Plants must undergo complex physiological, biochemical, morphological, developmental and metabolic changes to adapt to climate change. Therefore, stress signalling, metabolic and developmental adaption mechanisms have been studied by exploring the molecular mechanisms of stress tolerance in different plants (Zhu 2016; Deutsch et al. 2018; Zandalinas et al. 2021; Rivero et al. 2022). Helpful insights are provided by stress physiology against climate change-induced stresses, and studying stress physiology can help improve future crop productivity under changing climatic conditions (Mittler et al. 2022; Rivero et al. 2022; Zandalinas et al. 2021, 2024). Stress physiology also provides the link between biotechnological interventions and agronomic practices. Each stress scenario may require a distinct approach for the plants to acclimate or adapt, as different stresses affect plants differently (Zandalinas et al. 2021; Mittler et al. 2022; Rivero et al. 2022). As a result, depending on the combination of stresses, the plant may employ a different technique entirely, combine different responses, or give preference to one acclimation/adaptation strategy over the other (Rivero et al. 2022; Zandalinas et al. 2021, 2024).

Plants have stress tolerance behaviours that grow in response to adverse environmental circumstances to support their development, growth and yield. Over the past decades, researchers have focused on enhancing stress tolerance in crop species by discovering the complexities of plant responses to stress combinations (Rivero et al. 2022; Zandalinas et al. 2021, 2024). Plants sense external stress and communicate information to the cell via specific mechanisms. In contrast, plants maintain stress effects and cellular homeostasis by regulating the

expression of several genes associated with synthesizing important biomolecules such as plant growth regulators, secondary metabolites and compatible solutes (Zhu 2016; Raza, Bashir, et al. 2024).

Cellular integrity and energy production are affected in stress-exposed plants by disrupting the key metabolic and physiological processes (Rivero et al. 2022). Plants produce a new state of homeostasis known as acclimation via rapidly adjusting their metabolic and physiological responses to counteract the negative impacts of stress (Walters 2005). Adaptation is another significant strategy of plants that alters their anatomy, growth and reproductive aspects over longer periods (Bohnert et al. 1995; Rivero et al. 2022). In this framework, how plants perceive stress signals determines the appropriate response of plants to stress conditions, which ultimately induces stress-related genes and signalling cascades.

How do morphological modifications help adapt and mitigate stress factors? To answer it, we need to understand that the rate at which plants grow or survive under stress compared to control conditions is a common way for researchers to quantify stress tolerance. Due to the possibility of compromising growth to attain survivability and vice versa, the two metrics of stress tolerance: relative growth versus survival may be inconsistent (Zhang, Zhao, et al. 2020). Plants' morphological responses to stress conditions rely mainly on the leaf developmental stages and the age of the whole plant (Rankenberg et al. 2021). For instance, deepwater rice attempts to grow above water by elongating its internodes to confront flooding conditions successfully. This adaptation is shared by many other amphibious plant species, enabling them to thrive in challenging environments (Hattori et al. 2011). Root system is of key importance in conferring abiotic stress tolerance to make plants robust; nevertheless, root architecture and physiology are adapted in response to stress conditions to improve nutrient and water uptake (<https://www.wur.nl/en/research-results/chair-groups/plant-sciences/laboratory-of-plant-physiology/research/stress-resilience-in-crops.htm>). Plants exhibit compartmentation and the release of toxic Na^+ and Cl^- ions to alleviate the salinity induced alterations in the osmotic and ionic or hormonal homeostasis (Raza, Tabassum, et al. 2023; Raza, Charagh, Salehi, et al. 2023). Plants protect themselves from various abiotic and biotic stresses by creating a physical barrier and chemical protection by forming trichomes and releasing phenolic compounds, for example, flavonoids (Mymko and Avila-Sakar 2019; Karabourniotis et al. 2020). Plants can facilitate abiotic stress tolerance by altering their growth and adjusting certain morphological features by integrating ROS signals with hormonal pathways (Mittler et al. 2022). Additionally, plants adapt to waterlogged or water-deficient soils through the development of impermeable cell wall depositions or anatomical attributes by mature roots (Schneider et al. 2017; Pedersen et al. 2021). To limit oxygen and water or ion loss, older roots develop an endodermis and exodermis (Pedersen et al. 2021; Schneider et al. 2017), while a dedicated cuticle is developed by young root tips (Berhin et al. 2019). For example, some barley varieties produce aerenchyma in roots to enable the air to be transported to root zone when under waterlogging stress (Zhang et al. 2015). These diverse morphological changes and adaptation strategies could help design and deliver climate-smart crop plants.

At physiological levels, stress conditions negatively affect photosynthesis and respiration, which are plants' energy metabolism hubs. For example, as the relative water content of the soil decline, the rates of transpiration and photosynthetic activities decrease, making photosynthesis one of the primary processes impacted by water stress (Sales et al. 2021). In response to damage caused by stress conditions, plants employ various mechanisms to protect the photosynthetic apparatus, including photo destruction of the D1 protein of photosystem II, dissociation of the LHC from photosynthetic reaction centres, alterations in thermal dissipation of light energy, and so forth (Cui et al. 2014). One of the responses of crops to osmotic imbalance is water-use efficiency, which is inversely correlated with stomata closure during stress (Wang and Chang 2024; Peláez-Vico et al. 2024). Recent data on the hormonal alterations that occur during stress combinations have shown that proper stomatal responses and acclimation are triggered by a coordinated hormonal response to each specific stress combination (Zandalinas et al. 2024; Wang and Chang 2024; Peláez-Vico et al. 2024). By contrast, plants protect themselves from photo-oxidative stress by maintaining their Fv/Fm in young poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) leaves and accumulating anthocyanins (Moustaka et al. 2020). Stomatal closure, induced by abscisic acid (ABA) production under dehydration, reduces CO₂ influx, carbohydrate allocation and photosynthetic CO₂ fixation, creating a trade-off between growth and stress defence (Munemasa et al. 2015). Roots are the foremost indicators of lower water availability, triggering stomatal closure in leaves to conserve water (Wang and Chang 2024; Peláez-Vico et al. 2024), which makes this mechanism a key focus in research on plant drought response.

Plant stress tolerance mechanisms at the biochemical level include many important molecules such as carbohydrates, amino acids, phytohormones and secondary metabolites (Mittler et al. 2022; Raza, Salehi, et al. 2022; Rivero et al. 2022; Zandalinas et al. 2024; Raza et al. 2025). These molecules promote root development, reduce leaf abscission and leaf area, adjust ion leakage, help osmoregulation and detoxify ROS (Mittler et al. 2022; Rivero et al. 2022; Zandalinas et al. 2024). Decades of research have been directed to enhance antioxidant defence systems to mitigate oxidative stress, which causes cellular damage (Mittler et al. 2022; Raza, Salehi, et al. 2022). In addition to maintaining basal ROS levels, highly compartmentalized ROS production, scavenging and transport work together to enable the creation of particular ROS signalling signatures (Fichman and Mittler 2020; Mittler et al. 2022). Plants employ both enzymatic and non-enzymatic antioxidants in each subcellular compartment that are essential in modulating ROS homeostasis. Cellular processes involved in ROS generation, scavenging and transport must be carried out in a delicate balance for plants to grow, develop and adapt to their changing environments (Fichman and Mittler 2020; Mittler et al. 2022). To survive and adapt to stressful conditions, plants maintain their cellular redox homeostasis and signaling to prevent excessive ROS accumulation. Therefore, engineering crops with enhanced antioxidant machinery has led to climate-adapted varieties with enhanced oxidative stress tolerance (Kerchev and Van Breusegem 2022; Mittler et al. 2022). Diminished lipid peroxidation by declining ROS levels via accumulation of osmolytes (e.g., proline) in plants ultimately helps to maintain membrane integrity (Shinde et al. 2016).

Higher rates of plant survival, biomass production and grain yield were observed in plants that accumulate higher levels of proline in response to stresses, for example, drought (Yamada et al. 2005; Zhou et al. 2009).

Plants produce many secondary metabolites to survive stressful conditions. Optimum growth of plants requires a balanced production of primary and secondary metabolites under stress (Yadav et al. 2021; Raza et al. 2025). Scavenging of ROS occurs in plants by accumulating adaptable natural compounds, for example, flavonoids and polyphenols (Trembl and Šmejkal 2016). When plants are under stress, some secondary metabolites function as antioxidants and contribute to strengthen the cell wall, thereby reducing membrane lipid peroxidation and modulating the cell wall. To fast-track energy production and support the glutamic acid-mediated proline biosynthesis pathway, which is necessary to improve osmotic regulation, plants synthesize secondary metabolites to improve the tricarboxylic acid cycle and glycolysis (Qu et al. 2019). Plants synthesize chemicals known as phytohormones in small concentrations, which play a critical role in their growth, development and responses to environmental stress (Sabagh et al. 2021; Raza, Salehi, et al. 2022; Raza, Charagh, Najafi-Kakavand, et al. 2023). Coordination of differential signal transduction pathways is the major mechanism of phytohormones to strengthen stress tolerance, which brings key changes to plant development by regulating internal and external stresses. Furthermore, recent improvements in molecular processes have discovered the complicated multilevel nature of plant responses to stress conditions. These mechanisms involve various platforms, including sensing, transcript processing, transcription, translation and post-translation modifications (reviewed by Zhu 2016). Recent advances in molecular tools, such as RNA-seq and gene editing, help to identify target genes for stress tolerance and develop stress-smart high-yielding cultivars. Detailed arguments have been given in the next sections on how these modern molecular tools help to design and deliver climate-smart sustainable crops.

In short, we argue that integrating insights from stress physiology with modern molecular tools will open new windows for sustainable agriculture under climate change. This universal approach will enable the development of climate-smart crop varieties capable of surviving multiple stress factors, ensuring food security and economic stability.

3.3 | Sequence-Based Technologies: Bridging the Gap Between Lab to Field

In recent decades, significant advancements have transformed sequencing technologies, creating and refining high-quality reference genome sequences for numerous crop species and genotypes and facilitating climate-smart crop design (Xie et al. 2024). Re-sequencing and re-annotation of various crop accessions have provided enormous numbers of genetic variations, aiding in the discovery of functional genes associated with agronomic traits and stress tolerance across crops like rice, tomato, soybean, maize, cotton, wheat, chickpea and many others (<https://phytozome-next.jgi.doe.gov/>; <https://www.ncbi.nlm.nih.gov/genome/browse#!/overview/>). A recent review (Xie et al. 2024), offers a comprehensive picture of recent

advances in genome sequencing projects and their contributions to climate-smart and sustainable crop production.

In the current fast-forward research era, genomics (i.e., genomics-assisted breeding [GAB]) serves as the core of crop improvement and is widely applied for identifying the genetic variability concerning the phenotypic differences, novel traits, and most importantly, characterizing the pathways involved in stress tolerance and sustainable agriculture (Bohra et al. 2020; Varshney, Bohra, Yu, et al. 2021; Mishra et al. 2024). The sequence-based information obtained after effective usage of the genomics can be effectively translated from lab to field via cutting-edge genome editing tools such as precise clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated nuclease (Cas) technique or newly emerging machine learning approaches (Bohra et al. 2020; Varshney, Bohra, Roorkiwal, et al. 2021; Varshney, Bohra, Yu, et al. 2021; Raza, Chen, et al. 2024). These techniques provide in-depth insights regarding genes corresponding to desirable traits, their behaviour during climate change, and their interaction with other significant traits. To target and optimize the genetic candidates for crop improvement in the face of changing climate, it is crucial to know specific genotype-to-phenotype maps (Bohra et al. 2020; Varshney, Bohra, Roorkiwal, et al. 2021; Varshney, Bohra, Yu, et al. 2021; Mishra et al. 2024). Some successful stories on improving plant stress tolerance using GAB methods have been discussed in previous reviews (Bohra et al. 2020; Varshney, Bohra, Roorkiwal, et al. 2021; Varshney, Bohra, Yu, et al. 2021; Mishra et al. 2024).

Due to the advancement and cost-effectiveness of sequencing technologies, there is now a wealth of available data, setting the foundation for identifying genes linked to agronomic traits under changing climates (Varshney, Bohra, Yu, et al. 2021; Mishra et al. 2024; Xie et al. 2024). Over the years, several robust tools for trait mapping have emerged, utilizing deep sequencing methods such as RAD-seq, GBS, BSA-seq, SLAF-seq, and so forth (Varshney et al. 2019; Varshney, Bohra, Yu, et al. 2021; Raza, Chen, et al. 2024). While these strategies, being part of the quantitative trait loci mapping and genome-wide association studies (GWAS) have enabled the identification of candidate genomic regions and genes linked to multiple stress tolerance, they often suffer from imprecision due to the large candidate regions and reliance on parental traits. Nonetheless, the availability of plant genomes has fast-tracked the usage of genomic information for crop improvement (Bohra et al. 2020; Varshney et al. 2019; Varshney, Bohra, Yu, et al. 2021).

The newly constructed pangenomes, in combination with the presence or absence of variation-based GWAS analysis, have provided more power to the genomic as well as genetic analysis for exploring genomic resources (Wang, Yang, et al. 2023). For instance, the GWAS analysis was performed to study drought-related traits in rice (Ma et al. 2016), sorghum (Maina et al. 2022), sunflower (Wu, Shi, et al. 2022), drought and heat-related traits in wheat (Devate et al. 2022) and temperature-related traits in maize (Zhang, Zhang, et al. 2020). However, these studies have limitations in mapping multiple alleles and highly differentiated population structures (Nordborg and Weigel 2008; Zhou and Huang 2019). These limitations can be

overcome by using a combination of nested association mapping populations and multiparent advanced generation intercross populations, which are well-supported by the next-generation analysis as well as high-profile omics data (Zhou and Huang 2019; Varshney, Bohra, Yu, et al. 2021b). Nonetheless, irrespective of the implementation of such diverse approaches, phenotypic crop profiling in association with allelic variants and environment is still difficult to resolve (Yang et al. 2013; Tardieu et al. 2017).

Additionally, the ample resources and information obtained via structural genomics are ultimately utilized by functional genomics. Functional genomics, combined with other sequencing-based/omics technologies, informs the linkage between crop genomes and phenotypes under precise physiological states and environmental conditions (Varshney et al. 2019; Varshney, Bohra, Yu, et al. 2021). This has effectively enabled the identification of genes from several crops crucial for stress tolerance and yield determination, including the major crops such as soybean (Zhang et al. 2022), wheat (Wang et al. 2020), maize (Liu et al. 2020) and rice (Yu et al. 2022). Further, mutagenomics has also emerged as an approach to study the mutation event in the genome of the organisms causing the formation of mutated traits. Mutagenomics utilizes genomics information and modern omics tools to obtain desirable mutations in crop genomes, involving the development of diploid mutants, recombinant inbred lines or aneuploid/polyploid lines. The functional characterization of these mutant lines gives crucial information for formulating the breeding approach concerning the particular agroclimatic condition (Talukdar and Sinjushin 2015). The mutant traits can be characterized by high-throughput genomic approaches such as high-resolution melt, targeted induced local lesions in genomes (TILLING), serial analysis of gene expression and microarray analysis (Suprasanna Penna 2017). Out of these techniques, the TILLING technique is widely used in high throughput mutations in crops and acts as a crop breeding approach alternative to transgenic breeding. This genomic-based approach successfully modifies stress tolerance in crops such as rice and peanuts, reviewed by Singh et al. (2024). Moreover, mutagenomics combined with reverse genetics can effectively silence/interrupt candidate genes to functionally validate them (Suprasanna Penna 2017). Genomics combined with epigenetics has ascended to epigenomics, which may assist in characterizing the influence of environmental factors on the epigenome by providing the DNA methylation status of the genome. This assessment usually incorporates techniques such as bisulfite sequencing and methylation-sensitive amplified polymorphism (Saeed et al. 2022; Gallusci et al. 2023).

Another omics approach that has been heavily assisted by high-throughput sequencing is pan-genomics. The pangenome concept encompasses the entirety of a species' genome, consisting of core genes shared by all individuals and dispensable genes unique to certain individuals (Bayer et al. 2020; Shi et al. 2023). Advancements in sequencing technology have enabled the sequencing of multiple accessions of crop species, leading to a surge in pan-genomic studies across various crops like cabbage, rice, tomato, wheat, maize, barley, cotton, rapeseed, potato, citrus, pearl millet, chickpea (*Cicer arietinum*) and many others (Bayer et al. 2020; Shi et al. 2023; Raza, Bohra, and

Varshney 2023; Mishra et al. 2024; Xie et al. 2024). In recent years, the concept of super-pangenome has also emerged, which shed light on a whole genomic variation repertoire of a genus (Khan, Garg, et al. 2020; Khan, Garg, et al. 2024). These studies highlight the significance of structural variations and dispensable or nearby genes in maintaining crop diversity, enhancing quality and tolerance to multiple stresses (Bayer et al. 2020; Shi et al. 2023; Raza, Bohra, and Varshney 2023; Mishra et al. 2024; Khan, Garg, et al. 2024; Raza, Bohra, Garg, et al. 2023; Xie et al. 2024). We propose that integrating structural variations data from pan-genomics into future crop breeding programmes could increase crop efficiency and ensure food security in the context of climate change and the growing human population. Moreover, nearby or dispensable genes can be targeted via genetic engineering to design more climate-smart crop plants. Stress-associated genes could also be transferred to other major field food crops to help them adapt to changing climates and contribute to sustainable agricultural production and food security.

Moreover, high-throughput sequencing has been tremendously powerful to study the complete set of RNA transcripts of the plants, referred to as transcriptomics. This field has been demonstrated as a promising approach to assessing crop stress-responsive genes over time. The transcriptome analysis provides high throughput, sensitivity and efficacy and has been widely used to decipher the transcriptome of various model crops such as rice (Li, Jiang, et al. 2023), maize (Fu et al. 2021) and wheat (Ma et al. 2021) under diverse stress conditions. The single-cell omics approach is one of the newly emerged and promising approaches from these cutting-edge technologies. The single-cell multi-omics assessment helps to characterize the state and activities in the cell concurrently by integrating several single-modality omics methods, which profile genome, epigenome, transcriptome, epitranscriptome, proteome and metabolome (Baysoy et al. 2023; Depuydt et al. 2023). Such an ample amount of information from a single-cell leads to enlightening the knowledge regarding the non-anatomical markers for cell populations as well as their signalling during stress-mediated adaptations. Among various single-cell omics, novel progressions in transcriptomics have been achieved to elucidate the regulatory mechanisms of plant response to stresses via some advanced techniques such as in situ RNA-seq and spatially resolved transcriptomics or single-cell transcriptomics (Seyfferth et al. 2021; Yang et al. 2021; Bawa et al. 2024). The single-cell RNA-seq has demonstrated the differences in the tissue composition and developmental trajectories in *Arabidopsis* (Nolan and Shahan 2023). On a similar line, the single-cell transcriptome of the important crops, including rice, tomato and maize, was successfully performed, explained in Kaur et al. (2024). Due to the generation of huge datasets, online single-cell transcriptome databases and tools are also being established, for example, plant single-cell transcriptome database (PlantscRNAdb; <http://ibi.zju.edu.cn/plantscrnadb/>) which includes various marker genes from different cell types of four plants namely *Arabidopsis*, rice, tomato and maize (Chen et al. 2021), cellular stage predicting and biomarker mining tool such as NRTPredictor (<https://www.cgris.net/nrtip>) (Wang, Lin, et al. 2023), or a framework designing tool to explore single-cell atlases like scPlant (<https://compbionju.github.io/scPlant/>) (Cao, He, et al. 2023). Even though there are several reports

currently emerging from this area in the context of designing climate-smart crops, there is still a lot of scope to explore the single-cell approach.

While performing crop improvement-related operations, many other omics tools are usually employed for deeper knowledge advancement (Raza, Salehi, et al. 2024; Raza, Bashir, et al. 2024). The important omics tool, proteomics, acts as a bridge between genomics, transcriptomics and metabolomics and provides exact descriptions of the overall events in the cells (Yan et al. 2022; Raza, Salehi, et al. 2024). The accessibility of next-generation proteomic tools has notably improved our knowledge of cellular pathways, molecular physiology and regulatory processes under abiotic stress conditions (Yan et al. 2022). Proteomics can be complemented by metabolomics, which provides global identification and profile of the metabolites. Metabolomics describes the whole metabolic status of the cell, tissues or organs via a targeted or non-targeted approach (Yan et al. 2022; Raza, Salehi, et al. 2024; Raza et al. 2025). On the other hand, miRNAomics provides the profile of the non-coding miRNAs of the organism, which act as key post-transcriptional modulators. The miRNAomics hence sheds light on the post-transcriptional regulatory events in the cell at the given condition, such as protein re-folding, antioxidant machinery, reproductive events under stress, photosynthetic efficiency and hormonal regulations (Raza, Charagh, Karikari, et al. 2023). Altogether, these sequence-based technologies greatly accelerate the understanding of cellular metabolism and hence help portray the clearest approach for crop improvement in the face of changing climate. Nevertheless, the field of bioinformatics helps tremendously in this venture.

All these omics tools provide beneficial and more information when applied in combination (i.e., integrative multi-omics), and it is the current trend in the scientific community to read the total picture during the acquirement of stress tolerance in plants. For instance, these advanced sequencing techniques have been used with the integrative approach (along with non-sequencing-based omics tools such as metabolomics, ionomics and phenomics) to discover the regulatory mechanisms in major crops. The salt stress responses in rapeseed were evaluated using transcriptomics, proteomics, metabolomics and functional genomics approaches, and the results highlighted the key combined role of phytohormones (jasmonic acid and ABA) and ROS scavenging system in reducing salt damage in rapeseed (Shu et al. 2022). The integrated transcriptomic, proteomic and metabolic assessment discovered the secondary metabolites and auxiliary carbohydrate metabolism enhancing drought tolerance in rice (Dwivedi et al. 2023). The responses of wheat against drought were assessed using the physiological, proteomic, and metabolomic strategies, suggesting the key role of cell wall remodelling, modifications in cell signalling, endocytosis and biosynthesis of defence proteins for drought tolerance (Nešporová et al. 2024). The maize responses against controlled cold stress were recorded using metabolomic and proteomic approaches, and photosynthesis-related proteins and metabolites were reduced (Urrutia et al. 2021). Increasing patterns different proteins/metabolites such as *trans*-aconitate, hydroxycinnamate derivatives, benzoxazinoid, sucrose and allene oxide synthase, some glutathione transferases and peroxidases, were found to regulate cold tolerance (Urrutia et al. 2021). In

the near future, more integrated omics-based investigations are required to harness the adaptation and tolerance mechanisms, mainly against stress combinations.

The advances in sequencing techniques have given breeders various options for customizing climate-smart crops. GAB has been used effectively to counteract biotic and abiotic stress and to improve nutritional values in major crops (Bohra et al. 2020; Varshney, Bohra, Yu, et al. 2021; Raza, Chen, et al. 2024). Although these cutting-edge techniques have hastened genetic discovery, there remains a gap in implementing these findings in breeding programmes on the actual field level. It is now easier to establish GWAS for particular crops and/or traits (e.g., stress tolerance to multiple abiotic and biotic factors), but applying them to develop new crop varieties has been a real challenge. Though there are some success stories, several challenges hinder progress. These challenges primarily include the integration of GWAS results into genomic selection models, advancing modelling methods and algorithms to innovatively combine the diverse data type as well as considering nonlinear interactions like genotype-by-environment effects in genomic selection approaches to propel crop breeding objectives forward (Purugganan and Jackson 2021). Normally, crop improvement has principally relied on phenotypic annotations and quantitative breeding values but is missing the actual mechanistic understanding at the molecular level of how important traits develop. However, technological advancements have discovered the genetic basis of vital plant traits. The challenge now is to consistently integrate this molecular knowledge into crop improvement practices (Bailey-Serres et al. 2019). Irrespective of the availability of these cutting-edge technologies, it is crucial to understand the evolutionary process of the domestication and diversification of crops (Bohra, Tiwari, et al. 2022). The diversification has both imposed constraints and presented opportunities that can guide breeding endeavours (Bohra, Tiwari, et al. 2022). Contrariwise, the diversification of crops across multiple environments resulted in local adaptation during the evolution. These adaptations may provide vital genetic material that can boost the development of new climate-smart crop varieties (Purugganan and Jackson 2021; Bohra, Kilian, et al. 2022; Bohra, Tiwari, et al. 2022). The currently available advanced genome editing tools are certainly stimulating crop breeding efforts and will further assist in understanding the prompt association between mechanistic insights of gene function and agricultural output. However, there are always new challenges to address while bridging the gap between the lab-to-field application of improved crop varieties in the face of changing climate.

3.4 | Biotechnological Tools: Engineering Adaptation and Tolerance to Stressful Environments

Biotechnological tools, including genetic engineering techniques like CRISPR/Cas-based gene editing and transgenic breeding, empower scientists to directly manipulate plant genomes. By introducing or transferring genes conferring resistance to diseases, pests, or abiotic stresses, biotechnological interventions create genetically engineered crops designed for specific environmental challenges. These advancements are necessary for developing climate-smart crops and ensuring food

security. Additionally, precision breeding techniques enable the development of crops with enhanced nutritional profiles, addressing malnutrition issues globally. The use of CRISPR/Cas technique in developing climate-smart crops, also referred to as the advanced breeding technique, provides a promising possibility for the generation of both transgenic as well as non-transgenic crop varieties (Rönspies et al. 2021; Tuncel et al. 2023; Zaman et al. 2023).

Transgenic breeding has been able to generate stress-smart plants to cope with climate change in natural conditions. For instance, under drought conditions, transgenic wheat overexpressing *TaTR1* and *TaTR4* showed enhanced yield in field and greenhouse conditions (Beznec et al. 2021). Overexpression of *GmDREB1* from soybean enhances drought tolerance in transgenic wheat lines under field conditions by reducing membrane damage and improving osmotic adjustment and photosynthetic efficiency (Zhou et al. 2020). In another study, overexpression of *OsAAIL* in rice resulted in increased drought tolerance via ABA-dependent and ROS-scavenging regulatory pathways (Long et al. 2023). Under salinity stress, overexpression of *OsMADS27* boosted salinity tolerance and grain yield in transgenic rice lines when sufficient nitrate was available (Alfatih et al. 2023). The growing number of transgenic events suggests that transgenic breeding could serve as a promising tool for developing stress-smart crop plants while combining with speed breeding methods.

Non-transgenic variations can be created by producing null alleles using template-free genome editing and transferring an allele from one variety to another within the same species. This approach is particularly useful for creating crops that can bypass regulatory hurdles associated with transgenic varieties. This could include transferring a stress tolerance-related gene from a wild species to a commercial cultivar. Varieties generated in this manner are identical to those created using standard breeding processes, and as a result, their products can be quickly commercialized. Nevertheless, in some regions, such as the European Union, regulatory structures may enforce additional conditions, which can impact the speed of commercialization. In contrast, transgenic crops are created using the template-based targeted insertion of transgenes into specific sites (Visarada et al. 2009; Rönspies et al. 2021).

The CRISPR/Cas-based technologies have made precise genetic manipulation of crops pretty much possible (Rönspies et al. 2021; Zaman et al. 2023). This progress allows the manipulation of crop genomes to enhance the quality and quantity of agricultural output and stress tolerance via selective modulation of specific genes associated with traits of interest. There are several successful crop manipulations utilizing the CRISPR/Cas tool for designing climate-smart crop plants. For instance, a study by Santosh Kumar et al. (2020) demonstrated CRISPR/Cas9-mediated genome editing of the *OsDST* (drought and salt tolerance) in Indica mega-rice cultivar MTU1010 to improve grain yield under drought and salinity. The variant of *ARGOS8* gene, a negative regulator of the ethylene response, was generated using the gene editing in maize, resulting in increased grain yield under drought conditions (Shi et al. 2017). The cold tolerance in rice was improved by knockout of *OsPRP1* (proline-rich protein 1) in rice by creating the CRISPR/Cas9-

mediated knockout mutants (Nawaz et al. 2019). Furthermore, this technique has been effectively employed to combat infectious crop diseases and develop disease-resistant crops. This includes approaches such as indels-mediated gene disruption in coding regions/promoter regions, gene deletion via multiplex single guide RNA, homology-driven gene insertion and biomimicking (Zaidi et al. 2020). For example, the DICER-LIKE proteins were targeted using CRISPR/Cas to develop resistance against tomato mosaic virus and potato virus X in tomato (Wang, Deng, et al. 2018; Wang, Hardcastle, et al. 2018). The insect resistance against the common cutworm was developed in soybean using the *GmCPDK38* as a target for CRISPR/Cas (Li, Hu, et al. 2022). These interventions feature the versatility and broad application spectrum of CRISPR/Cas technology in crop protection. The rice blast, a fungal infection, was addressed for the resistance development in rice via targeting various genes, including *OsERF922*, *Ospi21* and *OsBsr-d1* (Wang et al. 2016; Zhou et al. 2022), and *OsSEC.3A* (Ma et al. 2018). In addition to stress-smart crops, the CRISPR/Cas system plays a key role in upgrading quality traits, such as those in oilseed crops, contributing to sustainable agriculture and enhanced food security (Li et al. 2024).

As many important agricultural traits stem from SNPs within non-coding intergenic regions or from dominant gain-of-function mutations in coding regions, CRISPR-based base editors are now widely utilized in crop engineering (Li et al. 2020; Zaman et al. 2023). Furthermore, the methods for targeted insertion using prime editing or chemically altered DNA, as well as refining the gene expression by dCas9-driven synthetic transcription modulator or CRISPRi-based circuits, have opened up a wide window of crop genome editing and controlled gene expression (Rönspies et al. 2021; Khan, Herring, et al. 2024). To date, CRISPR/Cas-mediated gene editing has proved to be successful in preparing gene knockout for silencing the individual gene, gene knock-in for overexpressing the gene, gene replacement, base editing, gene regulation and epigenome editing (Tuncel et al. 2023; Zaman et al. 2023). These diverse applications emphasize the transformative potential of CRISPR/Cas technology in modern agriculture.

Synthetic biology is one of the emerging approaches for crop improvement that combines biological principles with engineering to design a system to produce novel biological products (Rönspies et al. 2021; Sargent et al. 2022). This technology may facilitate the incorporation of multiple genes, sourced either from foreign organisms or synthetically created. It also allows for constructing new genomes from standardized genetic components, which can then be introduced into the target organism or cell, thus offering prospects for crop innovation. Synthetic biology presents fresh avenues to enhance crops via integrating novel genes with known functions, generating artificial genetic diversity, utilizing small RNAs for biotic stress control, and potentially accelerating the development of new cultivars with desirable traits, for example, multiple stress/disease tolerance. As reviewed elsewhere (Rönspies et al. 2021; Sargent et al. 2022; Lohani et al. 2022), synthetic biological tools help plants to cope with stressful conditions by regulating several mechanisms like photosynthetic rate, water use efficiency, enzyme interactions, microbial activities, nutrient acquisition, gene expression regulation.

Based on the available yet effective methods for crop improvement, the controlled expression of the transgene can be considered as key element. Hence, despite all the difficulties, genetic transformation is still considered a promising tool for crop improvement programmes. However, one of the bottlenecks in crop improvement through gene transformation is the lack of a universal protocol for effective plant transformation (Atkins and Voytas 2020). The process is further pushed back due to low regeneration rates in many economically important crops. Hence, despite the innovative success of the crop genome edition through modern tools such as CRISPR/Cas, effective plant transformation and regeneration approaches are in dire need of many crop improvement programmes. To address this hurdle, methods are being developed for de novo induction of gene-edited meristem via co-delivery of totipotency-inducing genes along with gene-editing reagents into somatic cells (Maher et al. 2020). Additionally, highly efficient plant virus-mediated transformation systems are also being standardized for gene editing (Ellison et al. 2020; Ma et al. 2020). These innovations could notably enhance the effectiveness and scope of plant genetic engineering.

Another emerging path to improve plant transformation efficiency is the application of nanomaterials, which may improve cargo delivery, species independence, germline transformation and gene editing efficiency. The rapid enhancement in gene delivery can be achieved via nanocarriers such as high-aspect ratio nanomaterials, which may empower the efficient transfer of functional genes (Demirer et al. 2021; Demirer et al. 2019). For instance, layered double hydroxide lactate nanosheets (LDH-lactate-NS) served as impressive carriers for transferring macro-molecules into plant cells. In this context, Wu, Zhang, et al. (2022) reported that LDH-lactate-NS improve root elongation in *Arabidopsis* by stimulating polar auxin transport, which improve nutrient and water uptake under stress conditions. This nanomaterial also detoxifies raw materials and serve as a fruitful tool for improving plant stress tolerance. Nanobiotechnology holds promise for beating some of the current limitations in plant transformation and could transform genetic engineering approaches. For instance, Raza, Charagh, Salehi, et al. (2023) reviewed the power of nano-mediated gene editing for crop improvement under stressful conditions (e.g., salinity and drought). They also highlighted the combined power of nanobiotechnology, gene editing and speed breeding for developing future stress-smart future crops. However, future efforts are required to fully harness the power of nanobiotechnology towards stress-smart agriculture.

Efficient plant breeding can create superior varieties that quickly displace outdated ones and handle ongoing difficulties efficiently and sustainably. Plant genome editing using the abovementioned approaches at specific targets allows customized plant breeding strategies based on objectives. This may effectively address the difficulties in food security, nutrient content, environmental adaptation, disease resistance and plant-based material manufacturing. There have been several successful attempts to modify the crop genome as per the requirement; however, there has been limited commercial success as only a few crops have been commercially released or are near to release to date, as reviewed by Tuncel et al. (2023).

The examples presented by Tuncel et al. (2023) demonstrate the potential for biotechnological innovations to address specific agricultural challenges and highlight the need for further development and regulatory approval.

Ultimately, developing a new, improved crop variety is a sequential cycle of developing newer genetic diversity, recombination and identifying the best transformant, followed by commercialization. Selecting and testing the best genetic variant compared to its classic counterpart is necessary. Hence, in transgenic breeding, the breeder specifically assesses the defined trait phenotype and then introgresses the transgenesis into the wider range of genetic traits (Visarada et al. 2009). The accuracy and precision of the new cutting-edge omics and transgenic approaches have helped transgenic breeding attain success. Collectively, we can state that the new biotechnological tools are heavily boosting crop improvement efforts. Though there are endless possibilities for developing innovative techniques for crop improvement, we cannot underestimate the emergence of new challenges as well.

3.5 | Microbial Partnerships: The Power of Microbiome for Sustainable Agriculture

Soil microorganisms contribute significantly to terrestrial biogeochemistry and the maintenance of plant health. Recent advances in high-throughput sequencing have enabled researchers to profile highly complex and taxonomically structured microbial communities associated with distinct parts of various plant species, including rice (Edwards et al. 2015), wheat (Chen et al. 2018) and soybean (Hussain et al. 2018). Importantly, the plant rhizosphere, root endosphere and phyllosphere microbiome have been demonstrated to establish complex interactions with the host and perform essential services, including nutrient acquisition, plant growth, flowering plasticity and disease suppression (Trivedi et al. 2020; Gao et al. 2021). However, several global challenges confront crop production, including climate change, demographic expansion and the growing demand of sustainable yield production, and all of these factors can also change the structure and functions of microbial communities associated with plants (Tito et al. 2018; Singh et al. 2023).

Structure and function of plant microbiome undergo dynamic changes in response to various stresses. For example, the pathogen invasion or changes in soil pH and temperature can shift the composition of plant microbiome and affect the level of disease suppressiveness (van der Voort et al. 2016; Carrión et al. 2019; Li, Chen, et al. 2023). However, it is also increasingly obvious that plants actively engage in mutualistic relationships with microbes to counter multiple stresses through 'cry for help' strategy, which involves the release of root exudates by the plant to recruit a subset of beneficial microbes when experiencing abiotic stresses (Bakker et al. 2018; Singh et al. 2023). Plant root exudates comprise organic acids, carbohydrates, fatty acids, amino acids and secondary metabolites. The specific analytes in root exudates, such as flavonoids and coumarins, are known to perform an indispensable function in coordinating the composition and dynamics of the root microbiome (Hussain et al. 2023).

Climate change parameters, such as drought, warming and elevated CO₂ concentration, can affect root exudate composition and plant immune responses, causing host-microbiome dysbiosis (Singh et al. 2023). For instance, the plant defence hormone salicylic acid has been shown to modulate the assembly of root microbiome (Lebeis et al. 2015), and its production decreases with an increase in temperature and CO₂ concentration in the environment which may impact microbiome assembly, making host susceptible to abiotic stresses (Singh et al. 2023). Similarly, drought-induced synthesis of ABA diminishes the plant immune response, thereby assisting large shifts in the root bacterial community while influencing plant stress responses (Arora and Jha 2023). Disruption of complex microbial interactions within the plant holobiont defines host fitness and disease outcomes. As microbiomes are critical for plant health, it has been hypothesized that the identification of factors that contribute to positive modulation of soil microbiome could be an attractive strategy for enriching beneficial microbes to mitigate the diverse set of climate-induced stresses in the era of the Anthropocene epoch (Trivedi et al. 2020, 2021; Hussain et al. 2023).

The optimization of plant production systems and increasing plant yield through host microbiome engineering highlights beneficial prospects for crop health and sustainable agriculture in the face of changing climate. In general, microbiome can be positively manipulated by direct application of (1) single microbial strain and microbial consortia (Mwaheb et al. 2017), (2) rhizosphere microbiome transplantation (Jiang et al. 2022) and/or (3) indirectly by agricultural practices such as crop rotation and intercropping (Hartman et al. 2018; Zhou et al. 2023) to drive shifts in microbial community composition and functions for reversing dysbiotic holobiont, protecting ecosystem and host health. The natural example of microbiome engineering in agricultural practices is particularly evident in disease-suppressive soils where naturally occurring microbiota inhibit the virulent pathogen in the presence of susceptible host and disease-conducive environmental conditions (Raaijmakers and Mazzola 2016; Hussain et al. 2024). In such specific suppressive soils, plant roots release specific molecules in the rhizosphere to enrich, stimulate and support the soil microbiome, acting as the first line of defence against soil-borne pathogens (Li, Chen, et al. 2023). The interaction between microbial consortia and a specific pathogen leading to disease suppression is biologically complex. If a pathogen breaches the first line of rhizosphere-induced disease resistance, endophytic microorganisms can offer an extra layer of defence by selectively enriching microbiota members with the genetic machinery to generate enzymes and secondary metabolites that counteract the pathogen (Carrión et al. 2019).

Microbial inoculants, whether single strain or consortium, provide various benefits with few limitations as they are eco-friendly, restore soil fertility, increase nutrient acquisition, protect against different stresses, decompose toxic substances and boost plant defence and immunity (Li, Wang, et al. 2022; Hussain et al. 2024; Olanrewaju et al. 2024). The demand for microbial inoculants grows by 12% annually due to eco-friendly technology and rising costs of chemical fertilizers. PGPB such as *Azotobacter*, *Pseudomonas*, *Azospirillum*, *Burkholderia*, *Rhizobia* and *Serratia* species are now commercially produced on a large

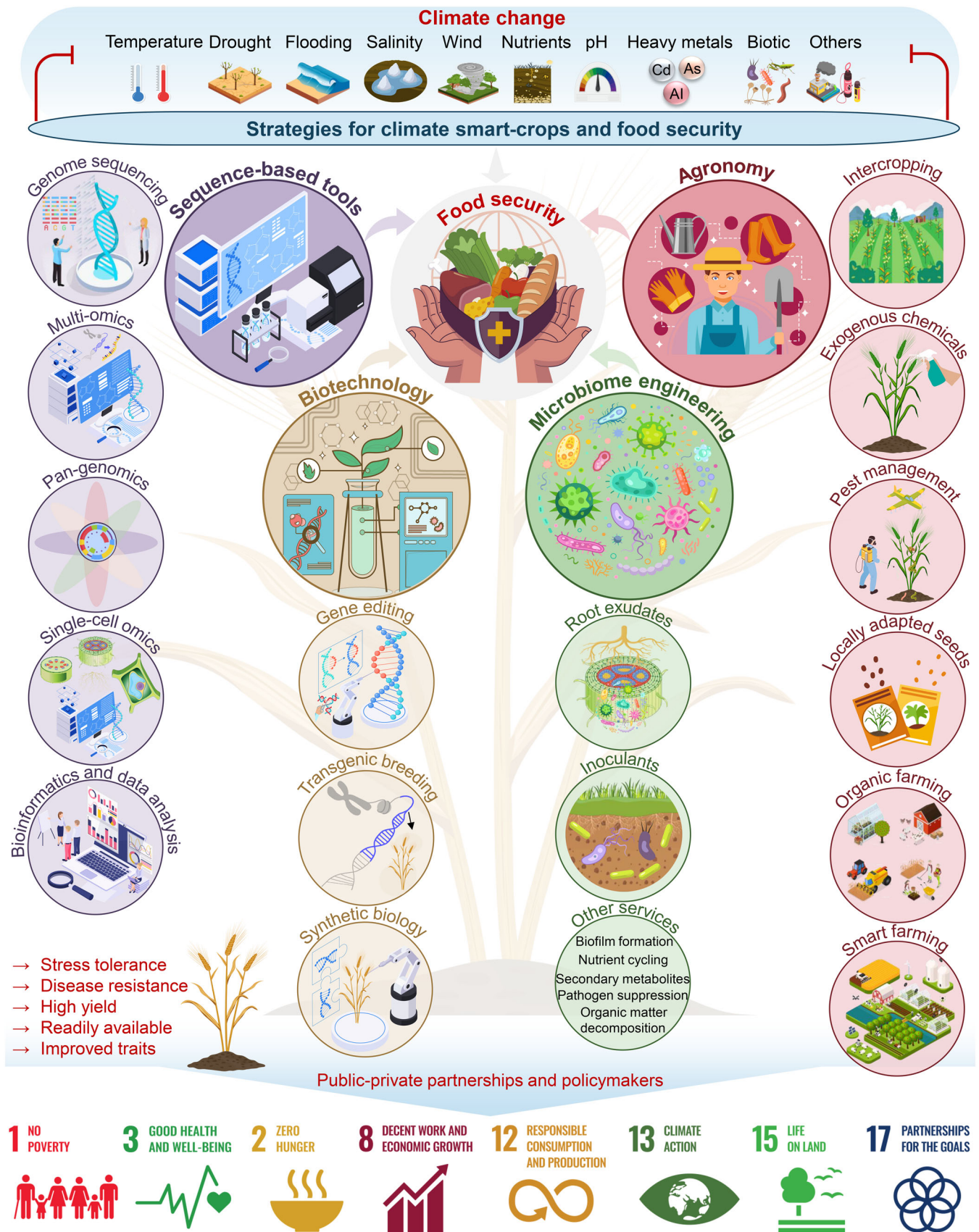


FIGURE 5 | Legend on next page.

scale (Vishwakarma et al. 2020). PGPB triggers defence responses such as induced systemic and systemic acquired resistance in host plants. In contrast, root-inhabiting bacteria induce biofilm formation that serves as both chemical and physical barriers against plant pathogens (Bai et al. 2022). Through plant–soil feedback and legacy impacts, the selective fortification of microbiota communities in response to biotic and abiotic stresses can affect plant immunity in subsequent generations (Kong et al. 2019; Trivedi et al. 2022). Exploiting the plant microbiota as an integrated biomarker can optimize the benefits of the entire microbiome. Engineering plant-linked microbiota for disease control will require a thorough understanding of plant–microbe–environment interaction beyond varied crops of interest.

Enhancing plant productivity by manipulating the plant soil microbiota in response to climate change has been identified as superiority by international policy agencies. These interventions may encompass direct manipulations of plant microbiota, function manipulation through land management practices, and the use of probiotics (Trivedi et al. 2020). The chemical interactions between plants and microbes, facilitated by various metabolites, are important in governing their symbiotic relationships and shaping the dynamics within the rhizosphere (Kim et al. 2022). Advanced genome editing tools and synthetic biology approaches will be feasible to engineer microbe-friendly plants efficiently releasing exudates that stimulate explicit beneficial plant–microbe interaction (Trivedi et al. 2021). Investigating microbial diversity depicts the discovery of new metabolites critical to plant growth and health (Olanrewaju et al. 2024). Genome mining tools and advances in metabolomics and genome sequencing of several microorganisms improve our understanding of microbial metabolites. The ecological and biological role of microbes will aid in developing sustainable strategies to improve crop tolerance and manage crop health to tackle climate change (Stassen et al. 2021).

The wild relatives of domesticated crops harbour a reservoir of genetic diversity (Bohra, Kilian, et al. 2022; Raza, Bohra, Garg, et al. 2023; Wang, Chen, et al. 2023), including traits that facilitate the formation of a unique microbiome (Raaijmakers and Kiers 2022). These microbiotas have the potential to aid in the adaptation of plants to climate change. Our understanding of the complex interaction between plants and their microbiome and the implications for plant fitness and productivity is beginning to unfold (Olanrewaju et al. 2024). However, the response of these interactions to climate change at evolutionary, ecological, biochemical and molecular levels is inadequate and, in some

instances, entirely unknown. A comprehensive approach where both plant and microbial ecophysiological outcomes are measured over time while considering multiple stresses and environmental conditions can interpret these interactions (Trivedi et al. 2022; Singh et al. 2023). Therefore, more efforts to obtain predictive insights into plant–microbiome interaction are required to advance new computational and modelling tools to predict the response of useful plant interaction to environmental stresses. Such knowledge will enable predictions of the effects of climate change on the plant-associated microbiome. It will open new avenues for applied research to leverage plant–microbe interaction to enhance the climate tolerance of plant communities.

4 | Conclusion and Future Recommendations

As climate change gradually threatens crop yields, developing a sustainable and productive agricultural system is decisive. A multifaceted approach is needed to tackle climate change-associated threats, integrating conventional agronomic practices with innovative management and mitigation strategies (Figure 5). Effective strategies for enhancing agricultural sustainability and resilience include soil health management, implementing intercropping systems, using locally adapted seeds, exogenous application of diverse chemical molecules, transitioning towards smart farming, and so forth. Moreover, progress in microbial engineering and plant–microbe interactions and an understanding of stress physiology are also needed for sustainable agriculture and future food security.

Understanding plant stress-related mechanisms is crucial for guiding the breeding of future stress-smart crops. In this context, extensive research has shown various adaptation and tolerance mechanisms in controlled environments, but open-field findings are often lacking. Therefore, to bridge this gap, employing tissue- and cell-specific phenotyping could offer new insights into how plants adapt to climate change, which can further boost our proficiency in designing stress-smart future crops. Literature advocates that single- and integrated-omics approaches have discovered numerous genes and pathways related to stress adaptation and tolerance. Nevertheless, significant questions remain unexplored regarding the number of genes to target and their specific roles in stress responses. It is still debated whether all significant genes are associated with specific stress conditions or if targeting a selective set of genes is more effective approach. This features the need for more in-depth investigations and advanced techniques, such as single-cell omics, to identify precise genetic elements important for stress tolerance in

FIGURE 5 | Strategies for designing climate-smart crops. These strategies include: sequence-based tools (i.e., whole genome sequencing or resequencing, pan-genomics ‘including pan-genomes and super-pangenomes’, multi-omics analysis ‘transcriptomics, proteomics, metabolomics, ionomics, epigenomics, miRNAomics, etc.’, single-cell omics, and key role of bioinformatics and data analysis); modern biotechnological tools (i.e., CRISPR-based gene editing, transgenic breeding ‘overexpression of key genes in the main crop for stress tolerance’, and emerging synthetic biology); soil microbiome engineering (e.g., by using suitable inoculants, etc.); and agronomics practices (e.g., intercropping, exogenous application of chemical compounds ‘such as phytohormones, neurotransmitters, gastrintransmitters, biostimulants, nanoparticles, etc.’, pest management, using locally adapted seeds in climate-affected lands, organic and smart farming. Data produced during the application of these strategies can be communicated and serve as feedback feeds to advance goal performance. These collaborative forces will improve the worth of climate-smart crop plants in the global schema on climate change, presenting the positive influences of adaptation and mitigation strategies to other correlated SDGs. Whereas integrating these diverse strategies can help us achieve SDG goals in the coming years, if not by 2030. The SDG logos were copied with permission from the United Nations (<https://www.un.org/sustainabledevelopment>). The content of this figure has not been approved by the United Nations and does not reflect the views of the United Nations or its officials or Member States.

major food crops. No single approach will be adequate since plants experience multiple stresses in natural conditions. Therefore, future research should focus on exploring the synergistic effects of combining various stress tolerance mechanisms and identifying key genetic and biochemical pathways that can be targeted for improvement. Understanding the interactions between different stress factors and their combined impact on plant physiology will deliver new insights into designing crops that can withstand multiple stresses simultaneously. Moving beyond conventional studies, we anticipate that comprehensive, integrated studies focusing on adaptation and tolerance mechanisms at cellular and tissue levels are essential to develop hardy crop varieties. Addressing these questions and employing advanced tools will be critical in optimizing genetic engineering strategies (e.g., overexpression of key genes in major field crops, gene editing and de novo synthesis of genes for specific traits) for improved stress tolerance and crop yield.

Integrating emerging pan-genomics, synthetic genomics, high-throughput phenotyping, remote sensing and artificial intelligence offers new ways for developing future climate-smart crops. Pan-genomics can fast-track breeding efforts by incorporating beneficial traits (e.g., disease and stress tolerance) from CWRs into modern crops. High-throughput phenotyping and AI-driven models will improve our ability to predict crop yields and understand climate impacts on plant physiology. Precision agriculture technologies, such as smart farming and advanced irrigation methods, will further mitigate climate change effects in everyday conditions. Synthetic genomics involves creating and modifying genomes, enabling scientists to design plants with enhanced traits altered for specific stress conditions. Synthetic genomics, combined with traditional breeding and modern biotechnological tools, offers a convincing strategy to design and engineer crops that can thrive in climate change.

Understanding variations in how genotypes of plants and microbes respond jointly to climate may be crucial for predicting and managing the recovery trajectories following climate disturbance. Experiments that manipulate the community composition of microbial guilds can determine how much microbes weaken or amplify the tolerance and resistance of plant populations to climate change, such as through feedback over time. Enhancing knowledge of microbial contributions to community and ecosystem resilience to climate disruption will be fruitful to farmers, land managers and restoration practitioners in developing climate-smart ecosystems.

To address these points, interdisciplinary collaboration is vital. Researchers from diverse fields, for example, breeders, agronomists, geneticists, stress physiologists, ecologists, molecular biologists, engineers and data scientists, must work together to build and apply these innovative tools. We believe such collaborations will be game-changing in harnessing the full potential of emerging technologies and integrating them with traditional practices. Additionally, adopting public-private partnerships and connecting with policymakers will be necessary to ensure that scientific advancements translate into practical applications in the agricultural sector. By addressing the current limitations and investigating new research directions, we can enhance crop stress tolerance, mitigate climate change effects, and ensure food security and sustainability in the face of a rapidly changing climate.

Author Contributions

Ali Raza and Rajeev K. Varshney conceived the idea. Ali Raza, Tushar Khare, Xinyue Zhang, Md. Mezanur Rahman and Muzammil Hussain participated in writing the original draft and literature search. Ali Raza designed the figures. Zhangli Hu and Rajeev K. Varshney supervised the work. Sarvajeet Singh Gill, Meixue Zhou, Zhong-Hua Chen, Zhangli Hu and Rajeev K. Varshney provided insightful suggestions and edited the manuscript. All authors have read and approved the final version of the manuscript.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

Ali Raza is an Editorial Board Member for *Journal of Sustainable Agriculture and Environment* and was not involved in the editorial review or the decision to publish this article. The other authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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