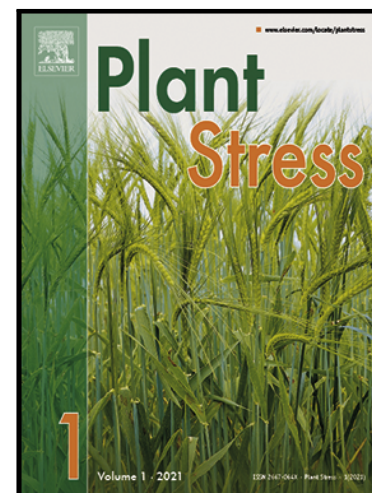


Integrative approaches to enhance reproductive resilience of crops
for climate-proof agriculture



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Highlights

- Enhancing reproductive resilience to stress is vital for food security.
- Modern breeding and genomics speed up stress-tolerant crop development.
- Agronomic practices and advanced tech support yields in extreme climates.
- Big data, AI, and omics enable integrative analyses for resilient crops.
- Integrative Agriculture is a holistic approach for climate-proofing crops.

Integrative approaches to enhance reproductive resilience of crops for climate-proof agriculture

RECROP COST⁺

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Abstract

Worldwide agricultural systems are threatened by rising temperatures, extreme weather events, and shifting climate zones. Climate change-driven failure in sexual reproduction is a major cause for yield reduction in horticultural and grain crops. Consequently, understanding how climate change affects reproductive processes in crops is crucial for global food security and prosperity. The development of climate-proof crops, including maize, wheat, barley, rice, and tomato, requires new genetic material and novel management practices to ensure high productivity under less favorable conditions. Safeguarding successful plant reproduction is challenging due to the complex nature of this biological process, and therefore, a multifaceted approach is the key to success. In this review, we provide an overview of the processes underlying plant reproduction and how they are affected by different abiotic stresses related to climate change. We discuss how genetics, advanced breeding technologies, biotechnological innovations, and sustainable agronomic practices can collectively contribute to the development of resilient crop varieties. We also highlight the potential of artificial intelligence (AI) in optimizing breeding strategies, predicting climate impacts, and improving crop management practices to enhance reproductive resilience and ensure food security. Lastly, we discuss the vision of a new era in agriculture where diverse actors and stakeholders cooperate to create climate-proof crops.

Keywords: abiotic stress, artificial intelligence, breeding, climate change, crop resilience, reproduction, sustainable agriculture

1. Introduction

The world's agricultural systems face significant challenges due to the ongoing effects of climate change and growing global demand for food production. An increase in global mean temperature of more than 1°C and strong thermal anomalies during the period 2011-2023 have been observed, and associated with a higher frequency and intensity of extreme weather events such as heat waves, cold or drought periods, as well as heavy rainfalls causing floods (Forster *et al.*, 2024). These phenomena have already caused disasters and have dire consequences for all actors along the food supply chain (Schmidt & Felsche, 2024).

Climate change impacts agricultural yields globally in varied ways. For maize, for example, it was estimated that each degree-Celsius increase in air temperature will reduce global yield by 7.4% leading to a 45% reduction by 2080 (Deryng *et al.*, 2014; Zhao *et al.*, 2017). In India, warming temperatures reduced wheat grain yields by 5.2% from 1981 to 2009 (Gupta *et al.*, 2017). Since 1979, Europe experienced reduced average production-weighted continent-wide wheat and barley yields by 2.5% and 3.8%, respectively (Faye *et al.*, 2023), while grain maize yield decreased by 4% during the past 14 years (EC, 2024). Moreover, short-term temperature and rainfall fluctuations also impact productivity. From 2010 to 2012, higher temperatures and lower precipitation in the Southern U.S., Western Russia, Western Australia, and East Africa caused a 14-80% grain yield decline in crops such as barley and wheat, leading to famine in East Africa (Anderson *et al.*, 2020). For processing tomatoes, a decline by 6% in yield is predicted till 2050 in certain regions (Camarano *et al.*, 2022). In addition, climate zones are shifting poleward, changing the distribution of productive agricultural areas (Parry *et al.*, 2005). In the future, warmer temperatures will extend growing seasons and open new areas for maize and wheat cultivation, among other crops, in Northern Europe, Russia and Canada, while conditions will become restrictive for important crops such as maize and wheat in other regions (Franke *et al.*, 2022). Notably, many developed countries in cooler climates are likely to benefit from increased yields in some crops, while the majority of developing countries in subtropics and tropics will likely face reduced yields, widening the wealth gap (Anderson *et al.*, 2020).

Considering the expected increase of 35-56% in global food demand by 2050, the current situation begs for adopting new strategies that can enhance the resilience of food production systems (van Dijk *et al.*, 2021). Such measures include the development of climate-proof crops and the improvement of crop management practices that are better adapted to new climatic conditions and are in line with sustainable policies that reduce negative environmental impacts, such as carbon emissions, and optimize the use of resources (Zhao *et al.*, 2022; Grados *et al.*, 2024). A comprehensive strategy for more sustainable food availability will support economic stability, environmental sustainability, and social equity (Hebinck *et al.*, 2021). Given the increasingly severe impacts of climate change, the transition to climate-smart agriculture using innovative technologies and modern practices is inevitable and likely one of the only viable paths to future food security.

Developing climate-resilient crops to withstand unpredictable climatic events is a fundamental aspect of climate-adapted agriculture (González Guzmán *et al.*, 2022; Rivero *et al.*, 2022). Plant growth relies on stem cells in meristems, which develop into essential tissues and organs, including leaves, flowers, and roots (Aichinger *et al.*, 2012). These stem cells enable long-term growth and adaptation to environmental changes, contributing to plant resilience against stresses (Lee, 2018). Many differentiated cells can dedifferentiate back into a stem cell-like state when needed. In crops, meristems generate key structures, including fruits and roots, which are vital for agriculture. Research on meristem regulation has greatly impacted agricultural practices, leading to crop varieties that are better adapted to different

environments and exhibit enhanced productivity (Lindsay *et al.*, 2024). In addition, differentiated tissues and organs can be protected against unfavorable environmental changes through specific signaling cascades that regulate avoidance and/or tolerance mechanisms that impact, for example, molecular chaperones, photosynthesis, cellular metabolism and gene expression (He *et al.*, 2018; Zhang *et al.*, 2023a) at early and advanced developmental stages (germination, seedling establishment, flowering induction). One should keep in mind that different species, varieties, growth stages and organs display different optimal temperatures and different temperature response and tolerance thresholds (Zhu *et al.*, 2021).

General plant fitness is a major determinant for successful plant reproduction leading to high quality crops. The products of plant sexual reproduction, seeds and fruits, are vital sources of nutrition and energy for a wide range of species including humans. Reproduction is a complex developmental process involving a finely orchestrated sequence of relatively short events and a disturbance at any stage of this chain can seriously hamper reproductive success. Thus, the reproductive process itself and the reproductive organs derived from it are particularly sensitive to stress conditions and failure to successfully complete a reproduction cycle may lead to lower quality and quantity of fruit/seed crops (Chaturvedi *et al.*, 2021). Flowering time is also sensitive to environmental conditions and can be accelerated or delayed by fluctuations in temperature, light quality, photoperiod, and water availability (Antoniou-Kourounioti *et al.*, 2021; Rivelli *et al.*, 2024). For pollinating insect-flower interactions, alterations in flowering time can disrupt the synchronization between the time window for pollination and the availability of pollinators (Čereković *et al.*, 2013; Scaven & Rafferty, 2013; Forrest, 2015). Extreme temperature and precipitation patterns can further affect the timing of fruiting, increase the fruit and seed vulnerability to pathogen attacks, and reduce seed survival and germination (Walck *et al.*, 2011; Liu *et al.*, 2018; Bevacqua *et al.*, 2023).

While global efforts to mitigate the effects of human activities on climate change are underway, parallel efforts to breed climate-resilient crops and adapt agricultural practices to the new and evolving environmental realities are equally essential to ensure food security and ecosystem sustainability. This article outlines the impact of extreme weather events driven by climate change on plant reproduction and explores strategies to enhance reproductive resilience to support food security worldwide. We propose that a new era of modernization in agriculture that integrates state-of-the-art genetics and genomics, advanced agronomic practices, digital farming technologies, and climate-smart strategies are crucial for addressing these challenges effectively. This holistic approach will involve leveraging genetic engineering, precision agriculture, and artificial intelligence (AI) to optimize resource use, enhance crop resilience, and ensure sustainable agricultural production in the face of climate change.

2. The importance of sexual reproduction for yield of seed and fruit crops

Crop plant reproduction involves several key developmental stages: floral transition, flower development, ovule and embryo sac development, pollen development and pollen tube growth as well as fertilization and seed/fruit development (Dresselhaus & Franklin-Tong, 2013; Hafidh *et al.*, 2016; Mendes *et al.*, 2016). Initially, the transition of a plant from a vegetative to a reproductive stage is characterized by the formation of flowers (Raihan *et al.*, 2021). Flowering is controlled by environmental and endogenous cues including light quality, intensity, photoperiod, temperature, and circadian rhythms, through the action of photoreceptors, clock components and autonomous pathway regulators, many of which converge in controlling the expression of the master regulators of flowering initiation, such as the *Arabidopsis thaliana* *FLOWERING LOCUS C* (*FLC*), *CONSTANS* (*CO*), *FLOWERING LOCUS T* (*FT*), and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*) genes, to name a few (Maple *et al.*, 2024). Flowering control primarily relies on the activation or repression of the afore-mentioned flowering regulators at the epigenetic, transcriptional and post-translational level. Within angiosperm flowers, the “hidden” haploid male and female gametophytes are formed (reviewed by Butel & Köhler, 2024). The embryo sacs (the female gametophytes) differentiate from megaspore mother cells within ovule primordia and at maturity are typically composed of seven cells including the female gametes, egg and central cell. Ovules grow directly from placenta tissue within the ovary of a pistil. In dicots, ovaries usually embed multiple ovules, whereas monocot flowers contain only a single ovule. Pollen grains (male gametophytes) develop from pollen mother cells in the anther of a stamen. Ovules, embryo sacs and embryos are continuously nourished by the mother plant, while pollen grains are nourished in anther loculi through the tapetum only during its early development. The mature pollen grain has a tough exine cell wall to survive unfavorable environmental conditions in a quiescent mature stage and to reach the stigmatic papillary cells in a viable state. Once there, the pollen grain rehydrates and forms a pollen tube that grows through the transmitting tract until it reaches the ovule and penetrates it via the micropyle, attracted by molecules produced by the synergid cells. At this point, both female and male gametophytes finally meet, the pollen tube bursts, the receptive synergid degenerates and the two male gametes, the sperm cells, are released. During the double fertilization process, one sperm cell fuses with the egg cell given rise to the embryo, while the second sperm cell fuses with the di-haploid central cell forming the triploid endosperm that will nourish the embryo during its development in eudicots and during germination in monocot cereals (Dresselhaus & Franklin-Tong, 2013; Hafidh *et al.*, 2016; Mendes *et al.*, 2016).

Several processes in sexual reproduction are critical for determining the final seed yield *per* fruit and *per* plant. Variations in flower structure, such as the gynoecium, including length of style, stigma, replum and the filament of the stamen, can affect pollination efficiency (Wu *et al.*, 2016; Pan *et al.*, 2019b; Lohani *et al.*, 2020; Baranzelli *et al.*, 2024). Pollination failure can arise from various abiotic factors that result in reduced pollen viability, insufficient pollen amount, unavailability of pollinators,

issues with pollen transfer to the stigma, and/or inhibited pollen germination and tube growth. Regardless of the cause, such pollination troubles typically limit reproduction success and may lead to (partial) sterility (Wilcock & Neiland, 2002). For insect-pollinated species, pollination efficiency greatly depends on the abundance of suitable insect species, the development of which can be differently affected by environmental conditions, especially extreme conditions (Sage *et al.*, 2015). Other factors, including ovule number, fitness of female and male gametophytes, synchronization of tissue development, gametophyte maturity, and pollen tube growth through the pistil, are essential pre-fertilization features required to ensure successful and efficient seed set (Dresselhaus & Franklin-Tong, 2013; Cucinotta *et al.*, 2020). During seed development, events affecting endosperm development and embryo morphogenesis can lead to seed abortion, while issues affecting seed maturation and dormancy can increase the risk of premature seed sprouting and seed germination (Young *et al.*, 2004; Chen *et al.*, 2021; Zhu *et al.*, 2021; Mácová *et al.*, 2022). Therefore, these reproductive failures have a direct impact on seed harvest (yield). In fruit crops, the number of seeds may affect fruit size (Bertin *et al.*, 1998; Aleemullah *et al.*, 2000) and shape, as in multilocular fruits such as tomato (Monselise, 2018).

Abiotic stresses can impair fruit setting, growth and ripening, often leading to reduced yield and compromised quality. Irrigation with water that has increased electrical conductivity can cause salinity stress and negatively impact water transport within the plant, limit gas exchange, and reduce fruit size due to inhibited xylem and phloem flow (Li *et al.*, 2023a). Mild heat stress can accelerate ripening whereas severe heat stress can delay ripening (Biggs & Handa, 1988; Miyazaki *et al.*, 2013; Gao *et al.*, 2017; Nakano *et al.*, 2021; Sharma *et al.*, 2023a). In some cases, abiotic stress can be beneficial in terms of fruit quality. In tomato, moderate salinity or drought stress can enhance fruit quality due to the increase of soluble solids, thereby improving fruit taste, even though smaller fruits are produced. Meanwhile, physiological disorders such as blossom end rot might be more frequent under moderate stress (Petersen *et al.*, 1998).

Climate change can significantly affect perennial fruit crops, particularly during flower initiation, leading to a reduced number of flowers in the following year or flower abortion (Čereković *et al.*, 2014). Higher temperatures and drought stress may inhibit floral transition by accelerating vegetative growth and reducing flower production (Čereković *et al.*, 2013; Bogdziewicz *et al.*, 2020). Contrastingly, for crops that require vernalization for flowering, winter warming can delay the onset of flowering through devernalization, and cause yield reduction as shown in winter wheat (Dixon *et al.*, 2019; Penfield *et al.*, 2021).

3. Sexual reproduction of crops in the face of climate change

The **impact of high temperatures on crop productivity** – Elevated ambient temperatures trigger a developmental program known as thermomorphogenesis that includes the elongation of organs and tissues, hyponastic growth, stomatal development, and accelerated flowering (Zioutopoulou *et al.*, 2021;

Delker *et al.*, 2022). While acceleration of flowering can help plants to avoid an upcoming hot period, it can also have trade-offs as it shortens the vegetative growth period, potentially leading to smaller plants with less biomass and lower yield potential and may disrupt synchronization with pollinators, affecting pollen and fruit set as well as their quality (Begcy *et al.*, 2019; Jagadish, 2020; Faust & Iler, 2022). Similarly, higher temperatures can speed up photosynthesis rate, and result in overall increase in plant biomass, but also drive modifications in sink-source relations and reduced partitioning in reproductive organs, concomitantly resulting in a lower yield (Suwa *et al.*, 2010; Lesjak & Calderini, 2017).

Beyond a certain temperature threshold, which may vary between species and genotypes, plants experience heat stress, which is typically manifested by reduced growth, but also affects all stages of plant development and, above all, reproductive development with major consequences on crop yield (Hedhly, 2011; Cucinotta *et al.*, 2020; Gonzalo *et al.*, 2020). During the reproductive phase, high temperatures cause both morphological and functional alterations in male and female reproductive structures contributing to reduced fertility (Figure 1; Pressman *et al.*, 2002; Hedhly, 2011; Begcy *et al.*, 2019; Jagadish, 2020; Lohani *et al.*, 2020; Miller *et al.*, 2021).

Heat stress impacts pollen quantity and morphology, the architecture of cell wall and, of utmost importance, pollen metabolism (Zinn *et al.*, 2010; Hedhly, 2011; Begcy *et al.*, 2019; Chaturvedi *et al.*, 2021). Developing pollen and growing pollen tubes are probably the most heat stress-sensitive plant organs (Rieu *et al.*, 2017; Gong *et al.*, 2024). In maize, a 2-day heat stress during different stages of pollen development and pollen tube growth can lead to severe reduction in fertility and grain yield (Gong *et al.*, 2024; Lv *et al.*, 2024). Interestingly, heat stress response mechanisms are activated during pollen development under physiological conditions, as a pro-active thermotolerance mechanism in case of an upcoming heat stress incident (Giorno *et al.*, 2010; Fragkostefanakis *et al.*, 2016; Sze *et al.*, 2024). However, limited male thermotolerance capacity does not explain all variation in reproductive outcomes, suggesting that the female part is also significantly affected by heat (Wang *et al.*, 2021a). In wheat, damages in female organs accounted for 34% of the gross fertility loss in plants exposed to a combination of heat and drought stress (Fábíán *et al.*, 2019).

The relative importance of female vs male effects for overall fertility is genotype-dependent for a particular crop and is dependent on the severity of the stress. A recent analysis of processing tomato cultivars concluded that the differences in heat tolerance for yield were not linked to pollen viability or pollination efficiency, but to female fertility (Miller *et al.*, 2021). A well-known female heat stress effect for many crops such as tomato and rice is “stigma exertion”, where the stigma of the flower extends beyond the anthers. In tomato stigma exertion impairs self-pollination and fertility, leading to fruit set reduction (Pan *et al.*, 2019a; Wu *et al.*, 2019, 2024; Shang *et al.*, 2021). In rice, however, stigma exertion can have both advantages and disadvantages under high temperatures. In particular, it can enhance pollen receptivity and mitigate heat-induced pollination issues, particularly under high nighttime

temperatures, but it can also negatively affect spikelet fertility during high daytime temperatures due to stamen-pistil asynchrony (Qi & Wu, 2022).

Heat stress also reduces stigma receptivity causing other abnormalities such as reduction in nutrient supply from the style to the growing pollen tube and in the production of pollen tube attractants (Wang *et al.*, 2021a). Moreover, heat stress is often accompanied by an increase in the levels of reactive oxygen species (ROS) to supra-optimal levels leading to cellular damage and thereby affecting ovule and pollen development, pollen-stigma interactions, and pollen tube growth and fertilization (Ali & Muday, 2024). Thus, balancing ROS levels by the use of scavengers holds a great potential for mitigating ROS-induced sterility during reproduction (Gong *et al.*, 2024).

Female reproductive traits play an important, though highly understudied role in reproductive heat tolerance, exhibiting variation in both pre-pollination (i.e. the proper development of female structures) and post-pollination (i.e., proper functioning of female structures) traits. Specifically, heat stress leads to morphological abnormalities of female organs, decreased ovule number and increased ovule abortion in various species (Zinn *et al.*, 2010; Jiang *et al.*, 2019).

The effect of low temperatures on crop productivity – Although global warming is expected to increase the length of the growing season and allow cultivation of warmer climate crops beyond their current range of cultivation, there is a higher risk of acute low temperature stress due to unpredictable cold episodes and late spring or early autumn frosts. Cold stress (i.e., temperatures below the growth limit) can cause chilling injury (typically between 0 °C and 12-15 °C) and freezing injury (below 0°C) (Kidokoro *et al.*, 2022; Soualiou *et al.*, 2022). The effects of chilling stress on plants include disruptions to cell membrane fluidity (Thomashow, 1999). Additionally, chilling stress reduces the activity of enzymes such as RuBisCO, leading to decreased CO₂ fixation and reduced energy production (Rivero *et al.*, 2022). This results in stunted growth and delayed development, especially impacting germination and early seedling growth. Chilling temperatures can also disrupt the production and action of growth hormones like gibberellins and auxins, altering growth patterns and developmental processes (Kidokoro *et al.*, 2022). In contrast, freezing stress results in ice formation within plant tissues, thereby causing more severe damage than chilling stress (Sanghera *et al.*, 2011). Ice crystals can physically damage cellular structures, leading to cell death. As ice forms, water is extracted from cells, leading to dehydration and concentration of toxic solutes in the cell sap (Ide *et al.*, 1998). Freezing temperatures halt metabolic processes such as photosynthesis, respiration, and enzymatic functions. Structural damage extends beyond the cellular level, impairing the vascular tissues of plants which affects nutrient and water transport, potentially leading to the death of the plant if exposed to low temperatures for prolonged periods (Ide *et al.*, 1998).

Freezing temperatures disrupt the development of crops, affect the timing of bud break and flowering in fruit trees, leading to a desynchronization between the flowering period and the availability of active pollinators (Thakur *et al.*, 2010), subsequently causing reduced fruit yield (Figure 1). Additionally, crops

that experience early or late season frosts may suffer from reduced vigor and delayed growth cycles, affecting overall productivity (Sanghera *et al.*, 2011). Rice is sensitive to low temperatures and when cold stress occurs during the reproductive phase, it causes significant damage to grain production (Thakur *et al.*, 2010). In wheat, a temperature drop of just 1°C below the threshold during reproduction can result in production losses ranging from 10% to 90% (Ji *et al.*, 2017), while in tomato cold stress induces malformed fruits (Wu *et al.*, 2023).

The combination of chilling stress with high light conditions disrupts thylakoid electron transport, reduces RuBisCO activity, and induces stomatal closure, thereby decreasing CO₂ uptake (Huang *et al.*, 2023a), and further leads to a reduction in mesophyll conductance (Fu *et al.*, 2016). Beyond a temperature threshold, the reduction in photosynthetic rate becomes irreversible and leads to a decreased source activity, ultimately limiting parental resources for reproduction (Snider *et al.*, 2009; Soualiou *et al.*, 2022). Low temperatures or chilling stress trigger abscisic acid (ABA) signalling, which is essential for cold tolerance due to its capacity to induce stomatal closure and osmolyte biosynthesis (Thomashow, 1999; Raza *et al.*, 2023). Other phytohormones, including ethylene, gibberellins, and auxin, also play roles in cold stress signaling (Lange *et al.*, 2020; Tang *et al.*, 2022; Huang *et al.*, 2023a; Liu *et al.*, 2024). Low temperatures often delay flowering, causing seeds to develop under suboptimal conditions later in the growing season. This leads to high rates of flower abortion, as documented in chickpea (Croser *et al.*, 2003) where reduced ovule size, viability, and missing embryo sacs impair pistil function (Srinivasan *et al.*, 1999). Nevertheless, the female fertility in key warmer climate crops, e.g. rice and maize, exhibits a relatively high cold stress tolerance (Hayase *et al.*, 1969; Dupuis & Dumas, 1990).

Cold stress causes pollen sterility by disrupting sugar metabolism in the tapetum, thereby preventing starch accumulation in pollen grains (Oliver *et al.*, 2005; Huang *et al.*, 2023a). This sterility is signaled by ABA, which down-regulates genes coding for cell wall invertase and monosaccharide transporters (Oliver *et al.*, 2007). Low temperatures also hinder pollen germination and inhibit pollen tube elongation which can lead to severe reduction in fertilization success (Parrotta *et al.*, 2019).

The impact of cold stress extends to grain filling, delaying the cell cycle and reducing cell division rates in species like maize (Rymen *et al.*, 2007). In chickpea, exposure to cold during the pod-filling stage impairs seed filling, increases flower and pod abortion, and significantly reduces seed growth rate, quality, and yield, with late pod-filling stage stress showing a more pronounced negative effect on seed composition and weight compared to early pod-filling stage stress (Kaur *et al.*, 2008). Additionally, chilling temperatures inhibit the accumulation of storage proteins, minerals, and amino acids, reducing both the rate and duration of grain filling (Nayyar *et al.*, 2007). Overall, cold stress limits resource availability for growth, and affects multiple stages of plant reproduction, from flower development to grain filling, leading to significant reductions in crop yield and quality across various economically important crops.

The impact of drought stress on crop productivity – Climate change is associated with the increased frequency and severity of drought periods in different regions of the world (Field *et al.*, 2012). Plant vegetative growth is often severely affected by drought stress but relatively only few studies have reported the effects of drought stress on reproductive organs (Barnabás *et al.*, 2008; Turc & Tardieu, 2018). Drought stress impairs physiological processes such as photosynthesis, and nutrient uptake. In maize, drought stress can cause up to 40% grain yield loss showing that wheat is particularly sensitivity to drought at the flowering and grain-filling stages (Daryanto *et al.*, 2016; Webber *et al.*, 2018; Cerekovic *et al.*, 2024). Additionally, drought often increases the susceptibility of crops to specific pathogens, further contributing to yield loss (Singh *et al.*, 2023).

Drought stress leads to a series of physiological and morphological changes (Su *et al.*, 2013; Čereković *et al.*, 2014; Sallam *et al.*, 2019; Sheoran, 2022; Duvnjak *et al.*, 2024). In drought-stressed plants, sink limitation due to curbed growth, and source limitation resulting from reduced photosynthesis may reduce plant growth and development, thereby adversely affecting crop yield and quality (Rodrigues *et al.*, 2019; Sallam *et al.*, 2019; Hageman & Van Volkenburgh, 2021).

Drought significantly affects the reproductive processes of crops, yet this critical aspect has received far less attention compared to the impact on vegetative tissues. A major effect is the reduction in flower development time, resulting in smaller flowers with lower quality and quantity of nectar, leading to the attraction of fewer pollinators (Figure 1; Al-Ghzawi *et al.*, 2009). Additionally, drought leads to pollen grain sterility, particularly when stress occurs during meiosis and mitosis, resulting in decreased pollen viability, germination, and pollen tube growth (Al-Ghzawi *et al.*, 2009; Fang *et al.*, 2010). The underlying causes of the damage to these issues include carbohydrate deprivation, increased endogenous ABA concentration, and impaired utilization of sucrose and starch by reproductive sinks (Sehgal *et al.*, 2018). In addition, reduced water availability interferes with normal embryo sac development, leading to malformed embryo sacs and increased ovule abortion (Barnabás *et al.*, 2008).

Grain filling can be severely affected by drought (Farooq *et al.*, 2017). The accumulation of non-reducing sugars to increase the osmotic potential as an acclimation response to drought and failure to build up starch during this period can lead to ovary abortion and reduced grain set and yield (Neumann Andersen *et al.*, 2002). The activity of acid invertase, a crucial enzyme in grain development, is reduced under low water potential, making it a limiting factor in starch biosynthesis and ovary development (Boyer & Westgate, 2004; Farooq *et al.*, 2017). Consequently, inadequate energy sources and elevated ABA levels during drought are key contributors to poor seed set (Liu *et al.*, 2005). Reduced water availability can limit the translocation of assimilates to the developing grains (Španić *et al.*, 2023) (Spanic *et al.*, 2023), resulting in smaller grain size and lower grain mass with overall reductions in crop yield as shown for wheat (Duvnjak *et al.*, 2024).

The impact of flooding and hypoxia stress on crop productivity - The erosive force of climate-induced precipitation is the leading cause of global soil degradation (Borrelli *et al.*, 2023; Panagos *et al.*, 2024). Waterlogging caused by extreme rainfall and flooding creates oxygen-deficient conditions with changes in soil redox status, accumulation of toxic substances that harm plant roots and aerobic soil organisms, affecting nutrient balance and soil properties (Bramley & Tyerman, 2010; Tyagi *et al.*, 2023). The inhibition of root physiological functions and impaired photosynthesis due to waterlogging stress have adverse effects both on vegetative and reproductive growth, leading to yield loss or even complete harvest failure (Zhou *et al.*, 2020; Pan *et al.*, 2021). Plants cope with stress caused by waterlogging through alterations in morphological traits such as development of distinct root structures and physiological responses including the regulation of hormone levels (Daniel & Hartman, 2024).

The impact of waterlogging on growth is crop-dependent. Few crops, such as rice, exhibit superior tolerance to waterlogged conditions due to developmental and physiological adaptations that allow them to thrive in flooded environments (Xu *et al.*, 2006; Bailey-Serres *et al.*, 2010; Langan *et al.*, 2022). However, other crops, e.g. barley, maize, wheat, bean, rapeseed etc., are particularly vulnerable to waterlogging, with yield losses ranging from 20% to 50%, depending on the duration and timing of the event (Tong *et al.*, 2021; Manik *et al.*, 2022). Moreover, extreme soil moisture increases microbial pathogen distribution and promotes plant vulnerability to diseases, augmenting agricultural losses (Moslemi *et al.*, 2018). Studies on hypoxia have been focused mainly on roots, while the effects of low oxygen on reproduction is less understood. How redox state under water deprivation conditions affects reproduction is important, considering that for example in maize hypoxic conditions naturally arising during growth affect germ cell fate, while oxidizing environment inhibit cell specification and cause ectopic differentiation in deeper tissues (Figure 1; Kelliher & Walbot, 2012).

The effect of salinity stress on crop productivity – Soil salinization is one of the main abiotic stresses threatening agricultural production, affecting an estimated 800 million hectares of arable land worldwide (Singh, 2022). Soil salinization is exacerbated by climate change factors such as increased evaporation and reduced rainfall in arid and semi-arid regions, which lead to salt accumulation, while poor management practices, including the use of saline irrigation water, inadequate drainage, and overuse of fertilizers, further contribute to salt buildup in agricultural soils (Uri, 2018). Unlike drought or heat episodes, salinity is a chronic stress, and as such, the impact of salinity on plant performance are well predictable. Most of the cultivated species are glycophytes, i.e. they are sensitive to salt, and their average yield is decreased by 50-80% already under moderate salinity (electrical conductivity of soil water of 4-8 dS m⁻¹) (Zörb *et al.*, 2019). Salinity stress, often a result of irrigation practices and sea-level rise, reduces the ability of plants to take up water and essential nutrients, leading to stunted growth and lower yields (Van Zelm *et al.*, 2020).

Salinity affects plants both through increased soil osmotic potential and raising ion concentration; the osmotic effects resemble drought stress, whereas ionic effects alter plant nutrient status and interfere

with cellular biochemical reactions (Munns & Tester, 2008). For example, exposure to sodium can delay flowering and trigger ABA-mediated stomatal closure for water conservation (Cai *et al.*, 2017). In addition, sodium impairs photosynthesis by disrupting the proton-motive force and inhibiting CO₂-fixation (Munns *et al.*, 2020). Na⁺ can be sequestered in vacuoles or transported back to the root via the high-affinity K⁺ transporter HKT1, which unloads Na⁺ to parenchymal cells (Hasegawa, 2013). The endodermis and Casparian strip act as barriers to Na⁺ influx and K⁺ efflux, while sodium that enters through non-selective cation channels is expelled by the sodium proton exchanger SOS1/NHX7 (Bassil & Blumwald, 2014). Salinity stress reduces meristem size and primary root elongation by lowering local auxin levels (Liu *et al.*, 2015).

Despite its importance for yield, the impact of salt stress on the development of reproductive organs remains poorly understood. In most crop species, salinity delays flowering, reduces the number of inflorescences and flowers, increases flower abortion and reduces stigma receptivity, pollen production and viability (Figure 1; (Khatun & Flowers 1995; Khan & Abdullah, 2003; Zhao *et al.*, 2021; Atta *et al.*, 2023).

Primary metabolites, including sugar alcohols, raffinose family oligosaccharides (RFOs; (Filippou *et al.*, 2021) and proline, function as osmolytes under salt stress and constitute a core mechanism in the salinity stress response (Flowers *et al.*, 2015; Mattioli *et al.*, 2020). Plants limit the entry of toxic ions into the reproductive organs compared to other organs (Bigot *et al.*, 2023). In tomato, Na⁺ accumulated in style, ovaries and anther intermediate layers but not in the tapetum nor in the pollen grains under salinity stress conditions (Ghanem *et al.*, 2009) and Na⁺ concentration was lower in the reproductive organs of the flower than in sepals and petals (Bigot *et al.*, 2023).

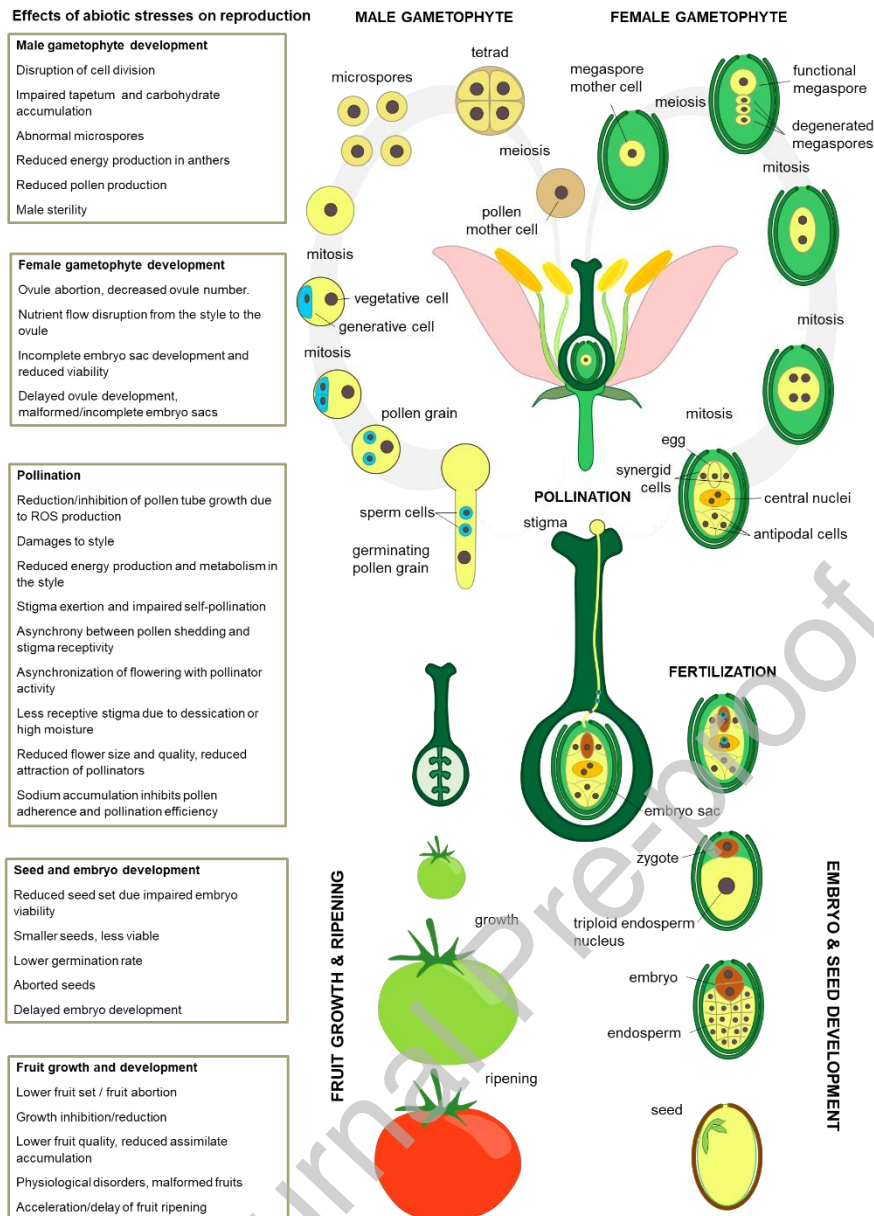


Figure 1. Impact of abiotic stresses on plant sexual reproduction. Left: effect of abiotic stresses on different stages of plant reproduction. Right: Reproduction (male and female gametophyte development) including fruit growth and development (tomato as an example) and seed development. Note that pollen grain in species is bicellular (e.g. tomato) and in others tricellular (e.g. grasses). The scheme is exemplary and variations in difference species exist that are not shown. Part of the scheme is inspired by Shutterstock image ID 1024272037.

4. Genetic approaches to crop improvement

4.1. Utilizing natural genetic variation to improve crop resilience

Climate-proof agriculture requires above all resilient crop varieties. Genetic diversity is a primary resource for breeding programs. It encompasses the genetic variability among lines and genotypes within a species, including different alleles, and allelic interactions (Salgotra & Chauhan, 2023). The focus on maximizing yield and the reduction of genetic diversity in modern domestication practices have led to

the development of crops and agricultural systems that have limited adaptive plasticity and are susceptible to climate change (Keneni *et al.*, 2012; Niinemets, 2020; Krug *et al.*, 2023). Indeed, modern cultivars of domesticated cereals are less tolerant to environmental stresses than their wild relatives (Toulotte *et al.*, 2022).

Genetic diversity analysis may be an indicator for breeders to evolve genotypes with diverse genetic components in order to achieve stability in wheat production and get favorable heterotic combinations (Spanic *et al.*, 2016). Therefore, expanding and utilizing the natural genetic variation in breeding programs is crucial for addressing emerging agricultural challenges. Genetic resources, including crop wild relatives (CWR), landraces, and modern varieties, are vital reservoirs of natural genetic variation.

Nowadays, advancements in next-generation sequencing and high-throughput phenotyping enable the effective utilization of plant genetic resources, especially in analyzing complex traits such as abiotic stress tolerance (Weckwerth *et al.*, 2020; Salgotra & Chauhan, 2023; Chaturvedi *et al.*, 2024). A Genome-Wide Association Study (GWAS) on a maize landrace-introgression pool developed from 20 populations collected in arid regions identified two markers associated with grain yield under drought conditions (Barbosa *et al.*, 2021). In cotton, a transcriptome-wide association study across more than 200 accessions identified the protein tyrosine kinase GhHRK1 to be associated with heat stress induced male sterility (Ma *et al.*, 2021). Despite the encouraging results, the explanatory power of genome-wide studies is still very limited, and challenges remain in translating these findings into practical breeding outcomes.

The release of crop genome assemblies has opened up new possibilities for mining alleles that confer tolerance to abiotic stresses. Assemblies are now available for large and complex genomes such as sunflower (3600 Mpb) (Badouin *et al.*, 2017), maize (2500 Mbp) (Schnable *et al.*, 2009), barley (5100 Mbp) (Mayer *et al.*, 2012) (Mayer *et al.*, 2012), and hexaploid bread wheat (17000 Mbp) (Lukaszewski *et al.*, 2014; Cavalet-Giorsa *et al.*, 2024). Analyzing the pan-genome diversity (representing the complete set of genes within a species) of crop relatives provides valuable insights into gene variation within secondary crop gene pools. For example, about 10% of the cultivated sunflower pan-genome and 1.5% of genes originate from introgressions from wild sunflower species (Hübner *et al.*, 2019). Tomato wild species, such as *Solanum pennellii*, carry stress-tolerant traits, which are crucial for breeding programs and can aid *de novo* domestication efforts, allowing breeders to develop entirely new varieties that are better adapted to environmental challenges (Bolger *et al.*, 2014).

Genebank collections play a crucial role for preserving the genetic diversity that underpins modern crop improvement efforts (Aubry, 2023). These collections house a vast array of genetic resources, including wild relatives, landraces, and traditional cultivars, which are essential for expanding the gene pool available for breeding programs. They serve as the foundation necessary for identifying and incorporating beneficial traits into modern cultivars (Mascher *et al.*, 2019). The genetic diversity stored

in Genebanks ensures that breeders have access to a wide range of alleles, enabling the development of resilient crops that can adapt to the increasing environmental challenges. The Focused Identification of Germplasm Strategy (FIGS) is used to select accessions or genotypes stored in Genebanks that have evolved in environments under natural selection pressure and are therefore likely to carry new allelic variation for useful traits (Haupt & Schmid, 2020). A combination of genomics and information on the evolutionary relationship between the trait and the environment with FIGS has the potential to improve the efficiency and accuracy of identifying the best for use in pre-breeding for target traits.

4.2. Breeding strategies for enhanced crop resilience to abiotic stresses

Breeding strategies aimed at enhancing crop resilience to abiotic stresses have become a critical focus in agricultural research. The first step of these strategies is the identification of reproductive traits associated with stress tolerance which is a long and complex process, requiring extensive research and careful selection to ensure the development of robust and adaptable crop varieties. For fruit and seed crops, reproductive traits include flowering, fertility rate, as well as pollen function, fruit and seed set under stress conditions. Traits such as pollen and egg viability, stigma receptivity, and seed filling are pivotal in maintaining productivity under stress. Furthermore, vegetative organs, such as roots, stems, and leaves, also contribute significantly to reproductive stress resilience, and therefore play a crucial role in overall plant health and yield stability. Deep and extensive root systems enhance water and nutrient uptake, and are therefore critical traits for water- and nutrient-limited conditions (Ghatak *et al.*, 2022). Leaves with reduced stomatal density or improved water-use efficiency maintain turgor and photosynthetic activity during stress periods (Bertolino *et al.*, 2019; Katanić *et al.*, 2021). Moreover, stems with enhanced structural integrity and efficient vascular systems support sustained reproductive development by ensuring the transport of nutrients and water, as well as the necessary mechanical strength to support leaves and reproductive organs (Agustí & Blázquez, 2020).

The evolution of genetic techniques from traditional to modern breeding methods has revolutionized the development of stress-resilient crops. Traditional breeding, relying on phenotypic selection and cross-breeding, laid the foundation for initial improvements in stress tolerance. However, the development of molecular genetics, genomics, and biotechnological tools has accelerated the identification and incorporation of stress-resilient traits, speeding up the development of varieties with enhanced resilience to abiotic stresses. Even more, the identification of signature profiles that are associated with thermotolerance such as the phosphorylation state of a specific set of proteins could aid in the identification of targets for breeding or targets for gene editing that will support crop improvement (Fonseca de Lima *et al.*, 2024).

A variety of molecular markers, from Restriction Fragment Length Polymorphisms (RFLP) to Simple Sequence Repeats (SSRs), and Single Nucleotide Polymorphisms (SNPs), have been extensively used to characterize genetic diversity within and between plant populations. These markers have been

instrumental in developing core collections in various crops, including rice (Yu *et al.*, 2011), soybean (Kumar *et al.*, 2022), and tomato (Blanca *et al.*, 2012). The advantages of molecular markers make them indispensable for studying genetic diversity and improving crop productivity and resilience. Recently, Pessoa *et al.* (2023) conducted a study on drought-tolerant *Solanum pennellii* introgression lines screened at the germination stage to investigate whether this tolerance persisted through the vegetative and reproductive stages. Of the five early-stage drought-tolerant lines two maintained their tolerance in later developmental stages. The authors also identified ten candidate genes for drought-tolerance with associated markers available for marker-assisted selection after validation.

4.2.1 Traditional breeding for abiotic stress tolerance

Crop breeders aim to improve abiotic stress tolerance in breeding germplasm and ultimately in commercial varieties and hybrids while maintaining high quality and yield traits. Screening and propagation of the genetic material in traditional breeding takes place at the production site where the resulting crop is located. This means that the development of lines and hybrids takes place in environmental conditions which are similar to those in which the crop is usually grown. The selection of the best performing lines includes higher yields under different environmental conditions that vary from year to year. Under stressful environmental conditions, there is unconscious selection for resilience because it leads to higher yield, whereas in other years with less severe stress conditions, selection for yield may be at the expense of resilience. On this ground, selection in the field is particularly problematic when resilience has a negative effect on yield (Sadok *et al.*, 2021). The likelihood of a crop being exposed to stress, along with the frequency and severity of that stress, determines whether investing in stress tolerance traits is economically viable and beneficial for long-term crop sustainability. There has been little effort to breed for enhanced phenotypic plasticity that could relax the resilience vs. yield trade-off; this largely reflects the overall limited phenotypic plasticity in modern crops (Shaar-Moshe *et al.*, 2019).

Despite the complexity of breeding for reproductive resilience, cultivars from hotter areas, such as parts of India, are often more resilient to heat than those bred in areas with temperate climates. Breeding germplasm, including varieties, hybrids, and landraces, are an important reservoir of genetic diversity and a rich source of resilience traits in high-yielding genetic backgrounds (Lazaridi *et al.*, 2024). Quantitative Trait Loci (QTLs) from breeding germplasm are less likely to be linked to negative pleiotropic effects than traits from wild accessions, known as negative linkage (Huang *et al.*, 2023b). This also means that a resilient germplasm is a very valuable source for academic research to better understand the molecular differences in breeding germplasm.

Breeding companies have already started implementing strategies for adaptation to climate change. These practices involve shifting sowing and planting dates to avoid detrimental effects of drought and high temperatures at flowering and seed set or could involve more logistically complex decisions such

as moving the sites of propagation of heat-sensitive crops (e.g. leek) to northern regions in response to low seed yields at the original southern production areas (Hampton *et al.*, 2016). While this may seem an elegant solution, it can come at the cost of the beneficial effect of selection under heat. For example, lettuce seed germination is temperature sensitive (Yoong *et al.*, 2016). However, seeds produced at high ambient temperatures germinate better at higher temperatures than seeds harvested from plants grown at lower temperatures, as the mother plant has a significant influence on seed traits (Penfield & MacGregor, 2017).

4.2.2 Modern breeding techniques

Molecular breeders can interrogate genome sequences using high resolution SNP platforms, genotyping by sequencing (GBS), or even by whole genome re-sequencing. QTLs can be transferred from one cultivar or wild accession to a breeding line (introgression) and the progress towards the generation of near isogenic lines (NILs) can be tracked based on genome sequence (Bita *et al.*, 2011). Genetic data can also be utilized to introduce mutations either derived from mutant populations with randomly generated mutations, or induced targeted mutations generated by gene editing. However, although many genes involved in abiotic stress related processes have been identified, not many stress tolerance loci have been successfully introduced into commercial material. A major reason for this is that reproductive resilience is a complex polygenic trait, as has been demonstrated in crops such as rice, maize, rice, *brassicaceae* and tomato (Wen *et al.*, 2019; Cappetta *et al.*, 2021; Seetharam *et al.*, 2021; Li *et al.*, 2023b). The ability of breeders to introduce QTLs into breeding lines and follow them through to a commercial product, alongside all other relevant quality and yield traits, is limited. This is particularly the case in the breeding of vegetable crops such as tomato, which is bred for many different market segments, each requiring a specific set of traits, including plant height, biotic resistance, fruit size, color, sweetness, flavor, shape, and vine architecture. Therefore, introducing more than one or two QTLs for abiotic stress resilience is often more economically feasible for field crops, such as processing tomatoes.

QTLs for increased pollen viability and pollen number under heat stress have been identified in tomato (Xu *et al.*, 2017). A major QTL conferring higher tolerance under continuous mild heat conditions (31°C day, 25°C night) was recently shown to act through enhanced cooling of young flower buds and to improve yield in heat wave-affected commercial production environments (Jansen *et al.*, 2024). A comparative study of QTL and RNA-seq in rice identified 45 heat-responsive genes, 24 of which showed specific expression patterns in reproductive tissues (Raza *et al.*, 2020). *OsBIP2* (Binding Protein 2) was identified as a potential candidate conferring thermotolerance of pollen tubes in response to heat stress. An earlier study provided a landmark of a QTL-identified rice gene, *THERMOTOLERANCE 1* (*TT1*), whose overexpression confers thermoprotection without compromising yield (Li *et al.*, 2015). In addition to the proteasomal TT1 subunit, chromatin remodeling factors, such as the *Brassica rapa* JUMONJI (JM18) histone 3 lysine 36 di- / trimethyl (H3K36me_{2/3}) demethylase were shown to

enhance thermal resilience without impairing plant parameters when grown under non-stress conditions (Xin *et al.*, 2024).

The complexity of abiotic tolerance in breeding germplasm was also highlighted by a study of heat stress tolerance in maize that identified 22 QTLs for leaf and tassel thermotolerance. However, tolerance QTLs from different cultivars did not co-localize, indicating that multiple, phenotypically differentiable pathways are involved in the development of foliar stress phenotypes that are relevant to the evaluation of yield reduction after heat stress (McNellie *et al.*, 2018).

One of the biggest challenges in crop breeding is the lengthy time required to develop stable, high-performing varieties, which can take several years. This issue can be addressed by speed breeding which aims to drastically shorten the breeding cycle, allowing the production of multiple crop generations within a year (Haroon *et al.*, 2022; Pandey *et al.*, 2022). Speed breeding is achieved typically by extending the photoperiod and providing continuous light to crops which in combination with single-seed descent method allows 4-6 generations of crops like wheat and barley within a year (Riaz *et al.*, 2016; Hickey *et al.*, 2017; Ghosh *et al.*, 2018). Speed breeding can be complemented by pollen-based selection, where stress application during the pollen development stage helps identify and select for stress-tolerant traits. By exposing pollen to biotic or abiotic stresses, breeders can screen for resilient pollen grains that carry beneficial alleles, which can then fertilize female gametes and produce stress-tolerant offsprings (Totsky & Lyakh, 2015; Mohapatra *et al.*, 2020; Singh *et al.*, 2020). Another proposed approach to make crop reproduction tolerant to abiotic stress has been to make the fruit set independent from pollination, and thus potentially bypassing the need for reproductive resilience for a successful fruit set (Klap *et al.*, 2017). A recessive knock-out mutation in the tomato *AGL6*-gene, for example, which was found to be the causal natural mutation in the facultative parthenocarpic *pat-k* mutant, resulted in high quality seedless fruits (Gupta *et al.*, 2021). However, although this tomato mutant has been described as facultatively parthenocarpic, seed set in this mutant after manual pollination is exceptionally low, making the trait unsuitable for seed production and commercial application. Another solution may be found in apomixis. While this phenotype is usually discussed in the frame of clonal reproduction (Underwood & Mercier, 2022), it may also render seed and fruit production less sensitive to environmental stress.

The combination of modern breeding techniques such as marker-assisted selection (MAS), advanced target genes identification, as well as the usage of CRISPR/Cas technology (see also below) with speed breeding, the development of resilient high-performing crop varieties can become more precise and faster than ever before (Haroon *et al.*, 2022; Pandey *et al.*, 2022; Cardi *et al.*, 2023).

4.2.3 Epi-breeding for stress resilience

Epigenetic regulation is crucial for plant stress resilience and reproductive development, as it modulates gene expression in response to environmental stimuli through mechanisms like DNA methylation, histone modification, and non-coding RNA activity (Begcy & Dresselhaus, 2018; Varotto *et al.*, 2020). Epigenetic modifications can lead to both, transient and heritable changes that impact stress tolerance and reproductive success. During reproductive development in cereals, epigenetic alterations, such as changes in DNA methylation and histone modifications, regulate the formation of gametophytes, fertilization, and seed development under stress conditions (Begcy & Dresselhaus, 2018; Dalakouras & Vlachostergios, 2021).

Heat stress affects reproductive tissues in plants through various epigenetic mechanisms. In rice, heat stress disrupts endosperm development by altering the expression of FERTILIZATION-INDEPENDENT ENDOSPERM 1 (*OsFIE1*), a component of the Polycomb Repressive Complex 2 (PRC2), leading to failure in cellularization due to changes in DNA methylation and histone modifications (Folsom *et al.*, 2014). Additionally, during male germline development, heat stress reduces expression of the multiple archesporial cells 1 (*MAC1*) gene in barley, potentially regulated by chromatin modifications, leading to anther abortion (Abiko *et al.*, 2005; Wang *et al.*, 2012). In submergence-stressed rice, H3K4me3-mediated regulation of alcohol dehydrogenase (*ADH*) expression shifts from di- to tri-methylation and increases H3 acetylation, promoting gene activation (Tsuji *et al.*, 2006).

Epigenetic variation can be subject to selection and result in stably inherited novel phenotypes, suggesting a role in rapid adaptive responses, and therefore presents a valuable tool for improving crop resilience (Schmid *et al.*, 2018). The use of epigenetic variation is explored using epigenetic recombinant inbred lines (epiRILs) (Johannes *et al.*, 2009; Reinders *et al.*, 2009). Screening of an *A. thaliana* epiRIL population based on the mutant parent line METHYLTRANSFERASE 1 (*met1-3* mutant), which has an almost complete erasure of CG methylation, identified delayed germination of several lines under salinity stress that was carried in the F9 generation, suggesting the stable inheritance of the trait (Reinders *et al.*, 2009). In an *A. thaliana ddm1*-based epiRIL population (DDM1: chromatin-remodeling gene decrease in DNA Methylation) heritable epigenetic variation was demonstrated in drought experiments (Johannes *et al.*, 2009; Zhang *et al.*, 2013). In tomato, mutation in one of the two *DDM1* paralogues resulted in increased thermotolerance in response to mild chronic heat stress, while silencing of *MutS HOMOLOG1 (MSH1)* in tomato positively affected fruit weight and fruit number under high temperature field conditions (Yang *et al.*, 2015; Singh *et al.*, 2021b). By combining epiRILs with epigenetic mapping techniques like epigenetic quantitative trait loci (epiQTL) analysis, key epigenetic loci associated with desirable traits can be identified, paving the way for epi-breeding (Zhang *et al.*, 2013). Therefore, through the selective application of epialleles, epiRILs can revolutionize crop improvement strategies for stress resilience.

4.3 Generation of climate-proof crops using New Genomic Techniques (NGTs)

Gene editing is a fascinating area of study in plant breeding and molecular biology. Gene editing can precisely modify specific genes to improve desirable traits, such as stress tolerance and crop yield, by introducing targeted mutations. New Genomic Techniques (NGTs) are a set of techniques that have emerged during the last 20 years and are used to alter the genetic material of an organism (Iqbal *et al.*, 2020). NGTs include gene editing methods such as CRISPR-Cas, Transcription Activator-Like Effector Nucleases (TALENs), and Zinc Finger Nucleases (ZFNs) which enable the precise manipulation of genomes, facilitating the incorporation of beneficial traits that confer stress tolerance in crops (Pixley *et al.*, 2023).

There is a plethora of examples from studies in crops that used NGTs and achieved increased stress resilience. CRISPR/Cas9 technology was used to create novel variants of the maize *ARGOS8* gene, a negative regulator of ethylene responses, by inserting the *GOS2* promoter into the gene's 5'-untranslated region (Shi *et al.*, 2017). These CRISPR-edited variants exhibited elevated *ARGOS8* transcript levels and grain yield increase without any yield loss under well-watered conditions. Similarly, advances in genome editing have shown promising results in improving drought tolerance in other crops such as tomato. Knockout of the gene coding for the transcription factor LATERAL ORGAN BOUNDARIES DOMAIN 40 (*SILBD40*) in tomato increased drought tolerance (Liu *et al.*, 2020). CRISPR/Cas9 mutagenesis of the ABA receptor *OsPYL9* in rice resulted in plants with higher ABA levels, antioxidant activities, chlorophyll content, leaf cuticular wax, and lower stomatal conductance and transpiration rates and consequently with increased drought tolerance (Usman *et al.*, 2020). Mutations in soybean *GmHDZ4* resulted in enhanced growth and improved root architecture with significantly greater root length, surface area, and root tips, which could maintain a higher turgor pressure through increased osmolyte accumulation and higher antioxidant enzyme activity, leading to reduced oxidative stress markers such as hydrogen peroxide, superoxide anion, and malondialdehyde (Zhong *et al.*, 2022).

Furthermore, CRISPR/Cas9 technology was used to enhance salinity tolerance in rice by knocking out the *OsRR22* gene, a B-type response regulator transcription factor involved in cytokinin signal transduction and metabolism, resulting in mutant plants with significantly improved salinity tolerance at the seedling stage without altering other agronomic traits (Zhang *et al.*, 2019). Similarly, a combination of CRISPR/Cas9-mediated editing of the *OsRR22* gene and heterosis utilization led to the development of novel salinity-tolerant rice lines, which maintained agronomic performance comparable to wild types under non-stress conditions (Zhang *et al.*, 2019; Sheng *et al.*, 2023). *OsWRKY63* negatively regulates chilling tolerance in rice and CRISPR/Cas9-generated *OsWRKY63*-knockout mutants showed increased chilling tolerance due to increased expression of cold-induced genes and ROS enzyme coding genes pushing beyond the limits of the genetically encoded capacity for tolerance (Zeng *et al.*, 2020). CRISPR-Cas9 gene editing on three genes in rice, namely *OsPIN5b*, *GS3*, and *OsMYB30*, was used to

create new mutants with significantly increased cold tolerance and yield (Zeng *et al.*, 2020). The *ospin5b* mutant resulted in increased panicle length, the *gs3* mutant contributed to larger grain size, and the *osmyb30* mutant provided enhanced cold tolerance, while the triple mutant combined the advantageous traits and cold tolerance. These examples demonstrate that CRISPR-based targeted gene editing can simultaneously modify multiple genes, combining different traits, conferring tolerance to various abiotic stresses. Furthermore, by targeting several genes, polygenic traits can be precisely engineered to enhance complex stress responses. In addition, the use of the CRISPR-Cas technology can be expanded to combine tolerance to multiple plant diseases, as CRISPR-edited intracellular nucleotide-binding leucine-rich repeat receptor *SINRC4a* mutants in tomato exhibited enhanced immunity against fungi, bacteria, and pests without penalty for growth or yield (Pizarro *et al.*, 2020).

Thus, CRISPR-Cas-based mutagenesis is clearly one of the key tools to accelerate the development of climate-resilient crops, crucial for keeping pace with the rapidly increasing severity of extreme climate phenomena. Optimized variants of Cas9 and other emerging Cas systems with increased efficiency, higher specificity and recognition of different Protospacer Adjacent Motif (PAM) sequences currently expand the plant genome engineering toolbox and will be on the frontlines of combating the effects of climate change on crops (Capdeville *et al.*, 2023; Cardi *et al.*, 2023).

CRISPR has been extended beyond genome editing to include CRISPR activation (CRISPRa) and interference (CRISPRi) (Carroll & Giacca, 2023). Catalytically inactive Cas9 (dCas9) is coupled with transcription activators or inhibitors to regulate gene expression at specific promoters, as well as chromatin modulators for epigenome editing. Targeted activation of *AREB1*, a major drought-responsive transcription factor, by utilizing dCas9HAT (dCas9-Histone acetyltransferase) triggered local chromatin rearrangement by acetylating histone H3K27, hence increasing gene expression during drought (Roca Paixão *et al.*, 2019). A CRISPR/dCas9-based targeted demethylation system was used to remove cytosine methylation at the targeted locus of the *FLOWERING WAGENINGEN* (*FWA*) promoter (Gallego-Bartolomé *et al.*, 2018). Early flowering allows plants to reproduce and set seeds before adverse environmental conditions arise, improving survival and reproductive success. Therefore, CRISPRa/i provide a potent and precise method to crop development that outperforms traditional breeding and transgenic procedures in terms of efficiency and specificity.

5. Agronomic practices to enhance the resilience of crops to extreme climate

Agronomic practices play a pivotal role in ensuring successful crop reproduction by creating optimal conditions for plant growth and development, which are essential for maximizing reproductive success and yield. In addition to the use of improved genetic material, several agronomic strategies need to be optimized in order to improve yields: (i) soil management; (ii) timely irrigation; (iii) pest and disease management; (iv) weed control; (v) crop rotation; (vi) proper spacing, planting density and dates of sowing; (vii) fertilizer management; (viii) cover/strip cropping; (ix) other agroecological techniques

(Figure 2; Balchin *et al.*, 2016; Bhaskar *et al.*, 2021; Franke *et al.*, 2022; Juventia *et al.*, 2022; Bogale & Bekele, 2023). As agricultural production is based on these principles, their prioritization is important in order to ensure a robust vegetative growth and a successful reproduction that will provide high yield of seeds and fruits. These practices particularly apply to open field farming systems, or to semi-controlled environment farming, while some are also relevant for modern closed or controlled-environment agriculture systems, such as greenhouses and vertical farms, which are not always immune to the effects of climate change.

Proper water management, including the sustainable use of water resources, maintaining appropriate water quality, and implementing a strategic irrigation plan, is essential for maximizing crop yield and ensuring long-term agricultural productivity. By optimizing these factors, farmers can enhance water use efficiency, support plant health, and mitigate the impacts of water scarcity and environmental stressors on crop production. For example, rising temperatures reduce wheat yields in India, and advancing wheat sowing by addressing delays in the preceding rice growing season, particularly through earlier rice nursery establishment and increasing groundwater irrigation access before monsoon rains, may help mitigate temperature impacts (Umashaanker *et al.*, 2024).

Maintaining soil health and sustaining the soil microbiome are crucial for boosting crop yields in stressful environments. Healthy soil enriched with organic matter and a diverse microbiome enhances nutrient cycling, improves soil structure, and increases water retention, all of which support plant growth under stress conditions (De Vries *et al.*, 2020). Beneficial soil microbes contribute to enhancing plant resilience in multiple ways, including the formation of self-colonized biofilms around roots, which improve nutrient uptake and protect roots from environmental stresses. They also influence plant physiology by altering root architecture, adjusting stress hormone levels (like ethylene and abscisic acid), and enhancing the production of antioxidants, volatile compounds, and osmolytes (Chatterjee & Niinemets, 2022; Barnawal *et al.*, 2017; Forni *et al.*, 2017; Rafique *et al.*, 2024). A notable example is the root endophytic bacterium *Pseudomonas argentinensis*, strain SA190, which significantly enhances drought tolerance in *Arabidopsis* and alfalfa by promoting root development and stress response through ABA signaling and epigenetic priming of aquaporin genes (Alwutayd *et al.*, 2023). Thus, utilizing beneficial microbial communities, or targeting the genes and pathways they affect in plants, offers a promising strategy for enhancing crop resilience and productivity in future agricultural practices under stress conditions.

Effective weed management is crucial for enhancing crop stress resilience by reducing competition for resources such as water, nutrients, and light, thereby promoting healthier plant growth and higher yields. Herbicides and tillage are currently the main methods used for weed management, with nowadays well documented negative effects on the environment. In addition, herbicide resistance in crops is an increasing problem for effective weed management. In modern agriculture with an emphasis on

sustainable farming practices the adoption of more holistic approaches that encompass practices aimed at reducing weed establishment, growth, and reproduction through methods that enhance the competitiveness of crops and minimize the ecological niches available for weeds (Monteiro & Santos, 2022; Brainard *et al.*, 2023). Key strategies include, among others, crop rotation, cover cropping, reduced tillage, mulching, optimization of planting density and row spacing, timely planting and harvesting, and intercropping which creates a more complex canopy and root structure that suppresses weed growth (Korres *et al.*, 2019). A shift towards biocontrol practices can reduce farmers' dependency on conventional synthetic herbicides, replacing them with botanical herbicides enhanced by modern encapsulation techniques for greater efficacy (Campos *et al.*, 2019).

In the 21st century, eco-friendly farming systems that implement integrated pest management through a better understanding of the underlying causes of diseases and pests, as well as incorporating sustainable agricultural practices, are essential for reducing chemical inputs and enhancing crop resilience (Barzman *et al.*, 2015). This approach promotes the use of biological control agents, crop rotation, and the cultivation of pest-resistant crop varieties, all of which contribute to a healthier ecosystem and more sustainable food production (Stenberg, 2017). Combined with appropriate fertilizer management, intercropping—the practice of growing non-crop plants or alternative crops alongside cash crops—is one of the most straightforward strategies to combat pests and diseases and diversify industrial agriculture. It can be used in several spatial arrangements (Huss *et al.*, 2022). Wide enough for separate cultivation, but thin enough for each crop to interact with other organisms in an ecosystem, is how strip intercrops flourish. Relay intercropping is the practice of growing many crops or living mulches in succession with some growth cycle overlap (Glaze-Corcoran *et al.*, 2020; Hatt & Döring, 2024).

In addition, incorporating traditional knowledge into modern agronomic practices may be beneficial for enhancing crop resilience and sustainability. Many indigenous farming methods, developed over centuries, emphasize biodiversity, soil health, and water conservation, offering potentially valuable solutions for the current agricultural challenges. Integrating these time-tested practices with modern techniques may help to create more robust farming systems that are better suited to withstand climate-related stresses. Agroforestry, a practice rooted in traditional knowledge, offers a potentially powerful approach to climate-proof agriculture in some regions such as Africa (Mbow *et al.*, 2014; Pantera *et al.*, 2021). By combining crops, animal husbandry, and trees, agroforestry enhances biodiversity, improves soil health, and increases water retention, all of which contribute to more resilient ecosystems and farming systems (Bogale & Bekele, 2023; Quandt *et al.*, 2023).

By adopting diverse agronomic practices in combination with advanced technologies, farmers can create conditions that enhance the stress resilience of sensitive cultivars but also further boost yields in tolerant varieties. Importantly, these approaches can contribute to sustainability by promoting soil health, reducing the reliance on chemical inputs, and supporting efforts for lower carbon emissions. By optimizing resource utilization and minimizing environmental impacts, these practices help create a

more sustainable agricultural landscape that mitigates the effects of climate change and supports long-term food security.

5.1 Optimizing resilience of crop reproduction through chemical applications

Chemical stimulants offer immediate and targeted solutions to a variety of agricultural challenges, including pest control, disease management, and nutrient deficiencies, but can also positively affect crop resilience and productivity under climate challenges (Martínez-Lorente *et al.*, 2024). They are natural or synthetic compounds with the potential ability to enhance plant growth and development under unfavorable environments. Phytohormones such as auxins, cytokinins, ABA, gibberellins, melatonin and jasmonates alter plant growth and productivity under stress conditions (Yakhin *et al.*, 2017). Cytokinins can affect fruit size and yield (Sosnowski *et al.*, 2023) and ethylene releasers such as ethephon can induce flowering, fruit ripening, and leaf abscission (Iqbal *et al.*, 2017). Additionally, synthetic brassinosteroid, glycine betaine, melatonin, polyamines, proline and nitric oxide donors such as sodium nitroprusside can be used to boost yield and improve plant biomass under stress conditions (Ashraf & Foolad, 2007; Simontacchi *et al.*, 2015; Ayub *et al.*, 2021; Hafeez *et al.*, 2021; Shao *et al.*, 2022; Sati *et al.*, 2023; Ullah *et al.*, 2024). Synthetic priming agents can also act as combined donors of compounds known for their priming effects. For instance, NOSH-aspirin (NBS-1120), a novel variant of aspirin that releases both nitric oxide and hydrogen sulfide, was originally developed as an anticancer drug. However, it has also demonstrated potential in mitigating abiotic stress in plants by leveraging the synergistic effects of its active components (Antoniou *et al.*, 2020; Gohari *et al.*, 2024). Similarly, the exogenous application of acetic acid induced the *de novo* jasmonic acid (JA) synthesis and histone H4 acetylation leading to increased tolerance to drought stress (Kim *et al.*, 2017).

Biostimulants on the other hand, such as beneficial microorganisms including mycorrhizal fungi and plant growth-promoting rhizobacteria, humic and fulvic acids, seaweed extracts, amino acids, chitosan, extracts derived from higher plants, or even plant metabolites offer a more sustainable approach (Canellas *et al.*, 2015; Hidangmayum *et al.*, 2019; Priya *et al.*, 2019a; Deolu-Ajayi *et al.*, 2022; Hnini & Aurag, 2024; Martínez-Lorente *et al.*, 2024). They enhance plant growth and development by improving the absorption of nutrients and water by the roots, which is essential for achieving high biomass production and successful harvests (Gilroy & Jones, 2000), stimulating beneficial microbial activity in the soil and enhancing stress tolerance (du Jardin, 2015; Shiade *et al.*, 2024), partly through the regulation of ROS metabolism (Gedeon *et al.*, 2022; Gong *et al.*, 2024). Also, they exert effects at the whole-plant level, influencing physiological processes such as germination, root and shoot growth and morphology, flowering, and fruit set. From the agronomic standpoint, these changes are highly important, as they are closely linked to crop yield and quality, thus determining economic profitability (Geelen & Xu, 2020). In this way, the use of exogenous biostimulants offers a simple and cost-effective strategy for short-term relief from abiotic stresses and can have immediate positive effects on stress sensitive varieties.

The exogenous addition of salicylic acid (SA) improves pollen mother cell meiosis under heat stress, resulting in increased pollen viability and seed-setting rates in rice (Feng *et al.*, 2018). SA treatment increased freezing tolerance in cold-primed wheat plants (Wang *et al.*, 2020, 2021b). The polyamine spermidine plays a crucial role in pollen germination and stimulates pollen tube growth by promoting protein synthesis under high temperatures (Gupta *et al.*, 2024). Improved pollen viability and germination was also observed in heat stressed tomatoes by exogenous melatonin application (Qi *et al.*, 2018). A brown seaweed (*Ascophyllum nodosum*) derived biostimulant significantly enhanced flower development, pollen viability, and overall fruit production in tomato plants under both normal and heat stress conditions (Carmody *et al.*, 2020). This effect was linked to an increased level of simple sugars and the higher expression of heat shock proteins (HSPs), in anthers and young fruits. In tomato plants, treatments with biostimulants coming from higher plants or algae increased fruit production and enhanced the concentration of minerals, bioactive compounds and soluble solids. The treated tomatoes also had greater antioxidant activity and fruit brightness and redness (Colla *et al.*, 2017; Rouphael *et al.*, 2017). Aminolevulinic acid improved yield in bell pepper under high temperatures when applied in its nano-encapsulated form (Hallaji *et al.*, 2024), while proline treatment enhanced pollen fertility and the overall mungbean plant performance under heat stress by increasing proline level and reducing the oxidative stress damage (Priya *et al.*, 2019a,b). In rice spikelets, exogenous application of ABA can reduce the heat-associated pollen sterility by increasing soluble sugars, starch, and non-structural carbohydrates, boosting the synthesis of the essential for thermotolerance HSPs, and upregulating sugar metabolism and transporter genes (Rezaul *et al.*, 2019). Flavonols, β -carotenoid and their derivatives have also a positive effect on pollen and consequently fertility (Rao *et al.*, 2024). Additionally, melatonin has been found to improve the reproductive success of rice under heat stress by enhancing antioxidant capacity and reducing oxidative damage in pollen and floral tissues (Barman *et al.*, 2024).

Chemical stimulants can be applied as seed coating material or by direct application on plants to ensure long-lasting effects by sustaining a stress tolerant status for a long period. Recent developments in nanotechnology with engineered nanocarriers have allowed the development of smart delivery systems that are eco-friendly and offer increased efficiency and reduced chemical usage (Gohari *et al.*, 2024). For example, melatonin-functionalized chitosan nanoparticles enhance spearmint tolerance to salinity (Gohari *et al.*, 2023), while putrescine-functionalized carbon quantum dots lead to protection of grapevine plants against cadmium stress (Panahirad *et al.*, 2023). Similarly, seed priming with hydrogen sulfide (H_2S) enhanced drought tolerance in sunflower (Fotopoulos *et al.*, 2013; Ocirk *et al.*, 2021). Taken together, a growing body of evidence suggests that chemical stimulants are practical and immediately available promising solutions for improving plant reproductive success and yield.

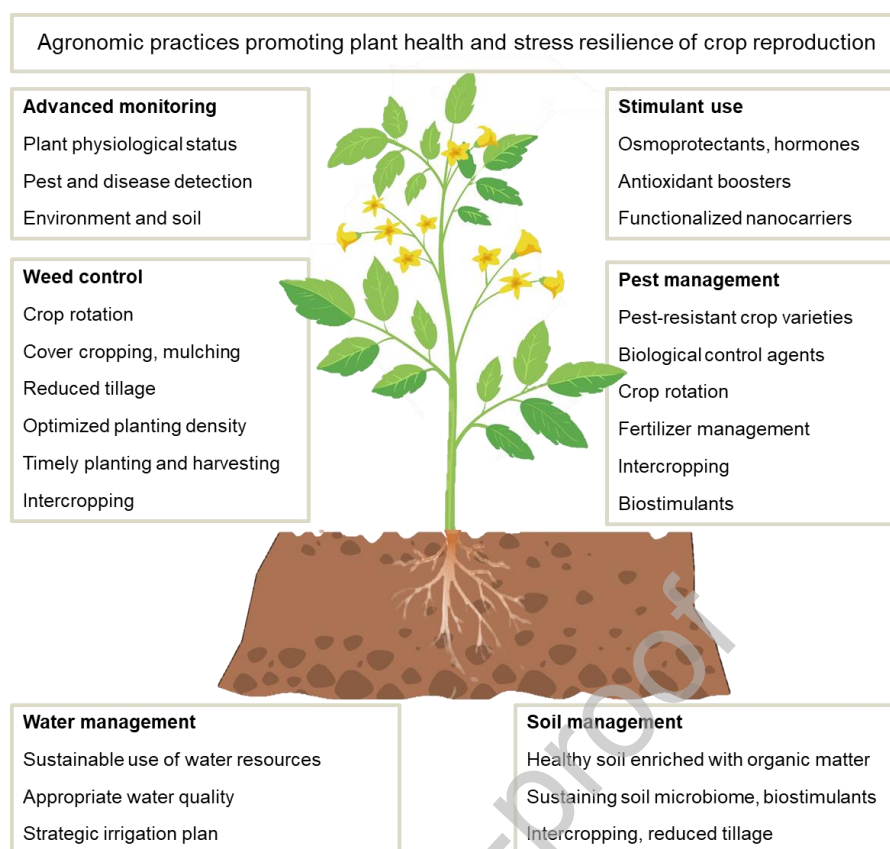


Figure 2. Overview of agronomic practices that can boost plant health and stress resilience of crop reproduction. Vectors have been designed by Freepik and modified.

6. Artificial Intelligence towards a climate-proof agriculture

Crop improvement approaches can be supported by “big data”, high-throughput technologies and AI which can support integrative analyses of genomic, phenotypic, and environmental data (Figure 3; Yan & Wang, 2023). The rise of omics technologies and next-generation phenotyping tools, like high spectral imaging, push research beyond traditional limits (Sheikh *et al.*, 2024). These technologies enable reliable analysis and application of complex data, fostering effective interventions for enhancing crop resilience (N. Govaichelvan *et al.*, 2024). In the pursuit of transformative and sustainable solutions within almost every aspect of the agriculture sector, AI has emerged as a revolutionary tool as it can perform efficient analysis of vast amounts of data, accurate classification and prediction (Yan & Wang, 2023).

Phenotyping - The traditional methods of phenotyping rely on manual measurements and observations, which are time-consuming, labor-intensive, and often subject to human error. AI-powered image analysis tools, utilizing deep learning algorithms, process large volumes of image data to assess leaf area, plant height, flowering period, and plant’s health status, but also flower morphology, pollen viability, and fruit set by analyzing and interpreting images captured by drones or cameras (Walsh *et al.*, 2024). Image-based phenotyping can be combined with Deep Learning (DL) approaches, based on

the establishment of artificial neural networks (ANNs) (Singh *et al.*, 2021a). Convolutional neural networks (CNNs) have been mostly applied for static images, while novel approaches based on recurrent neural networks and long-short term memories (LSTMs), have emerged in the last years to provide a dynamic time course of phenotyping studies (Taghavi Namin *et al.*, 2018). Machine Learning (ML) models can be utilized to generate agro-climatic models based on metadata concerning weather, soil, and crop parameters, to predict optimal yield for winter wheat (Mousavi *et al.*, 2023), and to evaluate the effects of flooding on yield based on different vegetation indices (Li *et al.*, 2023c).

CNNs have been used to improve maize tassel detection, ear counting and yield estimation of triticale, soybean yield prediction under different climate and growth conditions, or the determination of plant height in an oilseed rape population, among others (Zou *et al.*, 2020; Alexander *et al.*, 2024; Rodene *et al.*, 2024; Skobalski *et al.*, 2024; Stefański *et al.*, 2024). CNNs are also useful for the evaluation of the performance of reproductive tissues. ML approaches have been recently applied for the image-based discrimination of pollen germination rate and viability and DL has been utilized for the determination of the ideal temperature required for pollen germination (Tan *et al.*, 2022; Yamazaki *et al.*, 2023; Zhang *et al.*, 2023b). Moreover, CNNs have been used to predict the classification of pollen-carrying and pollen-free bees, offering a valuable tool to monitor the effects of climatic change on pollination (Pat-Cetina *et al.*, 2023). Finally, the automatic evaluation of seed germination across crop species has been made possible by DL employing CNN (Genze *et al.*, 2020; Krzyszton *et al.*, 2024).

-Omics - The integration of ML and AI into plant-omics has revolutionized the analysis and interpretation of complex biological data and helped to overcome barriers like high dimensionality, uncertainty, and non-independence among variables inherent in -omics data (Altman & Krzywinski, 2018). ML and particularly DL can provide more accurate and insightful analyses of plant characteristics affected by genotype and environment interactions (Rai *et al.*, 2019).

In addition, ML is becoming essential in genomics. Evolutionarily informed ML has been used for the annotation of genes and to support the characterization of genomes that are not yet fully understood, aiding breeding studies and genetic approaches (Zia *et al.*, 2023). Given the increasing importance of underutilized crops for food production and the expansion of diversity used for breeding, genomic characterization is crucial. In many cases, developing the pangenome of certain crops is necessary to fully harness their potential for breeding, as it captures the entire genomic diversity within a species, enabling the identification of novel alleles and traits that can be exploited to improve crop resilience and yield. ML and DL enhance the accuracy of variant calling, aiding crop breeding by identifying structural variations and novel alleles (Yocca & Edger, 2022). Haplotype-aware modeling and image-based analyses, enable researchers to extract meaningful patterns from complex data, advancing genomic selection and marker-assisted breeding for crop improvement and even AI-based models can forecast genomic crossovers in maternal and parental plants such as in maize, thereby allowing the identification of genomic regions with elevated mutation rates (Demirci *et al.*, 2021; Farooq *et al.*, 2024).

Moreover, ML algorithms have been successfully applied to predict gene promoters, *cis*-regulatory elements, tissue-specific biosynthetic gene expression, and structure and regulation of gene regulatory networks (GRNs), i.e. related to nitrogen signaling (Varala *et al.*, 2018; Uygun *et al.*, 2019). Tools like iDREM use hidden Markov models to reconstruct temporal GRNs in response to biotic and abiotic stresses (Ding *et al.*, 2018; Mishra *et al.*, 2021). The SCENIC analytical pipeline can analyze large datasets efficiently, facilitating cell-specific GRN inference (Van de Sande *et al.*, 2020). A comprehensive maize multi-omics network map was constructed, integrating genomic, transcriptomic, translomic, and proteomic data across development uncovered key regulatory factors for flowering time, including 18 genes with previously unknown roles in this process, and highlighted a histone modification pathway (Han *et al.*, 2023).

The integration of multi-omics data is important because it offers a comprehensive view of biological systems by combining different molecular layers, enabling a deeper understanding of complex gene interactions, improving predictions of phenotypic traits, and facilitating the discovery of biomarkers and regulatory networks for applications like crop breeding and disease research (Picard *et al.*, 2021). Algorithms have been designed and further employed for multi-omics integration, such as multivariate integrative method (MINT) and data integration analysis for biomarker discovery using latent variable approaches for omics studies (DIABLO, based on multiblock sPLS analysis) (Rohart *et al.*, 2017a,b).

Breeding - AI-powered predictive models can simulate how different crop varieties might perform under various climate scenarios, helping researchers anticipate and prepare for future environmental challenges. By integrating data from multiple sources, including field sensors, satellite imagery, and molecular analyses, AI can provide a comprehensive understanding of plant stress responses, guiding more targeted and efficient breeding strategies (Rivero *et al.*, 2022).

AI and ML, such as ML genomic selection are trained on extensive genomic datasets to identify desirable traits in crops in shorter time frames, than for example traditional marker-assisted selection (MAS), allowing for the acceleration of the breeding process (Tong & Nikoloski, 2021; Chao *et al.*, 2023). Several breeding programs have leveraged these techniques in various crops, including wheat and tomato (Cappetta *et al.*, 2020; Singh *et al.*, 2021c). ML clustering approaches, such as self-organising maps (SOM), can be used for the identification of putative biomarkers as shown for grape (Konecny *et al.*, 2023).

The traditional methods of genomic selection are often parametric, with limited flexibility and cannot sufficiently model the complex non-linear relationship commonly encountered in predicting complex phenotypic traits from genotypes (Sandhu *et al.*, 2021). Thus, a more efficient and assumption-free method that can also capture these non-linear relationships, incorporating different variables and their interaction, in addition to a genomic dataset is necessary to adapt GS analysis to complicated scenarios

and hidden patterns in datasets, and reliably predict untested individual progenies from genotypic data (Montesinos-López *et al.*, 2023).

The complexity and scaling issues inherent to omics analysis can be addressed by AI and ML, which facilitate -omics analysis as well as the association of genetic polymorphisms with plant traits (Murmu *et al.*, 2024). Moreover, ML, particularly deep neural networks, can learn nonlinear and complex relationships between genes and environmental conditions, combined with historical data, to make accurate predictions of yields for new hybrids planted in new locations with known weather conditions (Khaki & Wang, 2019). Several agritech companies use AI to develop *in silico* models to identify genetic combinations with the highest likelihood of field success (Waltz, 2017). These models are trained using vast datasets of phenotypic and genomic information. Furthermore, in the era of NGTs, AI and ML can support the development of the best editing strategy by assisting guide RNA selection and target prediction (Alipanahi *et al.*, 2022).

Hybrid breeding is a powerful strategy for crop improvement that enhances genetic diversity, resilience, yield, and trait combinations in response to climate change (Prohens *et al.*, 2017). However, conventional hybrid production through the creation of pure lines can be labor-intensive and challenging. To overcome this, plant breeders utilize double haploid (DH) production to rapidly achieve complete homozygosity in a single generation by inducing androgenesis at the optimal pollen development stage (Thakur *et al.*, 2024). A DL technique called Microscan has been developed to make it easier to select anthers at the optimal developmental stage, hence improving the output of double haploids from anther culture (García-Forteza *et al.*, 2020). DeepTetrad is a DL-based image recognition package that analyzes pollen tetrads for high-throughput measurements of crossover frequency and offer a framework for manipulating the meiotic recombination process in plants to create unique haplotypes with desirable combinations of alleles (Lim *et al.*, 2020). In speed breeding, ML and Neural Networks (NN) are employed to precisely and dynamically control multiple environmental conditions (light, temperature, and humidity) to accelerate plant growth cycles (Sharma *et al.*, 2024). The rate of flowering and seed set can be improved by using ML algorithms and neural networks (Rai, 2022).

Crop management - AI and ML are valuable tools for crop management, as they can perform yield prediction, disease and weed detection, and can assess crop quality (Shaikh *et al.*, 2022). They play a key role in making agricultural production more efficient and stable in the face of global environmental change (Kurek *et al.*, 2007; Niedbała *et al.*, 2024). Contemporary cloud-based systems and Internet-of-Things (IoT) infrastructure, supported by new AI algorithms, facilitate precision agriculture by optimizing the use of resources like water (e.g. the SWAMP project an IoT-based smart water management platform for precision irrigation) (Kamiński *et al.*, 2019), fertilizers, pesticides and herbicides, supporting sustainability and circular economy (Ayoub Shaikh *et al.*, 2022; Shaikh *et al.*, 2022; Sharma *et al.*, 2023b).

By processing data on soil health, remote sensing, weather patterns, and the physiological status of the plant, AI can forecast the best planting times and conditions for optimal reproductive success (Saxena *et al.*, 2022). For instance, AI algorithms have been used to predict the flowering times of various crops by analyzing climatic data and historical growth patterns (Qian-Chuan *et al.*, 2023). Optimizing reproductive resilience to climate change and extreme weather phenomena includes ensuring optimum growth conditions, and AI-driven tools that support systems like Precision Weed Management and Robotics (PWMR) can also be extended to weed control by identifying the most favorable conditions for crops while minimizing the spread and impact of weeds (Monteiro & Santos, 2022). This dual benefit allows for better resource allocation and enhanced crop resilience against both abiotic stressors and weed competition.

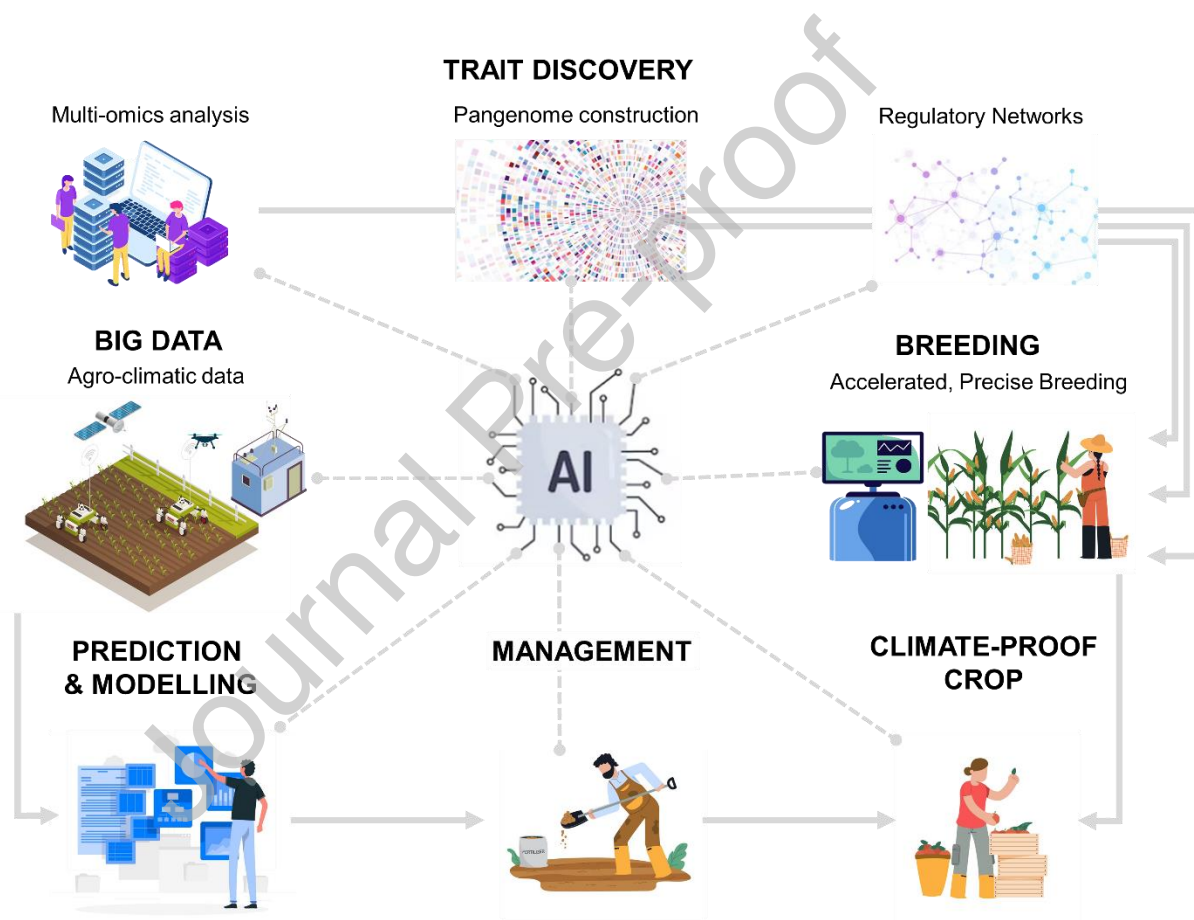


Figure 3. The role of Artificial Intelligence (AI) towards climate proof agriculture. Solid lines indicate the flow of information and arrows the contribution to specific aspects of science and technology related to agriculture. Dashed lines indicate how AI can collect and process all this information to develop integrated solutions for sustainable, climate-resilient agricultural systems, enabling real-time decision support, optimizing resource management, and advancing stress-tolerant crop varieties. Original vectors have been designed by Freepik and modified.

7. Integrated approaches as key drivers in the race for enhancing crop resilience

Reaching the goal of increased agricultural production by 28% over the next 10 years to ensure food security requires holistic approaches that utilize advanced genetics, modern agricultural techniques, cutting-edge technology, and sustainable practices (*State Food Secur. Nutr. World 2022*, 2022; Benitez-Alfonso *et al.*, 2023). This involves exploring plant resilience at the molecular level to identify stress-tolerant traits and breeding new varieties that are better adapted to fluctuating environmental conditions. These strategies are complemented by precision agriculture tools, AI, and data-driven decisions that optimize resource use, enhance crop health, and improve resistance to abiotic and biotic stresses, all of which are essential for meeting future food demands.

Accelerating the breeding process is essential to address the increasing challenges of climate change. The application of a synergized breeding strategy (SBS) including speed breeding, speed vernalization, phenotypic selection, backcrossing and marker-assisted selection has reduced time by around 53% to develop a BC₂ near-isogenic line in wheat (Cha *et al.*, 2024). Better integration of crop genome and pan-genome information along with linkage mapping, association mapping, joint linkage-association mapping strategies and genomic selection, which leads to the identification of the genes and pathways controlling important agronomic traits, can significantly reduce the time for developing new varieties ready for the farm (Graci & Barone, 2023). Bridging the genotype-phenotype gap will allow the identification of marker genes for desired traits. Particularly for resilience of reproduction in different stresses, which is likely a polygenic trait, the integration of multi-omics approaches is necessary together with the analytical power of ML supported by robust statistical models that can assist the integration of these complex datasets, and accelerate trait identification and breeding for resilience in diverse environmental conditions (Weckwerth *et al.*, 2020; Pazhamala *et al.*, 2021; Roychowdhury *et al.*, 2023). Moving from lab to farm is inevitable in order to accelerate breeding, while simulating future climate scenarios with the use of ML and high-throughput phenomic platforms will allow the simultaneous and continuous monitoring of key plant traits as selection markers to identify tolerant genotypes to abiotic stress (Gosa *et al.*, 2019). Such proactive measures can speed up the generation of climate-ready crops.

No doubt, the fastest route to generate stress-resilient crops is through gene editing. *De novo* domestication through targeted gene editing can fully harness the richness of wild species for improving agronomic traits for crops including stress resilience (Yu *et al.*, 2021). While the commercial use of NGT-based plants is currently restricted in many regions, including the European Union, it is likely inevitable that future generations will reap the benefits of this technology. As regulatory frameworks evolve, the potential of NGTs to revolutionize agriculture will become increasingly recognized and adopted, particularly considering that such crops will require less water, reduced chemical inputs and support better sustainable agriculture and circular economy than many conventional farming methods. This shift will be essential for addressing the growing challenges of food security and environmental sustainability.

It is likely, though, that genetic improvement alone might not be sufficient to meet the growing demands for food security. Therefore, maximizing yields will require the integration of advanced farming practices that optimize resource use, improve soil health, and reduce environmental impact. These practices, such as precision agriculture, optimized irrigation, and sustainable pest management, will work synergistically with stress resilient crops to boost productivity. Combining innovative crop genetics with smart, data-driven agricultural techniques can ensure higher yields, enhance resilience to climate stress, and promote more sustainable food production systems. Introducing sustainable priming practices, such as application of chemical stimulants, introducing diversified cropping systems (crop rotation, cover crops, crops diversification, and intercropping) and/or the use of plant growth-promoting rhizobacteria, arbuscular mycorrhizal and ectomycorrhizal fungi, cyanobacteria, and nitrogen-fixing bacteria will further improve productivity and minimize losses against extreme weather phenomena (De Vries *et al.*, 2020).

In conclusion, addressing the challenges of food security and crop resilience in the face of climate change requires a multifaceted, collaborative approach. It is essential to integrate cutting-edge strategies such as high-throughput phenotyping, genotyping, and gene editing, alongside advanced management practices. This holistic strategy will help us meet the demands of the future, ensuring a more secure and resilient global food system.

BOX 1 - Double fertilization

The pollen tube reaches the ovule through the micropyle, penetrates the embryo sac into one of the synergid cells, bursts, and discharges its two sperm nuclei, resulting in the degeneration of the synergid (Hater *et al.*, 2020). Angiosperms exhibit a double fertilization process: one sperm nucleus fertilizes the egg cell, forming a diploid zygote, while the other fuses with the di-haploid central cell forming a triploid endosperm (Baroux & Grossniklaus, 2019). Ovule integuments develop into the seed coat of eudicots, while cereals generate grains or caryopsis representing seeds that additionally contain a pericarp originating from ovary tissue. The coordination of the development of these seed components is vital for a viable seed. The endosperm initially develops as a coenocytic structure, undergoing a series of mitosis without cytokinesis, followed by cellularization. It accumulates starch, oil, and proteins to support embryo development. In eudicots, the endosperm is consumed during seed development, while in monocots, it persists to provide nutrients during seed germination (Doll & Nowack, 2024). The seed coat, a maternal tissue differentiated post-fertilization from the ovule integuments, is influenced by hormonal communication with the endosperm (Figueiredo & Köhler, 2016). Initially, seed coat cells elongate, allowing seed expansion (Zhang *et al.*, 2021). After endosperm cellularization, the seed coat becomes rigid and hydrophobic to protect the embryo from its environment, fixing seed size (Zhang *et al.*, 2024).

The zygote usually divides asymmetrically, forming a large basal cell and a small apical cell. The basal cell develops into the suspensor, a file of cells connecting the developing embryo to the maternal ovule tissues. The apical cell undergoes a series of symmetric and asymmetric cell divisions to form the embryonic shoot-root body axis, including cotyledons, shoot apex, hypocotyl, and root apex (morphogenesis phase). During embryo maturation, it accumulates especially storage proteins and lipids, acquiring desiccation tolerance and entering into dormancy (Dresselhaus & Jürgens, 2021; Verma *et al.*, 2022).

After fertilization, the ovary develops into a fruit. In cereals, the pericarp is fused with the thin seed coat to form a caryopsis representing a simple fruit. Fruits protect and nourish developing seeds and facilitate their dispersal. Fruit size often correlates with seed number and is influenced by phytohormones such as auxin, cytokinin and gibberellins (Ruan *et al.*, 2012; Walker & Bennett, 2024). However, parthenocarpy, fruit development without fertilization, occurs independently of seed formation. The fruit ripening process can be categorized into climacteric (tomato and peach) and non-climacteric (grapes, strawberries) types. Climacteric fruits rely on a complex interplay of hormones for ripening with ethylene and brassinosteroids playing major roles. In contrast, the onset of ripening in non-climacteric fruits depends strongly on ABA with the intervention of diverse hormonal regulation (Perotti *et al.*, 2023).

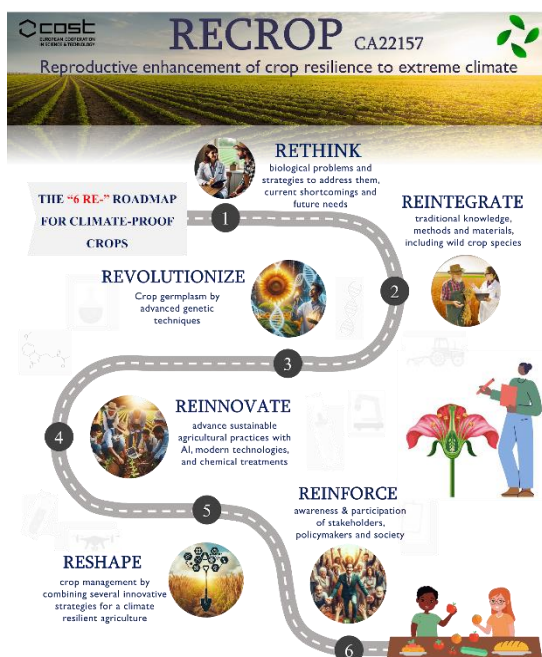
BOX 2 – Integrative Agriculture: Building the climate-proof agriculture of tomorrow

In the midst of the third decade of the 21st century, advances in science and technology have paved the way for more resilient agricultural practices. The target is clear: ensuring food security while reducing the negative effects of agriculture to climate change. The urgent actions towards this target require the integration of several key research and technology areas in order to enhance crop resilience, optimize resource use, and implement sustainable farming practices. Future integration of multi-omics approaches with high-throughput phenotyping and the assistance from AI and ML can reliably associate genes with desirable traits, while NGTs as well as modern breeding can speed up the development of climate-proof crops of high nutritive value. Of course, the full potential of these new varieties can only be obtained under optimum growth conditions. As discussed in this article, in non-fully controlled environments such as greenhouses, environment stress is often highly unpredictable, and fully optimal conditions are difficult or impossible to achieve. Thus, crop production will benefit from technologies that allow real time monitoring of different environmental and plant characteristics and proper decision-making systems for crop management. Promoting soil health through the use of biostimulants, cover crops, and beneficial microbes improves plant resilience to abiotic stresses and enhances productivity, while the adoption of integrated pest management, precision irrigation, and sustainable fertilization practices reduce the environmental impact of agriculture while maintaining high yields. AI will play an

essential role to improve crop management practices, and predict climate impacts on crop yields. Therefore, bringing this knowledge to the farmers is crucial. This can be achieved through extensive education, training programs, and extension services that ensure farmers are equipped with the necessary skills and tools to adopt these advanced practices, ultimately contributing to a more resilient and sustainable agricultural system.

This is not one researcher's job but requires interactions from researchers and stakeholders from different disciplines. In a global climate-proof agriculture system, plant biologists and geneticists offer the fundamental knowledge about plant responses; soil scientists and microbiologists provide insights into soil health, nutrient management, and the role of soil microbiome in enhancing plant resilience; and agronomists translate research findings into practical agronomic practices. Biotechnologists develop tools such as biostimulants or customized microbiome mixtures for specific crops and conditions. Data scientists and AI experts play a central role in this integrated approach, analyzing vast datasets to identify patterns and create predictive models that guide decision-making, while engineers develop new precision agriculture technologies to assist farmers in protecting their crops. Climate experts support this endeavor by assisting in the prediction of climate patterns, which can aid in the development of both short-term and long-term climate adaptation strategies. Further, environmental scientists and ecologists can contribute to the adoption and optimization of sustainable agricultural practices that mitigate environmental impacts.

In a global climate-proof agriculture system economists and policy makers build a local, national and regional framework to support sustainable agricultural practices and ensure they are economically viable for farmers. Social scientists assess the impact of climate change on farming communities, promote farmer education, and facilitate the adoption of resilient farming practices. In this global climate-proof agriculture system, a well-informed and engaged society supports the implementation of these integrated approaches, and fosters innovations that address global challenges with respect to humans, the society and the planet.



BOX 3 - RECROP COST Action: Advancing the Vision of Integrative Agriculture

RECROP is a strategic re-evaluation of agricultural practices to enhance crop resilience and productivity in response to climate change. It involves revisiting and rethinking traditional agricultural methods and incorporating innovative, climate-smart technologies and practices to ensure sustainable crop yields. It includes developing climate-resilient crops by implementing advanced breeding techniques, and adopting agronomic practices that mitigate the adverse effects of climate change. We propose a new era in crop science and technology, where RECROP

embodies “six RE-” strategies:

1. **Rethink biological problems and mitigation strategies:** Critically assess the biological questions underlying the sensitivity of crops to climate change and identify the approaches required to address these problems, and create flexible, long-term strategies that are adaptable to shifting climate patterns and future uncertainties.
2. **Reintegrate traditional and regional practices:** Combine traditional knowledge with modern innovations to create a more robust agricultural system that can be locally adapted to specific environmental and cultural contexts.
3. **Revolutionize crop germplasm:** Utilize advanced genetic and genomic techniques to create resilient crop germplasm capable of withstanding extreme weather conditions.
4. **Reinnovate agricultural technologies:** Focus on the continuous development and application of innovative technologies and practical solutions at every level of the agricultural process to address both present and future climate challenges.
5. **Reshape crop management:** Implement new technologies and methods to improve crop management and resilience, adaptable to both smallholder farms and large-scale agricultural systems.
6. **Reinforce societal engagement:** Promote awareness and active participation among communities and policymakers to support innovative genomic solutions, sustainable agricultural practices and climate adaptation strategies. This involves education, policy advocacy, and community-based initiatives to ensure widespread adoption and support for resilient agricultural systems.

RECROP (CA22157; www.recrop-cost.com) is a collaborative initiative supported by the Cooperation in Science and Technology (COST), which aims to advance these strategies by fostering international cooperation, research, and knowledge exchange to build a resilient agricultural future. This initiative brings together scientists, policymakers, farmers, and industry stakeholders to develop and implement innovative solutions that enhance crop resilience and productivity in the face of climate change.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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