Resilience of C_4 Crops to Climate Vagaries

ABSTRACT

Climate change poses significant challenges to agriculture worldwide, affecting productivity and threatening food security. Key drivers of climate change like altered water availability, temperature fluctuations and increased carbon dioxide concentrations, influence crop performance and ecosystem stability. The World has committed to eradicate extreme poverty and hunger by 2030. But climate change is undermining the livelihoods and food security of the rural poor, who constitute almost 80% of the world's poor. If plant genotypes that can withhold climate extremes are insufficient, food scarcity occurs, and the price of existing food resources would increase enormously, making it practically hard for the rural poor to obtain enough food. To avoid this happening, we need to develop plant genotypes that are climate resilient. Photosynthetic pathways in plants C_3, C_4, and CAM play a critical role in determining their adaptability to changing climatic conditions. Understanding the physiological responses of C_4 crops to various environmental stresses like water and temperature stress, highlights their potential for future climate resilience. Due to the efficient carbon concentrating mechanism, low stomatal conductance and high water use efficiency in C_4 plants, they are expected to show higher drought tolerance relative to C_3 plants. Studying the responses of C_4 crops to climate change is essential as they play a vital role in global food production, especially in tropical and subtropical regions prone to climate extremes. While C_4 crops are more resilient to heat and drought than their C_3 counterparts, their yield potential is still constrained by the increasing severity of abiotic stresses, such as prolonged droughts, heatwaves, and soil salinity. Understanding how C_4 crops respond to these challenges can provide insights into optimizing their growth and productivity in future climate scenarios. These insights are important for breeding stress-resilient varieties and improving crop management practices, to ensure global food security amidst escalating climate challenges.

Keywords: *Climate change, Drought, Heat stress, C_4 photosynthesis, Carbon concentrating mechanism*

1. INTRODUCTION

The climate of Earth has undergone alterations throughout history. There have been eight cycles of ice ages and warmer periods during the past 800,000 years, with the end of the last ice age approximately 11,700 years ago marking the beginning of the current climate era and the rise of human civilisation (NASA, 2024). Climate change occurs due to various factors, including atmospheric changes like El Niño, driven by winds and ocean currents. External forces, such as Earth's axial tilt and orbital shape, likely influence ice age cycles. Additionally, greenhouse gases like carbon dioxide (CO_2) trap heat, raising Earth's surface temperature (National Geographic Society, n.d.). Human activities, such as burning fossil fuels for energy and transportation or using technology to boost meat production, release greenhouse gases (Garnett, 2009; Stavi & Lal, 2013). Deforestation for timber or industrial development reduces the carbon dioxide absorbed by trees, while factories contribute to the greenhouse effect by emitting pollutants into the atmosphere (Rykowski, 2000; Aju et al., 2015; National Geographic Society, n.d). Global warming is linked to burning fossil fuels and tropical deforestation, with human activities increasing atmospheric CO_2 by about 30% over the past 150 years (National Geographic Society, n.d.). Greenhouse gases like methane and chemicals such as chlorofluorocarbons, hydrofluorocarbons, and hydrochlorofluorocarbons contribute significantly to climate change (Sovacool et al., 2021). Methane levels are rising due to agriculture, industrial activities, and decomposing waste in landfills (Karakurt et al., 2012). Similarly, these gases, used in refrigeration and aerosol sprays, trap heat in the atmosphere. While many countries are phasing them out through laws and regulations, their impact remains a concern (National Geographic Society, 2024). The effects of climate change are becoming increasingly evident. Global temperatures are rising, and oceans are getting warmer, with much of the heat being absorbed by the top layers of the ocean (Levitus et al., 2017; NASA, 2024). Ice sheets are shrinking, particularly in Greenland and Antarctica, while glaciers are retreating in many regions around the world (Velicogna et al., 2020). Snow cover is decreasing, and sea levels are rising because of melting ice and thermal expansion of seawater. Global sea level rose about 8 inches in the last century (Nerem et al., 2018). Arctic sea ice is declining, and ocean acidification is increasing. The ocean has absorbed between 20% and 30% of total anthropogenic CO_2 emissions in recent decades (Sabine et al., 2004). Carbon dioxide in the atmosphere warms the planet, causing climate change. Human activities have raised the atmosphere's CO_2 content by 50% in less than 200 years, with the current level of 424 ppm (NASA, 2024). C_4 crops, with their efficient carbon concentrating mechanism and higher water-use efficiency, present a promising solution to mitigate the impacts of these human-induced stresses. Understanding the interplay between anthropogenic climate change and the resilience mechanisms of C_4 crops is crucial for developing adaptive strategies that ensure sustainable food production in the face of escalating environmental challenges.

Climate change impacts on agriculture are being witnessed all over the world in the recent years affecting farm level productivity and adversely impacting stability in food grain availability at the national level. Temperature, water, and CO_2 are three of the main causes of climate change. Adopting sustainable methods that lower greenhouse gas emissions, encourage reforestation, and boost the use of renewable energy sources is crucial to addressing the issues caused by climate change, particularly in agriculture. Under drought, high temperatures, and nitrogen or CO_2 limitation, C_4 plants are more competitive than C_3 plants. (Watson-Lazowski and Ghannoum, 2021). C_4 plants possess the carbon concentrating mechanism, and can have increased photosynthetic rate, yield, water-use efficiency (WUE), and nitrogen-use efficiency (NUE) compared with ecologically similar C_3 plants. Sorghum is a promising C_4 crop for tackling extreme food insecurity because of its resistance to drought and capacity to flourish in a variety of soil types. Sorghum's ability to withstand water further increases its resilience (Mwamahonje et al., 2024). Implementing agricultural practices that favor C_4 plants could increase crop resilience to climate stressors, leading to higher productivity and better food security.

2. IMPACT OF CLIMATE VAGARIES ON CROPS

Climate change may adversely impact the yield of irrigated crops throughout the world, attributable to rising temperatures and alterations in water supply (Lal, 2000; Mall et al., 2017). Crops may experience severe weather events such as drought, flooding, excessive heat, and cold during their life cycle, leading to significant yield reductions (Raza et al., 2019). The effects of these factors may differ based on area, crop, cropping systems, soil types, and management practices. Sub-Saharan Africa frequently endures prolonged droughts and unpredictable weather patterns that threaten crop yields (Lombe et al., 2024). South Asia is projected to experience more frequent extreme weather events, such as heatwaves and intense rainfall, along with greater interannual variability in daily precipitation during the Asian summer monsoon (Sivakumar & Stefanski, 2011). India is among the most drought-prone nations globally, with around 53% of its geographical area classified as arid and semi-arid. Climate change affects crop production both directly and indirectly (Samuel et al., 2021). The immediate consequences primarily result from alterations in crop length and influence reproductive processes, including pollination and fertilisation. The indirect effects of climate change are mostly attributable to variations in water availability, as well as changes in insect, disease, and weed dynamics. Weather aberrations can impact numerous factors, particularly in rainfed regions where over 80 percent of farmers are smallholders, hence possessing limited capacity to mitigate adverse effects (Maheswari et al., 2015). Rainfed drylands, covering over 41% of Earth's surface, are vital for global food and fiber production while supporting biodiversity and ecosystem services. As temperatures increase, evapotranspiration increases, and precipitation decreases, 25–30% of drylands are already degraded, mostly because of soil erosion from wind and water in regions like Australia, East and Central Asia, and Sub-Saharan Africa (Chary et al., 2022).

3. CLIMATE RESILIENCE

The capacity to foresee, plan for, and react to potentially dangerous occurrences, patterns, or disruptions associated with the climate is known as climate resilience. Assessing how climate change will increase or change existing climate-related risks and acting to better manage them are key components of increasing climate resilience (C2ES, 2021).

3.1 Climate smart agriculture

Climate Smart Agriculture (CSA) is characterised as a methodology that directs the necessary actions to transform and realign agricultural systems to effectively promote development and guarantee food security in a changing climate. The initiative seeks to achieve three primary objectives: sustainably enhancing agricultural output and income; adapting to and fostering resilience against climate change; and minimising and/or eliminating greenhouse gas emissions, where feasible (Cordaid, 2016). CSA is frequently used interchangeably with climate-resilient agriculture (CRA); however, CRA is a subset of CSA that specifically addresses the impacts of climate change (Viswanathan et al*.,* 2020).

An on-farm trial in Karnal, India, assessed the greenhouse gas mitigation potential of CSA practices (CSAPs) in rice–wheat systems across six scenarios: Sc1 (conventional tillage without residue), Sc2 (conventional tillage with residue), Sc3 (reduced tillage + residue + fertilizer), Sc4 (reduced/zero tillage + residue + fertilizer), Sc5 (zero tillage + residue + fertilizer + GreenSeeker + Tensiometer), and Sc6 (Sc5 + nutrient-expert tool). CSAPs (Sc4, Sc5, Sc6) reduced global warming potential by 33–40% and emission intensity by 36–44% compared to conventional practices (Sc1). Additionally, they improved nitrogen productivity by 32–57%, eco-efficiency by 70–105%, and wheat yields by 0.62–0.84 Mg/ha, showing resilience to climate extremes. These results highlight CSAPs as effective for mitigating GHG emissions and enhancing sustainability in rice–wheat systems (Kakraliya et al., 2021).

Climate-smart agriculture has been promoted by the Department of Agricultural Extension in Bangladesh through climate field schools since 2010 to improve food security in the context of climate change. A study involving 118 farmers from Kalapara, Patuakhali, identified 17 CSA practices, including saline- and flood-tolerant crop varieties, floating-bed vegetables, the sorjan method, urea deep placement, and rainwater harvesting. On average, farmers adopted seven practices, with 32% of households classified as food secure, 51% mildly to moderately food insecure, and 17% severely food insecure. CSA adoption positively influenced food security (Hasan et al., 2018). Small-scale coconut farmers in Philippines frequently adopted CSA practices such as early harvesting and weather forecasting, driven by the recurring natural disasters like typhoons. However, practices like coconut-banana intercropping were rarely implemented due to the high initial investment and a lengthy payback period of approximately four years, challenges that were even greater for adopting typhoon-tolerant coconut varieties (Ruales et al., 2020).

In water-scarce regions, advanced irrigation strategies such as deficit irrigation and the use of non-conventional water resources, including treated wastewater and brackish groundwater, have emerged as effective measures to combat water scarcity. Protected cultivation systems like greenhouses equipped with artificial intelligence further enhance water productivity by creating controlled environments that reduce water loss (Nikolaou et al., 2020). These approaches collectively provide sustainable solutions for improving water management and mitigating the impacts of climate change on agriculture, especially in vulnerable areas like the Mediterranean region. Modernizing irrigation methods significantly improves water application efficiency, with systems like trickle irrigation achieving up to 90% water savings (Mesa-Jurado et al., 2012; Nikolaou et al., 2020). Agricultural water management plays a crucial role in mitigating unsustainable water use and improving water resilience and adaptation to climate change. Alternate wetting and drying (AWD) is another recommended irrigation alternative for irrigated rice systems. In AWD, rice fields experience alternating periods of saturation and desaturation, during which irrigation is paused and water is permitted to recede until the ponded water is eliminated and the soil attains a specific moisture content (Carrijo et al., 2017).AWD can decrease irrigation water inputs by 23%–43% and can lower the global warming potential by 45%–90% in comparison to continuously flooded rice (Sikka et al., 2022). A 25%–30% decrease in global warming potential through the implementation of intermittent flooding compared to continuous flooding was observed in rice cultivation (Pathak et al., 2011).

4. CLIMATE CHANGE AND PHOTOSYNTHESIS

Through the process of photosynthesis, all plants absorb CO_2 from the atmosphere and transform it into sugars and starches, but they do it in different ways (Paul & Foyer, 2001; Long et al., 2004). Each class of plants uses a different type of photosynthesis, known as a pathway, which is a variant on a series of chemical reactions known as the Calvin Cycle. A plant's capacity to tolerate low carbon atmospheres, higher temperatures, and decreased water and nitrogen is crucial for understanding climate change (Dusenge et al., 2019). These reactions also affect the quantity and kind of carbon molecules a plant produces, the locations where those molecules are stored, and more.

The processes of photosynthesis designated by botanists as C_3, C_4, and CAM, are directly relevant to global climate change studies because C_3 and C_4 plants respond differently to changes in atmospheric CO_2 concentration and changes in temperature and water availability. Scientists have started looking into how plants might be able to adapt to the changing climate as the world continues to warm. Modifying the processes involved in photosynthesis could be one approach to do it (Lara and Andreo, 2011). A promising approach is the introduction of a C_4 carbon concentration mechanism (CCM) into C3 crops, such as rice. The C_4 Rice project aims to achieve this, with predictions suggesting that incorporating a C_4 photosynthetic pathway into rice could increase yields by as much as 50 percent (Sheehy et al., 2008).

The C_4 Rice Consortium is employing strategies like metabolic C_4 engineering and the identification of leaf anatomy determinants through mutant screens to develop C_4 rice (Kajala et al., 2011).

The Crassulacean Acid Metabolism (CAM) cycle is a CO_2 fixation process occurring during the dark phase of photosynthesis in Crassulaceae plants, with malic acid as the first product (Black & Osmond, 2003; Osmond, 2007). Most CAM plants are succulents with fleshy leaves, abundant chloroplasts in mesophyll cells, and vascular bundles lacking well-defined bundle sheath cells. Their stomata open at night and close during the day. While less efficient in photosynthesis than C_4 plants, CAM plants are better adapted to extreme desiccation (Black & Osmond, 2003; Osmond, 2007; Schiller & Bräutigam, 2021). Poplar (*Populus* spp.) and willow (*Salix* spp.) which are fast-growing, short-rotation forestry bioenergy crops being susceptible to hydraulic failure following drought stress due to their relatively high stomatal conductance and isohydric nature. Improving water-use efficiency (WUE) by engineering crassulacean acid metabolism (CAM) into C_3 crops represents a viable strategy for sustaining plant productivity. CAM enhances water-use efficiency by enabling nighttime CO2 uptake when vapor pressure deficit is low. CAM in tree species like *Clusia* demonstrates its role in conserving water and maintaining carbon uptake during droughts. Bioengineering CAM into bioenergy trees offers a promising strategy for sustaining agroforestry amid climate change (Sekhar et al., 2021).

While the C_3 pathway is the most common, it is also inefficient due to the photorespiration, a process that wastes assimilated carbon when RuBisCO reacts not only with CO_2 but also O_2. Under prevailing atmospheric conditions, potential photosynthesis in C_3 plants is suppressed by O_2 as much as 40 %. The extent of that suppression increases under stress conditions such as drought, high temperatures and high light (Hirst, 2021). The C_4 plants are more efficient in photosynthesis than the C_3 plants (Schmitt & Edwards, 1981; Gowik & Westhoff, 2011). In C_4 plants, the photorespiration is suppressed by increasing the CO_2 concentration at the Rubisco site, hence suppressing the enzyme's oxygenase activity. C_4 photosynthesis relies on a biochemical CO_2 pump with spatial separation of CO_2 fixation and assimilation, typically involving Kranz anatomy where mesophyll and bundle sheath cells cooperate (Edwards et al., 2004; Lara and Andreo, 2011). The enzyme, phosphoenol pyruvate carboxylase of the C_4 cycle is found to have more affinity for CO_2 than the ribulose diphosphate carboxylase of the C_3 cycle in fixing the molecular CO_2 in organic compound during Carboxylation (Hatch, 1987; Lara and Andreo, 2011).

5. CARBON CONCENTRATING MECHANISM IN C_4 PLANTS

C_4 plants achieve high productivity through a carbon concentrating mechanism (CCM) that increases CO_2 concentration around RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase), the primary CO_2-fixing enzyme in plants, algae, and cyanobacteria. This CCM operates between two cell types: mesophyll cells, where CO_2 is initially fixed, and bundle sheath cells, where it is ultimately fixed (Watson-Lazowski & Ghannoum, 2021). In C_4 plants, PEP carboxylation occurs in specialized mesophyll cells, which also perform the full light-dependent reactions of photosynthesis (Schlüter & Weber, 2020; Romanowska & Wasilewska-Dębowska, 2022). Malate or aspartate is then transported to bundle sheath cells, characteristic of Kranz anatomy, where pre-fixed carbon is released for final CO_2 fixation by RuBisCO. This process raises the CO_2 concentration in bundle sheath cells to about 10 times that of ambient air, significantly reducing photorespiration. Notably, most bundle sheath cells do not complete the full light-dependent reactions of photosynthesis (Zabaleta *et al*., 2012; Watson-Lazowski & Ghannoum, 2021).

Table 1: C3 vs C4 cycle

	Calvin cycle or C_3 cycle	Hatch and Slack pathway or C_4 cycle
Enzyme	Ribulose bisphosphate carboxylase oxygenase (RuBisCO)	Phosphoenolpyruvate (PEP) carboxylase
Process	Convert CO_2 into a 3-carbon compound 3-phosphoglyceric acid	Convert CO_2 into 4-carbon intermediate
Steps	Carbon fixation, Reduction, Regeneration of RuBisCO	Carboxylation 2. Breakdown 3. Splitting 4. Phosphorylation
First stable product	Phospho glyceric acid (PGA)	Oxaloacetate (OAA)
Where carbon is fixed	All leaf mesophyll cells	The mesophyll cells (MC) and the bundle sheath cells (BSC). C4s have a ring of BSCs surrounding each vein and

		an outer ring of MCs surrounding the bundle sheath, known as the Kranz anatomy.
CO_2 compensation point	50-150 ppm CO_2	0-10 ppm CO_2
Photorespiration	Present and easily detectable.	Present only to a slight degree or absent.
Carbon concentrating efficiency	Low efficiency due to Rubisco's low affinity for CO_2 and high photorespiration rates (Jin et al., 2023).	High efficiency due to PEP carboxylase's high affinity for CO_2 and reduced photorespiration (Leegood, 2013).
The CO_2 concentration inside leaf	high (about 200 ppm)	low (about 100 ppm)
Net rate of photosynthesis in full sunlight	15-25 mg. of CO_2 per dm^2 of leaf area per hour	40-80 mg. of CO_2 per dm^2 of leaf area per hour

(Source: Ehleringer & Cerling, 2002 ; Lara and Andreo, 2011; Hirst, 2021).

6. ADVANTAGES OF THE C_4 PHOTOSYNTHETIC PATHWAY

The C_4 pathway increases CO_2 concentration in bundle sheath cells to 70 µM, compared to 4 µM in mesophyll cells, reducing RuBisCO's oxygenase activity by over 80%, though this effect varies with temperature. Consequently, C_4 plants exhibit up to double the photosynthetic rate and yield, 1.5 to 3 times greater WUE, and 2.5 times higher NUE compared to ecologically similar C_3 plants (Lin et al., 2019). In addition, elevating the concentration of CO_2 within the bundle sheath allows RuBisCO to increase its in vivo catalytic activity two- to fivefold in warm climates. As a result, C_4 plants have only 50–80% of the RuBisCO content found in C_3 plants, allowing them to sustain a higher leaf area production rate with lower leaf nitrogen levels compared to C3 species (Sage and Zhu, 2011b; Lin et al., 2019). WUE is enhanced in C_4 plants because CO_2 is fixed more effectively and stomata remain less open, reducing transpiration rates (Way et al., 2014; Leakey et al., 2019). This improved WUE allows C_4 plants to have longer growing seasons and more adaptable allocation patterns, such as directing more biomass to shoots in moist conditions or to roots in dry conditions (Lopes et al., 2011; Leakey et al., 2019). The C_4 pathway is particularly advantageous in hot, high-light environments that encourage high photorespiration rates (Long, 1983; Sage & Kubien, 2007; Lara & Andreo, 2011).

7. SUBTYPES OF C_4 PHOTOSYNTHESIS

C_4 species not only exhibit superior physiological traits compared to C_3 species but also display considerable diversity within themselves. C_4 photosynthesis is broadly categorized into three subtypes: NADP-malic enzyme (NADP-ME), NAD-malic enzyme (NAD-ME), and phosphoenolpyruvate carboxykinase (PEP-CK), each adapted to specific environmental conditions (Ghannoum *et al.*, 2011; Wang et al., 2014; Borghi, 2021).

Table 2: Differences between the C_4 subtypes in grasses

Characteristics	**NADP-ME**	**NAD-ME**	**PEP-CK**
Decarboxylation enzymes	NADP-ME	NAD-ME	PEP-CK
Main C4 acid exported to bundle sheath cells	Malate	Aspartate	Aspartate
Main 3C acid returned to mesophyll cells	Pyruvate	Alanine	Alanine/pyruvate
Site of	Chloroplast	Mitochondrion	Cytosol

decarboxylation			
Chloroplast position in the BSC	Reduced grana chloroplast with centrifugal arrangement	Granal chloroplast with centripetal arrangement	Centrifugal

(Sonawane, 2016)

In NADP-ME plants, malate serves as the main C_4 acid transported between mesophyll and bundle sheath cells, whereas aspartate is the primary transport acid in NAD-ME and PCK C_4 grasses. The C_4 subtypes are closely linked to specific grass subfamilies. Species with NADP-ME type anatomy are found in the Panicoideae subfamily within the Andropogoneae, Arundinelleae, and Paniceae tribes (Morrone et al., 2012; Venter, 2015). The NAD-ME and PEP-CK types are primarily associated with the Chloridoideae subfamily and have evolved only once in Panicoideae (Voznesenskaya et al., 2006; Koteyeva et al., 2023). Among major C_4 crops, sorghum exclusively uses NADP-ME, maize primarily employs NADP-ME with PEP-CK as a secondary decarboxylase, and millets exhibit a mix of NADP-ME, NAD-ME, and some PEP-CK species (Sonawane *et al.,* 2018).

Research on C_4 grasses, categorized into three biochemical subtypes—NAD-ME, PCK, and NADP-ME—grown under ambient (400 µL L^{-1}) and interglacial (280 µL L^{-1}) CO_2 conditions revealed that the Chloridoideae/NAD-ME group had higher leaf mass per area and leaf nitrogen content. In contrast, NADP-ME and PCK grasses exhibited enhanced photosynthetic nitrogen use efficiency (Pinto et al*.,* 2016).

8. C_4 CROPS

Approximately 60% of C_4 species are grasses, with around 40% of grasses utilizing the C_4 photosynthetic pathway. Most C_4 grasses belong to warm-origin taxa, particularly the PACMAD clade, and dominate warm-climate grasslands. These grasses include ecologically and economically significant species such as major staple food, fodder, and biofuel crops, as well as numerous prominent weeds (Sage et al., 2011a; Watson-Lazowski & Ghannoum, 2021). C_4 crops are particularly prevalent in warm (Korres et al., 2016), drought-prone climates (Lopes et al., 2011; Korres et al., 2016) and are becoming increasingly crucial for food and bioenergy security (Watson-Lazowski & Ghannoum, 2021).

Maize, sorghum, and sugarcane are major C_4 crops. Maize, the most produced cereal crop globally, is mainly grown in North and South America, as well as Eastern and Southern Africa, with over 60% of production in temperate regions (Watson-Lazowski & Ghannoum, 2021). Maize is primarily used in feed, starch, and biofuel industries, with 83% of its production allocated for industrial purposes. Among 125 developing countries, 75 consider maize a staple crop, accounting for 70% of global maize production (Burlakoti et al., 2024). Sorghum, more drought-tolerant than maize, thrives in dry climates and is valuable in areas with limited rainfall and resources for fertilizers (Watson-Lazowski & Ghannoum, 2021; Khalifa & Eltahir, 2023; Liaqat et al., 2024. Sorghum is a grain crop used for fodder, food, and bioenergy production. Its high photosynthesis rate makes it excellent for silage, while its stalks produce juice for jaggery, sugar, and ethanol (Wasi et al., 2023). The 2001–2020 global average harvested area for sorghum is 40.90 mha (Khalifa & Eltahir, 2023). All parts of sorghum like grain, juice, and bagasse are utilized for fodder, food, ethanol, and electricity. Sorghum thrives on waterlogged, saline-alkaline soils and is drought-resistant (Wasi et al., 2023). The drought resistance in sorghum is attributed to its root system, leaf rolling, osmotic adjustment, and ability to delay reproductive development (Nadew et al., 2021). Sugarcane, a key industrial crop for sugar and bioenergy, grows in tropical and subtropical regions (Raza et al., 2019). Worldwide, sugarcane ranks as the fifth largest crop in terms of production value and acreage, and it is the second largest bioenergy crop (Luo et al., 2023). It benefits from high CO_2 levels, showing improvements in biomass, photosynthesis, and overall growth, and is capable of coping with rising CO_2 concentrations due to its low CO_2 compensation point and carbon sequestration abilities (Watson-Lazowski & Ghannoum, 2021). Marin et al. (2013) observed improved sugarcane WUE and yield in parts of Brazil due to climate change using crop simulation models. As a C_4 plant with a CO_2 compensation point of 0-10 ppm, sugarcane can deplete atmospheric CO_2 under certain conditions. High CO_2 levels partially close stomata, reducing transpiration and sap flow, enhancing xylem potential and water status. Sugarcane also sequesters carbon naturally, mitigating CO_2 emissions and global warming by forming phytoliths (PhytOC), storing ~300 Mt of CO_2 annually in soil for thousands of years (Misra et al., 2019).

Millets, including pearl millet (*Pennisetum glaucum*) and foxtail millet (*Setaria italica*), are C_4 crops vital for food and fodder, with over 95% produced in developing countries. Their drought and heat tolerance make them suitable for harsh climates, and their short life cycle (12-14 weeks) helps escape stress. Traits like small leaves, thickened cell walls, and dense roots enhance stress resilience. The C_4 mechanism concentrates CO_2 around RuBisCO, reducing photorespiration

(~80%) and boosting photosynthesis, WUE, and NUE. This also improves growth, biomass allocation, and ecological performance in warm conditions (Lenka et al.,2020).

9. CLIMATE RESILIENCE IN C$_4$ GRASSES

Grass species are divided into two distinct clades: BOP (Bambusoideae, Oryzoideae, Pooideae) and PACMAD (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, Danthonioideae) (Hodkinson, 2018; Pardo and VanBuren, 2021; Gallaher et al., 2022). BOP grasses, primarily cool-season species found in temperate climates, utilize C3 photosynthesis, which outperforms C4 in these regions. Frost tolerance has independently evolved in many Pooideae grasses. PACMAD grasses, mainly warm-temperate and tropical species, include agriculturally significant crops like sugarcane, maize, sorghum, and various millets (Panicoideae) and underutilized grains like finger millet (Chloridoideae) (Pardo and VanBuren, 2021).

9.1 Climate resilience among PACMAD grasses

Grass stomatal anatomy enhances resilience with unique elongated, dumbbell-shaped guard cells and two subsidiary cells, enabling faster responses and higher WUE compared to kidney-shaped guard cells in eudicots and most non-grass monocots (Nunes et al., 2020; Pardo and VanBuren, 2021; Zahedi et al., 2024). Stomatal arrangement and density also influence drought tolerance (Mehri et al., 2009; Huang et al., 2020). Grasses typically have hypostomatic leaves with pores on the abaxial surface or amphistomatic leaves with pores on both surfaces, the latter promoting efficient CO$_2$ diffusion and higher photosynthetic rates. Unlike eudicots with dorsoventral leaves, grasses have isobilateral leaves oriented parallel to light, deeper veins, and vertical angles, minimizing WUE costs of amphistomaty (Pardo and VanBuren, 2021).

10. RESPONSE OF C$_4$ PLANTS TO CLIMATE VAGARIES

10.1 Effect of water stress on C$_4$ photosynthesis

Water stress significantly limits global plant productivity (Kijne, 2006). A study on the effects of water stress on winter wheat's photosynthesis, growth, yield, WUE, and irrigation water productivity (IWP) identified four stress levels based on field water capacity: severe (30–40%), moderate (40–50%), mild (50–60%), and well-watered (60–80%). Results showed that moderate and severe stress significantly reduced photosynthetic parameters (net photosynthetic rate, intercellular carbon concentration, stomatal conductance and transpiration), height, biomass, and grain size, leading to lower WUE and IWP. In contrast, mild stress only slightly decreased net photosynthetic rate compared to the well-watered group, with improvements in dry biomass and 1000-grain weight by 2.07% and 1.95%, respectively, during flowering and grain-filling (Zhao et al., 2020). Severe stress causes metabolic inhibition, including photoinhibition and damage to photosynthetic enzymes, leading to irreversible loss of photosynthetic activity (Goh et al., 2012) .C$_4$ plants, with high WUE and low stomatal conductance, exhibit greater drought tolerance, reducing water stress development. However, high WUE often prioritizes biomass production over water conservation in areas with high evapotranspiration (Ghannoum, 2016; Watson-Lazowski & Ghannoum, 2021).

The C$_4$ pathway enhances WUE, enabling C$_4$ grasses to thrive in drier, more exposed habitats. The high substrate affinity of PEPcase and the carbon-concentrating mechanism allow C$_4$ plants to function at lower mesophyll CO$_2$ levels and stomatal conductance, achieving higher instantaneous WUE than C$_3$ plants (Ghannoum et al., 2011; Pardo & VanBuren, 2021). Under drought stress, leaf-level WUE increases as reduced water loss from stomatal closure outweighs the decline in CO$_2$ assimilation. WUE also varies by C$_4$ subtype, with NAD-me grasses showing higher WUE than NADP-me grasses under drought condition (Ghannoum et al., 2002; Pardo & VanBuren, 2021).

Sorghum genotypes exhibit varied responses and tolerance to drought, influenced by the interaction between genotype and water stress levels. Research by Tingting (2010) found that sweet sorghum exhibited the highest WUE under moderate drought stress during early and middle growth stages, and under severe drought stress in the late growth stage. Increasing drought stress raised the light compensation point but reduced the light saturation point, apparent quantum yield, and dark respiration rate. Severe drought stress caused photoinhibition, lowering WUE and stem biomass. In contrast, normal water conditions avoided photoinhibition and increased stem biomass but reduced WUE. Overall, moderate drought stress conditions maximized both WUE and stem biomass. Jabereldar et al. (2017) identified sorghum genotype Tagat 10 as the most drought-tolerant, followed by Tagat 14, while Tagat 9 and cv. Gadambalea were the most drought-sensitive. Withholding irrigation at the 3-leaf stage improved crop WUE, reflecting the crop's ability to convert water into grain. Tagat 10 demonstrated superior WUE due to its higher seed yield compared to other genotypes.

10.2 Effect of high temperature on C_4 photosynthesis

Understanding temperature effects on C_4 plants is crucial for predicting their performance in future climates. As temperature rises, the oxygenation reaction increases, reducing RuBisCO's CO_2 specificity and limiting carbon gain. C_4 plants overcome photorespiration by concentrating CO_2 around RuBisCO in bundle sheath cells, maximizing carboxylation (Watson-Lazowski and Ghannoum, 2021)

C_4 crops like maize and sorghum show varying responses to temperature, with sorghum having higher photosynthetic temperature optima and greater heat and drought tolerance (Watson-Lazowski and Ghannoum, 2021). In a study by Correia et al. (2021), two maize genotypes, B73 and P0023, with contrasting drought and heat tolerance levels, were acclimatized to high temperatures (38°C vs. 25°C) under well-watered and water deficit (WD) conditions. Both genotypes successfully acclimatized to high temperatures, employing different mechanisms: B73 maintained photosynthetic rates by increasing stomatal conductance (g_s), while P0023 preserved g_s and exhibited limited transpiration. The study concluded that key traits for drought and heat tolerance in maize include limited transpiration rates and synchronized regulation of carbon assimilation metabolism.

Table 3. Results of warming and heat stress studies in Maize

Location	Ambient temperature	Continual warming	Heatwave (°C / hours / growth stage)	Photosynthesis	Yield	Reference
Yucheng, China	~ 13.1	~2	N.A.	Increase	N.A.	Zheng *et al*. (2018)
Illinois, USA	~22.7	~2.64	6 / 72 / Vegetative	Decrease	ns	Siebers *et al*. (2017)
Illinois, USA	~22.7	N.A.	6 / 72 / Reproductive	Decrease	Decrease	Ruiz-Vera *et al*. (2015)

10.3 CO_2 levels

Elevated CO_2 concentration can influence the growth of C_4 plants through several mechanisms. One effect is the increase in intercellular CO_2 partial pressure, which enhances CO_2 assimilation rate. Another is the reduction in stomatal conductance, leading to lower leaf transpiration rate. This decrease in leaf transpiration rate can boost leaf CO_2 assimilation rate and growth by conserving soil water, improving shoot water relations, and raising leaf temperature. Additionally, elevated CO_2 may lower mitochondrial respiration, which reduces overall plant respiratory losses and contributes to increased biomass (Ghannoum *et al.,* 2000).

As CO_2 concentrations rise, some regions will also experience increased frequency and severity of droughts (Lara & Andreo, 2011). The potential for enhanced growth and yield of C_4 plants at elevated CO2 concentrations is primarily attributed to reduced water use and decreased drought stress, rather than a direct increase in photosynthesis (Lara & Andreo, 2011; Pignon and Long, 2020). Pignon and Long (2020) found that C_4 species with CO_2 concentration in bundle sheath cells showed an indirect stimulation of photosynthesis when atmospheric CO_2 increased from 400 μmol mol^{-1} to 550 μmol mol^{-1}. However, no yield gains were observed under elevated CO_2 without drought stress.

Elevated CO_2 reduced midday stomatal conductance of FACE-grown sorghum by 32% with irrigation and by 37% under drought stress (Wall et al., 2001). As atmospheric CO_2 continues to rise, sorghum yield is expected to increase in areas with limited water availability (Ottman et al., 2001). Some C_4 plants grown under Free-Air Carbon Dioxide Enrichment (FACE) showed enhanced photosynthetic rates only during drought or under conditions of high atmospheric vapor pressure deficits (Leakey et al., 2009). Additionally, cultivating sorghum under elevated CO_2 mitigated the loss in grain quality caused by drought during the grain-filling stage by delaying physiological and metabolic responses to drought (De Souza et al., 2015).

In a future high-CO_2 environment, water requirements for irrigated sorghum will decrease, while dry-land productivity is expected to rise, assuming minimal global warming (Conley et al., 2001). Elevated CO_2 in controlled environments has been shown to increase sugarcane photosynthesis, WUE, biomass, and productivity. The improved WUE of sugarcane under elevated CO_2 is mainly due to reduced stomatal conductance. Sugarcane grown in elevated CO_2 had lower leaf stomatal conductance and transpiration, leading to greater leaf WUE. This helped delay the adverse effects of drought, allowing the plants to continue photosynthesis for at least an additional day during episodic drought cycles (Vu and Allen, 2009).

10.3.1 General effects of elevated CO_2 on photosynthetic heat tolerance

In C_3 species, elevated CO_2 generally enhances heat tolerance for photosynthesis, although at supra-optimal temperatures, this benefit may be diminished or even result in a decrease in photosynthesis. In contrast, C_4 species often experience reduced photosynthetic thermotolerance at both near-optimal and supra-optimal growing temperatures with elevated CO_2. While both C_3 and C_4 plants show similar reductions in stomatal conductance with increasing CO_2, C_4 plants have lower stomatal conductance at any given CO_2 level. This leads to reduced transpiration and higher leaf temperatures in C_4 plants, which could make them more susceptible to heat-related damage compared to C_3 plants in the same environment (Lara and Andreo, 2011).

The growth of maize and pearl millet under elevated CO_2 and temperature improved their cellular tolerance to osmotic stress and heat shock. However, maize appeared to benefit more from increased CO_2, while pearl millet seemed to benefit more from higher temperatures. The effects of current and anticipated global climate changes are likely to vary between these two species and may similarly impact other C_4 plant species across different ecosystems, whether natural or managed (Bordignon *et al*., 2019).

Elevated CO_2 is expected to enhance carbon uptake and water-use efficiency, leading to increased productivity of broomcorn millet in semi-arid regions under future high-CO_2 climates (Zhang et al., 2021). Similarly, elevated CO_2 significantly boosted grain yield and the accumulation of Zn, K, and Mn over three years, as well as enhancing the concentration and accumulation of P in foxtail millet (Gong et al., 2021).

11. ROLE OF C_4 CROPS IN THE FUTURE

Breeding crop varieties that can better withstand higher temperatures and extreme conditions is crucial for adapting to future climate challenges. Advances in technologies, particularly CRISPR-Cas9 gene editing, are significantly improving our ability to enhance germplasm. This technology allows for efficient overexpression, knockouts, and base pair edits within genetic sequences, making genetic improvements faster and more precise than traditional methods (Watson-Lazowski & Ghannoum, 2021). Conventional CRISPR technologies generally comprise two elements: a Cas protein that cleaves nucleic acids and a single guide RNA that associates with the Cas protein, directing it to a specific nucleic acid sequence, which is invariably adjacent to a conserved and compatible protospacer adjacent motif or protospacer flanking site for cleavage (Gaj, 2021). Studies have demonstrated its effectiveness in enhancing disease resistance in rice by correcting specific point mutations without causing double-strand breaks (Gupta et al., 2023; Chen et al., 2024). CRISPR/Cas technology allows precise genetic modifications to improve drought tolerance by targeting genes that regulate water use efficiency and osmotic balance (Shelake et al., 2022). Recent research has shown that modifying the ZmHDT103 gene in maize enhances drought tolerance by improving the plant's ability to withstand water scarcity while maintaining growth and yield under non-stress conditions (Chen et al., 2024). In wheat, engineering the TaRPK1 gene using CRISPR has been found to improve water absorption (Chen et al., 2024; Rahim et al., 2024). Additionally, CRISPR/Cas technology has been used to develop wheat with deeper root systems, improving water access from deeper soil layers. Another breakthrough involves manipulating Sal1 genes to increase osmoprotectant production, such as proline, which enhances drought resistance in wheat by helping plants endure dry periods (Mohr et al., 2022; Chen et al., 2024).

12. CLIMATE RESILIENT MAIZE FOR ASIA (CRMA)

The "Climate Resilient Maize for Asia" project is a collaborative initiative aimed at addressing the challenges faced by resource-poor maize farming communities in South and Southeast Asia, especially considering the anticipated impacts of climate change. Supported by Germany's development agency GIZ and implemented through a public-private partnership, the project focuses on enhancing the resilience of maize crops by developing and distributing abiotic stress-tolerant maize hybrids. These hybrids are specifically designed to thrive in rain-fed, stress-prone production systems, thereby promoting crop diversification, intensification, and higher yields. Building on the successes of the GIZ-funded "Abiotic Stress-Tolerant Maize for Increasing Income and Food Security among the Poor in South and Southeast Asia" project, this initiative addresses critical challenges related to improving maize production, enhancing food security, and building economic stability for smallholder farmers in the region (CIMMYT, 2020). Systematic breeding for heat stress-tolerant maize began at CIMMYT under the Heat Tolerant Maize for Asia project, funded by the United States Agency for International Development (USAID). The project focuses on breeding heat-tolerant maize through collaboration with public research institutions and private seed companies in Bangladesh, Bhutan, India, Nepal, and Pakistan (Zaidi et al., 2023). The Heat Tolerant Maize for Asia (HTMA-II) project, funded by CIMMYT with a budget of ₹73.50 lakhs, focused on developing climate-resilient maize through advanced breeding techniques and collaborations. The project successfully identified and deployed stress-tolerant maize hybrids, including ZH191085, which performed well under heat stress, and ZH182082, which yielded over 8.0 t/ha in heat-stressed conditions (IIMR, n.d.).

13. CLIMATE RESILIENCE IN C_4 WEEDS

Climate change is expected to cause shifts in weed community composition, impacting their population dynamics, life cycles, phenology, and infestation levels. Some weed species may go extinct, while others may become more aggressive and invasive. While elevated CO_2 levels are likely to boost the productivity of major C_3 crops, many of the troublesome agricultural weeds are expected to respond more positively to the increase in CO_2 than the crops themselves, potentially leading to their dominance in agro-ecosystems. Rising temperatures will likely favor the growth of C_4 weeds, which could result in significant crop yield losses. As climatic factors shift, crop-weed interactions may change, with weeds gaining an advantage and some previously non-threatening species taking over cultivated land. Under conditions of elevated temperature and drought, C_4 weeds are expected to dominate over C_3 crops, while C_3 weeds may prevail under higher CO_2 concentrations. However, when both CO_2 and temperature levels rise, C_4 weeds are predicted to dominate, further impacting crop production (Anwar *et al*., 2021). Barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.) a C_4 weed (Elmore & Paul, 1983) is a strong competitor of rice and can cause severe losses in grain yield across all rice cultures (Awan et al., 2024). A study conducted in China observed that grain yield losses ranged from 12.7% to 42.6% due to competition with *Echinochloa crus-galli* var. *mitis*, 22.3% to 55.2% with *Echinochloa crus-galli* var. *zelayensis*, and 1.5% to 12.1% with junglerice (*Echinochloa colona* (L.) Link) (Zhang et al., 2017; Damalas & Koutroubas, 2023). Another study demonstrated that an increase in the density of the C_4 weed pigweed redroot (*Amaranthus retoflexus*) led to a reduction in grain and biomass yield components, including ear length, ear diameter, the number of grains per row, the number of rows per ear, total grain number per ear, grain yield, and biological yield in corn (*Zea mays*) (Vazin, 2012).

Climate change is expected to significantly impact weed demographics, leading to shifts in weed species within agroecosystems (Peters et al., 2014; Ramesh et al., 2017). These shifts are crucial for weed management strategies and agricultural productivity. For species to persist in a particular habitat, they must adapt to environmental changes that can result in the alteration of weed flora, range expansion, and migration to new areas. Climate change will likely create opportunities for weeds to invade new ecosystems (Clements & Ditommaso, 2011; Peters et al., 2014). In fact, climate change is predicted to enhance the ability of introduced weed species to adapt to new environments, increasing their potential for invasion in both native and managed ecosystems. Weeds that are well-suited to altered environmental conditions, particularly with higher CO_2 concentrations, are expected to be more successful in utilizing available resources (Anwar et al., 2021). While C_3 crops may have a competitive edge over C_4 weeds under elevated CO_2 conditions alone, the simultaneous rise in both CO2 and temperature could favor the growth of C_4 weeds (Alberto et al., 1996). For instance, soybean yields were reduced from 45% to 30% when grown alongside *Amaranthus retroflexus* under elevated CO_2 compared to ambient levels (Ziska, 2003).

Table 4. Climate Resilient Varieties crop varieties from different states in India

Crop	Varieties	State	Seed source
Bajra	GHB-538 and GHB-719	Gujarat	Pearl millet Research Station, JAU, Jamnagar
	WCC-75	Karnataka	GKVK, UAS, Bangalore/ KSSC/ NSC
	RBH-177, RBH-154, RBH-173	Rajasthan	RSSC, Rajasthan
Foxtail Millet	RS-118, K-211-1, PS-4, SIA-326	Karnataka	GKVK, UAS, Bangalore/ KSSC/ NSC
Finger Millet	VR-708,HR-374	Chhattisgarh	IGKV / NRC millets, Bangalore
	MR-1, MR-6, GPU-66	Karnataka	GKVK, UAS, Bangalore/ KSSC

	Phule Nachani	Maharashtra	MPKV, Rahuri; ZARS, Kolhapur
Sorghum	CSH-5, CSH-9, CSV-4	Karnataka	GKVK, UAS, Bangalore/ KSSC
	Pant Chari 5, Pant Chari 7	Uttarakhand	GBPUA&T, Pantnagar
	Phule Chitra, M-35-1 Phule Vasudha, CSV18	Maharashtra	MPKV, Rahuri

(Lenka *et al*., 2020)

14. CONCLUSION

The changing climate has the potential to exert considerable adverse effects on plant physiology, soil fertility, carbon sequestration, and microbial activity, hence inhibiting plant growth and productivity, which would ultimately influence food production. C_4 plants are affected by significant global change variables in ways that contrast with C_3 plants. Comprehending the responses of C_4 plants to factors such as temperature, CO_2, nutrients, and water is essential for forecasting the adaptability of agricultural and wild C_4 populations to climatic variations, particularly those projected with global climate change. Understanding the mechanisms of stress responses in C_4 crops can aid in developing climate-resilient genotypes, thereby maintaining productivity amid fluctuating climatic conditions. This understanding should guide the formulation of targeted policies and programs that promote sustainable farming practices, strengthen climate resilience, and guarantee food security. Policymakers, researchers, and stakeholders must unite to prioritise investments in climate-resilient crops, enhance resource management, and alleviate the effects of climate change on global food systems.

Disclaimer (Artificial intelligence)

Authors hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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