



REVIEW ARTICLE

Climate change and crop-weed interactions: Unraveling the complex interactions between crops and weeds

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ABSTRACT

As the global climate continues to shift, the impacts of rising temperatures and elevated atmospheric CO₂ on agricultural systems have become increasingly significant, particularly in relation to crop-weed interactions. Several crops are especially vulnerable to climate-adaptable weeds, which possess higher fecundity, aggressiveness, and ecological resilience. Elevated CO₂ levels typically enhance the growth and competitive advantage of C₃ crops over C₄ weeds, due to the greater photosynthetic efficiency of C₃ plants under higher CO₂ concentrations. However, this advantage may diminish with rising temperatures, as C₄ weeds are more resilient to heat stress and can outcompete C₃ crops. The interaction between elevated CO₂ and temperature creates complex scenarios where the benefits of CO₂ enrichment for C₃ crops can be offset by the competitive edge gained by C₄ weeds under higher temperatures. Additionally, drought conditions further complicate these interactions, with C₄ weeds generally exhibiting greater resilience and competitive ability under moisture stress compared to C₃ weeds. Key outcomes of this review include the enhanced competitiveness of weeds under climate change, the altered physiological responses of both crops and weeds, and insights into the molecular and biochemical mechanisms driving weed adaptability to elevated CO₂ and temperature. These shifts in crop-weed dynamics present serious implications for crop yields. The review emphasizes the urgent need for adaptive, climate-resilient weed management strategies to mitigate these effects and sustain agricultural productivity in the future.

Keywords: Climate Change, Crop-weed interaction, Drought stress, C₃ weeds, C₄ weeds, elevated CO₂ and elevated temperature

INTRODUCTION

The world is currently off track in achieving the second Sustainable Development Goal (SDG2) to “end hunger, achieve food security and improved nutrition, and promote sustainable agriculture” by 2030 (UNICEF *et al.* 2019). Food security is vital for global sustainability, yet the increasing sensitivity of food production to climate change poses significant challenges (Porter *et al.* 2014). In recent decades, extreme weather events such as heatwaves, droughts, and prolonged precipitation have become more frequent, with devastating effects on agricultural productivity (Yan *et al.* 2022, Lobell *et al.* 2013, Vermeulen *et al.* 2013).

The impact of climate change on agricultural production is profound. Many regions worldwide have experienced reduced yields in essential crops such as wheat, maize, rice, and oilseed rape (Lachaud *et al.* 2022, Chandio *et al.* 2023). In India, for example, the annual average crop losses due to extreme weather events are estimated to account for around 0.25% of the nation's GDP (Singh *et al.* 2019). Without effective adaptation measures, global yields of critical food crops could decline by 12–20% by the end of the century (Aggarwal *et al.* 2019). This decline is expected to worsen as the current warming trend predicts average global temperature increases of 1.5–4.8 °C by 2100 (Malhi *et al.* 2021). The long-term warming patterns since pre-industrial times indicate a rise in temperatures by 0.1 to 0.3 °C per decade (IPCC, 2018). The Intergovernmental Panel on Climate Change (IPCC) forecasts that the average world temperature could increase by 2 °C by 2100 and 4.2 °C by 2400 (IPCC, 2021, NASA) (Figure 1). Simultaneously, the concentration of CO₂ in the atmosphere has been rising at an unprecedented rate, reaching 426 parts per million (ppm) in 2024 (<https://www.co2.earth/daily-co2>). Projections

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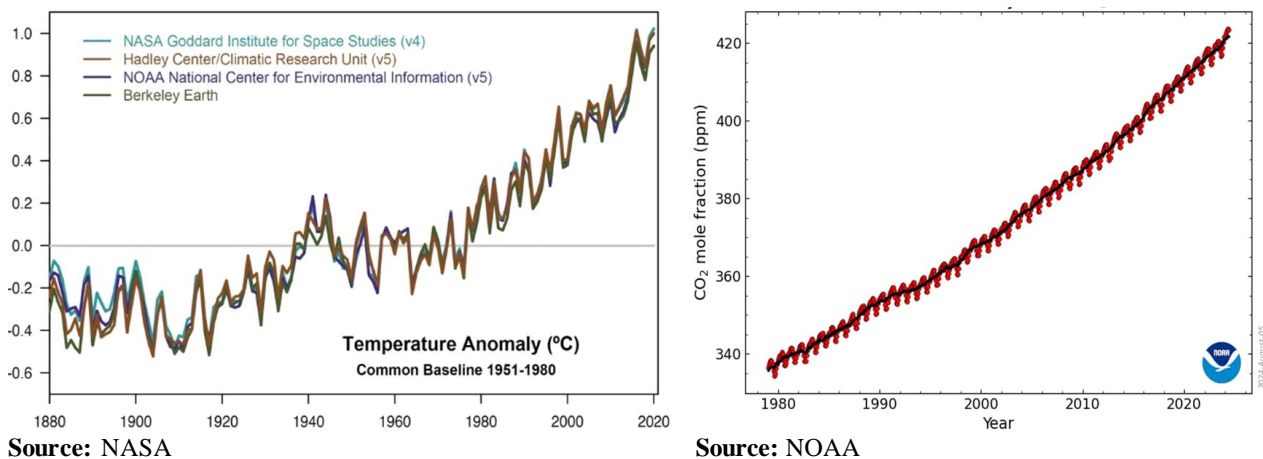


Figure 1. Global atmospheric temperature and CO₂ levels trend

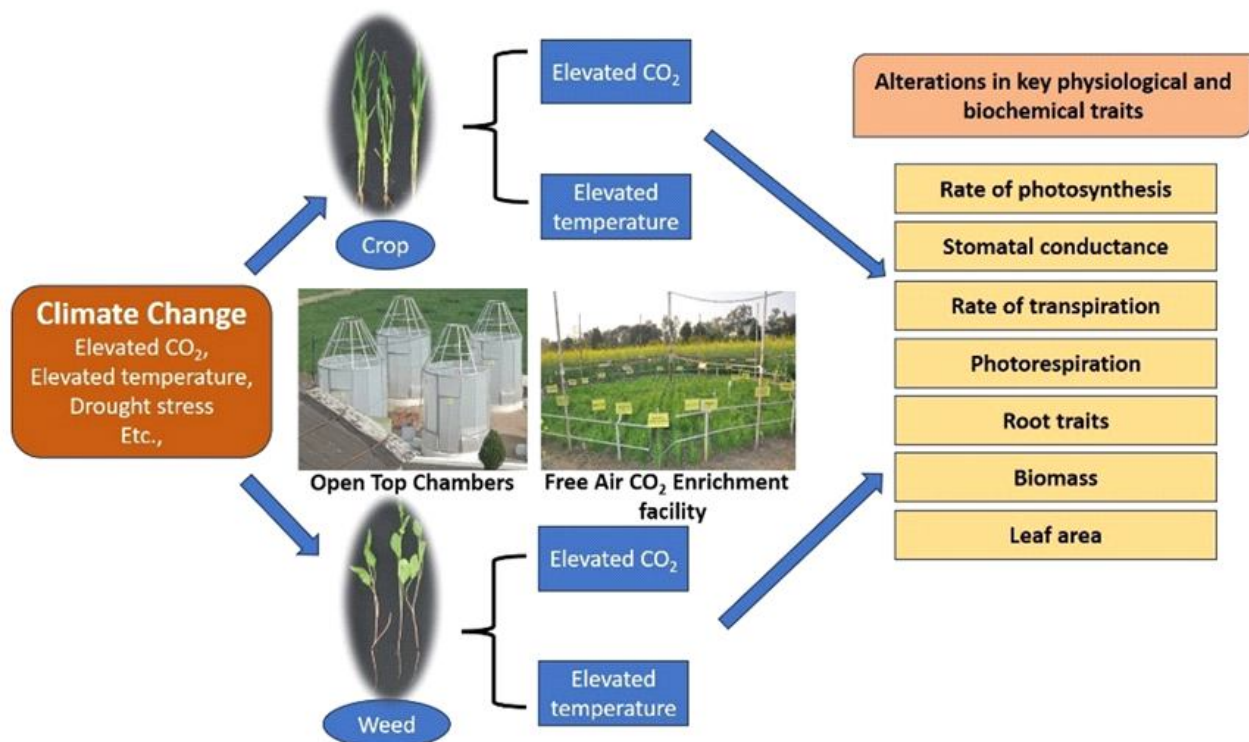


Figure 2. Impact of elevated CO₂ and temperature on crop-weed physiology and biochemistry

suggest that CO₂ levels may exceed 600 ppm in the near future (**Figure 1**), with a conservative estimate of 700 ppm by the end of the century (Ramanathan and Feng 2008, IPCC 2007, NOAA). Both elevated CO₂ and high temperatures are known to alter metabolic pathways in crop plants, generally leading to reduced yields and total biomass. However, elevated CO₂ can also have beneficial effects, such as increasing carbon uptake and improving water use efficiency through transcriptional reprogramming of metabolism (Leakey *et al.* 2009).

As the planet grapples with the effects of climate change, it becomes increasingly vital to understand how rising temperatures and atmospheric CO₂ levels influence various aspects of the natural world.

Among these considerations, the impact of elevated CO₂ and temperature on weed growth and physiology emerges as a critical area of research (Upasani *et al.* 2018) (**Figure 2**). Weeds, often seen as nuisances in agriculture, play a complex and multifaceted role in ecosystem dynamics. Globally, weeds are responsible for approximately 34% of crop yield losses (Oerke 2006), and they pose additional challenges under changing climate conditions (Sreekanth *et al.* 2023; Mahawar *et al.* 2023, Roy *et al.* 2023). These weeds can severely impact crop productivity and agricultural systems, affecting major crops like rice (Sreekanth *et al.* 2024, Pawar *et al.* 2022), wheat (Sondhia *et al.* 2023), soybean (Chander *et al.* 2023), and potato (Chethan *et al.* 2023) *etc.* These

opportunistic plant species exhibit remarkable adaptability, aggressiveness, competitiveness, and high fecundity, enabling them to thrive in diverse and challenging environmental conditions (Nguyen *et al.* 2015).

Given their adaptability and resilience, weeds are particularly responsive to changes in atmospheric composition and temperature regimes, making them formidable competitors to crops under climate change (Rodenburg *et al.* 2011, Blumenthal *et al.* 2013). Studying the effects of climate change on weed growth and physiology is essential not only for understanding the broader implications for ecosystems but also for devising effective strategies for sustainable agriculture (Mahajan *et al.* 2012, Grossman *et al.* 2014). While the influence of climate change on crops can be extrapolated to weeds, the dynamics often favor weeds, which, due to their plasticity, superior adaptability, and broader ecological tolerances, are more likely to outcompete crops.

Weeds' ability to compete with crops for scarce resources such as water and nutrients leads to significant reductions in crop yields (Ramesh *et al.* 2017). Furthermore, some weeds offer positive ecological benefits, such as absorbing heavy metals from contaminated soils (Roy *et al.* 2021). The genetic diversity and physiological flexibility of weeds often surpass that of crops, allowing weeds to survive and thrive under fluctuating environmental

conditions and resource availability. As climate change is projected to enhance weed competitiveness, ineffective weed management practices could lead to substantial yield losses (Miri *et al.* 2012, Valerio *et al.* 2013). Therefore, efficient weed management and control are critical to maintaining crop productivity.

This review explores the intricate relationship between rising atmospheric CO₂ levels, increasing temperatures, and their combined effects on crop-weed interactions and associated physiological responses. As global climate change continues to reshape environmental conditions, understanding how weeds respond to these changes is imperative for ensuring sustainable agriculture and effective ecosystem management. It provides an in-depth analysis of the underlying molecular and biochemical mechanisms governing weed responses to elevated CO₂ and temperature, offering a foundation for understanding the observed physiological changes and informing strategies for sustainable agriculture and ecosystem management.

CLIMATE CHANGE FACTORS INFLUENCING WEED GROWTH AND BIOMASS

Photosynthetic mechanism of C₃ and C₄ plants

The varying responses of C₃ and C₄ plants to altered climatic conditions require a more thorough understanding of the C₃ and C₄ photosynthetic cycles in weeds (Table 1).

Table 1. Differences in photosynthetic mechanism of C₃ and C₄ plants

Aspect	C ₃ Plants	C ₄ Plants	References
Photosynthetic Pathway	C ₃ pathway (Calvin Cycle)	C ₄ pathway (Hatch-Slack pathway)	Taiz & Zeiger, 2010, Sage <i>et al.</i> 2012
Initial CO ₂ Fixation	RuBisCO enzyme	PEP carboxylase enzyme	Raven <i>et al.</i> 2009
Initial CO ₂ acceptor	3-carbon compound (3-PGA)	4-carbon compound (oxaloacetate)	Long <i>et al.</i> 2006, Smith & Stitt, 2007
Carbon Fixation Location	Stroma of chloroplasts	Mesophyll cells and bundle sheath cells	Long <i>et al.</i> 2006
Photorespiration	High, significant loss of CO ₂ during photorespiration	Low, efficient CO ₂ use due to CO ₂ concentration mechanism	Walker <i>et al.</i> 2013, Tazoe <i>et al.</i> 2008
Oxygen Sensitivity	High sensitivity to photorespiration	Low sensitivity to photorespiration	Feng & Hu, 2013
Photosynthesis Efficiency	Lower efficiency in hot and dry conditions	Higher efficiency in hot and dry conditions	Sage & Monson, 1999
Leaf Anatomy	Simple anatomy; no specialized structures	Kranz anatomy (distinct bundle sheath cells)	Ehleringer <i>et al.</i> 1997
Energy Requirements	Lower energy cost for carbon fixation	Higher energy cost due to additional ATP and NADPH requirements	Lange <i>et al.</i> 2001
Water Use Efficiency (WUE)	Lower WUE compared to C ₄ plants due to higher photorespiration	Higher WUE due to reduced photorespiration and enhanced CO ₂ fixation	Condon <i>et al.</i> 2004
Optimal Temperature Range	Cooler temperatures (10–25 °C)	Warmer temperatures (30–45 °C)	Sage <i>et al.</i> 2012
CO ₂ compensation point	50–150 ppm	0–10 ppm	Taiz & Zeiger, 2010
Environmental Adaptations	Adapted to temperate and cooler climates	Adapted to hot and arid tropical and sub-tropical areas	Lichtenthaler & Buschmann, 2001
Examples	Wheat, Rice, Soybean	Maize, Sugarcane, Sorghum	Ehleringer <i>et al.</i> 1997

Elevated CO₂ levels

Increased carbon dioxide (eCO₂) levels are known to significantly enhance the growth and maturation of many plant species, with the response varying based on the photosynthetic pathway employed by the plant (C₃ or C₄) (Kimball and Idso, 1983). For C₃ crops like rice and wheat, eCO₂ levels can potentially improve their competitive advantage against C₄ weeds, as observed by Yin and Struik (2008). This advantage is attributed to the greater efficiency of C₃ plants in utilizing the increased CO₂ for photosynthesis. However, when both CO₂ and temperature rise simultaneously, the competitive edge shifts back to C₄ species, which are better adapted to higher temperatures. Patterson and Flint (1980) also support this, indicating that C₃ plants generally benefit more from CO₂ enrichment compared to C₄ plants.

For instance, Ziska (2000) demonstrated that under monoculture conditions, soybean (C₃) exhibited increases in yield (23%) and biomass (32%) under high CO₂ levels (ambient + 250 ppm). However, when grown in competition with the C₃ weed *Chenopodium album*, soybean's yield and biomass reductions were more pronounced under elevated CO₂, decreasing from 28% and 23% at ambient CO₂ to 39% and 34% at eCO₂, respectively, due to a 65% increase in the dry weight of *C. album*. Conversely, when competing with the C₄ weed *Amaranthus retroflexus*, the soybean yield decreased from 45% to 30% at higher CO₂ levels, suggesting that *C. album* might dominate under eCO₂, while *A. retroflexus* would be less competitive, potentially giving soybean an advantage over *A. retroflexus*.

Bunce and Ziska (2000) further argue that with rising atmospheric CO₂ levels, competition from weeds in C₃ plants might diminish. However, this benefit can be offset by simultaneous increases in temperature, which tend to intensify weed competition. Thus, while elevated CO₂ may favor C₃ crops over C₄ weeds, the combination of elevated CO₂ and temperature is likely to increase the overall competitive pressure from weeds, potentially reducing the crop's advantage. In summary, when CO₂ levels rise, C₃ crops may benefit if they compete with C₄ weeds, but under conditions of both elevated CO₂ and temperature, weeds may generally gain a competitive edge over crops. eCO₂ had a positive effect on overall growth and biomass of the following weeds (Table 2).

Increased temperatures

Under elevated temperatures, weeds utilizing the C₄ photosynthetic pathway often gain a competitive

Table 2. Effect of elevated CO₂ on major C₃ and C₄ weeds

Weed species	Reference
C₃ weeds	
<i>Abutilon theophrasti</i> Medic	Miri <i>et al.</i> 2012
<i>Alternanthera paronychioides</i> A. St.-Hil.	DWR 2020
<i>Avena fatua</i> L.	DWR 2008-09
<i>Bromus tectorum</i> L.	Zelikova <i>et al.</i> 2013
<i>Chenopodium album</i> L.	DWR 2010-11
<i>Cirsium arvensis</i> L.	O'Donnell and Adkins 2001
<i>Commelina diffusa</i> Burm. f.	DWR 2009-10
<i>Convolvulus arvensis</i> L.	Valerio <i>et al.</i> 2013
<i>Elymus repens</i> L.	Jia <i>et al.</i> 2011
<i>Euphorbia geniculata</i> Ortega.	DWR, 2008-09
<i>Lathyrus sativa</i> L.	DWR 2010-11, 2013-14
<i>Lolium multiflorum</i> Lam.	Davis and Ainsworth 2012
<i>Medicago denticulata</i> Willd.	DWR 2010-11, 2013-14
<i>Oryza</i> spp.	DWR 2013-14
<i>Parthenium hysterophorus</i> L.	DWR 2016-17
<i>Phalaris minor</i>	DWR 2010-11, 2013-14
<i>Polygonum convolvulus</i> L.	Ziska <i>et al.</i> 2004
<i>Xanthium strumarium</i> L.	Ziska 2013
<i>Parthenium hysterophorus</i> L.	Chandrasena 2009
<i>Chromolaena odorata</i> L.	Chandrasena 2009
C₄ weeds	
<i>Amaranthus viridis</i> L.	DWR 2016-17
<i>Amaranthus retroflexus</i>	Ziska and Bunce 1997
<i>Echinochloa crus-galli</i>	DWR 2014-15
<i>Sorghum halepense</i>	DWR 2008-09

edge over crops that rely on the more prevalent C₃ pathway (Yin and Struik 2008). High-temperature stress can impact growth rates during various developmental stages due to shifts in temperature thresholds. C₄ plant species are more resilient to heat stress and can stimulate meristematic regions, leading to rapid canopy growth and enhanced root proliferation, whereas such temperatures typically hinder growth in C₃ species (Morgan *et al.* 2001) (Table 3).

Table 3. Effect of elevated temperature on major C₃ and C₄ weeds

Weed species	Reference
C₃ weeds	
<i>Avena fatua</i>	O'Donnell and Adkins, 2001
<i>Chenopodium album</i>	Miri <i>et al.</i> 2012
<i>Cirsium arvensis</i>	Davis and Ainsworth, 2012
<i>Abutilon theophrasti</i>	Ainsworth, 2012
<i>Lolium multiflorum</i>	Ziska <i>et al.</i> 2004
<i>Polygonum convolvulus</i>	Valerio <i>et al.</i> 2013
<i>Convolvulus arvensis</i>	Ziska, 2013
<i>Xanthium strumarium</i>	Jia <i>et al.</i> 2011
C₄ weeds	
<i>K. scoparia</i> , <i>S. halepense</i>	McDonald <i>et al.</i> 2009
<i>E. indica</i>	Mahajan <i>et al.</i> 2012
<i>E. crus-galli</i>	Valerio <i>et al.</i> 2011;
<i>D. sanguinalis</i>	Satrapova <i>et al.</i> 2013
<i>A. retroflexus</i>	Zheng <i>et al.</i> 2011
<i>C. dactylon</i>	Rodenburg <i>et al.</i> 2011
<i>Sida spinosa</i>	Blumenthal <i>et al.</i> 2008

Interactive effects of elevated CO₂ and temperature on C₃ and C₄ weeds

Elevated CO₂ levels mitigate the effects of sub-optimal temperatures and other stressors on plant growth (Bazzaz 1990). As plants mature more rapidly under these conditions, they contribute a greater number of seeds to the soil seed bank. This increase in seed accumulation can lead to a higher density of *A. ludoviciana* populations. Specifically, at 480 ppm CO₂, *A. ludoviciana* produced 44% more seeds compared to plants exposed to 357 ppm CO₂ (Table 4).

Impact of drought on C₃ and C₄ weeds

Rice crops are vulnerable to both biotic (weeds) and abiotic (drought) stresses early in the season when they are most susceptible to weed competition, leading to oxidative stress in the plants (Table 5). Research indicates that the C₄ weed *E. colona* has a more pronounced negative impact on yield compared to the C₃-C₄ intermediate weed *A. paronychioides*, due to the greater physiological plasticity and mechanisms of C₄ weeds (Sreekanth *et al.* 2024). Low soil moisture significantly reduces the rate of photosynthesis, transpiration, and stomatal conductance (Kondo *et al.* 2004, Xu *et al.* 2007). The spread of weeds and crop productivity are highly influenced by fluctuations in rainfall patterns and aridity. With projected temperature increases of 1–5 °C for each doubling of atmospheric CO₂, aridity is expected to rise in many agriculturally significant regions. Increased evaporation and rainfall variability will likely lead to drier monsoon regions (Giannini *et al.* 2008), with a 5–8% increase in drought-prone areas (Rodenburg *et al.* 2011). Under these conditions, weed spread and prevalence will become significant issues in agricultural ecosystems, with summer droughts impacting weed control in spring-sown crops (Peters and Gerowitt 2014). C₄ and parasitic weeds, such as *Striga hermonthica*, are likely to survive better under extreme drought conditions (Rodenburg *et al.* 2010). Despite these challenges, there is limited information on how drought affects crop-weed interactions, highlighting the need for further research in this area.

Table 4. Interactive effect of elevated CO₂ and temperature on weed growth

Weed species	Reference
<i>Leptochloa chinensis</i> (L.) Nees	DWR 2020
<i>A. paronychioides</i>	DWR 2020
<i>E. geniculata</i>	DWR 2016-17
<i>C. album</i> and <i>P. minor</i>	DWR 2017-18
<i>E. colona</i>	DWR 2018-19
<i>Elytrigia repens</i>	Tremmel and Patterson, (1993)
<i>Echinochloa glabrescens</i>	Alberto <i>et al.</i> (1996), Carter and Patterson (1983)

PHYSIOLOGICAL AND BIOCHEMICAL RESPONSES

Photosynthesis and respiration

Increased atmospheric CO₂ levels induce various physiological changes in plants, including larger leaf areas, higher mass per unit area, enhanced photosynthesis, improved water use efficiency, increased tillering, accelerated flowering, greater grain weight, more grains per spikelet, elevated grain yields, and a higher harvest index (Jagadish *et al.* 2011). The rising CO₂ levels are expected to boost leaf photosynthesis in C₃ plants by increasing CO₂ concentrations within the leaf and reducing CO₂ loss through photorespiration. In contrast, C₄ plants, which utilize an internal biochemical pump to concentrate CO₂ at the carboxylation site, effectively minimize carbon loss through photorespiration and reduce the oxygenase activity of Rubisco (Naidu 2013). The specialized mesophyll cell arrangements in C₄ plants enhance CO₂ transfer and minimize photorespiration, giving them a photosynthetic advantage over C₃ plants (Drake *et al.* 1997). As a result, C₃ plants are anticipated to benefit more from CO₂ enrichment than C₄ plants, leading to lesser responses to elevated CO₂ in many C₄ weed species compared to C₃ crops. Under elevated temperatures, C₄ plants, which are commonly found among weeds, gain a competitive edge over C₃ crops (Yin and Struik 2008). For example, a 3°C increase in temperature significantly boosts the growth of itch grass (*Rottboellia cochinchinensis*), a C₄ weed that affects crops such as sugarcane, corn, cotton, soybean, grain sorghum, and rice (Patterson *et al.* 1999).

Relative water content (RWC) dynamics are influenced by root water absorption and transpiration-related water loss. Climate change generally reduces RWC across plant species, with non-stressed plants usually maintaining RWC levels between 85% and 90%, while those exposed to higher temperatures may see RWC drop to as low as 30% (Lee *et al.* 2017). Elevated temperatures and moisture stress can lead to more significant reductions in leaf elongation rates compared to net photosynthesis (Lyons *et al.* 1979).

Table 5. Effect of drought stress on weed growth (C₄ weeds)

Weed species	Reference
<i>Echinochloa crus-galli</i>	Patterson 1986
<i>Eleusine indica</i>	Patterson 1986
<i>Digitaria ciliaris</i>	Patterson 1986
<i>Bromus tectorum</i>	Patterson 1995
<i>Centaurea solstitialis</i>	Patterson 1995
<i>Striga hermonthica</i> (Del) Benth.	Rodenburg <i>et al.</i> 2010

Changes in photosynthesis and C assimilation

Increased CO₂ concentrations and rising temperatures significantly affect plant carbon metabolism and contribute to a feedback loop that influences future climate change. Elevated CO₂ enhances net photosynthesis by supplying more CO₂ to Rubisco and reducing photorespiration. However, this effect is nonlinear; at low internal CO₂ concentrations (C_i), photosynthesis is limited by Rubisco carboxylation rates, and as C_i increases, net CO₂ assimilation rates (A_{net}) rise sharply. Limitations on photosynthesis at higher C_i levels are influenced by the capacity to replenish RuBP and utilize triosephosphates for starch and sucrose production, which are less sensitive to CO₂ than Rubisco carboxylation (Sharkey *et al.* 2007). Although future CO₂ increases may have diminishing effects on carbon uptake, the rise in CO₂ since the Industrial Revolution has substantially stimulated photosynthesis (Gerhart and Ward 2010). For instance, elevated CO₂ has been shown to enhance rice yield due to the positive response of C₃ species, increasing carbon assimilation rates (Yang *et al.* 2006, Kim *et al.* 2003, Ma *et al.* 2007). There is limited research on how elevated CO₂ or temperature affects the distribution of photosynthetic carbon (C) and nitrogen (N) uptake across different rice organs (Yang *et al.* 2007).

Water use efficiency and transpiration rates

The concept of water use efficiency (WUE) was introduced by Briggs and Shantz (1913) to illustrate the relationship between plant productivity and water usage. They defined WUE as the amount of biomass produced per unit of water used by plants. To evaluate the impact of climate change on WUE, it is useful to start at the leaf level. This is because changes in CO₂ levels, water availability, and temperature are most apparent at this level, with fewer confounding factors such as canopy structure and soil interactions. WUE at the leaf level varies depending on the carboxylation pathway, including C₃ and C₄ photosynthesis as well as Crassulacean acid metabolism. Generally, C₄ plants exhibit higher inherent WUE compared to C₃ plants (Taylor *et al.* 2010).

Impact on nutrient uptake and metabolism

Climate change significantly impacts crop growth and production, primarily through changes in photosynthetic carbon assimilation (Reddy *et al.* 2010). Elevated CO₂ levels act as a carbon fertilizer, enhancing crop growth and development (Van der Kooi *et al.* 2016). The primary effect of increased atmospheric CO₂ is an enhanced rate of carbon

fixation in photosynthetic leaves (Taub 2010). Free-air carbon dioxide enrichment (FACE) trials have shown that many plant species can increase their photosynthetic rate by nearly 40% under higher CO₂ levels (475–600 ppm), leading to greater photosynthate production and dry matter accumulation (Ainsworth and Rogers 2007). Elevated CO₂ levels also impact plant development by increasing leaf area, leaf area index (LAI), leaf area duration (LAD), leaf thickness, and dry biomass production, as observed in crops like tomatoes (Pan *et al.* 2019).

This increase in dry matter under elevated CO₂ conditions enhances radiation interception by plants. Studies in rice and chickpeas have shown a linear relationship between solar radiation interception and total dry matter accumulation (Weerakoon *et al.* 2000). Elevated CO₂ often leads to higher LAI and LAD, which significantly affect radiation interception (Hikosaka 2005). However, the combination of elevated CO₂ and increased ambient temperatures can alter phenological phases and crop duration, leading to shorter crop cycles and faster initiation of phenological stages in crops like rice, wheat, maize, and mungbean (Cai *et al.* 2016). Elevated temperatures can negatively impact net photosynthesis, influencing processes such as photorespiration and ribulose-1,5-bisphosphate carboxylase activity, resulting in heat-induced physiological disorders and reduced crop yields (Cai *et al.* 2018).

The effects of elevated CO₂ on plants are influenced by additional meteorological conditions, including air temperature and moisture stress, which impact plant metabolism through photosynthesis, especially in high-altitude environments (Dusenge *et al.* 2019). While higher CO₂ levels are expected to increase photosynthetic rates, this effect depends on factors such as soil nutrition, leaf air temperature, and moisture availability (Leakey *et al.* 2009). Elevated CO₂ increases plants' access to carbon but also requires additional soil resources like mineral fertilizers. Essential nutrients such as nitrogen, phosphorus, and potassium play a crucial role in moderating crop responses to rising CO₂ levels, affecting soil nutrient dynamics (Raj *et al.* 2019).

CROP-WEED INTERACTION

Effect of enhanced atmospheric CO₂ concentration on crop-weed interaction

CO₂ enrichment has been shown to significantly stimulate the growth and development of many plant species (Kimball 1983, Kimball *et al.* 1993, Poorter

1993, Sage 1995). The variation in response to elevated CO₂ levels is largely influenced by the type of photosynthetic pathway (C₃ or C₄) in plants (Table 6). However, predicting the effects of increased atmospheric CO₂ on crop-weed interactions in isolated environments often leads to inadequate assessments of competition, as fields rarely host a single weed species (Ziska and Goins 2006). Although some studies have quantified the growth of crops and weeds under elevated CO₂ in competitive environments (Ziska 2004, Ziska and Goins 2006), more research combining various weed and crop species is urgently needed.

Under elevated CO₂, C₃ plants such as soybeans and *Chenopodium album* show significantly higher yields compared to C₄ plants like millet and pigweeds (Miri *et al.* 2012). The increase in biomass and yield of weedy rice, compared to cultivated rice at elevated CO₂ levels, suggests that future CO₂ concentrations may lead to a larger decline in the yield of cultivated rice in competition with C₃ weeds (Ziska *et al.* 2010). This could be due to the greater physiological flexibility and higher genetic variation found in wild species compared to cultivated lines (Treharne 1989).

Impact of elevated temperature on crop-weed interaction

Temperature alterations are poised to significantly impact the growth, development, and distribution patterns of weed plants. Generally, increased temperatures favor C₄ weeds over C₃ weeds due to the higher rates of photorespiration in C₃ plants under such conditions (Varanasi *et al.* 2016). Elevated temperatures enhance canopy growth and root proliferation in C₄ plants, giving them a competitive edge over C₃ crops (Morgan *et al.* 2001, Yin and Struik 2008). For instance, a 3°C rise in temperature has been shown to significantly boost the

growth of itch grass (*Rottboellia cochinchinensis*), a major C₄ weed that threatens crops like sugarcane, corn, cotton, soybean, sorghum, and rice, with potential expansion towards the central Midwest and California (Patterson *et al.* 1999).

Moreover, C₄ weeds like red root pigweed (*Amaranthus retroflexus*) and Johnson grass (*Sorghum halepense*) are predicted to fix CO₂ more efficiently than C₃ crops like soybean and cotton, particularly around noon when temperatures and light intensity peak. The enhanced water use efficiency and CO₂ compensation point of C₄ photosynthesis make these weeds better adapted to high evaporative demand (Bunce 1983). Under elevated CO₂ conditions, C₄ weedy species have demonstrated greater stimulation in photosynthesis and biomass production compared to C₄ crops (Ziska and Bunce 1997). Interestingly, during early growth stages before the differentiation of their 'Kranz anatomy,' C₄ plants initially rely on the C₃ pathway for carbon fixation, allowing them to benefit from elevated CO₂ (Nelson and Langdale 1989). Warmer conditions have also been observed to delay the germination of green foxtail (*Setaria viridis*), a C₄ weed that could become a more serious problem in maize crops globally due to its synchronization with maize germination, driven by increased temperature sensitivity (Peters and Gerowitt 2014).

Interactive effect of elevated CO₂ and temperature on crop-weed interaction

Several studies from ICAR-DWR have highlighted that *P. minor* gains a competitive edge over wheat when exposed to higher temperatures, either alone or in combination with elevated CO₂ (Table 7). Additionally, research indicates that a combination of high CO₂ and temperature delays

Table 6. Impact of elevated CO₂ on crop-weed interaction

Crops	Weeds	Response	Reference
C ₃ Rice, wheat, soybean, etc.	<i>Amaranthus palmeri</i> L., <i>Amaranthus rudis</i> , (C ₄ weeds)	Elevated CO ₂ favoured crops	Elmore and Paul, 1983, Yin and Struik 2008
Wheat	<i>Phalaris minor</i> (C ₃)	Elevated CO ₂ favoured weed	Naidu and Varshney, 2011
C ₄ crops (maize, sorghum, sugarcane, etc.)	C ₃ weeds <i>C. album</i> , <i>Ambrosia theophrasti</i> , <i>Ambrosia artemisiifolia</i> L., <i>Ambrosia trifida</i> L.	Elevated CO ₂ favoured weeds	Ziska <i>et al.</i> 2000
Chickpea	<i>Lathyrus sativa</i> , <i>Medicago denticulata</i>	Elevated CO ₂ favoured crop and weeds	DWR, 2013-14
Cultivated rice	weedy rice	Elevated CO ₂ favoured crop and weed	DWR, 2013-14
Maize	<i>Euphorbia geniculata</i>	Elevated CO ₂ favoured weed	DWR, 2008-09
Greengram	<i>Commelina diffusa</i> , <i>Euphorbia geniculata</i>	Elevated CO ₂ favoured weed	DWR, 2009-10
Greengram	<i>Brachiaria reptans</i> L., <i>Eragrostis diarrhena</i> (Schult.) Steud.	Elevated CO ₂ favoured crop and weed	DWR, 2012-13

Table 7. Combined effect of elevated CO₂ and temperature on crop-weed interaction

Crop	Weed	Response	Reference
Greengram	<i>E. geniculata</i> (C ₃), <i>A. viridis</i> (C ₄)	EC+ET favoured weed	DWR 2016-17
Wheat	<i>P. minor</i> (C ₃)	EC+ET favoured weed	DWR 2015-16
Maize	<i>C. album</i> and <i>P. minor</i>	EC+ET favoured crop and weed	DWR 2017-18
Soybean	<i>E. colona</i> and <i>I. rugosum</i>	EC+ET favoured crop and weed	DWR 2018-19
Rice	<i>A. paronychioides</i> (C ₃ -C ₄) and <i>L. chinensis</i> (C ₄)	EC+ET favoured weed	DWR 2020

panicle maturity in cultivated, weedy, and wild rice (DWR, 2014-15, DWR, 2015-16).

Impact of drought on crop-weed interaction

Water is a critical factor influencing plant growth, with each species requiring specific moisture conditions for optimal development. Climate change is expected to increase the frequency of droughts, floods, and erratic rainfall, leading to moisture stress in both arable and non-arable ecosystems. This stress affects crops and weeds alike, though weeds often exhibit greater physiological plasticity and genetic variation, making them somewhat less vulnerable to such conditions. Nonetheless, weeds will still respond to moisture stress, with their responses varying by species and environmental conditions. For example, some weeds release allelochemicals during drought to outcompete crops (Patterson 1995). C₃ weeds thrive under submergence, while C₄ weeds are better suited to dry conditions, explaining the dominance of C₃ weeds in flooded areas and C₄ weeds in arid soils (Matsunaka 1983).

A study highlighted that C₄ weed (*E. colona*) showed considerable negative impact on rice yield than C₃-C₄ intermediate weed (*A. paronychioides*) under drought stress due to C₄ weed physiological plasticity and mechanism (Sreekanth *et al.* 2024). The highest accumulation of MDA was observed under drought due to *A. paronychioides* (38.66 µg/g FW) and *E. colona* (66.21 µg/g FW) interference (Sreekanth *et al.* 2024). Drought and arid conditions favor the growth of C₄ weeds because of their strong internal physiological mechanisms. Competition of cotton with *A. theophrasti* and spurred anoda (*Anoda cristata* Schlecht.) is more under drought conditions (Patterson and Highsmith 1989). A decline in yield is due to *X. strumarium* was prominent in well-watered soybeans compared with water-stressed soybeans (Mortensen and Coble 1989). A raise in rainfall results in greater competition to wheat growth and yield against *C. arvense* (Donald and Khan 1992). Weed competition had little effect on crops under water deficit conditions, as the potential crop yield was already reduced by water stress Patterson (1995); Chauhan and Abugho (2013). By contrast, spiny amaranth (*Amaranthus spinosus* L.) and *L. chinensis*

survived under water stress conditions and produced a significant number of tillers/branches and leaves even at the lowest soil water content Chauhan and Abugho (2013). Only few studies have been conducted on this area, therefore, there is an urgent need to explore this aspect to cope up the upcoming climate change challenges.

EFFECT OF CLIMATE CHANGE ON CROP-WEED DYNAMICS AND WEED FLORA SHIFT

Changes in weed species composition and distribution

Climate change is expected to reshape the composition, distribution, and dominance of weed species in arable ecosystems, which are already influenced by human activities (Pautasso *et al.* 2010). Weeds, highly adapted to varying farming practices, will be affected by changes in land use, management practices, and climate conditions (Gunton *et al.* 2011). As climatic factors alter crop management, they will likely shift crop-weed interactions, potentially allowing some weeds to dominate (Fleming and Vanclay 2010). Key factors such as soil moisture, temperature, and CO₂ levels will drive these changes (Chauhan *et al.* 2014).

While most troublesome weeds are currently confined to tropical and subtropical regions, climate change may enable their expansion into cooler areas due to increased tolerance of low temperatures under elevated CO₂ (McDonald *et al.* 2009). Elevated temperatures and CO₂ are likely to enhance the growth of some weed species and shift the range of tropical and subtropical species northward (Chandrasena, 2009). C₄ weeds, benefiting from higher temperatures and drought, may outcompete C₃ crops, while C₃ weeds could dominate in high CO₂ conditions (Singh *et al.* 2016).

High temperatures and elevated CO₂ levels have been shown to affect weed growth and seed production, enhancing both for invasive and cropland weeds (Dukes *et al.* 2009). Increased CO₂, for example, has been linked to greater plant height in weedy rice, which aids in seed dispersal (Thomson *et al.* 2011). Similarly, temperature changes impact weed growth, seed production, and germination

(Benech-Arnold *et al.* 2000). These climatic shifts influence evolutionary pressures within plant communities, affecting species distribution and interactions (Grossman 2014).

Climate change significantly impacts weed populations, altering their distribution, abundance, and management in agroecosystems. As temperatures rise, weeds may either adapt locally, migrate to more suitable areas, or evolve to survive new conditions (Pautasso *et al.* 2010). Shifts in weed populations are expected as species respond to changes in climate, such as increased CO₂ and temperatures. For instance, many tropical weeds are expanding northward due to warming (Patterson 1995), with species like kudzu and itchgrass already moving into new regions (Patterson 1995).

Increased CO₂ levels and temperature may also enhance the growth and spread of invasive weeds, with species such as *Lonicera sempervirens* and *Pueraria lobata* becoming more common in cropland areas (Patterson 1995). In Australia, frost-intolerant species like rubber vine may shift to higher latitudes (Kriticos *et al.* 2003). The expansion of non-native weeds and the alteration of local weed dynamics due to climate change highlight the need for adaptive management strategies. Research should focus on the interactions between climate variables and weed traits to predict future shifts accurately (Hulme and Barrett 2013, Mack *et al.* 2000). Additionally, understanding how temperature and moisture stress interact is crucial for predicting weed behavior under global warming conditions.

Weed invasion

Weed species often spread beyond their native ranges, sometimes becoming invasive and negatively impacting native species (Mack *et al.* 2000). Approximately 10% of introduced species become invasive, threatening ecosystems and biodiversity (Kathiresan and Gualbert 2016). Climate change may further facilitate weed invasions by enhancing the adaptability of introduced species to new environments and increasing their competitive edge, especially with higher CO₂ levels (Hellmann *et al.* 2008). Invasive potential is influenced by genetic factors (*e.g.*, photosynthetic pathways, seed dormancy) and climatic factors (*e.g.*, temperature, CO₂ concentration) (Kathiresan and Gualbert 2016). Climate change interactions with land use practices may also convert benign species into invasive ones, affecting agricultural productivity (Irmaileh *et al.* 2010). Increased CO₂ may promote invasiveness, as observed with *Parthenium hysterophorus*, which shows higher coverage under warmer conditions

(Singh *et al.* 2011). While climate change impacts on invasiveness can be variable, increased CO₂ alone has been linked to higher risk. Understanding the mechanisms behind weed success in new areas is crucial. For example, C₄ weeds like *Panicum dichotomiflorum* and *Datura stramonium* are expected to spread northward or southward with climate changes (Clements and Ditommaso 2011, Weber and Gut, 2005). Winter annuals may thrive under milder winters, while thermophilic summer annuals may extend their range into cooler regions (Hanzlik and Gerowitt 2012).

Conclusion

The review highlights the multifaceted nature of crop-weed interactions in the context of changing climate conditions. Elevated CO₂ tends to benefit C₃ crops by improving their growth and competitive ability against C₄ weeds. However, this advantage is challenged by increased temperatures, which favor C₄ weeds due to their superior heat tolerance and growth characteristics. The combined effects of elevated CO₂ and temperature can exacerbate weed competition, potentially undermining the benefits of CO₂ enrichment for crops. Drought conditions further intensify these interactions, with C₄ weeds often outperforming C₃ weeds under water stress. As climate change continues to impact agricultural systems, it is crucial to develop adaptive management strategies that account for these complex interactions. Future research should focus on understanding the combined effects of CO₂, temperature, and drought on crop-weed dynamics to inform effective weed management practices and safeguard crop yields in a changing climate. Future strategies must focus on developing climate-resilient crops, optimizing weed control methods, and adjusting agricultural practices to mitigate the adverse effects of these environmental changes. Continued research and adaptation will be essential to ensure sustainable crop production in an evolving climate.

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