Research, Society and Development, v. 10, n. 8, e16710817060, 2021
(CC BY 4.0) | ISSN 2525-3409 | DOI: http://dx.doi.org/10.33448/rsd-v10i8.17060

Drought and climate change impacts on plant metabolism: A review

Impactos da seca e das mudanças climáticas no metabolismo das plantas: Uma revisão

Impactos de la sequía y el cambio climático en el metabolismo de las plantas: Una revisión

Received: 06/10/2021 | Reviewed: 06/22/2021 | Accept: 06/23/2021 | Published: 07/10/2021

Juracy Barroso Neto
ORCID: https://orcid.org/0000-0002-0424-8447
Universidade Federal Rural de Pernambuco, Brazil
E-mail: jnetobarroso@gmail.com
José Raliuson Inácio Silva
ORCID: https://orcid.org/0000-0003-0483-0514
Universidade Federal Rural de Pernambuco, Brazil
E-mail: raliuson.agro@gmail.com
Cinara Wanderléa Felix Bezerra
ORCID: https://orcid.org/0000-0002-4375-8730
Universidade Federal Rural de Pernambuco, Brazil
E-mail: cinarawfb@gmail.com
Thialla Larangeira Amorim
ORCID: https://orcid.org/0000-0001-7738-6448
Universidade Federal Rural de Pernambuco, Brazil
E-mail: thialla.lamorim@gmail.com
Pedro José Hermínio
ORCID: https://orcid.org/0000-0003-2408-6278
Universidade Federal Rural de Pernambuco, Brazl
E-mail: pedro9281@gmail.com
Renilson Pessoa Morato
ORCID: https://orcid.org/0000-0002-7063-2420
Universidade Federal Rural de Pernambuco, Brazil
E-mail: renilsonpessoa@gmail.com
Marcela Maria Albuquerque-Silva
ORCID: https://orcid.org/0000-0002-4056-5458
Universidade Federal Rural de Pernambuco, Brazil
E-mail: marcelaalbuquerque.efl@gmail.com
Vicente José Laamon Pinto Simões
ORCID: https://orcid.org/0000-0002-0448-2698
Universidade Federal Rural de Pernambuco, Brazil
E-mail: laamoneng.agro@gmail.com

Abstract

Drought and predicted changes in climate, such as increased atmospheric CO_2 concentration and high temperature, may affect the growth and productivity of crop plants and generate varying responses, including morphological, physiological, biochemical and molecular changes. Water deficit negatively affects photosynthesis, while increasing CO_2 can benefit plants and attenuate photo-oxidative damage, especially in C3 metabolism species. However, the excess heat associated with this increase can affect photosynthetic efficiency differently, depending on the species and/or variety studied. In addition, the responses to the combination of these factors are poorly understood and cannot be extracted directly from the effects of each of these agents applied in isolation. This review sought to address the isolated and combined effects of water deficit and climate change on agricultural production, reporting how plant metabolism is affected by rising temperatures and high CO_2 concentration. This understanding is important to monitor the behavior of plants in the face of future climatic scenarios in order to develop strategies that can confer resistance to plants and ensure food security for agricultural production.

Keywords: Climate change; Crop production; Drought; Plant metabolism.

Resumo

A seca e as mudanças previstas no clima, como aumento da concentração de CO_2 atmosférico e a elevada temperatura, poderão afetar o crescimento e a produtividade das plantas agrícolas e gerar respostas variadas, incluindo mudanças morfológicas, fisiológicas, bioquímicas e moleculares. O déficit hídrico afeta negativamente a fotossíntese, enquanto o aumento do CO_2 pode beneficiar as plantas e atenuar o dano fotooxidativo, especialmente em espécies do metabolismo C3. No entanto, o excesso de calor associado a este aumento pode afetar diferentemente a eficiência fotossintética, dependendo da espécie e/ou variedade estudada. Além disso, as respostas à combinação desses fatores são mal compreendidas e não podem ser extraídas diretamente dos efeitos de cada um desses agentes aplicados isoladamente.

Esta revisão procurou abordar os efeitos isolados e combinados do déficit hídrico e das mudanças climáticas na produção agrícola, relatando como o metabolismo das plantas é afetado pelo aumento da temperatura e elevada concentração de CO_2. Esse entendimento é importante para monitorar o comportamento das plantas frente aos cenários climáticos futuros e para desenvolver estratégias que possam conferir tolerância às plantas e garantir a segurança alimentar para a produção agrícola.
Palavras-chave: Metabolismo vegetal; Mudanças climáticas; Produção agrícola; Seca.

Resumen

La sequía y los cambios climáticos previstos, como el aumento de la concentración de CO_2 atmosférico y las altas temperaturas, pueden afectar el crecimiento y la productividad de las plantas agrícolas y generar respuestas variadas, incluidos cambios morfológicos, fisiológicos, bioquímicos y moleculares. El déficit de agua afecta negativamente a la fotosíntesis, mientras que el aumento de CO_2 puede beneficiar a las plantas y atenuar el daño fotooxidativo, especialmente en especies de metabolismo C3. Sin embargo, el exceso de calor asociado con este aumento puede afectar la eficiencia fotosintética de manera diferente según la especie y/o variedad estudiada. Además, las respuestas a la combinación de estos factores son poco conocidas y no pueden extraerse directamente de los efectos de cada uno de estos agentes aplicados de forma aislada. Esta revisión buscó abordar los efectos aislados y combinados del déficit de agua y el cambio climático en la producción agrícola, informando cómo el metabolismo de las plantas se ve afectado por el aumento de las temperaturas y la alta concentración de CO_2. Esta comprensión es importante para monitorear el comportamiento de las plantas en escenarios climáticos futuros y para desarrollar estrategias que puedan proporcionar resistencia a las plantas y garantizar la seguridad alimentaria para la producción agrícola.
Palabras clave: Cambio climático; Metabolismo vegetal; Producción agrícola; Sequía.

1. Introduction

Water constraints caused by changing weather conditions, especially rainfall, tend to impact crop production in many areas, affecting food security in vulnerable environments such as arid and semi-arid regions, creating a level of uncertainty for agricultural systems (Daryanto, Wang & Jacinthe, 2017). The challenge of drought is a global reality affecting agriculture in both developed and developing countries and is expected to worsen if climate change persists (Elliott, et al., 2017).

The precipitation pattern has been changing, indicating a tendency to increase the rainfall intensity, but a decrease in its frequency, which plays a major role in determining the spatial patterns and variations of the globe (Chen & Dai, 2017). Parallel to this, global warming is also a strong contributor to drought intensifies in the subtropics (Hansen & Sato, 2016), this is directly related to an increase in surface warming and consequent real crop evapotranspiration, being the heat responsible for the increasing occurrence of drought, establishing it faster and more intensely (Trenberth, et al., 2013).

A study of national grain production losses worldwide, based on extreme weather disasters reported during 1964-2007, found that drought resulted in a reduction of approximately 10.1% of all production, and that this damage is mainly associated with a decrease in harvested area and crop yields of 5.1% and 4.1% respectively (Lesk, Rowhani & Ramankutty, 2016). Another estimate ensures that in China, average drought-related grain loss reaches nearly 39.2 billion kilograms per year (Leng, Tang & Rexburg, 2015).

Another concern is the increasing concentration of CO_2 observed in the atmosphere in the last 150 years, which, although it has been accompanied by greater CO_2 assimilation and storage in terrestrial ecosystems, there is evidence that this increase causes high temperatures and intensifies the stress caused by drought (Ainsworth, et al., 2020). This could limit the ability of future terrestrial ecosystems to protect themselves from atmospheric emissions (Stuart Chapin & Díaz, 2020).

Based on this, different sectors, including agriculture, will be in the process of adapting to address global change (Ludwig & Asseng, 2010), being the understanding plant metabolism an important tool for breeding programs, a technological alternative to produce varieties that adapt well under these restrictive growing conditions (Langridge & Reynolds, 2015). Therefore, studies on multifactorial interactions, which simulate the natural conditions under which plants are imposed, become more important than isolated analyzes, as they reach strategies to subsidize the development of increasingly resistant cultivars and minimize the impact of these and other conditions in the future.

2. Methodology

This qualitative study is a literature review, that has the objective to gather information on the effects of climate change, especially drought, increased temperature, and increased carbon dioxide in the photosynthetic metabolism of plants. This understanding is important to help plant improvement programs, in the search for technologies and varieties that are tolerant to the conditions foreseen for the coming years. For this, we carry out vast research in databases, using articles published in national and international scientific journals, covering data from research institutes, as well as master's dissertations, books, and technical press releases.

3. Results and Discussion

Impacts of drought on crop production

Metabolic, molecular disorders and growth restrictions

Water stress due to deficit can limit plant germination and development (Vibhuti, et al., 2015) and among the various consequences of drought on plant development, changes in growth, dry matter and yield are commonly reported (Jaleel, et al., 2009; Lipiec, et al., 2013), being the tolerance mainly dependent on the specie (Maréchaux, et al., 2015). These changes can be explained by the malfunctioning or inhibition of the vital processes of plants under stress that require water, such as metabolic functions, ion and nutrient transport, cell development and solute translocation (Zargar, et al., 2017).

Analysis of plant performance patterns under water stress is important mainly because impacts are related to both endogenous factors such as size and stomatal density, root size or plant height, as well as environmental conditions such as temperature of air and soil, moisture, and photosynthetically active radiation (PAR) (Bollig & Feller, 2014). In water deficit conditions there is induction of stomatal closure and consequent reduction of stomatal conductance, affecting the gas exchange process by restricting the influx of atmospheric CO_2 into the carboxylation sites in the leaf mesophyll (Andrianasolo, et al., 2016; Lawlor & Cornic, 2002). As a result, the net CO_2 assimilation decreases and may result in a significant increase in the $NADPH/NADP^+$ ratio in chloroplasts as a result of reduced Calvin cycle activity and photosynthetic restriction (Foyer & Noctor, 2000).

Many plant species naturally accumulate some substances when exposed to different abiotic stresses, such as water deficit. Osmotic adjustment and accumulation of compatible solutes are directly related to the plant's role in adapting to dehydration, mainly by maintaining turgor and protecting specific cellular functions (Blum, 2017). These compounds are known to play an adaptive role in osmotic mediation and protection of subcellular structures when the plant is under stress (Vibhuti, et al., 2015).

In addition to hormonal signaling and anatomical adaptations at the cellular level caused by water stress, the accumulation of these low molecular weight compounds (e.g. proline and gibberellins) (Lipiec, et al., 2013), as well as specifically increasing carotenoids (Jaleel, et al., 2009) are important for stress tolerance. Blum (2017) states that the relationship of osmotic adjustment to produce under stress is mediated by a cell turgor support or higher stomatal conductance, confirming that within some crops, such as wheat, corn, sorghum and sunflower, adjustment is associated with higher root growth and consequent improvement in soil water uptake.

At the roots, plants also manifest numerous adaptive changes in response to dehydration. Decreased root hydraulic conductivity is induced, reducing water flow to the plant while preventing loss of water from the plant to dry soil (Lipiec, et al., 2013). However, time to stress exposure can also influence the type of response. In the short term drought promotes higher root growth as a strategy to improve water uptake (Comas, et al., 2013), having this opposite effect with prolonged exposure, which results in shrinkage and anatomical deformations of the root, disrupting the defense mechanisms and leading to a reduction in yield or even death (Zargar, et al., 2017).

Changes in photorespiratory activity

In dry conditions the photorespiratory activity is intensified, which occurs mainly in species of C3 metabolism (Foyer, et al., 2009). In these species, the photorespiratory activity may contribute to dissipate the excess of reducing power and energy from the photochemical phase of photosynthesis (Embiale, et al., 2016; Takahashi & Badger, 2010). Photorespiratory activity is present in both C4 and C3 species, being most intense in the latter, and may be increased in both species by abiotic stresses such as elevated temperatures, water deficit and excess light (Foyer & Noctor, 2003; Rivas, et al., 2016; Takahashi & Badger, 2010; Zelitch, et al., 2009).

In theory, the most accepted metabolic function performed by photorespiration is the dissipation of excess reducing power, which, although decreasing the quantum yield of photosynthesis can be considered physiologically favorable under water stress conditions (Foyer, et al., 2012). This energy dissipation through photorespiration can prevent damage such as photoinhibition due to excess light by allowing the metabolism to continue using electron chain products (Takahashi, Bauwe & Badger, 2007; Wingler, et al., 2000).

The dissipation of excess energy through increased photorespiration occurs associated with the production of hydrogen peroxide in peroxisome through the action of glycolate oxidase (GO) enzyme (Foyer, et al., 2009). GO is a photorespiratory enzyme that catalyzes the oxidation of glycolate in peroxisome, producing during this reaction equimolar amounts of glyoxylate and hydrogen peroxide (H_2O_2) (Xu, et al., 2009), being dependent on glycolate supply through oxygenation of 1,5-bisphosphate (RuBP) ribulose in the chloroplast (South, et al., 2019).

In photosynthetic cells peroxisomes are considered the main H_2O_2 producing sites, followed by chloroplasts and mitochondria, other potentially H_2O_2 producing organelles as byproducts of photosynthetic and respiratory metabolism, respectively (Foyer & Noctor, 2003). Therefore, GO activity is favored by conditions that limit the diffusion of CO_2 from the outside of the leaf to photosynthetic cells, such as stomatal closure caused by water stress (Noctor & Mhamdi, 2017).

However, this photosynthetic repair process causes losses for proper carbon assimilation through Rubisco carboxylation. About 25% is not recovered (Hodges, et al., 2016). Therefore, some recent studies use various strategies to reduce the costs of photorespiration. Chamber and greenhouse plants with altered photorespiratory pathways within the chloroplast showed promising results, including increased photosynthetic rates, plant size, and yield, as reported in *Camelina sativa* (Dalal, et al., 2015). South et al. (2019), for example, they have built metabolic pathways in transgenic tobacco plants that are able to more efficiently recapture the unproductive byproducts of photosynthesis with less lost energy. In field trials, these transgenic tobacco plants were ~ 40% more productive than wild type tobacco plants.

Impact of temperature rise

Temperature fluctuations are challenges facing agricultural environments over time, and concern crop production in the coming years (IPCC, 2013). Temperature, directly influenced by the increase in greenhouse gases, has changed atypically over the past two decades, and is warming up to almost 0.2 °C per decade, which is a 50 times faster rate than the natural glacial-interglacial cycle (Nobre, et al., 2012). According to the Intergovernmental Panel on Climate Change report (IPCC, 2007) the likely range of temperature increase is between 1.8 °C and 4.2 °C by the end of the century and warming appears unambiguous. Given this scenario, there is the following question: can climate changes allow for acclimatization and adaptation of species, as these changes will occur gradually? Some say that in many cases the adaptation of plants is unlikely to match the pace or magnitude of predicted climate change (Jump & Penuelas, 2005), and this can have considerable impacts on crop yield.

Photosynthesis is light dependent and is modulated by leaf temperature (Greer, 2015) and other environmental conditions, and it is important to understand how variations in climate affect this process (Bagley, et al., 2015). Photorespiratory activity is present in species with higher intensity in C3 metabolism, and may be intensified by abiotic stresses such as elevated temperatures, water deficit and excess light. (Foyer & Noctor, 2003; Rivas, et al., 2016; Takahashi & Badger, 2010; Zelitch, et al., 2009). The solubility of CO_2 in water increases with lower heat intensity compared to the solubility of O_2 under the same conditions. Thus, raising the temperature may reduce the CO_2/O_2 ratio in the cell and may lead to lower CO_2 availability of the Rubisco carboxylation site, which favors Rubisco oxygenase activity and stimulates photorespiration (Foyer & Noctor, 2000). In addition, excess heat can affect Rubisco's kinetic properties, stimulating oxygenase activity to the detriment of carboxylase activity (Ehleringer & Helliker, 1997).

Studies show that under high temperature plants can have their photosynthetic activity compromised (Dusenge, et al., 2019), or even modulate transpiration parameters and stomatal conductance in the hope of keeping the leaves cool (Barroso Neto, et al., 2018). Keeping the leaf temperature at or slightly below the air temperature proves the cooling capacity of the various cultivars or species, via transpiration, in order to keep the plant protected from very high thermal bands (Oliveira, Fernandes & Rodrigues, 2005).

Moreover, the high temperature can cause even greater damage, directly related to the photosynthetic apparatus (Wise, et al., 2004). This can lead to changes in the thylakoid membrane and alter the physical-chemical properties and, also, the functional organization of these cellular structures (Alberto & Borges, 2009). As a consequence, there may be a blocking of the reaction centers of the PSII and, then, the dissociation of the protein-pigment complex of the central nucleus of the PSII light-collecting apparatus (Armond, Schreiber & Björkman, 1978).

From germination to reproduction, thermal stress can harm all growth stages of vegetables, especially in the main crops, causing negative impacts on agricultural production (Hussain, et al., 2019). In wheat, for example, this stress is linked to the reproductive and grain filling stages (Abdelrahman et al. 2020), and an increase of 1 °C can cause a 4-6% reduction in the average global production (Asseng, et al., 2014). Other processes and organs that are quite affected and vulnerable to temperature rise are those related to seeds, including regulation of the development of fertilization or abnormalities in flowering (Pareek, et al., 2020)

The resilience of cultures in this scenario depends on genetic mechanisms, which play an important role in responding to rising temperatures (Janni, et al., 2020). Genotypes more tolerant to high temperatures showed a significant increase in sugars, alcohols and phosphate when performed an analysis of the metabolite profile of wheat genotypes (Impa, et al., 2019). The main effects caused by the increase in temperature in plants are related to the alteration of photosynthetic processes, phenology and biomass partition; reduced growth, productivity and quality; inhibition of germination and photosynthesis; among others, such as improper development, oxidative stress and water loss (Chiu, et al., 2016; Eyshi Rezaei, et al., 2015; Hasanuzzaman, et al., 2012, 2013a, 2013b; Mathur, et al., 2014; Xiong, et al., 2017).

Impacts of increased CO_2 concentration

Interaction with climate change and agriculture

The high concentration of atmospheric carbon dioxide (CO_2) is a major component of climate change (IPCC, 2018), increasing from pre-industrial level from 280 μmol mol^{-1} in 1750 to 400 μmol mol^{-1} today, and with forecasts for 900 μmol mol^{-1} in the late 21st century (IPCC, 2007; Xu, et al., 2016). Although disputed, this prediction has raised major concerns about plant behavior, mainly because this increase in CO_2 may come combined and/or cause other climate changes, such a global warming and reduced rainfall.

There is a positive interaction between climate change and the increase in CO_2 concentration, which can significantly dampen the decrease in global gross domestic product (GDP) by the end of the 21st century (Pan, et al., 2018). Combining climate change with increasing CO_2 concentration would increase global water use efficiency (WUE), suggesting that this increase could mitigate climate change-induced WUE decline, especially in high latitude regions (Weiwei, et al., 2018). However, these answers will be more reliable when we get more detailed studies on evapotranspiration in an environment with twice the CO_2 concentration we have today.

Potential changes in growth and development

Increasing atmospheric CO_2 concentration will likely affect plant development and physiology (Broughton, et al., 2017), being generally associated with an increase in vegetative growth and total leaf area, which may consequently increase plant water use (Lewis, et al., 2013). This response to growth is mainly determined by increasing the photosynthesis rate per unit area of leaf and decreasing specific leaf area (Poorter & Navas, 2003).

Despite the acclimatization of photosynthetic capacity, as measured by the maximum carboxylation and electron transport rates, recent studies with high ambient CO_2 concentrations on photosynthetic responses in C3 plants show that photosynthetic carbon absorption is enhanced (Leakey, et al., 2009). In addition, carbon dioxide enrichment often reduces leaf transpiration, which can increase soil water content, improving plant development in water-constrained environments, and increasing community productivity (Fay, et al., 2015).

Two are the reactions commonly related to the effects of high CO_2 on plants: one linked to stomatal effects and the other effects metabolic. In addition to providing plus carbon and causing the partial closure of the stomata, the high CO_2 can also induce metabolic changes involving levels of reactive oxygen species, possibly resulting in an increased protective capacity of the antioxidant defense system (AbdElgawad, et al., 2016). A defense system study, analyzed in *Arabidopsis thaliana*, revealed that high CO_2 activates some multiple defense pathways, leading to greater resistance to biotic and abiotic stresses, but when analyzing specific mutant genes, the evidence that activation of these plant defense pathways to this condition were caused by stomatal closure, being partly related to the metabolic effects involving redox signaling (Mhamdi & Noctor, 2016).

Although the explanations of the crucial biochemical pathways that regulate this signaling to high CO_2 have not been completed, the increase in plant growth is often reported. In your experiment with wheat, O'leary et al. (2015) observed a significant increase in biomass, leaf area index and photosynthetic area index under high CO_2, and this increased vegetative growth resulted in a 26% increase in grain yield. Although most responses reveal increased growth related, this effect is also dependent on the species and its possible tolerance to some stresses. For example, the effects of drought on three maize genotypes were also attenuated by CO_2 enrichment, but reduced growth was observed in a highly drought-resistant hybrid, the first effect being related to improved stress tolerance, reducing loss, improving soil moisture content and increasing the potential of water in the leaves (Yang, et al., 2014).

Gas exchange and stomatal functions

The large variability in plant responses to high CO_2 concentrations, especially among species, gives different strategies for controlling gas exchange, and it is not yet clear whether there is a coordinated action between the physiology and morphology of these plants. These responses are mainly dependent on species, plant age, type of experiment, exposure time, nutritional availability and other factors (Ainsworth & Long, 2005; Nowak, Ellsworth & Smith, 2004).

Many experiments have reported an increase in photosynthesis, evidenced mainly in C3 plants, attributed to a higher carbon availability at the carboxylation sites, reducing the photorespiration process (Gamage, et al., 2018; Bowes, 1991) and increasing biomass (O'leary, et al., 2015). In addition, a decrease in stomatal conductance (g_s) is usually observed when plants are subjected to an increase in high CO_2 concentration in the growing environment (Flexas, et al., 2007; Gao, et al., 2015; Uddin, et al., 2018).

An atypical response to these findings was that found by Lahive, Hadley & Daymond (2017), when they tested this condition in cocoa, obtaining significantly higher stomatal conductance in plants at high CO_2, which could be explained by the reflection of the environment in which the crop is submitted (moist). However, contrary to this hypothesis, and despite being a rare response, a higher stomatal conductance associated with CO_2 increase may also occur in species adapted to hot and low humidity conditions (Purcell, et al., 2018).

Although not interfering with carbon absorption processes, the stomatal partial closure under high CO_2 can alter the water balance of the plants. When stomatal conductance decreases, there is automatically less perspiration, and consequently the greater efficiency in water use (Easlon, et al., 2015). This fact is explained by the lower water loss due to partial stomatal closure under higher CO_2 concentration. This stomatal control is accomplished by regulating stomatal opening through changes in guard cell turgor and by changes in stomatal density and leaf area during development (Haworth, Elliott-Kingston & Mcelwain, 2013).

The increase in temperature due to the concentration of greenhouse gases in the environment should also influence gas exchange in plants, since the solubility of CO_2 in water increases with less intensity in the heat compared to the solubility of O_2 under the same conditions. Thus, raising the temperature may reduce the CO_2/O_2 ratio in the cell and may lead to lower CO_2 availability at the Rubisco carboxylation site, which favors Rubisco oxygenase activity and stimulates photorespiration (Foyer & Noctor, 2000). In addition, excess heat can affect Rubisco's kinetic properties, stimulating oxygenase activity to the detriment of carboxylase activity (Ehleringer, Cerling & Helliker, 1997).

Accordingly, while the increase in ambient carbon dioxide facilitates the water issues of stomatal regulation (Barroso Neto, 2019), and increasing photosynthetic efficiency (Ainsworth & Long, 2005), in contrast, the high temperatures stimulate the photorespiratory cycle reactions in plants (Betti, et al., 2016; Walker, et al., 2016). This heterogeneity of plant responses between high CO_2 and its consequences on the environment is a pertinent question that has been heavily studied, showing that other climate variables, such as the projected increase in global temperature, may nullify the possible benefits by itself of the high concentration of CO_2 (Eller, et al., 2014; Wang, et al., 2016).

A recent question is whether increasing CO_2 concentrations will influence plant sensitivity to water stress, and whether increased growth may mean less water requirement under these conditions through better water use efficiency. As a result of decreased transpiration and increases in net photosynthesis, plants have been shown to maintain higher water use efficiency when grown under high CO_2 than when grown under ambient conditions (Tyree & Alexander, 1993), considered the main effect of CO_2 enrichment on growth enhancement (Morgan, et al., 2001).

High plant growth by increasing CO_2, however, may be limited by other aspects, such as available water, making the presence of a positive effect of CO_2 increment dependent on this factor (Reich, Hobbie & Lee, 2014). Lewis et al. (2013) suggest in their results with eucalyptus that gas was the main factor regulating the effects of increasing atmospheric CO_2 on photosynthetic responses to short term drought. Among the favorable effects, an increase in net CO_2 assimilation rates has been reported, both in the absence (Aspinwall, et al., 2018) of as in the presence of abiotic stresses, such as water deficit (Paudel, et al., 2018). Oliveira et al. (2013) on your results showed that CO_2 increase favored the maintenance of tissue turgor, contributing to the maintenance of high rates of CO_2 assimilation in a native Cerrado plant under water stress.

On the other hand, exposure time can influence plant responses to high CO_2. The increase in photosynthesis in the early stages of exposure to high CO_2 concentration may not be sustained for a longer period (Gamage, et al., 2018). This phenomenon is known as “photosynthetic acclimatization” and has been widely reported in the literature and has been attributed to several mechanisms such as the decline in nitrogen supply to leaves (Seneweera, et al., 2011), accumulation of nonstructural carbohydrates, or by inhibition by feedback and physical damage to chloroplast (Delucia, Sasek & Strain, 1985).

Photorespiratory modulation in the absence and under drought

As has been said, photorespiration, increased by water stress, is an important source of H_2O_2, and is certainly affected by the change in CO_2 concentration (Zinta, et al., 2014). It is then believed that high CO_2 can mitigate the impact of stress by decreasing photorespiration, resulting in lower hydrogen peroxide production (Abdelgawad, et al., 2016; Foyer, et al., 2009). The hypotheses supporting these claims are that high CO_2 increases the supply of chloroplast electron acceptors (Mhamdi & Noctor, 2016), which can ultimately limit electron leakage to oxygen, ensuring $NADP^+$ regeneration (Foyer, et al., 2012), and avoiding the formation of reactive oxygen species in exacerbated amounts, thus avoiding the consequent oxidative stress.

This pathway, however, is not the only hydrogen peroxide producer, the which may not be a very confident direct relationship. In addition, photorespiration appears to be a part of the stress response to prevent the formation of reactive oxygen species (ROS), despite being a source of production in peroxisomes. The importance of photorespiratory reactions in keeping reactive oxygen species levels low and therefore protect against oxidative damage under a variety of stress conditions (Voss, et al., 2013). Another important point is that photorespiration also provides metabolites for other processes of plant metabolism, for example glycine for glutathione synthesis, which is also involved in protecting against stress (Wingler, et al., 2000).

This still persistent impasse over the real role of photorespiration is due to the fact that this process involves metabolic communication between various subcellular compartments (Noctor & Mhamdi, 2017). In addition, some recent studies have already used in research that seeks alternative pathways for this process in order to increase photosynthesis in plants. Important findings have been made using genetically modified models deficient in various photorespiration enzymes, such as those found in *Arabidopsis thaliana*, and also for other crops such as rice (Noctor & Mhamdi, 2017).

4. Conclusion

Plant production will be directly influenced by the lack of water and climate change, such as the increase in CO_2 concentration and temperature rise, expected by the end of the century. Although there is evidence that increased CO_2 can benefit and even mitigate the detrimental effects of drought, the rise in temperature caused by this increase in greenhouse gases tends to nullify this improvement. Alternatives that alleviate this tension between environmental phenomena and plant growth are needed to ensure world food security. This will only be possible, with the help of science, which will understand plant behavior in order to modify management or improve the mechanisms and alter genes that confer resistance to plants against future abiotic stresses.

Acknowledgments

The Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) and Coordenação de Aperfeiçoamento de Pessoal Docente (CAPES), Brazil, by fellowship.

References

Abdelrahman, M., Burritt, D. J., Gupta, A., Tsujimoto, H., & Tran, L. S. P. (2020). Heat stress effects on source–sink relationships and metabolome dynamics in wheat. *Journal of Experimental Botany*, 71, 543–554. 10.1093/jxb/erz296.

AbdElgawad, H., Zinta, G., Beemster, G. T. S., Janssens, I. A., & Asard, H. (2016.) Future Climate CO_2 Levels Mitigate Stress Impact on Plants: Increased Defense or Decreased Challenge? *Frontiers in Plant Science*, 7, 556. 10.3389/fpls.2016.00556.

Ainsworth, E. A., Lemonnier, P., & Wedow, J. M. (2020). The influence of rising tropospheric carbon dioxide and ozone on plant productivity. *Plant Biology*, 22, 5–11. 10.1111/plb.12973.

Ainsworth, E. A., & Long, S. P. (2005). What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist*, 165 (2), 351-371. 10.1111/j.1469-8137.2004.01224.x.

Alberto, S., & Borges, B. (2009). Fotoinibição da Fotossíntese. *Revista Brasileira de Biociências*, 7 (4), 463–472.

Andrianasolo, F. N., Casadebaig, P., Langlade, N., Debaeke, P., & Maury, P. (2016). Effects of plant growth stage and leaf aging on the response of transpiration and photosynthesis to water deficit in sunflower. *Functional Plant Biology*, 43 (8), 797–805. 10.1071/FP15235.

Armond, P. A., Schreiber, U., & Björkman, O. (1978). Photosynthetic Acclimation to Temperature in the Desert Shrub, *Larrea divaricata*: II. Light-harvesting Efficiency and Electron Transport. *Plant Physiological*, 61 (3), 411–415. 10.1104/PP.61.3.411.

Aspinwall, M. J., Blackman, C. J., de Dios, V. R., Busch, F. A., Rymer, P. D., Loik, M. E., Drake, J. E., Pfautsch, S., Smith, R. A., Tjoelker, M. G., & Tissue, D. T. (2018). Photosynthesis and carbon allocation are both important predictors of genotype productivity responses to elevated CO_2 in *Eucalyptus camaldulensis*. *Tree Physiological*, 38 (9), 1286–1301. 10.1093/treephys/tpy045.

Asseng, S., Ewert, F., Martre, P., Rötter, R. P., Lobell, D. B., Cammarano, D., & White, J. W. (2015). Rising temperatures reduce global wheat production. *Natural Climate Change*, 5, 143–147. 10.1038/nclimate2470.

Bagley, J., Rosenthal, D. M., Ruiz-Vera, U. M., Siebers, M. H., Kumar, P., Ort, D. R., & Bernacchi, C. J. (2015). The influence of photosynthetic acclimation to rising CO_2 and warmer temperatures on leaf and canopy photosynthesis models. *Global Biogeochemistry Cycles*, 29, 194–206. 10.1002/2014GB004848.

Barroso Neto, J. (2019). *Efeito do aumento da concentração ambiente de CO_2 na eficiência fotossintética e proteção oxidativa em plantas de arroz submetidas ao déficit hídrico*. Dissertação de Mestrado, Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada. Serra Talhada, Pernambuco, Brasil. 99p.

Barroso Neto, J., Hermínio, P. J., Amorim, T. L., Morato, R. P., & Ferreira-Silva, S. L. (2018). Influência da temperatura nas respostas fotossintéticas de ora-pró-nobis (*Pereskia aculeata*) crescidas em ambiente semiárido. *Anais III SIMPROVS – Simpósio Nacional de Estudos para Produção Vegetal no Semiárido, Campina Grande, Paraíba, Brasil*. (1), ISSN 978-85-7946-272-6.

Betti, M., Bauwe, H., Busch, F. A., Fernie, A. R., Keech, O., Levey, M., Ort, D. R., Parry, M. A. J., Sage, R., Timm, S., Walker, B., & Weber, A. P. M. (2016). Manipulating photorespiration to increase plant productivity: Recent advances and perspectives for crop improvement. *Journal of Experimental Botany*, 67 (10), 2977-2988. 10.1093/jxb/erw076.

Blum, A. (2017). Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant, Cell & Environmental*, 40(1), 4–10. 10.1111/pce.12800.

Bollig, C., & Feller, U. (2014). Impacts of drought stress on water relations and carbon assimilation in grassland species at different altitudes. *Agriciculture, Ecosystems & Environmental*, 188, 212–220. 10.1016/j.agee.2014.02.034.

Bowes, G. (1991). Growth at elevated CO_2 - Photosynthetic responses mediated through Rubisco. *Plant Cell and Environment*, 14, 795–806. 10.1111/j.1365-3040.1991.tb01443.x

Broughton, K. J., Smith, R. A., Duursma, R. A., Tan, D. K. Y., Payton, P., Bange, M. P., & Tissue, D. T. (2017). Warming alters the positive impact of elevated CO_2 concentration on cotton growth and physiology during soil water deficit. *Functional Plant Biology*, 44 (2), 267-278. 10.1071/FP16189.

Chapin, S. F., & Díaz, S. (2020). Interactions between changing climate and biodiversity: Shaping humanity's future. *Proceedings of the National Academy of Sciences.* 117, 6295–6296. 10.1073/pnas.2001686117.

Chen, D., & Dai, A. (2017). Dependence of estimated precipitation frequency and intensity on data resolution. *Climate Dynamics*, 50, 3625-3647. 10.1007/s00382-017-3830-7.

Chiu, R. S., Pan, S., Zhao, R., & Gazzarrini, S. (2016). ABA-dependent inhibition of the ubiquitin proteasome system during germination at high temperature in *Arabidopsis*. *The Plant Journal*, 88, 749–761. 10.1111/tpj.13293.

Comas, L. H., Becker, S. R., Cruz, V. M. V., Byrne, P. F., & Dierig, D. A. (2013). Root traits contributing to plant productivity under drought. *Frontier Plant Science*, 4, 442. 10.3389/fpls.2013.00442.

Dalal, J., Lopez, H., Vasani, N. B., Hu, Z., Swift, J. E., Yalamanchili, R., Dvora, M., Lin, X., Xie, D., Qu, R., & Sederoff, H. W. (2015). A photorespiratory bypass increases plant growth and seed yield in biofuel crop *Camelina sativa*. *Biotechnology Biofuels*, 8, 175. 10.1186/s13068-015-0357-1.

Daryanto, S., Wang, L., & Jacinthe, P. A. (2017). Global synthesis of drought effects on cereal, legume, tuber and root crops production: A review. Agric. *Water Management*, 179 (1), 18–33. 10.1016/j.agwat.2016.04.022.

Delucia, E. H., Sasek, T. W., & Strain, B. R. (1985). Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research*, 7, 175–184. 10.1007/BF00037008.

Dusenge, M. E., Duarte, A. G., & Way, D. A. (2019). Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist.*, 221 (1), 32-49. 10.1111/nph.15283.

Easlon, H. M., Carlisle, E., McKay, J. K., & Bloom, A. J. (2015). Does Low Stomatal Conductance or Photosynthetic Capacity Enhance Growth at Elevated CO_2 in Arabidopsis?. *Plant Physiology*, 167, 793–799. 10.1104/pp.114.245241.

Ehleringer, J. R., Cerling, T. E., & Helliker, B. R. (1997). C-4 photosynthesis, atmospheric CO_2 and climate. *Oecologia,* 112 (3), 285–299. 10.1007/s004420050311.

Eller, F., Lambertini, C., Nguyen, L. X., & Brix, H. (2014). Increased invasive potential of non-native *Phragmites australis*: Elevated CO_2 and temperature alleviate salinity effects on photosynthesis and growth. *Global Change Biology*, 20 (2), 531–543. 10.1111/gcb.12346.

Elliott, J., Glotter, M., Ruane, A. C., Boote, K. J., Hatfield, J. L., Jones, J. W., Rosenzweig, C., Smith, L. A., & Foster, I. (2017). Characterizing agricultural impacts of recent large-scale US droughts and changing technology and management. *Agricultural Systems*., 159 (1), 275-281. 10.1016/j.agsy.2017.07.012.

Embiale, A., Hussein, M., Husen, A., Sahile, S., & Mohammed, K. (2016). Differential sensitivity of *Pisum sativum* L. cultivars to water-deficit stress: Changes in growth, water status, chlorophyll fluorescence and gas exchange attributes. *Journal of Agronomy*, 15(2), 45–57. 10.3923/ja.2016.45.57.

Eyshi-Rezaei, E., Webber, H., Gaiser, T., Naab, J., & Ewert, F. (2015). Heat stress in cereals: Mechanisms and modelling. *Europan Journal Agronomy*, 64, 98–113. 10.1016/j.eja.2014.10.003.

Fay, P. A., Newingham, B. A., Polley, H. W., Morgan, J. A., LeCain, D. R., Nowak, R. S., & Smith, S. D. (2015). Dominant plant taxa predict plant productivity responses to CO_2 enrichment across precipitation and soil gradients. *AoB Plants*, 7, 1-7. 10.1093/aobpla/plv027.

Flexas, J., Diaz-Espejo, A., Galmés, J., Kaldenhoff, R., Medrano, H., & Ribas-Carbo, M. (2007). Rapid variations of mesophyll conductance in response to changes in CO_2 concentration around leaves. *Plant, Cell Environmental*., 30, 1284–1298. 10.1111/j.1365-3040.2007.01700.x.

Foyer, C. H., Neukermans, J., Queval, G., Noctor, G., & Harbinson, J. (2012). Photosynthetic control of electron transport and the regulation of gene expression. *Journal of Experimental Botanic,* 63 (4), 1637–1661. 10.1093/jxb/ers013.

Foyer, C. H., Bloom, A. J., Queval, G., & Noctor, G. (2009). Photorespiratory Metabolism: Genes, Mutants, Energetics, and Redox Signaling. *Annuals Review of Plant Biology*, 60, 455–484. 10.1146/annurev.arplant.043008.091948.

Foyer, C. H., & Noctor, G. (2003). Redox sensing and signalling associated with reactive oxygen in chloroplasts, peroxisomes and mitochondria. *Physiology Plant*, 119, 355–364. 10.1034/j.1399-3054.2003.00223.x.

Foyer, C.H., & Noctor, G. (2000). Oxygen processing in photosynthesis: Regulation and signalling. *New Phytologist*, 146 (3), 359-388. 10.1046/j.1469-8137.2000.00667.x.

Gamage, D., Thompson, M., Sutherland, M., Hirotsu, N., Makino, A., & Seneweera, S. (2018). New insights into the cellular mechanisms of plant growth at elevated atmospheric carbon dioxide concentrations. *Plant Cell Environmental*, 41 (6), 1233-1246. 10.1111/pce.13206.

Gao, J., Han, X., Seneweera, S., Li, P., Zong, Y. Z., Dong, Q., Lin, E. Da, & Hao, X. Y. (2015). Leaf photosynthesis and yield components of mung bean under fully open-air elevated [CO_2]. *Journal of Integrative Agriculture*, 14, 5, 977–983. 10.1016/S2095-3119(14)60941-2.

Greer, D. H. (2015). Photon flux density and temperature-dependent responses of photosynthesis and photosystem II performance of apple leaves grown in field conditions. *Functional Plant Biology*, 42, 782-791. 10.1071/FP15068.

Hansen, J., & Sato, M. (2016). Regional climate change and national responsibilities. *Environmental Research Letter*, 11 (3), 034009. 10.1088/1748-9326/11/3/034009.

Hasanuzzaman, M., Nahar, K., Alam, M. M., Roychowdhury, R., & Fujita, M., (2013a). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Scince*, 14 (5), 9643-9684. 10.3390/ijms14059643.

Hasanuzzaman, M., Nahar, K., & Fujit, M., (2013b). Extreme Temperature Responses, Oxidative Stress and Antioxidant Defense in Plants, in: Abiotic Stress - Plant Responses and Applications in Agriculture. 10.5772/54833.

Hasanuzzaman, M., Hossain, M. A., Da Silva, J. A. T., & Fujita, M., (2012). Plant response and tolerance to abiotic oxidative stress: Antioxidant defense is a key factor, in: Crop Stress and its Management: Perspectives and Strategies. *Springer Netherlands*, p. 261–315. 10.1007/978-94-007-2220-0_8.

Haworth, M., Elliott-Kingston, C., & McElwain, J. C. (2013). Co-ordination of physiological and morphological responses of stomata to elevated [CO_2] in vascular plants. *Oecologia*, 171 (1), 71–82. 10.1007/s00442-012-2406-9.

Hodges, M., Dellero, Y., Keech, O., Betti, M., Raghavendra, A. S., Sage, R., Zhu, X. G., Allen, D. K., & Weber, A. P. M. (2016). Perspectives for a better understanding of the metabolic integration of photorespiration within a complex plant primary metabolism network. *Journal of Experimental Botany,* 67 (10), 3015-3026. 10.1093/jxb/erw145.

Hussain, H. A., Men, S., Hussain, S., Chen, Y., Ali, S., Zhang, s., Zhang, K., Li, Y., Xu, Q., Liao, C., & Wang, L. (2019). Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. *Scientific Reports*, 9, 3890. 10.1038/s41598-019-40362-7.

Impa, S. M., Sunoj, V. S. J., Krassovskaya, I., Bheemanahalli, R., Obata, T., & Jagadish, S. V. K. (2018). Carbon balance and source-sink metabolic changes in winter wheat exposed to high night-time temperature. *Plant Cell Environmental*, 42 (4), 1233-1246. 10.1111/pce.13488.

IPCC. (2018). Summary for policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H-O,, et al., eds. Geneva, Switzerland: World Meteorological Organization, 32.

IPCC, (2013). Climate Change 2013: The Physical Science Basis, Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 10.1017/CBO9781107415324.

IPCC, (2007). IPCC Fourth Assessment Report (AR4). 1, 976.

Jaleel, C. A., Manivannan, P., Wahid, A., Farooq, M., Al-Juburi, H. J., Somasundaram, R., & Panneerselvam, R. (2009). Drought stress in plants: A review on morphological characteristics and pigments composition. *International Journal of Agriculture Biology*, 11 (1), 100-105. 08–305/IGC-DYT/2009/11–1–100–105.

Janni, M., Mariolina, G., Maestri, E., Marmiroli, M., Valliyodan, B., Nguyen, H. T., & Marmiroli, N. (2020). Molecular and genetic bases of heat stress response in crop plants for increased resilience and productivity. *Journal of Experimental Botany*, 71, 1-23. 10.1093/jxb/eraa034.

Jump, A. S., & Peñuelas, J. (2005). Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letter,* 8, 1010–1020. 10.1111/j.1461-0248.2005.00796.x.

Lahive, F., Hadley, P., & Daymond, A. J. (2017). The impact of elevated CO_2 and water deficit stress on growth and photosynthesis of juvenile cacao (*Theobroma cacao* L.). *Photosynthetica*, 56 (3), 911-920. 10.1007/s11099-017-0743-y.

Langridge, P., & Reynolds, M. P. (2015). Genomic tools to assist breeding for drought tolerance. *Current Opinion in Biotechnology,* 32, 130-135. 10.1016/j.copbio.2014.11.027.

Lawlor, D. W., & Cornic, G. (2002). Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environmental*, 25, 275–294. 10.1046/j.0016-8025.2001.00814.x.

Leakey, A. D. B., Ainsworth, E. A., Bernacchi, C. J., Rogers, A., Long, S. P., & Ort, D. R. (2009). Elevated CO_2 effects on plant carbon, nitrogen, and water relations: Six important lessons from FACE. *Journal of Experimental Botany*, 60 (10), 2859–2876. 10.1093/jxb/erp096.

Leng, G., Tang, Q., & Rayburg, S. (2015). Climate change impacts on meteorological, agricultural and hydrological droughts in China. *Global. Planet Change*, 126, 23–34. 10.1016/j.gloplacha.2015.01.003.

Lesk, C., Rowhani, P., & Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature*, 529, 84–87. 10.1038/nature16467.

Lewis, J. D., Smith, R. A., Ghannoum, O., Logan, B. A., Phillips, N. G., & Tissue, D. T. (2013). Industrial-age changes in atmospheric [CO_2] and temperature differentially alter responses of faster- and slower-growing Eucalyptus seedlings to short-term drought. *Tree Physioly*, 33 (5), 475–488. 10.1093/treephys/tpt032.

Lipiec, J., Doussan, C., Nosalewicz, A., & Kondracka, K. (2013). Effect of drought and heat stresses on plant growth and yield: a review. *International Agrophysics*, 27 (4), 463–477. 10.2478/intag-2013-0017.

Ludwig, F., & Asseng, S. (2010). Potential benefits of early vigor and changes in phenology in wheat to adapt to warmer and drier climates. *Agriculture Systems* 103, 3, 127–136. 10.1016/j.agsy.2009.11.001.

Maréchaux, I., Bartlett, M. K., Sack, L., Baraloto, C., Engel, J., Joetzjer, E., & Chave, J. (2015). Drought tolerance as predicted by leaf water potential at turgor loss point varies strongly across species within an Amazonian forest. *Functional Ecology*, 29 (10), 1268–1277. 10.1111/1365-2435.12452.

Mathur, S., Agrawal, D., & Jajoo, A. (2014). Photosynthesis: Response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology*, 137, 116–126. 10.1016/j.jphotobiol.2014.01.010.

Mhamdi, A., & Noctor, G. (2016). High CO_2 Primes Plant Biotic Stress Defences through Redox-Linked Pathways. *Plant Physiology*, 172, 929–942. 10.1104/pp.16.01129.

Morgan, J. A., Lecain, D. R., Mosier, A. R., & Milchunas, D. G. (2001). Elevated CO_2 enhances water relations and productivity and affects gas exchange in C3 and C4 grasses of the Colorado shortgrass steppe. *Global Change Biology*, 7, 451–466. 10.1046/j.1365-2486.2001.00415.x.

Nobre, C. A., Reid, J., & Veiga, A. P. S. (2012). Fundamentos Científicos das Mudanças Climáticas, Inpe.

Noctor, G., & Mhamdi, A. (2017). Climate Change, CO_2, and Defense: The Metabolic, Redox, and Signaling Perspectives. *Trends Plant Science*, 22 (10), 857–870. 10.1016/j.tplants.2017.07.007.

Nowak, R. S., Ellsworth, D. S., & Smith, S. D. (2004). Functional responses of plants to elevated atmospheric CO_2 - Do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytology*, 162, 253-280. 10.1111/j.1469-8137.2004.01033.x.

O'Leary, G. J., Christy, B., Nuttall, J., Huth, N., Cammarano, D., Stöckle, C., Basso, B., Shcherbak, I., Fitzgerald, G., Luo, Q., Farre-Codina, I., Palta, J., & Asseng, S. (2015). Response of wheat growth, grain yield and water use to elevated CO_2 under a Free-Air CO_2 Enrichment (FACE) experiment and modelling in a semi-arid environment. *Global Change Biology*, 21, 2670–2686. 10.1111/gcb.12830.

Oliveira, A. D. de, Fernandes, E. J., & Rodrigues, T. J. D. (2005). Condutância estomática como indicador de estresse hídrico em feijão. *Engenharia Agrícola*, 25 (1), 86–95. 10.1590/S0100 -69162005000100010.

Oliveira, V. F., Silva, E. A., Zaidan, L. B. P., & Carvalho, M. A. M. (2013). Effects of elevated CO_2 concentration and water deficit on fructan metabolism in *Viguiera discolor* Baker. *Plant Biology*, 15, 471–482. 10.1111/j.1438-8677.2012.00654.x.

Pan, S., Chen, G., Ren, W., Dangal, S. R. S., Banger, K., Yang, J., Tao, B., & Tian, H. (2018). Responses of global terrestrial water use efficiency to climate change and rising atmospheric CO_2 concentration in the twenty-first century. *International Journal Digital Earth*, 11 (6), 558–582. 10.1080/17538947.2017.1337818.

Pareek, A., Dhankher, O. P., & Foyer, C. H. (2020). Mitigating the impact of climate change on plant productivity and ecosystem sustainability. *Journal of Experimental Botany*, 71 (9), 451-456. 10.1093/jxb/erz518.

Paudel, I., Halpern, M., Wagner, Y., Raveh, E., Yermiyahu, U., Hoch, G., & Klein, T. (2018). Elevated CO_2 compensates for drought effects in lemon saplings via stomatal downregulation, increased soil moisture, and increased wood carbon storage. *Environmental Experimental Botany*., 148, 117–127. 10.1016/j.envexpbot.2018.01.004.

Poorter, H., & Navas, M. L. (2003). Plant growth and competition at elevated CO_2: On winners, losers and functional groups. *New Phytology*, 157 (2), 175-198. 10.1046/j.1469-8137.2003.00680.x.

Purcell, C., Batke, S. P., Yiotis, C., Caballero, R., Soh, W. K., Murray, M., & McElwain, J. C. (2018). Increasing stomatal conductance in response to rising atmospheric CO_2. *Annaus Botany*, 121 (6), 1137-1149. 10.1093/aob/mcy023.

Reich, P. B., Hobbie, S. E., & Lee, T. D. (2014). Plant growth enhancement by elevated CO_2 eliminated by joint water and nitrogen limitation. *Nature Geoscience*, 7, 920–924. 10.1038/ngeo2284.

Rivas, R., Falcão, H. M., Ribeiro, R. V., Machado, E. C., Pimentel, C., & Santos, M. G. (2016). Drought tolerance in cowpea species is driven by less sensitivity of leaf gas exchange to water deficit and rapid recovery of photosynthesis after rehydration. *South African Journal Botany*, 103, 101–107. 10.1016/j.sajb.2015.08.008.

Seneweera, S., Makino, A., Hirotsu, N., Norton, R., & Suzuki, Y. (2011). New insight into photosynthetic acclimation to elevated CO_2: The role of leaf nitrogen and ribulose-1,5-bisphosphate carboxylase/oxygenase content in rice leaves. *Environmental Experimental Botany*, 71 (2), 128–136. 10.1016/j.envexpbot.2010.11.002.

South, P. F., Cavanagh, A. P., Liu, H. W., & Ort, D. R. (2019). Synthetic glycolate metabolism pathways stimulate crop growth and productivity in the field. *Science*, 363, 6422, eaat9077. 10.1126/science.aat9077.

Takahashi, S., & Badger, M.R. (2010). Photoprotection in plants: A new light on photosystem II damage. *Trends Plant Science*, 16(1), 53-60. 10.1016/j.tplants.2010.10.001.

Takahashi, S., Bauwe, H., & Badger, M. (2007). Impairment of the Photorespiratory Pathway Accelerates Photoinhibition of Photosystem II by Suppression of Repair But Not Acceleration of Damage Processes in Arabidopsis. *Plant Physiology*, 144, 487–494. 10.1104/pp.107.097253

Trenberth, K. E., Dai, A., Van der Schrier, G., Jones, P. D., Barichivich, J., Briffa, K. R., & Sheffield, J. (2013). Global warming and changes in drought. *Nature Climate Change*, 4(1), 17–22. 10.1038/nclimate2067.

Tyree, M., & Alexander, J. (1993). Plant water relations and the effects of elevated CO_2: a review and suggestions for future research. *Vegetation*, 104, 47–62. 10.1007/BF00048144.

Uddin, S., Löw, M., Parvin, S., Fitzgerald, G. J., Tausz-Posch, S., Armstrong, R., O'Leary, G., & Tausz, M. (2018). Elevated [CO_2] mitigates the effect of surface drought by stimulating root growth to access sub-soil water. *PLoS One*, 13 (6), 1-20. 10.1371/journal.pone.0198928.

Vibhuti, S. C., Bargali, K., & Bargali, S. S. (2015). Seed germination and seedling growth parameters of rice (*Oryza sativa*) varieties as affected by salt and water stress. *Indian Journal Agriculture Science*, 85 (1), 102–108.

Voss, I., Sunil, B., Scheibe, R., & Raghavendra, A. S. (2013). Emerging concept for the role of photorespiration as an important part of abiotic stress response. *Plant Biology*, 15 (4), 713-722. 10.1111/j.1438-8677.2012.00710.x.

Walker, B.J., VanLoocke, A., Bernacchi, C. J., & Ort, D. R. (2016). The Costs of Photorespiration to Food Production Now and in the Future. *Annuals Review Plant Biology*, 67(1), 107–129. 10.1146/annurev-arplant-043015-111709.

Wang, D. R., Bunce, J. A., Tomecek, M. B., Gealy, D., McClung, A., McCouch, S. R., & Ziska, L. H. (2016). Evidence for divergence of response in Indica, Japonica, and wild rice to high CO_2 × temperature interaction. *Global Change Biology*, 22 (7), 2620–2632. 10.1111/gcb.13279.

Weiwei, L. U., Xinxiao, Y. U., Guodong, J. I. A., Hanzhi, L. I., & Ziqiang, L. I. U. (2018). Responses of Intrinsic Water-use Efficiency and Tree Growth to Climate Change in Semi-Arid Areas of North China. *Science Reports*, 8 (14), 1-8. 10.1038/s41598-017-18694-z.

Wingler, A., Lea, P. J., Quick, W. P., & Leegood, R. C. (2000). Photorespiration: metabolic pathways and their role in stress protection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355, 1517–1529. 10.1098/rstb.2000.0712.

Wise, R. R., Olson, A. J., Schrader, S. M., & Sharkey, T. D. (2004). Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant, Cell Environmental*, 27 (6), 717–724. 10.1111/j.1365-3040.2004.01171.x.

Xiong, D., Ling, X., Huang, J., & Peng, S. (2017) Meta-analysis and dose-response analysis of high temperature effects on rice yield and quality. *Environmental of Experimental Botany*, 141,1–9. 10.1016/j.envexpbot.2017.06.007.

Xu, Z., Jiang, Y., Jia, B., & Zhou, G. (2016). Elevated-CO_2 Response of Stomata and Its Dependence on Environmental Factors. *Frontiers Plant Science*, 7, 657. 10.3389/fpls.2016.00657.

Xu, H., Zhang, J., Zeng, J., Jiang, L., Liu, E., Peng, C., He, Z., & Peng, X. (2009). Inducible antisense suppression of glycolate oxidase reveals its strong regulation over photosynthesis in rice. *Journal Experimental Botany,* 60 (6), 1799–1809. 10.1093/jxb/erp056.

Yang, J., Sicher, R. C., Kim, M. S., & Reddy, V. R. (2014). Carbon dioxide enrichment restrains the impact of drought on three maize hybrids differing in water stress tolerance in water stressed environments. *International Journal Plant Biology*, 5 (1), 38-44. 10.4081/pb.2014.5535.

Zargar, S. M., Gupta, N., Nazir, M., Mahajan, R., Malik, F. A., Sofi, N. R., Shikari, A. B., & Salgotra, R. K. (2017). Impact of drought on photosynthesis: Molecular perspective. *Plant Genetic*, 11, 154-159. 10.1016/j.plgene.2017.04.003.

Zelitch, I., Schultes, N. P., Peterson, R. B., Brown, P., & Brutnell, T. P. (2009). High Glycolate Oxidase Activity Is Required for Survival of Maize in Normal Air. *Plant Physiology*, 149 (1), 195–204. 10.1104/pp.108.128439.

Zinta, G., Abdelgawad, H., Domagalska, M. A., Vergauwen, L., Knapen, D., Nijs, I., Janssens, I. A., Beemster, G. T. S., & Asard, H. 2014. Physiological, biochemical, and genome-wide transcriptional analysis reveals that elevated CO_2 mitigates the impact of combined heat wave and drought stress in *Arabidopsis thaliana* at multiple organizational levels. *Glob. Chang. Biol*., 20 (12), 3670–3685. 10.1111/gcb.12626.