

Elevated CO₂ and Water Stress in Combination in Plants: Vanguarders for Adaptation to Changing Climate

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The changing dynamics in climate is the primary and important determinant of agriculture productivity. The effects of this changing climate on overall productivity in agriculture can be understood when we study the effects of individual components contributing to the changing climate on plants and crops. Elevated CO₂ and drought due to low variability in rainfall is one of the important manifestations of the changing climate. There is considerable amount literature that addresses these aspects in terms of effects on plants systems from molecules to ecosystems. Of particular interest is the effect of increased CO₂ on plants in relation to drought and water stress. As it is known that one of the consistent effects of increased CO₂ in the atmosphere is increased photosynthesis, especially in C3 plants, it will be interesting to know the effect of drought in relation to elevated CO₂. The possible mechanisms by which this occurs will be discussed in this minireview. Interpreting the effects of short term and long term exposure of plants to elevated CO₂ in context of ameliorating the negative impacts of drought will show us the possible ways by which there can be effective adaption to crops in the changing climate scenario.

Keywords: Elevated CO₂, Drought, Photosynthesis, Transpiration rate, Stomatal conductance

Introduction

Agriculture is one of the dominant drivers of change in the Anthropocene era, at present about 11 percent which is about 1.5 billion ha of the total land surface area is used for production of crops which is about 36 percent of land which is suitable for agriculture (Alexandratos and Bruinsma 2012). Agriculture on one hand is affected by the changing climate and on the other hand is also contributing to it. The changing dynamics in climate is the primary and important determinant of agriculture productivity. The effects of this changing climate on overall productivity in agriculture can be understood when we study the effects of individual components contributing to the changing climate on plants and crops.

There is a continuing need to feed the growing population and globally, human population of 7.2 billion in mid-2013 is expected to increase to almost 8.1 billion in 2025, and to further grow to 9.6 billion in 2050 (UN 2013). Food security in terms of food availability is imperative in such a scenario. Changing

climate is a reality and slowly we are learning to adapt to it and also in the process devising mitigation strategies so that we can put the brakes on the changes which in general is harmful. The competition for natural resources like land, water and energy will keep growing at a pace with which it would be difficult for us to catch up, unless we have sound strategies in place to adapt to the harmful effects of changing climate and further mitigate the effects of changing climate.

The effects of changing climate on particular areas specifically like agriculture is difficult to predict with a great degree of accuracy although the overall effects are known and understood. Reports indicate that global average temperatures have increased by about 1 °C since the pre-industrial era and that anthropogenic warming is adding around 0.2 °C to global average temperatures every decade (IPCC 2018). The global CO₂ in the atmosphere has reached 407 ppm in 2018 (Friedlingstein et al 2019). Given the current rate of generation of CO₂, it can be expected that it will exceed 600 ppm by the end of this Century (IPCC 2007). The levels of greenhouse gas (GHG) is changing rapidly, CO₂ concentration in the atmosphere can directly affect the growth and development of vegetation in general and it is indirectly affecting plant growth due to seasonality and variability in rainfall it causes.

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Elevated CO₂ and drought due to low variability in rainfall is one of the important manifestations of the changing climate. There is considerable amount literature that addresses these aspects in terms of effects on plants systems from molecules to ecosystems. Of particular interest is the effect of increased CO₂ on plants in relation to drought and water stress. Increases in the source of carbon can have favorable effects in plants in relation to their growth and development, this can be all the more pronounced in the presence of optimum to high levels of nutrients in the soil and increased water available. These effects may be of short duration and can vary according the photosynthesis types of the plant like in C₃, C₄, CAM and C₃- C₄ intermediate plants. In addition, there are studies which show that C₃ crops show increased growth and yield under both wet and dry growing conditions. C₄ crops show increased growth and yield only under dry growing conditions and drought leads to stomatal limitations of C₃ and C₄ crops and is alleviated by eCO₂.

The forecasts for the coming decades have projected varying changes in precipitation that can result increasing frequency of droughts and floods (Shanker et al 2014). Drought is one of the important abiotic stresses in the present changing climate scenario and the study of the mechanism by which it affects plants is metabolism, growth and development is of paramount importance. In the past decade, global losses in crop production due to drought totaled ~\$30 billion (Gupta et al 2020). The loss in crop production due to drought in the past ten years has been close to about 30 billion and with the estimate that about 5 billion people will be in water scarce regions of the world by 2050, emphasizes the importance of studying all the facets of drought and plant growth. Interestingly there are studies that crops grown under field conditions, the positive impact of elevated atmospheric CO₂ concentrations on productivity was found to be significantly stronger under soil water limitation than under potential growth conditions, as reported in Kimball et al. (1994) for cotton, Pinter et al. (1996) for wheat, De Luis et al. (1999) for alfalfa and also for temperate pasture species (Clark et al., 1999). There is also evident interactive effects of elevated CO₂ and other environmental conditions which are indicative of changing climate like drought, heat and other stresses which invariably accompany elevated CO₂ conditions in the atmosphere. The importance in understanding this complex relationship is imperative in a high CO₂ atmosphere which is envisaged in future to counter the

effects of changing climate. As it is known that one of the consistent effects of increased CO₂ in the atmosphere is increased photosynthesis, especially in C₃ plants, it will be interesting to know the effect of drought in relation to elevated CO₂. The possible mechanisms by which this occurs will be discussed in this minireview. Interpreting the effects of short term and long term exposure of plants to elevated CO₂ in context of ameliorating the negative impacts of drought will show us the possible ways by which there can be effective adaptation to crops in the changing climate scenario.

Water relations, transpiration and stomatal conductance

Elevated CO₂ concentration is known to mitigate effects of drought stress, in a study in *Populus* spp. and *Salix* spp. by Johnson et al (2002) it was found that when these two species were grown in ambient (350 μmol mol⁻¹) or elevated (700 μmol mol⁻¹) predawn water potential reduced as water stress increased as against midday water potential which did not show any changes. The changes observed were 0.1 MPa at predawn and 0.2 MPa at mid-day. An increased elasticity of the cell wall is usually observed when there is altered water relations. These cellular changes allow the tress to maintain higher turgor at lower water potentials and tissue water content. The mitigating effect of higher CO₂ was by increasing ψ_p at the same levels ψ_w which can result in osmotic adjustment. This mechanism of osmotic adjustment can improve plant metabolism or at least maintain plant metabolism at optimal levels resulting in acclimation to drought. Stomatal dynamics drives the carbon uptake during water deficit stress and when there is an accompanying stress like short term elevated CO₂, the role of stomatal limitation in assimilation of carbon may reduce with reduction in photorespiration and increase in the partitioning of soluble sugars and increase in water use efficiency.

In a study on the possible adaptive response of semi dwarf durum wheat cultivars by physiological and molecular mechanisms (Medina et al 2016) it was seen that elevated CO₂ and water stress increased d₁₅N, which was cultivar dependent and the effect diminished as water stress increased. Shifts in N metabolism and this could reflect in decreased root to shoot translocation of a decrease in N. The authors observed d₁₃C increased under moderate stress irrespective of the CO₂ concentration indicative of higher water-use efficiency. PEPC expression was increased under water stress and elevated CO₂ combination. Carbohydrates which are the

substrates for PEPC increased under these stresses and this showed the roles of PEPC in providing carbon skeleton for amino acid and lipid biosynthesis. It is seen that a transcript level coordination in C and N metabolism is seen under a combination of water stress and elevated CO₂. The dehydrin genes DHN11 and DHN16 showed changes in expression under water stress and elevated CO₂ with genotype dependent change in transcript levels, this shows that the interactive effects of both elevated CO₂ and water stress varies according to the genotype in wheat.

In a study with field experiments and process based simulations Kellner et al (2019) have shown that CO₂ enrichment contributes to decreased water stress and also contributed to higher yields of maize under restricted water conditions. They showed from their studies that elevated CO₂ decreases transpiration without effect on soil moisture at the same time it increases evaporation. Modelling has shown that water stress reduced to an extent of – 37 percent under elevated CO₂, a simulated increase in stomatal resistance being the reason for this.

Some of the effects water stress in combination with elevated CO₂ can be understood when see the effects observed in FACE experiments. In maize elevated CO₂ reduces transpiration and this in turn contributed to the increase in soil moisture and evaporation. In a simulated study by Kellner et al (2019) it was seen that transpiration was reduced by 22 percent in 2007 (wet and dry) and in 2008 (wet). Hussain et al (2013) showed that in a FACE experiment transpiration in maize was reduced significantly under 550 ppm CO₂ concentration. Daily sap flow and vapour pressure deficit (VPD) of maize was investigated by Manderscheid et al (2016). Whole plant transpiration was reduced by 50 percent in drought as compared to wet in ambient CO₂ concentrations and 37 percent reduction was observed in elevated CO₂ concentration of 550 ppm. Enrichment of CO₂ did not affect sapflow under drought and a 20 percent decrease was seen under wet conditions. Maize under elevated CO₂ had a higher transpiration rate which was due to lower sap flow in the preceding period when plant available soil water was minimum, this shows that reduction in canopy transpiration by elevated CO₂ can delay the effects of water stress and can contribute to increased plant biomass production.

Another study by Mwendia et al (2019) on the physiological response of two C3 and C4 mechanisms syndromes, Napier grass (*Pennisetum purpureum* Schumacher × *Pennisetum glaucum* (L.) R. Br) and hydric common reed grass (*Phragmites australis* (Cav.) Trin.

Ex Steud) under water stress and elevated CO₂ it was seen that there was a general response of increase in Photosynthesis, reduced leaf water potential and increase in transpiration in both the grass species. A contrasting response was seen in the two grasses to elevated CO₂ and water stress, the difference in the species response was due to the stomatal characteristics as evident by the changes in transpiration rate and osmotic adjustment. Water status adjustment by modification of xylem anatomy and hydraulic properties is a mechanism found in many plants, its relationship with the observed effect of elevated CO₂ to increase plant water potential via reduced stomatal conductance and water loss was studied by Liu et al (2020). One the known adaptation to water stress by plants is to maintain high water potential and turgor pressure under water deficient conditions. The authors saw in their study that water deficit significantly decreased xylem vessel diameter, conduit roundness and stem cross section area, it was seen that these impacts of water deficit were relieved at elevated CO₂. In another study by Wang et al (2018) where the adverse effects of drought was studied on soyabean under elevated CO₂, the authors found that elevated CO₂ increased WUE contributing towards countering drought, they did not find any positive effects on osmotic adjustments.

The effects of Elevated CO₂ individually and in combination with water deficit in Soyabean was studied by Bencke-Malato et al (2019). In instantaneous water stress treatment elevated CO₂ reverted the expression of genes related to stress, transport and nutrient deficiency that were induced by water stress, the interaction of drought and elevated CO₂ affected the expression of genes with physiological and transcriptomic analysis showing that elevated CO₂ can mitigate the negative effects of water stress in soyabean roots.

Photosynthesis, growth and biomass

In addition to understanding the acclimation pattern of plants under a combination of water stress and elevated CO₂, future yield prediction can also be done under the changing climate scenario from precise data on effects of elevated CO₂ and drought on biomass and soil water conditions. Growth modelling under these conditions have contributed to our knowledge on these effects. Under sufficient water supply C3 crops recorded increased yield under elevated CO₂ where as C4 crops did not show much change in the yield. A 10 – 15 percent increase in biomass has been seen in C3

crops under FACE experiments due to the CO₂ fertilizing effect (Andresen et al 2018; Weigel and Manderscheid 2012), on the other hand C4 crops maize and sorghum did not respond similarly under water sufficient conditions (Leakey et al 2006; Manderscheid et al 2014). In a study by Diksaityte et al (2019), it was seen that adverse effects of heat and drought was alleviated by improved water relations under elevated CO₂. The authors also saw that the mechanism of photosynthesis reduction under combination of heat and drought was due to increased drying of soil and decrease in stomatal conductance.

In a study on Macauba palm by Rosa et al (2019) the author investigated the effects of elevated CO₂ and drought on photosynthesis, they found that at elevated CO₂ the plants were capable of recovering more from water stress due to increased Rubisco carboxylation rate and electron transport rate thus preventing reduction in total dry matter production. The authors noted that drought and increased CO₂ affected stem length and total drymatter production, it was seen that at elevated CO₂ there was no reduction in stem length and total biomass due to drought.

In coffee, it was seen by Avila et al (2020) that at 723 ± 83 ppm concentration of CO₂ for a period of seven months has increased biomass accumulation even water deficit treatments with reduced rates of photorespiration and oxidative pressure under drought. The plants under drought and elevated CO₂ showed high respiratory carbon flux which is high respiration rates and also an energy status that supported increased root growth under drought. These results show a new mitigating method of elevated CO₂ for maintenance of photosynthetic performance under drought. Other studies have shown that in soyabean (Li et al 2020) drought effect on photosynthesis was not alleviated by elevated CO₂, the authors found that net photosynthetic rate and chlorophyll b content reduced under drought and elevated CO₂. In another study Andresen et al (2016) evaluated biomass accumulation in long term experiments under elevated CO₂ and drought and saw that there was

a multiple response pattern and the pattern itself was likely to change and they suggested long term experiments to access future impact of climate change.

Future perspectives

Deficit irrigation to economize water use and to induce acclimation by plant physiological adjustments is an approach that can be advocated to counter the adverse effects of changing climate, our mini review here shows that this can be an important strategy in future agriculture under elevated CO₂ which effectively decrease the impact of low soil water on photosynthesis and in turn biomass accumulation and yield in crops. Plant water relations is mainly affected by gas exchange and stomatal physiology which in turn is affected by elevated CO₂ and drought and there are complex manifestation when these stresses act in combination, these are the critical factors when the goal is to evolve climate ready cultivars. In order to devise strategies for adaption in crops in agricultural systems we have understand and elucidate how these processes operate across a range from ecosystems to organismal and from cellular, biochemical to molecular level.

Adaptation in agriculture to changing climate is occurring all over the world, the practices should now be based on the findings that drought and water stress conditions can be effective in alleviating the effects of climate change. There is a general consensus and better understanding of effects not that can be put to use for tackling climate related effects on crop production.

One of the important facets that has come out of this mini review is that most of the effects observed needs to be looked into with a mechanistic perspective to arrive at correct inferences that can help us move ahead with the goal of evolving climate ready cultivars. In many of the studies the casual association are observed which need further investigations which we trust this mini review will invigorate in researchers.

Table 1 Summary of effects of Elevated CO₂ and drought in plants

Plant/Crop/Tree	CO ₂ concentration	Water stress imposition	Effect	Reference
Poplar	700 ± 50 μmol mol ⁻¹	Soil drying cycle by withholding water	Reduced Gas exchange, decreased leaf conductance, increased photosynthesis, increased transpiration efficiency	Johnson et al (2002)
Wheat	400 μmol mol ⁻¹ , 790 μmolmol ⁻¹	Progressive restriction of water from 10 percent to 60 percent pot capacity	Reduced plant biomass,	Medina et al (2016)

			Stomatal conductance and carbon isotope signature indicated water saving strategy. PEPC expression increased	
<i>Tabernaemontana divaricata</i>	1000 $\mu\text{mol mol}^{-1}$, 700 $\mu\text{mol mol}^{-1}$	70 percent of field capacity (FC) for 4 days and 30 percent of FC for 4 days	Increase in stomatal conductance (gs), plant height (PH) and plant girth (PG)	Thruppoyil et al (2020)
Maize	550 $\mu\text{mol mol}^{-1}$	Half water in water stress treatment compared to control	37 percent reduction in whole plant transpiration	Manderscheid et al (2016)
Napier grass (<i>Pennisetum purpureum</i> Schumach \times <i>Pennisetum glaucum</i> (L.) R. Br) and hydric common reed grass (<i>Phragmites australis</i> (Cav.) Trin. Ex Steud)	563 \pm 6.7 $\mu\text{mol mol}^{-1}$ 541 \pm 6.9 $\mu\text{mol mol}^{-1}$ 601 \pm 9.1 $\mu\text{mol mol}^{-1}$	Withdrawing irrigation	Increase in Photosynthesis, reduced leaf water potential and increase in transpiration	Mwendia et al (2019)
Maize	700 $\mu\text{mol mol}^{-1}$, 900 $\mu\text{mol mol}^{-1}$, and 1,200 $\mu\text{mol mol}^{-1}$	deficit irrigation	Decreases in stomatal conductance and reduced transpiration rate	Liu et al (2020)
Soyabean	Ambient + 200 $\mu\text{mol mol}^{-1}$	35- 45 percent of RWC	Elevated CO_2 enhanced the resistance to drought by improving the capacity of photosynthesis and WUE in soybean leaves	Wang et al (2018)
<i>Pinus halepensis</i> (Aleppo pine)	867 \pm 157 $\mu\text{mol mol}^{-1}$	10 Percent Relative Substrate Water Content	Under drought, the effect of CO_2 on WUE was pronounced, with intercellular CO_2 being increased near stomatal closure,	Birami et al (2020)
Lemon	650 and 850 $\mu\text{mol mol}^{-1}$	leaf water potential of -3.5 MPa	Stomatal downregulation at elevated CO_2 reduced water-use but not photosynthesis.	Paudel et al (2018)
Soybean	800 $\mu\text{mol mol}^{-1}$	water deficit was applied by randomly removing plants out of the hydroponic solution exposing the roots to ambient- or elevated-air	Responses of soybean roots to short-term water deficit are buffered by Elevated CO_2	Bencke-Malato et al (2019)
Cassava (<i>Manihot esculenta</i> Crantz)	750 $\mu\text{mol mol}^{-1}$	Stopping irrigation for 7 days	Elevated CO_2 reduced the negative effect of drought on transpiration, water use efficiency, all growth measures and harvest index.	Cruz et al (2018)
Faba bean (<i>Vicia faba</i> L.)	550 $\mu\text{mol mol}^{-1}$	Water was withheld until 30 percent FC	Elevated CO_2 -induced stimulation of nodulation and nodule	Parvin et al (2019)

			density helped maintain N ₂ fixation under drought	
Andiroba (<i>Carapa surinamensis</i>)	700 $\mu\text{mol mol}^{-1}$	50 percent field capacity	Whole-plant water-use efficiency (WUEP) improved under combination treatments	de Oliveira et al (2019)
<i>Hymenaea stigonocarpa</i> Mart. ex Hayne, <i>Solanum lycocarpum</i> A. St.-Hil. and <i>Tabebuia aurea</i> (Silva Manso) Benth. and Hook. f. ex S. Moore	700 $\mu\text{mol mol}^{-1}$	Water stress was introduced three times during the experiment by halting irrigation 1 month before the fourth (360 days old), fifth (450 days old) and sixth (540 days old) morphophysiological surveys	Water stress decreased biomass production under high CO ₂	Souza et al (2016)
Grapevines (<i>Vitis labrusca</i>)	800 $\mu\text{mol mol}^{-1}$	Stopping irrigation	Elevated CO ₂ delayed drought effects on both net photosynthetic rate and Rubisco activity for four days, by reducing stomatal conductance, transpiration and stomatal density	da Silva et al (2017)
<i>Brassica napus</i>	800 $\mu\text{mol mol}^{-1}$	Withholding water for 7 days	Elevated CO ₂ diminished the adverse effect by improved water relations	Diksaityte et al (2019)
Maize	550, 700, and 900 $\mu\text{mol mol}^{-1}$	Deficit irrigation	Photosynthetic rate in elevated CO ₂ concentrations was higher under Deficit irrigation than under regular irrigation.	Li et al (2018)
<i>Acrocomia aculeata</i>	700 $\mu\text{mol mol}^{-1}$	Water withholding	Higher Rubisco carboxylation rate (V_c max) and electron transport rate (J max) contributed to recovery from drought	Rosa et al (2019)
Cucumber (<i>Cucumis sativus</i> L.)	800 \pm 20 $\mu\text{mol mol}^{-1}$	$\psi_w = -0.05$ MPa and $\psi_w = -0.15$ with PEG 6000	Higher photosynthetic performance and increased grana thickness under moderate drought stress, increased palisade cells length and chloroplasts number per palisade cell under severe drought stress.	Liu et al (2018)

CO₂ on tree water-use efficiency and carbon metabolism. *New Phytologist*.

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