

INFLUENCE OF ELEVATED CO₂ ON AGRICULTURAL SYSTEMS: A REVIEW

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ABSTRACT

Agriculture constitutes the second largest biome on Earth's surface and is responsible for a third of the world's net primary production. Carbon dioxide (CO₂) is directly linked to the primary production of ecosystems through its major role in photosynthesis. CO₂ levels on Earth's atmosphere have increased substantially since the Industrial Revolution and increase at a rate of 3.2 ppm per year. Along with such rises, shifts in precipitation patterns and global annual temperature averages have occurred, which might affect food production worldwide. The present work aimed at assessing how elevated CO₂ concentrations affect net accumulation of carbon in this biome, increasing net photosynthesis and nitrogen and water use efficiency. Interactions among elevated atmospheric CO₂, temperature and precipitation – major climate parameters driving current changes - are discussed, as well as means by which crop physiological responses to elevated CO₂ can help mitigate some of the deleterious effects predicted in many agricultural systems worldwide.

Keywords: Carbon dioxide, photosynthesis, nitrogen, water use efficiency

INFLUÊNCIA DO CO₂ ELEVADO SOBRE SISTEMAS DE PRODUÇÃO AGRÍCOLA: REVISÃO

RESUMO

A agricultura constitui o segundo maior bioma terrestre, responsável por um terço da produção primária líquida mundial. O dióxido de carbono (CO₂) está diretamente relacionado à produção primária de ecossistemas através de seu papel crucial na fotossíntese; sua concentração atmosférica aumentou substancialmente desde a Revolução Industrial e eleva-se a uma taxa de 3,2 ppm ao ano. Simultaneamente a esta elevação, alterações em parâmetros climáticos como pluviosidade e temperaturas médias anuais têm ocorrido, com potencial impacto sobre a produção mundial de alimentos. Objetivou-se analisar efeitos da elevação de CO₂ atmosférico sobre a acumulação de carbono neste bioma, elevando a eficiência fotossintética e de uso da água e nitrogênio. Foco foi dado às interações entre CO₂ atmosférico, temperatura e pluviosidade -

variáveis climáticas ligadas às mudanças climáticas, e como respostas fisiológicas de culturas agrícolas à sua elevação podem auxiliar a mitigar alguns dos efeitos deletérios previstos em diversos sistemas agrícolas ao redor do globo.

Palavras-chave: Dióxido de carbono, fotossíntese, nitrogênio, eficiência do uso da água

INTRODUCTION

Agricultural lands can be defined as intensively human-managed ecosystems in which the production of essential goods for human well-being (food, wood, fuel, and fiber) is maximized through transformations of the landscape (VANDERMEER, 1995). In this review, the word “agriculture” will be employed to characterize a major biome which combines many crop groups, such as forage, oilcrops, sugarcrops, vegetables, and production of fruit, cereal, root, and fiber (MONFREDA et al., 2008).

Land conversion to agriculture is among the most substantial ways by which humans can alter ecosystems (VITOUSEK et al., 1997). Ellis & Ramankutty (2008), in a pioneer work on Earth’s biomes, integrated human population, land use and land cover to produce eighteen “Anthropogenic Biomes”. This novel view of human-driven modifications on ecosystems went beyond the traditional view over Earth’s biomes as function of different vegetation types and climates, and ranked croplands as the second largest anthropogenic biome. By using procedures that integrated the variables above and other authors results, these authors were able to show that croplands cover around 20% of the free-ice lands worldwide, or approximately 15 million km², which represents 12% of Earth’s surface. An additional area of 31.5 million km² is currently occupied by pastures.

Croplands account for a third of Earth’s net primary production (NPP), which is defined as the carbon net gain by vegetation after losses through respiratory processes are subtracted (CHAPIN et al., 2002). Increases in NPP don’t always translate in gains in net ecosystem production (NEP, net accumulation of carbon in an ecosystem), which in agricultural lands is ultimately determined by the balance of how much biomass is removed from the field during harvest processes and how much stays in the system (ALBERTI, 2010). Therefore, the net accumulation of carbon in agricultural lands is highly variable according to the type of cropping system implemented (e.g., annual and perennial crops, fuel or food production). A broad analysis over agricultural ecosystems done by Lal et al. (2003) showed that NEP experienced in croplands

is of an equal or greater intensity than what is seen in many natural systems, which can help recover carbon lost during land conversion.

By combining census statistics with two sources of satellite land cover data, Monfreda et al. (2008) produced a very comprehensive cropland map (below), which includes 175 cultivated plants.

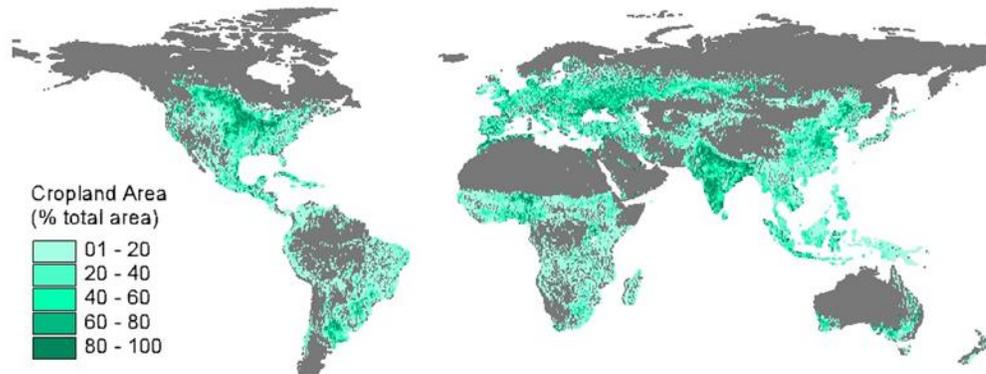


Figure 1. World cropland area. Extracted from Monfreda et al. (2008).

As can be inferred, agriculture distribution is primarily controlled by water availability, climate, soil type, and topography. As an ecosystem driven by decisions made by humans, biotic and abiotic properties such as soil chemistry, soil physics, and mainly biodiversity are modified to favor the growing crop, leading to an ecosystem that is kept at early successional stages through disturbances of many different types (DORA et al., 2010). As a very diverse ecosystem concerning the types of cropping systems existent, many interactive factors take place. Flooding techniques are usually employed in many rice (*Oryza sativa* L.) fields worldwide to favor the growing crop in detriment of weed species and maximize yields. Moreover, sugarcane (*Saccharum officinarum* L.) fields located in some countries are burnt prior to harvest to decrease biomass and ease its processing (OSBORNE et al., 2010).

Although agriculture intensifies production of goods, other important ecosystem services can be severely impaired. Ribaudo et al. (2010) suggest ways of improving ecological services performed by agricultural lands by the adoption of alternate management procedures, such as no-till practices for increased carbon sequestration and establishment of vegetation buffers for water quality maintenance. Most agricultural lands are carbon sources due to the management practices used (mainly tillage), but a shift toward carbon sink occurs by the adoption of conservative soil management practices, such as no-till or use of green cover crops.

THE ROLE OF CARBON DIOXIDE (CO₂) ON EARTH'S PRIMARY PRODUCTION

CO₂: a major greenhouse gas

Carbon dioxide (CO₂) is critical for life on the planet due to its major role in global surface warming and photosynthesis, among many other processes. CO₂ is a trace gas since more than 99.9% by volume of Earth's atmosphere is composed of nitrogen, oxygen, and argon (CHAPIN et al., 2002). CO₂, along with other gases such as methane (CH₄), nitrous oxide (N₂O), and water vapor play an active role on Earth's energy budget due to their ability to absorb long-wave radiation emitted by Earth, which is then reradiated in all directions. This fundamental phenomenon is known as the greenhouse effect, responsible for warming the terrestrial surface – without an absorbing atmosphere, Earth's surface temperature would be around 33°C cooler, potentially affecting its ability to support life (CHAPIN et al., 2002; McKIBBEN, 2007).

Studies combining air samples collected since the 1950s and analysis of air bubbles trapped in glacial ice cores revealed that the levels of CO₂ in the atmosphere have ranged from 180 to 280 ppm during the past 800,000 years (CHAPIN et al., 2002; McKIBBEN, 2007). Since the beginning of the Industrial Revolution, the concentration of atmospheric CO₂ (hereinafter referred to as “CO₂”) has increased from 275 to 407 ppm (LINDSEY, 2019), and will top 700 ppm or more by the year 2100 (McKIBBEN 2007; DaMATTA et al., 2016). Spatial variations of [CO₂] are minimal since the atmosphere is mixed enough to have a constant CO₂ concentration worldwide and up to 80 km in height (DaMATTA et al., 2016).

Agricultural lands are areas in which the original vegetation was removed, exposing the soil to higher temperatures, and allowing for a high microbial activity and release of CO₂ through many processes (VANDERMEER, 1995). Land conversion to agriculture is expected due to the rapid-growing human population worldwide, and is among the events that show the greatest release of CO₂ to the atmosphere, increasing the effects of high [CO₂] on plants as well as indirect effects on ocean acidity and temperature rise. This may ultimately result into a positive feedback leading to even highest microbial activity and highest amounts of CO₂ released to the atmosphere.

Photosynthesis: from CO₂ to sugars

Crops can be divided into two major groups concerning the photosynthetic pathway used: C₃ and C₄ crops (TAIZ et al., 2014). The CAM pathway is not found on major crops. A brief

overview of the biochemistry of photosynthesis performed by C₃ and C₄ crops is discussed in order to best elucidate crop responses to CO₂ rise. For an overall view of photosynthesis, refer to the vast literature available.

Rubisco is the enzyme responsible for the carboxylation of CO₂ into the Calvin-Benson Cycle for both C₃ and C₄ plants. This enzyme catalyzes the attachment of CO₂ to an electron acceptor or substrate, ribulose-biphosphate (RuBP). Due to its affinity for CO₂ and oxygen (O₂), Rubisco can either catalyze carboxylation reactions – leading to photosynthesis and incorporation of carbohydrates, or oxygenation reactions. The process of oxygenation performed by Rubisco is called photorespiration (TAIZ et al., 2014).

C₄ plants have a very effective mechanism for concentrating CO₂ at the site where Rubisco fixes carbon, which makes them less reliable upon atmospheric [CO₂] and ultimately leads to virtually no photorespiration. More specifically, C₄ species have two main cells in which the carbon-fixation reactions occur – the mesophyll and the bundle sheath cells. At the mesophyll cell, C₄ species have a special enzyme responsible for catalyzing CO₂ carboxylation with phosphoenolpyruvate (PEP, the electron acceptor). This enzyme is called PEP carboxylase and has little affinity for oxygen (TAIZ et al., 2014). Organic acids are produced through this first step at the mesophyll cell and are transported to the bundle sheath cells, where they are decarboxylated. CO₂ then enters the Calvin-Benson Cycle through carboxylation processes catalyzed by Rubisco. Since PEP carboxylase has very low affinity to O₂, mainly CO₂ (as organic acids) is taken to the site where Rubisco fixes carbon (the bundle sheath cell), saturating the cell interior and inhibiting possible oxygenation reactions by Rubisco, maximizing carbon assimilation and net photosynthesis.

Photosynthesis of C₃ species take place exclusively at the mesophyll cells, in which all carbon-fixation reactions occur. Since there is no mechanism for saturating [CO₂] at the site where Rubisco fixes carbon (as seen in C₄ species), at the interior of these cells the CO₂:O₂ ratio reflect mostly the outside air ratios of both gases. Therefore, Rubisco can either catalyze photosynthetic reactions (carboxylation) or photorespiration (oxygenation). At current [CO₂], C₃ plants are Rubisco-limited (some authors prefer CO₂-limited) since the CO₂:O₂ ratio inside the mesophyll cell leads to an average carboxylation to oxygenation ratio of 3:1, or even less than this (NASH, 1996, TAIZ et al., 2014), meaning that oxygenation reactions directly respire away up to 40% of the carbon fixed by C₃ photosynthesis (CHAPIN et al., 2002). Thus, at current [CO₂],

photorespiration limits the net photosynthetic gain of C₃ crops, which is defined as the balance between CO₂ that is assimilated through photosynthesis, and leaf respiration in the light (photorespiration and mitochondrial respiration combined).

Three main considerations can be drawn from the differences seen between the C₃ and C₄ photosynthetic pathways. Firstly, as already mentioned, at current [CO₂] C₄ species show a greater net photosynthesis due to their effective mechanism for inhibiting photorespiration. Due to their very efficient photosynthetic apparatus and efficiency of Rubisco, C₄ species also show a reduced quantity per leaf area of this enzyme. Since Rubisco accounts for 25% of the total leaf nitrogen, less of this commonly limiting macronutrient is required to build the C₄ photosynthetic apparatus (TAIZ et al., 2014), and highest nitrogen use efficiency rates are then observed. Lastly, due to their efficient mechanism for saturating CO₂ where Rubisco is located, C₄ plants can absorb CO₂ with a smaller stomata aperture than do C₃ species. This leads to lower water losses through transpiration in C₄ species and higher water use efficiency compared to C₃ species.

These differences on the carbon-fixation reactions ultimately lead to different crop responses to elevated [CO₂]. Due to their effective mechanism for saturating CO₂ inside the bundle sheath cell, many C₄ species are already CO₂-saturated at current atmospheric [CO₂] and show little responses to high CO₂ (WAND et al., 1999). C₃ species thus have the greatest potential for photosynthetic gains in scenarios with elevated [CO₂] because they are currently limited by losses through photorespiratory processes, which are directly connected to the CO₂:O₂ ratio in the carboxylation site (chloroplast) (FOYER et al., 2009).

DIRECT EFFECTS OF ELEVATED [CO₂] ONTO CROP PRODUCTION

Enhancement of Net Primary Production (NPP) and yields of C₃ crops

Results from a number of studies show a CO₂-fertilization effect, i.e. increases in photosynthesis and yields. The magnitude of responses to elevated [CO₂] is 3 times greater in C₃ than C₄ crops (KIMBALL, 1983; LLOYD & FARQUHAR, 1996; DRAKE et al., 1997; AINSWORTH & LONG, 2005; LEAKEY et al., 2005; BLOOM, 2010).

While reviewing 15 years of FACE (free-air carbon enrichment) studies, Ainsworth & Long (2004) reported an average 38% increase in yields of fertilized C₃ crops. FACE is a common way of experimenting with elevated [CO₂] that opposes the also common open-top chambers due to its

nature as a field experiment, in which no confinement structures are used to hold [CO₂] steady - CO₂ is constantly released through pipes over the crop canopy instead.

Hogy et al. (2009), in a 3-year FACE study with spring wheat (*Triticum aestivum* L. cv. TRISO), found interactions that went beyond the predicted results. Spring wheat was grown at current (380 ppm) and elevated [CO₂] (535 ppm), in a randomized complete block design with three replicates. Fertilizers were applied according to standard recommendations in different crop stages. Soil moisture was monitored using reflectometry sensors and irrigation was applied when necessary. Results can be seen in Figure 2. Wheat growing under elevated [CO₂] had a 12% increase in total biomass, and 11% increase in grain yield, reflecting increases in net primary production of C₃ crops.

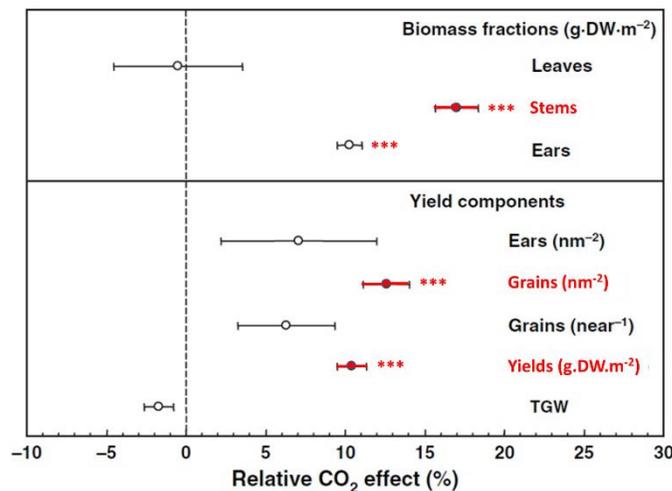


Figure 2. Responses of spring wheat growing under 535 ppm of CO₂ relative to plants growing under 380 ppm (current [CO₂]). Parameters highlighted in red are statistically significantly different at 99.9% confidence level (indicated by three asterisks). Leaves biomass was not significantly different among treatments. Total plant biomass (the sum of leaves, stems and ears) which potentially stays in the field showed a consistent increase over this 3-year study, indicating that a long-term gain in the soil carbon can be expected. Adapted from Hogy et al. (2009).

Since nitrogen (N) content was also significantly reduced, the biomass C:N ratio is greater than the C:N ratio of wheat grown under current [CO₂], hence slower decomposition rates in the soil are expected (HOGY et al., 2010), contributing to a buildup in soil organic matter. Other parameters not shown in Figure 2 were also significantly different among treatments. Wheat grown under elevated [CO₂] had a 7.4% lower total grain protein, and grain size was smaller compared to

wheat grown under current [CO₂]. Such attributes lower the grain quality and raise concerns about future food security. Market value is also impaired due to the resulting smaller grains. Additionally, a 7% reduction in gluten quantity was observed, altering processing properties of the flour produced.

Responses of C₄ crops growing under elevated [CO₂]

Little stimulation of photosynthesis under high [CO₂] is expected for C₄ species due to the virtual absence of photorespiration resulting of the CO₂-saturating mechanism in C₄ leaves (NASH, 1996). Accordingly, studies with maize (*Zea mays* L.) conducted by Kim et al. (2007) reported that neither biomass nor net photosynthesis measured at elevated [CO₂] was changed. Improvements of 15% on net photosynthesis of C₄ crops were reported by Ainsworth & Long (2004), while Wand et al. (1999) found increases of 25% in the assimilation of carbon. Such inconsistent results may be attributed to differences in the CO₂ saturation levels among C₄ species. Wand et al. (1999) states that “while some species appear to be CO₂ saturated at ambient [CO₂], other C₄ grasses are not necessarily saturated at that level”. This explanation may account for the wide variability observed regarding stimulation of C₄ crop photosynthesis when cultivated under elevated [CO₂].

Improvements on the water use efficiency of C₃ and C₄ crops

Water use efficiency (WUE) is a measure of carbon gained per unit of water used and is generally expressed as g C m⁻² mm⁻¹ (CONDON et al., 2004). Elevated [CO₂] has been shown to directly induce lower stomatal apertures on both C₃ and C₄ crops. Such leads to lower conductance of CO₂ and water vapor, enhancing WUE by lowering transpiration rates and increasing biomass production per mm of water transpired (CONLEY et al., 2001; CONDON et al., 2004; LEAKEY et al., 2005).

FACE experiments with soybeans (*Glycine max* (L.) Merr., a C₃ crop) growing at 718 ppm of CO₂ showed a 28% reduction in water loss by leaf unit area, resulting in a 45% increase in WUE, despite a 9% increase in leaf area in comparison to plants growing at 369 ppm of CO₂ (BOOKER et al., 2004). Such results are explained by the capacity of performing a more efficient carbon assimilation while transpiring less water due to lower stomatal conductance, and is in agreement with results available on the literature for other C₃ crops (rice, YOSHIMOTO & KOBAYASHI, 2005; wheat, QIAO et al., 2010; peanuts, VU, 2005).

C₄ species do not show the same magnitude of increases in WUE, perhaps due to their already very efficient water use (CONLEY et al., 2001). Studies done with sugarcane grown at FACE experiment reported a slight increase in WUE (VU & ALLEN, 2009), although De Souza et al. (2008) reported increases of 62% in WUE of sugarcane grown in open-top chambers. Conley et al. (2001) grew sorghum (*Sorghum bicolor* (L.) Moench) at 570 ppm of CO₂ for two years using the FACE approach, and two irrigation regimes. Based on grain yield, there was a 9% and 19% increase in WUE in wet and dry plots, respectively, showing an enhanced capacity of withstanding drought stress, whereas total biomass results indicate WUE increased by 16% and 17% in wet and dry plots, respectively. Such contradictory results for C₄ crops indicate a need of specific research on interactions among high [CO₂], C₄ crops and experimental approach (e.g., FACE or open-top chambers).

Increased nitrogen use efficiency (NUE) and reduction in respiration rates

NUE (nitrogen use efficiency) is a measure of organic matter produced per unit of N taken up (HOGY et al., 2009). Studies show nitrogen (N) cycle is greatly impacted and modified as [CO₂] increases, especially for C₃ crops. In one of these studies, rice was grown under FACE approach at 570 and 370 ppm of CO₂ in two consecutive growing seasons. Rice plants growing under elevated [CO₂] had increases in NUE of 7.5%, 15.1%, and 6% at 30, 60, and 120 days after transplanting (ZENG et al., 2010), which was attributed to a lower leaf nitrogen concentration. Wheat has shown similar results regarding lower leaf nitrogen and grain protein (HOGY et al., 2009; ERBS et al., 2010). However, C₄ crops show a shorter decrease in nitrogen content, but still a 5% increase in NUE was noticed (AINSWORTH & LONG, 2004). A broader view is offered by Kimball et al. (2002), who concluded that total nitrogen content recorded in C₃ species is reduced by 16% in chamber and 9% in FACE under elevated [CO₂], compared to only 7% for C₄ plants.

The underlying mechanism for a highest NUE seen under elevated [CO₂] lies on the role of Rubisco, and on its shift in content seen under high CO₂. Firstly, Rubisco accounts for the largest single share of leaf N. Continuous increases in [CO₂] shift the photosynthesis-limiting factor from Rubisco activity to RuBP regeneration, i.e. high CO₂ leads to higher CO₂:O₂ ratios in the leaf intracellular spaces, inhibiting photorespiration performed when Rubisco catalysis oxygenation of RuBP, and the factor limiting greater carbon assimilation is then regeneration of the electron acceptor RuBP, which has to be done by the end of the Calvin-Benson Cycle (TAIZ et al., 2014).

Therefore, less Rubisco is required at the same photosynthetic efficiency, and the lowest content of this enzyme generally accounts for the lowest leaf N noticed and lowest total plant N. Two major considerations can be drawn at this point. Crops can reach the same levels of photosynthetic activity and yields while less nitrogen is used to build their photosynthetic apparatus (which can therefore reduce use of N fertilizers), or crops could reach higher yields at the nitrogen availability seen today. In both cases NUE is increased, and optimization of this commonly limiting factor is increased (LONG & DRAKE, 1991).

The lowest N content noticed under elevated [CO₂] leads to an effect known as “Acclimation of CO₂”. Crops (C₃ mainly) growing under high CO₂ get more NUE but less efficient to do photosynthesis due to the lowest Rubisco content, and thus reach lowest maximum carboxylation rates, which are counterbalanced by the much lower photorespiration rates seen under high CO₂ (BLOOM et al., 2010).

High [CO₂] has also a direct inhibitory effect on plant respiration rates. Such effect is expected due to the lowest nitrogen content noticed when crops (mainly C₃ species) are grown under high CO₂. More specifically, respiration rates follow nitrogen content of a tissue, i.e. the greater the leaf N quantity, the higher the respiration rates will be. This is further clarified by analyzing leaves from the top and low canopy of a tree which is growing in densely vegetated areas. Leaves from the top canopy are N-enriched in order to maximize photosynthesis, and thus show greater respiration rates than leaves from the lower canopy, which are shaded and have lower nitrogen, and lower respiration rates as well (CHAPIN et al., 2002).

Mitochondrial O₂ uptake of soybeans growing at 720 ppm was 15% lower than the uptake seen when plants were grown at current [CO₂], which was explained by lower N content and concentration of photosynthetic enzymes in soybeans growing at high CO₂ (GONZALEZ-MELER et al., 1996).

The outcome of weed-crop competition under elevated CO₂ concentrations

Zeng et al. (2010) analyzed competitiveness traits of rice, a C₃ crop, and the C₄ weed barnyardgrass (*Echinochloa crusgalli* L.), when plants were allowed to compete under either ambient or elevated [CO₂]. Barnyardgrass and other species in the *Echinochloa* genus are considered the most troublesome weed species in rice systems. Herbicides are commonly employed for *Echinochloa* spp. control in rice fields; however, their management has been greatly

complicated by the evolution of resistance to multiple herbicides (Heap, 2020), threatening the sustainability of rice production worldwide. Results by Zeng et al. (2010) showed that elevated [CO₂] enhanced rice biomass, tillers, leaf area index and net assimilation rate, while reducing those of barnyardgrass after elongation, suggesting that rising atmospheric [CO₂] could favor rice when growing in competition with barnyardgrass in paddy fields. However, whether such results could also be observed with long-term exposure and acclimation to elevated [CO₂] remains to be elucidated.

HIGH CO₂ INTERACTIONS WITH CLIMATE VARIABLES

Interactions between elevated [CO₂] and temperatures

Due to its role as a greenhouse gas, changes in [CO₂] and temperature (T) are likely to occur concomitantly (KIM et al., 2007). Accordingly, projections for 2050 indicate temperature (T) increases from 0.5 to 5° C for different regions worldwide (MEEHL et al., 2007), and a mean global T increase from 1.8 to 4°C until 2100 (DaMATTA et al., 2016).

Direct effects of increasing T on crop physiology are dependent on soil water status, plant species, and magnitude of increases in T (TAIZ et al., 2014). Soil water status is the variable that more closely determines the photosynthetic efficiency under high T, since the hormone abscisic acid is produced on the root during drought stress and transported to the leaves determining stomatal closure (TAIZ et al., 2014). Therefore, crops grown in rainfed or irrigation systems will behave differently in the future if only effects of high T are considered.

Species vary in their optimum and upper T for photosynthesis, thus warming will benefit colder areas by approximating day T and the crop optimum T for photosynthesis, while on warmer regions T can go beyond the optimum T and thus decrease net photosynthesis (MEEHL et al., 2007). Extended growing season will also benefit crops at temperate zones.

Increases in T above optimum tilt the balance toward photorespiration on C₃ crops. High T lead to highest evapotranspiration rates, lower stomatal apertures, and slower intracellular diffusion of CO₂ compared to O₂. These effects combined with lowest Rubisco affinity for CO₂ noticed at high T will ultimately increase photorespiration rates and decrease net photosynthesis. C₄ crops are favored under high T due to their absence of photorespiration (TAIZ et al., 2014).

When high CO₂ inhibitory effects on photorespiration are coupled with scenarios of higher T, deleterious effects of T on C₃ photosynthesis seems counterbalanced (KIMBALL et al., 2002).

Specifically, higher respiration rates seen under high T are counterbalanced by lowest respiration rates under high CO₂, and higher evapotranspiration is softened by highest WUE. Additionally, highest photorespiration rates under high T are offset by inhibition of photorespiration under high CO₂ - plants growing under elevated [CO₂] have an increase in their optimum and upper T for photosynthesis that can be up to 5°C for some species, mainly due to CO₂ inhibition of photorespiration (DRAKE et al., 1997). Therefore, CO₂ strongly affect responses of C₃ crops to elevated temperatures.

Can positive effects of elevated [CO₂] compensate for decreases in precipitation?

Changes in precipitation patterns have occurred worldwide and are projected to intensify in the coming decades, leading to greater weather extremes between drought and flooding events (MEEHL et al., 2007). Although variations are region-dependent, projections indicate generalized decreases in water availability and increases in extreme events frequency, such as intense drought or extreme T. Since high CO₂ is been shown to benefit plant growth through increases in dry matter produced per quantity of water used, and increases in the optimum and upper T for photosynthesis are noticed as well, increasing [CO₂] can help mitigate the deleterious impacts of both lowest precipitation and water stress (especially for rainfed crops, but important for the whole ecosystem), as well as increases in T until a certain limit related to the crop physiology (CONLEY et al., 2001; BOOKER et al., 2004; CONDON et al., 2004; TUBIELLO et al., 2006).

CONCLUSION

By considering the direct effect of elevated [CO₂] on carbon assimilation of C₃ and C₄ crops, it is safe to assume that C₃ species will take more advantage of a forthcoming CO₂-enriched environment. Increased WUE will also play a major role, decreasing crop vulnerability to drought stress and allowing for increases in NPP. This becomes especially important for rainfed crops, which remain the primary means for food production worldwide, though 80% of the world allocable water is used for irrigation. Improved plant development and growth is often observed at elevated [CO₂] and attributed to reductions in moist limitations rather than direct photosynthesis stimulation. Benefits of CO₂ fertilization in a long-term scale is hard to be predicted since changes on several other variables that interfere in a plant growth are still uncertain or highly regional-dependent. It is important to state that such photosynthetic improvements only happen under

absence of stressful conditions (abundance of water, as well as proper nutrient availability), which is not always true for most of the agricultural lands. High-input agriculture is likely to take more advantage of the upcoming [CO₂] since yields are generally not limited by water nor nutrients, but by losses through photorespiration. As noticed for high-input agriculture, low-input agriculture is benefited by highest WUE and lowest N dependency, but improvements are likely to be limited by other factors, such as drought stress, nutrients deficiency, and weed competition. In this scenario, management recommendations are difficult to be placed since increases in inputs on subsistence agriculture may also lead to higher CO₂ and other greenhouse gases emissions (fossil-fuel burning, fertilizers). Establishing CO₂ emissions worldwide through reforestation of abandoned agricultural lands, as well as more conservative soil management (no-till practices) can certainly help slow or even avoid future scenarios of unpredictable extreme events, while favor crops through increases soil fertility.

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REFERENCES

- AINSWORTH, E.A.; LONG, S. P. 2005. What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. **New Phytologist**, Lancaster, v. 165, p. 351-371.
- ALBERTI, M. 2010. Maintaining ecological integrity and sustaining ecosystem function in urban areas. **Current opinion in Environmental Sustainability**, Amsterdam, v. 2(3), p. 178-184.
- ALTIERI, M.A. 2009. Agroecology, Small Farms, and Food Sovereignty. **Monthly Review-an Independent Socialist Magazine**, Nova York, v. 61, p. 102-113.
- BLOOM, A.J.; BURGER, M.; RUBIO-ASENSIO, J.S.; COUSINS, A.B. 2010. Carbon Dioxide Enrichment Inhibits Nitrate Assimilation in Wheat and Arabidopsis. **Science**, Washington DC, v. 328, p. 899-903.
- BOOKER, F.L.; FISCUS, E.L.; MILLER, J.E. 2004. Combined effects of elevated atmospheric carbon dioxide and ozone on soybean whole-plant water use. **Environmental Management**, Zuri, v. 33, p. S355-S362.
- CHAPIN, F.S.I.; MATSON, P.A.; MOONEY, H. 2002. Principles of terrestrial ecosystem ecology. **Springer-Verlag**, Nova York, NY.
- CONDON, A.G.; RICHARDS, R.A.; REBETZKE, G.J.; FARQUAR, G.D. 2004. Breeding for high water-use efficiency. **Journal of Experimental Botany**, Oxford, v. 55, p. 2447-2460.
- CONLEY, M.M.; KIMBALL, B.A.; BROOKS, T.J.; PINTER, P.J.; HUNSAKER, D.J.; WALL, G.W.; ADAM, N.R.; LAMORTE, R.A.; MATTHIAS, A.D.; THOMPSON, T.L.; LEAVITT,

- S.W.; OTTMAN, M.J.; COUSINS, A.B.; TRIGGS, J.M. 2001. CO₂ enrichment increases water-use efficiency in *Sorghum*. **New Phytologist**, Lancaster, v. 151, p. 407-412.
- COUSINS, A.B., BLOOM, A.J. 2003. Influence of elevated CO₂ and nitrogen nutrition on photosynthesis and nitrate photo-assimilation in maize (*Zea mays* L.). **Plant Cell and Environment**, Liverpool, v. 26, p. 1525-1530.
- DaMATTA, F.M.; GODOY, A.G.; MENEZES-SILVA, P.E.; MARTINS S.C.V.; SANGLARD, L.M.V.P.; MORAIS, L.E.; TORRE-NETO, A.; GHINI, R. 2016. Sustained enhancement of photosynthesis in coffee trees grown under free-air CO₂ enrichment conditions: disentangling the contributions of stomatal, mesophyll, and biochemical limitations. **Journal of Experimental Botany**, Oxford, v. 67, p. 341-352.
- DE SOUZA, A.P.; GASPAR, M.; SILVA, E.A.; ULIAN, E.C.; WACLAWOVSKY, A.J.; NISHIYAMA, M.Y.; SANTOS, R.V., TEIXEIRA, M.M.; SOUZA, G.M.; BUCKERIDGE, M.S. 2008. Elevated CO₂ increases photosynthesis, biomass and productivity, and modifies gene expression in sugarcane. **Plant Cell and Environment**, Liverpool, v. 31, p. 1116-1127.
- DORA, V.; ORSOLYA, S.; SZILARD, C.; ZITA, D.; MIHALY, Z. 2010. Study of secondary succession on recently abandoned fields, with special attention to their weed relations. **Novenyvdelem**, Budapest, v. 46, p. 109-116.
- DRAKE, B.G.; GONZALEZ-MELER, M.A., LONG, S.P. 1997. More efficient plants: A consequence of rising atmospheric CO₂? Pages 609-639 in R. L. Jones, editor. **Annual Review of Plant Physiology and Plant Molecular Biology**. Palo Alto, Annual Reviews Inc.
- ELLIS, E.C.; RAMANKUTTY, N. 2008. Putting people in the map: anthropogenic biomes of the world. **Frontiers in Ecology and the Environment**, Washington DC, v. 6(8), p. 439-447.
- ERBS, M.; MANDERSCHIED, R.; JANSEN, G.; SEDDIG, S.; PACHOLSKI, A.; WEIGEL, H.J. 2010. Effects of free-air CO₂ enrichment and nitrogen supply on grain quality parameters and elemental composition of wheat and barley grown in a crop rotation. **Agriculture Ecosystems & Environment**, Amsterdam, v. 136, p. 59-68.
- FOYER, C.H.; BLOOM, A.J.; QUEVAL, G.; NOCTOR, G. 2009. Photorespiratory Metabolism: Genes, Mutants, Energetics, and Redox Signaling. **Annual Review of Plant Biology**, Palo Alto, v. 60, p. 455-484.
- GONZALEZ-MELER, M.A.; RIBAS-CARBO, N.; SIEDOW, J.N.; DRAKE, B.G. 1996. Direct inhibition of plant mitochondrial respiration by elevated CO₂. **Plant Physiology**, Fairfax, Rockville, v. 112, p. 1349-1355.
- HEAP, I. 2020. The international survey of herbicide resistant weeds. Available at: <www.weedscience.org>. Accessed on: Jan. 15, 2020.
- HOGY, P.; KECK, M.; NIEHAUS, K.; FRANZARING, J.; FANGMEIER, A. 2010. Effects of atmospheric CO₂ enrichment on biomass, yield and low molecular weight metabolites in wheat grain. **Journal of Cereal Science**, Davis, v. 52, p. 215-220.
- HOGY, P.; WIESER, H.; KOEHLER, P.; SCHWADORF, K.; BREUER, J.; FRANZARING, J.; MUNTIFERING, R.; FANGMEIER, A. 2009. Effects of elevated CO₂ on grain yield and quality of wheat: results from a 3-year free-air CO₂ enrichment experiment. **Plant Biology**, Stuttgart, v. 11, p. 60-69.
- KIM, S.H.; GITZ, D.C.; SICHERB, R.C.; BAKER, J.T.; TIMLIN, D.J.; REDDY, V.R. 2007. Temperature dependence of growth, development, and photosynthesis in maize under elevated CO₂. **Environmental and Experimental Botany**, Amsterdam, v. 61, p. 224-236.
- KIMBALL, B.A. 1983 Carbon dioxide and agricultural yield an assemblage and analysis of 430 prior observations. **Agronomy Journal**, Madison, v. 75, p. 779-788.

- KIMBALL, B.A.; KOBAYASHI, K.; BINDI, M. 2002. Responses of agricultural crops to free-air CO₂ enrichment. **Advances in Agronomy**, Washington DC, v. 77, p. 293-368.
- LAL, R. 2003. Offsetting global CO₂ emissions by restoration of degraded soils and intensification of world agriculture and forestry. **Land Degradation & Development**, Nova York, v. 14, p. 309-322.
- LEAKEY, A.D.B.; BERNACCHI, C.J.; LONG, S.P.; ORT, D.R. 2005. Elevated CO₂ does not stimulate C₄ photosynthesis directly, but impacts water relations and indirectly enhances carbon gain during drought stress in maize (*Zea mays*) grown under free-air CO₂ enrichment (FACE). **Comparative Biochemistry and Physiology Part A Molecular & Integrative Physiology**, Amsterdam, v. 141, p. S305-S306.
- LINDSEY, R. 2019. Climate change: atmospheric carbon dioxide. **Climate.gov – science & information for a climate-smart nation**. Available at: <<https://www.climate.gov/news-features/understanding-climate/climate-change-atmospheric-carbon-dioxide>>. Accessed on: Jan. 12, 2020.
- LI, L.; NIELSEN, D.C.; YU, Q.; MA, L.; AHUJA, L.R. 2010. Evaluating the Crop Water Stress Index and its correlation with latent heat and CO₂ fluxes over winter wheat and maize in the North China plain. **Agricultural Water Management**, Amsterdam, v. 97, p. 1146-1155.
- LLOYD, J.; FARQUHAR, G.D.; 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. **Functional Ecology**, London, v. 10, p. 4-32.
- LONG, S.P.; DRAKE, B.G.; 1991. Effect of the long-term elevation of carbon dioxide concentration in the field on the quantum yield of photosynthesis of the C₃ sedge *Scirpus olneyi*. **Plant Physiology**, Rockville, v. 96, p. 221-226.
- MCKIBBEN, B. 2007. Climate change 2007: The physical science basis: Summary for policymakers. **New York Review of Books**, New York, v. 54, p. 44-45.
- MEEHL, G.A.; STOCKER, T.F.; COLLINS, W.D.; FRIEDLINGSTEIN, P.; GAYE, A.T.; GREGORY, J.M.; KITOH, A.; KNUTTI, R.; MURPHY, J.M.; NODA, A.; RAPER, S.C.B.; WATTERSON, I.G.; WEAVER, A.J.; ZHAO, Z.C. 2007. Global Climate Projections. IPCC WG1 Fourth Assessment Report. Cambridge University Press. Available at: <<https://www.ipcc.ch/site/assets/uploads/2018/08/ar4-wg1-chapter10-supp-material-1.pdf>>. Accessed on Dec.15, 2019.
- MONFREDA, C.; RAMANKUTTY, N.; FOLEY, J.A. 2008. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. **Global Biogeochemical Cycles**, Washington DC, 22:19.
- NASH, T.H.I. 1996. Photosynthesis, respiration, productivity and growth. In Lichen Biology; Nash III, T. H. Ed.; **Cambridge University Press**, Cambridge, 1996, p 88.
- OSBORNE, B.; SAUNDERS, M.; WALMSLEY, D.; JONES, M.; SMITH, P. 2010. Key questions and uncertainties associated with the assessment of the cropland greenhouse gas balance. **Agriculture Ecosystems & Environment**, Amsterdam, v. 139, p. 293-301.
- QIAO, Y.Z.; ZHANG, H.Z.; DONG, B.D.; SHI, C.H.; LI, Y. X.; ZHAI, H.M.; LIU, M.Y. 2010. Effects of elevated CO₂ concentration on growth and water use efficiency of winter wheat under two soil water regimes. **Agricultural Water Management**, Amsterdam, v. 97, p. 1742-1748.
- RAMANKUTTY, N.; HERTEL, T.; LEE, H. L.; ROSE, S. K. 2010. Global agricultural land use data for integrated assessment modeling, in Human-Induced Climate Change: An Interdisciplinary Assessment. **Cambridge University Press**, Cambridge, p. 252-265.

- RIBAUDO, M.; GREENE, C.; HANSEN, L.; HELLERSTEIN, D. 2010. Ecosystem services from agriculture: Steps for expanding markets. **Ecological economics**, Amsterdam, v. 69, p. 2085-2092.
- STRIGEL, G. 2008. WMO Statement on the Status of the Global Climate 2007. **Hydrologie Und Wasserbewirtschaftung**, Berlin, 52:137-139.
- TAIZ, L.; ZEIGER, E.; MOLLER, I.A.; MURPHY, A, 2014. Plant physiology and development. Sixth Edition. **Oxford University Press**, Oxford.
- TUBIELLO, F.N.; AMTHOR, J.S.; BOOTE, K. J.; DONATELLI, M.; EASTERLING, W.; FISCHER, G.; GIFFORD, R. M.; HOWDEN, M.; REILLY, J.; ROSENZWEIG, C. 2006. Crop response to elevated CO₂ and world food supply - A comment on "Food for Thought..." by Long et al., Science 312: 1918-1921, 2006. **European Journal of Agronomy**, Amsterdam, v. 26, p. 215-223.
- VANDERMEER, J. 1995. The ecological basis of agriculture. **Annual Review of Ecology and Systematics**, Washington DC, v. 26, p. 201-224.
- VITOUSEK, P.M.; MOONEY, H.A.; LUBCHENCO, J.; MELILLO, J.M. 1997. Human Domination of Earth's Ecosystems. **Science**, Washington DC, v. 277, p. 494-499.
- VU, J.C.V. 2005. Acclimation of peanut (*Arachis hypogaea* L.) leaf photosynthesis to elevated growth CO₂ and temperature. **Environmental and Experimental Botany**, Amsterdam, v. 53, p. 85-95.
- VU, J.C.V.; ALLEN, L.H. 2009. Growth at elevated CO₂ delays the adverse effects of drought stress on leaf photosynthesis of the C₄ sugarcane. **Journal of Plant Physiology**, Amsterdam, v. 166, p. 107-116.
- YAN, H.M.; FU, Y.L.; XIAO, X.M.; HUANG, H.Q.; HE, H.L.; EDIGER, L. 2009. Modeling gross primary productivity for winter wheat-maize double cropping System using MODIS time series and CO₂ eddy flux tower data. **Agriculture Ecosystems & Environment**, Amsterdam, v. 129, p. 391-400.
- YOSHIMOTO, M.; OUE, H.; KOBAYASHI, K. 2005. Energy balance and water use efficiency of rice canopies under free-air CO₂ enrichment. **Agricultural and Forest Meteorology**, Amsterdam, v. 133, p. 226-246.
- WAND, S.J.E.; MIDGLEY, G.F.; JONES, M.H.; CURTIS, P.S. 1999. Responses of wild C₄ and C₃ grass (Poaceae) species to elevated atmospheric CO₂ concentration: A meta-analytic test of current theories and perceptions. **Global Change Biology**, London, v.5, p.723-741.
- ZENG, Q.; LIU, B.A.; GILNA, B.; ZHANG, Y.L.; ZHU, C.W.; MA, H.L.; PANG, J.; CHEN, G.P.; ZHU, G.J. 2010. Elevated CO₂ effects on nutrient competition between a C₃ crop (*Oryza sativa* L.) and a C₄ weed (*Echinochloa crusgalli* L.). **Nutrient Cycling in Agroecosystems**, Amsterdam, v. 89, p. 93-104.

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