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IMPACT OF CLIMATE CHANGE ON PLANTS, FRUITS AND GRAINS[1]

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ABSTRACT - Over the past few years, the increased use of fossil fuels as well as the unsustainable use of land, through the reduction of native forests has increased the greenhouse gas emissions, contributing definitively to the rise in temperature on earth. In this scenario, two environmental factors, directly related to the physiology of crop production, are constantly being changed. The first change is the increase in the partial pressure of carbon dioxide (CO_2), which directly affects photosynthetic efficiency and the associated metabolic processes. The other change is the temperature increase which affects all the physiological and metabolic processes mediated by enzymes, especially photosynthesis and respiration. Therefore, this review aims to discuss the main effects caused by increased CO_2 pressure and the temperature rise in the physiology, productivity and post-harvest quality of plants with photosynthetic metabolism C3, C4 and CAM. Based on physiological evidence, the increased atmospheric CO_2 concentration will benefit net photosynthesis, stomatal conductance and the transpiration of C3 plants, however in hot, dry and saline environments, the C4 and CAM species present an advantage by having low photorespiration. Studies show controversial conclusions about the productivity of C3 and C4 plants, and the quality of their fruits or grains under different CO_2 concentrations or high temperatures. Thus, there is a need for more testing with C3 and C4 plants, besides of more researches with CAM plants, in view of the low number of experiments carried out in this type of plants.

Keywords: Carbon dioxide. Greenhouse gases. Photosynthetic metabolism. Plant physiology. Temperature.

IMPACTO DAS MUDANÇAS CLIMÁTICAS EM PLANTAS, FRUTOS E GRÃOS

RESUMO - Ao longo dos últimos anos, o aumento na utilização de combustíveis fósseis, bem como o uso não sustentável da terra, pela redução das florestas nativas, tem aumentado a emissão dos gases de efeito estufa, contribuindo de maneira definitiva para a elevação da temperatura na terra. Nesse cenário, dois fatores ambientais, diretamente ligados à fisiologia da produção vegetal, estão sendo constantemente alterados: a elevação na pressão parcial de dióxido de carbono (CO_2), que afeta diretamente a eficiência fotossintética e os processos metabólicos associados. A outra mudança é o aumento da temperatura, que afeta todos os processos fisiológicos e metabólicos mediados por enzimas, com destaque para a fotossíntese e a respiração. Diante disso, esta revisão teve como objetivo discutir os principais efeitos causados pelo aumento da concentração do CO_2 e elevação da temperatura na fisiologia, produtividade e qualidade pós-colheita das plantas com metabolismo fotossintético C3, C4 e CAM. Com base nas evidências fisiológicas o aumento da concentração de CO_2 atmosférico irá incrementar a fotossíntese líquida, a condutância estomática e a transpiração das plantas C3. Porém em ambientes quentes, secos e salinos, as espécies C4 e CAM apresentarão vantagem por possuir baixa fotorrespiração. Os estudos apresentam conclusões controvérsias sobre a produtividade das plantas C3 e C4, e a qualidade de seus frutos ou grãos submetidos a diferentes concentrações de CO_2 ou temperaturas elevadas. Assim, existe a necessidade de mais experimentação com plantas C3 e C4, além de mais pesquisas com plantas CAM, tendo em vista, o reduzido número de experimentos realizados com esse tipo de planta.

Palavras-chave: Dióxido de carbono. Gases de efeito estufa. Metabolismo fotossintético. Fisiologia de plantas. Temperatura.

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INTRODUCTION

Today's agenda is the debates about global climate change. This approach is recent. It began in the 80's when the World Meteorological Organization (WMO) and the United Nations Environment Program (UNEP) decided to monitor and simulate the changes climate occurring on our planet. The Intergovernmental Panel on Climate Change (IPCC) was created in order to gather information and indicate the causes and effects of these environmental impacts.

According to the IPCC (2007): the increased use of fossil fuels, inadequate agricultural practices and changes in the use of land are the human activities that contribute most to increasing the concentration of greenhouse gases (GHGs) in the atmosphere, and creating as a result, global warming (SOLOMON et al., 2007).

The main greenhouse gases are water vapor, methane, ozone, nitrous oxide and carbon dioxide (CO_2), the latter being responsible for 70% of the potential of raising the temperature of the Earth (MARENGO, 2006; BRENNAN et al., 2007; PIMENTEL, 2011). Studies show that by the end of this century the concentration of CO_2 will go from the current 384ppm to 720ppm, and as a consequence, the Earth's average temperature could rise 1.8 to 4.0°C (IPCC, 2007; LEAKEY et al., 2009).

Based on this problem, researchers have been trying to figure out how plants will behave with the possible increase of CO_2 concentration and temperature in the future.

Thus, this review aims to discuss, based on research results, the physiological and productive performance of the C3, C4 and CAM plants as well as the quality of their fruits or grains.

EFFECTS OF CO_2 AND TEMPERATURE ON PLANT PHYSIOLOGY

In nature, there are three types of plants with different photosynthetic metabolism: C3, C4 and CAM. Each one presents unique characteristics in regard to absorption and assimilation of the carbon as well as to the adaptation to temperature variations.

These different types of plants show changes in physiology, morphology, anatomy, chemistry and gene expression profile when grown in elevated CO_2 concentrations and high temperatures (BRAGA et al., 2006; SOUZA et al., 2008). Pimentel (2004) argues that the physiological responses to different environmental conditions are variable and may be a function of genotype, the environment and the phenotype interaction.

According to Marin and Nassif (2013), the increase in the atmospheric CO_2 concentration increases the gradient that drives the diffusion of CO_2 from the atmosphere to the chloroplast. Therefore higher rates of photosynthesis for a given stomatal conductance are expected. In addition, one has to maintain the same deficit in the stomata-atmosphere vapor pressure, so that a reduction in the transpiration rate will occur (TAIZ; ZAIGER 2013).

C3 photosynthetic metabolism plants in optimal temperature and humidity conditions will benefit the most from the increase in CO_2 concentration, but will suffer from stress if subjected to high temperatures due to a number of morphological, morpho-anatomical, physiological and biochemical changes, that affect their development and can result in drastic reduction in productivity (WAHID et al., 2007).

Contrary to the C3 plants, C4 and CAM photosynthetic metabolism plants in adverse conditions (high temperatures and low humidity) present less perspiration and a more efficient use of water and nutrients, especially nitrogen (STRECK, 2005; TAIZ; ZEIGER, 2013).

Barbosa et al. (2011) in an experiment with C3 photosynthetic metabolism plants, observed that the increase in CO_2 concentration (550ppm) in a growth chamber, decreased stomatal conductance in cowpea 'Marataoã' and 'Tapaihum' cultivars, 33.57% and 60.10%, respectively, compared to the control (360ppm). The transpiration rate reduced (26.82%) only in the Marataoã variety. The rate of net photosynthesis was not affected in either one of the cultivars. In sugar beet (*Beta vulgaris*), grown in an atmosphere rich in CO_2 (700ppm), Ignatova et al. (2005) noted an increase in net photosynthesis of 85%, 47% and 52% at days 3; 6 and 8 of analysis.

In an experiment with tropical tree species, Lloyd and Farquhar (2008) observed that the photosynthetic rates in the trees reduced when subjected to temperatures above 30°C. This condition caused an increase in respiration and transpiration and a reduction in stomatal conductance, due to the high leaf vapor pressure deficit. The same authors believe that the increase in CO_2 in the coming decades will compensate for any reduction in photosynthesis caused by increased temperature.

C3 photosynthetic mechanism land plants show positive responses (increase in net photosynthesis and decreased transpiration) when submitted in short term to an environment with high concentrations of CO_2. In the long term, this increase is compensated many times over by the down-regulation of photosynthetic capacity in the C3 species (LONG et al., 2004). According to Long et al. (2006) and Leakey et al. (2009), with the increase in the atmospheric CO_2 concentration, throughout the whole plant cycle, increased mitochondrial respiration occurs due to increased transcription and the activity of several glycolysis enzymes, the Krebs cycle, and the mitochondrial electron transportation chain.

In plants with C4 photosynthetic metabolism, the physiological responses can be variable. Vu et al. (2006) and Vu and Allen Jr (2009), working with sugar cane submitted to elevated CO_2 (720ppm) in a greenhouse, observed an increase of 17% and 26% in net photosynthesis and a reduction of over 30% in stomatal conductance and transpiration. Souza et al. (2008) reached similar conclusions, a reduction of over 30% in stomatal conductance and transpiration and a 30% increase in net photosynthesis of sugar cane, grown in an open-top chamber with 720ppm of CO_2. High CO_2 concentrations in C4 species, can improve the efficiency of water use, as it will reduce the periods of depletion of soil moisture, softening the period of stress during the dry season, decreased stomatal conductance and transpiration (MORGAN et al., 2011). Thus, the efficiency of water use per plant and per cultivated area would be greater (LEAKEY et al., 2009).

Long et al. (2006) observed reduction in stomatal conductance and water saving in corn growing in a high CO_2-concentration atmosphere (550ppm). However the CO_2 assimilation showed no significant increase. The cause of this is believed to be saturation, because the C4 photosynthetic metabolism plants allow high rates of photosynthesis even in environments with little atmospheric CO_2 and low stomatal conductance (TAIZ; ZAIGER, 2013).

The result of stomata partial closure are decreased transpiration and xylem flow protection, which allow the stomata efficiency under conditions of low humidity in the atmosphere and soil (OSBORNE; SACK, 2012). Stomatal conductance plays a key role in the exchange of leaf gases, limiting both the water outlet and the inlet of CO_2 (BUCKLEY, 2005).

It is noteworthy, too, that the stomatal closure is generally observed when the concentration of CO_2 is high and may be associated with a lower loss of latent heat and a consequent increase in leaf temperature (KIMBALL; BERNACCHI, 2006). According to Taiz and Zeiger (2013), in conditions of stress, stomatal movement constitutes in an important mean of plant defense against excessive water loss and eventual death by desiccation. Moreover, the guard cells are considered sensitive to the levels of CO_2 (SAGE, 2002).

Several of the observed photosynthetic responses can be attributed to differences in experimental technologies, plant species used, age of the plant, type of soil in which the plant was grown, climate of the region, as well as the duration of the treatment and the phenological phases in which the treatment was applied (DAVEY et al., 2006; DAMATTA et al., 2010; POLLEY et al., 2011).

Therefore, the general expectation, based on physiological evidence is that the increase of atmospheric CO2 benefits net photosynthesis, stomatal conductance and the transpiration of C3 plants. However, in hot, dry and salty environments, C4 and CAM species would have an advantage due to the fact that they show a very low photorespiration.

EFFECTS OF CO_2 AND TEMPERATURE ON THE PRODUCTIVITY OF PLANTS

With the increasing concentration of CO_2 on our Planet and the consequent global warming, several simulations of climate changes are being held. The main simulation model is based on CO_2 application in the atmosphere or soil, but controlled-environment studies are needed (GOMES et al., 2005), especially in growth or open-top chambers.

Studies under controlled conditions of temperature and humidity point to average increases of 30% in productivity in many C3 crops submitted to the atmosphere at twice the current CO_2 concentration. In less controlled field conditions, the productivity gain was lower, between 10-28% (FUHRER, 2003; LIMA; ALVES, 2008).

Ainsworth and Long (2005) also observed an increase (10-20%) in the production of air biomass in pastures of C3 plants. However in C4 plants, the increase was between 0% and 10%. Therefore these values should be lower in commercially cultivated areas because of limiting factors such as pests, diseases, competition with weed, nutrient availability and stress caused by temperatures and drought (GHINI et al., 2012).

According to Dias Filho (2007), in Brazil, most established pastures are formed by plants with the C4 photosynthetic pathway, which according to Fuhrer (2003), virtually do not present positive results at elevated CO_2 concentrations. However, the results are controversial. The sugar cane presents a high yield when grown in a high CO_2 concentration (SOUZA et al., 2008; VU; ALLEN Jr, 2009). On the other hand, well-fertilized and irrigated corn, does not respond positively to this factor (LEAKEY et al., 2006).

Experiments with other crops in a controlled environment, demonstrate positive responses when using the CO_2 enrichment method (FLORIDES; CHRISTODOULIDES, 2009; REDDY et al., 2010). Studies by Paula et al. (2011) with tabasco peppers, Kosobryukhov (2009) with cucumbers (*Cucumis sativus*) and Richter and Semenov (2005) with wheat (*Triticum aestivum*) reported an increase in productivity.

In protected environments, similar results were also observed by Frizzone et al. (2005a). They reported an increase in commercial productivity of yellow hybrid Bonus II melon fruits when doses of CO_2 combined with doses of potassium (K_2O) were applied through irrigation water, the optimal combination was 301.8 kg ha^{-1} and 300 kg ha^{-1}, respectively.

Field experiments also show satisfactory results: Furlan et al. (2001), Pinto et al. (2006) and Branco et al. (2007) with lettuce, melon and tomato, respectively. Studies by Krishnan et al. (2007), Shimono et al. (2009) and Walter et al. (2010), using outdoor CO_2 enrichment with rice and Crous et al.

(2008), with pine trees, found positive results

Experiments with C3 tree species corroborate with the positive results obtained in other crops. Higher production of biomass was observed in species such as Guapinol (*Hymenaea courbari*), Sickle Pigeonwings (*Clitoria falcata*), *Piptadenia gonoacantha* (commonly known in Brazil as "Pau-Jacaré"), Guapuruvu (*Schizolobium parahyba*) and Brazilian Rosewood (*Dalbergia nigra*) when submitted to high concentrations of CO_2, due to higher rates of photosynthesis (BUCKERIDGE et al., 2007; BUCKERIDGE et al., 2008; GRANDIS et al., 2010). According to Tremblay et al. (2005), species used for reforestation can also be stimulated with the enrichment of CO_2, especially after the burning of a deforested area due to loss of soil carbon to the atmosphere.

Enrichment of CO_2 in a short time period, when the demand for carbohydrates is high, as in the early development of the organs of economic interest, is an alternative to increase the dry matter production of certain crops (PIMENTEL, 2004). However, the effects of using this technique should be tested for each crop and its stage of development, goal of cultivation and treatment duration (LONG et al., 2006).

The application of CO_2 should be performed at appropriate phenological stages. According to technical recommendations by Frizzone et al. (2005b), the applications should occur in the determined period between the beginning of flowering, when 80% of the male flowers are open, and the beginning of the fruit stage, when 80% of the melon's fruit-set occurs.

Similar behavior was observed by D'Albuquerque Junior et al. (2007), who concluded that CO_2 applications at flowering and fruiting stages contributed to increase the melon production in 17% and 18%, respectively, when compared with the control (no application of CO_2). For the Guapinol species (commonly known in Brazil as "Jatobá") which also belongs to the C3 group, Grandis et al. (2010) claim that it is in the young stage where most CO_2 absorption occurs.

The enrichment of CO_2 combined with high temperatures may have both beneficial and non-beneficial effects in the crops with C3 and C4 photosynthetic pathways. According to Streck and Albert (2006) the increase of air temperature in 2; 3 and 6ºC nullified the beneficial effects of increased CO_2 in the productive yield of corn, wheat and soybeans, respectively. Walter et al. 2010, corroborate with this information in rice crops.

On the other hand, Grandis et al. (2010) observed that in physiological terms it is possible that the effects of the increase of the CO_2 concentration combined with high temperatures positively join together, in a controlled environment, increasing crop yields, especially in fast-growing species.

The positive effect of the combination of factors (temperature + CO_2) were observed in alfalfa (*Medicago sativa*) (ARANJUELO et al., 2005), cotton (*Gossypium hirsutum*) (YOON et al., 2009), Mongolian oak (*Quercus mogolica*) (WANG et al., 2008) and wheat (*Triticum aestivum*) (LUO et al., 2005), in which a growth productivity were observed. Positive responses are mainly due to improved photosynthetic rates that are associated with increased biomass (LUO et al., 2005; RICHTER; SEMENOV, 2005; BATTIST; NAYLOR, 2009; FRIEND et al., 2009).

According to Taiz and Zaiger (2013), the higher concentration of CO_2 stimulates photosynthesis and reduces stomatal conductances. Other responses are secondary, such as: accelerated growth, decreased transpiration and decreased leaf nitrogen. This is all due to the increased supply of carbon and its interaction with water loss. The temperature affects all of the biological processes such as: photosynthesis, respiration, cell division, transport and phenology.

As stated above, this issue still has conflicting reports on the productivity of C3 and C4 plants under different CO_2 concentrations and / or high temperatures. Therefore, there is need for more experimentation with C3 and C4 plants, in addition to implementation of experiments with CAM plants, in view of the low number of experiments carried out in this type of plants.

EFFECTS OF CO_2 AND TEMPERATURE ON QUALITY OF FRUITS OR GRAINS

The increased concentration of CO_2 in the atmosphere also presents different effects on the postharvest quality of fruits and grains; it can be beneficial as well as harmful. In working with wheat, Hogy et al. (2009) found that the enrichment of CO_2 in the atmosphere has decreased the quality of the grain, because it modified the amino acid concentrations, reducing the amount of protein 7.4% compared to the control.

In melon, CO_2 application in irrigation water increased the pulp acidity, soluble solids, thickness and firmness (FRIZZONE et al., 2005a). Using the same method and culture, Pinto et al. (2006) found no influence to acidity, soluble solids and pH. D'Albuquerque Junior et al. (2007) also reached the same conclusion, disagreeing only on the acidity, which reduced.

Positive results were also obtained in a protected environment. Tomato plants with liquid CO_2 enrichment (700 to 900ppm) presented larger fruits, strong coloring, higher ascorbic acid and total sugar content compared to the control 250 to 400 ppm CO_2 (ISLAM et al., 1996). Experiments with Niitaka pears corroborate the efficacy of this treatment. The fruits subjected to elevated CO_2 condition (700ppm) had larger dimensions (size and diameter) and soluble solids when compared with control fruits (HAN et al., 2012).

However in an experiment with yellow pitaya (*Selenicereus megalanthus*) and red pitaya (*Hylocereus undatus*), two species of CAM photosynthetic metabolism, no significant differences in soluble solids and pulp percentage were observed when two CO_2 concentrations were used (380 and 1000ppm) in an open-top chamber housed in a greenhouse. However, an average increase of 52g of the fresh weight in the yellow pitaya fruit was verified when using 1000ppm of CO_2 when compared with control fruits. As far as the red pitaya fruits, there were no statistical differences (WEISS et al., 2010).

The results also show differences in the quality of the fruits and grains of the C3 and C4 plants when submitted to different CO_2 concentrations and / or high temperatures. Therefore, more experiments are needed with all kinds of plants, especially the CAM photosynthetic metabolism ones.

METHODS OF TESTING

As noted earlier, the experimental methods for the analysis of responses to climate change are being used in order to indicate the actual interference of abiotic factors in physiology and in the productivity of plants, besides the quality of fruits and grains. These environment simulation models demonstrate the importance of examining the isolated and combined effects of elevated atmospheric CO_2 concentration and global warming.

Currently some methods are being tested for environments with and without control, such as outdoor CO_2 enrichment (HOGY et al., 2009) and water irrigation (FRIZZONE et al., 2005a), CO_2 injection in an open top chamber (WEISS et al., 2010) and in a growth chamber (PAULA et al., 2011). However, these methods should be further studied with the aim of seeking information about which method is best suited for each condition (local and environmental conditions) given the need for objective and clear methods that obtain accurate responses that ensure reliability for the scientific community.

According to Norby and Luo (2004) outdoor experiments are difficult to conduct and interpret, since their results may be masked by interference from other factors not foreseen such as excessive rainfall, drought stress, wind speed, incidence of pests and diseases, among others. However, this method has the advantage of indicating the actual results, taking into account that plants may encounter these factors in the field.

The CO_2 enrichment experiments with irrigation water can be developed in the field, a greenhouse and a controlled environment. This method has some advantages such as increasing the amount of carbon in the soil, improving its chemical quality, increasing the availability of macro and micronutrients present in the soil, reducing the risk of the plant suffering water stress, as they will be irrigated constantly.

The disadvantage is that it requires a large amount of CO_2 to be effective, which increases the production costs. According to Skok et al. (1962) and Stolwijk and Thimann (1957), cited by Storlie and Heckman (1996), fewer than 5% of CO_2 fixed by the plants is absorbed through the roots. So, the productivity increase as a result of CO_2 absorption by the root system, due the CO_2 application by irrigation water, should be quite unlikely.

Another method used in the field and in greenhouses is the injection of the CO_2 in an open-top chamber (WEISS et al., 2010). This method aims to inject CO_2 into the chamber, forming a type of microclimate; therefore it will increase the concentration of this gas, and still allowing gas exchanges, given the presence of a surface opening on the chamber.

The advantage of this methodology is that the plant can absorb both the CO_2 from the atmosphere as well as what is being injected artificially. The disadvantage is that loss of gas injected to the atmosphere without being tapped by the plant can occur and can burden the cost of experimentation.

Experiments in a controlled environment are also being conducted (BARBOSA et al., 2011). This method aims to control some abiotic factors (temperature, humidity, solar radiation, excess or deficit of water, etc.) that may influence the outcome of the experiments.

The advantage of this method is the possibility to test one or more factors in isolation without the risk of interference. The disadvantages are: high cost of system implementation and the uncertainty of obtaining the same environmental conditions when the crop is deployed in the planting areas.

CONCLUSION

The constant climate changes on our planet are the biggest concerns of the scientific community. It is unclear what will actually happen with the C3, C4 and CAM plants in the future. As shown in this review, the researchs showed conflicting results: while some species will be benefited, others will be harmed - which will depend mainly on the physiological metabolism of each type of plant.

This issue still has controversial conclusions about the productivity of C3 and C4 plants, and the quality of its fruits and grains under different CO_2 concentrations or high temperatures. Therefore, there is need for more experimentation with these three types of plants, particularly with CAM plants, in view of the low number of experiments carried out on this type of plant.

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