American Journal of Plant Sciences, 2018, 9, 150-162
http://www.scirp.org/journal/ajps
ISSN Online: 2158-2750
ISSN Print: 2158-2742

Elevated CO_2 Levels Affect Phytochemicals and Nutritional Quality of Food Crops

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How to cite this paper: Rajashekar, C.B. (2018) Elevated CO_2 Levels Affect Phytochemicals and Nutritional Quality of Food Crops. *American Journal of Plant Sciences*, **9**, 150-162.
https://doi.org/10.4236/ajps.2018.92013

Received: November 21, 2017
Accepted: January 21, 2018
Published: January 24, 2018

Abstract

Rising atmospheric CO_2 levels pose many challenges to global climate, thus to all forms of life including plants. The impact of elevated CO_2 on plant growth and development and the nutritional quality in relation to major nutrients in many crops has been explored extensively. However, information on the elevated CO_2 effects on the health-promoting phytochemicals in food crops is rather limited. Major nutrients in food crops including protein, phosphorus, potassium, calcium, iron, zinc and other micronutrients in many food crops are known to be suppressed at elevated CO_2 levels. Elevated CO_2 increases carbohydrate accumulation but decreases nitrogen accumulation in plants thus affecting their C-N ratio. A number of studies show that high C-N ratio and nitrogen limiting conditions in plants can result in the accumulation of carbon-based secondary metabolites, many of which are health-promoting phytochemicals and allelochemicals involved in plants' defense against pathogens and herbivory. Although the results from these studies are variable, it can be concluded that while elevated CO_2 is known to suppress the content of major nutrients, it may actually have a favorable impact on the accumulation of carbon-based phytochemicals in food crops.

Keywords

Elevated CO_2, Food Crops, Nutritional Quality, Phytochemicals, Secondary Metabolites

1. Introduction

The world population is projected to increase to nearly 10 billion by the middle of this century [1]. The rapidly growing population poses two important challenges, first, to be able to produce enough food to feed the growing population and second, to maintain the quality of food produced, especially in the face of rapidly changing climate and rising global CO_2 level. The rising CO_2 concentration is both an immediate and a long term concern to plants and animals including humans because in recent decades, global atmospheric CO_2 concentration has risen at an alarmingly rapid rate and is expected to reach dangerous levels in the near future. Presently, the global CO_2 level exceeds 400 ppm, [2] nearly a 30% increase since the 1950s and is projected to double by the end of this century [3].

Increasing amount of CO_2 in the atmosphere affects the global climate, especially temperature, which can have an adverse effect on all life forms on this planet. In addition to the direct impact of elevated CO_2 on the global temperature, CO_2 has a unique role in plants. That is because it plays a key role in photosynthesis which produces sugars, complex carbohydrates and carbon skeletons for most organic compounds in plants, and in fact, more than 90% of the plant dry matter is derived from photosynthesis. Thus, numerous studies have focused on understanding the CO_2 effects on various aspects of plant growth, productivity and survival in crops and as well as in native flora [4] [5] [6]. However, only a few studies have dealt with the nutritional quality of food crops and even fewer studies on the health-promoting phytochemicals in food crops. Health-promoting phytochemicals have been known to play an important role in preventing numerous chronic and degenerative diseases and in the well-being of humans [7]. Plants produce myriad classes of secondary metabolites, many of which are known to have health-promoting qualities while others (allelochemicals) are involved in plant defense against pathogens and herbivores. The purpose of this review is to focus more on the studies dealing with the health-promoting phytochemicals in plants and in food we consume, and look for a common theme in plants' responses to elevated CO_2. In order to provide a broader context to this subject, the review includes a brief discussion on the effects of elevated CO_2 on the overall growth characteristics of plants and the general nutritional quality of food crops relating to major nutrients.

2. Plant Growth and Major Nutrients

The effect of elevated CO_2 on plant growth and development and yield responses has been extensively studied both under controlled and field conditions [8] [9]. Although the overall responses under these experimental conditions produce similar pattern, they are subdued in field experiments, especially those involving Free Air Carbon dioxide Enrichment (FACE) approach compared to the controlled environmental studies [10] [11]. Typically, high CO_2 levels can result in a larger canopy and an increase in plant height, dry biomass and crop yields [10] [11] [12] [13]. Generally, C_3 crops and trees respond more strongly to elevated CO_2 than do C_4 or legumes. An overwhelming number of studies on field crops and on the native flora show an increase in the biomass accumulation at elevated CO_2 [8] [10]. In fact, this finding has been exploited in many horticultural crops including fruits and vegetables by increasing the ambient CO_2 levels during crop growth under protected environments such as greenhouse and high tunnels [14] [15]. The rationale behind using CO_2 enrichment is that the protective production systems can often experience lower CO_2 concentration during day time, especially in fall and winter [16] [17] [18]. However, what is not known is the effect of CO_2 enrichment on the nutritional quality of these crops. Thus, the potential challenge for horticultural food crop production is that these crops are likely to be exposed to high CO_2 not only in the protective production systems but also in open fields because of the rapidly rising atmospheric CO_2 levels.

It is well established that with higher CO_2 levels, the rate of photosynthetic activity increases initially, however, this response tends to diminish over the long term, as plants acclimate to this new condition [9]. The acclimation may not necessarily be due to the elevated CO_2 per se, but rather due to the changing C-N balance in the plants, resulting from the exposure to elevated CO_2. In C_3 plants, CO_2 is fixed by the enzyme, ribulose-1,5 biphosphate carboxylase (Rubisco), its content and activity in the leaves are reduced at elevated CO_2 levels [10] [19]. Thus, high CO_2 which is likely to increase C-N ratio in plants could also make nitrogen potentially a limiting factor for the synthesis of Rubisco, thereby negatively affecting the photosynthetic capacity, but increasing the nitrogen use efficiency [20] [21]. Nevertheless, in response to elevated CO_2, despite their acclimation, plants show a net accumulation of starch and sugars [20]. Thus, high CO_2 favors carbon accumulation with concomitant decrease in nitrogen content [9]. In fact, nitrogen metabolism is closely linked to carbon metabolism and plays an important role in signaling and in inducing significant changes in the regulation of a wide array of genes affecting a large swath of metabolic pathways involved in many cellular functions including primary and secondary metabolisms [22] [23]. Another important impact of elevated CO_2 on plants is that it can significantly reduce the leaf stomatal conductance [6] which can suppress leaf CO_2 exchange, thus potentially affecting photosynthesis, and also transpiration in a number of both C_3 and C_4 species [10] [21]. Thus, reduced transpiration improves the water use efficiency and may actually ward off the adverse affects of drought at elevated CO_2 [4] [21] [24] [25]. So, in a broader sense, C-N balance can affect not only plant functions but also the ecosystem at large including nutrient cycling, ecosystem dynamics, plant defense against biotic and abiotic stresses and plant interaction with herbivores and microbes [26] [27] [28].

While elevated CO_2 has a direct effect on photosynthetic activity and carbon accumulation in plants, it can also affect the profile of chemical composition in cells and tissues. It has long been known to affect the mineral or nutrient contents of plants including N, P, K, Ca and Mg [29]. As mentioned earlier, there is an overwhelming evidence that elevated CO_2 decreases nitrogen concentration in plant tissues including in edible parts of the plants, which has an enormous implication on the nutritional quality of human diet [30] [31]. Diminished nitrogen content of plants, which mostly reflects on their protein content, is a major concern as it plays an important role in the human diet. Malnutrition and public health issues resulting from protein deficiency are a common problem globally, especially in regions where C_3 cereal crops are the staple food. Thus, crops growing under elevated CO_2 will pose a serious health threat to a wide swath of global population. The decreased nitrogen concentration in plants has been attributed to several factors including the dilution effect caused by the accumulation of carbon at high CO_2 levels. However, after examining the concentrations of other nutrients in plant tissues exposed to elevated CO_2, Myers *et al.* [31] concluded that the decrease in nitrogen content in tissue may not be as a result of dilution caused by the accumulation of carbohydrates. Also, Taub and Wang [32] have outlined other possible factors for low nitrogen concentration in plants at high CO_2 including: a decrease demand for nitrogen, a decrease in uptake of nitrogen and other nutrients by plants as elevated CO_2 can reduce the transpiration rate, and a reduced assimilation of inorganic nitrogen into organic forms. Indeed, studies have shown that nitrate uptake by plants and its assimilation into organic compounds are known to be affected at elevated CO_2 in a wide variety of C_3 plants [33] [34].

In addition to decreased protein level in edible portion of many crops, study by Myers *et al.* [31] demonstrated a suppression of mineral nutrients in response to elevated CO_2 in several genotypes of commonly cultivated crops including rice, wheat, corn, sorghum, soybean and peas grown in diverse geographical locations over many growing seasons. The results showed a significant decrease in levels of important micronutrients such as zinc and iron in the edible portions of C_3 cereal and legume crops. This turns out to be significant because a large part of our global population receive their dietary zinc and iron from C_3 grains and legumes, and an estimated 2 billion people world-wide may suffer from deficiency of these micronutrients [35]. Thus, depressed levels of these nutrients in staple foods are likely to exacerbate this global health problem. Similar results were noted in leafy vegetables, such as lettuce and spinach, where elevated CO_2 showed a significant decrease in a number of major and micronutrients including protein and zinc [36]. In a meta-analysis of nutritional quality of many food crops as affected by elevated CO_2, Loladze [37] showed that the overall pattern in many C_3 plants was that elevated CO_2 depressed not only nitrogen but many other nutrients including iron, zinc, calcium, potassium, sulfur and other micronutrients.

Thus, rising atmospheric CO_2 level, in addition to inducing many adverse predictable climatic changes like warming and extreme weather-related events and the dire consequences on food security and safety, is likely to pose a real threat to the nutritional quality of food we consume. Ironically, in the face of the uncertainty of being able to produce enough food going forward because of the accelerated climatic changes, people may have to actually consume more food to get adequate nutrition. In fact, many studies have shown that herbivores and insect pests of plants consume more food at elevated CO_2 to successfully complete their life cycles [38] [39] [40].

3. Phytochemicals

There is limited information with a great deal of variability with regard to the impact of elevated CO_2 on the phytochemical content of plants. Thus, the major challenge has been to make valid comparisons of studies that often use different experimental conditions or methods to treat plants with CO_2, methods ranging from closed chambers with protected environmental conditions to open-top chambers and FACE system under field conditions, especially, when we know that plant responses vary greatly depending on the experimental conditions [10]. In addition, the concentrations of most phytochemicals in most tissues are likely to be low compared to major nutrients and strongly depend on many factors including genotype, plant part and plant developmental stage [41]. Therfore, a good deal of caution is warranted in comparing such disparate studies to draw valid conclusions.

Carbon and nitrogen metabolisms are tightly controlled in plants and typically, there is an inverse relationship between the contents of carbon and nitrogen in plants. The interrelationship between these nutrients (balance) has been explored quite extensively in relation to allelochemicals, plant defense and ecosystem characterization, but not so much with regard to health-promoting phytochemicals in crop plants. Higher atmospheric CO_2 can lead reallocation of resources with in the plant affecting many physiological process including changes in primary and secondary metabolisms, growth, and development. Elevated CO_2 can result in increased carbohydrate reserves in the plants, which affects not only the nutrient balance in plants but also serve as a source of secondary metabolites, many of which are health-promoting phytochemicals and others regarded as allelochemicals which can play an important role in plant defense against biotic and abiotic stresses. It is important to note that the distinction between health-promoting phytochemicals and allelochemicals is not always clear as many health-promoting phytochemicals can also play a key role in plant defense.

Considerable research on allelochemicals and plant defense has focused on the basic hypothesis that reallocation of plant resources, especially to secondary metabolites, is based on the premise of carbon–nutrient balance (CNB). Many studies have supported this hypothesis that a higher carbon accumulation can to lead to the accumulation of carbon-based secondary metabolites such as phenolic compounds [42] [43] [44]. However, this premise has also been a subject of considerable debate as some studies subsequently have failed to show the reliability of CNB in predicting the accumulation of carbon-based secondary metabolites in plants [45] [46]. The results are variable depending on the specific phytochemicals and plant species used in these studies. For example intermediates of phenylpropanoid pathway, a source of many phytochemicals, are a dynamic part of a complex network of pathways and many are likely to be in a state of flux as they may have rapid turnover rates. Some examples of such labile intermediates are phenolic glycosides, monoterpenes and sesquiterpenes whose concentrations are typically low and show great variability temporally and between plant organs. Thus, one would expect to see a lack of consistency in the results when these intermediates are measured in response to elevated CO_2. On the other hand, more stable intermediates or end products like condensed tannin or lignin are likely to show more consistent positive response with high carbon accumulation [44] [47]. Nonetheless, it should be noted that many of the labile intermediates of secondary metabolism are often likely to be more important with regard to the health-promoting qualities of food than the stable end products.

Many studies have shown that higher carbohydrate levels can lead to the accumulation of certain carbon-based secondary metabolites such as phenolic compounds including flavonoids in numerous plant species [48] [49] [50] [51]. In response to elevated CO_2, accumulations of phenolic acids, many flavonoids including condensed tannins have been observed in birch, willows and as well as in other species [52] [53] [54] [55]. Similarly, several flavonoid glycosides and other phenolic compounds accumulate in lettuce in response to high CO_2 [51]. High CO_2 has also been shown to improve the nutritional quality of tomato fruits by increasing the level of their carotenoids such as lycopene and β-carotene, and ascorbic acid [18] and in broccoli by increasing its glucosinolate content [56]. Furthermore, many studies have also shown that some of these phytochemicals, which are antioxidants, induced by elevated CO_2, play not only a key role in plant defense against many biotic and abiotic stresses but also mitigate the adverse effects caused by these stresses [57]-[62].

However, on the other hand, there are also studies that show negative or conflicting responses to elevated CO_2 in relation to carbon-based secondary metabolites. For example, elevated CO_2 produced low phenolic accumulation in needles of pine [48] and Norway spruce [63]. It has also been shown to reduce the quality of rice grains as measured by the contents of phytochemicals including total phenolics, flavonoids, tocopherol and tocotrienols [64]. In addition, it is not unusual to find contrasting results of CO_2 effects reported in the same species. For example, Sun *et al.* [65] reported lower antioxidant activity in strawberry fruits while Wang *et al.* [66] observed higher amounts of ascorbic acid, glutathione and phenolic compounds with higher antioxidant activity against many reactive oxidative species. Similarly in birch leaves, high CO_2 favored low accumulation of flavones while, in contrast, it was found to increase the accumulation of many flavonoids including condensed tannins [53].

Notwithstanding these conflicting results, a comparative review of secondary metabolite responses to elevated CO_2 by Pennuelas and Estiarte [67] suggests that in a majority of plant species studied there was a positive response to elevated CO_2 and N-limiting conditions leading to the accumulation phenolic compounds and condensed tannins.

4. Role of Nitrogen

A number of studies have examined the role of nitrogen in the secondary metabolism and the results show that N-limiting conditions lead to the accumulation of carbon-based secondary metabolites [68]. Bryant *et al.* [68] showed that low leaf nitrogen in Alaska paper birch seedlings, induced by defoliation, resulted in the accumulation of condensed tannin. Fritz *et al.* [69] examined the regulation of synthesis of secondary metabolites in relation to C-N status in tobacco plants. They found that nitrate nutrition can suppress the accumulation of many carbon-based secondary metabolites but increase the content of N-containing alkaloid such as nicotine. On the other hand, nitrate deficient tobacco plants induced many genes involved in phenylpropanoid pathway including PAL, 4CL-2 and HQT and thus, accumulated a number of phenylpropanoids and flavonoids, such as benzoic acid, coumaric acid, caffeic acid, chlorogenic acid, rutin and lignin. They demonstrated that this response is driven by the lack of adequate nitrate nutrition to the plants rather than the organic nitrogen status of plants. This is consistent with the results observed in Arabidopsis where a number of genes involved phenylpropanoid and flavonoid metabolism were activated in N-deficient plants while nitrate addition resulted in a coordinated repression of genes involved in these pathways [23].

Thus form these studies, it can be concluded that nitrogen nutrition of plants plays a major role in the accumulation of carbon-based secondary metabolites. This is supported by many field studies where limited nitrogen fertilization can produce results very similar to those in response to elevated CO_2. Low nitrogen fertilization in numerous crops including many fruits and vegetables can result in increased accumulation of a whole host of phenolic compounds (see the excellent review by Treutter [70]). Low nitrogen favored the accumulation of several phenolic compounds including flavonoids and chlorogenic acid in apple fruits [71]. Similar results were observed in apple leaves by Leser and Treutter [72] with regard to a number of secondary metabolites including hydroxyl cinnamic acids and many flavonoids. In field trials, low nitrogen application to cabbage stimulated the accumulation of nitrogen and sulfur containing phytochemicals such as glucosinolates [73]. Similar results have been reported in other brassica species as well [74]. However, it should be noted that while there is a strong evidence from these studies that low nitrogen fertilization can induce the synthesis of carbon-based phytochemicals, it is not clear whether carbon accumulation also played any role in this as carbon accumulation was not measured in these studies. However based on many other studies [42] [67] [69], it is safe to assume that both nitrogen nutrition and carbon accumulation have a significant role in the accumulation of phytochemicals in plants.

5. Conclusion

In conclusion, elevated CO_2 is known to have a positive effect on photosynthetic activity, plant growth, biomass accumulation and yield. It can also reduce transpiration, increase water use efficiency and improve drought resistance. Higher photosynthetic activity can result in carbon accumulation and a higher C-N ratio which can affect a wide range of metabolic functions including primary and secondary metabolisms in plants. Elevated CO_2 depresses nitrogen content (protein) along with a number of major nutrients including phosphorus, potassium, calcium, iron, zinc and others in food crops which certainly can lead to serious global health crisis and malnutrition. As carbon and nitrogen metabolisms are tightly controlled, carbon accumulation and nitrogen limitation are known to coordinate and regulate numerous genes across several metabolic pathways, including secondary metabolism, thus affecting many cell functions. Elevated CO_2 and N-limiting conditions have been known to favor the accumulation of carbon-based secondary metabolites which have a key role in health-promoting qualities of food crops and in plant defense against herbivory in many plant species. While the results are variable with regard to the effect of elevated CO_2 on the health-promoting phytochemical accumulation in food crops, a great number of studies support the fact that elevated CO_2 may favor the accumulation carbon-based phytochemicals. Thus, although elevated CO_2 can suppress the contents of major nutrients, it may enhance certain group of health-promoting phytochemicals in food crops.

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