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The Impact of Elevated CO₂ and High Temperature on the Nutritional Quality of Fruits - A Short Review

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ABSTRACT

Fruits are essential components of modern diet. Fruit nutrients provide important benefits to human in various ways for better health. Phytochemicals in fruit vary in quality and quantity depending mainly on fruit species and cultivar. Additionally, these phytonutrients can also be affected by different environmental factors including atmospheric carbon dioxide (CO₂) and temperature. The current changes and the continuous anticipated increase in the CO₂ concentrations and temperature in the atmosphere has become a major challenge in crop production. The literature is rich with investigations of individual and combination effects of elevated CO₂ and temperature on growth, development and yield of plants, including fruits. The purpose of this review is to evaluate the impacts of elevated CO₂ and high temperature individually and interactively on nutritional quality of fruits. According to the reviewed literature, both elevated CO₂ and temperature significantly influenced fruit nutrient content and availability. Elevated CO₂ is expected to affect positively the fruits nutrient content, while mixed responses found for high temperature. Interaction effects of these factors are the most important since they are predicted to increase concomitantly. With available literature, the combination impact of these factors on fruit nutrients was discussed under three different hypotheses in this review. (1) high temperature may offset the positive effects of elevated CO₂, (2) elevated CO₂ would compensate for the negative effects of high temperature and (3) interactively, both elevated CO₂ and temperature may increase or decrease the phytonutrients in fruits.

Keywords: carbon dioxide, fruits, phytochemicals, temperature

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Introduction

The world is currently experiencing significant environmental and socioeconomical impacts due to the ongoing climate changes. Those impacts are already evident on agriculture and have been widely researched. Atmospheric carbon dioxide concentration (CO₂) and surface temperature are key factors in driving climate changes, affecting crop production [1]. The current atmospheric CO₂ level (400 ppm in September, 2018)¹ has far exceeded the pre-industrial level (280 ppm) and predicted to further increase beyond 1000 ppm by the end of this decade[2]. Increased greenhouse gasses, primarily CO₂ has caused global warming of 1.5 °C above the pre-industrial level [3]. It has been also predicted that temperature is likely to rise by a maximum of 4.9 °C by 2100 IPCC [1]. Both, elevated CO₂ and higher surface temperature influence crop growth, development and yields [4, 5]. Further, these factors can be accompanied by the anticipated increase in variability and uncertainty of precipitation with increasing tendency for extreme events (floods, droughts, heat waves and frosts) across the world[1].

Plants are directly affected by atmospheric CO₂ and showed different morphological, physiological, biochemical and molecular responses to elevated CO₂. Significant increases in photosynthesis and water use efficiency have been observed under elevated CO₂ with decreased transpirations and stomatal conductance in plants. Such increases in the photosynthetic capacity profits higher growth and yields in plants [6]. However, those positive effects can be altered by other factors of climate change such as temperature, precipitation and tropospheric ozone concentration [5]. Generally, higher temperatures in plant growth environment have been shown to reduce plant photosynthesis, biomass production and adversely affect flowering and fruiting in plants [7].

Consequences of climate change have been analysed in relation to the impact on quantity and quality of different crop species [5]. Effect of climate changes on growth and yield have been mainly investigated wheat, rice, canola, and legumes [8-15] for being the staple foods in different regions in the world. It is a fact that these main crops are more important when considering the food security. However, in recent years, fruits and vegetables have greatly attracted scientists' attention to examine the effect of climate changes on their phytochemicals which are important for human health and immune systems. Recent epidemiological studies have that increased consumption of fruits has reduced the occurrence of most of the diseases including cancers and cardiovascular [16]. Therefore, fruits have become a major part of modern diet supplying essential dietary micronutrients and fibres. Additionally, the nutritional quality of fruits can be detrimentally affected by various factors including climate change [17-20]. Therefore, it is important to understand the influences of elevated atmospheric CO₂ and higher temperature individually and interactively on fruit crops for food security and better health in future.

In this context, the current study reviewed the results of past studies to understand the separate and combined effects of elevated CO₂ and high temperature in growth environment on nutritional quality of fruits. In addition, the study highlights the research gaps and finally the potentials for future research.

Discussion

Effects of elevated CO₂ on nutritional quality of fruits

Elevated CO₂ in the growth environment potentially increase the net photosynthesis of plants specially in C₃ plants as CO₂ is limited in C₃ photosynthesis under current conditions. It has been reported that net photosynthesis can increase by more than 50% in respond to

¹ <https://www.co2.earth/>

elevation of CO₂ which was attributed to higher carboxylation rates as a result of abundant availability of CO₂ as a substrate [21]. Hence, most of fruit crops as C₃ species are expected to respond favourably to future CO₂ trend. Moreover, some C₃ fruit species have shown higher photosynthetic efficiency and greater sensitivity to elevated CO₂ in comparison to the plants that have same photosynthetic pathway [22]. Enhanced CO₂ in the growth environment promotes accumulation of carbohydrates in plants as a result of stimulated photosynthetic responses [23]. The main function of these carbohydrates is growing the plant biomass and then utilises the surplus in the production of plant secondary metabolites or micronutrients [24]. Many studies have discussed the relationship between CO₂ elevation in growth environment and the production of carbon-based secondary metabolites [25-27], and de Rezende et al. [28] and Chen et al. [29] confirmed that plants increased the synthesis of phenolic compounds when they have higher carbohydrate reservoirs. Increased fruit yields under enhance CO₂ have been widely reported in strawberry [30-36], raspberry [37], and grapes [38].

The fascinating factor of fruits is that different fruit species contain different flavours, aromas and skin colours, in addition to sugars and organic acids such as citric, malic, and tartaric. Sugars act as the fuel for plant metabolic processes and also as precursors of flavour compounds in fruits. Further, soluble sugars contribute directly to the sweetness, and it is considered that fruits will have the richest flavour when they have a good balance in sugars and organic acids [36, 38]. Elevated CO₂ (650 and 950 ppm) enhanced the glucose, fructose and sucrose contents as well as the total sugars which contribute most to the fruity flavour in strawberries [36]. Consequently, aroma compounds such as ethyl hexanoate, ethyl butanoate, methyl hexanoate, methyl butanoate, hexyl acetate, hexyl hexanoate, methyl methanoate, butyl acetate, methyl acetate, furaneol, linalool, and methyl octanoate were

increased significantly when growing strawberry at elevated CO₂. Among these strawberry aromatic compounds, methyl hexanoate, ethyl hexanoate, and ethyl butanoate were increased by 68%, 48%, and, 35% respectively, at 950 ppm CO₂. The same authors [36] suggested that the increased amounts of sugars; importantly fructose may contribute to enhance aroma compounds *via* furanone synthesis. However, elevated CO₂ reduced the organic acid contents (-17%) and increased total sugar to acid ratio (40%), reflecting lowered sourness in strawberry [36, 39]. Moreover, elevated CO₂ has positively affected both acids and sugar contents of grapes. Growing the grapes at 700 ppm CO₂, increased the acid concentration by 8-9% and sugar content by 13-14% [38], however, a study by Kizildeniz et al. [40] demonstrated that CO₂ elevation (700 ppm) under ambient growth conditions did not influence either malic or tartaric acids concentrations in grapes.

Fruits also contain polyphenols which are a major group of phytonutrients contribute to the antioxidant capacity of fruits. These compounds are important in reducing the oxidative stresses and promote better health. Fruit species reveal different polyphenol profiles varied both in quality and quantity. Elevated CO₂ during plant growth significantly increased the contents of total polyphenols, flavonoids and anthocyanins in fruits [40, 41]. Anthocyanin composition and content are important quality attributes in fruits which influence the fruit colour. Pelargonidin is the dominant anthocyanin pigment responsible for the colour of strawberry, and cyanidin for raspberry and blackberry [42]. Strawberries grown under enriched CO₂ (650 and 950 ppm) conditions had greater amounts of polyphenols including flavonoids and anthocyanins [41]. Enhanced CO₂ up to 950 ppm increased the contents of pelargonidin-3-glucoside, p-coumaroylglucose, cyanidin 3-glucoside, pelargonidin 3-glucoside-succinate, and dihydroflavonol respectively by 72%, 76%, 105%, 110%, and 269% in strawberries [41]. The same study reported that the levels of

ascorbic acid, glutathione, ascorbic acid to dehydroascorbic acid ratio, glutathione to oxidised glutathione ratio were increased and the content of dehydroascorbic acid decreased at the higher CO₂ levels. The ascorbic acid is considered a major antioxidant that attacks free radicals and protect the cells against the oxidative damages space[43]. Elevated CO₂ up to 700 ppm increased the total anthocyanin content by 48% and the skin colour density in grapes. These anthocyanins are produced in grapes *via* the flavonoid synthesis pathway and pigmented the berry skin in red, purple and blue colours [40]. Tannins and flavonoids are considered the major polyphenols found in guava plants and 25% increase in tannin contents has been reported under enhanced CO₂ (780 ppm) conditions [28]. The same authors suggested that the observed increase in tannin might be attributed to the increased starch accumulation, higher carbon/nitrogen ratio, and defence related metabolism in plants. These previously reported studies confirmed that rising CO₂ in the atmosphere would lead to improve growth and yield of fruits as well as the nutrient contents.

Effects of elevated temperature on nutritional quality of fruits

Temperature is an important factor in crop production that affects crop growth and development. Air temperature varies across the world depending on the geographical location as well as the season of the year [44]. Plants response to temperature can be highly variable with genetic make-up and the developmental stage of plant and other abiotic factors in growth environment. Therefore, it is hard to predict the effects of rising air temperature on crop production and quality. According to previous studies, in general, higher temperature is expected to cause varying degrees of negative impacts on plant growth, development and yield [44-46]. Commercial strawberry cultivation has already been affected by the rising air temperatures in some parts of the world. For example, 4 °C increase in average air

temperature was reported in Turkey in 2008 compared with 2007 and as a result, the strawberry yield had declined by 32%. In the mean time, the predicted increase in the surface temperature by 6 °C in 2091 – 2100 in Europe , is expected to shorten the duration of crop cycle and to cause significant yield reductions [20]. Kadir [46] reported that when the temperature rose well above the optimum, it caused detrimental effects on fruit crops. For instant, high temperature (40/35 °C day/night) reduced the net photosynthesis of strawberries by 44%, reducing the fruit yields to zero [46].

In contrast to the effect of elevated CO₂ on carbohydrates contents in plants [29, 39], carbohydrates and sugars contents were significantly reduced by higher day/night temperature (30/22 °C) in strawberries in comparison to ambient temperature (25/12 °C) [47]. As a result, it affected the sensory qualities of strawberry and reduced its sweetness and the flavour [47]. However, similar to the effects observed under CO₂ elevation, total polyphenols [48], flavonols and anthocyanin concentrations were significantly increased by elevated temperature (30/22 °C) in strawberries [47]. The contents of p-coumaroylglucose, dihydroflavonol, quercetin-3-glucoside, quercetin-3-glucuronide, kaempferol-3-glucoside, kaempferol-3-glucuronide, cyanidin-3-glucoside, pelargonidin-3-glucoside, pelargonidin-3-rutinoside, cyanidin-3-glucoside-succinate, and pelargonidin-3-glucoside-succinate were greater in strawberries under higher temperature and resulted in significant increase in antioxidant capacity by 54% [48, 49]. Additionally, such increment in polyphenol contents were associated with more redder and darker fruit surface colour in strawberries [47]. Increased anthocyanin contents were also observed in grapes when grown at higher temperature [50, 51]. Contradictory to these positive impacts of high temperature observed on strawberry and grape, hot climates (>30 °C) in summer had markedly reduced the anthocyanin accumulation in apple skin caused

by down regulation of anthocyanin synthesise pathway [52]. Cyanidin-3-galactoside in the main anthocyanin pigment responsible for the red colour of apple skin and lower temperature was very much favourable in synthesis and accumulation of anthocyanin pigments in apples [53]. Further, higher temperature (22/12 °C) during the post bloom in apple enhanced the soluble solids content, greater starch hydrolysis and more yellow colour peel in comparison to cooler conditions [54].

Higher day/night temperature (30/22 °C) in growth environment during fruiting made significant reductions in organic acid contents especially, citric acid (-18%) and ellagic acid (-15%) in strawberries [47]. Further, the soluble solids, titratable acidity, soluble solids to titratable acidity ratio, and ascorbic acids contents were decreased by 36%, 14%, 25%, and 41%, respectively at 30/22 °C in comparison with 25/12 °C. In contrast, strawberry grown under high temperature (30/20 °C) during the whole crop cycle had no effect on ascorbic acid content in fruits [48]. Further, kiwi fruits exposed to high temperature during the cell division phase in growth had lower concentrations of ascorbic acid. At the same time, kiwi fruits contained remarkably lower concentrations of carbohydrates, total sugars, and fruit acidity under high temperature. Therefore, the study demonstrated a positive correlation between sugar and ascorbate metabolism in plants at elevated temperature [55]. Similarly, malic acid content in grapes declined significantly at higher temperature possibly due to the increase in respiration. The higher temperature stimulates the enzyme activity responsible for the degradation of malic acid to glucose which is utilised in respiration [40]. As a result, grapes lost organic acids in respiration under warmer growth conditions and had decreased acidity which could directly influence the grape juice quality [40].

Some studies have reported that high temperatures (33 and 42 °C) reduced protein synthesis and final total protein content in

strawberries. Typical cellular protein content decreased in respond to the higher growth temperatures, however strawberry leaves and flowers synthesized new heat-shock proteins as a result of imposed heat stress [56]. Moreover, strawberries showed greater heat-stress tolerance under gradual heat stress with the synthesis of more new heat stable proteins. Plant protein was declined only by 51% due to the gradual heat stress but 67% protein reduction was observed due to the sudden heat stress [57]. In conclusion, rising temperature may cause both positive and negative impacts on fruits nutritional quality. In addition, synthesis of antioxidants and heat stress proteins under elevated temperature may help fruits and plants to survive the anticipated harsh future climate conditions.

Interactive effects of elevated CO₂ and temperature on nutritional quality of fruits

The previous discussions in sections 2.1. and 2.2. demonstrated the independent effects of elevated CO₂ and temperature on fruit phytochemicals. However, as both atmospheric CO₂ and temperature will increase simultaneously, their interactive effects on plants may be more pronounced. Consequently, the individual effects of elevated CO₂ and temperature on plants would be considerably different from their interactive effects. Under these circumstances, the available literature could be categorized into three different hypotheses in order to predict the adjustments of above climatic factors in crop production. These categories are: (1) High temperature may offset the positive effects of elevated CO₂ on fruit nutrients, (2) Elevated CO₂ may compensate the negative effects of rising temperature and stabilize or neutralize the content of phytochemicals or (3) Both factors in combination would contribute either to increase or decrease in fruit nutrient contents.

A study by Vu et al. [58] revealed that under both elevated CO₂ and temperature, sweet orange trees performed well and had higher photosynthetic rates, water use efficiency and

lower rates of transpiration and stomatal conductance. In strawberry, elevated CO₂ increased the net photosynthesis by around 50% under 25 °C, while, both elevated CO₂ and high temperature only increased the net photosynthesis approximately by 35% [59]. Further, strawberries showed highest fruit yield under elevated CO₂ (720 ppm) however, the yield was reduced by 35% due to the increase temperature by 5°C under elevated CO₂ [60]. These results and observations agree with our first hypothesis (High temperature may offset the positive effects of elevated CO₂). The interaction effect of elevated CO₂ and temperature (720 ppm and 25/20 °C) on the concentrations of fructose and glucose, and sweetness index of strawberries was significant. In comparison with the control treatment, the sugar concentrations were increased by elevated CO₂ but slightly decreased by the elevated temperature. However, highest contents of fructose, glucose and greater sweetness index were found under both elevated CO₂ and temperature conditions [60]. Similarly, Elevated temperature remarkably enhanced the amounts of malic acid and tartaric acid in grapes thereby negatively affected the pH of the juice. However, elevated CO₂ compensated that negative effects of elevated temperature and stabilized the juice acidity in grapes [40]. Once more, such observations agree with the second hypothesis (Elevated CO₂ may compensate the negative effects of rising temperature). Further, both elevated CO₂ and temperature enhanced the anthocyanin contents in grape [61]. Additionally, the combined elevated CO₂ and temperature with drought increased the total soluble solid contents and reduced the total polyphenol index and colour density of grapes [40]. The stronger interaction of elevated CO₂ and temperature was also detected in strawberry fruits, which showed greater polyphenols contents under these condition [Balasooriya et al. [62] (unpublished work)]. According to these results, increased CO₂ (650 and 950 ppm) and higher temperature (ambient+5 °C) together enhanced the amounts of total polyphenol, antioxidant, flavonoid and

anthocyanin contents to the highest. The individual phenolic compounds in strawberry such as pelargonidin rutinoside, cyanidin, quercetin derivatives, kaempferol derivatives, catechin, ferulic acid, coumaroyl, and resveratrol were also significantly increased under elevated growth conditions (950 ppm and 30 °C). However, higher temperature considerably offset the positive effects of elevated CO₂ for the contents of some individual polyphenols like pelargonidin-3-glucoside. These reported findings supported the third hypothesis (Both high CO₂ and temperature would contribute together either to increase or decrease the nutrient contents).

Finally, it should be emphasised that individual and interactive effects of elevated CO₂ and high temperature on fruit phytochemicals can be affected by the other factors in the growth environment such as; irrigation [40], UV level [53], light [63], soil nutrients [60], and ozone concentration etc. and the crop factors like growth stage [47, 54, 55] and cultivar [40, 52].

Conclusion

This review suggests that the nutritional quality of fruits can seriously be affected by elevated CO₂, high temperature and their interactions depending on the fruit species, cultivar, growth stage and interactions with other environmental factors. Elevated CO₂ may or may not alleviate the deleterious effects of higher temperatures and enhance the fruit performance under future climatic conditions. However, the effects of climate changes are complex and hard to predict the exact effects of the combined factors on fruit development, nutrition values and chemical composition. To the best of our knowledge, studies are scarce in recent literature to draw a clear picture of the interaction effects of elevated CO₂ and higher temperature on fruit nutritional quality. Therefore, the authors suggest that more investigations should be carried out to evaluate the combined effects of elevated CO₂ and high temperature on fruit phytochemicals in different crop species and cultivars. Such works will be more beneficial in order to predict how

various fruits will respond to individual and combined climate change factors, and how to screen and choose the better plants that can thrive under the future climate changes, and while sustaining the economic yield and better fruit quality.

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