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Impacts of Elevated Carbon Dioxide and Temperature on Physicochemical and Nutrient Properties in Strawberries

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Abstract

Strawberry (*Fragaria x ananassa* Duch.) is one of the most popular edible fruit worldwide. Strawberries are generally cultivated in open fields or under protected cropping, and are available all year round. Consumers prefer fruit with a bright red color, sweet taste, and distinct aroma. Over the past two decades, strawberry has shown one of the highest growth rates in terms of fresh fruit consumption. Such increment in consumer demand for strawberry could be attributed to its high nutrient content and perceived health benefits. Phenolic compounds and vitamins are the main antioxidants in the strawberry phytochemical profile. However, the predicted climate changes in the near future are expected to cause major challenges in modern agriculture due to its significant potential negative impacts on both quantity and quality of various crops, including strawberry. Increasing atmospheric CO_2 levels and ambient temperature are the key factors in a changing climate scenario. The effects of either high CO_2 or high temperature on growth, development, yield, and quality of strawberry plant has been relatively well-investigated. However, information on the effects of combined high CO_2 and temperature on strawberry is lacking. This review will examine the literature available about the relationship between climate changes and strawberry production and quality, and address the information needed in the future research in this area.

Keywords

Antioxidants, Biological availability, Climate change, Polyphenolic compounds, Quality

Introduction

Climate change is considered to be the most serious global challenge faced by humanity today [1]. It is predicted to cause varying degrees of negative impacts across agro-ecosystems of the world and is flagged as a major threat to global food production systems as we know them. Rapidly rising greenhouse gases such as carbon dioxide (CO_2) caused by various human activities appears to be altering the global climate. In particular, rainfall distribution and frequency, due to heating of Earth's surface, oceans, and atmosphere [2]. Based on global climate modelling atmospheric CO_2 concentrations may increase over 1000 ppm, and the global surface temperature may also increase by 2.5 C to 7.8 C by the end of the 21st-century [1]. These environmental factors, individually and in combination, are expected to have significant impacts on crop growth, development and production. For example, increased CO_2 levels have been reported to enhance plant photosynthesis and water use efficiency, but to reduce transpiration and there by directly affecting growth and yield. On the other hand, higher temperature levels have reduced plant photosynthesis, increased transpiration, and interestingly, shortened crop cycles [3]. However, it should be noted that the effects of climate change on crops quality and

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quantity may also be affected by a range of other factors, including region [4], crop species, harvestable yield components, and crop management [5].

Strawberry is one of the most nutritious fruits which can supplement high contents of micro-nutrients including phenolic compounds and vitamins into human diets. Over the past decade, significant changes have been attributed to strawberry production areas in the world due to climate change [6-10]. This paper discusses the importance of strawberry as a micronutrient rich fruit in the human diet, and reviews the independent and combined effects of high CO_2 and high temperature on growth, development, production, and nutritional quality of strawberries. Further, it attempts to identify the current gaps in knowledge and future research directions in order to develop strategies for maintaining the quality and productivity of strawberries under future anticipated environmental changes. This review is an initial milestone in a current PhD research project at the University of Melbourne to define the optimum combined high CO_2 and temperature for good strawberry quality and quantity.

Strawberry

Strawberry is one of the commonest and highly demanded edible fruits, produced worldwide. It is a member of the family *Rosaceae* and belongs to the genus *Fragaria* which refers to fragrant in Latin. There are two types of strawberries: wild and cultivated. The wild European strawberry is *F. vesca* L., whereas *F. ananassa* Duch. is the cultivated type among the 23 *Fragaria* species [11].

Strawberry is a perennial herb with a prostrate growth habit, which prefers a cool and moist climate [11] and requires full sun for optimum growth performance. It prefers well-drained soils with an optimal pH range from 5.3 to 6.5. Among all soft fruits, strawberry is considered as the most economically important fruit, with its very high crop production value per ha [12]. The world leading strawberry producers in 2013 were China, the USA, Mexico, Turkey, and Spain. The total global annual strawberry production was around 7.7 million tons produced on 361,662 ha [13]. The Food and Agriculture Organization (FAO) data show that global strawberry production has more than doubled in the last 2 decades from 3.2 million tons in 1993.

Common quality parameters of strawberry involve consumer acceptance of color, size, shape, firmness, and flavor as perceived by the combination of taste and aroma. Good-quality strawberries have high sugar and aroma levels, along with acid balance and preferred physical properties like color and firmness. It has been reported that strawberry flavor depends on the content of sucrose, glucose, and fructose, which are the organoleptic factors of sweetness [14]. Additionally, the higher sugar concentration, acid balance, active aromatic volatile composition, and polyphenols contents contribute to aroma and flavor. Organic acids like citric acid and malic acid mainly create fruit sourness and alter fruit colour by affecting pH and anthocyanin compounds [15]. The physicochemical characteristics of strawberry also change during fruit maturity. Total soluble solids (TSS)/titratable acidity (TA) ratio (TSS/TA), and levels of sucrose,

Table 1: Composition of fresh strawberry (per 100 g of edible fruit) based on country of origin. Values depend on cultivar, growth conditions, and the geographical location.

Nutritional component	**Country or Region***				
	USA [54]	**Australia and NZ** [54]	**UK** [54]	**Asia** [54]	**Japan** [54]
Proximates and carbohydrates					
Water (g)	90.95	92.1	91.6	92.4	90.0
Energy (kcal)	32	25	30	26	34
Protein (g)	0.67	0.7	0.6	0.8	0.9
Total lipids (g)	0.3	0.2	0.5	0.2	0.1
Ash (g)	0.4	0.5	-	0.4	0.5
Carbohydrates (g)	7.68	3.9	6.1	4.3	8.5
Dietary fibre (g)	2.0	2.5	-	1.9	1.4
Total sugar (g)	4.89	3.8	6.1	-	6.1
Minerals					
Calcium (mg)	16	18	17	21	17
Magnesium (mg)	14	8	12		13
Phosphorus (mg)	24	24	26	16	31
Potassium (mg)	153	158	170	66	170
Sodium (mg)	1	3	1	3	-
Vitamins					
Vitamin C, total ascorbic acid (AA) (mg)	58.8	45.0	57.0	59.0	62.0
Folate (µg)	24	39	61		90
Vitamin A, RAE (µg)	1	0	-	2	1
Beta-carotene (µg)	7	0	-	23	17

*__Source:__ USDA [54], AUSNUT [55], CoFIDS [56], ASEAN [57], MEXT [58].

glucose, fructose, and malic acid increase with maturity, while TA and citric acid levels decrease [16]. Data on the composition of strawberry based on the country of origin are shown in Table 1. A considerable variation could be found in the Table 1 due to the genetic differences, environmental conditions, pre and postharvest management practices and the methods of analysis used.

Health benefits of strawberry antioxidants

Strawberries are rich in natural antioxidant compounds, including polyphenols and vitamins (vitamin C and folate). Phenolic compounds are diverse in content and include; flavonoids, phenolic acids, lignans, stilbenes, tannins, and coumarins (Table 2) and accounts for numerous health benefits [17]. Among selected popular fruits, strawberry shows the second highest polyphenol content of 146 mg/100 g after blueberries (445 mg/100 g) and is higher than orange and apple [18]. The level of total phenols in strawberry could vary between 43 and 273 mg/100 g fresh weight (FW) [14]. Due to this highly nutritious features, strawberry extracts has been recently consumed as an ingredient in functional foods and dietary supplements as a human health promoting agent [19].

Strong research evidence on health benefits of strawberry has been well-documented through the outcomes of numerous recent epidemiological and clinical studies [19-21].

Table 2: Phenolic compounds found in Strawberry.

Phenolic group	**Source***	**Phenolic group**	**Source***
Flavonoids		**Phenolic acids**	
Flavonols		Gallic acid	8
Quercetin	7,3	Vanillic acid	8
Quercetin-3-glucuronide	4	Hydroxycinnamic acids	3
Quercetin-3-malonylglucoside	2,4	p-coumaroyl hexose	4
Quercetin-rutinoside	4	cinnamoyl glucose	2
Quercetin-glucoside	4	ferulic acid derivatives	3
Quercetin-glucuronide	4		
Kaempferol	7,3		
Kaempferol-3-glucoside	4		
Kaempferol-3-malonylglucoside	2,4	**Stilbenes**	
Kaempferol-coumaroyl-glucoside	4	Resveratrol	11
Kaempferol-glucuronide	4		
Flavanols	3,5	**Tannins**	
Catechin	1,2,4	***Hydrolysed***	
Proanthocyanidin B1	4	**Ellagitannins**	
Proanthocyanidin trimer	4	Ellagitannin	2,4,6
Proanthocyanidin B3	4	Bis-HHDP-glucose	4
Procyanidinpentamer	2	Galloyl-HHDP-glucose	4
Procyanidin trimer	2	Galloyl-diHHDP-glucose	2
		digalloyl-tetraHHDP-diglucoses	2
Anthocyanins	3	HHDP-galloyl-glucose	4
Cyanidin-3-glucoside	2,4,6	Galloyl-bis-HHDP-glucose	4
Cyanidin-3-malonylglucoside	2,4	Dimer of galloyl-bis-HHDP	4
Cyanidin-3-malonylglucosyl-5-glucoside	4	Sanguiin H-6	4
Cyanidin-3-rutinosode	4	Agrimoniin	2
cyanidin-3-sukcynyloglucoside	6	Methyl-EA-pentose conjugates	4
Pelargonidin-3-galactoside	4	Methyl-EA-pentose conjugates	4
Pelargonidin-3-glucoside	2,4,6	Ellagic acid	1,2,3,4,7
Pelargonidin-3-diglucoside	4	Ellagic acid pentoside	4,10
Pelargonidin-3-arabinoside	4,6	Ellagic acid glucoside	1,2,4,10
Pelargonidin-3-rutinoside	2,4	***Condensed***	
Pelargonidin-3-acetylglucoside	2,4	Proanthocyanin	7
Pelargonidin-3-malylglucoside	4		
Pelargonidin-3-malonylglucoside	2,4	**Coumarins**	
5-pyranopelargonidin-3-glucoside	4	Coumaroylhexoses	2,4
Delphinidin	8	Cinnamoyl glucose	2
Pelargonidin-3-sukcynyloglucoside	6	p-Coumaric acid	7,9

***Source:** 1. Aaby, et al. [59], 2. Aaby, et al. [60], 3. Buendia, et al. [61], 4. Giampieri, et al. [62], 5. Halbwirth, et al. [63], 6. Jimenez-Garcia, et al. [64], 7. Oszmianski and Wojdylo [65], 8. Benzie and Wachtel-Galor, [66], 9. Bordonaba and Terry [10], 10. Wang, et al. [67], 11. Wang, et al. [68].

Strawberry products were used as the main dietary supplement in those studies and were tested using either *in-vitro* cell cultures or *in-vivo* in humans or animals [19,22].

The *in-vitro* effect of strawberry extract on the inhibition of α-amylase was studied by McDougall, et al. [23] and they concluded that strawberry polyphenols show an antidiabetic effect by limiting post-meal blood glucose levels, and they confirmed the antidiabetic properties recorded earlier by Bordonaba and Terry [22]. Therefore, strawberry could be a good source to prevent and treat metabolic complications related to diabetes as further confirmed by Moazen, et al. [24] who investigated the impact of freeze-dried strawberry supplementation in patients with type 2 diabetes. Another study by Abdulazeez [25] tested the effect of freeze-dried strawberry powder in diabetic rats and observed a significant reduction in serum lipid profile up to the control condition. The effect of strawberry phytochemicals on neuronal structure and function has also been tested [26]. Importantly, the rich polyphenol profile of strawberries caused a marked reduction in oxidatively induced neurotoxicity in general. Further, Heo H and Lee C [26] reported that strawberry exhibited the highest cell protective ability over banana and orange. Strawberry anthocyanins were the major contributors that performed higher protective effects. More recently, Amatori, et al. [27] demonstrated that a polyphenol-rich strawberry extract (PRSE) was able to decrease the cellular viability of breast cancer cells *in-vitro* and *in-vivo* in a time- and dose-dependent manner.

Strawberry response to environmental changes

Strawberry is a C_3 species and plants with the C_3 photosynthetic pathway respond favourably to increases in atmospheric CO_2 concentrations. As a result, CO_2 enrichment of horticultural crops, including strawberry, grown in protected production systems is gaining interest, mostly in temperate regions during winter through spring to increase yields [28]. Further, strawberry is highly sensitive to the ambient temperature, importantly the day and night temperatures. Photoperiod and number of other environmental factors including management greatly influence the growth and productivity of strawberries; which however, are not addressed here. This review has focused on impacts of the two main climate change variables, i.e. CO_2 and temperature on yield and quality of fresh strawberries at harvest, but it does not cover the effects of those two parameters during storage/preservation.

Effect of Elevated Carbon Dioxide on Strawberries

Effect on photosynthesis

Photosynthesis is a primary physicochemical process which drives the dry matter accumulation and synthesis of plant organic compounds. Experimental outcomes to date clearly demonstrate that net photosynthesis of strawberry plants increases under enhanced CO_2 levels compared to normal atmospheric levels [29-34]. The average effect of CO_2 enrichment on strawberry resulted in 73% and 55% increase in net photosynthesis and 43% and 63% increase in overall plant dry biomass, respectively, at 300 ppm and 600 ppm of atmospheric CO_2 [35]. The large variation in photosynthetic response to elevated CO_2 appears to be the result of various factors, including CO_2 concentration (400 ppm to 1000 ppm), duration of exposure to a particular CO_2 level, fruiting period, method of CO_2 enrichment, growth medium, space availability to plant growth, cultivar, nutrient and water application, and other growth conditions including light and temperature.

Any CO_2 levels above the normal ambient CO_2 concentration increased net photosynthetic rate of strawberries [30,32,36]. Overwintering strawberry plants grown under 700 ppm to 1000 ppm had nearly 50% higher leaf photosynthetic rates compared to the plants grown under ambient CO_2 levels of 360 ppm to 390 ppm [30]. Increased rates of photosynthesis generally results in greater dry matter accumulation which in turn support extensive and rapid growth of strawberry plants in spring. Leaf photosynthetic rates strongly correlated with leaf age, therefore, leaf age appeared to have significant influence on photosynthetic responses to elevated CO_2 levels. For example, greater improvements in photosynthetic rates at 450 ppm to 900 ppm CO_2 concentrations were observed primarily in younger leaves, while the older leaves showed an increase in net photosynthesis rate only up to 600 ppm. The negative or lack of response in photosynthesis in older leaves at higher CO_2 levels greater than 600 ppm was attributed to photo-inhibition at higher CO_2 concentrations [32,36].

Effect on yield

Increased CO_2 in the growth environment is reported to improve the fruit yield of strawberry crops [31]. Increases in yield under elevated CO_2 were due to increases in either individual fruit weights [15,33] or the number of fruits per plant [30] or both [37]. The same authors reported that strawberry plants exposed to higher CO_2 levels during growth and development had enhanced photo assimilation which promoted development of branch crowns, pedicels, and flower bud differentiation [37], with increased flowering and more fruits per plant, consequently resulting greater total fruit yields.

Enriched CO_2 concentrations of 450, 600, 750, and 900 ppm, in comparison with 300 ppm, enhanced strawberry fruit productivity due to increased pedicel number per plant, fruit setting per pedicel, fruit size, dry matter content of the fruits, and an increase in average fruit yield per plant of 0.7, 2.7, 3.6, and 4.1 fold, respectively [37]. An increase in strawberry yield of 62% at higher CO_2 concentrations (700-1000 ppm) was reported due to increased number of flowers and fruits compared with plants grown at ambient concentrations of CO_2 [30]. However, the increment in strawberry fruit yields at high CO_2 levels have also been attributed to increased individual fruit dry matter content [33,15] and increased fruit set [34].

Effect on fruit flavor

Flavor and aroma of strawberries are important factors in determining consumer acceptability. Strawberries produce complex mixtures of volatile compounds including more than 100 esters, as well as alcohols, aldehydes and also sulphur containing compounds. Many of those compounds determine the unique strawberry aroma and contribute directly to the characteristic strawberry flavor [15].

The major volatile aromatic 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, have been identified and analyzed in strawberries [15]. Fruits grown under higher CO_2 levels contained significantly greater levels of flavor compounds compared to the fruits under normal CO_2 levels. The concentrations of ethyl hexanoate, ethyl butanoate, and methyl hexanoate increased by 48%, 35%, and 68%, respectively, at the highest CO_2 level (950 ppm). Moreover, CO_2 at 950 ppm lowered organic acid (citric and malic) contents by 17% and increased total sugar to organic acids ratio by 40%, which represents a reduction in fruit sourness. Similarly, Chen, et al. [36-38] observed improved strawberry fruit quality at enriched CO_2 concentrations due to higher sugar accumulation and sugar/acid ratios in fruits as a result of decreased titratable acid content. Moreover, the higher CO_2 levels (600 and 900 ppm) raised non-structural carbohydrate production efficiency of strawberry plants compared to 300 ppm [38]. Penuelas and Estiarte [39] has discussed the increases in carbon-based secondary or structural compounds concentrations (CBSSC) like phenols with risen atmospheric CO_2 concentrations. Increments in CBSSC could be a result of highly regulated plant defensive change in biosynthesis pathways to response external abiotic changes such as elevated CO_2 levels [40].

Finally, it appears that strawberry flavor and aroma increase with rising CO_2 levels, thereby increasing the eating quality of the fruits.

Effect on antioxidant compounds

In common with many other plant constituents discussed so far the antioxidant content of strawberry increased at CO_2 levels of 650 and 950 ppm compared to the ambient conditions [41].

Flavonoids identified in strawberry fruits include pelargonidin 3-glucoside, cyanidin 3-glucoside, p-coumaroyl-glucose, pelargonidin 3-glucoside-succinate, and dihydroflavonol. Their levels increased by 72%, 105%, 76%, 110%, and 269%, respectively, at 950 ppm of CO_2 [41] compared with those at ambient CO_2 level. Moreover, the increased CO_2 promoted ascorbic acid/dehydroascorbic acid (AA/DHA) ratio and GSH/GSSG (oxidized GSS) ratio which are associated with increased free radical scavenging capacity. The increase in antioxidant compounds may be due to enhanced metabolism and production of antioxidant compounds as a result of greater availability of carbohydrate reservoir. Fruits exposed to the 950 ppm CO_2 concentration exhibited the highest antioxidant capacity compared to fruit treated with ambient CO_2 concentrations.

A summary of various studies on the effect of elevated CO_2 concentration on strawberry yield and quality is presented in Table 3. In general, those results support the proposition that, in the future, strawberry plants grown under higher CO_2 environments will produce high yields of high-quality strawberries.

Effect of High Temperature on Strawberries

Effect on growth and yield

Temperature is a key environmental variable that affects strawberry plant growth and development and is identified as a limiting factor in crop productivity depending on the geographical location and the season of year [9]. Strawberry is highly sensitive to day and night temperatures and their interactions with other environmental factors, especially photoperiod. Therefore, in temperate regions, strawberry production is seasonal and concentrated in the warmer months under traditional open field cultivation systems. However, production can be extended to year-round using different varieties and planting techniques and particularly if produced using protected cropping techniques [42]. Higher temperatures alter morphological, anatomical, physiological, and ultimately, biochemical and molecular changes in strawberry plants [9]. In addition, the temperature response can be highly dependent on the genetic makeup or cultivar of strawberry grown.

Mean temperatures between 15 °C to 23 °C have been identified as optimum for strawberry photosynthesis depending on cultivar [43]. However, different studies have proposed different day/night temperatures as the best for strawberry growth; such as 30/25 ˚C [44]., or 25/12 ˚C [45]. Another study by Palencia, et al. [9] indicated that temperatures higher than 20 ˚C decreased the yields, while growth and yield were drastically reduced at temperatures above 35 ˚C [44].

Table 3: Effect of increased CO_2 concentrations on physical and chemical properties of strawberry fruit.

CO_2 concentrations	Observations in strawberry fruit due to increased CO_2 levels	Reference
Ambient + 300 ppm Ambient + 600 ppm 353/400 to 600 ppm day/ and night	■ Increased fruit dry matter contents by 18% with extra 300 ppm and 39% at extra 600 ppm CO_2. ■ Increased total sugar by 12% in air enriched with 300 ppm and 20% in air enriched with 600 ppm due to increased net photoassimilate production Increased sweetness due to increased sugar contents. ■ Increased organic acids in fruits grown at ambient plus 600 ppm to 17.4% as compared to 8.4% at ambient plus 300 ppm. Reduced sourness of fruit. ■ Enhanced levels of flavor compounds in fruit including ethyl hexanoate, ethyl butanoate and methyl hexanoate as increased sugars act as precursors for flavor compounds.	Wang and Bunce [15]
Ambient + 300 ppm Ambient + 600 ppm 353/400 to 600 ppm day/ and night	■ Enhanced ascorbic acid content by 10% at ambient + 300 ppm and 13% at ambient + 600 ppm and decreased dehydroascorbic acid content thereby increased the AA/DHA ratio. ■ Increased glutathione (GSH) by 171% at ambient + 600 ppm and GSH/GSSG (oxidized GSH) ratio. ■ Yielded significantly higher anthocyanins and flavonoid, content. ■ Increased oxygen radical absorbance activity in fruit of strawberry plants grown in the CO_2 enrichment conditions.	Wang, et al. [41]
390 ppm (ambient) 560 ppm	■ Increased yield by 17% to 42% due to increased carbohydrate accumulation, total fresh fruit weight, and flower and fruit number per plant.	Deng and Woodward [31]
300 ppm, 450, 600, 750, and 900 ppm	■ Increased average fruit yield per plant by 0.7, 2.7, 3.6, and 4.1-fold, daily growth per fresh fruit by 0.4, 1.0, 1.1, and 1.3-fold, and growth rate of fruit biomass per plant by 1.0, 3.9, 5.5, and 6.9-fold. ■ Enhanced fruit development and branch-crown and pedicel development and flower bud differentiation. ■ Enhanced fruit productivity through increased pedicel number per plant, fruit setting per pedicel, fruit size and dry matter content of the fruits. ■ Increased total sugar content of fruits with higher sugar/acid ratio due to decreased titratable acid content. ■ Promoted early and prolonged flowering and fruiting period.	Chen, et al. [36-38]
400, 600, and 900 ppm	■ Increased yields by 15%, 20%, and 31% at 400 ppm, 600 ppm, and 900 ppm respectively due to increased fruit weight with shorter fruit development time.	Lieten [33]
340 ppm 1000 ppm	■ Increased fruit yield by 47% due to increased fruit set per plant.	Sung and Chen [34]

High temperatures reduced strawberry fruit size, weight, and caused irregular shaped fruit [44-46]. The reduced fruit size and weight can be attributed to lower dry matter accumulation due to higher fruit transpiration rate and decreased photosynthetic rates at higher temperatures [46]. Generally, cooler day/night temperatures favored plant and fruit growth, while rising temperatures resulted in smaller irregular shaped fruits. In a study by Wang S and Camp [45], strawberries grown at various day/night temperatures (18/12 °C, 25/12 °C, 25/22 °C, and 30/22 °C) in growth cabinets showed that a day/night temperature of 30/22 °C negatively affected plant growth, fruit development and fruit quality of strawberry cultivars. The fruit weights reduced by 10%, 33% and 66% at day/night temperatures of 25/12 °C, 25/22 °C, and 30/22 °C, respectively, compared to 18/12 °C. Maintaining temperature at 40/35 °C caused complete absence of fruit formation and zero yield [44].

Effect on photosynthesis

Although the light dependent reactions of photosynthesis are not sensitive to temperature the light-independent reactions catalysed by enzymes are. In general, the rate of reaction increases as temperature increases and reaches an optimum after which the overall rate declines. As the temperature continues to increase enzymes are denatured until all activity stops [47]. Depending on cultivar, temperature rises of 10 °C to 15 °C could cause reversible alteration in photosynthesis (PS), however, fluctuations below or above this level may cause irreversible damage to the photosynthetic system [48]. In strawberries, higher day/night temperatures (40/35 °C) appeared to cause detrimental and irreversible damage to PS II as indicated by chlorophyll fluorescence and PS II efficiency measurements [44].

Net photosynthesis rate in strawberries decreased with increasing temperatures (20/15 °C, 30/25 °C, and 40/35 °C) and the response was cultivar-dependent. When 2 varieties, "Sweet Charlie" and "Chandler", were exposed to these increasing day/night temperatures, net photosynthetic ratedecreased by 44% and 20%, respectively, in "Sweet Charlie" and "Chandler" at the highest day/night temperatures (40/35 ˚C) over those exposed to 20/15 °C and 30/25 °C [44]. Additionally, the higher day/night temperatures of 30/25 °C and 40/35 °C had a major effect on stomatal and mesophyll conductance, transpiration, water use efficiency, and it reduced chlorophyll content [43,44]. "Sweet Charlie" and "Chandler" varied in their response to elevated temperature with "Chandler" displaying higher tolerance than "Sweet Charlie". Chandler plants were less sensitive to short term exposure to high temperatures and were able to maintain a significantly higher net CO_2 assimilation rate, intercellular CO_2 concentration, and water use efficiency for at least 3 weeks in higher day/night temperatures [44].

Overall, higher temperatures appear to have negative impacts on strawberry photosynthesis and there by plant growth and development. However, strawberry response to variations in temperature is cultivar-dependent. Identification and development of heat-tolerant strawberry cultivars will be essential to enable strawberry producers to adapt to the anticipated climatic changes, particularly increased temperature and CO_2 levels.

Effect on fruit development and sugar content

As high temperatures can have a significant negative impact on the vegetative growth of strawberry plants, it is anticipated that high temperatures will also have a detrimental effect on the reproductive development of strawberry. It has been reported that heat stress under high temperatures can cause sterility, lower fruit set, there by lower yields, and in extreme cases complete crop failure [9,43,49]. High temperatures can have detrimental effects on fruit size, shape, yield, color, texture, flavor, nutritional composition, and nutrient content. Consequently, increasing temperatures may reduce strawberry development significantly and lower fruit quality substantially.

Higher temperatures could also affect fruit quality by reducing sweetness [45]. The sweetness of strawberry is directly related to the sugar content of fruit flesh including glucose, fructose, and sucrose. Fruits produced at 30/22 ˚C (day/night) showed lower sugar and total carbohydrate contents than fruits from plants grown at 18/12 °C, 25/12 °C and 25/22 °C [45]. Consequently, strawberry production at higher temperatures may have a negative impact on the flavor of strawberries.

Effect on antioxidants

Ascorbic acid and total organic acids, including ellagic acid content, showed a significant decline in strawberry fruits as day/night temperatures increased from 18/12 °C to 25/12 °C, 25/22 °C and 30/22 °C [45]. A substantial increase in phenolic compounds in strawberries grown at the higher day/night temperature (30/22 °C) was documented by [50]. It appears that strawberries grown at warmer day/night temperatures (30/22 °C and 22/25 °C) produce more antioxidants as a defence mechanism in response to the applied stress. In support of this view, strawberries grown at 30/22 °C had greater amounts of phenolic acids, flavonols, and anthocyanins than those grown at lower temperatures [50]. The level of the response was cultivar-dependent, with the cultivar "Kent" showing higher antioxidant levels as well as greater antioxidant capacity compared with "Earliglow" fruit [50]. Although sweetness of strawberry fruit is reduced when the environments become warmer, the fruits will have high nutritional value due to the increased phenolic compounds and higher antioxidant activity. However, strawberries grown under warmer conditions will have reduced yields, due in part to small and uneven-sized fruit which will make them unattractive to producers and consumers [45]. If this is the case then there may be opportunities to utilize the fruit for high antioxidant value-added processed products.

Effect on fruit color

Strawberry fruit color is a key fruit-intrinsic visual cue that consumers use to decide fruit quality before they buy or eat. An attractive fruit appearance with dark red color and higher flesh pigment intensity were exhibited by fruits which developed at a higher growth temperature (30/22 °C) [45,50]. It was suggested that increased polyphenolic compounds especially anthocyanin, may make the strawberries redder and cause darker fruit surfaces [50]. However, it should be noted that results of Kadir [44] were in disagreement and showed reduced fruit skin color intensities at high temperature (30/25 °C). Such contradiction in these reported results may be attributed to various factors, other than temperature, including cultivars and other growth conditions. From a consumer perspective, colour alone is insufficient to determine consumer preferences for strawberry fruit without acceptable fruit size and shape. Consequently, when judging the impact of climate change on strawberry fruits, changes in all quality traits need to be considered.

Effect on proteins

Plant proteins are important macromolecules involved in every stage of plant growth and development, including biological reactions (enzymes) and cellular, structural, and membrane transport systems. Some studies reported that protein synthesis and final total protein content declined significantly in plants grown at high temperatures of 33 °C and 42 °C [51]. Although the typical cellular protein content decreased at higher growth temperatures, new heat-shock proteins were synthesized as a result of imposed heat stress in strawberry leaves and flowers. The detected stress proteins were cultivar- and temperature-dependent with substantial differences in the level of expression between the cultivars "Nyoho" and "Toyonaka" [51]. The newly synthesized heat-shock proteins could act as protectors (molecular chaperones) in preventing thermal aggregation of denatured proteins due to high temperatures and thermal stress [51,52].

Another response to high temperature stress is the production of reactive oxygen species (ROS) which can cause significant damage to cells. Plant peroxidases can detoxify ROS in the presence of H_2O_2. Peroxidase activity has been observed to increase in strawberry plant cells subjected to heat stresses there by providing some protection from oxidative damage to cells [52]. The impact of heat on stress-protein production was analysed by Gulen and Eris [52] in 2 ways; with gradual growth temperature increases in 5 °C increments from 25 °C to 45 °C, and by imposing heat shocks. Both treatments showed a significant increase in peroxidase activities against ROS. The strawberry plants exposed to gradual, incremental increases in temperature had greater heat-stress tolerance due to the synthesis of more new heat stable proteins than the plants that received a sudden shock heat-stress. Therefore, strawberry plants may cope with future warmer environments by acclimatizing to rising temperatures through the production of enzymatic antioxidants. Furthermore, strawberry plants subjected to sudden heat events also have the capacity to respond and produce protective proteins, but at a reduced rate.

The reported positive and negative effects of high temperatures on strawberries are summarized in Table 4.

Interactive Effect of CO_2 and Temperature on Strawberry Physicochemical Properties

Many studies have shown that strawberries respond differently to increases in temperature than to higher CO_2 levels when they are applied independently. Higher yields and better-quality strawberries were recorded under higher CO_2 levels, while high temperatures reduced yield and fruit quality. However, both factors caused a similar response in increasing fruit polyphenol contents. Strawberry plants produced higher-quality fruits at lower temperatures (Table 4). Despite some very good research demonstrating the independent effect of increased temperature and CO_2, the combined impact of anticipated future increases in both, due to climate change, on strawberry growth and development is unclear.

The magnitude of the effects of individual CO_2 or temperature factors on the strawberry can be considerably different from their combined effects. To our knowledge, only one study has reported the combined effects of both elevated CO_2 and temperature on strawberry. Sun, et al. [53] observed decreased fruit yields of 12% to 35% at high CO_2 (720 ppm) and high temperature (25/20 ˚C). Plants grown at

Table 4: Effect of increasing temperature on physical and chemical properties of strawberry fruit.

Temperature	Reported features	Reference
15 ˚C and 19 ˚C	■ Decreased fruit size by 29% of FW and 33% of DW at 19 ˚C compared. to 15 ˚C due to lower dry matter accumulation attributed to increased photorespiration and higher fruit transpiration.	Miura, et al. [46]
Day/night: 18/12, 25/12, 25/22, and 30/22 (˚C)	■ Greater pigment intensity resulted in darker and redder fruit due to increased anthocyanin content; Chroma color values increased by 39%. ■ Decreased fruit quality. Soluble solids content (SSC) decreased by 36%, titratable acidity (TA) by 14%, SS/TA ratio by 25%, and AA by 41%. ■ 18/12 ˚C was the best temperature for fruit growth with higher fructose (~390 mg/DW of fruit), glucose (~350 mg/DW of fruit), and total carbohydrates (~770 mg/DW of fruit). ■ Reduced fruit quality with smaller and irregularly shaped fruits. ■ Decreased organic acid content by 18% (mainly citric acid) and ellagic acid by 15%.	Wang and Camp [45]
Day/night: 18/12, 25/12, 25/22, and 30/22 (˚C)	■ Significantly increased phenolic acid, flavonol, and anthocyanin content. ■ Increased antioxidant capacity by nearly 54%.	Wang and Zheng [50]
25, 30, 35, 40 and 45 (˚C)	■ Largest increase in peroxidase activity from 3 to 35 µmol/g min DW with gradual increase in temperature (GHS). ■ Smaller increase in peroxidase activity in response to sudden temperature increase (SHS) of 3 to 19 µmol/g min DW. ■ Decreased cellular protein by 51% under GHS and by 67% under SHS.	Gulen H and Eris [52]

high CO_2 and low temperatures produced the highest fruit yields, while fruit number per plant and the yield decreased as CO_2 and temperature increased. They proposed that yield reduction may be due to lower fruit set, decreased carbohydrate metabolism during flowering, inhibition of flower induction, a smaller number and size of inflorescences, and decreased pollen viability. In addition, high CO_2 levels combined with high temperatures reduced anthocyanins by 27%, total flavonoids by 31% to 36%, and antioxidant capacity by 18% to 28% in strawberry fruits [53].

Future Research Needs

Information on the combined effects of elevated CO_2 levels and temperature on strawberry growth and development, particularly berry yield, quality, and nutritional value is lacking. Therefore, it is important to investigate the effect of combined CO_2 and temperature at the levels anticipated to result from climate change, particularly the physical, chemical, and nutritional properties of different strawberry cultivars. Additionally, studies on the impact of climate changes on nutritional and health value of strawberry fruits in terms of bio-accessibility or bioavailability is virtually unresearched. Such information will be helpful to develop adaptation strategies to reduce the yield losses for commercial strawberry producers under future climates. It has been well documented that the responses of strawberries to different climatic conditions are variety-dependent so existing strawberry varieties which thrive under adverse climatic conditions should be identified for their tolerance to climate change through selection and breeding.

Conclusions

Strawberry is widely consumed globally, is highly nutritious and is a major source of vitamin C, folate, dietary polyphenols, and antioxidants. Its total Antioxidant Capacity is greater than the most common fruits including plum, orange, red and white grape, kiwi, pink grapefruit, banana, apple, tomato, pare honey dew and melon. However, strawberry is highly sensitive to growth temperature and CO_2 levels. For example, increases in CO_2 concentrations enhanced photosynthesis, fruit size and numbers, overall fruit yield, flavour compounds, and antioxidant contents. On the contrary, high temperature reduced strawberry yield, photosynthesis, plant development, and fruits characteristics (size, shape, colour, flavour, and nutrients composition). Although the individual effects of high CO_2 and high temperature on strawberry growth, quality, and nutritional composition are relatively well-studied, the interactive effects of temperature and atmospheric CO_2 particularly at evaluated levels above the normal average conditions, on strawberry growth, productivity and quality lacking.

This is particularly important as the global warming due to elevated CO_2 is said to be a reality; therefore, such information on the combined effects of high CO_2 and high temperature levels during crop growth and development on strawberry quantity and quality will be of great benefit for understanding mechanisms behind the responses and in developing research strategies to overcome negative impacts while maximising the gains from any potential positive responses. The anticipated results from research currently being conducted in this area at The University of Melbourne will contribute towards achieving the above objectives, and eventually leading to generate knowledge, technology and best management practices, so strawberry industry could prepare and to adapt to the anticipated changes in climate and weather patterns.

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