Interaction of Elevated Carbon Dioxide and Temperature on Strawberry (*Fragaria × ananassa*) Growth and Fruit Yield

Himali N. Balasooriya, Kithsiri B. Dassanayake, Saman Seneweera, Said Ajlouni

Abstract**—**Increase in atmospheric CO_2 concentration [CO_2] and ambient temperature associated with changing climatic conditions will have significant impacts on agriculture crop productivity and quality. Independent effects of the above two environmental variables on the growth, yield and quality of strawberry were well documented. Higher temperatures over the optimum range (20-25ºC) lead to crop failures, while elevated [CO_2] stimulated plant growth and yield but compromised the physical quality of fruits. However, there is very limited understanding of the interaction between these variables on the plant growth, yield and quality. Therefore, this study was designed to investigate the interactive effect of high temperature and elevated [CO_2] on growth, yield and quality of strawberries. Strawberry cultivars 'Albion' and 'San Andreas' were grown under six different combinations of two temperatures (25 and 30ºC) and three [CO_2] (400, 650 and 950 µmol mol^{-1}) in controlled-environmental growth chambers. Plant growth measurements such as plant height, canopy area, number of flowers, and fruit yield were measured during phonological development. Photosynthesis and transpiration, the ratio of intercellular to atmospheric [CO_2] (Ci/Ca) were measured to estimate the physiological adjustment to climate stress. The impact of temperature and [CO_2] interaction on growth and yield of strawberry was significant ($p < 0.05$). Across both cultivars, highest fruit yields were observed at 650 µmol mol^{-1} [CO_2], which was particularly clear at 25°C. The fruit yield gradually decreased at 30°C under all the treatment combinations. However, photosynthesis rates were highest at 650 µmol mol^{-1} [CO_2] but no increment was found at 900 µmol mol^{-1} [CO_2]. Interestingly, Ci/Ca ratio increased with increasing atmospheric [CO_2] which was predominant at high temperature. Similarly, fruit yield was substantially reduced at high [CO_2] under high temperature. Our findings suggest that increased Ci/Ca ratio at high temperature is likely reduces the photosynthesis and thus yield response to elevated [CO_2].

Keywords**—**Atmospheric [CO_2], fruit yield, strawberry, temperature.

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I. Introduction

It has been reported that the atmospheric [CO_2] is rising and the recent predictions are that current atmospheric [CO_2] levels will be doubled that of the pre-industrial levels and may even increase up to 970 µmol mol^{-1} by 2100 [1]. Increase in atmospheric [CO_2] is concomitant with a rise in mean global air temperature due to the greenhouse effect. The global mean temperature is predicted to increase by 2.6 to 4.8 ºC at the late 21st century relative to the period of 1986 to 2005 [2] at the current rate of GHG emissions bringing in significant changes to global climates. Scientific investigations conducted over the past decades indicated that increase in atmospheric [CO_2] and ambient temperature associated with changing climatic conditions will cause varying degree of negative effects, but significant impacts on plant growth, development and production [3].

Strawberry (*Fragaria × ananassa)* is a popular berry fruit, which is rich in various antioxidants including polyphenols and vitamins. This crop is widely cultivated all around the world in open fields for commercial cultivation systems and intensively under protected environments. However, various studies indicated that strawberry production have been affected by climate change in last decades [3]-[6]. Calleja [4] thoroughly examined the impacts of climate change on the strawberry production, including the vulnerability to disease incidence in strawberry fields in the United Kingdom. Similarly, Neri, Baruzzi [3] indicated that European strawberry farmers are facing climate change and searching for new varieties and cultural practices to optimize the yield with changing environments. For example, the commercial strawberry yield in Turkey was declined by 32% due to an increased average temperature by 4 °C in 2008 compared with 2007 [6]. Temperatures between 15 °C and 20 °C is ideal for strawberry fruitification in Europe consequently, the anticipated increasing mean temperature by 6 °C in future (2091 – 2100), is predicted to shorten the crop cycle duration hence reducing the total fruit yield [6].

With the clearest evidence of global warming since late 19th century [7], numerous studies provided a more comprehensive picture of growing strawberry under warmer environments and its effects on quality and productivity. Effect of temperature on plant growth, yield and quality is complex due to different temperature optima of different growth stages and variations among strawberry cultivars. For example, the plant growth could be accelerated by a small increase in temperature if the temperature is below the optimum. However, the opposite is also true when the temperature is close to the maximum. Depending on cultivar, average temperatures between 15 °C to 25 °C is favored for optimum growth of strawberry plant [8], [9] and, temperature beyond 35 °C will cause adverse effects on strawberry production [10]. The same author reported also that increasing day/night temperatures (20/15, 30/25, and 40/35°C) reduced the net photosynthesis rate in strawberry plant by affecting stomatal and mesophyll conductance, transpiration, water use efficiency, and chlorophyll content [10].

Additionally, the higher temperatures (30/25, and 40/35°C) increased the respiration rate, metabolic activities and finally restricted the net photo assimilation by around 50% [8], [10]. Such decline in photosynthesis rate at high temperature could be also the result of irreversible damages on the leaf photosynthesis systems [10], [11] and photosynthetic enzymes [12]. Moreover, high temperature (40 °C) may affect the plant water and nutrient status by restricting root biomass and preventing fruit formation [9]. The same study revealed that growth and development of both strawberry plant and fruit were negatively affected by higher temperatures compared to ambient [10]. The overall, and most visible influence of high temperature on strawberries can be summarized by less quality fruits with lower weight, smaller and irregular shape [9], [10], [13]. This kind of misshapen and malformed fruits could be due to higher pollen infertility [3]. Therefore, it could be concluded that global warming might be a threaten to this crop, as it could cause noticeable yield losses.

Un-similar to the effect of high temperature, strawberry plants grown under controlled elevated [CO_2] showed divergent responses. It is well established that C_3 plants showed higher sensitivity to rising atmospheric [CO_2] as the current level is below the optimal for C_3 photosynthesis [14]. In fact, the increased CO_2 exhibited greater photosynthesis rates in strawberry plants [15]-[18]. Bushway [15] indicated that increasing CO_2 levels up to 700 and 1000 µmol mol^{-1} improved the net photosynthesis rate by nearly 50%. Short term CO_2 enrichment up to 1000 µmol mol^{-1} during the fruiting period in strawberry decreased stomatal conductance and increased leaf CO_2 exchange rate (CER), photosynthetic photon flux density, chlorophyll content and mesophyll conductance with a resultant increase in plant photosynthesis [18]. However, a long-term CO_2 enrichment, showed different results. For example, photosynthesis acclimation to elevated [CO_2] suppressed the initial stimulation of photosynthesis due to decrease in rubisco activity and content and reduced the intercellular CO_2 concentration [19]. Though the CO_2 concentrations above 750 and 900 µmol mol^{-1} decreased leaf chlorophyll content and depressed the CO_2 assimilation rates [16]. Greater CO_2 uptake by overwintering strawberry plants produced higher contents of carbohydrates in plants crowns, leaves and roots which also encouraged a rapid and extensive growth in the spring [15]. Additionally, growth at higher CO_2 (700 to 1000 µmol mol^{-1}) increased strawberry yield by around 62%. Such improvement in strawberry yield at high [CO_2] level was attributed to the increased flower and fruit number compared with the ambient condition [15]. Comparatively higher fruit yield under elevated [CO_2] resulted from a simultaneous higher fruit set and individual fruit weight [15], [18], [20].

These observations clearly demonstrated the obvious impact of above climatic factors (high temperature and elevated [CO_2]) on strawberry growth, development, and final yield [21]. However, considering the correlated increases in both air temperature and [CO_2], it is of upmost importance to investigate the combined effects of those factors on vegetative and reproductive development of plants. Generally, elevated [CO_2] increases the photosynthesis by reducing photorespiration. Such effect may become greater at high temperature due to partial or fully mitigation of the dramatic effects of high temperatures on crop growth, development and yields [22]. Nevertheless, the rising temperature and CO_2 concentration showed a strong interaction in canopy photosynthesis [22].

The detailed and possible synergistic/antagonistic interaction of high temperature and elevated [CO_2] and their effect of plant growth has not been previously investigated. The objective of this study was to determine the interactive effect of temperature and elevated [CO_2] on strawberry plant growth, development and productivity. This current study reports the growth and yield responses of two different strawberry cultivars to the simulated climate stress (high temperature and [CO_2]) through physiological adjustment.

II. Materials and Methods

A. Experimental Location and Plant Materials

This research was conducted under controlled-environmental plant growth facility of the glasshouse complex at the Parkville Campus of the University of Melbourne, Australia. Two controlled plant growth chambers (Model: TPG-2400-TH-CO_2, Thermoline Scientific Equipment Pty. Ltd., Wetherill Park, NSW, Australia) which facilitated fully automated control of all plant growth environmental conditions within each chamber were used for growing experimental plants. Rooted runners of two popular day neutral strawberry cultivars, ‘Albion’ and ‘San Andreas’ were used in these experiments. The fresh runners were purchased from Toolangi Certified Victorian Runner Growers’ Co-Op Ltd, Toolangi, Victoria, Australia. The runners were transported under refrigerated storage to the Parkville glasshouse, sorted for their uniformity and planted on the same day in 1.65 L plastic pots filled with sterilized, well drained, commercial potting media. Potted runners were then kept in a glasshouse chamber under ambient environmental conditions nearly for six weeks for their initial growth. At the end, plants were screened for the health, vigor and uniformity in size, selected plants were then transferred into the growth cabinets and grown under controlled elevated temperature and [CO_2] conditions.

B. Treatments and Plant Growth Conditions

In addition to the strawberry cultivars, this experiment consisted of six different combinations of two main environmental treatments; i.e. two levels of day temperature and three levels of [CO_2] (a total of 12 treatment combinations: 02 Cultivars **X** 02 temperature treatments **X** 03 [CO_2] levels). The temperature treatments were 25 °C (ambient) and 30 °C (elevated) and [CO_2] treatments were 400 µmol mol^{-1} (ambient); 650 µmol mol^{-1} (intermediate) and 950 µmol mol^{-1} (high). Each treatment was replicated four times and each replicate consisted of 3 pots with a single strawberry crown in each pot. Two separate but identical growth chambers were deployed to maintain two temperature treatments. CO_2 treatments were imposed in stages; where CO_2 level in each chamber were increased from ambient to highest level in three separate stages. At stage 1, strawberry plants were raised initially at ambient CO_2 level (400 µmol mol^{-1}) for a complete fruiting cycle (eight weeks). At the end of the first stage, both growth cambers were cleaned out and CO_2 concentrations were raised to 650 µmol mol^{-1} and screened, two almost identical, fresh set of strawberry plants (in the same growth stage to the previous plants at the start) were introduced. This step was repeated for the final [CO_2] too. Placements of strawberry plants in growth chambers were randomized to eliminate the position effect inside the growth chamber. The growth cambers were swopped for temperature treatments at each [CO_2] level to avoid any effect from the growth chambers during the experimental period. Temperature treatments were applied only during set daytimes while night temperature across treatments was maintained at 20 °C.

Desired [CO_2] within growth chambers were maintained by injecting pressurized CO_2 gas through a reticulated tubing with a combination of pressure regulator, CO_2 gas sensor/monitor and a feedback controller for each chamber. Compressed food grade CO_2 (≥ 99.5%) gas supplied by Coregas Pty. Ltd., NSW, Australia in standard 'D' size gas cylinders (Product code: 376142) was used for this purpose. Same CO_2 levels were maintained during both day and night throughout the crop growth. The relative humidity (RH) within growth cabinets was maintained around 70%. Temperature, [CO_2], and RH were monitored all the times during the experimental period and the treatments were continued until harvesting the fruits.

Plants in growth chambers were provided with close to natural daylight of PAR around 300 – 500 µmol m^{-2} s^{-1} with a day length of 12 hours (06.00 to 18.00) using supplementary light [23]. 12 hours of day length maintained during the initial period of 3-4 weeks to promote vigorous plant growth. Depending on the variety and type of runner, the runners took around four weeks to reach their mature growth stage. During this initial growth period, newly emerging runners and the first set of flowers were removed to enhance plant vigor. Plants were then subjected a day length of 14 hours (06.00 to 20.00) [23] to promote flowering and continued through fruiting period until harvesting at around eighth week.

All the plants were irrigated by an automated drip irrigation system to maintain moisture levels of the growth medium at field capacity. Commercially available nutrient solutions consisting all essential macro and micro plant nutrients (Diamond 19 carrot® at seedling stage and Aquasol® at flowering and fruiting stage) were fed to all plants at regular intervals. All other crop management practices were applied equally to all experimental plants across various treatments.

C. Measurements

Physiological performances of strawberry plants during the initial vegetative growth phase under various treatments were monitored after four weeks by measuring leaf gas exchange parameters including, net assimilation rate, photosynthesis rate, stomatal conductance, intercellular CO_2 concentration (C_i) and transpiration rate using a portable photosynthesis system (LI-COR 6400, Lincoln, NE, USA). The measurements were made non-destructively *in vivo* inside growth chambers on three different strawberry leaves per plant with a minimum of three repeated measurements for each leaf. Photosynthetic water use efficiency (WUE) of strawberry leaf was estimated as the ratio of carbon assimilation rate to water evaporation rate. Leaf photosynthetic efficiency was derived from net photosynthesis rate divided by intercellular CO_2 concentration [17].

The vegetative growth of strawberry plants was monitored *via* the means of plant height, number of crowns, number of leaves and canopy area. Strawberry canopy area was measured using digital images of plant canopy analyzed by "Easy Leaf Area" software [24]. Further, total number of inflorescences, flowers and fruits in each plant were manually recorded to determine the reproductive development of strawberry plants. Ripen fruits with 90% red color, free from defects and decay were harvested separately from each chamber for each cultivar and for each replicate. Finally, the fresh fruit weight was measured to determine the average individual fruit weight and the final fruit yield. The fruit setting percentage was calculated by using flower number and fruiting.

D. Statistical Analysis

The data were statistically analyzed using Minitab® 17 Statistical Software applying a General Linear Model analysis of variance (ANOVA) with three factors; Temperature, [CO_2] and cultivar. Differences among the means of plant physiological and plant and fruit growth parameters between the treated combinations of increased temperature and elevated CO_2 concentrations were determined using the Tukey's multiple comparison method at 95% confidence level. All data were reported as means ± standard deviation.

III. Results

A. Leaf Gas Exchange Properties

Leaf gas exchange measurements and derived photosynthetic efficiency parameters for strawberry plants in response to the elevated CO_2 concentrations and temperature are summarized in Table I. The interaction effect of temperature and [CO_2] was significant ($p<0.05$) for net photosynthesis rate, stomatal conductance, intercellular [CO_2], and transpiration rate of strawberry plants.

Elevated [CO_2] up to 650 µmol mol^{-1} increased the net photosynthesis rate of strawberry leaves at 25 and 30 °C temperature in both cultivars (Fig. 1 (a)). Under ambient temperature, net photosynthesis rate did not change significantly (P>0.05) due to enhanced [CO_2] from 650 to 950 µmol mol^{-1} in either cultivar, but significant reductions (p < 0.05) were found under 30 °C in both cultivars (Fig. 1 (a)). Overall, elevated [CO_2] increased the net photosynthesis rate of strawberry leaves (by 41% in Albion and 55% in San Andreas) under ambient temperature but, increasing temperature by 5 °C reduced the net photosynthesis rate by 16% in Albion and 14% in San Andreas (Table I).

TABLE I
LEAF GAS EXCHANGE, CI/CA RATIO, PHOTOSYNTHETIC WATER USE EFFICIENCY AND LEAF PHOTOSYNTHESIS EFFICIENCY OF STRAWBERRY PLANTS AS AFFECTED BY ELEVATED TEMPERATURE AND CO_2 CONCENTRATIONS

Cultivar	Temperature	[CO_2]	Photosynthesis rate	Stomatal conductance	Intercellular [CO_2]	Transpiration rate	Ci/Ca	WUE	Leaf photosynthesis efficiency
Albion	25°C	400	10.71±1.76^{cd}	0.27±0.05^{a}	302.36±17.09^{ns}	3.36±0.44^{b}	0.76±0.04^{cd}	3.26±0.57^{e}	35.76±7.12^{ns}
		650	14.84±1.98^{a}	0.27±0.06^{a}	465.38±22.44^{ns}	4.65±0.63^{a}	0.72±0.03^{efg}	3.27±0.63^{e}	32.03±4.91^{ns}
		950	15.13±1.32^{a}	0.18±0.05^{def}	746.80±54.80^{ns}	3.02±0.63^{bc}	0.79±0.06^{bc}	4.79±0.63^{b}	20.06±2.44^{ns}
	30°C	400	12.07±1.52^{bc}	0.23±0.05^{bc}	274.84±13.10^{ns}	4.57±0.63^{a}	0.69±0.03^{g}	2.64±0.86^{f}	44.04±6.19^{ns}
		650	14.22±1.89^{a}	0.21±0.06^{cd}	481.03±36.96^{ns}	4.34±0.80^{a}	0.74±0.06^{de}	3.33±0.76^{e}	29.95±4.11^{ns}
		950	11.88±1.98^{bc}	0.20±0.04^{cd}	800.94±26.73^{ns}	3.28±0.80^{b}	0.84±0.03^{a}	3.43±0.76^{de}	14.26±3.51^{ns}
San Andreas	25°C	400	9.97±1.70^{d}	0.17±0.03^{def}	274.49±20.37^{ns}	2.53±0.39^{c}	0.69±0.01^{g}	3.96±0.57^{c}	36.06±7.59^{ns}
		650	15.44±1.90^{a}	0.25±0.05^{ab}	447.79±22.75^{ns}	4.46±0.62^{a}	0.69±0.04^{fg}	3.51±0.63^{cde}	34.63±5.05^{ns}
		950	14.95±1.75^{a}	0.14±0.03^{f}	714.32±34.83^{ns}	2.62±0.63^{c}	0.75±0.04^{cde}	5.72±0.63^{a}	21.02±2.98^{ns}
	30°C	400	10.22±1.33^{d}	0.15±0.04^{ef}	247.74±26.68^{ns}	3.31±0.54^{b}	0.62±0.06^{h}	3.04±0.86^{ef}	41.68±6.41^{ns}
		650	14.14±2.07^{a}	0.20±0.05^{cd}	471.51±36.50^{ns}	4.18±0.71^{a}	0.73±0.06^{def}	3.56±0.76^{cde}	30.50±4.85^{ns}
		950	12.14±1.63^{b}	0.18±0.05^{de}	779.69±31.73^{ns}	3.19±0.80^{b}	0.82±0.03^{ab}	3.91±0.76^{cd}	15.79±2.86^{ns}
Interaction Effect	CO_2*Temperature		**	**	**	**	**	**	**
	CO_2*Temperature *Cultivar		**	**	ns	**	**	**	ns

Reported results are the means ± standard deviation. Means within each column followed by different superscript letters are significantly different (P<0.05), (**) - Significant, ns – Not significant). Units; [CO_2] = µmol CO_2 mol^{-1}, photosynthesis rate = µmol CO_2 m^{-2} s^{-1}, stomatal conductance = mol H_2O m^{-2} s^{-1}, intercellular [CO_2] = µmol CO_2 mol^{-1}, WUE = CO_2 10^{-3} H_2O^{-1}, leaf photosynthesis efficiency = mmol CO_2 m^{-2} s^{-1}.

Stomatal conductance decreased when the CO_2 increased from 400 to 950 µmol mol^{-1} in strawberry cultivar "Albion" (Table I). In contrast, stomatal conductance increased from 400 to 650 µmol mol^{-1} reaching to the highest of 0.25 mol H_2O m^{-2} s^{-1} at 25 °C and 0.20 mol H_2O m^{-2} s^{-1} at 30 °C in "San Andreas". Stomatal conductance decreased thereafter to 0.14 and 0.18 mol H_2O m^{-2} s^{-1} respectively at 25 and 30 °C as [CO_2] increased to 950 µmol mol^{-1}. However, cultivar 'Albion' always had comparatively higher stomatal conductance than 'San Andreas' at each interaction showing a significant difference between the cultivars (Table I).

Intercellular [CO_2] of leaves increased gradually with increasing atmospheric [CO_2] in strawberry leaves without indicating any saturation (Fig. 1 (b)). When [CO_2] was raised from 400 to 650 µmol mol^{-1} and 950 µmol mol^{-1} at ambient temperature, the intercellular [CO_2] of leaves were increased by 67% and 80%, respectively. That trend was greater at 30 °C and caused 86% and 96% increase in the intercellular [CO_2]. However, no significant differences (P>0.05) in intercellular [CO_2] were observed between cultivars under these conditions.

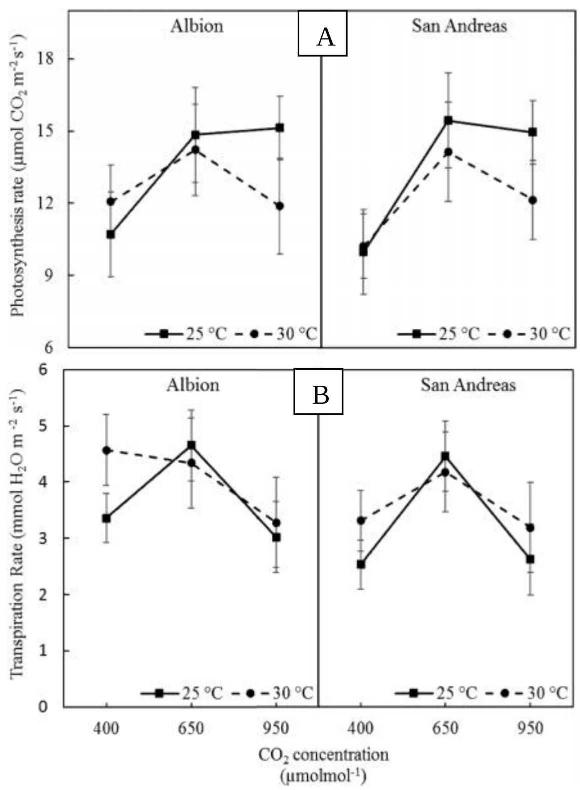

Fig. 1 (a) The influence of different combinations of temperature and CO_2 concentrations on strawberry leaf photosynthesis (A) photosynthesis rate, (B) transpiration rate in different strawberry cultivars

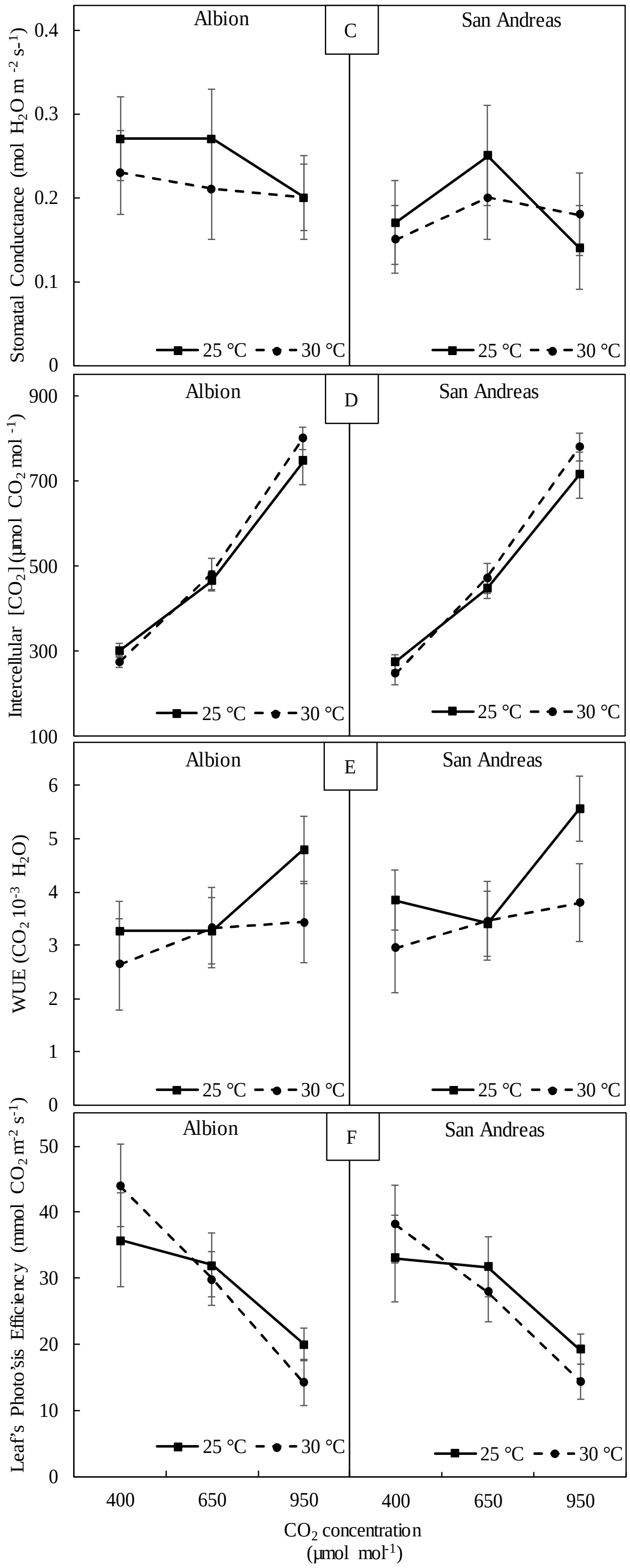

Fig. 1 (b) The influence of different combinations of temperature and CO_2 concentrations on strawberry leaf photosynthesis. (A) photosynthesis rate, (B) stomatal conductance, (C) intercellular CO_2 concentration (Ci), (D) transpiration rate, (E) WUE and (F) photosynthesis efficiency of leaf commonly in different strawberry cultivars

B. Ci/Ca, WUE and Photosynthesis Efficiency

Temperature, [CO_2] and cultivar interactively contributed to Ci/Ca and WUE of strawberry plants. However, in contrast, the photosynthesis efficiency was only influenced by direct effects temperature and [CO_2] rather than interactive effects of those two factors (Table I). Ci/Ca or carboxylation efficiency of leaves gradually increased with rising [CO_2] at high temperature in both cultivars. The highest Ci/Ca (0.84) was observed at treatment combinations of 30 °C and 950 µmol mol^{-1} in strawberry cultivar 'Albion'. Similar to Ci/Ca, photosynthetic WUE was greater at elevated [CO_2] (950 µmol mol^{-1}) at both temperatures in cultivar 'Albion' and at 30 °C in cultivar 'San Andreas' (Table I). Under 950 µmol mol^{-1} elevated [CO_2], WUE of strawberry leaves was generally higher at ambient temperature in compared to high temperature (Fig. 1 (b)).

Unlike Ci/Ca and WUE, photosynthesis efficiency of leaves decreased at elevated [CO_2] (Table I). Leaf photosynthesis efficiency was lowered by elevated [CO_2] (950 µmol mol^{-1}) when the plants grown at 30 °C than at ambient temperature (Fig. 1 (b)). This implies that the increasing temperature and [CO_2] might reduce the photosynthesis efficiency of leaves with unlimited availability of carbon. Photosynthesis efficiency of leaves was maximum (44.04 mmol CO_2 m^{-2} s^{-1}) at high temperature and ambient [CO_2] and it was less than a half (14.26 mmol CO_2 m^{-2} s^{-1}) at lowest at both elevated growth conditions in cultivar 'Albion' (Table I).

C. Plant Growth

Vegetative growth of strawberry plants as indicated by canopy area, number of leaves, plant height, and crown number is shown in Table II. The temperature and [CO_2] interactively influenced on phonological development of strawberry plants. However, the main treatments and cultivar interaction was not significant and Table II presents the average results of both strawberry cultivars. The maximum growth of strawberry plants was observed at 650 µmol mol^{-1} [CO_2] and 25 °C temperature. Elevated [CO_2] from 400 to 650 µmol mol^{-1} increased the plant height by 25% at 25 °C and 20% at 30 °C. However, plants were comparatively shorter at 950 µmol mol^{-1} [CO_2], and the shortest plants were observed at 950 ppm and 25 °C combination (Table II). Those plants recorded a significant ($p<0.05$) height reduction (12%) compared to plants grown at ambient conditions. Similarly, canopy area of strawberry plants was significantly higher ($p<0.05$) at elevated 650 µmol mol^{-1} [CO_2] and at ambient temperature (Table II). However, the canopy areas of strawberry plants were significantly lower at elevated 950 µmol mol^{-1} [CO_2] when compared to 400 ppm at ambient temperature. Conversely, at 30 °C plants exhibited a well grown plant canopy ranged from 436 cm^2 to 626 cm^2 when rising [CO_2] from 400 ppm to 950 ppm. Therefore, the rising CO_2 levels over 650 ppm at ambient temperature could suppress the plant height and canopy expansion of strawberry. Nonetheless, at the combination of 650 µmol mol^{-1} [CO_2] and 25 °C, the plants had more number of leaves and crowns per plant in comparison with other CO_2 levels. Therefore, the plant growth associated with 650 µmol mol^{-1} [CO_2] and 25 °C seems to be more favorable for strawberry plant growth.

D. Flowering and Fruiting

Temperature and [CO_2] interactively influenced the reproductive development of strawberry plants, but no significant differences (P>0.05) between cultivar were found. The number of inflorescences and flowers per plant were higher when plants were grown at 650 µmol mol^{-1} [CO_2] at 25 and 30 °C (Fig. 2). There were three inflorescences and 16 flowers per plants at 650 µmol mol-1 [CO_2] at both temperatures. However, the flowering of strawberry plants did not change significantly (P>0.05) due to 5 °C increased temperature at 950 µmol mol^{-1} [CO_2] treatment (Fig. 2). Under those conditions, the plants produced similar number of inflorescences and flowers per plant to those at ambient. Fig. 2 shows the influence of varied combinations of temperature and [CO_2] levels during reproductive development. Fruit setting is a key component in strawberry yield and it was affected by both temperature and [CO_2]. The fruit setting percentages were significantly lower at 650 µmol mol^{-1} [CO_2] at both temperatures, and at 400 µmol mol^{-1} [CO_2] at high temperature (30 °C) only (Fig. 2). The increased temperature strongly reduced the fruit setting by 43% at ambient CO_2 levels. Increased fruit setting% at elevated [CO_2] at both temperatures did not lead to a greater number of fruit possibly due to less number of flowers. However, the highest number of fruits were recorded from the 650 µmol mol^{-1} [CO_2] with the concurrent occurrence of increased number of inflorescences and flowers.

E. Fruit Development and Yield

Table III shows the total fruit yield, individual average fruit weight and average primary fruit weight of strawberry plants as influenced by different combinations of temperature and [CO_2]. Interaction effect of temperature, [CO_2] and cultivar was significant (p<0.05) on all the fruit characters. However, Higher temperature effect was particularly pronounced on fruit development and yield. Compared to ambient 25 ºC temperature, 30 °C suppressed fruit development by reducing fruit size, fruit weight and finally the fresh fruit yields at all the [CO_2] levels (Table III). The average fresh fruit weight per plant was reduced by high temperature compared to ambient temperature at all CO_2 levels and the reduction was 83% at ambient [CO_2]. For some extent, CO_2 enhancement could overcome the negative effects of high temperature on fruit yields (Table III). The average maximum fruit length and width were greater at all the [CO_2] at ambient temperature in both cultivars.

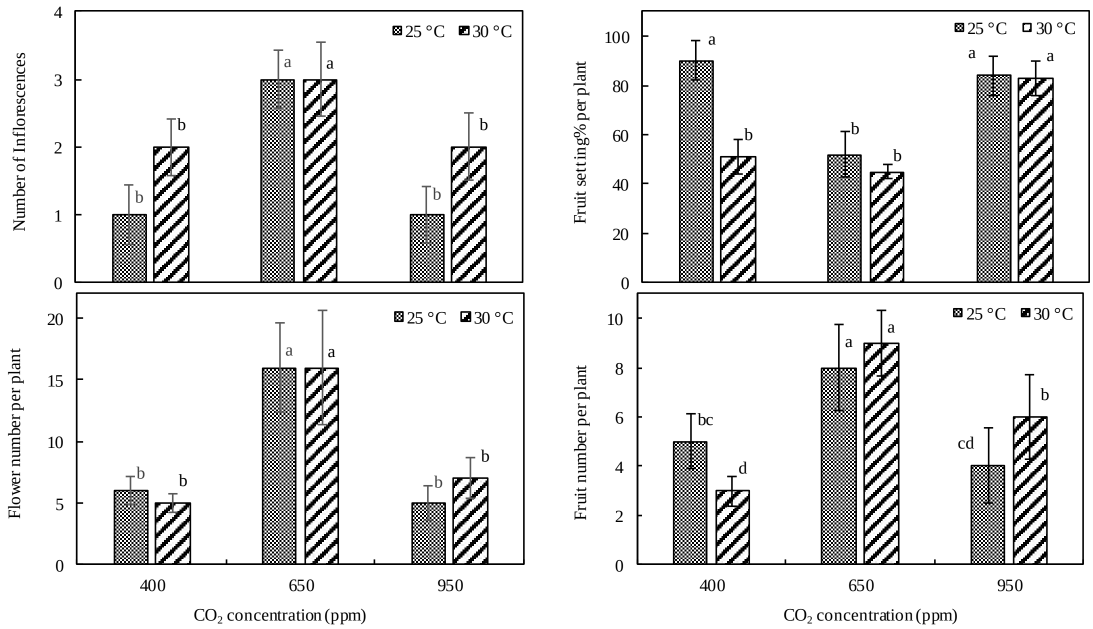

Fig. 2 Reproductive characteristics of strawberry plants as affected by different combinations of temperature and CO_2 concentrations. Cultivar effect on strawberry reproductive growth and development was insignificant (P>0.05). Columns with different letters within each category denote significant difference among the different CO_2 treatments

TABLE II
VEGETATIVE GROWTH OF STRAWBERRY PLANTS AS AFFECTED BY DIFFERENT COMBINATIONS OF TEMPERATURE AND CO_2 CONCENTRATIONS

Tem.	[CO_2]	Plant height	Canopy Area	No. of leaves per plant	No. of crowns per plant
25 °C	400	12.4 ± 1.6^{b}	526 ± 110^{c}	11 ± 2^{b}	2 ± 0.72^{b}
	650	15.6 ± 2.0^{a}	722 ± 108^{a}	16 ± 2^{a}	3 ± 0.83^{a}
	950	10.9 ± 1.2^{c}	568 ± 108^{bc}	10 ± 2^{b}	2 ± 0.46^{b}
30 °C	400	11.8 ± 1.5^{bc}	436 ± 92^{d}	11 ± 2^{b}	2 ± 0.71^{b}
	650	14.2 ± 1.2^{a}	525 ± 101^{c}	9 ± 3^{b}	3 ± 0.64^{a}
	950	12.2 ± 2.4^{bc}	626 ± 101^{b}	11 ± 3^{b}	2 ± 0.65^{b}
Interaction effect					
CO_2*Temperature		**	**	**	**
CO_2*Temperature *Cultivar		ns	ns	ns	ns

Reported results are the means ± standard deviation. Means within each column followed by different superscript letters are significantly different (P<0.05) (** - Significant, ns – Not significant). Tem. stands for temperature. Units; [CO_2] = µmol mol^{-1}, plant height = cm, canopy area = cm^2

TABLE III
EFFECT OF VARIOUS GROWTH TEMPERATURES AND CO_2 CONCENTRATIONS ON FRUIT YIELD OF STRAWBERRY PLANTS

Cultivar	Temperature	[CO_2]	Total fruits weight per plant	Avg. fruit weight per plant	Avg. primary fruit weight	Avg. Maximum Fruit length	Avg. Maximum Fruit width
Albion	25 °C	400	33.80 ± 6.44^{c}	8.20 ± 1.34^{ab}	12.07 ± 0.73^{ab}	3.0 ± 0.4^{ab}	2.6 ± 0.3^{ab}
		650	45.09 ± 4.90^{abc}	7.35 ± 0.65^{b}	8.92 ± 0.76^{cd}	2.8 ± 0.3^{abc}	2.5 ± 0.1^{ab}
		950	37.14 ± 5.66^{abc}	10.13 ± 1.90^{a}	13.5 ± 1.87^{a}	2.9 ± 0.7^{abc}	2.7 ± 0.3^{a}
	30 °C	400	9.60 ± 2.41^{d}	3.20 ± 0.37^{cd}	4.79 ± 0.31^{ef}	1.9 ± 0.5^{de}	1.8 ± 0.2^{ce}
		650	37.82 ± 2.47^{abc}	4.38 ± 0.32^{c}	6.32 ± 0.56^{de}	2.2 ± 0.3^{cd}	2.0 ± 0.3^{cd}
		950	16.48 ± 0.57^{cd}	4.10 ± 0.19^{c}	9.22 ± 1.97^{bcd}	2.1 ± 0.4^{de}	2.0 ± 0.2^{cd}
San Andreas	25 °C	400	60.05 ± 10.4^{a}	10.30 ± 0.73^{a}	14.58 ± 1.03^{a}	3.1 ± 0.5^{a}	2.8 ± 0.2^{a}
		650	59.48 ± 7.92^{ab}	8.10 ± 0.34^{ab}	11.70 ± 1.03^{abc}	3.1 ± 0.4^{a}	2.7 ± 0.3^{a}
		950	41.34 ± 3.51^{abc}	7.38 ± 0.87^{b}	11.81 ± 1.78^{abc}	2.4 ± 0.6^{a}	2.3 ± 0.3^{bc}
	30 °C	400	7.00 ± 1.70^{d}	1.99 ± 0.35^{d}	2.68 ± 0.41^{f}	1.5 ± 0.5^{e}	1.5 ± 0.2^{e}
		650	33.40 ± 4.03^{bc}	3.52 ± 0.39^{cd}	3.73 ± 0.42^{ef}	2.4 ± 0.3^{bcd}	2.1 ± 0.3^{cd}
		950	29.98 ± 6.98^{cd}	4.96 ± 0.61^{c}	9.27 ± 1.83^{bcd}	2.0 ± 0.3^{de}	2.0 ± 0.3^{cd}
Interaction effect	CO_2*Temperature		**	**	**	**	**
	CO_2*Temperature*Cultivar		**	**	**	**	**

Reported results are the means ± standard deviation. Means in each category and within each column followed by different superscript letters are significantly different (P<0.05) (** - Significant, ns – Not significant). Units; [CO_2] = µmol mol^{-1}, fruit weights = g, fruit length = cm.

IV. DISCUSSION

The present study clearly demonstrated that the interactions of elevated temperature and [CO_2] were significant (P<0.05) on leaf gas exchange properties of strawberry. On average, elevated [CO_2] increased the net photosynthesis rate by 41% at 25 ºC and at 950 µmol mol^{-1} [CO_2] in ‘San Andreas’ and by 55% at 25 °C and at 650 µmol mol^{-1} [CO_2] in ‘Albion’. Similarly, Bushway [15] reported increased net photosynthesis rates by 50% at 700 – 1000 µmol mol^{-1} [CO_2] and 15 ºC. According to our results, the CO_2 enrichment improved the net photosynthesis rates of strawberry leaves even at 30 ºC. Wang, Wang [25] also observed increased net photosynthesis rates in Oak seedlings at elevated temperature (ambient + 4 °C). The elevated temperature significantly increased the irradiance saturation point, apparent quantum yield, maximum photosystem II efficiency, chlorophyll content, and finally maximum net photosynthesis rate of plants [25].

Photosynthesis is affected by numerous internal leaf factors including photosynthetic apparatus, enzymes and their status photochemical reactions [25]. It is well-known that the [CO_2] is a limiting substrate in leaf photosynthesis in C3 plants thus net photosynthesis rate is highly dependent on intercellular [CO_2] concentration of leaves [11], [14]. The increased availability of CO_2 inside the leaf would increase leaf photosynthesis through increased activity of rubisco enzyme and reduced photorespiration [14]. In this study, the intercellular [CO_2] increased continuously in a range of 260 to 800 µmol mol^{-1} when external [CO_2] was increased from 400 to 950 µmol mol^{-1}. Chen, Hu [17] experienced the same trend for intercellular [CO_2] of strawberry leaves. When the strawberry plants exposed to 300 to 900 µmol mol^{-1}, intercellular [CO_2] levels ranged from 276 to 886 µmol mol^{-1}. Under higher [CO_2] in outside environment, generally closes stomatal aperture, which is apparent in these current results, and limits the gas exchange [26]. However, intercellular [CO_2] in strawberry leaves increased continuously with increased [CO_2] even at lower stomatal conductance at both temperatures. Therefore, it is possible that strawberry is unlikely to be photosynthetically saturated under very high [CO_2] concentrations.

However, elevated temperature (30 °C) and [CO_2] of 950 µmol mol^{-1} reduced net photosynthesis rate of leaves by 20% compared to 25 °C and 950 µmol mol^{-1}. High temperature can influence in plant photosynthesis in both positively (as explained earlier) and negatively by increasing dark respiration [25]. The rubisco down regulation associated with both elevated temperature and [CO_2] may also reduce the rate of net photosynthesis of leaves [27]. Both elevated temperature and [CO_2] could reduce the content and activation of rubisco protein thus influence the leaf photosynthesis rate. It has been reported that high temperatures above the optimum would change the solubility of gasses *via* declining the photosynthesis enzymes of ribulose bisphosphate (RuBP) carboxylase/oxygenase (RuBPCO). Because of changing the activity of RuBPCO, the Ci/Ca ratio which is an indication of carboxylation efficiency might be reduced [28]. In this study there was a clear reduction in Ci/Ca ratio and high temperature at ambient [CO_2]. However, the Ci/Ca ratio was significantly ($p<0.05$) greater at elevated [CO_2]. Increased CO_2 supply can support to a better carboxylation efficiency which is apparent in this study.

Temperature and [CO_2] individually and interactively can affect WUE in plants [28]. These factors highly influence stomatal conductance of leaves which regulates the plant water loss and thereby influence the leaf WUE [28]. WUE of strawberry leaves was highest at 25 °C and 950 µmol mol^{-1} where the plants had higher CO_2 storage under lowest water loss (Table I). The lowest WUE was observed at high temperature and 400 µmol mol^{-1} combination.

But elevated [CO_2] could partially alleviate the detrimental effects of the high temperature thus increasing the WUE. The net photosynthesis rates remained constant at 650 and 950 µmol mol^{-1}, but the reduced transpiration rates of leaves and improved the WUE at 25 °C and 950 µmol mol^{-1}. Higher [CO_2] in external environment suppresses the stomatal opening and consequently limits the water loss from leaves. These water savings in the plants improve the WUE at elevated [CO_2] [29]. Therefore, under the predicted future climate change, particularly under elevated [CO_2], C3 plants are likely to perform better under water limited conditions.

The vegetative growth was significant in plants grown at 25 °C temperature and 650 µmol mol^{-1} [CO_2]. At this combination, plants were comparatively taller and plants had a larger canopy cover, and higher number of leaves and crowns. Reddy, Rasineni [14] also observed taller *Gmelina arborea* plants under elevated CO_2 (ambient + 100 µmol mol^{-1}). Elevated [CO_2] increased cell division, expansion, differentiation and organogenesis, encouraged by carbon assimilation and WUE [14]. However, at elevated 950 µmol mol^{-1} [CO_2], strawberry plants experienced lower growth. Lower growth of plants could be due to end-product inhibition associated with limited sink capacity and resulted with down regulation of photosynthesis [14]. It is expected that more carbon moves to the roots and stems than the leaves under elevated [CO_2]. Therefore, restricted root growth at elevated [CO_2] decreases the root/shoot ratio in potted pants. A down regulation photosynthesis would occur as a result of root induced signaling [30]. Significant reductions in rubisco activity and chlorophyll contents in leaves of pot grown plants [31] would further support the down regulation photosynthesis. However, the increased CO_2 compensated to the negative effects of high temperature (30 °C) on growth of plants for some extent having similar vegetative growth to ambient temperature. In comparison to ambient growth conditions (25 °C and 400 µmol mol^{-1}), the combination of both elevated temperature and [CO_2] did not noticeably influence on plant growth or development. Both strawberry cultivars responded similarly to the combinations of the elevated growth conditions at vegetative development.

Similarly, reproductive development of the plants was significantly ($P<0.05$) accelerated at 650 µmol mol^{-1} [CO_2] at 25 °C and 30 °C. Increased CO_2 promoted more number of flower clusters, flowers and ultimately more fruits. None of the other combinations significantly influenced flower initiation. However, temperature adversely affected fruit number due to lower fruit setting percentage at 400 µmol mol^{-1}. Although the fruit setting percentage was lower at 650 µmol mol^{-1} [CO_2], plants produced the highest number of fruits due to increased flowering. Therefore, the rising CO_2 in future up to 650 µmol mol^{-1} may be favorable on reproductive development of strawberry but, concentrations near 950 µmol mol^{-1} at ambient and + 5 °C may be not. Further, yield response to elevated [CO_2] highly depends on the sensitivity of reproductive phase of individual plant cultivar to the high temperature [32], [33]. Ahmed, Hall [33] tested two cowpea cultivars of heat sensitive and heat tolerant under elevated temperature and [CO_2]. Their results suggested that the CO_2 enrichment was not able to increase the tolerance of cowpea plants to overcome the heat stress during the reproductive phase. The results were also true for the tested strawberry cultivars in this study.

The number of inflorescences, flowers and fruits together with average fruit weight decide the harvestable yields in strawberry. Results from current study revealed that temperature individually and interactively with higher [CO_2] (650 and 950 µmol mol^{-1}) declined the fruit yield in strawberry plants. Higher temperature often erodes the yield benefits of strawberry of improved by CO_2 enrichment. In this study, high temperature reduced the average fruit weights and fruit yields except at 650 µmol mol^{-1}. The plants grown at 650 µmol mol^{-1} at both temperatures produced similar fruit yields to the ambient conditions. Those higher fruit yields were caused by encouraged blooming. Enriched [CO_2] from 400 to 950 µmol mol^{-1} at 30 °C increased average fruit weight and average primary fruit weight per plant by overcoming the inhibitory effects of increased temperature. Similarly, increased fruit weights and fruit sizes were reported for pear fruits under elevated climate conditions (Ambient + 4 °C and 700 µmol mol^{-1}) [34]. Though [CO_2] enrichment would be beneficial on plant growth process more at high temperature than low, but supra-optimal temperatures (above 40 °C) could lead the plants to considerable yield losses even at enriched [CO_2] [29], [35].

Theoretically it is expected that rising [CO_2] levels would compensate the detrimental effects of high temperature on strawberry yield in future. However, none of the varieties tested in this study were able to produce better yields under elevated temperature and [CO_2]. Therefore, this study suggests that higher temperatures (ambient + 5 °C) and very high [CO_2] levels (i.e. 950 μmol mol^{-1}) in future may not favor high quality and economical strawberry cultivations.

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