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Effects of Root-Zone Temperature on Photosynthesis, Productivity and Nutritional Quality of Aeroponically Grown Salad Rocket (*Eruca sativa*) Vegetable

Jie He*, Xin Er See, Lin Qin, Tsui Wei Choong

Natural Sciences and Science Education Academic Group, National Institute of Education, Nanyang Technological University, Singapore
Email: *jie.he@nie.edu.sg

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Abstract

Although tropical high ambient temperature and humidity severely reduced the productivity of temperate plants, temperate vegetable crops such as lettuce have been successfully grown in Singapore by only cooling its root-zone. In this paper, a cool Meditteranean vegetable, *Eruca sativa*, was studied to understand how different RZTs can impact its shoot productivity, photosynthesis and nutritional quality. All plants were cultivated using aeroponic systems in a tropical greenhouse under hot ambient conditions where roots were subjected to four different root-zone temperatures (RZTs) of 20˚C-RZT, 25˚C-RZT, 30˚C-RZT and fluctuating ambient temperatures ranged from 25˚C to 38˚C [25˚C/38˚C (ambient)]-RZT. Parameters studied include shoot fresh weight (FW), photosynthetic gas exchange, midday chlorophyll (Chl) fluorescence F_v/F_m ratio, Chl fluorescence photochemical quenching (qP), non-photochemical quenching (qN) and electron transport rate (ETR), total phenolic compounds and mineral content such as potassium (K), calcium (Ca), magnesium (Mg) and iron (Fe). Among the 4 different RZT treatments, *E. sativa* plants grown under ambient-RZT (25/38˚C-RZT) had the lowest shoot and root FW while those plants grown under 20˚C-RZT had highest productivity of shoot and root. However, there were no significant differences in shoot and root FW in plants grown at 25˚C- and 30˚C-RZT. Compared to plants grown under 25˚C/38˚C (ambient-RZT), light-saturated photosynthetic CO_2 assimilation rate (A_{sat}) and stomatal conductance (g_{ssat}) were similarly higher in 20˚C-, 25˚C- and 30˚C-RZT. All plants had midday Chl fluorescence F_v/F_m ratio lower than <0.8 ranged from 0.785 to 0.606 with the highest and lowest ratios recorded in 20˚C-RZT and ambient-RZT plants, respectively. These results indicate that cooling the RZ of *E. sativa* plants protected their PS II from photoinactivation during midday in the greenhouse. There were no significant differences observed in photochemical quenching (qP), non-photochemical quenching (qN) and electron transport rate among plants grown under 20˚C-, 25˚C- and 30˚C-RZT. However, plants grown under ambient-RZT had lower qP, qN and ETR compared to all other plants. *E. sativa* at 20˚C-RZT with the best developed roots had the highest dietary mineral (K, Mg, Ca and Fe) contents but lower total phenolics content. In contrast, ambient-RZT, plants with poorly developed roots had the lowest mineral content but highest total phenolic content. The results of this study suggest that cooling of roots is a feasible method for the cultivation of *E. sativa* in the tropic, which enhances the content of dietary minerals in shoots.

Keywords

Chlorophyll Fluorescence, Dietary Minerals, Root-Zone Temperature,
Phenolic Compounds, Photosynthetic CO_2 Assimilation Rate, Stomatal Conductance

1. Introduction

A leafy vegetable characterized by its strong distinctive flavours, *Eruca sativa*, commonly known as rocket, is well known for their antioxidant and medicinal properties. As such, they are widely consumed by people or researched as alternative medications to synthetic drugs [1]-[3]. However, *E. sativa* are mediterranean plants which require cool temperatures for optimum growth and development. Dolezalova *et al.* [4] reported that *E. sativa* is best grown at temperatures from 10˚C to 25˚C. In contrast, temperatures in the tropical greenhouse can fluctuate from 26˚C to 38˚C. Temperate crops are vulnerable to heat stress when grown under these temperatures due to the poor root development and mineral deficiency [5]-[9] and limitation of photosynthesis [10]-[15]. Other effects of heat-stress were scorching of shoots, abscission and senescence of leaves, growth inhibition and decreased plant productivity [10] [11] [16].

A study on *Brassica albogabra* also showed detrimental effects of high temperatures on root morphology, such as total root length and mineral nutrition [9]. Berry (1975) studied on *Atriplex glabriuscula*, a cool marine climate plant, and found that photosynthetic capabilities decrease as a trade-off to adapt to higher temperatures [15]. He *et al.* reported that temperate crops grown in a tropical greenhouse exhibited both stomatal and non-stomatal limitation of photosynthesis [12]. Thus, a Mediterranean plant such as *E. sativa* is not suitable for cultivation in Singapore under natural conditions due to the negative impacts of high tropical temperature on its growth and photosynthesis. However, the cultivation of *E. sativa* in Singapore is possible through the use of aeroponic systems by cooling the root zone. We have previously reported that subtropical and temperate vegetable crops could be grown in the tropics with the cooling of root zones, even though aerial parts were exposed to ambient tropical temperatures [14]. Our previous results showed that cooling of RZ reduced depression of photosynthesis during periods of bright sunlight, mitigated stomatal limitations on photosynthesis due to water deficit and alleviated non-stomatal limitation resulting from protecting leaves from photo inactivation, and improved overall plant growth and development [12] [13].

This study aimed to invest if photosynthetic capabilities, productivity and nutritional qualities of *E. sativa* were affected under tropical conditions with different RZTs, namely at 20˚C-, 25˚C-, 30˚C- and 25˚C/38˚C (ambient)-RZT. Fresh weights (FW) of root and shoot were measured to determine productivity of plant at harvest. Light-saturated photosynthetic CO_2 assimilation rate (A_{sat}), stomatal conductance ($g_{s\ sat}$) and midday chlorophyll (Chl) fluorescence F_v/F_m ratio were measured in the greenhouse to investigate the effects of RZT on stomatal and non-stomatal limitations of photosynthesis [12]. Light response curves of photochemical quenching and non-photochemical quenching were determined to study the impacts of RZT on photosynthetic utilization of radiant energy [13]. Effects of RZT on nutritional qualities were also analysed by the comparison of total phenolic compounds and various minerals such as K, Ca, Mg and Fe.

2. Materials and Methods

2.1. Plant Material and Cultural Methods

E. sativa seeds were germinated on moist Whatman filter papers in petri dishes under laboratory conditions. Three days after germination, the seedlings were inserted into polyurethane cubes soaked in water for adaptation. After nine days of adaptation, these seedlings were transplanted into four aeroponic troughs of different temperatures. To maintain the different RZTs, all troughs were insulated using aluminum-laminated polyethylene sheets. Three water tanks were regulated using chillers to maintain the different constant RZTs at 20.1˚C ± 0.1˚C, 25.0˚C ± 0.1˚C, 29.6˚C ± 0.1˚C while one of them was kept at ambient temperature range from 25˚C to 38˚C. Full nutrient solution was supplied by misting roots at a frequency of 30 seconds at every three min. The electrical conductivity and pH of nutrient solutions were maintained at 2.0 ± 0.2 mS and pH 6.5 ± 0.5 respectively. The aerial parts of the plants were subjected to prevailing greenhouse conditions, where temperatures fluctuate from 25˚C to 38˚C and maximal photosynthetic photon flux density (PPFD) was about 600 μmol photon $m^{-2}\cdot s^{-1}$.

2.2. Measurements of Shoot and Root FW

Four weeks after transplant, random plants from each treatments were harvested at 0700 h. Shoot and roots were separated for FW measurement. The roots of each plant were washed and dabbed dry before weighing.

2.3. Measurements of A_{sat} and $g_{s\ sat}$

Three weeks after transplanting, readings were taken between 0900 h to 1100 h in the greenhouse with an open infrared gas analysis system with a 6 cm^2 chamber (LI-6400, Biosciences, US). Readings were taken with a LED light source, which supplied 1000 $\mu mol\cdot m^{-2}\cdot s^{-1}$ of PPFD. The light source emitted in the wavelength ranged between 420 to 510 nm and 610 nm to 730 nm. The spectral output of the light source has one peak centred at about 465 nm and second peak centred at about 670 nm. Average ambient [CO_2] and relative humidity in the chamber were 400 ± 3.5 $\mu mol \cdot mol^{-1}$ and 70% respectively. Measurements were recorded when both A_{sat} *and* $g_{s\ sat}$ were stable.

2.4. Measurement of Midday Chl Fluorescence F_v/F_m Ratio

Three weeks after transplanting, measurements of midday F_v/F_m ratio were made with the Plant Efficiency Analyser, PEA, (Hansatech Instruments Ltd., England). All F_v/F_m ratios were taken from the same leaves from which A_{sat} and g_{ssat} were recorded. The readings were carried out 1230 h to 1330 h. Attached leaves were pre-darkened with clips for 15 min prior to measurements. Dark-adapted leaves were placed under the light pipe and irradiated with the pulsed lower intensity-measuring beam to measure F_0, initial chlorophyll fluorescence. F_m, maximum chlorophyll fluorescence was assessed by 0.8 s of saturated pulse (>6000 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The variable fluorescence yield, F_v, was determined by F_m-F_0. The efficiency of excitation energy captured by open PSII reaction centres in dark-adapted plant samples was estimated by the fluorescence F_v/F_m ratio.

2.5. Measurements of Photochemical Quenching (qP), Non-Photochemical Quenching (qN) and Electron Transport Rate (ETR)

Leaf discs (1 cm diameter) were punctured and placed on moist filter papers in Petri dishes. They were pre-darkened for 15 min prior to measurements. Via the Imaging-PAM Chl Fluorometer (Walz, Effeltrich, Germany), images of fluorescence emission were digitized within the camera and transmitted via a Firewire interface (400 megabits/s) (Firewire-1394, Austin, TX, USA) to a personal computer for storage and analysis. Measurements and calculations of qP, qN and ETR were determined according to He *et al.* [17].

2.6. Determination of Total Phenolic Compounds

The concentration of total phenolic compounds was determined in methanol extracts using a colorimetric method [18] [19]. To extract the phenolic compounds, 0.5 g of fresh shoot tissues were grinded with liquid nitrogen and 5 ml of 80% methanol. The extracts were shaken for 30 min at 2000 rpm and centrifuged for 20 min at 3500 rpm. The supernatants were transferred to clean tubes. 0.5 ml of extract was diluted with 0.5 ml of diluted Folin-Ciocalteau reagent and 1 ml of 7.5% Na_2CO_3 solution. After 20 min, the absorbances were measured at 765 nm using UV-2550 spectrophotometer (Shimadzu, Japan). Total phenolic compounds of the samples were expressed as gallic acid equivalents in micrograms per gram of FW.

2.7. Determination of Inorganic Dietary Minerals

Dried shoot tissues of 0.2 g were microwave-digested in 4 ml of 65% HNO_3 using UltraWAVE single reaction chamber microwave digestion system (Milestone, US). Digested samples were diluted with the addition of Milli-Q water to a total volume of 25 ml. Inductively coupled plasma optical emission spectrophotometry (ICP-OES) was performed using Optima 8300 ICP-OES Spectrometer and WinLab 32 (Perkin Elmer, US). The data retrieved were then used to calculate the concentrations.

2.8. Statistical Analysis

Levene's test was used to ensure equal variances across samples of the four treatments. One-way analysis of variances (ANOVA) and Tukey's multiple comparison test were used to discriminate between means of the different treatments, where means with $p < 0.05$ has significant differences. All statistical analyses were performed using MINITAB software (MINITAB Inc., US).

3. Results

3.1. Shoot and Root Productivity

Figure 1 shows *E. sativa* plants that were grown in a tropical greenhouse with aeroponic system at 20˚C-RZT (Figure 1(a)) and other different RZTs for 4 weeks (Figure 1(b)). Plants grown under ambient-RZT (25˚C/38˚C-RZT) had the lowest shoot FW while those plants grown under 20˚C-RZT had highest productivity of shoot (Figure 2(a)). However, there were no significant differences in shoot FW implants grown at

Figure 1. *E. sativa* plants grown in a tropical greenhouse with aeroponic system at 20˚C -RZT (a) and grown under different RZTs for 4 weeks (b).

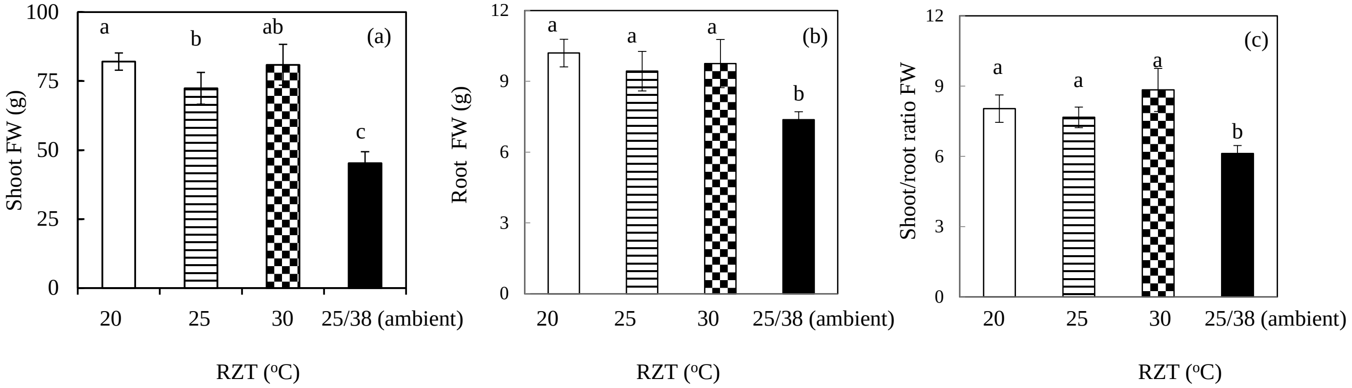

Figure 2. Shoot (a), root (b) FW and shoot/root ratio FW of *E. sativa* grown under different RZTs. Each bar represents the mean measurements from 5 plants (n = 5). Vertical bars represent standard errors. Means with the same alphabet above the bars are not statistically different ($p > 0.05$) as determined by Tukey's multiple comparison test.

25˚C- and 30˚C-RZT. For root FW (**Figure 2(b)**) and shoot/root ratio FW (**Figure 2(c)**), there were no significant differences among *E. sativa* grown under 20˚C-, 25˚C- and 30˚C-RZT and they were significantly higher than plants grown at ambient-RZT.

3.2. Photosynthetic Gas Exchanges at Different RZTs

No significant differences in A_{sat} (**Figure 3(a)**) and $g_{s\ sat}$ (**Figure 3(b)**) were observed among plants grown under 20˚C-, 25˚C- and 30˚C-RZTs. However, these two parameters were significantly higher than those of ambient-RZT plants (25˚C/38˚C -RZT).

3.3. Photosynthetic Utilization of Radiant Energy at Different RZTs

20˚C-RZT and A-RZT plants had the highest and lowest midday F_v/F_m ratio respectively (**Figure 4**). High midday PPFD induced dynamic photo inactivation, indicated by <0.8 F_v/F_m ratios. Decreasing F_v/F_m ratio was observed with increasing RZTs. In fact, *E. sativa* grown under 20˚C-RZT had very mild photo inhibition as midday Fv/Fm ratio was very close to 0.8. **Figure 5** shows the light response curves of ETR, qP and qN from *E. sativa* grown under different RZTs. For all plants, ETR increased with increasing PPFD from 15 to 715 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and decreased with further increasing PPFD beyond 715 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (**Figures 5(a)-(d)**). Although the light response curves were similar for all plants, at a PPFD of 605 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which was close to their growth PPFD, the ETR values indicated by black arrows, for plants grown under 20˚C-, 25˚C- and 30˚C-RZT were similarly but significantly higher than those of plants grown under ambient-RZT. Although qP decreased and qN increased with increasing PPFDs from 15 to 1585 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for all plants, under higher PPFDs, the values of qP and qN were similarly but significantly higher in plants grown at 20˚C-, 25˚C- and 30˚C-RZTs than at ambient-RZT. For instance, the average values of qP and qN measured at a PPFD of 605 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (indicated by blank arrows), were 0.767 (**Figure 5(e)**), 0.782 (**Figure 5(f)**), 0.765 (**Figure 5(g)**), and 0.617 (**Figure 5(h)**), respectively for 20˚C-, 25˚C- and 30˚C- and ambient-RZT.

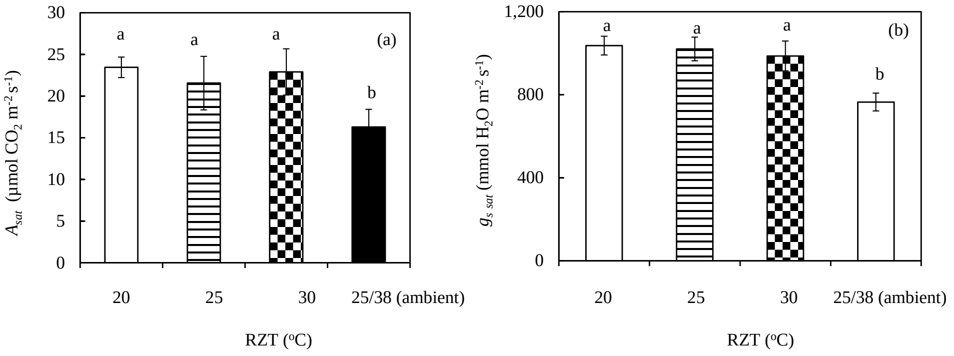

Figure 3. A_{sat} (a) and $g_{s\,sat}$ (b), of *E. sativa* grown under different RZTs (n = 4). Means with the same alphabet above the bars are not statistically different ($p > 0.05$) as determined by Tukey's multiple comparison test.

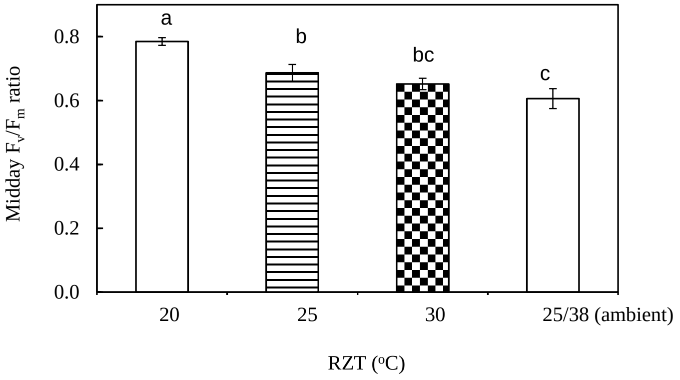

Figure 4. Midday F_v/F_m ratio of *E. sativa* grown at different RZTs (n = 8). Means with the same alphabet above the bars are not statistically different ($p > 0.05$) as determined by Tukey's multiple comparison test.

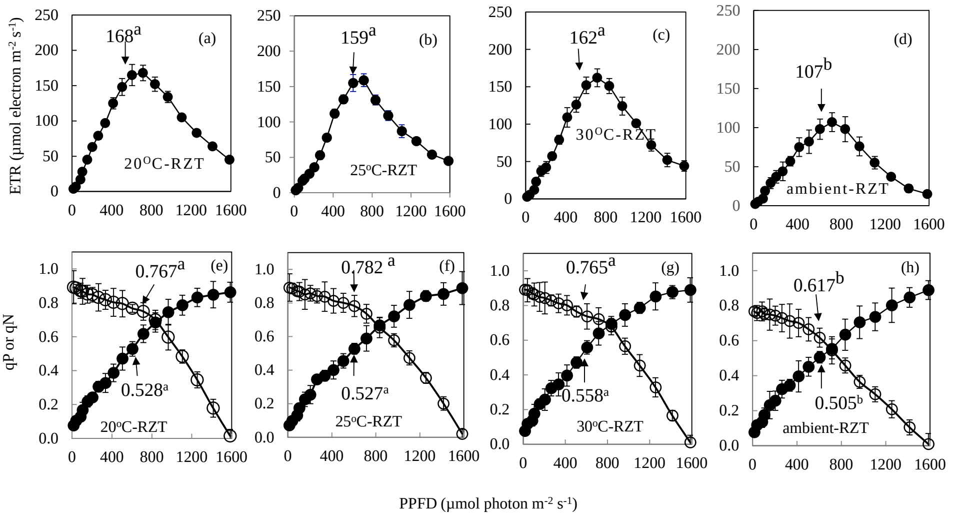

Figure 5. Light responses curves of ETR (a, b, c, d), qP (open circle) and qN (solid circle) (e, f, g, h) of *E. sativa* grown at different RZTs (n = 15). Black arrows show the values measured at a PPFD of 605 μmol photon $m^{-2}\cdot s^{-1}$). Means with the same alphabet above the bars are not statistically different ($p > 0.05$) as determined by Tukey's multiple comparison test.

3.4. Nutritional Qualities

The content of total phenolic compounds was significantly higher in ambient-RZT plants as compared to plants of other RZTs, which had similar levels (Figure 6(a)). On the other hand, the contents of inorganic minerals such as K, Mg, Ca and Fe in *E. sativa* were different among the different RZT treatments. For example, K and Ca contents were highest in *E. sativa* grown at 20˚C-RZT followed by those grown under 25˚C- and 30˚C-RZT and *E. sativa*grown at ambient-RZT had the lowest K and Ca contents (Figure 6(b) and Figure 6(d)). For Mg, *E. sativa* grown under 20˚C-, 25˚C- and 30˚C-RZT had similar higher content than that of ambient-RZT plants (Figure 6(c)). *E. sativa* grown at 30˚C-RZT had the highest Fe content followed by those grown under 20˚C- and 25˚C-RZT whereas plants grown under ambient-RZT had the lower Fe content.

4. Discussion

In the present study, the biomass of both shoot and root of *E. sativa* were significantly higher at 20˚C-RZT compared to those grown at ambient-RZT (Figure 1(b) and Figure 2). The lowest shoot and root FW and shoot/root ratio FW observed in *E. sativa* grown under high ambient-RZTimply that high RZT affected not only the productivity of *E. sativa* grown in the tropical greenhouse but also photoassimilate partitioning between shoot and root. *E. sativa* grown under high RZT with more photoassimilates partitioned to roots than shoot (Figure 1(c)) and this has been previously reported by our team in lettuce [5] [6] and other researchers in other plant species [20] [21]. However, similar to temperate lettuce, cooling the RZ of *E. sativa* could alleviate such adversely effects on productivity [5] [6] [22]. Our ^{14}C feeding experiments suggested that the younger developing leaves of lettuce grown under cooling-RZT had greater sink strength [6]. It was interesting to note that there were no significant differences in root FW and shoot/root ratio FW among *E. sativa* grown under 20˚C-, 25˚C- and 30˚C-RZT, indicating that the optimal cool-RZT for *E. sativa* was much broader that the temperate lettuce that had a narrow optimal cool-RZT at about 20˚C [10] [11]. Mature

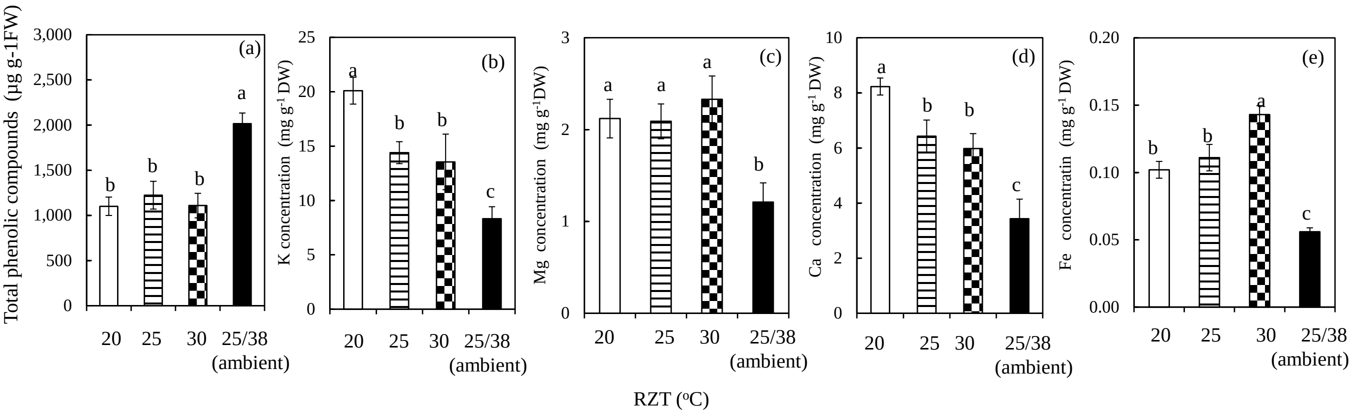

Figure 6. Total phenolic compound (a), ptassium, K (b), calcium, Ca (c), magnesium, Mg (d) and iron, Fe (e) concentrations of *E. sativa* grown at different RZTs (n = 4). Means with the same alphabet above the bars are not statistically different ($p > 0.05$) as determined by Tukey's multiple comparison test.

E. sativa plants (4 weeks after transplanting, **Figure 1**) showed that ambient-RZT plants had much smaller root system with shortest root length but thick root diameter (data not shown) compared to that of *E. sativa* grown under other cooler RZT. These concur with the discussion of our various studies where inhibitory effects on root elongation and lateral growth but promoting root thickening were observed in plants grown at high RZTs [5]-[7] [23]. The root thickening may be due to the synthesis of chemical signals such as ethylene [8] [24], that was further confirmed by our team recently [25]. Effects of RZTs on ethylene production and root chickening of *E. sativa* merits our future study.

Contrary to our previous studies on lettuce [10] [11] [14], RZT did not seem to have significant impact on photosynthesis of *E. sativa* from 20˚C to 30˚C although their A_{sat} (**Figure 3(a)**) and $g_{s\ sat}$ (**Figure 3(b)**) were significantly lower under hot ambient-RZT. A_{sat} of *E. sativa* grown under different RZTs correlate well with $g_{s\ sat}$. Lower $g_{s\ sat}$ indicated stomatal closure or partially closure when roots were subjected to high RZTs [12] [14]. Stomatal closure could deplete CO_2 in the intercellular spaces and at the chloroplast level, thus reducing *Asat* [26] and this is termed a stomatal limitation of photosynthesis [12] [14] that occurred in *E. sativa* grown under ambient-RZT. High RZT resulted in stomatal limitation of photosynthesis was also reported in the studies of tomatoin a greenhouse [27]. Tomato plants that were grown at similar shoot temperature of 25˚C but 5 different RZTs of 12˚C, 18˚C, 24˚C, 30˚C and 36˚C showed that photosynthetic CO_2 uptake, was the highest at 24˚C-RZT but the lowest at 36˚C-RZT [27]. We have also reported that temperate lettuce exposed to high solar irradiation (maximum PPFD *circa* 1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the tropical greenhouse accompanied by high RZT experienced not only stomatal but also non-stomatal limitations of photosynthesis supported by decreases of leaf Chl content and Chl fluorescence F_v/F_m, ratio [12]. In the present study, average midday fluorescence F_v/F_m, ratios were 0.785, 0.678, 0.652 and 0.606, respectively measured from *E. sativa* grown under 20˚C-, 25˚C-, 30˚C- and ambient-RZT (**Figure 4**). These results indicated that dynamicPSII photo inhibition was rather mild or moderate and was not accompanied by decreases of predawn F_v/F_m, ratio and leaf Chl content (data not shown). These could be due to the lower solar irradiation inside the greenhouse (maximum PPFD *circa* 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the present study compared to our previous experiment with lettuce discussed earlier [12]. However, there was still a significant lower midday F_v/F_m, ratio in *E. sativa* grown under ambient-RZT compared to those grown under cooler RZT (**Figure 4**). It well known that photo inhibition could occur at low and moderate light when other adverse conditions such as super- or sub-optimal temperature were present [28]. At optimal growing temperature and low light, the electron flow from PSII does not exceed the capacity of PSI electron acceptors to cope with electrons, and PSI remains stable [29]-[31]. Recently, it has been reported that PS II photo inhibition was regarded as an ultimate mechanism for protecting PSI activity [31]. In the present study, lower ETR (**Figure 5(d)**) and qP (**Figure (5h)**) in *E. sativa* grown under ambient-RZT compared to other cooler RZT (**Figures 5(a)-(c)** and **Figures 5(e)-(g)**) seemed to supported this conclusion. Non-photochemical quenching (qN or NPQ) help to regulate and protect photosynthesis in environments in which light energy absorption exceeds the capacity for light utilization and thus, avoid over reduction and potential damage to PS II [32] [33]. However, instead of higher qN, lower qN was observed in *E. sativa* grown under ambient- RZT (**Figure 5(h)**). High levels of qN were typically associated with higher level of carotenoids [34] [35]. However, in the present study, levels of carotenoids varied little among the different RZT treatment (data not shown).

Plant phenolic compounds of plants are essential human diet, and are of considerable interest due to their antioxidant properties [36]. It has been reported that low growth temperature decreased the content of some phenolic compounds in pea (*Pisum sativum* L.) seedlings [37]. In the present study, while plants grown under other cooler RZTs had low total phenolic content, plants grown under ambient-RZT had the highest total phenolic content (**Figure 6(a)**). Bita and Gerats reported that heat stress led to the production of reactive oxygen species (ROS). Anti-oxidants such as phenolics compounds are produced by plants in order to resist oxidative stress [38]. Results from this study thus indicate that phenolic compounds may produce to counter the oxidative stress at ambient-RZT. At other RZTs, the cooler RZTs had alleviated the oxidative effects of heat stress.

RZT affects the root morphology and productivity of *E. sativa.* Would RZT also affects the dietary mineral uptake of *E. sativa* since high RZT results in poor root development, reductions of uptake and transport of mineral and inhibition of nitrogen metabolism [14] [39]? Compared to plants grown at cooler RZT, ambient-RZT plants had lower shoot K (**Figure 6(b)**), Mg (**Figure 6(c)**), Ca (**Figure 6(d)**) and Fe (**Figure 6(e)**) concentration. When comparisons made among 20˚C-, 25˚C- and 30˚C-RZT, 20˚C-ZT plants had higher K and Ca concentration, indicating that the roots of *E. sativa* need much cooler temperature to absorb and translocate these two elements to the shoot, resulting from well-established root systems under cool-RZTs [5] [7]. For Mg, there were no significant differences among the plants grown under three cool-RZTs. It was surprise to note that Fe concentration was the highest in plants grown under 30˚C-RZT. Based on the above results, a general trend was observed, where increase in RZTs generally led to increase in total phenolic content and decrease in mineral content. These hinted a possible manipulation of organic and mineral nutrient quality and productivity in *E. sativa* using different RZTs.

5. Conclusion

In conclusion, the growth of *E. sativa* plants was adversely affected by hot ambient-RZT in a tropical greenhouse. Ambient-RZT led to heat stress effects on *E. sativa*, such as poor growth, midday photo inhibition, stomotal limitation of photosynthesis and generally low mineral concentrations. 20˚C-RZT would be a suitable RZT for the cultivation of *E. sativa*, as plants had enhanced productivity, mild midday photoinhibition, high photosynthetic ate and generally high mineral concentrations. However, plants growing at 20˚C-RZT have low antioxidants such as total phenolic compounds. As this is a preliminary study to provide a potential method of cultivating *E. sativa* in the tropics, more studies should be carried out to manipulate the nutritional values by adjusting other factors such as light or CO_2 levels.

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