Photooxidative Stress Modulation of Endogenous Phytohormone and Antioxidant Accumulations and Fruit Maturity in Date Palm (*Phoenix dactylifera* L.)

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Abstract

A common modern cultivation practice is bagging the fruit bunch if date palm (*Phoenix dactylifera* L.) which may influence fruit maturity and nutraceutical quality. Exposure of fruits to photooxidative stress induces changes in the endogenous concentrations of plant hormones and other metabolites, which may cause accelerated fruit maturity. This study was conducted to examine the effect of exposure to direct and indirect sunlight on date palm fruit development. The indirect sunlight treatment was simulated by fruit bunch bagging, a common practice in modern date production. The exposure of date palm fruits to direct sunlight-induced photooxidative stress causing an increased concentration of ascorbic acid and decreased content of chlorophyll, anthocyanins, carotenoids, and phenols compared to the fruit bagging treatment. Direct sunlight also reduced the concentration of phytohormones, including indoleacetic acid, gibberellin, and zeatin, but increased abscisic acid accumulation. The directly-exposed fruits reached a partially-mature stage (*Rutab*) in August, whereas the bagged fruits remained at the immature stage (*Khalal*). This study is the first to describe the biochemical basis of the observed improvement of date palm fruit development in response to reduced light intensity. Besides, it provides insights into controlling date palm fruit maturity and subsequently prolonging the shelf life dates on the tree; thus, extending the marketing period for the benefit of the farmers.

Keywords Abscisic acid · Anthocyanin · Ascorbic acid · Carotene · Chlorophyll · Direct sunlight · Fruit bagging · Phenol

Introduction

Sunlight contributes to the ripening of many fruits, including date palm. Date palm (*Phoenix dactylifera* L.) is the leading fruit crop in Iraq and surrounding countries (Khierallah et al. 2015). It is an evergreen tree bearing fruit during the summer and continuing into autumn in some varieties. The fruits have high nutritional value and are used in many food industries and have a high market value (El Hadrami and Al-Khayri 2012). Among the palms, dates occupy third place in terms of economic importance in the world after oil palm and coconut. The desired qualities of the consumer are cleanliness, bright color and size of the fruit. Field practices that help increase fruit size involve covering the clusters to block the sunlight from reaching the fruits (Shareef and Alapresm 2012).

Sunlight reaching the fruit can cause damage at the cellular level, including the breakdown of photosynthesis and peroxidation of the lipid and photooxidative of phytohormones such as indoleacetic acid (IAA), which is considered most affected by high radiation (Šebela et al. 2017). Light accelerates the process of fruit maturation through the process of photooxidation as the light-emitting plant hormones such as gibberellin (GA_3) and zeatin (ZT) break down (Shareef 2010). Some plant hormones, such as abscisic acid (ABA), are known as stress hormones that play a critical role in plant growth, regulation of growth, stomata closure, and fruit abscission (Yang et al. 2011). IAA is a multifunctional plant hormone that is necessary not only for plant growth and development but also contributes to plant growth under stress conditions (Takisawa et al. 2019). Besides, there is significant importance in the development of plant and phenotypic plasticity. These hormones include IAA, ABA, GA_3, and ZT (Torres and Kahlaoui 2017). However, the cytokinin (CK) receptor system appears to contribute to the regulation of photosynthesis mechanisms (Márquez et al. 2019). Thus CK plays a vital role in response strategy of the *Arabidopsis* plant for adaptation to high light intensity (Alabadí and Blázquez 2009). Moreover, GA_3 decreases when the plant is exposed to light, while shade increases the levels of GA_3, leading to the elongation of cells (Rosenwasser et al. 2010).

Photooxidation is a sequential process involving a large number of antioxidants following the first event-photon absorption, which stimulates the collapse of radical free products (Elgendy and Al-Ghamdy 2007). Light is the primary atmospheric stress that works on plants and inhibits growth primarily by disabling the pathway of photosynthesis (Singla et al. 2006). Sunlight is one of the main factors that regulate chlorophyll building pathways, while growth regulators enhance the growth of the plant (Gomes et al. 2011). The plant performs a defensive mechanism for the reduction of damage, including the accumulation of secondary metabolites to minimize plant tissue breakdown (Sulusoglu 2014). The content of plant hormones and antioxidants changes the effect of

environmental factors on plant tissue to protect the pigments of these substances in flavoxate, anthocyanins, and polyamine (Sun et al. 2017). Light influences the content of ascorbic acid (AsA) in the leaves and fruits of the plant, leading to increased vitamin C in the leaves as compared to the fruits (Massot et al. 2012). Awad and Al-Qurashi (2012) found that the bagged fruit of cv. Barhee dates covered with perforated craft bags for 4 weeks after pollination exhibited increased ascorbic acid and phenolic contents.

Light stress is the least studied and most neglected type of abiotic stress. Previous studies have shown the extent to which date palm fruit varieties need different levels of thermal units to reach maturity (Klein and Zaid 2002); however, studies on the influence of light stress on fruit maturity are lacking. The present study elucidates the effect of photooxidative stress on the levels of hormones and antioxidants in the date palm fruit as it matures.

Materials and Methods

Plant Material and Growth Conditions

This experiment was carried out in a date palm orchard at the district of Abi Al-Khaseeb, Basrah, Iraq, during the 2018 growing season. Twenty 17-year old trees of cv. Hillawi, subjected to regular field practices including fertilization, pruning, and irrigation, were used in this experiment. The inflorescence number was reduced to seven per palm by removing early- and late-merging inflorescences. Artificial pollination was used by harvesting the male spathes (cv. Al-Ghannami Al-Akhdar) and manually placing a few strands inside the female spathes. The fruit bunch was bagged immediately after pollination with 50 x 70 cm brown paper bags. Unbagged bunches in the same tree represented the direct sunlight treatment. Two months after pollination, fruit samples (100 fruits) were collected every month for analysis. Light intensity was measured daily at 11 am using a photometer. Furthermore, at the same time, the temperatures of the field and under the bags were measured using a hygro-thermometer. The monthly average of light and temperature averages are presented in Table 1. No precipitation occurred during the duration of the experiment.

Table 1 The change in daily light intensity and temperature during 2018 growth season

Month	Light intensity, (cd)	Air temperature, (ºC)	Temperature under bag, (ºC)
June	0.976	41	36
July	1.092	42	38
August	1.140	44	38

Estimation of Photosynthetic Pigments

Pigment contents were extracted from the fruits according to the method described by Lichtenthaler and Wellburn (1983). Samples of 200 mg of fresh fruit were homogenized in 8 ml acetone (80%) and centrifuged at 3000 rpm for 3 min. The supernatant was used to measure absorbance at 645, 663, 534, and 470 nm, to determine the total chlorophyll, anthocyanins, and carotenoids, respectively.

Total Phenolic Content

The total concentration of phenols in the extract was determined according to the Folin-Ciocalteu method (Waterman and Mole 1994). In a 1.5 ml Eppendorf tube, 790 µl pure water, 10 µl sample, and 50 µl of Folin–Ciocalteu reagent was included and vortexed for 5 min 150 µl of Na_2CO_3 (20%) was included, and the blend was vortexed for 5 min and permitted to rest at room temperature in the dark for 2 h. The absorbance was measured at 750 nm. The phenol content was determined spectrophotometrically at 750 nm based on gallic acid as a standard curve and expressed in mg of gallic acid counterparts (mg GAE) per 100 g fresh tissue.

Ascorbic Acid Content

Ascorbic acid (AsA) content was determined using the Luwe and Takahama (1993) technique with slight modifications. Samples (0.5 g) were ground in liquid nitrogen using a mortar and pestle and then homogenized in 1% cold trichloroacetic acid. The homogenate was then centrifuged at 12,000 xg for 20 minutes at 4 °C, and the supernatant (50 µl) was mixed with 100 mM potassium phosphate buffer and the ascorbic acid estimated spectrophotometrically at 265 nm.

Hormones Analysis

Determination of indoleacetic acid (IAA), abscisic acid (ABA), gibberellic acid (GA_3) and zeatin (ZT) was performed using the same tissue extracts to assure data reliability. Samples of gathered date fruits were washed, surface dried with a paper towel, promptly placed in liquid nitrogen, and stored at -20℃. One g of fresh mass (FM) samples were ground in liquid nitrogen, extracted medium-term with 30 ml 80% cold methanol at 4 ℃. The concentrate was centrifuged at 2000 xg and 4 ℃ for 15 min, and the supernatant gathered. At that point, new cold methanol was used to fill the remainder, extracted four times with the strategies above. The all-out methanolic separate was dried in a rotary

evaporator and separated into 10 ml methanol aliquots. IAA, ABA, GA_3, and ZT estimated by the infusion of the concentrate into a turnaround stage HPLC on a switch stage C18 section (250 × 4.60 mm, 5 microns) in an isocratic elution mode utilizing a portable stage comprising of acetonitrile: water (26:74) with 30mM phosphoric acid according to Tang et al. (2011).

Statistical Analysis

The experiment was conducted as a randomized block design consisting of two factors (light intensity) at two levels (direct and indirect sunlight, i.e., without and with a bag) and months after pollination at three levels (June, July, and August). Each of these six treatments consisted of five replications. The data were subjected to analysis of variance (ANOVA) using SPSS variant 21.0 (SPSS, Chicago, IL), and the means were separated using the Duncan test at the 5% significance level.

Results

Photosynthetic Pigments Content

Total chlorophyll content decreased as fruits matured. The light increased the chlorophyll content fruit compared to bagged fruit, especially in the early stage of fruit formation. The highest level of chlorophyll under light was in June at 62.14% compared with bagged fruits (Fig. 1A). The content of anthocyanins increased as fruits matured. In August, anthocyanins increased in bagged fruits to be higher than in unbagged fruits. Bagging of fruits caused a maximum increase in the percentage of anthocyanins in August at 15.38% compared with the effect of light (Fig. 1B). The content of carotenoids increased as the fruit matured. Fruit bagging increased the content of carotenoids significantly, compared to unbagged fruits. The percentage increase of carotenoids in August under bags was 9.23%, compared with unbagged fruits (Fig. 1C).

Phenols and Ascorbic Acid Antioxidants

Phenols decreased as fruits matured. The effect of light significantly reduced the content of phenols in fruits. The decrease of phenol percentage under light stress was 21.65%, compared with the bagged fruit treatment in August (Fig. 2A). The content of AsA differed in fruits exposed to direct light and indirect sunlight. AsA decreased as the fruits matured. In light, the increased percentage of AsA was 12.9% in August, compared with bagged fruits (Fig. 2B).

Phytohormone Levels

Figure 3 shows that the plant hormones IAA, GA_3, and ZT increased in July, except for ABA, which increased in August. Direct light reduced the levels of phytohormones in fruits compared to bagged fruits, except for the rise in the content of the ABA of the fruits exposed to light in August, when fruits reached the *Rutab* stage, while the fruits were still bagged in the *Khalal* stage. The decrease in hormone content in light-exposed fruits compared with bagged fruit was 10.83% IAA, 49.49% GA_3, and 32.91% ZT in August, whereas ABA increased by 3.57%.

Discussion

The fruits of date palm turn from green to a distinctive yellow or red color depending on the variety. In this study, the yellow variety of cv. Hillawi was used. Dates vary in their photosynthetic pigments during the different stages of growth under natural light, as in the first stage of growth that increases the chlorophyll, while in the stage of physiological maturity increases the pigment of carotene or anthocyanins depending on the variety (Al-Farsi et al. 2005). However, blocking the sun's rays from reaching the fruits, using brown paper in these stages, led to a difference in the amount of these pigments. Anthocyanins and carotenoids increased in fruits under bags, while chlorophyll decreased (Fig. 1). Placing the plant at low light intensity stimulates the mechanism of shade avoidance leading to a reduction in chlorophyll production and the appearance of other pigments (Banerjee and Roychoudhury 2016). Whereas, the arrival of photons to photosynthesis in the fruit, as a result of exposure to light, leads to the high activity of photosynthesis and distinguishes chlorophyll from other pigments in the early stages of growth (Apichatmeta and Ritchie 2017). The difference in photosynthesis and, therefore, the type of dominant pigments depends on the growth and amount of light intensity experienced by the plant organ (Croft and Chen 2018). The direct light caused the breakdown of the anthocyanin and may have increased the activity of enzymes responsible for the decrease of this pigment. Similar results were obtained with carotenoids in response to direct light, which led to the breakdown, while the indirect light and low the temperature (Table 1) within bags led to the preservation of carotene and anthocyanin pigments in the unbagged fruit (Fig 1 A, B). These findings agree with those of Lee et al. (2007) in Indian ginseng (*Withania somnifera*) where light exposure led to the breakdown of photosynthetic pigments while the fruit bagging increased the concentration of secondary pigments and reduced the formation of primary pigments by preventing the photooxidative process.

Photooxidation leads to the stimulation of biochemical responses in plants (Liu and Zhong 2017). The content of phenols in dates reaches the upper limit at the *Khalal* stage and then decreases in subsequent stages (*Rutab* and *Tamar*) (Al-Alawi et al. 2017). The fruits exposed to light reached the *Rutab* stage; whereas, the bagged fruit was still in the *Khalal* stage (Fig. 4). Thus, the high content of phenols in bagged fruits is present

because they did not reach the beginning of the *Rutab* stage. The increase in the phenolic content of the bagged fruits is attributable to the decrease in the breakdown of the polyphenol oxidase enzyme and the hydrolysis of the phenols (Al-Farsi et al. 2005). Date palm fruits at the *Rutab* stage are sensitive to storage conditions because of their softness at this stage, which limits marketing due to increased damage (Shareef 2010). Polyphenol oxidase activity was noted to increase in Malabar spinach (*Basella alba*) when exposed to oxidative stress induced by exposure to high temperature (Siddika et al. 2015). Increasing the concentration of phenols protects the fruits from insects, allowing it to reach final maturity and thus improve its texture (Pérez-Llorca et al. 2019). Thus, the firmness of the date flesh leads to the possibility of storing it longer, which is what happened to the bagged fruits.

Ascorbic acid is one of the main components of chloroplasts in a plant. Therefore, the intensity of light is strongly associated with the formation of chlorophyll and photosynthetic activity, which increases the content of AsA in fruits under high light (Izumi et al. 1992). In August, AsA accumulation under light was more than bagged fruit (Fig. 2 B). Exposure of fruits to direct sunlight leads to the raising of the temperature of fruits to 10 ºC higher than the temperature of the fruits in shade and thus leads to a rise in the accumulation of antioxidants (Helyes et al. 2007). Ascorbic acid is an essential antioxidant and is increasingly concentrated when exposed to oxidative stress (El-Bassiouny and Sadak 2015). The low concentration of ascorbic acid under the bags is a result of lower light exposure; therefore, these fruits have a better texture.

The interaction between light and plant hormones plays a vital role in modifying the development and plant behavior in response to different environmental conditions (Alabadí and Blázquez 2009). The decrease of indoleacetic acid content in light-exposed fruits (Fig 3, A) may be explained by the breakdown of the molecules of the hormone or the occurrence of crosstalk with the ethylene, which leads to the rapid development of fruits to the final maturity stage due to photooxidative stress. Light rays reduce the concentration and activity of IAA through photo-degradation (Sawicki et al. 2015). Blocking light from access to bagged fruits increased IAA content (Fig. 3a). Preventing photons from reaching the fruits has a direct effect on cell physiology; cells are no longer able to metabolize and use IAA (Banerjee and Roychoudhury 2015). Fruits exposed to light showed a decreased concentration of gibberellin (Fig. 3b). The high light conditions lead to a reduction in GA_3 and an increase in the content of ABA (Rosenwasser et al. 2010). Stavang et al. (2007) found that high temperature caused by exposure of pea plants to light leads to the expression of the *PsGA2ox2* gene responsible for the deactivation of GA_3.

Zeatin decreased in fruit effect by light while it increased under bags (Fig. 3c). Plants suffer from senescence-like symptoms under stress due to an increase in reactive oxygen species (ROS) production (Duarte et al. 2013). ZT is often portrayed as an antioxidant due to its anti-senescence properties (Buchanan-Wollaston et al. 2002). There was a

decrease in ZT content in response to the oxidase/dehydrogenase inhibition caused by photooxidative stress (Vaseva et al. 2006).

The acceleration of fruit ripening and the accumulation of light-induced secondary metabolites are linked to the enhancement of the ABA signal transduction essential for the stress endurance mechanisms (Berli et al. 2011). The increase of ABA in fruits accompanied the rapid maturity at the *Rutab* stage (Fig. 3D). The light irradiation improves the ABA signal transduction by stimulating the plant protection mechanism. The high concentration of ABA as a result of light stress is involved in mitigating plant damage (Banerjee and Roychoudhury 2015).

Conclusions

Both plant hormone and antioxidant responses contribute to the ripening of date palm fruits by stimulating the intensity of the high light that leads to a modification in the metabolism of fruits. On the contrary, shading the fruit and preventing direct light leads to the non-oxidation of many of the substances involved in metabolism, which renews the state of the fruit tissue and thus prolongs the stages of growth. This study has identified a cultural practice to prolong the shelf life of dates on the trees and explained the relevant biochemical rationale. Bagging fruits lengthens the stage of *Khalal* by about two months and increases the storability of fruits during the *Rutab* stage. This method could contribute to extending the marketing season of date and increase farmers' income.

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Author Contributions HJS and JMA contributed equally to the manuscript preparation.

Conflict of Interest The authors declare no conflict of interest.

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Figures Legends

Fig. 1 Changes in chlorophyll (A), anthocyanin (B), and carotene (C) content of cv. Hillawi fruit during 3 months of growth unbagged under direct solar radiation or covered with bags. The means of 5 replicates ±SE. Bars with different letters are significantly different at $p \leq 0.05$ after a Duncan correction.

Fig. 2 Changes in phenols (A) and ascorbic acid (B) content of cv. Hillawi fruit during 3 months of growth unbagged under direct solar radiation or covered with bags. The means of 5 replicates ±SE. Bars with different letters are significantly different at $p \leq 0.05$ after a Duncan correction.

Fig. 3 Changes in indoleacetic acid, IAA (A), gibberellin, GA_3 (B), zeatin, ZT (C), and abscisic acid, ABA (D) content of cv. Hillawi fruit during 3 months of growth unbagged under direct solar radiation or covered with bags. The means of 5 replicates ±SE. Bars with different letters are significantly different at $p \leq 0.05$ after a Duncan correction.

Fig. 4 Effect of growth direct sunlight (unbagged) and indirect sunlight (bagged) on photosynthetic pigments of date palm fruit

Figure 1

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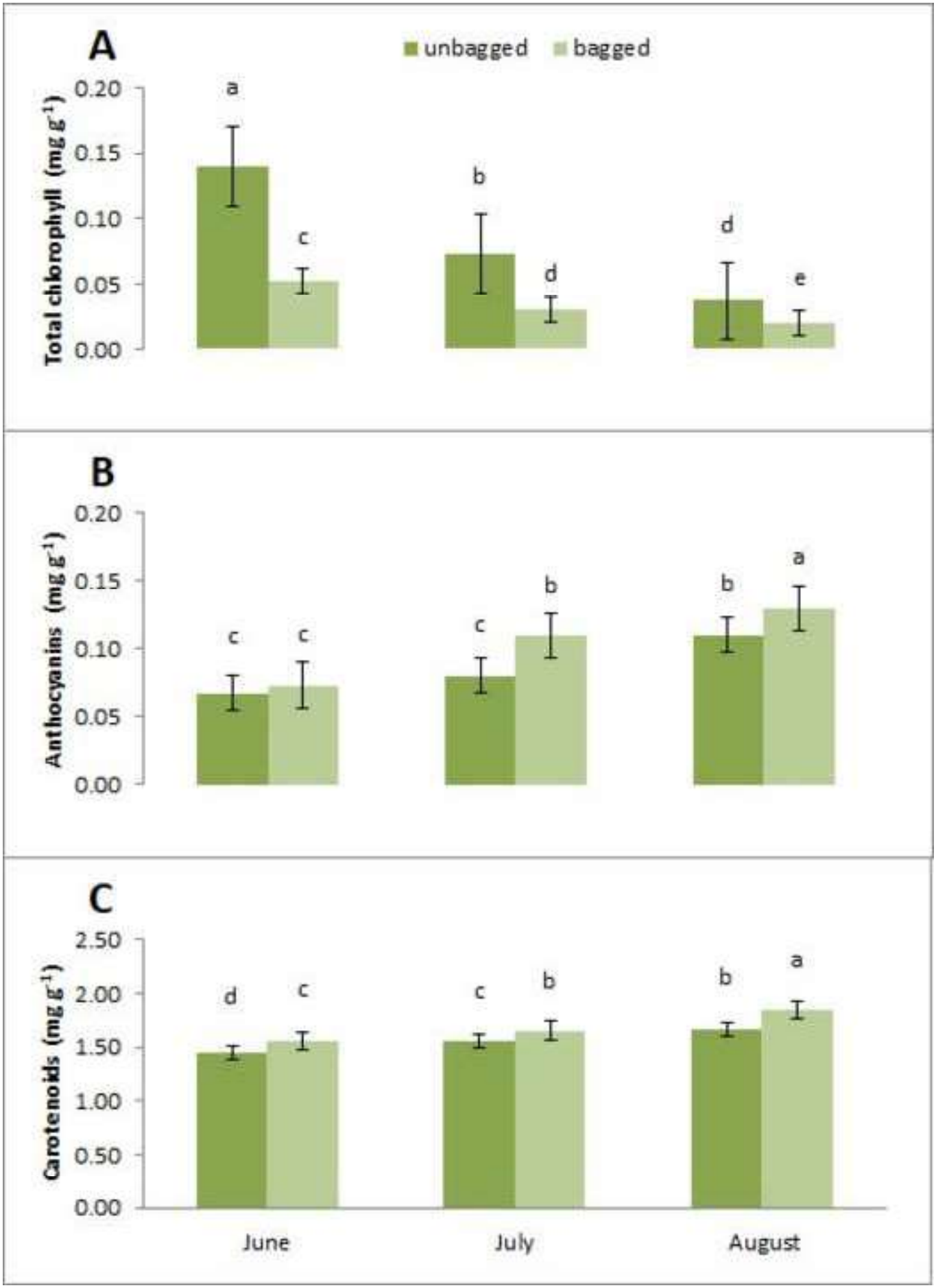

Figure 2

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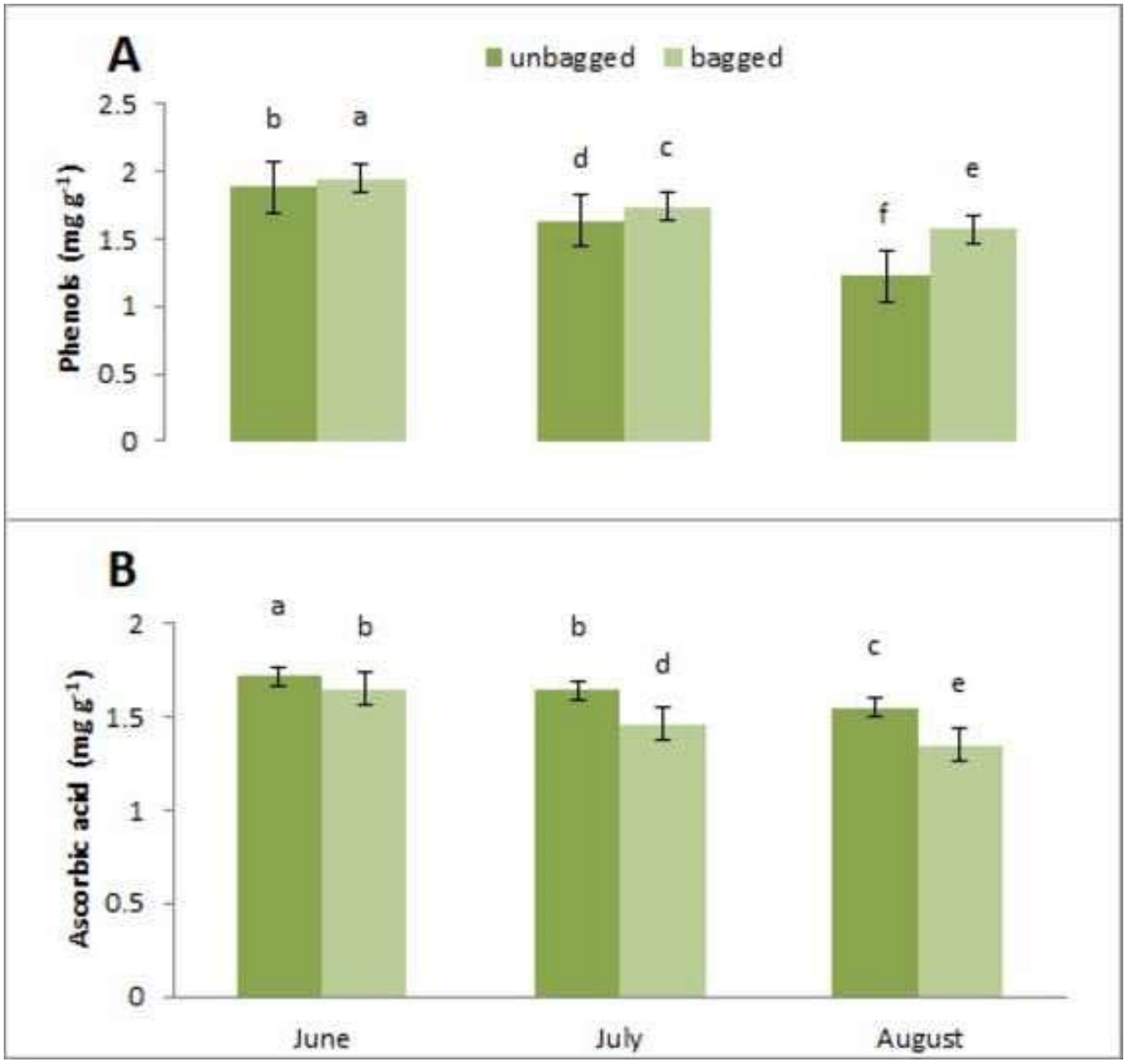

Figure 3

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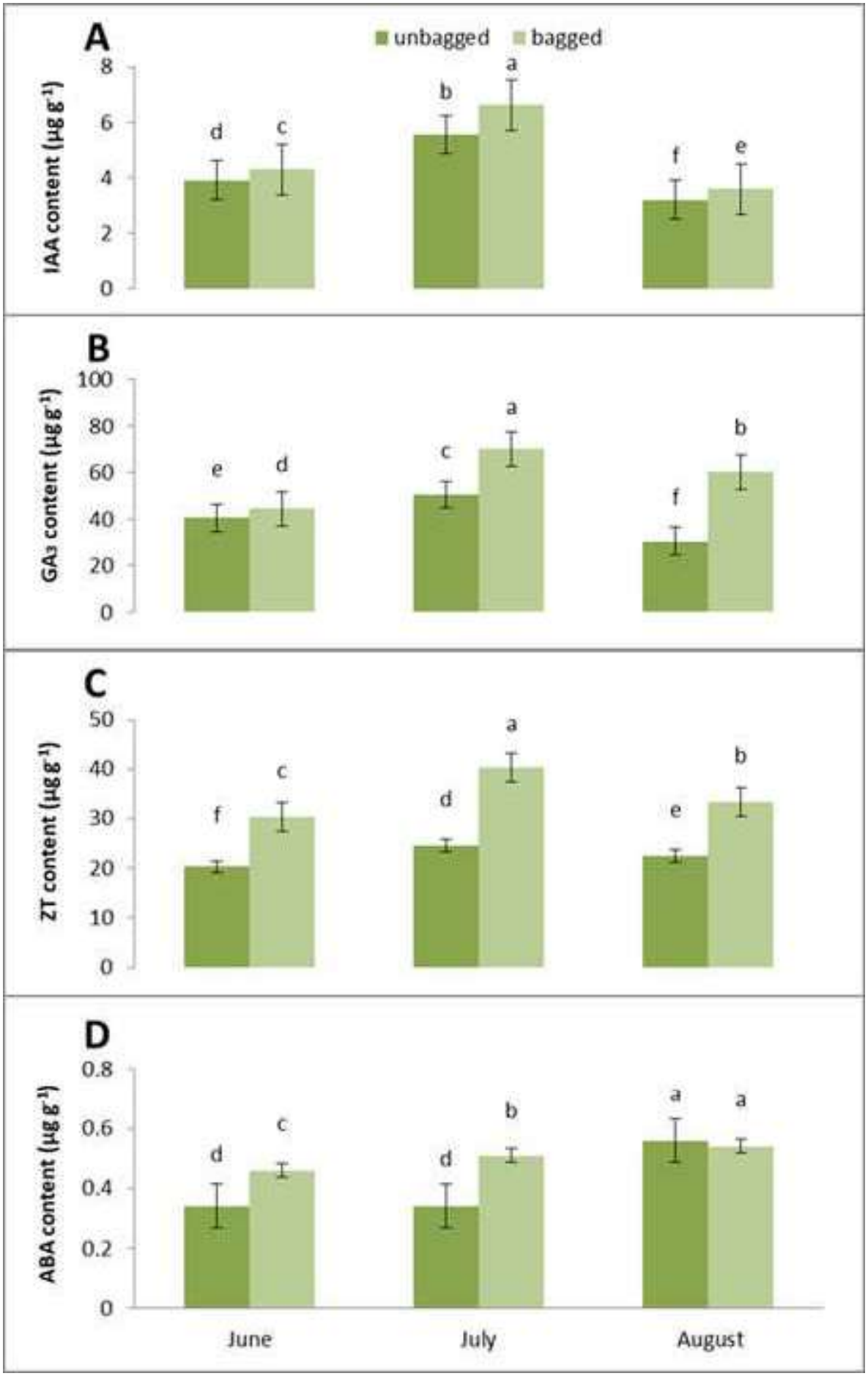

Figure 4

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