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The difference in temperature between day and night affects the strawberry soluble sugar content by influencing the photosynthesis, respiration and sucrose phosphatase synthase

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Abstract: Plenty of studies have demonstrated that DIF has an effect on the fruit growth. To study the effects of day and night temperature differences on the strawberry sugar quality, an experiment using climate chambers was conducted. Five different differences between the day and night temperatures (DIF) were set, which were 6 °C (28 °C/22 °C, day/night temperature), 8 °C (29 °C/21 °C), 10 °C (30 °C/20 °C), 12 °C (31 °C/19 °C), 14 °C (32 °C/18 °C). The results showed the following indices peaked with a DIF of 12 °C, including the photosynthesis rate, glucose content, fructose content, sucrose content, soluble sugar content and sugar metabolic enzyme activity. The respiration rate increased with the DIF during the day and decreased with the DIF at night. The root dry weight peaked at a DIF of 10 °C, the stolon dry weight peaked at a DIF of 8 °C and the leaf dry weight peaked at a DIF of 6 °C; however, the fruit dry weight reached maximum values at a DIF of 12 °C. The Grey correlation analysis showed that the most important factor in our experiment affecting the fructose content was the sucrose phosphate synthase; however, for the sucrose, glucose, and soluble sugars, the most important factor was the photosynthesis. We found that a DIF of 12 °C (31 °C/19 °C, day/night temperature) was the most suitable for strawberry growth, especially for the sugar content accumulation.

Keywords: sugar accumulation; grey correlation analysis; sugar metabolic enzymes; photosynthesis rate; respiration rate

In strawberry production, the temperature is one of the most important factors affecting the seedling growth and fruit photosynthesis (Patil et al. 2001; Zhou et al. 2005; Verheul et al. 2007). It has been showed the DIF (difference between daytime temperature and night temperature) also has an effect on the fruit quality, which consists of the soluble sugar content, fruit colour, vitamin C content, organic-acid content and so on (Erwin et al. 1989; Guo, Li 2000; Gulen et al. 2003; Blanchard, Runkle 2011).

Photosynthesis was dominant in plants during the day, and high temperatures were conducive to the formation of photosynthetic products (Bunce 1985; Cockshull et al. 1995). At night, lowering temperatures could reduce the material consumption (Berghage et al. 1990). Plenty of studies have reported that the DIF also has an impact on the photosynthesis. It has been indicated that the P_n (net photosynthesis rate) was affected by the DT (daytime temperature), instead of the NT (night temperature) (Lasseigne et

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al. 2007). It has also been proved that DIF, during cultivation, influences the morphology and dry matter distribution in crop transplants (Kliewer et al. 1972; Heuvelink 1989; Kumakura 1995; Inthichack et al. 2013); a higher DIF resulted in an increase in the growth and more dry matter distribution of the root (Grimstad, Frimanslund 1993).

It has been perceived that the DIF influenced the fruit quality significantly; there have been many studies on the fluctuation of the soluble sugar content with the temperature (Hansen, Waldo 1944; Ranwala 1992; Wang 2001; Bachman, McMahon 2006; Bradford et al. 2010). The temperature greatly affected the soluble sugar (fructose, glucose, and sucrose), the decline in the amount of sugar in various plant parts at high temperatures could be attributed to the fact that plants grown at high temperatures used photosynthetic products to support higher metabolic activities, and cool temperatures favoured sugar accumulation (Wang 2001; Yan et al. 2010). The soluble sugar of kaki fruit, muskmelon fruit and beets have proven to be sensitive to changes in the DIF (Chujo et al. 1973). A proper DIF significantly increased the vitamin C and organic acid content of tomatoes, which was confirmed by several studies (Khanal 2012; Li et al. 2015; Yuan 2016). Some studies revealed that the difference in the sucrose content among three pear cultivars was mainly caused by the SS-s enzyme activity, and the difference in the glucose and fructose content was related to the enzyme activity of the acid invertase (AI), neutral invertase (NI) and sucrose synthase decomposition direction(SS-d) (Wang 2001).

However, studies on how the DIF acts on the strawberry's quality are lacking, it is hard to know how the DIF influences the photosynthesis and respiration of strawberries. This study aimed to (1) investigate the effects of different DIFs on the morphology and photosynthesis of the strawberry, (2) clarify the influence of the DIF on the strawberry's quality, (3) evaluate the effects of the DIF on various strawberry indices by the Grey correlation analysis, and (4) reveal the mechanism of the DIF that affects the strawberry's quality.

MATERIALS AND METHODS

Experimental design. The experiment was conducted in the agricultural meteorology key laboratory of Nanjing University of Information Science and Technology (Jiangsu province, China) from April to May 2018. Fifteen strawberry seedlings (*Fragaria × ananassa* Duch. HongYan) in the budding period were transferred into plastic pots (25 cm in diameter), which contained a medium loam soil. The relative humidity (RH) was controlled in the range of 60%–70%, the plants were watered as needed, the fertiliser application was 80 kg/ha (urea), 75 kg/ha (superphosphate) and 60 kg/ha (potassium chloride). The DIF treatment started at the mature stage and lasted for 12 days; all the plants were still in the mature stage at the end of treatment.

The strawberries were divided into five treatments according to the DIF, which were 6 °C (22 °C/28 °C, day/night temperature), 8 °C (29 °C/21 °C), 10 °C (30 °C/20 °C), 12 °C (31 °C/19 °C) and 14 °C (32 °C/18 °C), each group dealing with three levels. The above treatments were set according to the actual possible range of the temperature in the experimental area. They were respectively placed in five kinds of day and night temperature difference environments until the mature fruits were ripe. During the treatment, the water and nutrient conditions were kept in an appropriate range, and no obvious diseases occurred or pests observed.

The experiment was carried out by using intelligent plant growth chambers (A1000, Conviron, Winnipeg, Canada). The temperature and relative humidity (RH) in the automatic control chambers reached the set value according to the real-time monitoring results of the sensor. The fluctuation in the indoor air temperature and RH was less than 0.5 °C and 3%, respectively. In the experiment, the indoor relative humidity was 60%, the light intensity was 700 μmol/m^2·s, and the photoperiod was 14/10 h D/N (06:00/20:00). Before the dark period, the measured soil moisture content was manually watered to achieve the optimum soil moisture content for strawberry growth. Each measurement index of the experiment was repeated three times.

Morphological index measurements. The different organs (roots, stolons, leaves and fruits) of each strawberry plant were washed and stored separately. After 5 min of drying at 105 °C, they were placed in an oven at 85 °C and dried to a constant weight. The dry mass of each organ was measured by an electronic balance with an accuracy of 0.01 g. The selected strawberries were measured for each treatment after 12 days of processing.

Photosynthesis and respiration index measurements. The 5th–7th functional leaves from the top of the strawberry plants were selected, the photosynthetic rate was measured between 9 am–11 am

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using a portable photosynthesis measurement system (LI-6400, LI-COR Bioscience, Lincoln, USA), using a standard leaf chamber and an open gas path. The temperature in the leaf chamber was 25 °C, the CO_2 concentration was 380 ± 10 μmol (CO_2)/mol, and the relative humidity was 60–70%. Three repetitions were measured for each treatment after 12 days of processing.

Soluble sugar measurements and sugar metabolic enzyme extraction and assays. The contents of the soluble sugar, fructose, sucrose and glucose were determined by an evaporative light scattering detector (Alltech-ELSD2000) according to Chen's method (Chen et al. 2007). The soluble acid invertase (AI) and neutral invertase (NI) activity were measured by using an acetic acid-sodium acetate buffer, the directional activity of the sucrose synthase synthesis (SS-s) and sucrose phosphatase (SPS) activity were measured by using a Tris-HCL buffer, the sucrose synthase decomposition (SS-d) activity was measured by using a Mes-NaOH buffer (Bashir et al. 2017). The enzyme activity unit is expressed as (μmol/min·g).

Statistical analysis. The data were statistically evaluated using an analysis of variance (ANOVA) and Duncan's multiple range tests. All the statistical analyses were considered significant at a $P < 0.05$ level. Excel 2010 (Microsoft Systems Inc., USA) and Origin 2018 (Originlab Corp., US) were used for the data processing and chart making. IBM SPSS Statistics 26 (SPSS Inc., Chicago, IL, USA) was used for the differences in the significance and the Grey correlation analysis.

RESULTS

Photosynthesis and Respiration. When the light intensity was within the range of 500 μmol/m²·s, the photosynthetic rate of the strawberries under each treatment increased rapidly. When the light intensity increased to 500 μmol/m²·s, the photosynthetic rate increased slowly. Under every Photosynthetically active radiation (PAR), the photosynthetic rate with a DIF of 12 °C was the highest; the strawberry with a DIF of 6 °C was the lowest (Figure 1).

It can be seen from Table 1 that the light compensation point of the strawberries treated in the 5 groups was between 31.14–53.9 μmol/m²·s, they had the highest compensation point and the lowest compensation point when there was a DIF of 6 °C and 14 °C, respectively. The light saturation point

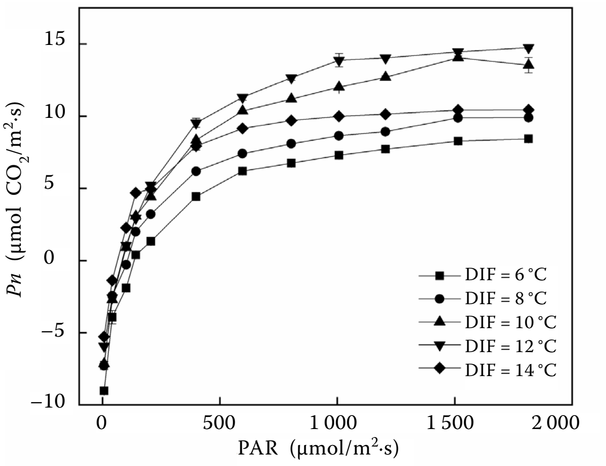

Figure 1. Photosynthetic rate in the strawberry leaves under the different DIF treatments; the vertical bars are the standard deviation

DIF – the difference between the day and night temperatures; PAR – photosynthetically active radiation; *Pn* – net photosynthesis rate

was between 410.05–536.41 μmol/m²·s, with a maximum DIF of 12 °C and a minimum DIF of 6 °C.

The respiration rate is the difference between the photosynthetic rate and the net photosynthetic rate. The DR (day respiration rate) increased with an increase in the DIF and the NR (night respiration rate) decreased with an increase in the DIF. The change in the respiration rate during the day is related to: DIF 6 °C < DIF 8 °C <DIF 10 °C < DIF 12 °C < DIF 14°C (Figure 2). The change in the respiration rate was almost opposite to that of the photosynthesis, DIF 6 °C > DIF 8 °C > DIF 10 °C > DIF 12 °C > DIF 14 °C.

Table 1. Light compensation point and light saturation point under different DIFs

DIF	Light compensation point (μmol/m²·s)	Light saturation point (μmol/m²·s)
DIF 6 °C	53.9 ± 0.12[b]	410.05 ± 64.6[a]
DIF 8 °C	33.64 ± 0.27[a]	416.82 ± 52.5[a]
DIF 10 °C	34.78 ± 0.15[a]	492.78 ± 65.1[b]
DIF 12 °C	36.26 ± 0.08[a]	536.41 ± 34.7[c]
DIF 14 °C	31.14 ± 0.41[a]	460.057 ± 62.5[ab]

DIF – the difference between the day and night temperatures; values are mean ± SD ($n = 3$) and small letters indicate a significance of $P < 0.05$ by Duncan's significance test

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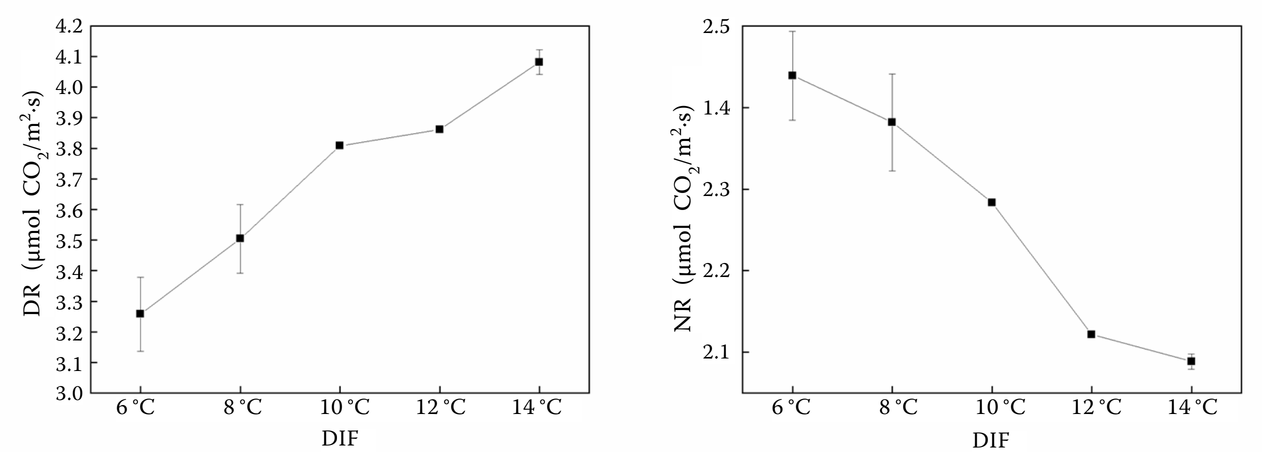

Figure 2. Respiration of the strawberry leaves during the day and night under the different DIF treatments

DR – day respiration rate; NR – night respiration rate; the vertical bars are the standard deviation; DIF – the difference between the day and night temperatures

The chlorophyll a and chlorophyll b content of the strawberries with a DIF of 10 °C and 12 °C were the highest, the chlorophyll *a* and chlorophyll *b* content of the strawberries with a DIF of 8 °C and 14 °C were the lowest. For the same kind of pigment, the pigment content with a DIF of 12 °C was always higher than the other treatments (Figure 3).

The proportion of the dry matter distribution was similar for each organ under each treatment, which was the root > leaf > stolon > fruit. The dry matter accumulation of the root and stolon was highest at a DIF of 14 °C, the leaf accumulation was highest at a DIF of 6 °C, and the fruit accumulation was highest at a DIF of 10 °C in all the treatments (Figure 4).

Quality index. The fructose, sucrose and glucose all presented a unimodal distribution with an increase in the DIF. When the DIF was 12 °C, the fructose, sucrose and glucose sugar content reached its peak, with a maximum value of 43.04%, 37.38% and 19.56%, respectively. With an increase in the DIF, the content of the three sugars all decreased (Figure 5).

The SPS activity increased with an increase in the DIF. The SS-s and SS-d activity under each temperature difference treatment were significantly higher than that of the other three enzymes. When the DIF

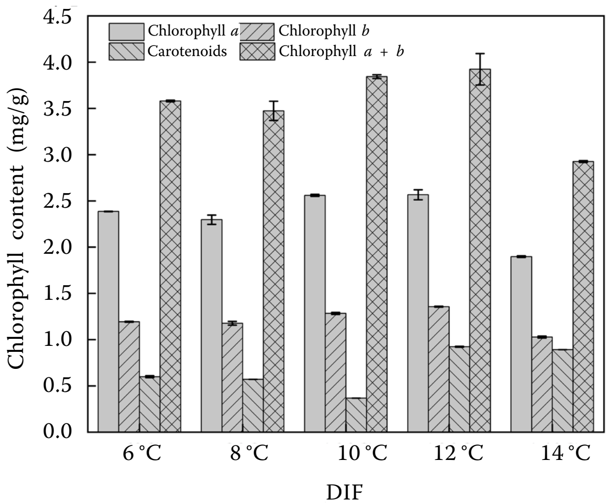

Figure 3. Chlorophyll *a*, chlorophyll *b*, carotenoid and chlorophyll contents under the different DIF treatments;

The vertical bars are the standard deviation; DIF – the difference between the day and night temperatures

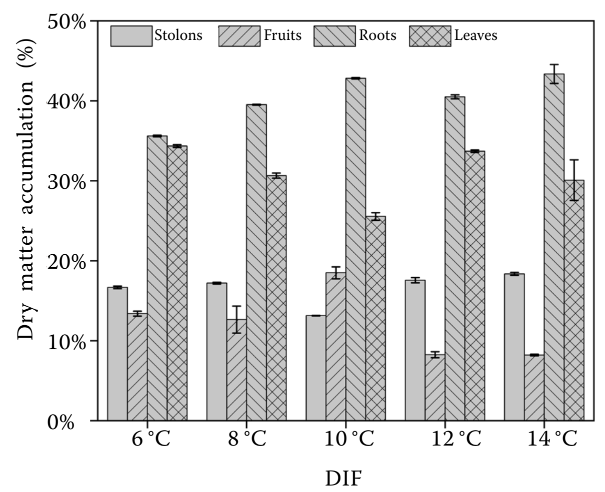

Figure 4. Dry matter distribution of the strawberry organs under the different DIF treatments

The vertical bars are the standard deviation; DIF – the difference between the day and night temperatures

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Table 2. Grey correlation analysis of the influence degree of each factor on the soluble sugar content

	Pn	DR	NR	AI	NI	SPS	SS-s	SS-d	LDW	SDW	RDW	FDW
Fructose	0.6895	0.5951	0.5229	0.6397	0.7213	0.7358	0.5752	0.7283	0.5129	0.5305	0.5906	0.4424
Glucose	0.7265	0.5022	0.4965	0.4562	0.4969	0.7025	0.682	0.6851	0.4925	0.4521	0.4989	0.5069
Sucrose	0.7376	0.6206	0.5955	0.5857	0.6137	0.7215	0.6389	0.6811	0.588	0.559	0.617	0.6342
Soluble sugar	0.7275	0.6484	0.5503	0.6309	0.7004	0.7028	0.6124	0.7033	0.5523	0.5887	0.6361	0.4806

Pn – net photosynthesis rate; DR – daytime respiration; NR – night respiration; AI – acid invertase; NI – neutral invertase; SPS – sucrose phosphate synthase; SS-s – sucrose synthase synthesis direction; SS-d – sucrose synthase decomposition direction; LDW – dry weight of the leaf; SDW – dry weight of the stolon; RDW – dry weight of the root; FDW – dry weight of the fruit

was 6 °C, the SS-s activity was lower than that in of the SS-d. When the DIF was 12 °C, the SS-d activity reached the highest, and most of the sucrose decomposed. The NI activity was slightly lower than the AI. The sucrose content increased sharply with a decrease in the invertase (including AI and NI) activity, and the invertase activity increased with an increase the DIF (Bashir 2018). The SS-s and SS-d activity increased with an increase in the DIF (Figure 6).

Grey correlation analysis. The Grey correlation analysis (Table 2) showed that the SPS was the most important factor affecting the fructose content, followed by the SS-d and NI; the photosynthesis had the greatest influence on the glucose and sucrose content, fol-

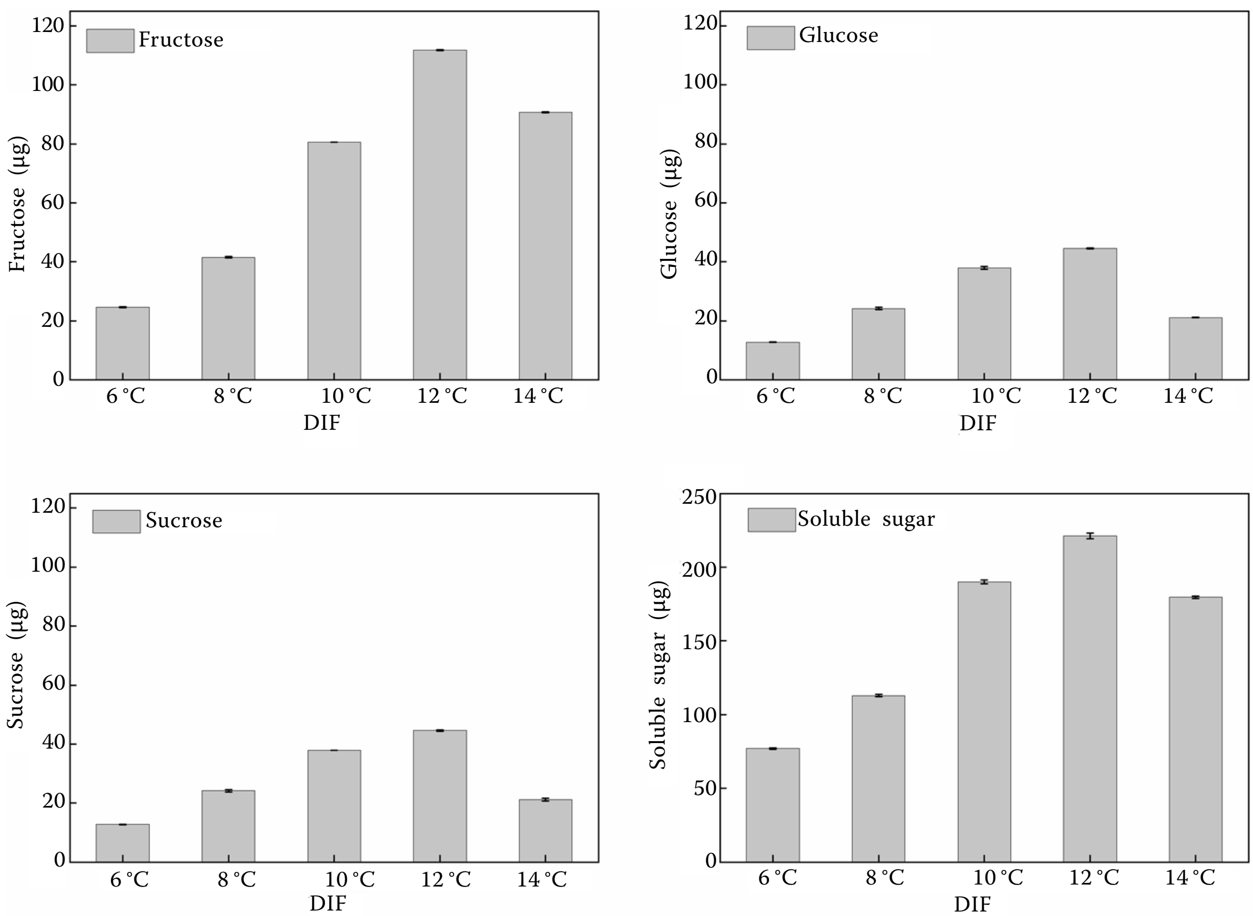

Figure 5. Fructose (A), glucose (B), sucrose (C) and soluble sugar (D) content in the strawberry fruit under the different DIF treatments

The vertical bars are the standard deviation; DIF – the difference between the day and night temperatures

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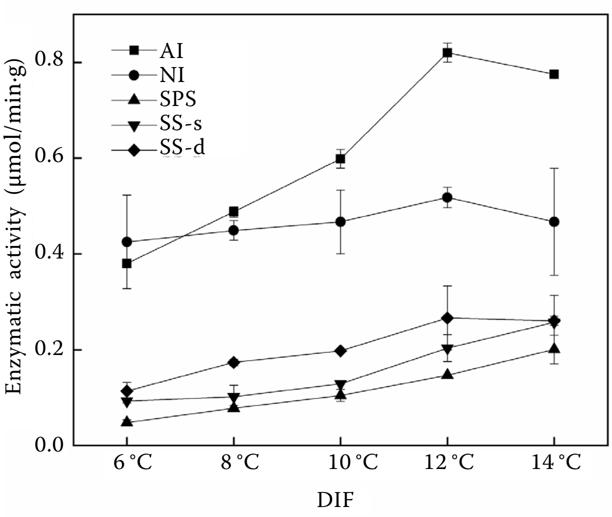

Figure 6. Acid invertase (AI) activity, neutral invertase (NI) activity, sucrose phosphatase (SPS) activity, directional activity of the sucrose synthase synthesis (SS-s) activity, sucrose synthase decomposition (SS-d) activity in the strawberry fruit under the different DIF treatments

The vertical bars are the standard deviation; DIF – the difference between the day and night temperatures

lowed by the SPS and SS-d. For the soluble sugar content, the photosynthesis had the greatest effect, followed by the SS-d and SPS.

DISCUSSION

Effects of photosynthesis, respiration and dry matter distribution under different DIF. The net photosynthetic rate (P_n) is the difference between the photosynthetic rate and the respiration rate. In this study, the P_n increased as the DIF increased except at a DIF of 14 °C. Baker and Ding (Makino et al. 1994; Ding et al. 2003; Baker 2008) reported that when the temperature was not over 30 °C, the P_n increased as the DIF increased. The P_n peaked at a DIF of 12 °C, decreased at a DIF of 14 °C (Figure 1), the reason might be that the day temperature in the DIF of 14 °C was higher than that of the DIF of 12 °C, the high temperature in the daytime (32 °C) in the DIF of 14 °C may have led to high temperature stress; excessive daytime temperatures reduce the activity of the photosynthesis enzymes in the cells. It may also be due to the fact that excessive daytime temperatures reduce the chlorophyll synthesis (Liu et al. 2010; Na et al. 2014; Choi et al. 2016), which weaken the light absorption efficiency of the leaves and, thus, reduces the net photosynthetic rate.

The respiration rate of the strawberries was also different under the different treatments. During the day, the respiration rate ranged from: DIF 6 °C > DIF 10 °C > DIF 14 °C > DIF 12 °C > DIF 8 °C (more than 400 μmol·mol) (Figure 2). We presumed the main influencing factors were the temperature and photosynthetic rate, however, it did not agree with the results of Gerhart, who found that the maximum initial rate at which strawberries respire was 36.5 °C, at the higher temperatures (35 °C, 36.5 °C, 37.5 °C, and 40 °C), the respiration quickly falls (Gerhart 1930). On the other hand, the night respiration rate ranged from: DIF 6 °C > DIF 8 °C > DIF 10 °C > DIF 12 °C > DIF 14 °C (Figure 2). The main influencing factor was the temperature. The higher the night temperature was, the higher the enzyme activity on the respiration would be and the respiration rate would be enhanced, and this was confirmed by Cockshull and Nei (Cockshull et al. 1982; Nei et al. 2005). This indicates that when the temperature difference was 12 °C in the daytime, the net photosynthetic rate was the highest, the accumulation of the photosynthetic products was the highest, and the nutrient consumption was less when the night respiration rate was lower, so it was the most favourable for the dry matter accumulation.

In this study, we found that the treatment with highest sugar content in the strawberry fruits was a DIF of 12 °C instead of a DIF of 14 °C, which was inconsistent with the existing research views. Traditional studies found that the higher the DIF was, the higher the soluble sugar content in the fruits was, usually because of the low temperature, low respiration rate and small dry matter consumption at night. In our opinion, an appropriate DIF would affect the dry matter distribution, and the temperature difference between the day and night would improve the nutritional development, leading to a high sugar content in the strawberry fruits.

When the DIF was lower (6 °C/8 °C/10 °C), it was conducive to the morphological development of the strawberries, which was specifically reflected in promoting the stem elongation, increasing the leaf area, dry weight of the leaf stem and root. The reason was the daytime temperature of several treatments with a lower DIF was relatively low and the temperature was more appropriate. A higher DIF (14 °C) increased the content of the organic acid, vitamin C and sucrose metabolising enzyme, because the higher DIF treatment was accompanied by a higher daytime temperature and stronger radiation, which was conducive

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to the accumulation of acids and vitamin C, while the higher daytime temperature was not conducive to the action of the sucrose metabolising enzyme, so more enzymes were accumulated. The most proper DIF strawberry development in this experiment was 12 °C; under this treatment, the temperature of strawberries showed the strongest photosynthetic capacity, the reddest appearance in colour and the sweetest fruit, the main reason was that the photosynthetic enzymes and fluorescence reactions had the highest activity when the DIF was 12 °C, the accumulation of chlorophyll and red pigment in the strawberry leaves was also the best, the SS-d activity was the worst, and the sugar being accumulated content was the highest.

Effects of sugar metabolic enzymes under different DIF. Fructose and sucrose are the major sugars in fruit, accounting for more than 65% of the total sugar (Wang 2001). The low sucrose content in strawberry fruits may be due to the enzymatic hydrolysis of sucrose to glucose after translocation from the leaves (Forney, Breen 1985). The fructose, glucose, sucrose and soluble sugar all reached the maximum and minimum value at a DIF of 12 °C and 6 °C (Figure 5), respectively, we presumed that most of the sucrose decomposed into fructose and glucose due to the optimal temperature of the sucrose decomposing enzyme activity under the DIF treatment of 6 °C.

Sucrose metabolism is the main metabolic pathway of plants. The key enzymes involved in the sucrose accumulation and metabolism in the fruits were the sucrose phosphate synthase (SPS), sucrose synthase (SS), and invertase (Ivr). Ivr can be divided into acid invertase (AI) and neutral invertase (NI) according to its optimal pH value. The sucrose in strawberries was synthesised from SPS rather than SS (Hubbard et al. 1989; Nascimento et al. 1997). When the DIF was 12 °C, the sucrose synthase decomposition activity increases, the Ivr decomposition activity also increases, the sucrose phosphate synthase activity was slightly lower, which makes the sucrose decompose into glucose and fructose faster (Figure 6). This result was consistent with the research results of Chen, who concluded that there was a significant negative correlation between the Ivr activity and the sucrose accumulation in fruits, he also reported that the invertase activity in mature fruits was low, which led to the rapid accumulation of sucrose in the fruits (Chen et al. 2007).

Different DIFs impacted soluble sugar content by affecting photosynthesis, respiration and sucrose phosphate synthase (SPS). Strawberries are a non-respiratory jump variant fruit, research has shown that sucrose phosphate synthase is a key enzyme in the sucrose accumulation. Sucrose phosphate synthase played an important role in the sucrose metabolism process (Baxter et al. 2003). Its dynamic adjusted the synthesis of the sucrose and photosynthetic primary product allocation between the starch and sucrose, in sucrose metabolism, it had strong impact on the source and the library, it adjusted the the distribution of photosynthetic product in the sugar and starch (Liu et al. 2005). Huber had pointed out that the higher SPS activity, the more sucrose accumulation (Huber, Huber 1996), and this was consistent with our findings. The sucrose accumulation is closely related to an increase in the activity during fruit ripening. During the ripening process of Wenzhou mandarin oranges, the SPS activity increased, indicating that SPS played a very important role in the accumulation of fruit sugars (Komatsu et al. 2002).

CONCLUSION

The photosynthetic rate, saturation point and chlorophyll content reached maximum values at a DIF of 12 °C, and the respiration rate (day and night) and the compensation point reached their maximum values at a DIF of 14 °C. All of the sugar (fructose, glucose, sucrose, soluble sugar) content peaked at a DIF of 12 °C, the AI, NI, SS-d content also peaked at a DIF of 12 °C, while the SPS and SS-s content reached their maximum values at a DIF of 14 °C. The Grey correlation analysis showed that the SPS was the most important factor affecting the fructose content, the photosynthesis was the most important factor affecting the glucose and sucrose content, the photosynthesis had the greatest effect on the soluble sugar content. All of the above results indicated that the DIF (12 °C) was suitable for the strawberry sugar content. This study is expected to provide a theoretical basis for strawberry production, which is helpful in improving the strawberry yield and quality. Further studies are needed to set different DIF treatments with equal daytime temperatures.

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