

# Potential Effects of Temperature Differences on the Soluble Sugar Content in Pear Fruit during the Growing Seasons of 2018 and 2019

Jeong Hwa Cho<sup>1†</sup>, Ung Yang<sup>2†</sup>, Seung Gon Wi<sup>2</sup>, Bok-Rye Lee<sup>2</sup>, Seungwon Oh<sup>3</sup>, Min-Soo Kim<sup>3</sup>, and Sang-Hyun Lee<sup>1,2,4\*</sup>

<sup>1</sup>Department of Horticulture, College of Agriculture and Life Sciences, Chonnam National University, Gwangju 61186, Korea

<sup>2</sup>Asian Pear Research Institute, Chonnam National University, Gwangju 61186, Korea

<sup>3</sup>Department of Mathematics & Statistics, Chonnam National University, Gwangju 61186, Korea

<sup>4</sup>Interdisciplinary Program in IT-Bio Convergence System, Chonnam National University, Gwangju 61186, Korea

\*Corresponding author: [pear@chonnam.ac.kr](mailto:pear@chonnam.ac.kr)

†These authors contributed equally to this work.

## Abstract

The impacts of climate change on crop yields and fruit quality are projected to accelerate with increased atmospheric carbon dioxide levels; however, few studies have focused on the impacts of climate change on the accumulation pattern and content of soluble sugars in pear (*Pyrus pyrifolia*) fruit. We compared the soluble sugars content and accumulation patterns during the 2018 and 2019 growing seasons throughout the developmental stages of pear fruit with climate data collected over the same period. Between the two years, we observed differences in the fructose and sucrose contents at the maturation stage of the pear fruit, resulting from differences in sugar accumulation following 132 days after full bloom (DAFB). Differences were also found in the meteorological data measured over the two years. In particular, the daily average temperatures from late-June to mid-August (73 to 132 DAFB) were all higher in 2018 than in 2019, and differences in the cumulative amounts of both fructose and sucrose were observed since 132 DAFB. Notable differences were confirmed in the comparison of the meteorological variables for each time interval. Among the meteorological variables, those related to temperature showed clear differences between the two years. Correlation coefficient matrices showed that sucrose and fructose accumulation responded differently depending on the meteorological variables over the two years. Furthermore, only accumulated temperature and air temperature were correlated with changes in the sucrose and fructose content in 2018, unlike in 2019. Taken together, our results indicate that temperature differences may have contributed to differences in the fructose and sucrose contents and their accumulation patterns over the two years.

**Additional key words:** annual, comparisons, environmental, extreme, maturity, summer

## Introduction

According to the Korea Meteorological Administration, the average temperature nationwide in summer 2018 was 25.4°C, the highest recorded since 1973. This anomalous heat wave was strongly

Received: January 17, 2021

Revised: April 7, 2021

Accepted: June 1, 2021

 OPEN ACCESS



HORTICULTURAL SCIENCE and TECHNOLOGY  
39(5):560-571, 2021  
URL: <http://www.hst-j.org>

pISSN : 1226-8763  
eISSN : 2465-8588

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

Copyright©2021 Korean Society for Horticultural Science.

The present study was supported by a grant from the Korea Institute of Planning and Evaluation for Technology in Food, Agriculture, Forestry and Fisheries (IPET) through Export Promotion Technology Development Program (No. 617075-5) and Advanced Production Technology Development Program (No. 318065-03) funded by the Ministry of Agriculture, Food and Rural Affairs (MAFRA).

affected by high atmospheric pressure from Tibet and the North Pacific anticyclone. However, in summer 2019, the extension of the North Pacific anticyclone to the Korean peninsula was delayed by frequent inflows of cold air from the northern Bering Sea, resulting in fewer heat waves than those in summer 2018.

The global changes in climate have largely been attributed to increased CO<sub>2</sub> emissions and human activities (Masson-Delmotte et al., 2018). The global mean surface temperature has increased by approximately 1°C above the average in the pre-industrial era (1,850–1,900). Global warming is estimated to increase by 0.2°C per decade owing to ongoing anthropogenic emissions (greenhouse gases). Over the coming decades, climate change and increased CO<sub>2</sub> levels are projected to impact the yield of all crops (Lobell and Gourdj, 2012; Sultan et al., 2019).

Extreme high temperatures owing to global warming caused a drastic reduction in the yield of pome fruit (Thomson et al., 2014; Darbyshire et al., 2015). Extreme high temperature, which occurs during summer seasons, can adversely affect the quality of pome fruit through sunburn damage (Schrader et al., 2003; McClymont et al., 2016), poor color development (Steyn et al., 2004; Thomson et al., 2018), and reduced carbon assimilation (Han et al., 2012). In addition, extreme heat may result in increased insect pests and disease incidence (Rosenzweig et al., 2001). In recent years, pear orchards have frequently experienced weather conditions that have compromised the quantity and quality of the fruit.

Many previous studies have focused on the relationship between the content of soluble sugars and the gene expression and enzyme activities involved in the sugar metabolism during the developmental stages of pear fruit (Moriguchi et al., 1992; Tanase and Yamaki, 2000; Yamada et al., 2007; Zhang et al., 2014; Jia et al., 2021; Lee et al., 2021). However, to date, there is little research on the impact of climate change on the accumulation patterns and composition of soluble sugars during the developmental stages of pear fruit through comparisons of annual meteorological variables.

In this study, we aimed to identify whether differences in fruit sugar composition are related to changes in atmospheric and soil conditions observed over the two years. We investigated the content of three major soluble sugars (glucose, fructose, and sucrose) and their accumulation patterns throughout the developmental stages of pear fruit and collected atmospheric and soil environmental data during the growing seasons of 2018 and 2019 through real-time sensor-based monitoring. Therefore, the results obtained may provide a better understanding of the impacts of climate change on the sugar composition of pear fruit.

## Materials and Methods

### Experimental Site

This study was conducted at a pear orchard (34°58'34.1"N 126°42'12.7"E; 25–30 m above sea level; 0.83 ha) utilizing Information and Communication Technology (ICT)-based equipment, located in Naju, Korea.

### Plant Material

Pear (*Pyrus pyrifolia*) cv. Niitaka fruit were harvested throughout two successive seasons (2018 and 2019) from the pear orchard, which received standard horticultural management including fertilizer application, irrigation, and disease control. Between 10 and 15 fruit were randomly sampled from the same fruit-bearing position at 15-day intervals during the period of 42 to 177 days after full bloom (DAFB) in each year. The fruit collected at each sampling period were frozen

in liquid nitrogen and then stored at  $-60^{\circ}\text{C}$  until analyzed. Unless otherwise stated, all experiments were performed independently and in triplicate.

### Analysis of Soluble Sugar

The stored samples were freeze-dried and then ground into a fine powder. Soluble sugars were extracted from 30 mg of the powdered samples with occasional shaking for 3 hours in 3 mL of distilled water. The extracts were centrifuged at  $13,000 \times g$  for 5 min. The supernatants were passed through a  $0.45 \mu\text{m}$  membrane filter and then injected into the chromatographic system. Soluble sugars were analyzed using high-performance liquid chromatography equipped with a refractive index detector (2414, Waters, MA, USA) and a REZEX RPM (Phenomenex, CA, USA) column ( $300 \times 7.8 \text{ mm}$ ).

### Measurement of Atmosphere and Soil Conditions in the Pear Orchard

Meteorological data were recorded automatically on a data logger (Xspark, Nare Trend Inc., Korea) at 5-min intervals. Soil temperature and soil moisture were measured at a 15-cm depth using Hydra Probe II soil sensors (SDI-12, Stevens Water Monitoring System Inc., OR, USA). The daily mean values of temperature, atmospheric humidity, and solar insolation were calculated during the period of 80 to 180 DAFB in 2018 and 2019. The mean daily values were determined by calculating the average of all the 5-min interval values for each day. Daily mean temperature and humidity values for soil were calculated during the same period using similar metrics.

### Statistical Analysis

To confirm whether there was a difference in the meteorological data over the two years, we compared the meteorological data measured prior to 147 DAFB, when the difference in the contents of fructose and sucrose occurred, at 15-day intervals. That is, t-1, t-2, t-3, t-4, and t-5 indicate 15, 30, 45, 60, or 75 days before 147 DAFB, respectively. For meteorological data at 15-day intervals, we used 15 observations per time interval, and each observation was assumed to be independent. Seven meteorological variables—air temperature, atmospheric humidity, accumulated temperature, diurnal temperature range, solar insolation, soil temperature, and soil humidity—were analyzed.

All analyses were performed using python (version 3.8.3). Pearson correlation analysis, Shapiro-Wilk test, T-test, and Wilcoxon signed-rank test were performed in the python packages “scipy” (version 1.6.1). Normality of the meteorological data for each time interval was assessed using the Shapiro – Wilk test of normality ( $\alpha=0.05$ ) (Shapiro and Wilk, 1965). T-tests were conducted when the distribution of both groups satisfied normality (when the value of the Shapiro-Wilks test for both groups is greater than 0.05). However, if normality is not valid (when the value of the Shapiro-Wilks test is less than 0.05 in either or both groups), the Wilcoxon signed-rank tests were performed (Wilcoxon, 1945). The significance level was set to 0.05.

## Results

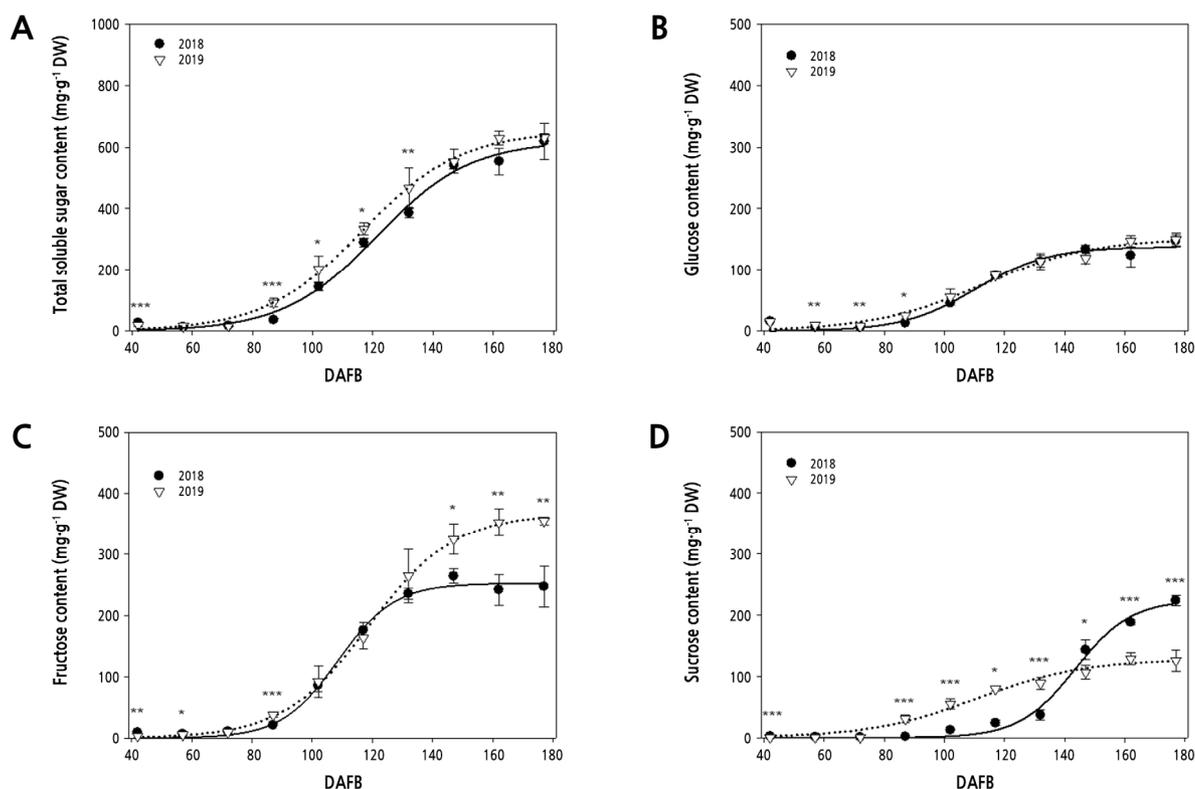
### Accumulation Pattern of Soluble Sugars

As illustrated in Fig. 1A, a steady increase in the content of total soluble sugars occurred during the period from 87 to 147 DAFB, and then remained at a high level until maturity. We noted a difference in the accumulation of total soluble

sugars between the two years; their contents were higher in 2019 than in 2018 during the period from 87 to 132 DAFB. There was no significant difference in glucose accumulation between the two years. In both years, a negligible amount of glucose was detected during the period from 42 to 72 DAFB, but thereafter, the glucose content increased gradually until maturity (Fig. 1B). However, the accumulation pattern of fructose and sucrose during the two years differed from that of glucose; differences in fructose and sucrose contents were observed between the two years at the maturation stage of pear fruit. In both years, the fructose content steadily increased during the period from 87 to 147 DAFB and then remained at the highest level until maturity, with little fluctuation (Fig. 1C). A notable difference in the fructose content was observed in mature fruit harvested at 177 DAFB, with contents of  $247.27 \text{ mg} \cdot \text{g}^{-1} \text{ DW}$  and  $355.3 \text{ mg} \cdot \text{g}^{-1} \text{ DW}$  in 2018 and 2019, respectively. In 2018, no sucrose was detected during the period from 42 to 87 DAFB, but thereafter, the sucrose content increased gradually until 132 DAFB, followed by a rapid increase from 132 DAFB until maturity, accounting for about 36.13% of the total soluble sugars (Fig. 1D). The sucrose accumulation after 87 DAFB differed between the two years; the sucrose content at maturation in 2018 was about 1.8-fold higher than that observed in 2019.

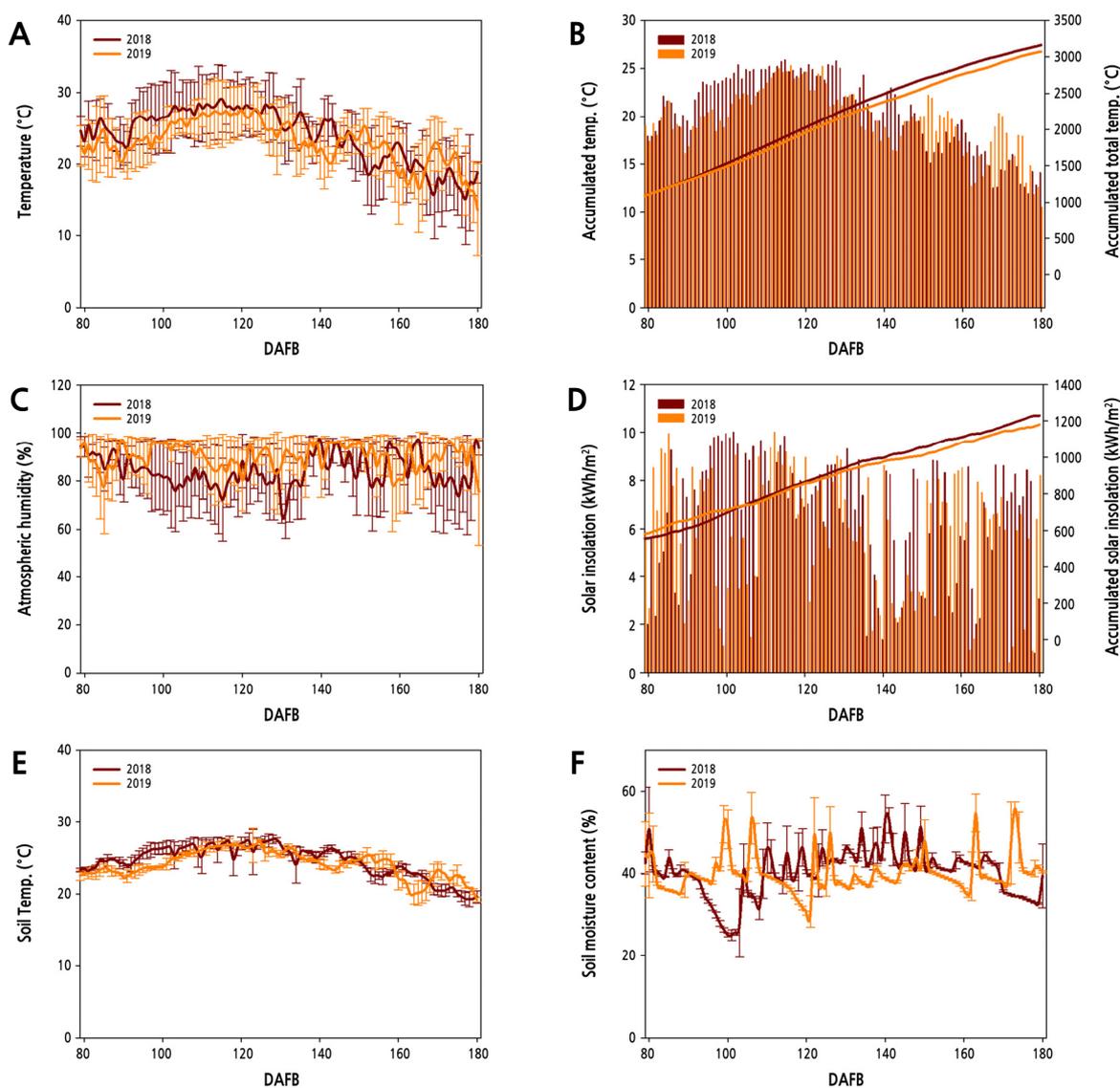
## Measurement of Environmental Factors Over the Two Years

Climate data were collected over the two years from multiple sensors installed in the pear orchard with an applied



**Fig. 1.** Changes in the soluble sugar content during pear fruit development. Measurements were taken at 15-day intervals during the period from 42 to 177 days after full bloom (DAFB) in 2018 (closed circles) and 2019 (open reversed triangles). The solid line represents a smooth trend line for the data points in 2018. The dotted line represents a smooth trend line for the data points in 2019. (A) Total soluble sugars. (B) Glucose. (C) Fructose. (D) Sucrose. Values represent the mean  $\pm$  SD of three replicates. Asterisks indicate a significant difference at each sampling time. \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

ICT-based platform. Similar patterns in both air temperature and humidity were observed for both years; however, average daily temperatures from late-June to mid-August (73-132 DAFB) varied, with a mean temperature 2°C higher in 2018 (26.3°C) than in 2019 (24.3°C) (Fig. 2A). The mean diurnal temperature range over the same period was 1.4°C higher in 2018 (7.8°C) than in 2019 (6.4°C). The mean air humidity values from late-June to mid-August were 82.2% and 89.7% in 2018 and 2019, respectively, with values ranging from 66.5 to 94.2% in 2018 and 77.7 to 96.0% in 2019 (Fig. 2C). The total accumulated temperature from late-June to mid-August was calculated as 1373.6°C in 2018 and 1277.5°C in 2019; the accumulated temperature in 2018 was 96.1°C greater than that in 2019 (Fig. 2B). In the comparison of average solar insolation from late-June to mid-August, the mean value was 0.7 kWh/m<sup>2</sup> higher in 2018 (7.4 kWh/m<sup>2</sup>) than in 2019 (6.7 kWh/m<sup>2</sup>) (Fig. 2D).



**Fig. 2.** Seasonal patterns of (A) temperature, (B) accumulated temperature, (C) atmospheric humidity, (D) solar insolation, (E) soil temperature, and (F) soil moisture content from 2018 to 2019 at the study site. Each value represents a daily observation during the period from 80 to 180 days after full bloom (DAFB) in 2018 (solid maroon line) and 2019 (solid orange line). Values represent the mean  $\pm$  SD.

No perceptible difference was observed in the seasonal patterns of soil temperatures between the two years. However, the average daily soil temperature from late-June to mid-August was 1.1°C higher in 2018 than in 2019 (Fig. 2E). In addition, the deviation of daily mean temperatures was about 0.2°C higher in 2018 than in 2019. Soil moisture was measured daily over the two years, and a greater fluctuation was observed in soil moisture than in soil temperature (Fig. 2F). However, the average daily soil moisture value over the same period was similar between the two years.

**Table 1.** Comparison of meteorological variables for each time difference at 15-day intervals between 2018 and 2019

Meteorological variables	Time interval	Mean ± SD (2018)	Mean ± SD (2019)	<i>p</i> value	comparison
Temperature <sup>z</sup>	t-5	24.379 ± 1.026	22.304 ± 1.179	< 0.001*	18 > 19
Temperature <sup>y</sup>	t-4	25.219 ± 1.597	22.774 ± 1.168	< 0.001*	18 > 19
Temperature <sup>z</sup>	t-3	27.946 ± 0.530	26.515 ± 0.645	< 0.001*	18 > 19
Temperature <sup>y</sup>	t-2	27.391 ± 1.003	26.132 ± 1.176	< 0.001*	18 > 19
Temperature <sup>z</sup>	t-1	24.904 ± 1.406	22.543 ± 1.421	< 0.001*	18 > 19
Atmospheric humidity <sup>z</sup>	t-5	85.036 ± 7.902	88.617 ± 5.374	0.172	18 = 19
Atmospheric humidity <sup>y</sup>	t-4	85.047 ± 3.589	91.876 ± 3.905	< 0.001*	18 < 19
Atmospheric humidity <sup>z</sup>	t-3	78.916 ± 3.132	90.436 ± 4.304	< 0.001*	18 < 19
Atmospheric humidity <sup>y</sup>	t-2	80.302 ± 5.843	88.488 ± 4.006	< 0.001*	18 < 19
Atmospheric humidity <sup>y</sup>	t-1	87.472 ± 6.422	92.164 ± 3.826	< 0.001*	18 < 19
Accumulated temp <sup>z</sup>	t-5	18.513 ± 2.211	18.713 ± 1.554	0.784	18 = 19
Accumulated temp <sup>y</sup>	t-4	22.020 ± 1.932	19.160 ± 1.332	< 0.001*	18 > 19
Accumulated temp <sup>y</sup>	t-3	24.787 ± 0.776	23.287 ± 1.275	< 0.001*	18 > 19
Accumulated temp <sup>y</sup>	t-2	24.440 ± 1.093	22.973 ± 1.353	< 0.001*	18 > 19
Accumulated temp <sup>z</sup>	t-1	21.260 ± 1.567	18.807 ± 1.564	< 0.001*	18 > 19
Diurnal temp range <sup>z</sup>	t-5	7.915 ± 3.087	7.427 ± 2.458	0.647	18 = 19
Diurnal temp range <sup>z</sup>	t-4	7.267 ± 2.188	5.391 ± 2.609	0.049*	18 > 19
Diurnal temp range <sup>y</sup>	t-3	8.556 ± 1.718	5.930 ± 2.582	< 0.001*	18 > 19
Diurnal temp range <sup>z</sup>	t-2	7.434 ± 1.553	6.459 ± 1.988	0.159	18 = 19
Diurnal temp range <sup>z</sup>	t-1	5.245 ± 2.586	5.450 ± 2.208	0.823	18 = 19
Solar insolation <sup>y</sup>	t-5	5.989 ± 2.762	6.929 ± 2.730	< 0.001*	18 < 19
Solar insolation <sup>y</sup>	t-4	7.680 ± 2.354	5.383 ± 2.620	< 0.001*	18 > 19
Solar insolation <sup>y</sup>	t-3	8.475 ± 1.542	7.073 ± 2.617	< 0.001*	18 > 19
Solar insolation <sup>z</sup>	t-2	7.634 ± 0.953	6.994 ± 1.744	0.238	18 = 19
Solar insolation <sup>z</sup>	t-1	5.250 ± 2.616	4.491 ± 2.093	0.404	18 = 19
Soil temp <sup>z</sup>	t-5	23.391 ± 0.729	22.565 ± 0.631	0.003*	18 > 19
Soil temp <sup>z</sup>	t-4	25.248 ± 0.886	23.270 ± 0.498	< 0.001*	18 > 19
Soil temp <sup>z</sup>	t-3	26.420 ± 0.589	25.896 ± 0.661	0.035*	18 > 19
Soil temp <sup>y</sup>	t-2	26.836 ± 0.739	26.373 ± 0.509	< 0.001*	18 > 19
Soil temp <sup>z</sup>	t-1	25.563 ± 0.568	24.631 ± 0.914	0.003*	18 > 19
Soil moisture <sup>z</sup>	t-5	38.980 ± 4.507	37.122 ± 6.370	0.381	18 = 19
Soil moisture <sup>y</sup>	t-4	33.994 ± 5.754	40.581 ± 4.651	< 0.001*	18 < 19
Soil moisture <sup>y</sup>	t-3	37.419 ± 5.737	40.383 ± 4.319	< 0.001*	18 < 19
Soil moisture <sup>y</sup>	t-2	42.634 ± 2.537	37.309 ± 5.539	< 0.001*	18 > 19
Soil moisture <sup>y</sup>	t-1	46.052 ± 3.753	39.281 ± 1.623	< 0.001*	18 > 19

Temp = temperature.

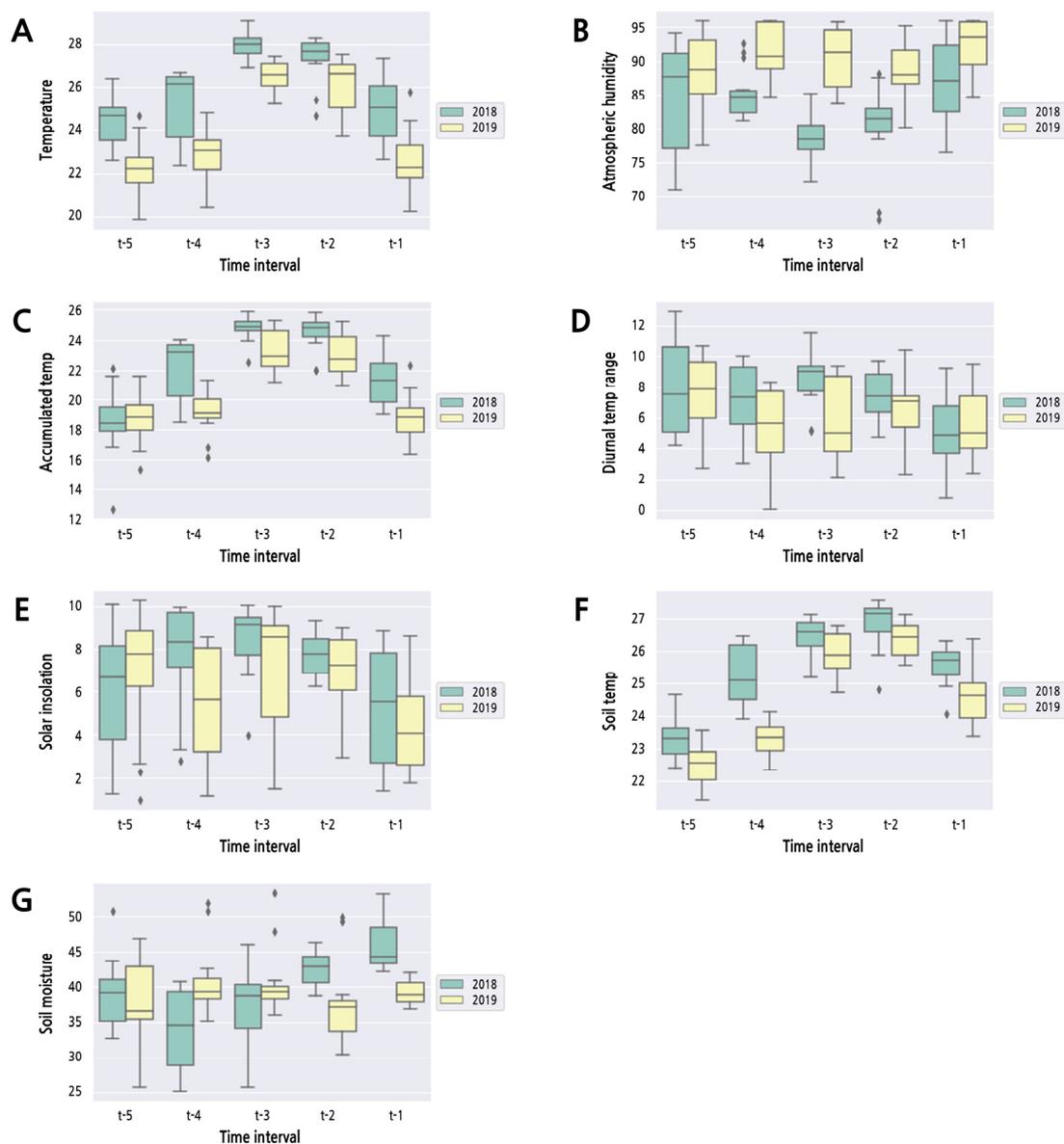
<sup>z</sup>T-test.

<sup>y</sup>Wilcoxon signed rank test.

\*significant at  $p < 0.05$ .

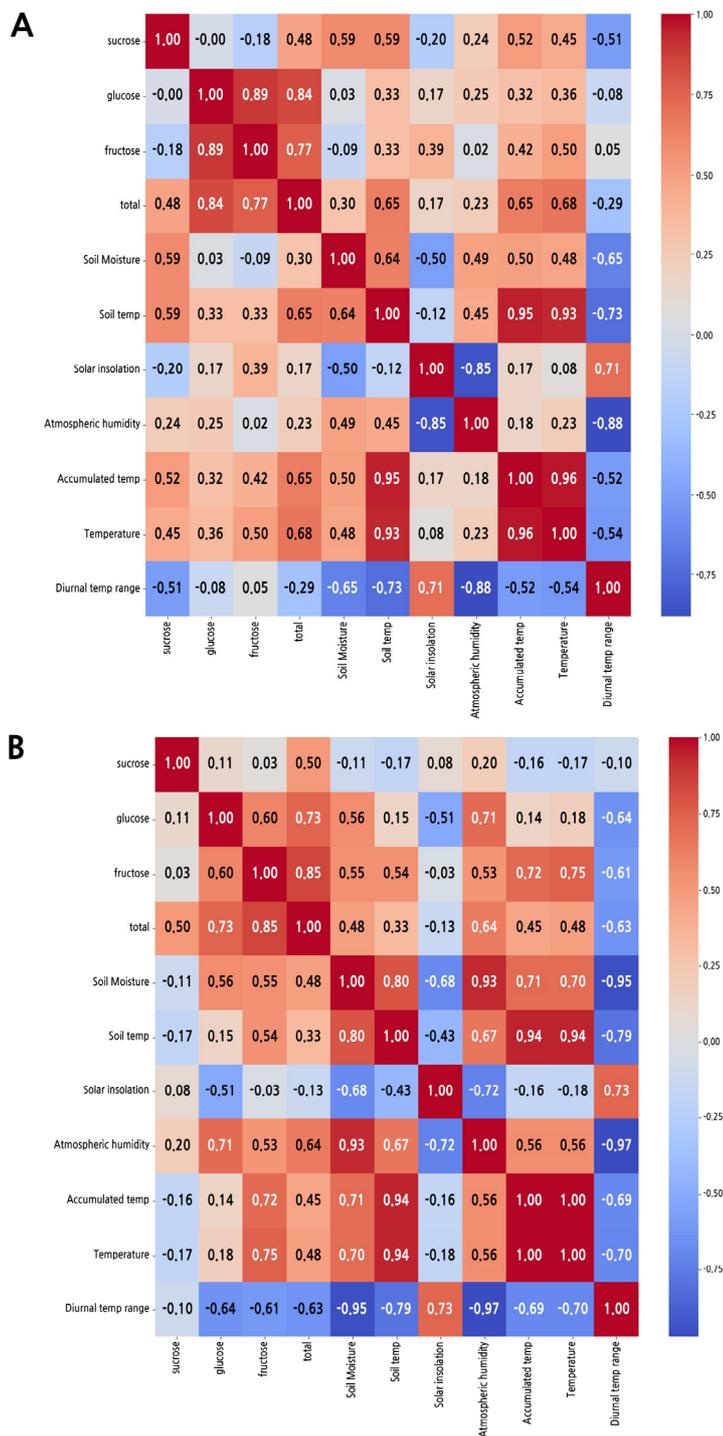
### Difference in Meteorological Variables between the Two Years

Over the two years, we compared meteorological data measured prior to 147 DAFB at 15-day intervals (t-1 – t-5) as depicted in Table 1 and visualized using a box plot (Fig. 3). For air temperature, all values were higher ( $p < 0.05$ ) in 2018 than in 2019 from t-5 to t-1. There was no significant difference in atmospheric humidity between the two years at t-5, but the values of atmospheric humidity from t-4 to t-1 in 2019 were significantly higher ( $p < 0.05$ ) than those in 2018. Further, the accumulated temperature values showed no difference between the two years at t-5, but those from t-4 to t-1 in 2018



**Fig. 3.** Box plots comparing values of meteorological variables at 15-day intervals between the two years. (A) Temperature. (B) Atmospheric humidity. (C) Accumulated temperature. (D) Diurnal temperature range. (E) Solar insolation. (F) Soil temperature. (G) Soil moisture. The boxplots consist of two parts: a box and a set of whiskers. Upper and lower whiskers in boxplots indicate the maximum and minimum values of data, respectively. The lower line in the box means quantile 25% (Q1), and the upper line in the box means quantile 75% (Q3). The center line in the box means median (Quantile 50%; Q2). The data points that lie outside of  $Q2 \pm 1.5 \times (Q3-Q1)$  are considered outliers and are represented as diamond-shaped dots.

were higher ( $p < 0.05$ ) than those in 2019. For soil temperature, all values were higher ( $p < 0.05$ ) in 2018 than in 2019. However, the values of other meteorological variables, such as diurnal temperature range, solar insolation, and soil moisture, were not biased to a particular year, showing no consistent pattern.



**Fig. 4.** Multiple correlation analysis. The heatmap of multiple correlation matrices represents the correlations for the change in the soluble sugars content with meteorological variables in 2018 (A) and 2019 (B). Positive correlations are displayed in red and negative correlations in blue.

## Multiple Correlation Analysis

The heatmap of multiple correlation matrices between the soluble sugars content and meteorological variables is shown in Fig. 4. Multiple correlation matrices represent the correlations for the changes in the soluble sugars content with meteorological variables between the two years. In 2018, sucrose was found to be correlated with soil moisture, soil temperature, accumulated temperature, air temperature, and the diurnal temperature range. Fructose was correlated with accumulated temperature and air temperature in 2018. However, in 2019, fructose had a close correlation with accumulated temperature and air temperature, whereas sucrose showed no correlation with meteorological variables. This indicated that differences in the contents of fructose and sucrose might be attributed to differences in meteorological variables over the two years.

## Discussion

This study was conducted to investigate the impacts of climate change on the quality of pear fruit during the growing seasons of 2018 and 2019. Between the two years, notable differences in the accumulation patterns of fructose and sucrose were noted from 132 DAFB until maturity of pear fruit; however, no difference in glucose accumulation was observed (Fig. 1). While sucrose accounted for approximately one-third of the total soluble sugar measured in 2018, fructose was the predominant sugar in 2019, accounting for 56.3% of the total soluble sugar at maturity. These differences in sugar composition might be responsible for the differences in the sweetness of pear fruit over the two years. The composition and overall amount of sucrose, fructose, and glucose directly impact the perceived sweetness of the fruit (Tanase and Yamaki, 2000). During fruit development, annual differences in the soluble sugars content and their accumulation patterns identified in this study have also been reported in previous studies (Fadda and Mulas, 2010; Oikawa et al., 2015; Mesa et al., 2016).

Over the two years, we found differences in the meteorological data measured (Fig. 2). In particular, the daily average temperatures from late-June to mid-August (73 to 132 DAFB) were all higher in 2018 than in 2019 (Fig. 2A), and differences in both fructose and sucrose accumulation were observed after 132 DAFB between the two years (Fig 1C and 1D). Notable differences were also observed in the meteorological variables for each time interval between the two years (Table 1 and Fig. 3). In the comparison based on each time interval, the values of air temperature, accumulated temperature, and soil temperature in 2018 were all higher than those in 2019, excluding the value of accumulated temperature at t-5 in 2018. In addition, as shown in the multiple correlation analysis (Fig. 4), we found that sucrose and fructose accumulation responded differently depending on the meteorological variables over the two years. These results implied that the differences in meteorological conditions may affect the soluble sugars content and their accumulation patterns. It also indicated that the difference in temperature observed over the two years may have contributed to differences in the fructose and sucrose contents and their accumulation patterns. This is because, unlike in 2019, only accumulated temperature and air temperature were found to be correlated with the change in sucrose and fructose content in 2018 among other meteorological variables.

Factors that contributed to differences in the cumulative amounts of both fructose and sucrose over the two years can be found in a previous study by Richardson et al. (2004) who investigated the deleterious effects of high temperatures on

carbohydrate metabolism in kiwifruit. In their experiments, a transient reduction in the soluble sugars content was observed immediately after heat treatment of kiwifruit at any stage of fruit development. The soluble sugars content in kiwifruit receiving heat treatment during the cell division phase was recovered to the level of the control group thereafter, whereas kiwifruit subjected to heat treatment during starch accumulation or fruit maturation had a significantly lower soluble sugars content than that of the control group. In addition, the finding that the sugar to starch ratio of kiwifruit receiving heat treatment during the fruit maturation stage was lower than that of the control group indicates that mobilization of sugar from starch was delayed by heat treatment. Interestingly, sucrose was more affected by high temperatures than hexoses. However, the effect of high temperatures on the sensitivity of sucrose seems to be temporary. Although the hexose to sucrose ratio was raised immediately after heat treatment, the ratio returned to a level similar to that of the control group after the high temperatures were removed. Thus, it can be assumed that the delay in sucrose accumulation observed in 2018 was due to delayed starch decomposition by high temperatures, as revealed in the results of Richardson et al. (2004).

The effect of temperature on the sugar content during fruit development is well documented in the literature. In a previous study of Liu et al. (2013), the sucrose content in pear flesh increased significantly by 11.8% two weeks after a high-temperature treatment when compared with that in untreated flesh at harvest. Their result is consistent with our finding, where the sucrose content in 2018 increased dramatically after 132 DAFB. The average temperature from late-June to mid-August (73 to 132 DAFB) was 1.8°C higher in 2018 (26.3°C) than in 2019 (24.5°C). Kano (2006) observed that sucrose accumulation in melon fruit on 40 DAFB was much more promoted in a high-temperature treatment than that in unheated fruit. The sucrose content was higher in rice grains grown in a greenhouse than in grains grown in the field (Li et al., 2006); the day and night temperatures in the greenhouse were 2°C and 0.3°C higher than the ambient air temperature, respectively. Their results also showed that activities of sucrose synthase and invertase decreased in high-temperature-treated grains. Therefore, our finding that fructose accumulation at the maturation stage in 2018 was lower than that in 2019 suggests that it is related to a decrease in the activity of sucrose synthase by high temperatures (Schmolzer et al., 2016; Stein and Granot, 2019). Sucrose synthase has been shown to play a role in sucrose cleavage rather than sucrose synthesis (Turner and Turner, 1975; Stein and Granot, 2019).

In contrast to our results, Yamada et al. (1994) reported that the sucrose content in the flesh of two apple cultivars decreased with increasing fruit temperature from 21 to 35°C, but the content of fructose and glucose increased. However, the results obtained by Yamada et al. (1994) are thought to be due to a raised hexose to sucrose ratio in the fruit immediately after the high-temperature treatment, similar to the findings of Richardson et al. (2004). Besides, a high-temperature treatment negatively affected the sucrose content compared with plants subjected to a low-temperature treatment in sugarcane (Bonnett et al., 2006) and watermelon (Fukuoka et al., 2009). Sun et al. (2012) investigated the combined effects of elevated CO<sub>2</sub>, nitrogen, and temperature on sugar composition in strawberry. However, the effect of high-temperature treatment on the sugar composition was negligible. The contents of fructose and glucose increased 1.3-fold under elevated CO<sub>2</sub> treatment compared to those under the ambient CO<sub>2</sub> condition, regardless of temperature. Taken together, changes in the sugar content and the types of sugar accumulated under high temperature stress differ depending on the intensity and duration of the stress and the fruit crop species.

The meteorological conditions differed over the two years in the present study; likewise, the fructose and sucrose contents and their accumulation patterns also differed. Among the meteorological variables, the variables related to

temperature showed a clear difference over the two years at each time interval. Correlation coefficient matrices showed that accumulation of soluble sugars responded differently depending on the meteorological conditions over the two years. Furthermore, only accumulated temperature and air temperature were correlated with the change in sucrose and fructose contents in 2018, unlike in 2019. This indicates that temperature differences may have contributed to the differences in the fructose and sucrose contents and their accumulation patterns over the two years.

However, our results are still insufficient to elucidate the effects of extreme high temperatures, especially during the summer period, on the accumulation pattern and composition of soluble sugars in pear fruit. The extent of the effects of these temperature changes on fructose and sucrose content during fruit development stages and/or at maturity of pear fruit remains unclear. Given the acceleration of global warming, further studies are needed to evaluate the effects of extreme high temperatures, particularly during the summer period, on the sugar composition at different developmental stages of pear fruit, especially in terms of the intensity, duration, and frequency of the high temperature.

## Literature Cited

- Bonnett G, Hewitt M, Glassop D** (2006) Effects of high temperature on the growth and composition of sugarcane internodes. *Aust J Agri Res* 57:1087-1095. doi:10.1071/AR06042
- Darbyshire R, McClymont L, Goodwin I** (2015) Sun damage risk of Royal Gala apple in fruit-growing districts in Australia. *NZ J Crop Hortic Sci* 43:222-232. doi:10.1080/01140671.2015.1034731
- Fadda A, Mulas M** (2010) Chemical changes during myrtle (*Myrtus communis* L.) fruit development and ripening. *Sci Hort* 125:477-485. doi:10.1016/j.scienta.2010.03.024
- Fukuoka N, Masuda D, Kanamori Y** (2009) Effects of temperature around the fruit on sugar accumulation in watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) during the latter half of fruit developmental period. *J Jpn Soc Hortic Sci* 78:97-102. doi:10.2503/jjshs1.78.97
- Han J-H, Cho JG, Son I-C, Kim SH, Lee I-B, Choi IM, Kim D** (2012) Effects of elevated carbon dioxide and temperature on photosynthesis and fruit characteristics of 'Nittaka' pear (*Pyrus pyrifolia* Nakai). *Hortic Environ Biotechnol* 53:357-361. doi:10.1007/s13580-012-0047-x
- Jia B, Cheng Z, Wang Q, Zhang S, Heng W, Zhu L** (2021) Characterization of the composition and gene expression involved the shikimate pathway in the exocarp of 'Dangshansuli' pear and its russet mutant. *Hortic Environ Biotechnol* 62:125-134. doi:10.1007/s13580-019-00207-8
- Kano Y** (2006) Effect of heating fruit on cell size and sugar accumulation in melon fruit (*Cucumis melo* L.). *HortScience* 41:1431-1434. doi:10.21273/HORTSCI.41.6.1431
- Lee BR, Cho JH, Wi SG, Yang U, Jung WJ, Lee SH** (2021) The Sucrose-to-Hexose Ratio is a Significant Determinant for Fruit Maturity and is Modulated by Invertase and Sucrose Re-Synthesis During Fruit Development and Ripening in Asian Pear (*Pyrus pyrifolia* Nakai) Cultivars. *Hortic Sci Technol* 39:141-151. doi:10.7235/HORT.20210013
- Li T, Liu Q-H, Ohsugi R, Yamagishi T, Sasaki H** (2006) Effect of high temperature on sucrose content and sucrose cleaving enzyme activity in rice grain during the filling stage. *Rice Sci* 13:205-210
- Liu D, Ni J, Wu R, Teng Y** (2013) High temperature alters sorbitol metabolism in *Pyrus pyrifolia* leaves and fruit flesh during late stages of fruit enlargement. *J Amer Soc Hort Sci* 138:443-451. doi:10.21273/JASHS.138.6.443
- Lobell DB, Gourdji SM** (2012) The influence of climate change on global crop productivity. *Plant Physiol* 160:1686-1697. doi:10.1104/p.p.112.208298
- Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, et al.** (2018) Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C
- McClymont L, Goodwin I, Turpin S, Darbyshire R** (2016) Fruit surface temperature of red-blushed pear: threshold for sunburn damage. *NZ J Crop Hortic Sci* 44:262-273. doi:10.1080/01140671.2016.1216867
- Mesa K, Serra S, Masia A, Gagliardi F, Bucci D, Musacchi S** (2016) Seasonal trends of starch and soluble carbohydrates in fruits and leaves of 'Abbé Fétel' pear trees and their relationship to fruit quality parameters. *Sci Hort* 211:60-69. doi:10.1016/j.scienta.2016.08.008
- Moriguchi T, Abe K, Sanada T, Yamaki S** (1992) Levels and role of sucrose synthase, sucrose-phosphate synthase, and acid invertase in sucrose accumulation in fruit of Asian pear. *J Amer Soc Hort Sci* 117:274-278. doi:10.21273/JASHS.117.2.274
- Oikawa A, Otsuka T, Nakabayashi R, Jikumar Y, Isuzugawa K, Murayama H, Saito K, Shiratake K** (2015) Metabolic profiling of developing pear fruits reveals dynamic variation in primary and secondary metabolites, including plant hormones. *PLoS ONE* 10:e0131408. doi:10.1371/journal.pone.0131408

- Richardson AC, Marsh KB, Bolding HL, Pickering AH, Bulley SM, Frearson NJ, Ferguson AR, Thornber SE, Bolitho KM, et al. (2004) High growing temperatures reduce fruit carbohydrate and vitamin C in kiwifruit. *Plant Cell Environ* 27:423-435. doi:10.1111/j.1365-3040.2003.01161.x
- Rosenzweig C, Iglesias A, Yang X-B, Epstein PR, Chivian E (2001) Climate change and extreme weather events-Implications for food production, plant diseases, and pests. *Global Change & Human Health* 2:90-104. doi:10.1023/A:1015086831467
- Schmolzer K, Gutmann A, Diricks M, Desmet T, Nidetzky B (2016) Sucrose synthase: a unique glycosyltransferase for biocatalytic glycosylation process development. *Biotechnol Adv* 34:88-111. doi:10.1016/j.biotechadv.2015.11.003
- Schrader L, Zhang J, Sun J (2003) Environmental stresses that cause sunburn of apple. *Acta Hort* 618:397-405. doi:10.17660/ActaHortic.2003.618.47
- Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). *Biometrika* 52:591-611. doi:10.1093/biomet/52.3-4.591
- Stein O, Granot D (2019) An Overview of Sucrose Synthases in Plants. *Front Plant Sci* 10:95. doi:10.3389/fpls.2019.00095
- Steyn W, Holcroft D, Wand S, Jacobs G (2004) Anthocyanin degradation in detached pome fruit with reference to preharvest red color loss and pigmentation patterns of blushed and fully red pears. *J Amer Soc Hort Sci* 129:13-19. doi:10.21273/JASHS.129.1.0013
- Sultan B, Defrance D, Izumi T (2019) Evidence of crop production losses in West Africa due to historical global warming in two crop models. *Sci Rep* 9:1-15. doi:10.1038/s41598-019-49167-0
- Sun P, Mantri N, Lou H, Hu Y, Sun D, Zhu Y, Dong T, Lu H (2012) Effects of elevated CO<sub>2</sub> and temperature on yield and fruit quality of strawberry (*Fragaria×ananassa* Duch.) at two levels of nitrogen application. *PLoS ONE* 7:e41000. doi:10.1371/journal.pone.0041000
- Tanase K, Yamaki S (2000) Sucrose synthase isozymes related to sucrose accumulation during fruit development of Japanese pear (*Pyrus pyrifolia* Nakai). *J Jpn Soc Hortic Sci* 69:671-676. doi:10.2503/jjshs.69.671
- Thomson G, McCaskill M, Goodwin I, Kearney G, Lolicato S (2014) Potential impacts of rising global temperatures on Australia's pome fruit industry and adaptation strategies. *NZ J Crop Hortic Sci* 42:21-30. doi:10.1080/01140671.2013.838588
- Thomson GE, Turpin S, Goodwin I (2018) A review of preharvest anthocyanin development in full red and blush cultivars of European pear. *NZ J Crop Hortic Sci* 46:81-100. doi:10.1080/01140671.2017.1351378
- Turner JF, Turner DH (1975) The regulation of carbohydrate metabolism. *Annu Rev Plant Physiol* 26:159-186. doi:10.1146/annurev.pp.26.060175.001111
- Wilcoxon F (1945) Individual comparisons by ranking methods. *Biometrics Bull* 1:80-83. doi:10.2307/3001968
- Yamada H, Ohmura H, Arai C, Terui M (1994) Effect of preharvest fruit temperature on ripening, sugars, and watercore occurrence in apples. *J Amer Soc Hort Sci* 119:1208-1214. doi:10.21273/JASHS.119.6.1208
- Yamada K, Kojima T, Bantog N, Shimoda T, Mori H, Shiratake K, Yamaki S (2007) Cloning of two isoforms of soluble acid invertase of Japanese pear and their expression during fruit development. *J Plant Physiol* 164:746-755. doi:10.1016/j.jplph.2006.05.007
- Zhang HP, Wu JY, Qin GH, Yao GF, Qi KJ, Wang LF, Zhang SL (2014) The role of sucrose-metabolizing enzymes in pear fruit that differ in sucrose accumulation. *Acta physiol plant* 36:71-77. doi:10.1007/s11738-013-1387-6