INTRODUCTION

Strawberry (Fragaria x ananassa Duch.) is a rich source of bioactive compounds, including ascorbic acid (ASA), and polyphenols, such as anthocyanins and phenolic acids, most of which exhibit high antioxidant activities both in vitro and in vivo (Giampieri et al., 2012). As antioxidant compounds are associated with health benefits, the dietary intake of strawberry is highly recommended (Hannum, 2004; Cervantes et al., 2019). However, in the strawberry fruit, the content of antioxidant compounds varies because of genetics, environmental factors, and cultural practices.

Previously, several studies on strawberry focused on the effects of environmental factors, such as harvest season (Cho et al., 2016), air temperature (Balasooriya et al., 2019; Shin et al., 2007; Sun et al., 2012), and light-related factors, such as light intensity, light duration, and ultraviolet (UV) exposure (Palmiere et al., 2017; Cervantes et al., 2019), on antioxidant compounds. In general, environmental conditions such as air temperature and irradiation have great impacts on plant growth because of changes in the photosynthetic apparatus, such as the photoinhibition of photosystem II (PSII) (Xu et al., 2020). Changes in the photosynthetic apparatus affect antioxidant metabolism through the generation of reactive oxygen species in photosynthesizing tissues (Hajiboland, 2014), which affect plant growth and/or photosynthetic performance, leading to changes in the level of antioxidant compounds. However, the effects of plant growth and photosynthetic performance on fruit antioxidant compounds have not yet been investigated. Therefore, to enhance the level of antioxidant compounds in the strawberry fruit, it is necessary to understand the interactions of antioxidant compounds with plant growth and photosynthetic performance.

A correlation network analysis can be used widely to visualize interactions among various factors (Newman, 2003). From the agricultural viewpoint, the correlation network analysis of plant metabolism can provide key insights into biochemical processes and their regulation (Toubiana et al., 2013). Previously, correlation network analysis has been used to perform metabolic data analysis of several horticultural crops, such as tomato (DiLeo et al., 2011; Zushi and Matsuzoe, 2011, 2015), pepper (Silva et al., 2016), and strawberry (Fat et al., 2008). In these studies, the correlation network and its structure have been characterized extensively in efforts to elucidate the design principles of metabolic interactions. For example, in strawberry fruit, the correlation network suggested that metabolism is
substantially coordinated during early development in different organs, and indicated a higher degree of connectivity within and between metabolic pathways in the achenes (Fait et al., 2008). However, in these correlation network analyses, the information generated was limited to metabolite–metabolite interactions, and little was learned about plant growth–photosynthetic performance–metabolite interactions.

In this study, we aimed to visually identify the interactions of antioxidant compounds with plant growth, leaf photosynthesis performance, and agronomic quality in strawberry, and to elucidate the significance of these interactions using the correlation network analysis. In addition, we screened the key factors needed to enhance the level of fruit antioxidant compounds. To perform this study, we established three research farms of commercially grown strawberry, and measured plant growth, leaf photosynthetic performance–related parameters, agronomic quality, and antioxidant content at 2-week intervals during 2 months, and then constructed the correlation network.

MATERIALS AND METHODS

Plant material and agronomic practices

The strawberry (Fragaria×ananassa Duch.) cultivar Sagahonoka was used in this study. Plants were grown commercially from September 2018 to April 2019 on the three farms in Miyazaki, Japan. The coordinates, altitude, and size of each farm are as follows: farm A (32°14′07″ N, 131°31′22″ E; 92 m above sea level [masl]; 42.5 m), farm B (32°12′47″ N, 131°29′51″ E; 96 masl; 50.0 m×26.0 m), and farm C (32°16′14″ N, 131°34′28″ E; 5 masl; 42.5 m×18.6 m). At each farm, plants were grown in a multispan gutter-connected greenhouse with an arch roof, which was covered with a conventional plastic film. In each greenhouse, daughter plants were transplanted in late September 2018 on raised beds prepared according to commercial standards. Plants were grown according to current commercial cultivation and pest management practices.

The air temperature and irradiation at each farm were measured with an all-in-one weather station (ATMOS-41; METER Group, Inc., WA, USA) connected to a data logger (ZL6; METER Group, Inc., WA, USA) located above a multispan gutter-connected greenhouse with an arch roof, which was covered with a conventional plastic film. In each greenhouse, daughter plants were transplanted in late September 2018 on raised beds prepared according to commercial standards. Plants were grown according to current commercial cultivation and pest management practices.

The air temperature and irradiation at each farm were measured with an all-in-one weather station (ATMOS-41; METER Group, Inc., WA, USA) connected to a data logger (ZL6; METER Group, Inc., WA, USA) located above tested plants. Measurements were recorded every 10 minutes, and the daily mean air temperature and daily light integral (DLI) were calculated.

Measurement of growth and photosynthetic performance–related parameters

Plant growth and photosynthetic performance–related parameters were measured at 2-week intervals during March and April 2019 (Fig. 1). At each farm, the following measurements were taken at 10:00-13:00 from two plots (6 plants/plot) established at the center row of each greenhouse: plant height, leaf length, width, thickness, and color, transpiration rate, leaf area index (LAI), and photosynthetic performance. The leaf characteristics, transpiration rate, and photosynthetic performance were measured on a leaflet of the fully expanded third leaf. Among the leaf characteristics, leaf length and width were measured with a tape measure, leaf thickness was measured using a micrometer (OMV-25MX; Mitsutoyo Co., Kanagawa, Japan), and leaf color was measured using a chlorophyll meter (SPAD 502; Konica Minolta, Inc., Tokyo, Japan). The transpiration rate was measured twice per leaf with a steady-state diffusion porometer (AP4; Delta-T Devices Inc., Cambridge, UK) and the LAI was measured using a portable LAI meter (MJ-15LAI/P; Environmental Measurement Japan Co., Ltd., Fukuoka, Japan) (Kume et al., 2011).

Leaf photosynthetic performance was measured twice per leaf, with Y(II) as the light-adapted quantum yield of PSII and chlorophyll a (Chl a) fluorescence transient (OJIP transient) as a highly useful and sensitive signature of photosynthesis, both of which provide valuable information on the structure and function of the photosynthetic apparatus (Stirbet et al., 2018; Tsimilli-Michael, 2020). The Y(II) was measured with a Y(II) meter (Opti-Sciences, Inc., NH, USA), according to a single multiphase flash method of sub-saturating intensity based on Lorhauts et al. (2013). The OJIP transient was measured with a portable Chl a fluorometer (OS-30P+; Opti-Sciences, Inc., NH, USA). Before taking the measurements, the leaves were exposed to the dark for 30 minutes using special plastic clips (Opti-Sciences, Inc., NH, USA). The OJIP steps measured the fluorescence intensity when all PSII reaction centers (RCs) are open (O; minimal fluorescence intensity), at 100 μs (T100), 300 μs (K), 2 ms (J), and 30 ms (I), and when all PSII RCs are closed (P; maximal fluorescence intensity). In addition, the measured OJIP steps were analyzed by the JIP-test method (Strasser et al., 2004; Tsimilli-Michael, 2020) (Table 1).

Measurement of agronomic qualities

Fully mature fruits (at least 15–20 fruits per research farm) were harvested in 2019 from March 1 to April 26 at
the time of measurement of growth and photosynthetic performance-related parameters (Fig. 1). The harvested fruits were stored on ice and delivered to the laboratory within 1–2 hours of harvest, and agronomic qualities were measured immediately. Ten fruits of uniform size and color were selected, and the weight and surface color of each fruit were measured. The fruit surface color was determined using the CIE L*a*b* color space with a colorimeter (CR-310; Konica Minolta, Inc., Tokyo, Japan) at three different spots around the equatorial plane of each fruit. The L*a*b* method was used to calculate the lightness (L), chroma (C* = [a*² + b*²]¹/²), which indicates the color intensity, and hue angle (h* = arctangent [b*/a*]), where 0° = red; 90° = yellow; 180° = green; and 270° = blue.

After measuring the weight and fruit surface color, fruits were sliced vertically into quarters. A quarter was squeezed, and the extract was used to measure the total soluble solids (TSS) and acidity with a portable sugar-acid meter (PAL-BX/ACID3; ATAGO Co., Ltd., Tokyo, Japan). In addition, one slice was freeze-dried for 72 hours (FDU-2100; EYELA Co., Ltd., Tokyo, Japan) and then ground to a fine powder. Each sample was weighed before and after freeze-drying, and the measurements were used to calculate the percentage of dry matter (DM%). The other slices were stored at −80°C until needed to measure antioxidant compounds.

### Measurement of antioxidant compounds

To evaluate antioxidant compounds, levels of ASA, dehydroascorbic acid (DHA; the oxidized form of ASA), total polyphenols, antioxidant activity, and anthocyanins were measured. To measure ASA and DHA, 1.8–2.5 g of frozen tissue was homogenized in 20 mL of cold 2% metaphosphoric acid (w/v). The homogenate was centrifuged at 15,000×g for 15 minutes at 4°C, and the supernatant was analyzed by high-performance liquid chromatography, as described previously (Zushi and Matsuzoe, 2007).

To measure the total polyphenol content and antioxidant activity, ~0.1 g of freeze-dried sample was placed in a centrifuge tube containing 4 mL of cold 70% methanol (v/v) and 1.5% formic acid (v/v) (Nowicka et al., 2019), and sonicated at a low temperature (~10°C) in an ultrasonic bath (US-3KS; SND Co., Ltd., Nagano, Japan) for 1 hour. The sample was then centrifuged at 15,000×g for 15 minutes at 4°C. Total polyphenol content was evaluated using Folin–Ciocalteu reagent after the solid-phase extraction, and antioxidant activity was measured using the 1-diphenyl-2-picrylhydrazyl radical scavenging assay, as described previously (Zushi and Matsuzoe, 2015).

To measure the anthocyanin content, ~0.1 g of freeze-dried sample was placed in a centrifuge tube containing 3 mL of methanol with 1% HCl (v/v) at 4°C for 24 hours, and then centrifuged at 15,000×g for 10 minutes at 25°C. The anthocyanin content was expressed as pelargonidin 3-glucoside at 520 nm (Ferreira et al., 2007).

### Statistical analysis and correlation network analysis

All data were presented as the mean±SE, and significant differences between means within each research farm and research period were determined using the Tukey-Kramer test (P < 0.05). The statistical analysis was performed using JMP Version 14 (SAS Institute, Inc., NC, USA).

To visualize the interactions among plant growth, photosynthetic performance, agronomic quality, and antioxidant compound content, a correlation network analysis was performed as described previously (Zushi and Matsuzoe, 2011). Briefly, pairwise correlation coefficients and P values were calculated using mean values of each trait, and a correlation network was constructed using the Pajek 5.00 software (http://pajek.imfm.si/doku.php). The correlation network was defined as a set of nodes (growth parameters, photosynthetic performance-related parameters, agronomic quality, and antioxidant compounds) and edges (correlation). Two nodes were connected by a link if the correlation (positive or negative) was significant (P < 0.05). The size of a node indicates the degree centrality.

### RESULTS

**Environmental factors**

The daily mean air temperature and DLI at each farm increased gradually during the research period (Fig. 1). However, the daily mean air temperature at farm A was lower than that at the other farms during March, and the DLI at farm C was lower than that at the other farms from March to April.

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**Table 1** Selected JIP-test parameters calculated based on the OJIP transients.

| JIP-test parameters | Description |
|---------------------|-------------|
| Area                | Total complimentary area between the fluorescence induction curve and F₀ reflecting the size of the plastoquinone pool |
| M₁                  | Approximated initial slope of the fluorescence transient |
| F₀                  | Maximum quantum yield of primary photochemistry (= Fₐ/Fᵣ) |
| Ψₑ                  | Probability that a trapped exciton moves an electron into the electron transport chain beyond Q₂ |
| Ψₑ/Q₂              | Quantum yield of electron transport |
| Fₐ/Fᵣ              | Potential photochemical efficiency of PSII |
| PI                  | Performance index on absorption basis for energy bifurcations from the absorption events to the reduction of the intersystem electron transport chain |
| ABS/RC             | Specific absorption flux per RC |
| TRₑ/RC             | Trapped energy flux per RC |
| ETₑ/RC             | Electron flux per RC |
| DLₑ/RC             | Energy dissipation flux per RC |
| TRₑ/F₀ or CS₀ or CSₑ | Trapped energy flux per cross-section at F₀ or Fₑ |
| ETₑ/C₀ or CS₀ or CSₑ | Electron flux per cross-section at F₀ or Fₑ |
| DLₑ/C₀ or CS₀ or CSₑ | Energy dissipation flux per cross-section at F₀ or Fₑ |
| RC/C₀ or CS₀ | Density of active RCs (Qₑ reducing RCs) per cross-section at point F₀ or Fₑ |

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**NETWORK ANALYSIS IN STRAWBERRY**
Seasonal and inter-grower variations in plant growth and leaf photosynthetic performance at the three farms

Among the plant growth parameters measured in this study, the plant height averaged over the three research farms increased during the research period (Fig. 2). The leaf color, indicated by the SPAD value, was high on March 1, 2019. Other parameters were maintained at a relatively constant level. However, among the three research farms, farm B showed the lowest values of plant height, leaf length, leaf width, and LAI. The leaf thickness was the highest at farm B and the lowest at farm C during the research period.

Among the photosynthetic performance-related parameters, the values of $F_{\text{Po}}$, area, and $Y(\text{II})$ averaged over the three research farms were low on March 29, whereas the average $F_{\text{Do}}$ was high on March 29 (Fig. 2). $M_{\text{O}}$ increased gradually until March 29 and then was maintained at a constant level. By contrast, $P_{\text{I}}$, $Y_{0}$, and $F_{\text{Eo}}$ decreased until March 29 and then increased, reaching the starting value. The $Y(\text{II})$ differed among the research farms, whereas other parameters showed little differences among the research farms. In addition, other photosynthetic performance-related parameters either decreased or were maintained at a constant level until March 29 (Figs. S1, S2).

Seasonal and inter-grower variations in agronomic quality and antioxidant content at the three farms

Among the agronomic qualities measured in this study, the mean fruit weight value across the three research farms remained constant during the research period (Fig. 3). The DM%, TSS, and acidity decreased during the research period. The lightness of fruit color was low on March 29. No differences were detected in almost all the parameters among the three research farms.

The mean values of ASA, total ASA, and anthocyanin content across the three farms decreased during the research period (Fig. 3). By contrast, the antioxidant activity and total polyphenol content were high on March 29 and then decreased gradually to the initial value on March 1. The DHA content remained relatively constant throughout the research period. No differences were detected in almost all the parameters among growers as well as agronomic qualities at each farm.

Correlation network analysis of plant growth, leaf photosynthetic performance, agronomic quality, and fruit antioxidant compounds

A significant correlation was detected among all 325 pairs of measured traits ($P < 0.05$). The correlation network included 48 nodes interlinked by 325 edges (Fig. 4). The degree of nodes varied from 2 to 23, and the topological properties were different among nodes (Fig. 4). In antioxidant compounds, total polyphenol, total ASA and ASA contents, and antioxidant activity were highly connected with other nodes, and the degrees of these nodes were greater than 10 (Table 2).

Additionally, leaf thickness, plant height, and leaf color were connected with ASA and total ASA contents, but not with the DHA content, total polyphenol content, and antioxidant activity (Fig. 4, Table 2). Anthocyanin was connected with only leaf color. Several photosynthetic performance parameters ($\Phi_{\text{tr}}, \Psi_{\text{w}}, \Phi_{\text{psii}}, P_{\text{i}}, ET_{\text{r}}/RC, F_{\text{v}}/F_{\text{m}},$ and area) showed a negative correlation with the total polyphenol content and antioxidant activity; however, ASA and total ASA were connected with only two parameters.
NETWORK ANALYSIS IN STRAWBERRY

Fig. 3  Seasonal and inter-grower variations in agronomic quality and antioxidant compound content of strawberry fruit grown at the three research farms. Data represent the mean ± SE (n = 6-10) in each farm. The antioxidant compound content was calculated on a fresh weight (FW) basis. Mean values at each farm and across all farms are shown. Different lowercase letters indicate significant differences (P < 0.05; Tukey-Kramer test).

Fig. 4  Correlation network analysis of plant growth parameters, leaf photosynthetic performance-related parameters, agronomic qualities, and antioxidant compounds of strawberry fruit grown at the three research farms. Only significant correlations (P < 0.05) are drawn. Yellow, light blue, green, and red nodes denote plant growth parameters, photosynthetic performance-related parameters, agronomic qualities, and antioxidant compounds, respectively. Correlations are indicated with solid lines (positive correlations) or dotted lines (negative correlations). The size of the vertices indicates the degree centrality.
Almost all JIP parameters were low on March 29; however, 
the temporal decline in JIP parameters, such as \( \Phi_{\text{PSII}} \), was highly connected with total polyphenol, ASA and total 
ASA contents, and antioxidant activity. The agronomic 
qualities including DM% and TSS were connected with 
anthocyanin, and ASA and total ASA contents, but not 
with the total polyphenol content and antioxidant activity 
(Fig. 4, Table 2).

**DISCUSSION**

**Seasonal and inter-grower variations in plant growth, photosynthetic performance, agronomic quality, and antioxidant compound**

In several studies, environmental conditions such as 
light and temperature have been shown to have a signifi-
cant impact on the growth and development of strawberry 
plants (Kadir et al., 2006; Choi et al., 2016; Xu et al., 
2020). Consistently, in our study, as the daily mean air tem-
perature and DLI differed among the three research farms 
and fluctuated during the research period (Fig. 1), the 
growth parameters and photosynthetic performance 
showed seasonal and inter-grower variations. However, 
except these variations, our results indicate that agronomic 
qualities and antioxidant compounds remained stable 
between growers, but fluctuated greatly during the research 
period.

The JIP parameters derived by OJIP transients are 
suitable for photosynthetic performance as a stress indica-
tor (Stirbet et al., 2018) and monitoring physiological 
changes in the strawberry plant (Xu et al., 2020). Our 
results indicated that photosynthetic performance param-
eters, such as several JIP parameters and Y(II), could be 
used to monitor seasonal and inter-grower variations. 
Almost all JIP parameters were low on March 29; how-
ever, \( \Phi_{\text{PSII}} \) was high on this date (Fig. 2). In a previous 
report, PSII inhibition, as indicated by \( F_{v}/F_{m} \) (and by \( \Phi_{\text{PSII}} \) 
in our study), was the lowest when the ambient light inten-
sity in the greenhouse was the brightest, suggesting a pho-
toinhibition state under high light intensity (Choi et al., 
2016). In the current study, the daily mean temperature and 
DLI increased until March 29 and then were maintained at 
a relatively high value compared with the values observed 
from February to March (Fig. 1). Therefore, we suggest 
that the temporal decline in JIP parameters, such as \( \Phi_{\text{PSII}} \), 
area, and Y(II), and the high level of dissipation of 
absorbed photons (as indicated by \( \Phi_{\text{PSII}} \)) occurred owing to 
the photo-inhibition of PSII in leaves because of high tem-
perature and DLI.

In strawberry fruits, plant growth and light conditions 
are important factors affecting the ASA and polyphenol 
contents (Atkinson et al., 2005; Palmieri et al., 2017; 
Fenech et al., 2019). Previously, the content of antioxidant 
compounds in strawberry fruits decreased under high tem-
perature and irradiation conditions (March to April in 
Spain) (Cervantes et al., 2019). In addition, the harvest 
time significantly affected the content of antioxidant com-
 pounds in strawberry fruits (Kawanobu et al., 2010; Ariza 
and Neocleous and Nikolaou, 2019). In another study, the accu-
mulation of anthocyanins was promoted by exogenous 
sugar treatment because of the activation of the anthocya-
nin biosynthesis pathway (Li et al., 2019). Thus, the sea-
onal variation in our study probably resulted from low 
synthesis activity due to the reduction in the carbohy-
drate pool, as indicated by lower TSS and DM%, because 
of environmental changes during the research period.

**Correlation network analysis of antioxidant com-
 pounds in strawberry**

Correlation network analysis provided useful informa-
tion on metabolite–metabolite interactions in several horti-
cultural crops (Fait et al., 2008; Mounet et al., 2009; DiLeo 

| Table 2 List of the number of degrees and connected nodes with antioxidant compound in the correlation network. |
|---|---|---|---|---|---|
| Node| Number of degree| \( \Phi_{\text{PSII}} \)| \( \Psi_{\text{P}} \)| \( \Phi_{\text{PSII}} \)| ET0/RC |
| Polyphenol| 12| DL/RC| ET0/CSM| TR/CSI| RC/CSA| Area |
| ASA| 11| Plant height| Leaf thickness| Leaf color| \( \Psi_{\text{P}} \)| M |
| Total ASA| 11| Plant height| Leaf thickness| Leaf color| \( \Psi_{\text{P}} \)| M |
| Antioxidant activity| 10| Plant height| Leaf thickness| Leaf color| \( \Psi_{\text{P}} \)| M |
| Anthocyanin| 5| Leaf color| TSS| DM%| ASA| Total ASA |
| DHA| 2| Lightness| Total ASA| |

*The underlined nodes showed negative correlations.*

including \( M_{o} \) and \( \Psi_{\text{P}} \) (Fig. 4, Table 2). Furthermore, \( \Psi_{\text{P}} \) 
was highly connected with total polyphenol, ASA and total 
ASA contents, and antioxidant activity. The agronomic 
qualities including DM% and TSS were connected with 
anthocyanin, and ASA and total ASA contents, but not 
with the total polyphenol content and antioxidant activity 
(Fig. 4, Table 2).
growth parameters, leaf thickness acted as a key factor, as described below.

In the correlation network analysis, the most elementary characteristics of a node are its degree, which indicates the number of links to other nodes, and connectivity (Steuer and López, 2008). Our results indicated that the degree and connectivity differed clearly for each antioxidant compound (Fig. 4, Table 2). For example, the total polyphenol content and antioxidant activity were connected negatively with many leaf photosynthetic performance parameters, but were not connected with any plant growth parameters. By contrast, ASA and total ASA were connected with only two leaf photosynthetic performance parameters, but with several plant growth parameters. These results suggest that interactions of antioxidant compounds with plant growth and photosynthetic performance parameters differed for each compound. In general, the ASA content could be linked to the level of sugars as a substrate for ASA biosynthesis (Wheeler et al., 1998; Fenech et al., 2019), but polyphenol content not linked because of generally biosynthesized via the shikimate pathway (Tomás-Barberán and Espín, 2001). Our results showed that sugar (as indicated by TSS) was correlated positively with ASA and total ASA, but not with polyphenol (Fig. 4).

Therefore, the different interaction of each antioxidant compound may be due to variations in their biosynthesis pathway and/or their response to sugar.

Interestingly, although anthocyanins are a group of polyphenols, the degree and connectivity of anthocyanin and total polyphenol differed distinctly. For example, although anthocyanin was connected positively with TSS, the total polyphenol was not (Fig. 4). In strawberry fruit development, changes in sugar content coordinate with anthocyanin accumulation, but not with total polyphenol (Ferreya et al., 2007). Therefore, our results may be caused by the coordinated changes between sugar (as indicated by TSS) and anthocyanin. In contrast, in strawberry fruit, anthocyanins are the major class of polyphenol compounds, but other phenolic compounds, such as ellagic acid, are also present (Giampieri et al., 2012). Thus, in our study, the different network traits of total polyphenols and anthocyanins may be affected by the seasonal and inter-grower variations in polyphenol compounds other than anthocyanin; for example, while anthocyanin content decreased during the research period, total polyphenol content was high on March 29 because other phenolic compounds may have accumulated during the research period (Fig. 3).

Furthermore, a few plant growth and photosynthetic performance parameters contributed to the key factor in the link of each antioxidant compound. Among the plant growth parameters, leaf thickness acted as a key factor, as it was highly negatively connected with several JIP parameters and positively connected with TSS, DM%, ASA, and total ASA (Fig. 4, Table 2). Thicker leaves allow a greater concentration of the photosynthetic apparatus per unit leaf area, and variations in leaf thickness can have a major influence on crop growth and productivity (White and Montes-R, 2005). Therefore, we hypothesized a positive correlation between leaf thickness and photosynthetic performance. However, our findings were inconsistent with the hypothesis, indicating that thicker leaves induce the low photosynthetic performance in strawberry. By contrast, as ASA and total ASA content were positively correlated with leaf thickness, practical management with thicker leaves may be necessary to increase these components.

In addition to leaf thickness, our results indicated that $\Psi$ also acts as a key factor to increase the fruit antioxidant compounds because $\Psi$ was positively or negatively connected with the total polyphenol content, antioxidant activity, ASA, and total ASA in the correlation network (Fig. 4, Table 2). The $\Psi$ indicates the probability that a trapped excitation moves an electron into the electron transport chain beyond $Q_a$ (Strasser et al., 2004). Therefore, we suggest that the fruit antioxidant compound is correlated with the performance of electron transport chain in the leaf PSII. Thus, we propose that photosynthetic performance parameters such as $\Psi$ should be suppressed to increase the polyphenol content and antioxidant activity, but promoted to increase the ASA content.

CONCLUSIONS

Our results revealed seasonal and inter-grower variations in plant growth, photosynthetic performance, agronomic quality, and antioxidant compounds of strawberry. Additionally, the interaction of traits was visualized using correlation network analysis, and the identified interactions differed among all antioxidant compounds. Thus, we conclude that the significance of connectivity and the key factors identified, such as the leaf thickness and $\Psi$, using the correlation network analysis provided useful information to enhance fruit antioxidant compounds.

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