JEE
ISSN: 2288-1220
https://doi.org/10.5141/jee.23.040
Journal of Ecology and Environment (2023) 47:09

RESEARCH

Ecophysiological characteristics of *Rosa rugosa* under different environmental factors

Young-Been Kim[1,4†], Sung-Hwan Yim[2,3†], Young-Seok Sim[2] and Yeon-Sik Choo[1,2,3*]

[1]Department of Integrative Natural Sciences for the East Sea Rim, Kyungpook National University, Daegu 41566, Republic of Korea
[2]Department of Biology, Kyungpook National University, Daegu 41566, Republic of Korea
[3]Research Institute for Dok-do Ulleung-do Island, Kyungpook National University, Daegu 41566, Republic of Korea
[4]Seed Vault Center, Baekdudaegan National Arboretum, Bonghwa 36209, Republic of Korea

ARTICLE INFO
Received July 3, 2023
Revised July 27, 2023
Accepted July 29, 2023
Published on August 25, 2023

***Corresponding author**
Yeon-Sik Choo
E-mail yschoo@knu.ac.kr

†These authors contributed equally to this work.

Background: Ecophysiological characteristics of *Rosa rugosa* were analyzed under different environmental factors from May to October 2022. Photosynthesis, chlorophyll fluorescence, chlorophyll content, leaf water content (LWC), osmolality, carbohydrate content, and total ion content were measured to compare the physiological characteristics of *R. rugosa* at two study sites (i.e., in large pots and in the Goraebul coastal sand dune area).
Results: When *R. rugosa* was exposed to high temperatures, photosynthetic parameters including net photosynthetic rate (P_N) and stomatal conductance (g_s) in both experiment areas declined. In addition, severe photoinhibition occurs when *R. rugosa* is continuously exposed to high photosynthetically active radiation (PAR), and because of this, relatively low Y(II) (i.e., the quantum yield of photochemical energy conversion in photosystem II [PSII]) and high Y(NO) (i.e., the quantum yield of non-regulated, non-photochemical energy loss in PSII) in the *R. rugosa* of the pot were observed. As the high Y(NPQ) (i.e., the quantum yield of regulated non-photochemical energy loss in PSII) of *R. rugosa* in the coastal sand dune, they dissipated the excessed photon energy through the non-photochemical quenching (NPQ) mechanism when they were exposed to relatively low PAR and low temperature. *Rosa rugosa* in the coastal sand dune has higher chlorophyll *a* and carotenoid content. The high chlorophyll *a* + *b* and low chlorophyll *a*/*b* ratios seemed to optimize light absorption in response to low PAR. High carotenoid content played an important role in NPQ. As a part of the osmotic regulation in response to low LWCs, *R. rugosa* exposed to high temperatures and continuously high PAR used soluble carbohydrates and ions to maintain high osmolality.
Conclusions: We found that F_v/F_m was lower in the potted plants than in the coastal sand dune plants, indicating the vulnerability of *R. rugosa* to high temperatures and PAR levels. We expect that the suitable habitat range for *R. rugosa* will shrink and move to north under climate change conditions.

Keywords: climate change, coastal sand dune, environmental change, photosynthesis, *Rosa rugosa*

Introduction

Plants are exposed to various environmental factors throughout their life span due to their sedentary life. Environmental factors are divided into several categories, including pathogen infection, biotic stress (e.g., herbivory), and abiotic stress (e.g., drought, high temperature, nutrient deficiency, and exposure to salt or heavy metals; Suzuki et al. 2014). Of these factors, abiotic stress is a major threat to plants that limits their growth and distribution and should be overcome (Rajaniemi and Allison 2009; Rajkumar et al 2017; Thakur and Nayyar 2013). The intensity and frequency of abiotic stress varies with habitat. In coastal sand dune habitats, abiotic stresses include temperature, light intensity and duration, wind, wind-driven sand movement, and salinity, all of which occur at a higher intensity and frequency than in other habitats (Frosini et al. 2012). These stresses induce ionic imbalances in plant tissues and lead to decreased photosynthetic efficiency due to reduced enzyme activities (e.g., rubisco) and increased leaf respiration rates (Allakhverdiev et al. 2008; Chang et al. 2020; Medina and Francisco 1997; Sudhir and Murthy 2004). Furthermore, stress-generated reactive oxygen species (ROS) induce negative effects, such as oxidative damage in plant tissues (Chang et al. 2020; Singh and Thakur 2018).

Various abiotic stresses combine in outdoor environments to affect plants (Billings 1952; Suzuki et al. 2014). The effects of such combined abiotic stresses on plants are limited to the plant's response to a single stressor, since plants utilize specific mechanisms in response to abiotic stresses that are dependent on specific stress combinations in addition to their unique response mechanisms for single stresses (Suzuki et al. 2014). The metabolic and signaling responses of plants to multiple stresses are highly diverse and include photosynthesis, osmolytes synthesis, and hormonal signaling mechanisms (Iyer et al. 2013; Prasch and Sonnewald 2013; Suzuki et al. 2014). However, these mechanisms remain poorly understood.

Among the components of a plant, the leaf is the primary organ where photosynthesis, the key process that converts light energy from photons into chemical energy usable by the plant, takes place. Leaves are also recognized as a representative organ that can be used to assess physiological traits, including plant growth and adaptation, can be assessed (Ashraf and Harris 2013; Givnish 1987; Hohmann-Marriott and Blankenship 2011). Photosynthesis occurs through a complex interaction of structures (e.g., photosystem II [PSII], PSI, and cytochrome b6f complex) and enzymes (e.g., rubisco and ATP synthase) inside chloroplast thylakoids (Allen et al. 2011; Ashraf and Harris 2013; Jensen and Leister 2014). In particular, PSII and the light harvest complex (LHC) catalyze water oxidation and harvest and convert photons to electronic energy to initiate photosynthesis (Albanese et al. 2020; Kawakami and Shen 2018). Since PSII is affected by a wide range of environmental factors, including moisture, temperature, and day length, there has been great interest in the relationship between photosynthetic capacity and PSII activity to obtain a better understanding of how plants respond to their environment (Adams and Langton 2005; Ashraf and Harris 2013; Villar et al. 2006). Abiotic stresses often cause osmotic pressure changes within plants, to which lead plants to respond by utilizing osmolytes such as soluble carbohydrates and ions (Vicente et al. 2016). Soluble carbohydrates are products of photosynthesis and are known to be primarily involved in osmotic pressure regulation (Gil et al. 2013; Singh and Thakur 2018). Thus, the accumulation of osmolytes can be assessed to understand how plants respond to abiotic stresses (Chapin et al. 1990).

The inability of plants to respond appropriately to abiotic stresses results in photoinhibition, which limits photosynthesis and the activity of the plant's photosynthetic machinery. Photoinhibition causes photon energy to be captured rather than absorbed, leaving the remaining energy as a potential threat to the PS, especially PSII (Takahashi and Badger 2011). Plants have developed photoprotective mechanisms to overcome photoinhibition, prevent the inactivation of PSII, restore an already closed PSII to an active state (Takahashi and Badger 2011). Various morphological and physiological characteristics of plants are involved in photoprotection, including non-photochemical quenching (NPQ) mechanisms that utilize carotenoids, such as xanthophylls, and D1 protein reconstitution (Kitao et al. 2000).

Rosa rugosa is a representative native, coastal dune, woody plant that grows in the outermost hinterland of coastal dunes and is protected as a Phytosystematic Specific Plant Class II (National Institute of Ecology 2018). It is a boreal plant adapted to relatively low temperatures on the Korean Peninsula and is known to have a lower growth limit at 37° 68′N in the central part of the peninsula, although this limit is gradually moving northward due to climate changes (Han et al. 2013). Various studies have focused on this species as its conservation value increased,but these studies have focused primarily on pharmacology (Choi et al. 1997; Kim et al. 2001; Young 1990; Yu et al. 2014) and horticulture (Joung et al. 2010; Lee et al. 2011). Only a few studies have been conducted on its physiological and ecological characteristics of the native Korean plant.

This study aimed to investigate the physiological and ecological characteristics of *R. rugosa* in response to environmental changes by analyzing its photochemical characteristics under seasonal and diurnal variations. In addition, its chlorophyll contents and leaf composition were analyzed under seasonal variations. This study provides basic data for the establishment of coastal dune conservation strategies to mitigate future climate change and coastal dune disturbance in Korea and East Asia.

Materials and Methods

Study site and plant materials

Rosa rugosa was planted at two sites: (1) in a rear pine windbreak forest (36°35′03.5″N, 129°24′41.4″E) of the Goraebul coastal sand dune (36°35′03.5″N, 129°24′41.4″E), which is a representative coastal sand dune located on the east coast of Gyeongsangbuk-do, Republic of Korea; and (2) in large pots (R = 1.0 m, H = 0.9 m) in the biology building of Kyungpook National University (35°53′12.0″N 128°36′ 20.8″E), where they were allowed to settle for approximately 1 year. The soil used in the large pots was sandy soil from the Goraebul coastal sand dunes, and the pots were exposed to direct sunlight by removing the shielding structure. The soil moisture content was maintained above 5% by periodic watering in the large pots, and a modified Hoagland's medium (0.5 mM NH_4NO_3, 0.5 mM $MgSO_4 \cdot 7H_2O$, 0.5 mM KH_2PO_4, 0.5 mM $CaCl_2 \cdot 2H_2O$, 0.5 mM K_2SO_4, 19 mM Fe-EDTA, and trace elements) was used to treat 2 L per pot each every week.

Photochemical characteristics of seasonal changes

Environmental factors and meteorological data

The environmental factors measured were leaf temperature, vapor pressure deficit based on leaf (VPDL) temperature (kPa), soil moisture content (%), and photosynthetically active radiation (PAR) (μmol $m^{-2}s^{-1}$). Leaf temperature, VPDL and PAR were measured using a portable photosynthesis meter (Li-Cor 6400; LI-COR Biosciences, Lincoln, NE, USA). Soil moisture content was measured using a soil moisture meter (Theta Probe ML3; Delta-T Devices, Cambridge, UK).

Meteorological data for the period May–October 2022 at the Kyungpook National University, where the research tree species is located, and at Goraebul coastal sand dunes, Yeongdeok-gun, Gyeongsangbuk-do, Republic of Korea, are presented in terms of daily average temperature (°C), daily maximum temperature (°C), and daily minimum temperature (°C), relative humidity (%), daily precipitation (mm), maximum instantaneous wind speed (m/s), maximum wind speed (m/s), and average wind speed (m/s). These data were collected from the Korea Meteorological Administration Longitudinal Observation Data.

Photosynthetic metrics

A portable photosynthesis meter (Li-Cor 6400) was used to measure photosynthetic metrics. For accurate measurements, a reference CO_2 concentration of 400 μmol/mol and a flow rate of 500 mmol/s were maintained using a 6400-01 CO_2 mixer. In brief, fully grown leaves were combined in a 6 cm^2 leaf chamber to ensure stabilization of ΔCO_2 and CO_2 reference, and then net photosynthesis rate (P_N), stomatal conductance (g_s), transpiration rate (E), and intercellular CO_2 concentration (C_i) were measured. Instantaneous water use efficiency (WUE) was calculated as the ratio of P_N and E (P_N/E). Instantaneous carboxylation efficiency (CE) was calculated as the ratio of P_N and C_i (P_N/Ci).

Chlorophyll fluorescence

Chlorophyll fluorescence was measured using a portable chlorophyll fluorometer (PAM-2500; Heinz Walz GmbH, Pfullingen, Germany) to determine Y(II) (i.e., the quantum yield of photochemical energy conversion in PSII), Y(NPQ) (i.e., the quantum yield of regulated non-photochemical energy loss in PSII), and Y(NO) (i.e., the quantum yield of non-regulated, non-photochemical energy loss in PSII) in fully grown leaves exposed to light. After a dark adaptation period of more than 25 minutes, the minimum fluorescence yield of the dark-adapted state (F_o) and the maximum fluorescence yield of the dark-adapted state (F_m) were measured, and the F_v/F_m ratio (i.e., the maximum photochemical quantum yield of PSII) was calculated using the formula $(F_m - F_o) / F_m$.

Physiological characteristics of *Rosa rugosa* under diurnal variation

Environmental factors and meteorological data

Leaf temperature, VPDL, and PAR were measured using a portable photosynthesis measuring device (Li-Cor 6400) in large pots at Kyungpook National University in June and August 2022, and in the corresponding dune at Goraebul coastal dunes in August 2022. Soil moisture content was measured using a soil moisture meter (Theta Probe ML3).

Photosynthesis indicators

To measure the diurnal variations in photosynthetic indicators, P_N, g_s, E, chloroplast C_i, WUE, and CE were measured using a portable photosynthesis measurement device at 3-hour intervals (i.e., five times a day from 06:00–18:00 hour) in June and August 2022.

Chlorophyll fluorescence

To measure the diurnal variation in chlorophyll fluorescence, F_v/F_m, Y(II), Y(NPQ), Y(NO), and F_o, and F_m were measured using a portable chlorophyll fluorescence measurement device at 3-hour intervals (i.e., five times a day from 06:00–18:00 hour) in June and August 2022.

Analyzing leaf composition over the season

Chlorophyll content

A certain area of the leaves of the collected target plant was separated and extracted by immersion in 5 mL of dimethyl sulfoxide for 48 hours at 30°C. The extract was subjected to absorbance measurements using a UV/VIS Spectrophotometer (OPTIZEN 2120; Mecasys Co. Ltd., Daejeon, Korea) at wavelengths of 665 nm, 649 nm, and 480 nm. The absorbance measurements were calculated as follows (Wellburn 1994):

$$C_a = 12.47\,A_{665} - 3.62\,A_{649}$$
$$C_b = 25.06\,A_{649} - 6.5\,A_{665}$$
$$C_{a+b} = C_a + C_b$$
$$C_{a/b} = C_a / C_b$$
$$\text{Carotenoid} = (1{,}000\,A_{480} - 1.29\,C_a - 53.78\,C_b) / 220$$

Leaf water content, osmolarity, total ion content, and soluble carbohydrate content

The corresponding leaves were collected and fresh weight (FW) of the collected leaves was measured, and then the leaves were dried at 70°C for 72 hours using a desiccator (Forced Convection Oven, JSOF-150; JS Research Inc., Gongju, Korea). Next, their dry weight (DW) was measured, and the leaf water contents (LWCs) was calculated using the following equation.

LWC (%) = [(FW – DW) / FW] × 100

Leaf extracts were prepared by grinding dried plant leaves into a homogeneous powder using a grinder (Polymix Laboratory Dry Mill Drive Unit, Polymix^{TM} PX-MFC 90 D; Kinematica AG, Luzern, Switzerland), and then placing taking a constant weight aliquot and placing it in a 25 mL measuring flask in a 90°C water bath for 1 hour. After allowing to cool at room temperature for sufficient time, the final volume was adjusted to 25 mL and extracted by filtering through a 0.45 μm GF/C filter (Whatman, Maidstone, UK). Osmolality was measured with an osmometer (Micro-Osmometer; Precision System Inc., Natick, MA, USA) using the principle of freezing point enhancement method by taking 50 μL of the extracted sample liquid. Total ion content (TIC) was determined using a conductivity meter (Mettler Check Mate 90; Mettler Toledo, Columbus, OH, USA) by diluting 1 mL of the extracted sample with 4 mL of distilled water, and was calculated as the Na^+ and Cl^- ion equivalents (NaCl equivalent). The soluble carbohydrate content was determined by adding 400 μL of 5% phenol solution and 2 mL of crude H_2SO_4 to a solution of 20 μL of plant extract and 780 μL of distilled water, mixing well after 10 minutes, cooling at room temperature for 30 minutes, and measuring the absorbance at a wavelength of 490 nm using a UV/VIS Spectrophotometer. Glucose (20–800 μL in 1,000 μL) was used as a standard solution and the sugar content was quantified based on this (Pazur 1994).

Statistical analysis

T-test was performed using SPSS 26.0 (IBM Co., Armonk, NY, USA) to determine whether there were a significant differences between the measurements ($p < 0.05$). Measurements were expressed as mean with standard deviations.

Results

Seasonal changes in photochemical indicators

Meteorological and environmental factors during the seasonal change measurement period

To investigate the changes in physiological characteristics of *R. rugosa* due to seasonal changes, the study was conducted from May 2022, when the leaves grew sufficiently and reached a size (6 cm^2 ≤) where photosynthesis could be measured, to October, when the leaves molted. The weather conditions at Kyungpook National University and Goraebul coastal sand dunes, the two study sites selected for this research, were different (Figs. 1 and 2). During the study period, the average daily temperature at both locations increased until August and then decreased, but the lowest daily temperature at Kyungpook National University was recorded in late June and the highest daily temperature was recorded in early August. At Goraebul coastal sand dunes, the minimum temperature was recorded in early August and the maximum temperature was recorded in late June, indicating that leaf temperature was related to the mean temperature at both sites (Figs. 1A, 2A, and 3B). In addition, at Kyungpook National University, where the maximum temperature in June was 37.1°C, the leaf temperature was the highest at 42.0°C. On the other hand, at Goraebul coastal sand dunes, the leaf temperature was 34.8°C when the maximum temperature was 36.6°C, showing a clear difference between the regions. Considering that the measurement time for this study was 12:00–14:00 hour, when photosynthesis is most active and the temperature is the highest of the day, it can be seen that the maximum temperature is closely related to the leaf temperature (Figs. 2A and 3B).

The difference in wind speed between the two areas is related to geographical characteristics, as the coastal dunes of Goraebul, adjacent to the sea, are known to have higher average and instantaneous peak wind speeds and more frequent gusts compared to Kyungpook National University (Figs. 1C and 2C).

Soil moisture content also appears to be influenced by the time of measurement (Fig. 3C), and July and August, which recorded high soil moisture content, were periods of intensive precipitation during the study period, suggesting that the high soil moisture content measurements during these months were due to precipitation (Figs. 1C, 2C, and 3C). There was no significant seasonal difference in soil moisture content between the large pots at Kyungpook National University and the coastal dunes at Goraebull, where moisture was continuously supplied. This is likely due to the mulching effect of the undecomposed pine needles in the windbreak forest at the far end of the coastal dune where the plant grows, which suppresses the evaporation of soil moisture. Therefore, neither site appears to have been affected by severe water stress.

The VPDL, which is known to be influenced by temperature and relative humidity, was highest in June at both sites, but was 29.5% higher at Kyungpook National University than at Goraebul coastal sand dunes (Fig. 3D), indicating that the atmosphere was drier at Kyungpook National University. PAR, a measure of photon density in the wavelength bands available to plants for photosynthesis, was lower at Kyungpook National University than at Goraebul coastal sand dunes for most of the study period, which is likely due to frequent sun flecking by the pine tree crowns (Fig. 3A).

Photosynthetic indicators

Seasonal changes in environmental factors affect the photosynthetic metrics of lichens, and these effects are

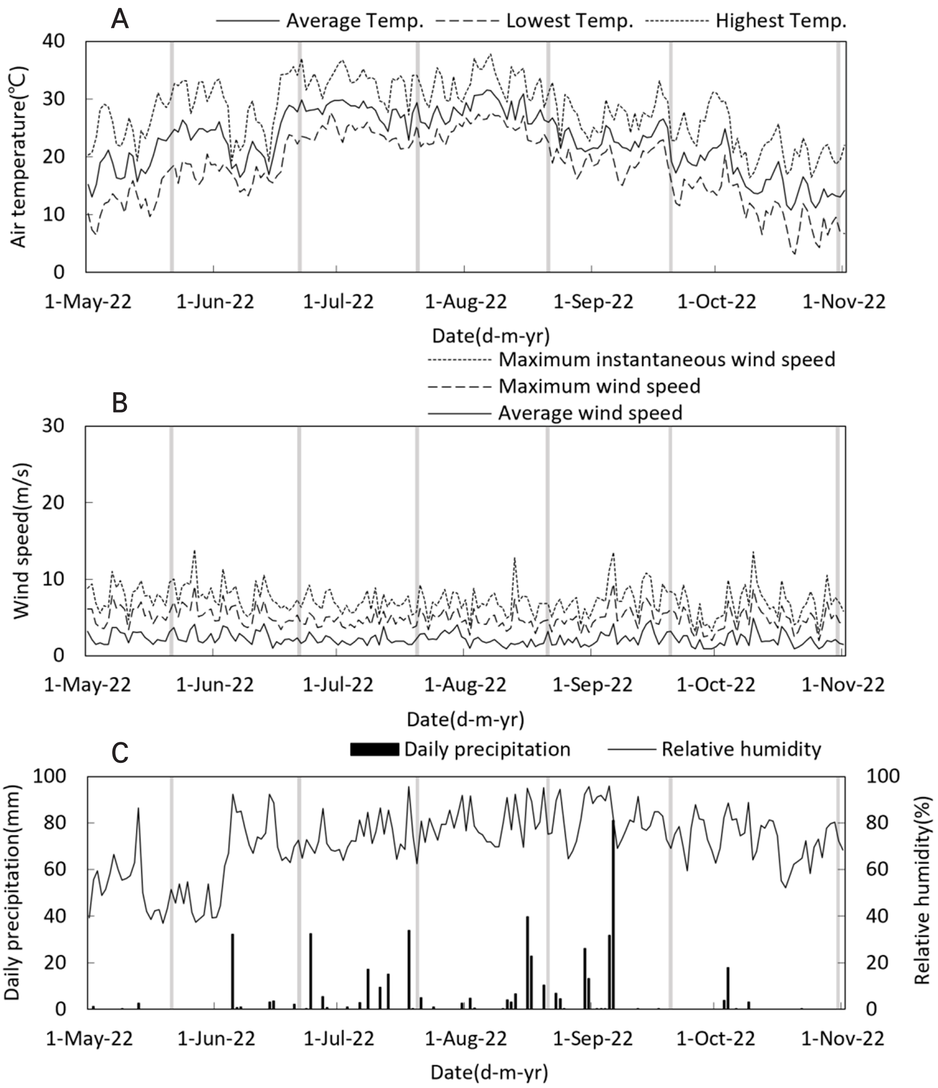

Fig. 1 Seasonal variations in (A) average air temperature (°C), lowest air temperature (°C), highest air temperature (°C), (B) maximum instantaneous wind speed (m/s), maximum wind speed (m/s), average wind speed (m/s), (C) daily precipitation (mm), relative humidity (%) during the study period (May–October 2022) in Daegu where the pot of Kyoungpook National University is located. Light grey box indicate the measured period.

shown in Fig. 4. The net photosynthetic rate (P_N) of *R. rugosa* in large pots showed a 33.9% decrease in June, when leaf temperatures were at their highest, compared to May. On the other hand, the corresponding decrease in P_N in the coastal dunes was 27.2%, indicating a significant decrease in P_N in the large pot (Fig. 4A). In addition, both sites showed a steady increase in P_N until August, when leaf temperature decreased. This suggests that P_N is closely related to leaf temperature. In general, tree species have an optimal temperature range for growth, and when the temperature is lower or higher than the optimal range, photosynthesis is inhibited (Yamori et al. 2014), and the August leaf temperature (ca. 30°C) is considered to be the optimal temperature for the most active photosynthesis.

In addition, photosynthetic indicators such as CE and stomatal conductance (g_s) also show a similar trend to net photosynthetic rate (P_N), decreasing with increasing leaf temperature (Fig. 4B and 4F). However, in the case of transpiration rate (*E*), the correspondence of coastal sand dune shows a similar trend to stomatal conductance (g_s) and does not show a significant change in transpiration rate (*E*), while *R. rugosa* in large pots showed the highest transpiration rate (*E*) in June when the leaf temperature was highest and then decreased (Fig. 4C). When foliar temperature increases, plants tend to either decrease foliar temperature by increasing transpiration (*E*) by increasing stomatal conductance (g_s) or maintain LWC by decreasing stomatal conductance (g_s) (Ball et al. 1988; dos Santos et al. 2022; Gates 1964; Wang et al. 2021).

Water use efficiency can determine how much carbon a plant gains through photosynthesis while losing water through transpiration, and is known to be directly linked to physiological processes that regulate the gradient of CO_2 and H_2O at the leaf level (Hatfield and Dold 2019; Stanhill 1986). Large pot *R. rugosa* had the lowest WUE in June and coastal dune *R. rugosa* in July, with a steady increase through October with decreasing leaf temperature (Fig. 4E).

Chlorophyll fluorescence

We investigated the seasonal response of chlorophyll fluorescence, which can identify the activity of photosynthet-

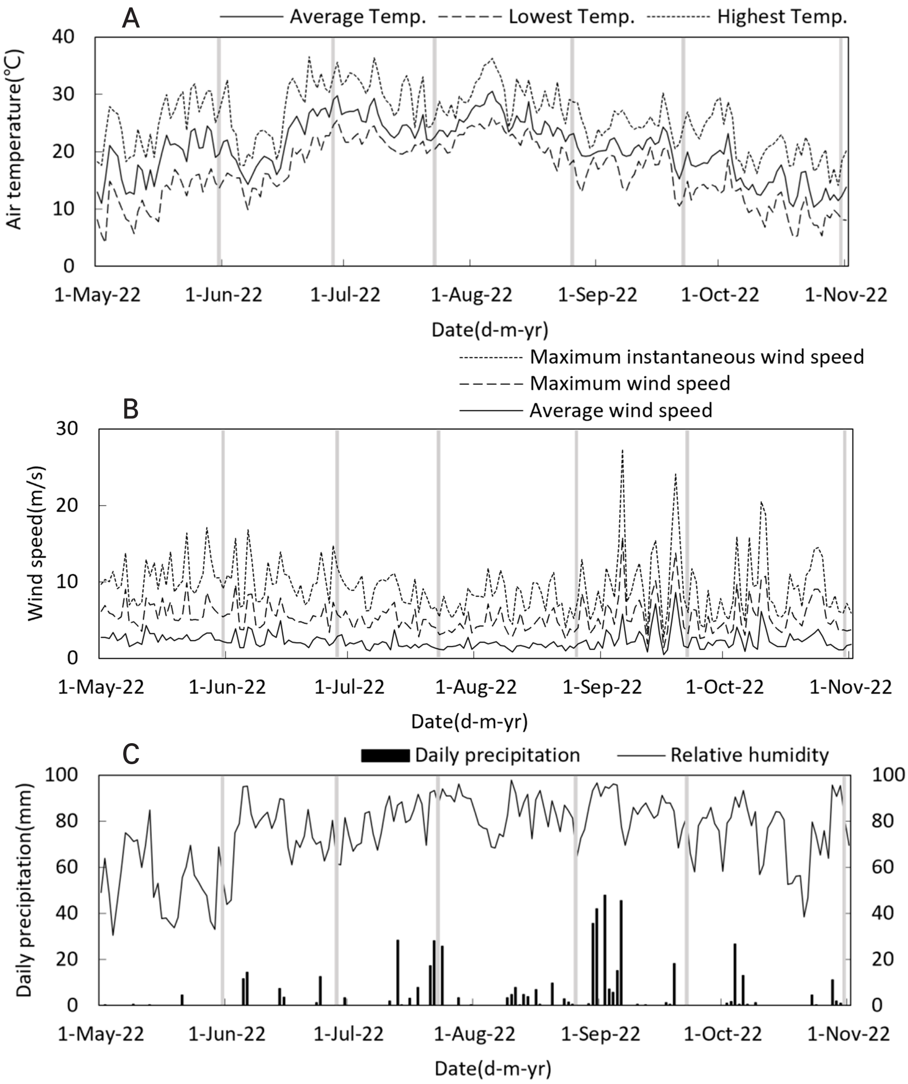

Fig. 2 Seasonal variations in (A) average air temperature (°C), lowest air temperature (°C), highest air temperature (°C), (B) maximum instantaneous wind speed (m/s), maximum wind speed (m/s), average wind speed (m/s), (C) daily precipitation (mm), relative humidity (%) during the study period (May–October 2022) in Yeongdeok-gun where the Goraebul coastal sand dune is located. Light grey box indicate the measured period.

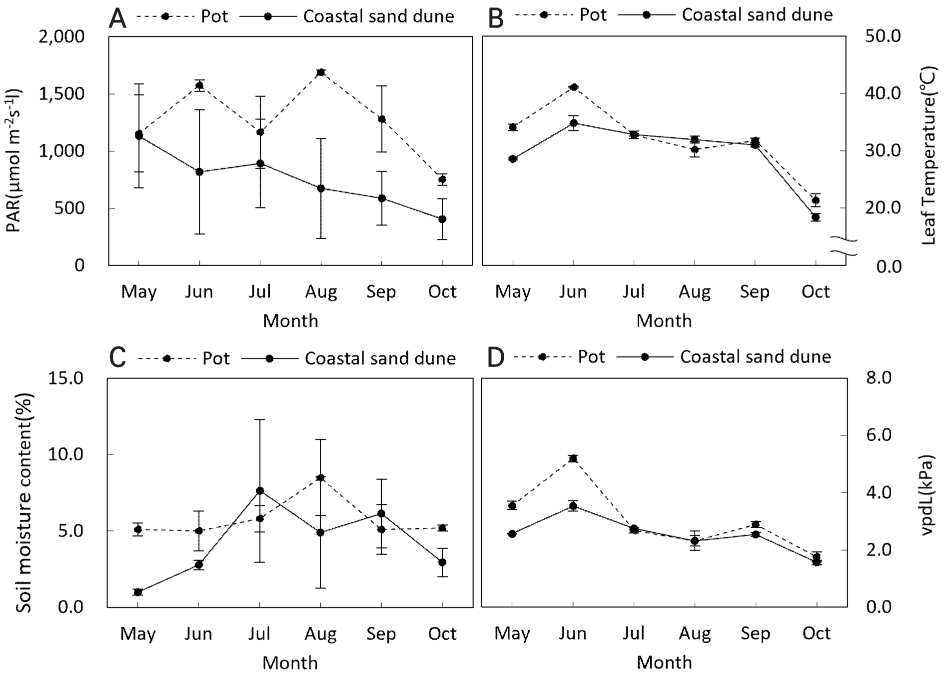

Fig. 3 Seasonal variations in environmental factors in the Goraebul coastal sand dune (solid line) and the pot (dashed line). (A) Photosynthetically active radiation (PAR) (μmol m^{-2}s^{-1}), (B) leaf temperature (°C), (C) soil moisture content (%), (D) vapor pressure deficit based on leaf (VPDL) (kPa).

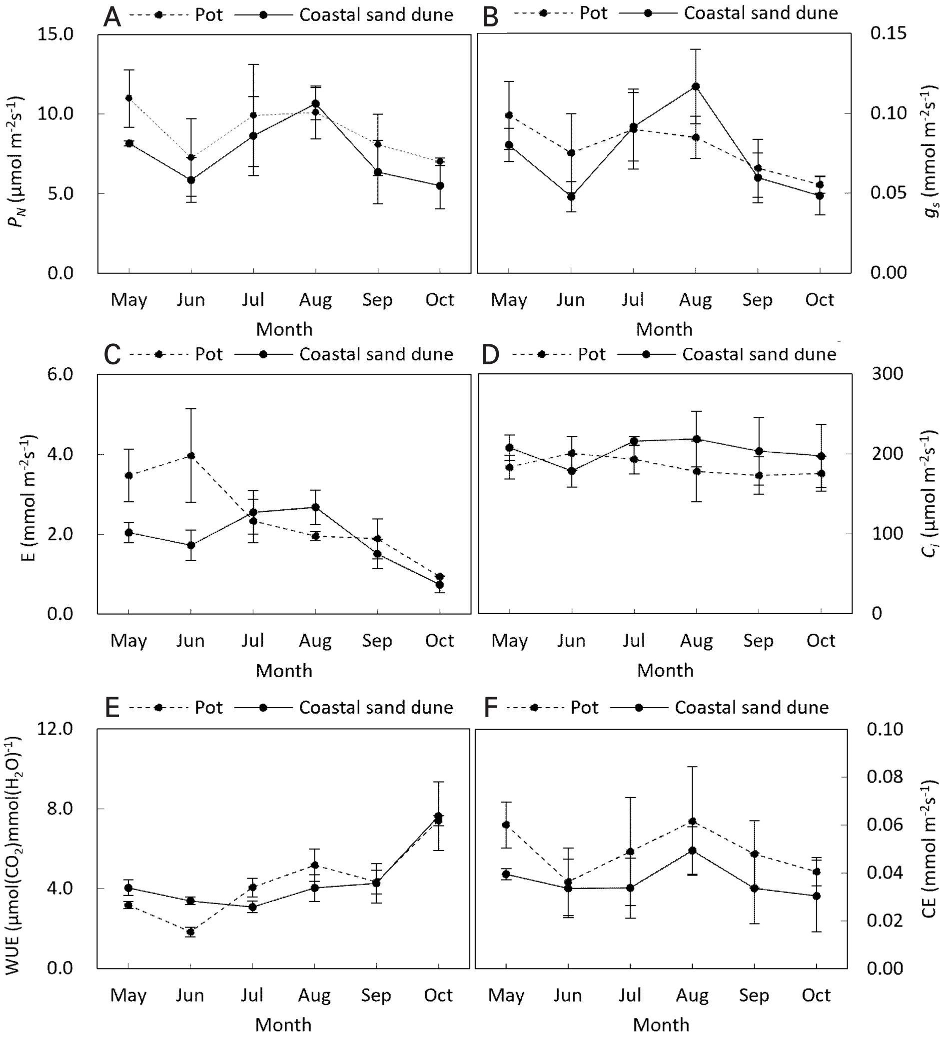

Fig. 4 Seasonal variations in photosynthetic parameters of *Rosa rugosa* in the Goraebul coastal sand dune (solid line) and the pot (dashed line). (A) Net photosynthetic rate (P_N), (B) stomatal conductance (g_s), (C) transpiration rate (E), (D) intercellular CO$_2$ concentration (C_i), (E) instantaneous water use efficiency (WUE), (F) instantaneous carboxylation efficiency (CE).

ic machinery, and found differences in chlorophyll fluorescence indicators among the study areas (Fig. 5). Light is the driving force of PSII, but it interferes with electron transfer, damages reaction centers including protein D1 in PSII, and causes photoinhibition, which inhibits the entire photosynthetic process (Aro et al. 1993a; Aro et al. 1993b). The proportion of Y(II) that processes the energy of photons in PSII was relatively low in most seasons in *R. rugosa* in large pots that were continuously exposed to high PAR compared to coastal dunes (Fig. 5A and 5B). High PAR appears to have caused photoinhibition of *R. rugosa*, which is primarily caused by light but can also be caused by a combination of various environmental factors including temperature (Aro et al. 1993a; Takahashi and Murata 2008). The lowest Y(II) values were common in July, when high leaf temperatures were observed.

In general, when plants are exposed to high PAR, they release excess photon energy in the form of heat through the NPQ mechanism to avoid photodamage, and a relatively small proportion is used for photosynthesis (Chen et al. 2016). *Rosa rugosa* is thought to adequately regulate photoinhibition by high PAR and leaf temperature through the NPQ mechanism. Mean Y(NPQ) over the seasons was higher for *R. rugosa* in coastal dunes than in large pots. This probably indicates that *R. rugosa* in Goraebul coastal dunes effectively regulates light stress, including sun fleck in windbreak forest, through the NPQ mechanism (Fig. 5B). On the other hand, *R. rugosa* in large pots showed relatively low Y(NPQ) and high Y(NO), indicating that under continuous exposure to strong light, the excess energy over photochemical reactions is passively released in the form of heat and fluorescence with PSII largely inactive, rather than through the NPQ mechanism (Fig. 5A).

The F_v/F_m ratio is referred to as the maximum quantum yield and is an important indicator of the physiological state of a plant, which can be used to diagnose whether stress is occurring (Parkhill et al. 2001; Sharma et al. 2015). The F_v/F_m ratio measurements showed that compared to the coastal dunes, the *R. rugosa* in the large pots had lower values in all seasons, indicating that the *R. rugosa* in the large pots exposed to high light intensity and high temperature were under higher stress conditions (Fig. 5C).

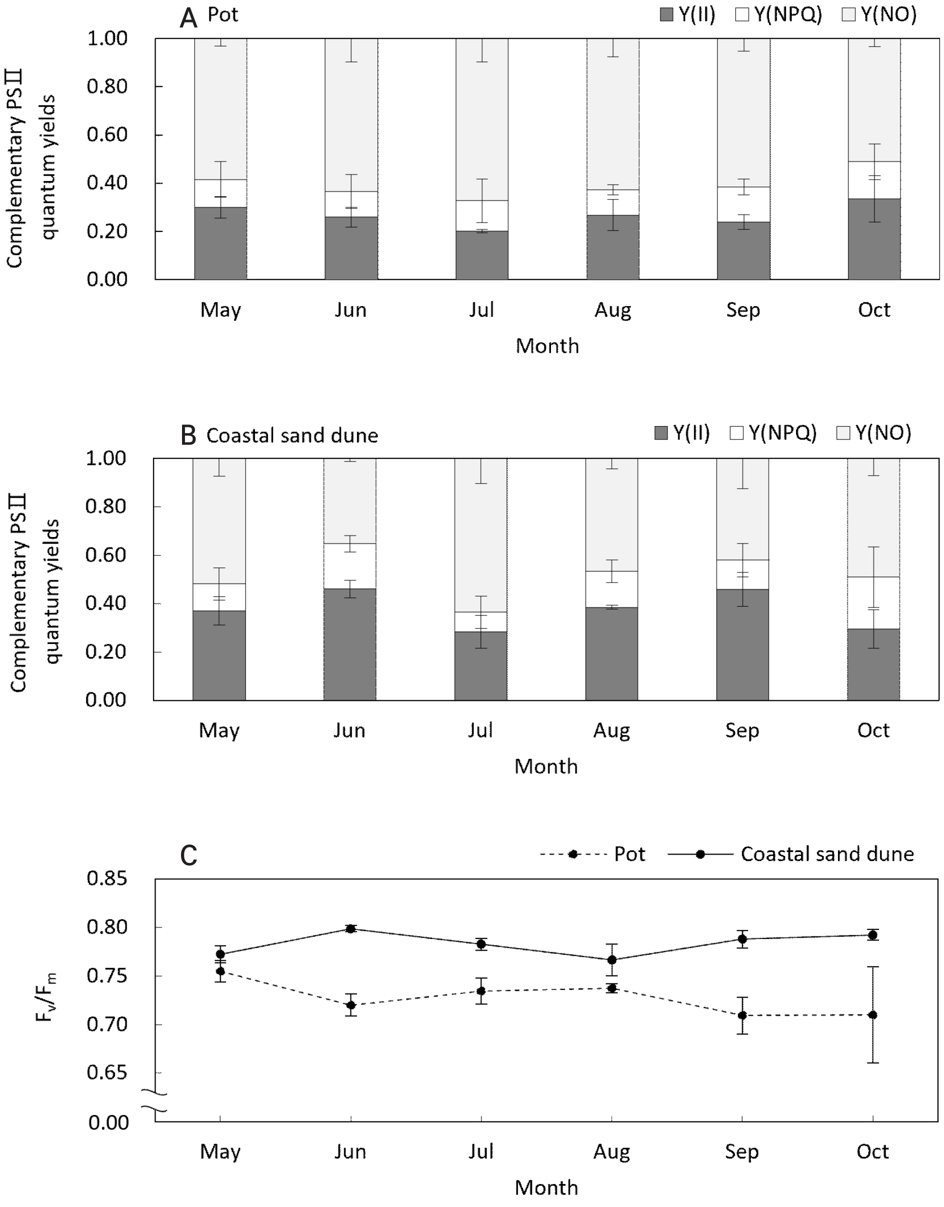

Fig. 5 Seasonal variations in chlorophyll parameters. (A) Y(II), Y(NPQ), and Y(NO) of *Rosa rugosa* in the pot, (B) Y(II), Y(NPQ), and Y(NO) of *R. rugosa* in the Goraebul coastal sand dune, (C) F_v/F_m (maximum quantum yield) of *R. rugosa* in the Goraebul coastal sand dune (solid line) and the pot (dashed line). Y(II): The quantum yield of photochemical energy conversion in PSII; Y(NO): The quantum yield of non-regulated, non-photochemical energy loss in PSII; Y(NPQ): The quantum yield of regulated non-photochemical energy loss in PSII.

Changes in photochemical properties during diurnal variations

Meteorological and environmental factors during diurnal variation

To understand the physiological response of *R. rugosa* to changes in environmental factors within a short period of time, diurnal variation in large pots and Goraebul coastal dune correspondents was measured in June, when the highest leaf temperature was recorded, and in August, when net photosynthetic rate (P_N) recovered in response to decreasing leaf temperature. Leaf temperature was generally higher in June than in August (Fig. 6B), and VPDL followed a similar trend to leaf temperature, indicating that the atmosphere became drier with increasing leaf temperature (Fig. 6C). PAR was highest at 12:00 hour, indicating that the Goraebul coastal dunes had lower light intensity compared to the large pots, and *R. rugosa* in large pots compared to the coastal dunes were affected by strong light from the morning (Fig. 6A).

Photosynthetic properties

The photosynthetic characteristics of the diurnal variation showed different patterns depending on the time of measurement (Fig. 7). The June net photosynthetic rate (P_N) of *R. rugosa* in large pots showed the highest value at 09:00 hour and tended to decrease with increasing leaf temperature. It has been reported that P_N is affected not only by various environmental factors, including temperature and PAR, but also by physiological factors within the plant body, such as leaf age and hormones, and that the younger the leaf age, the higher the P_N tends to be (Bozarth et al. 1982; Weis and Berry 1987). In general, changes in stomatal conductance (g_s) affect the CO_2 concentration (C_i) in mesophyll cells. In June, the stomatal conductance (g_s) peaked at 09:00 hour and decreased thereafter, resulting in

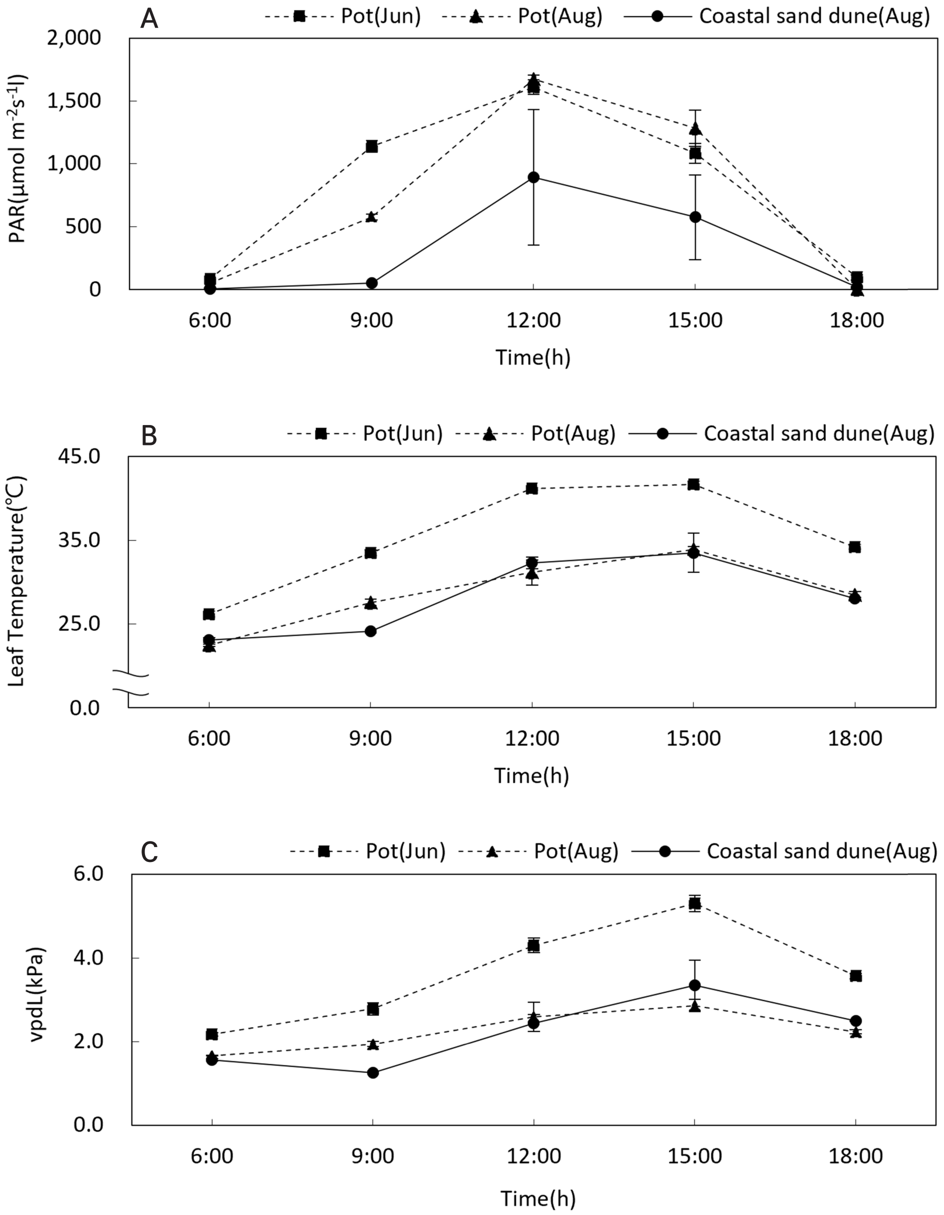

Fig. 6 Diurnal variations in environmental factors of *Rosa rugosa* measured in July in the pot (quadrangle), August in the pot (triangle), and August in the Goraebul coastal sand dune (circle). (A) Photosynthetically active radiation (PAR) (μmol m^{-2}s^{-1}), (B) leaf temperature (°C), (C) vapor pressure deficit based on leaf (VPDL) (kPa).

a steady decrease in CO_2 concentration (C_i) from 06:00 hour to 12:00 hour or 15:00 hour, as stomatal conductance (g_s) restricted gas movement into the leaf, reducing the amount of CO_2 supplied to the leaf compared to the CO_2 used for photosynthesis. The resulting decrease in photosynthetic activity led to an increase in chloroplast CO_2 concentration (C_i) again (Fig. 7D). Unlike the case in June, the net photosynthetic rate (P_N) in August showed the highest value at 12:00 hour and then tended to decrease, which is thought to be due to the lower temperature of the corresponding leaves in August compared to June (Fig. 7A). Comparison of PAR and net photosynthetic rate (P_N) in August showed that the coastal dune *R. rugosa* had a similar P_N to the large pots despite the relatively low PAR, which is likely a result of the highly efficient photosynthesis of the coastal dune *R. rugosa*. Stomatal conductance (g_s) and transpiration rate (E) were lower in August compared to June (Fig. 7B and 7C). In particular, transpiration rate (E) was lower at all time points than in June, suggesting that transpiration rate (E) may be regulated by leaf temperature and VPDL independently of stomatal conductance (g_s).

In August, the WUE of the two sites showed the highest value at 12:00 hour and then decreased, which was related to the change in CE (Fig. 7E and 7F). This is believed to be a result of the inability to assimilate carbon effectively even with sufficient moisture supply, as the increase in leaf temperature under high temperatures leads to stomatal closure in addition to an increase in transpiration (E), which affects photosynthetic activity.

Chlorophyll fluorescence characteristics

Y(II), an indicator of using the energy of photons for photochemical reactions, showed the lowest rate at 12:00

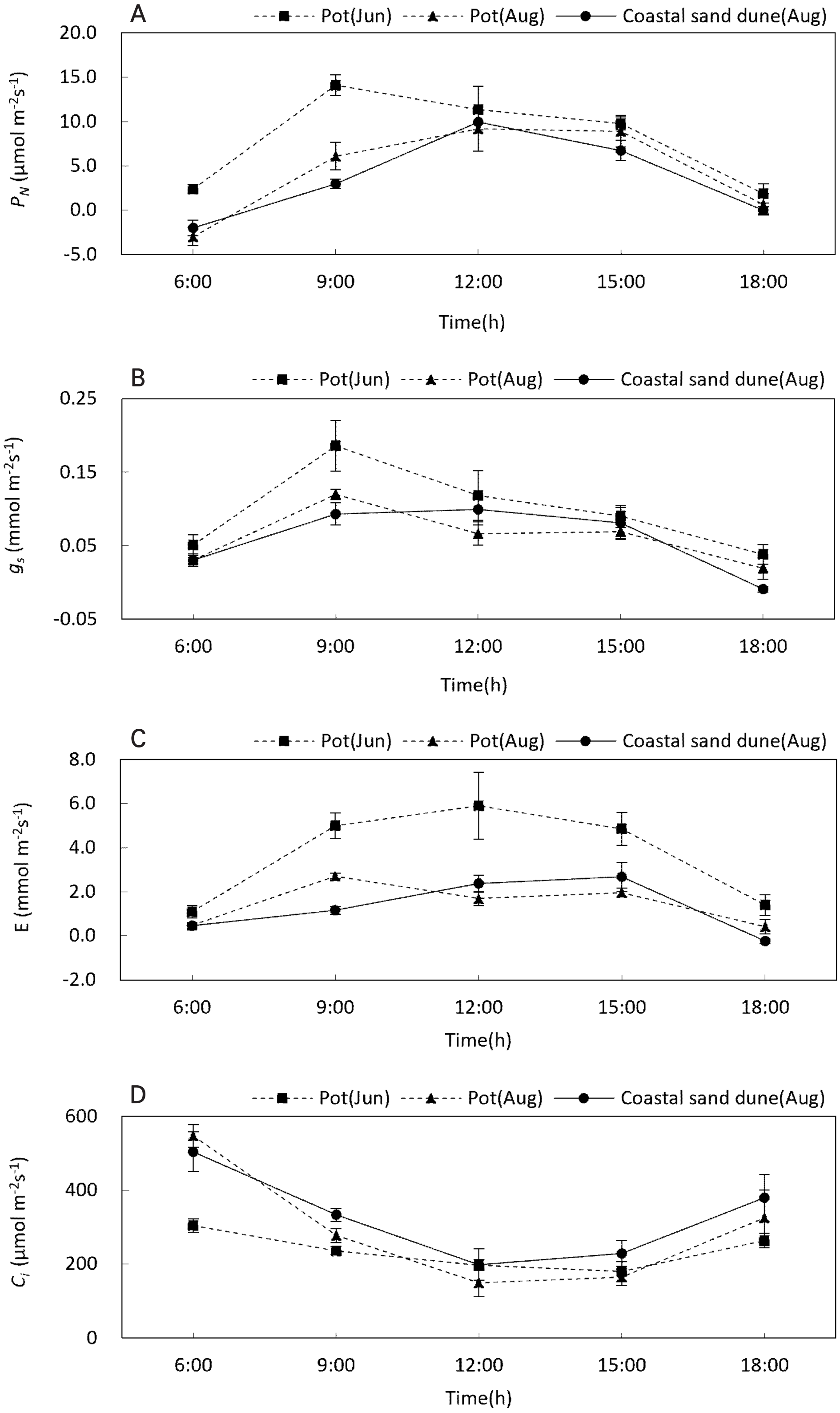

Fig. 7 Diurnal variations in the photosynthetic parameters of *Rosa rugosa* measured in July in the pot (quadrangle), August in the pot (triangle), August in the Goraebul coastal sand dune (circle). (A) Net photosynthetic rate (P_N), (B) stomatal conductance (g_s), (C) transpiration rate (*E*), (D) intercellular CO_2 concentration (C_i), (E) instantaneous water use efficiency (WUE), (F) instantaneous carboxylation efficiency (CE).

hour and the lowest Y(II) in June when the leaf temperature was the highest (Fig. 8).

The Y(II) value at 15:00 hour, when the temperature remained as high as 12:00 hour, recovered to the level at 09:00 hour. It is known that a combination of environmental factors such as high leaf temperature and PAR induce reversible inactivation of PSII. The recovery of Y(II) values suggests that *R. rugosa* can restore a portion of the inactivated PSII to an active state within a few hours, despite the persistence of negative environmental factors such as high leaf temperature and PAR.

Various mechanisms, including the NPQ mechanism, are utilized to protect PSII from degradation, and differences in photoprotective mechanisms are known to occur

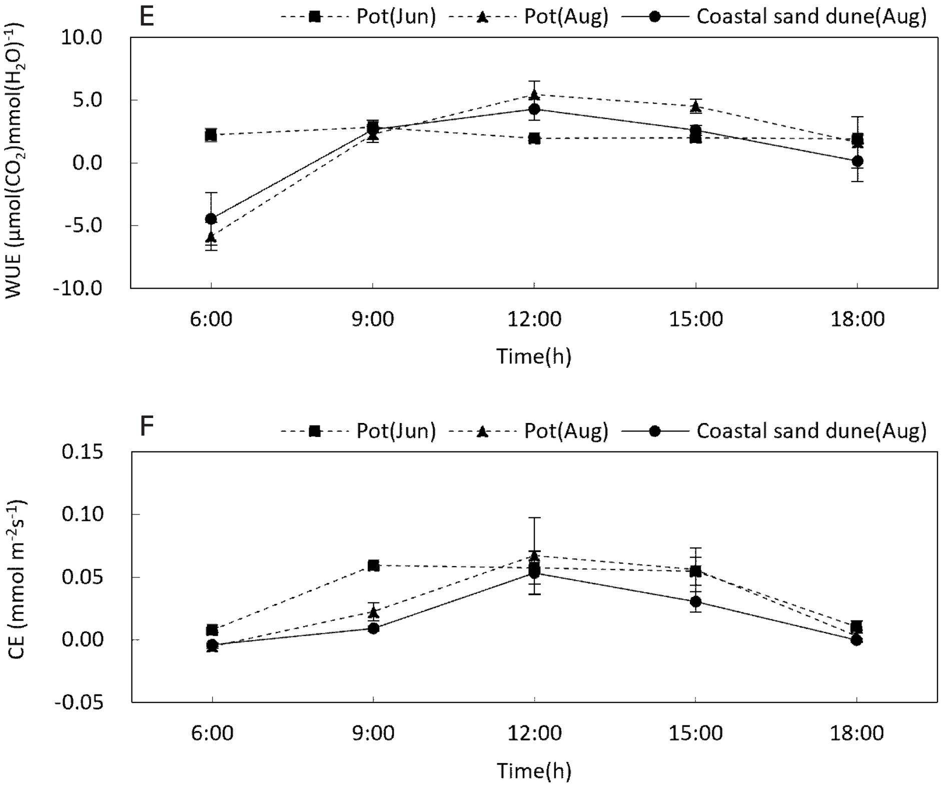

Fig. 7 Continued.

depending on the time of year of measurement (Long et al. 1994). June measurements of Y(NPQ), which represents the proportion of NPQ mechanisms, decreased by 27.3% from 12:00 hour to 15:00 hour, whereas August measurements of large pots increased by 54.6% from 12:00 hour to 15:00 hour and August measurements of coastal dunes increased by 70% from 12:00 hour to 15:00 hour (Fig. 8). High foliar temperatures in June may inhibit the activity of the NPQ mechanism, and other mechanisms are utilized to prevent photoinhibition, including increased production of D1 protein, increased activity of photosynthetic enzymes used for carbon fixation, and activation of ROS scavenging systems (Aro et al. 1993b; Demmig-Adams and Adams 1992; Jahnke et al. 1991).

In August, *R. rugosa* on the coastal dunes had higher Y(NPQ) values than the large pots (Fig. 8B and 8C). Based on the high Y(NO) values of the large-pot *R. rugosa*, it seems that when *R. rugosa* is exposed to high light intensity within a short period of time, PSII shifts to a closed state and dissipates excess energy in other forms in a passive manner rather than through the NPQ mechanism pathway. This behavior is known to be more prevalent in shade-adapted plants than in light-adapted plants (Demmig-Adams 1998). *R. rugosa* in coastal dunes appears to utilize the NPQ mechanism for photoprotection effectively at lower light levels.

As a result, the F_v/F_m ratio, which indicates the physiological state of the plant, had the lowest value at 15:00 hour in *R. rugosa* in large pots compared to the coastal dunes (June), showing that high foliar temperature and strong PAR negatively affect the physiological state of the plant (Fig. 9). In addition, the low Y(NO) ratio in August in the Goraebul coastal dune suggests that a large number of PSsII were active and maintained a high F_v/F_m ratio, suggesting that *R. rugosa* is well adapted to the pine forest behind the coastal dune.

Analyzing leaf composition over the season

Chlorophyll content

Chlorophyll plays a pivotal role in the photosynthesis process by transferring the energy of photons to the reaction center of PSII (Taiz and Zeiger 2010). In general, chlorophyll content can reflect the amount of photon energy absorbed per unit area and is a well-known indicator of physiological characteristics such as plant productivity (Anderson 1967; Zhang et al. 2021). Measurements of chlorophyll content over the season showed that *R. rugosa* in the Goraebul coastal dunes had higher chlorophyll *a* and carotenoid content, while there was no significant difference between the two habitats for chlorophyll *b* (Fig. 10). The high chlorophyll content of *R. rugosa* in the Goraebul coastal dune windbreak forest is likely a response to low light and frequent photoperiod events, while the relatively low chlorophyll content of the large pots is attributed to chlorophyll destruction by high temperatures (Larkindale and Huang 2004). The higher chlorophyll *a* + *b* values measured in the Goraebul coastal dune environment are believed to be due to the low PAR inside the Goraebul coastal dune windbreak forest, and under these conditions, *R. ru-*

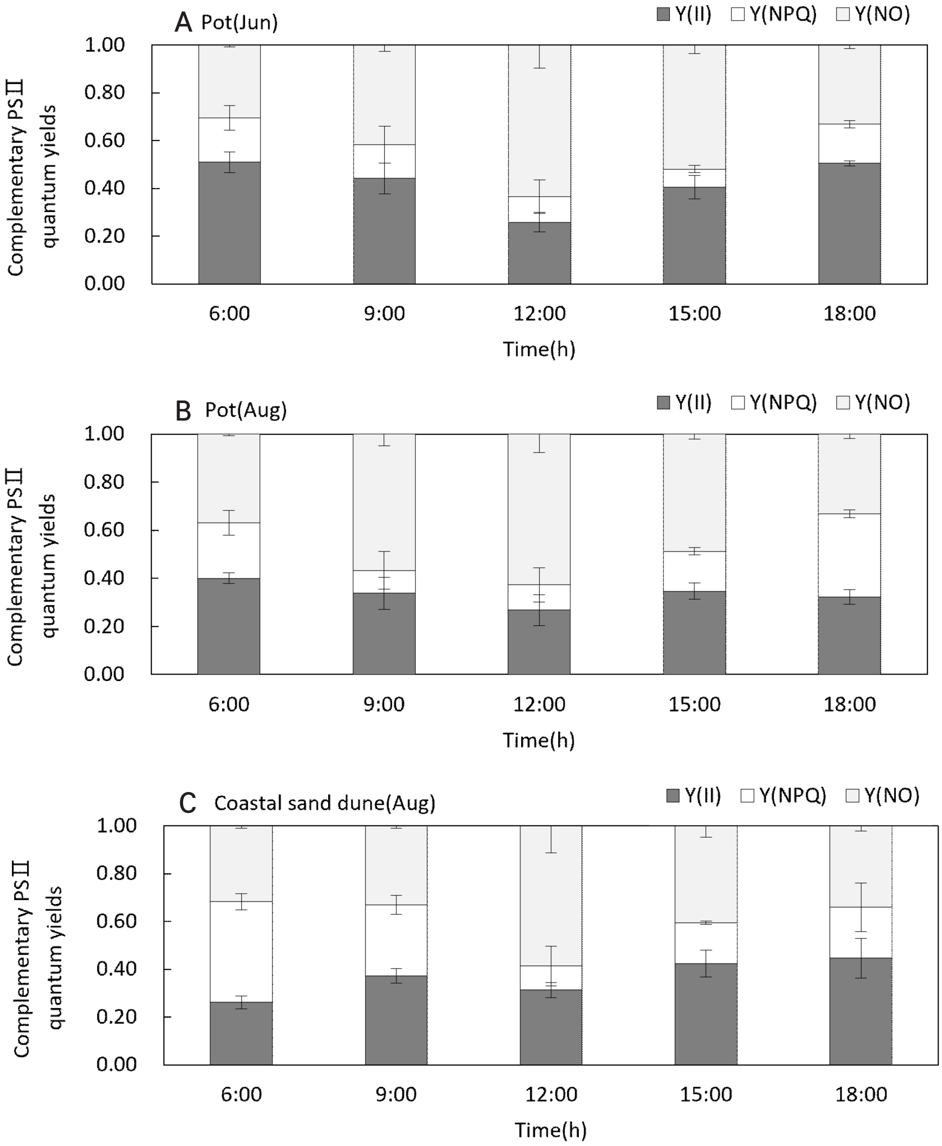

Fig. 8 Diurnal variations in chlorophyll parameters. (A) Y(II), Y(NPQ), and Y(NO) of *Rosa rugosa* in the pot measured in June, (B) Y(II), Y(NPQ), and Y(NO) of *R. rugosa* in the pot measured in August, (C) Y(II), Y(NPQ), and Y(NO) of *R. rugosa* in the Goraebul coastasl sand dune measured in August. Y(II): The quantum yield of photochemical energy conversion in PSII; Y(NO): The quantum yield of non-regulated, non-photochemical energy loss in PSII; Y(NPQ): The quantum yield of regulated non-photochemical energy loss in PSII.

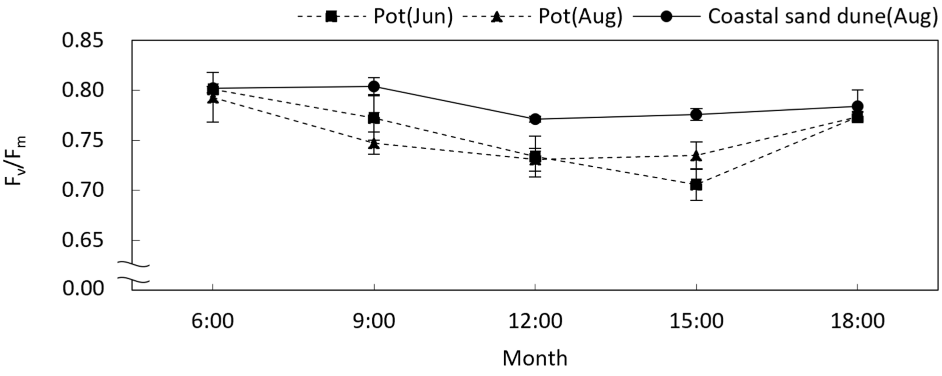

Fig. 9 Diurnal variations in F_v/F_m (maximum quantum yield) of *Rosa rugosa* in the pot measured in July (quadrangle), in August (triangle) and *R. rugosa* in the Goraebul coastal sand dune in August (circle).

gosa increases its pigment density per unit leaf area, resulting in efficient photon capture (Dai et al. 2009; Dale and Causton 1992; Kappel and Flore 1983; Wittmann et al. 2001). The relatively low chlorophyll content in large pots is thought to be a mechanism to protect against excess photon energy through increased activity of chlorophyllase and Chl-degrading peroxidase under high temperature conditions (Hu et al. 2020).

The chlorophyll *a*/*b* ratio indicates the size of the PSII antenna and the amount of LHC protein; a decrease in the chlorophyll *a*/*b* ratio leads to an increase in the antenna size and the amount of LHC protein, and conversely, an increase in the chlorophyll *a*/*b* ratio leads to a decrease in the antenna size and the amount of LHC protein (Pfündel

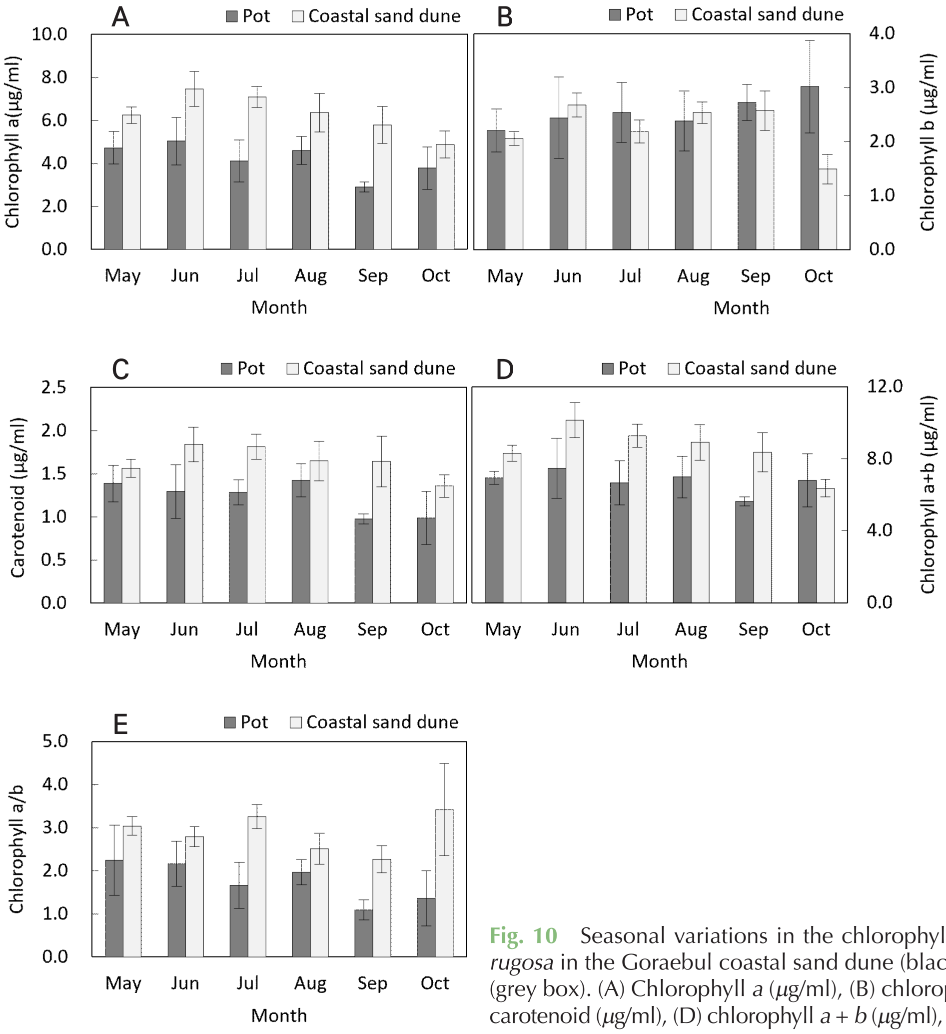

Fig. 10 Seasonal variations in the chlorophyll contents of *Rosa rugosa* in the Goraebul coastal sand dune (black box) and the pot (grey box). (A) Chlorophyll *a* (μg/ml), (B) chlorophyll *b* (μg/ml), (C) carotenoid (μg/ml), (D) chlorophyll *a* + *b* (μg/ml), (E) chlorophyll *a*/*b*.

et al. 2008; Tanaka et al. 2001). The high chlorophyll *a*/*b* ratio in the coastal sand dune *R. rugosa* means that the antenna size of PSII is relatively small, and reducing the antenna size may be a factor in increasing photosynthetic efficiency under conditions of high frequency of sun fleck (Shin et al. 2016).

In general, environments with continuous cycles of strong and weak light, such as sun fleck, can induce inhibition of PSII as much as exposure to continuous strong light (Adams et al. 1999). The NPQ mechanism, the primary photoprotective response to PSII degradation, requires carotenoids such as violaxanthin, zeaxanthin, and antheraxanthin, which are utilized in the xanthophyll cycle (Gilmore 1997). The relatively high carotenoid content in the Goraebul coastal dune environment appears to be a mechanism for photoprotection of *R. rugosa* against phototoxicity.

Analyzing leaf water content, osmolarity, total ion content, and soluble carbohydrate content

Leaf water content, leaf osmolarity, TIC, and soluble carbohydrate content in June, when temperatures were at their highest, are shown in Table 1. *Rosa rugosa* in large pots exposed to high leaf temperatures and high PAR had relatively low water content and high osmolarity. High osmolarity is known to be part of an osmotic adjustment that increases the amount of solute content per unit cell under water deficit conditions, reducing osmotic potential (Flowers and Yeo 1986; Munns et al. 1979). Increased transpiration(*E*) due to high leaf temperatures can also cause water stress, and soluble carbohydrates and ions are used to regulate leaf water potential (Flowers and Yeo 1986; Hessini et al. 2009). *Rosa rugosa* in large pots maintained high osmolarity by increasing the TIC and soluble carbohydrate content. The accumulation of soluble carbohydrates is an osmotic adaptation response to a decrease in LWC. In addition, they are known to act as osmoprotective substances to dissipate ROS generated by inhibition of enzymes and metabolism due to stresses caused by high temperature and high insolation, and to prevent cell degeneration caused by abiotic factors such as high temperature (Blum 2005; Fedotova 2019; Girija et al. 2002; Hasanuzzaman et al. 2013; Silva et al. 2013). *Rosa rugosa* in large pots contained 82.0% higher soluble carbohydrates than coastal dunes, suggesting that *R. rugosa* actively utilizes soluble carbohydrates for osmotic adjustment to overcome water stress conditions.

Table 1 Water content and solute contents in *Rosa rugosa* leaves in the Goraebul coastal sand dune and the pot

Parameter	Number	Mean	Standard deviation	t (*p*-value)
LWC				
Coastal sand dune	6	63.1	1.5	–5.983 (<0.001)***
Pot	6	57.7	2.1	
Osmolality				
Coastal sand dune	6	310.1	10.4	–11.062 (<0.001)***
Pot	6	393.7	15.2	
TIC				
Coastal sand dune	6	219.9	1.1	–12.934 (<0.001)***
Pot	6	235.4	2.7	
Carbohydrate				
Coastal sand dune	6	98.3	14.5	–5.306 (<0.001)***
Pot	6	178.9	31.0	

LWC: leaf water content; TIC: total ion content.
***$p < 0.001$.

Discussion

When summarizing the results of the meteorological and environmental factors of the two regions, the biggest difference between the two regions is temperature and sunlight, with Kyungpook National University's environment having a high temperature and strong light, while Goraebul coastal sand dunes has a relatively low sunlight and low temperature.

*Rosa rugo*sa in large pots in environments with high air temperatures and rapidly increasing VPDL do not appear to respond effectively to high temperatures by showing a decrease in transpiration (*E*) due to high stomatal conductance (g_s) despite a decrease in stomatal conductance (g_s). Therefore, the decrease in water content, which is essential for photosynthesis, caused a decrease in net photosynthetic rate (P_N) and carbon fixation efficiency. *Rosa rugosa* of Goraebul coastal sand dunes did not show a significant decrease in LWC due to a concomitant decrease in stomatal conductance (g_s) and transpiration rate (*E*) in June, when the highest leaf temperature was recorded, and carbon fixation efficiency did not decrease significantly despite a decrease in net photosynthetic rate (P_N).

Water use efficiency of *R. rugosa* decreases when *R. rugosa* is exposed to high temperatures, which is thought to be part of a mechanism to counteract high leaf temperatures (Sinclair et al. 1984). In particular, *R. rugosa* in large pots showed a decrease in WUE in June compared to May, which was attributed to an increase in transpiration (*E*) due to an increase in VPDL (Hatfield and Dold 2019; Sinclair et al. 1984). The increase in WUE with decreasing temperature is thought to be due to a decrease in transpiration rate (*E*) due to a decrease in stomatal conductance (g_s) (Sinclair et al. 1984) or to more efficient utilization of water at lower cost in colder environments (Jiang et al. 2022). Thus, it can be seen that *R. rugosa* is more favorable to growth in low temperature environments than in high temperature.

In *R. rugosa*, high leaf temperature is known to indirectly affect protein synthesis and inhibit the repair system of PSII by inactivating Rubisco activase, which is essential for Rubisco activity, accelerating the production of ROS (Murata et al. 2007; Takahashi and Murata 2008). An adequate level of ATP must be maintained for the smooth operation of the PSII repair system after photoinhibition. However, as shown in Fig. 4B and 4D, high leaf temperature seems to have restricted the Calvin circuit by decreasing stomatal conductance (g_s) and CO_2 concentration (C_i) in the chloroplasts, thereby inhibiting the synthesis of PSII components such as D1 protein. Thus, it is thought to have negatively affected the PSII repair system (Murata et al. 2007; Takahashi and Murata 2008).

The decrease in Y(NPQ), the ratio of the NPQ mechanism, which is known to be one of the photoprotective mechanisms, is not only due to inhibition by strong light, but also to inhibition of the entire photosynthetic process. In order for the NPQ mechanism to operate, a ΔpH gradient must be established through the low pH of the thylakoid lumen (Ruban 2016; Tyystjärvi 2013). For this to occur, an adequate amount of ATP must be available. However, due to the high leaf temperature, the stomatal conductance (g_s) was reduced, the Calvin's circuit was limited, and a large number of PSsII were inactivated. The entire photosynthesis process is thus inhibited and the amount of ATP synthesized is reduced (Gilmore 1997; Lu et al. 2017).

In plants, ions, like soluble sugars, contribute to osmotic regulation and play a variety of roles, including redox reactions, energy storage, and carbon compound organization (Flowers and Yeo 1986; Taiz and Zeiger 2010). Thus, *R. rugosa* appears to overcome the stress of high temperatures by increasing the content of ions or soluble carbohydrates when exposed to stressful conditions.

Conclusions

In order to analyze the physiological and ecological characteristics of *R. rugosa*, a species native to the Korean Peninsula, classified as a boreal plant and designated as a plant systematic class II, according to environmental factors, photochemical characteristics, chlorophyll content, LWC, osmolarity, soluble carbohydrate content, and TIC according to seasonal and diurnal changes were measured and analyzed during the study period (May 2022–October 2022).

The results of the photochemical characterization of *R. rugosa* showed that both the corresponding plants in both environmental conditions exhibited a significant decrease in photosynthetic indicators, including net photosynthetic rate (P_N) and stomatal conductance (g_s), during the period of exposure to high leaf temperature, and the decrease in photosynthetic indicators with decreasing leaf temperature was closely related to leaf temperature. Furthermore, it appears that *R. rugosa* suffers from severe photoinhibition when exposed to high light levels continuously. This explains why it exhibits relatively low Y(II) and high Y(NO). On the other hand, in the coastal dune environment, *R. rugosa* was found to be degraded due to its high Y(NPQ). Therefore, the low F_v/F_m ratio of *R. rugosa* in large pots indicates that *R. rugosa* is constantly exposed to high light intensity and high temperature stress.

The coastal dune *R. rugosa* showed significant differences between chlorophyll *a* and carotenoid content, which appears to be an adaptation to low light intensity and sun fleck effects, the higher chlorophyll *a* + *b* values measured were a result of negative resistance to efficient photon capture by increasing pigment density per area in response to low light intensity, while the chlorophyll *a*/*b* ratio was lower in the coastal dune *R. rugosa*, which appears to be a factor that increases photosynthetic efficiency under conditions of high frequency of sun fleck effects.

In addition, *R. rugosa* in large pots exposed to high temperatures and sustained high light levels utilizes soluble carbohydrates and ions to maintain high osmolarity, which appears to be part of osmotic regulation in response to low LWC; specifically, *R. rugosa* maintains its osmotic potential by increasing its soluble carbohydrate content.

Based on the analysis of the photochemical characteristics of *R. rugosa* and the physiological characteristics of its leaves in this study, it is expected that exposure to high temperatures and continuous and intense light intensity will inhibit the photochemical characteristics of *R. rugosa*, limiting its growth and distribution, due to the physiological and ecological characteristics of *R. rugosa* that prefer somewhat lower temperatures to higher temperatures.

Abbreviations

LWC: Leaf water content
PAR: Photosynthetically active radiation
Y(II): The quantum yield of photochemical energy conversion in PSII
Y(NO): The quantum yield of non-regulated, non-photochemical energy loss in PSII
Y(NPQ): The quantum yield of regulated non-photochemical energy loss in PSII
PS: Photosystem
ROS: Reactive oxygen species
LHC: Light harvest complex
NPQ: Non-photochemical quenching
VPDL: Vapor pressure deficit based on leaf
WUE: Water use efficiency
CE: Carboxylation efficiency
FW: Fresh weight
DW: Dry weight

Acknowledgements

All the authors are deeply grateful to plant ecophysiology lab in Kyungpook National University, Republic of Korea.

Authors' contributions

YBK did data curation, investigation, and writing-original draft. SHY did data curation, funding acquisition, writing-review and editing. YSS did data analysis, writing-review and editing. YSC did conceptualization, supervision, writing-original draft, and writing-review and editing. All the authors approved the manuscript.

Funding

This research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (2016R1A6A1A05011910 & 2016R1D1A1B03934927), and by grants from the National Institute of Ecology (NIE-A-2023-20 & NIE-B-2023-02).

Availability of data and materials

The data sets generated and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

References

Adams SR, Langton FA. Photoperiod and plant growth: a review. J Hortic Sci Biotechnol. 2005;80(1):2-10. https://doi.org/10.1080/14620316.2005.11511882.

Adams WW 3rd, Demmig-Adams B, Logan BA, Barker DH, Osmond

CB. Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II efficiency in two vines, *Stephania japonica* and *Smilax australis*, growing in the understory of an open *Eucalyptus* forest. Plant Cell Environ. 1999;22(2):125-36. https://doi.org/10.1046/j.1365-3040.1999.00369.x.

Albanese P, Tamara S, Saracco G, Scheltema RA, Pagliano C. How paired PSII-LHCII supercomplexes mediate the stacking of plant thylakoid membranes unveiled by structural mass-spectrometry. Nat Commun. 2020;11(1):1361. https://doi.org/10.1038/s41467-020-15184-1.

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P. Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res. 2008;98(1-3):541-50. https://doi.org/10.1007/s11120-008-9331-0.

Allen JF, de Paula WB, Puthiyaveetil S, Nield J. A structural phylogenetic map for chloroplast photosynthesis. Trends Plant Sci. 2011;16(12):645-55. https://doi.org/10.1016/j.tplants.2011.10.004.

Anderson MC. Photon flux, chlorophyll content, and photosynthesis under natural conditions. Ecology. 1967;48(6):1050-3. https://doi.org/10.2307/1934566.

Aro EM, McCaffery S, Anderson JM. Photoinhibition and D1 protein degradation in peas acclimated to different growth irradiances. Plant Physiol. 1993a;103(3):835-43. https://doi.org/10.1104/pp.103.3.835.

Aro EM, Virgin I, Andersson B. Photoinhibition of Photosystem II. Inactivation, protein damage and turnover. Biochim Biophys Acta. 1993b;1143(2):113-34. https://doi.org/10.1016/0005-2728(93)90134-2.

Ashraf M, Harris PJC. Photosynthesis under stressful environments: an overview. Photosynthetica. 2013;51(2):163-90. https://doi.org/10.1007/s11099-013-0021-6.

Ball MC, Cowan IR, Farquhar GD. Maintenance of leaf temperature and the optimisation of carbon gain in relation to water loss in a tropical mangrove forest. Funct Plant Biol. 1988;15(2):263-76. https://doi.org/10.1071/PP9880263.

Billings WD. The environmental complex in relation to plant growth and distribution. Q Rev Biol. 1952;27(3):251-65. https://doi.org/10.1086/399022.

Blum A. Drought resistance, water-use efficiency, and yield potential-are they compatible, dissonant, or mutually exclusive? Aust J Agric Res. 2005;56(11):1159-68. https://doi.org/10.1071/AR05069.

Bozarth CS, Kennedy RA, Schekel KA. The effects of leaf age on photosynthesis in rose[1]. J Am Soc Hortic Sci. 1982;107(5):707-12. https://doi.org/10.21273/JASHS.107.5.707.

Chang B, Ma K, Lu Z, Lu J, Cui J, Wang L, et al. Physiological, transcriptomic, and metabolic responses of *Ginkgo biloba* L. to drought, salt, and heat stresses. Biomolecules. 2020;10(12):1635. https://doi.org/10.3390/biom10121635.

Chapin FS 3rd, Schulze E, Mooney HA. The ecology and economics of storage in plants. Annu Rev Ecol Syst. 1990;21(1):423-47. https://doi.org/10.1146/annurev.es.21.110190.002231.

Chen JW, Kuang SB, Long GQ, Yang SC, Meng ZG, Li LG, et al. Photosynthesis, light energy partitioning, and photoprotection in the shade-demanding species Panax notoginseng under high and low level of growth irradiance. Funct Plant Biol. 2016;43(6):479-91. https://doi.org/10.1071/fp15283.

Choi YH, Kim MJ, Lee HS, Hu C, Kwak SS. Antioxidants in leaves of Rosa rugose. Korean J Pharmacogn. 1997;28(4):179-84.

Dai Y, Shen Z, Liu Y, Wang L, Hannaway D, Lu H. Effects of shade treatments on the photosynthetic capacity, chlorophyll fluorescence, and chlorophyll content of *Tetrastigma hemsleyanum* Diels et Gilg. Environ Exp Bot. 2009;65(2-3):177-82. https://doi.org/10.1016/j.envexpbot.2008.12.008.

Dale MP, Causton DR. Use of the chlorophyll *a/b* ratio as a bioassay for the light environment of a plant. Funct Ecol. 1992;6(2):190-6. https://doi.org/10.2307/2389754.

Demmig-Adams B, Adams WW 3rd. Photoprotection and other responses of plants to high light stress. Annu Rev Plant Biol. 1992;43:599-626. https://doi.org/10.1146/annurev.pp.43.060192.003123.

Demmig-Adams B. Survey of thermal energy dissipation and pigment composition in sun and shade leaves. Plant Cell Physiol. 1998;39(5):474-82. https://doi.org/10.1093/oxfordjournals.pcp.a029394.

dos Santos TB, Ribas AF, de Souza SGH, Budzinski IGF, Domingues DS. Physiological responses to drought, salinity, and heat stress in plants: a review. Stresses. 2022;2(1):113-35. https://doi.org/10.3390/stresses2010009.

Fedotova MV. Compatible osmolytes - bioprotectants: is there a common link between their hydration and their protective action under abiotic stresses? J Mol Liq. 2019;292:111339. https://doi.org/10.1016/j.molliq.2019.111339.

Flowers TJ, Yeo AR. Ion relations of plants under drought and salinity. Funct Plant Biol. 1986;13(1):75-91. https://doi.org/10.1071/PP9860075.

Frosini S, Lardicci C, Balestri E. Global change and response of coastal dune plants to the combined effects of increased sand accretion (burial) and nutrient availability. PLoS One. 2012;7(10):e47561. https://doi.org/10.1371/journal.pone.0047561.

Gates DM. Leaf temperature and transpiration[1]. Agron J. 1964;56(3):273-7. https://doi.org/10.2134/agronj1964.00021962005600030007x.

Gil R, Boscaiu M, Lull C, Bautista I, Lid N A, Vicente O. Are soluble carbohydrates ecologically relevant for salt tolerance in halophytes? Funct Plant Biol. 2013;40(9):805-18. https://doi.org/10.1071/fp12359.

Gilmore AM. Mechanistic aspects of xanthophyll cycle-dependent photoprotection in higher plant chloroplasts and leaves. Physiol Plant. 1997;99(1):197-209. https://doi.org/10.1111/j.1399-3054.1997.tb03449.x.

Girija C, Smith BN, Swamy PM. Interactive effects of sodium chloride and calcium chloride on the accumulation of proline and glycinebetaine in peanut (*Arachis hypogaea* L.). Environ Exp Bot. 2002;47(1):1-10. https://doi.org/10.1016/S0098-8472(01)00096-X.

Givnish TJ. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytol. 1987;106(s1):131-60. https://doi.org/10.1111/j.1469-8137.1987.tb04687.x.

Han YH, Lee YH, Kim JB, Cho KJ. Vegetation characteristics of coastal sand dune in the East Coast. J Korean Soc Environ Restor Technol. 2013;16(1):55-69. https://doi.org/10.13087/KOSERT.2013.16.1.055.

Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci. 2013;14(5):9643-84. https://doi.

org/10.3390/ijms14059643.

Hatfield JL, Dold C. Water-use efficiency: advances and challenges in a changing climate. Front Plant Sci. 2019;10:103. https://doi.org/10.3389/fpls.2019.00103.

Hessini K, Martínez JP, Gandour M, Albouchi A, Soltani A, Abdelly C. Effect of water stress on growth, osmotic adjustment, cell wall elasticity and water-use efficiency in *Spartina alterniflora*. Environ Exp Bot. 2009;67(2):312-9. https://doi.org/10.1016/j.envexpbot.2009.06.010.

Hohmann-Marriott MF, Blankenship RE. Evolution of photosynthesis. Annu Rev Plant Biol. 2011;62:515-48. https://doi.org/10.1146/annurev-arplant-042110-103811.

Hu S, Ding Y, Zhu C. Sensitivity and responses of chloroplasts to heat stress in plants. Front Plant Sci. 2020;11:375. https://doi.org/10.3389/fpls.2020.00375.

Iyer NJ, Tang Y, Mahalingam R. Physiological, biochemical and molecular responses to a combination of drought and ozone in Medicago truncatula. Plant Cell Environ. 2013;36(3):706-20. https://doi.org/10.1111/pce.12008.

Jahnke LS, Hull MR, Long SP. Chilling stress and oxygen metabolizing enzymes in *Zea mays* and *Zea diploperennis*. Plant Cell Environ. 1991;14(1):97-104. https://doi.org/10.1111/j.1365-3040.1991.tb01375.x.

Jensen PE, Leister D. Chloroplast evolution, structure and functions. F1000Prime Rep. 2014;6:40. https://doi.org/10.12703/p6-40.

Jiang Y, Wang XX, Meng H, Xu YW, Wang S, Wang SD. Photosynthetic physiology performance and expression of transcription factors in soybean of water use efficiency difference. Russ J Plant Physiol. 2022;69(1):9. https://doi.org/10.1134/S102144372201006X.

Joung YH, Kim ST, Kim GJ, Lee JH, Gi GY, Han TH. Genetic relationship of genus Rosa germplasm and genetic diversity of Rosa rugosa in Korea. Korean J Hortic Sci Technol. 2010;28(6):1003-13.

Kappel F, Flore JA. Effect of shade on photosynthesis, specific leaf weight, leaf chlorophyll content, and morphology of young peach trees. J Am Soc Hortic Sci. 1983;108(4):541-4. https://doi.org/10.21273/JASHS.108.4.541.

Kawakami K, Shen JR. Purification of fully active and crystallizable photosystem II from thermophilic cyanobacteria. Methods Enzymol. 2018;613:1-16. https://doi.org/10.1016/bs.mie.2018.10.002.

Kim MJ, Kim JS, Kim KE, Shin KH, Heo K, Cho DH, et al. Comparison of antioxidative activities from different organs of Rosa rugosa Thunb. Korean J Med Crop Sci. 2001;9(1):40-4.

Kitao M, Lei TT, Koike T, Tobita H, Maruyama Y. Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. Plant Cell Environ. 2000;23(1):81-9. https://doi.org/10.1046/j.1365-3040.2000.00528.x.

Larkindale J, Huang B. Changes of lipid composition and saturation level in leaves and roots for heat-stressed and heat-acclimated creeping bentgrass (*Agrostis stolonifera*). Environ Exp Bot. 2004;51(1):57-67. https://doi.org/10.1016/S0098-8472(03)00060-1.

Lee JY, Lee JH, Ki GY, Kim ST, Han TH. Improvement of seed germination in Rosa rugosa. Korean J Hortic Sci Technol. 2011;29(4):352-7.

Long SP, Humphries S, Falkowski PG. Photoinhibition of photosynthesis in nature. Annu Rev Plant Physiol Plant Mol Biol. 1994;45(1):633-62. https://doi.org/10.1146/annurev.pp.45.060194.003221.

Lu T, Meng Z, Zhang G, Qi M, Sun Z, Liu Y, et al. Sub-high temperature and high light intensity induced irreversible inhibition on photosynthesis system of tomato plant (*Solanum lycopersicum* L.). Front Plant Sci. 2017;8:365. https://doi.org/10.3389/fpls.2017.00365.

Medina E, Francisco M. Osmolality and δ13C of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. Estuar Coast Shelf Sci. 1997;45(3):337-44. https://doi.org/10.1006/ecss.1996.0188.

Munns R, Brady CJ, Barlow EWR. Solute accumulation in the apex and leaves of wheat during water stress. Funct Plant Biol. 1979;6(3):379-89. https://doi.org/10.1071/PP9790379.

Murata N, Takahashi S, Nishiyama Y, Allakhverdiev SI. Photoinhibition of photosystem II under environmental stress. Biochim Biophys Acta. 2007;1767(6):414-21. https://doi.org/10.1016/j.bbabio.2006.11.019.

National Institute of Ecology. Floristic Target Species (FT Species) in Korea. Seocheon: National Institute of Ecology; 2018.

Parkhill JP, Maillet G, Cullen JJ. Fluorescence-based maximal quantum yield for PSII as a diagnostic of nutrient stress. J Phycol. 2001;37(4):517-29. https://doi.org/10.1046/j.1529-8817.2001.037004517.x.

Pazur JH. Neutral polysaccharide. In: Chaplin MF, Kennedy JF, editors. Carbohydrate analysis: a practical approach. 2nd ed. Oxford: IRL Press; 1994. p. 90-2.

Pfündel E, Klughammer C, Schreiber U. Monitoring the effects of reduced PS II antenna size on quantum yields of photosystems I and II using the Dual-PAM-100 measuring system. PAM Appl Notes. 2008;1:21-4.

Prasch CM, Sonnewald U. Simultaneous application of heat, drought, and virus to Arabidopsis plants reveals significant shifts in signaling networks. Plant Physiol. 2013;162(4):1849-66. https://doi.org/10.1104/pp.113.221044.

Rajaniemi TK, Allison VJ. Abiotic conditions and plant cover differentially affect microbial biomass and community composition on dune gradients. Soil Biol Biochem. 2009;41(1):102-9. https://doi.org/10.1016/j.soilbio.2008.10.001.

Rajkumar M, Bruno LB, Banu JR. Alleviation of environmental stress in plants: the role of beneficial *Pseudomonas* spp. Crit Rev Environ Sci Technol. 2017;47(6):372-407. https://doi.org/10.1080/10643389.2017.1318619.

Ruban AV. Nonphotochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants from photodamage. Plant Physiol. 2016;170(4):1903-16. https://doi.org/10.1104/pp.15.01935.

Sharma DK, Andersen SB, Ottosen CO, Rosenqvist E. Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. Physiol Plant. 2015;153(2):284-98. https://doi.org/10.1111/ppl.12245.

Shin WS, Lee B, Jeong B, Chang YK, Kwon JH. Truncated light-harvesting chlorophyll antenna size in *Chlorella vulgaris* improves biomass productivity. J Appl Phycol. 2016;28(6):3193-202. https://doi.org/10.1007/s10811-016-0874-8.

Silva EN, Vieira SA, Ribeiro RV, Ponte LFA, Ferreira-Silva SL, Silveira JAG. Contrasting physiological responses of *Jatropha curcas* plants to single and combined stresses of salinity and heat. J Plant Growth Regul. 2013;32(1):159-69. https://doi.org/10.1007/s00344-012-9287-3.

Sinclair TR, Tanner CB, Bennett JM. Water-use efficiency in crop production. BioScience. 1984;34(1):36-40. https://doi.org/10.2307/1309424.

Singh J, Thakur JK. Photosynthesis and abiotic stress in plants. In: Vats S, editor. Biotic and abiotic stress tolerance in plants. Singapore: Springer; 2018. p. 27-46.

Stanhill G. Water use efficiency. Adv Agron. 1986;39:53-85. https://doi.org/10.1016/S0065-2113(08)60465-4.

Sudhir P, Murthy SDS. Effects of salt stress on basic processes of photosynthesis. Photosynthetica. 2004;42(4):481-6. https://doi.org/10.1007/S11099-005-0001-6.

Suzuki N, Rivero RM, Shulaev V, Blumwald E, Mittler R. Abiotic and biotic stress combinations. New Phytol. 2014;203(1):32-43. https://doi.org/10.1111/nph.12797.

Taiz L, Zeiger E. Plant physiology. 5th ed. Sunderland: Sinauer Associates is an imprint of Oxford University Press; 2010.

Takahashi S, Badger MR. Photoprotection in plants: a new light on photosystem II damage. Trends Plant Sci. 2011;16(1):53-60. https://doi.org/10.1016/j.tplants.2010.10.001.

Takahashi S, Murata N. How do environmental stresses accelerate photoinhibition? Trends Plant Sci. 2008;13(4):178-82. https://doi.org/10.1016/j.tplants.2008.01.005.

Tanaka R, Koshino Y, Sawa S, Ishiguro S, Okada K, Tanaka A. Overexpression of chlorophyllide a oxygenase (CAO) enlarges the antenna size of photosystem II in Arabidopsis thaliana. Plant J. 2001;26(4):365-73. https://doi.org/10.1046/j.1365-313x.2001.2641034.x.

Thakur P, Nayyar H. Facing the cold stress by plants in the changing environment: sensing, signaling, and defending mechanisms. In: Tuteja N, Gill SS, editors. Plant acclimation to environmental stress. New York: Springer; 2013. p. 29-69. https://doi.org/10.1007/978-1-4614-5001-6_2

Tyystjärvi E. Photoinhibition of photosystem II. Int Rev Cell Mol Biol. 2013;300:243-303. https://doi.org/10.1016/b978-0-12-405210-9.00007-2.

Vicente O, Al Hassan M, Boscaiu M. Contribution of osmolyte accumulation to abiotic stress tolerance in wild plants adapted to different stressful environments. In: Iqbal N, Nazar R, Khan NA, editors. Osmolytes and plants acclimation to changing environment: emerging omics technologies. New Delhi: Springer; 2016. p. 13-25.

Villar R, Robleto JR, De Jong Y, Poorter H. Differences in construction costs and chemical composition between deciduous and evergreen woody species are small as compared to differences among families. Plant Cell Environ. 2006 Aug;29(8):1629-43. https://doi.org/10.1111/j.1365-3040.2006.01540.x.

Wang F, Zhang F, Gou X, Fonti P, Xia J, Cao Z, et al. Seasonal variations in leaf-level photosynthesis and water use efficiency of three isohydric to anisohydric conifers on the Tibetan Plateau. Agric For Meteorol 2021;308-309:108581. https://doi.org/10.1016/j.agrformet.2021.108581.

Weis E, Berry JA. Quantum efficiency of Photosystem II in relation to 'energy'-dependent quenching of chlorophyll fluorescence. Biochim Biophys Acta Bioenerg. 1987;894(2):198-208. https://doi.org/10.1016/0005-2728(87)90190-3.

Wellburn AR. The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. J Plant Physio. 1994;144(3):307-13. https://doi.org/10.1016/S0176-1617(11)81192-2.

Wittmann C, Aschan G, Pfanz H. Leaf and twig photosynthesis of young beech (*Fagus sylvatica*) and aspen (*Populus tremula*) trees grown under different light regime. Basic Appl Ecol. 2001:2(2):145-54. https://doi.org/10.1078/1439-1791-00047.

Yamori W, Hikosaka K, Way DA. Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation. Photosynth Res. 2014;119(1-2):101-17. https://doi.org/10.1007/s11120-013-9874-6.

Young HS. Antihypertensive activity and triterpene from the underground parts of Rosa rugose. J Oriental Bot Res 1990;3(2):83-9.

Yu HS, Mun YJ, Woo WH, Song JH. Anti-melanogenic effects of ethanol extracts from Rosa rugosa thunb. J Korean Soc Cosmetol. 2014;20(1):36-41.

Zhang Y, He N, Yu G. Opposing shifts in distributions of chlorophyll concentration and composition in grassland under warming. Sci Rep. 2021;11(1):15736. https://doi.org/10.1038/s41598-021-95281-3.