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ORIGINAL ARTICLE

Photosynthetic responses to soil water stress in summer in two Japanese urban landscape tree species (*Ginkgo biloba* and *Prunus yedoensis*): effects of pruning mulch and irrigation management

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Abstract

Key message **Stomatal regulation involves beneficial effects of pruning mulch and irrigation on leaf photosynthesis in *Prunus yedoensis* and *Ginkgo biloba* under moderate drought. *G. biloba* showed conservative water use under drought.**

Abstract Leaf photosynthesis is highly sensitive to soil water stress via stomatal and/or biochemical responses, which markedly suppress the growth of landscape trees. Effective irrigation management to maintain leaf photosynthesis and information on species-specific photosynthetic responses to soil water stress are essential for the sustainable management of landscape trees in Japan, in which summer drought often occurs. In order to investigate effective irrigation management, we used plants with moderate soil water stress as controls, and examined the effects of daily irrigation and pruning mulch on leaf photosynthesis in container-grown *Ginkgo biloba* and *Prunus yedoensis*, which are the first and second main tall roadside trees in Japan. Stomatal conductance was significantly increased by pruning mulch and daily irrigation, with similar increases in leaf photosynthesis being observed in *P. yedoensis* and *G. biloba*. In order to obtain information on species-specific photosynthetic responses to soil water stress, we compared the responses of leaf photosynthesis and leaf water status to reductions in soil water content (SWC) between the two species. *G. biloba* maintained a constant leaf water potential, leaf water content, maximum carboxylation rate, and electron transport rate with reductions in SWC, whereas reductions were observed in *P. yedoensis*. We concluded that pruning mulch and irrigation effectively offset the negative impact of moderate water stress on leaf photosynthesis in summer in *P. yedoensis* and *G. biloba* via stomatal regulation, and also that *G. biloba* maintained its photosynthetic biochemistry and leaf water status better than *P. yedoensis* under severe water stress.

Keywords Water-use efficiency · Leaf water potential · Soil water content · Stomatal conductance · Carbon isotope ratio

Abbreviations

A_{sat}	Light-saturated CO_2 assimilation rate
Δ	Carbon isotope discrimination
g_s	Stomatal conductance
J	CO_2-saturated electron transport rate
PPFD	Photosynthetic photon flux density
RWC	Relative leaf water content
SWC	Soil water content
VPD	Vapor pressure deficit
V_{cmax}	Maximum carboxylation rate

Introduction

Urban landscapes create different growth conditions from the surrounding rural and natural environments. A limited water supply due to a small volume of soil available and poor infiltration by paved roads, combined with low nutrient levels, the extremes of temperature, and high

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irradiance have been shown to markedly affect the growth of isolated urban trees in parking lots and along streets (Vico et al. 2014). Among the various environmental factors in urban landscapes, soil water stress has been identified as the main factor reducing growth and/or leading to the failure of transplanted urban trees (Kaushal and Aussenac 1989; Fini et al. 2009). Soil water stress is one of the most important factors negatively impacting leaf photosynthetic performance, which is an essential factor for determining tree growth, through stomatal regulation and/or photosynthetic biochemistry (e.g., Lambers et al. 2008; Chaves et al. 2009).

Although the climate in Japan is classified as humid subtropical in the summer, summer drought often occurs when the absence of precipitation is prolonged. Summer drought has become more serious due to the effects of urban and global warming; average air temperature and atmospheric relative humidity in Kyoto in August increased by 0.23 °C and decreased by 1.6 % per decade, respectively, between 1951 and 2012 (Japan Meteorological Agency); this rise in temperature was markedly larger than that of the global average in the same period (0.12 °C per decade between 1951 and 2012, IPCC 2014). Higher atmospheric temperatures and lower soil water content were reported in urban areas in Kyoto city than in rural areas in the summer (Kagotani et al. 2013). Summer drought has been shown to cause severe damage to landscape trees in Japan (Iijima et al. 1993; Ikeda and Hashimoto 1996). Osone et al. (2014) reported declines in leaf photosynthesis and stomatal conductance in urban trees in hot-dry summers than in average summers in Tokyo, Japan. Such declines may prevent landscape trees from playing important social, economic, and environmental roles including urban heat island mitigation and reducing energy use (Vico et al. 2014).

Supplemental irrigation management has been suggested to ameliorate the negative impact of soil water stress on landscape trees in summer (Fain et al. 1999; Vico et al. 2014). However, a smaller irrigation interval and amount of water are essential for the effective and sustainable management of landscape trees. One possible and promising management is mulching by organic materials; organic mulching is considered to be environmentally friendly and has been shown to have positive effects on plant growth and physiology (e.g., reviewed by Ferrini and Fini 2011), with increases in soil water content and/or decreases in evaporation by organic mulch (pine wood chip, pine bark) being reported for urban trees (Iles and Dosman 1999; Montague et al. 2000; Montague and Fox 2008). In this context, using pruning from landscape trees as mulch materials, as described previously by Youkhana and Idol (2009), may be particularly beneficial because it reduces waste materials and CO_2 emission with their incineration and also increases soil water content. However, the effects of pruning mulch on tree photosynthetic performance by Japanese landscape trees have not yet been examined.

Information on the species-specific responses of urban trees to water stress is important for effective irrigation management for urban trees. Physiologically, it is widely recognized that the photosynthetic response and its underlying mechanisms to water stress markedly vary between species (Warren 2008; Medrano et al. 2009; Tomás et al. 2014). Nevertheless, information on urban tree physiological performance to water stress is limited because trees in urban landscapes are mainly selected for their esthetic qualities (Percival and Sheriffs 2002), which intensified after the 1980s in Japan (Kurihara et al. 2014). To the best of our knowledge, only a few studies have compared the species-specific physiological responses of urban trees to water stress in Japan; Osone et al. (2014) recently reported that *Ginkgo biloba* was less sensitive to summer drought under urban street conditions than *Prunus yedoensis* and *Zelkova serrata*. Environmental conditions in the field vary between study sites and species, and have led to difficulties in comparing species-specific responses; therefore, studies performed under controlled conditions will provide valuable information on the species-specific physiological responses of urban trees to drought. Comparisons and evaluations of the effects of soil water content on photosynthetic performance between landscape tree species may have a significant impact by improving leaf photosynthetic function and, thus, contributing to the more effective management of landscape trees.

The aims of the study were to test the hypotheses that

1. The soil water content and leaf photosynthetic performance of landscape trees are increased by pruning mulch and irrigation under moderate soil water stress, and
2. Photosynthetic responses and the leaf water status to soil water stress differ between tree species in a manner that depends on stomatal and/or biochemical responses.

We selected two landscape tree species, *Ginkgo biloba* (maiden hair tree) and *Prunus yedoensis* (Yoshino cherry). In 2009, 6.75×10^6 tall trees and 1.40×10^8 shrubs were planted as roadside trees in Japan, with *G. biloba* and *P. yedoensis* being the first (5.70×10^5, 8.4 %) and second (5.22×10^5, 7.7 %) main tall tree species (Kurihara et al. 2014). *G. biloba* is considered to be a good species for street planting (Handa et al. 1997; Bassuk et al. 2009) because it grows in a wide range of soil moisture from wet to very dry soil (Bassuk et al. 2009). On the other hand, urban *Prunus* trees are declining in Japan, partly due to inappropriate management including the cutting of roots

(Satomura et al. 2005). We performed two experiments on container-grown *G. biloba* and *P. yedoensis*. In the first experiment, the effects of pruning mulch and daily irrigation on leaf photosynthesis were investigated from the rainy season to subsequent hot summer; the rainy season and summer season are from early June to late July and late July to late September, respectively, in a typical year in Kyoto city (Japan Meteorological Agency). In the second experiment, photosynthetic performance and the plant water status in relation to soil water content were monitored with reductions in soil water content in summer under controlled conditions.

Materials and methods

Site description and tree seedlings

This study was conducted in a glasshouse in Kyoto Institute of Technology (35°01′N, 135°41′E, 50 m of altitude). The climate of Kyoto city is warm temperate, with annual precipitation of 1490 mm and an annual mean temperature of 15.9 °C (Japan Meteorological Agency). Rainy season accounts for 29.5 % of annual rainfall, lasting from early June to late July, and is followed by a hot and clear summer season with daytime maximum temperatures regularly exceeding 30 °C, lasting to late September.

This study focused on two species of the deciduous broadleaved tall tree *Ginkgo biloba* L. and *Prunus* × *yedoensis* Matsum. (Figure 1a, b), the leaves of which begin to expand in April and fall in November. Stomatal density was higher in *P. yedoensis* than in *G. biloba* (230 and 110 stomata mm^{-2} for mature sun leaves, Fig. 1c, d).

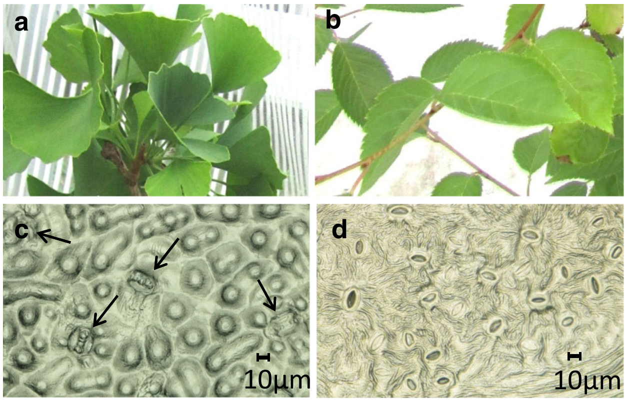

Fig. 1 Images of fully expanded mature leaves in June for *G. biloba* (**a**) and *P. yedoensis* (**b**), and microscopic images of stomata at the lower side of the leaves for *G. biloba* (**c**) and *P. yedoensis* (**d**). *Arrows* indicates stomata in *G. biloba.* Light photographs were obtained for the secondary replica using a digital microscope (VHX-1000, Keyence, Osaka, Japan)

Seedlings of the trees were grown under natural sunlight with a 50 % shading cloth in a glasshouse (7 m × 5 m × 5 m) in Kyoto Institute of Technology. In 2009, 150-cm tall, 3-year-old *P. yedoensis* seedlings (Nihon Kaki, Saitama, Japan) and 80-cm tall, 4-year-old *G. biloba* seedlings (Archinet, Tokyo, Japan) were obtained commercially. These seedlings were transplanted into 12-l Wagner pots with a diameter of 25.2 cm and depth of 30 cm (AlphaPurchase, Tokyo, Japan), filled with loamy soil:sand:muck soil = 2:2:1. Plants were irrigated daily and fertilized once a week with 500 mL of 1/500 nutrient solution (N:P:K = 6:10:5, Hyponex, USA) per container until the treatments were started. We selected nine healthy seedlings for each species, and pruned them in May 2010 so that they had similar numbers of leaves.

Irrigation and mulch treatments

Pruning mulch was made in 2009 from pruning of the *G. biloba* and *P. yedoensis* trees, which were planted on the campus of the Kyoto Institute of Technology. Pruned materials were dried for approximately 1 week and shredded into chips of approximately 2 cm in length using a chipper (Chipper & Shredder CSE 220-DC, Shindaiwa, Hiroshima, Japan), and their properties have been summarized in Table 1.

The effects of pruning mulch on evaporation from soil were tested in the glasshouse, using pots containing the same soil with the same thickness (5 cm) of pruning mulch as those used for plant growth. All pots were well-watered with 1.2 l of water on the first day of the experiment, and evaporation from soil was then estimated from weight lost from the pots for 4 days.

The pruning mulch and irrigation treatments were performed between June 19 and September 11, 2010 in the glasshouse with a 50 % shading cloth. Measurements were performed on the first day of the experiment (June 19) after all of the plants were well-watered. The irrigation and mulch treatments were started thereafter. We set the treatment of “irrigated once every 5 days with no mulch” as the control because Kyoto government irrigates roadside trees after 5 days without precipitation during the summer season. We compared the effects of the two treatments: (1) irrigated daily with 1.2 l of water with no mulch (well-watered) and (2) irrigated with 1.2 l of water once every 5 days with mulch (mulch) to control plants, for three plants for each treatment ($n = 3$). The thickness of the pruning mulch was 5 cm, which was previously determined to have no effect on soil oxygen levels (Hanslin et al. 2005). Atmospheric temperature, vapor pressure deficit (VPD), and PPFD in the glasshouse were monitored by a data logger (U23-002 and UA-002-64, Onset Computer Corporation, MA, USA) that was set 2 m above the

Table 1 Properties of soil and pruning mulch materials, and evaporation rate from soils with or without mulch materials

Materials	Soil in the pots	Pruning mulch from *G. biloba*	Pruning mulch from *P. yedoensis*
Water content (g g^{-1})	0.299	0.469	0.473
pH	6.9	7.8	6.2
EC (mS cm^{-1})	0.11	0.37	0.14
Evaporation rate (kg m^{-3} day^{-1})	8.0 (1.1)^{a}	2.7 (1.2)^{b}	2.5 (1.1)^{b}

Differences in the evaporation rate from soil were analyzed using a one-way ANOVA, tested by Tukey's test ($p < 0.05$). Different letters indicate that the difference was significant

Mean values (SD) were shown for the evaporation rate ($n = 4$)

floor, from which data were collected at 30-min intervals. The soil water content (SWC, g g^{-1}) was measured 3 weeks (rainy season) and 9 weeks (summer season) after the onset of the treatments, and was determined by weighing the pots daily from the second to fifth days after irrigation using the following equation: SWC = remaining water/maximum amount of water, where remaining water = maximum amount of water — water loss. The maximum amount of water available per container (SWC of 1.0 g g^{-1}) was obtained by subtracting the pot weight at the wilting point from that at field capacity for three sample plants of *G. biloba* and *P. yedoensis* after finishing the treatments, as described previously by Medrano et al. (2009). In the present study, SWC = 0 means the wilting point.

Leaf photosynthesis

The light-saturated CO_2 assimilation rate (A_{sat}) and stomatal conductance (g_s) were measured using a Li-6400 photosynthesis system (Li-Cor, NE, USA). In 2010, the effects of irrigation and mulch on leaf photosynthesis were investigated by measuring photosynthetic parameters between June and September every 3 weeks (0, 3, 6, 9, and 12 weeks) for two attached fully expanded mature leaves from three plants 3 days after irrigation ($n = 6$). Photosynthesis chamber conditions were set as follows: light provided from red–blue LED, 1500 µmol m^{-2} s^{-1} PPFD, leaf temperature, 25.0 °C, VPD, 1.1 kPa, and 380 µmol mol^{-1} of CO_2 supplied by a CO_2 mixer, considering that leaf photosynthesis by *G. biloba* and *P. yedoensis* was light-saturated at 1500 µmol m^{-2} s^{-1} PPFD, and the mean daily atmospheric temperature and VPD between June and September in an average year in Kyoto city are 25.5 °C and 1.1 kPa, respectively, with the daytime (6:00–18:00) atmospheric temperature being 26.6 °C (monthly values varied from 24.0 to 29.2 °C, Japan Meteorological Agency). The lowest atmospheric CO_2 concentration in the daytime was approximately 370 µmol mol^{-1} between June and September in Kyoto Institute of Technology in 1998 (Kawamukai et al. 2000), and was approximately 390 µmol mol^{-1} in 2009 in Nagoya city, Japan (Wada et al. 2011).

In summer (August) in Kyoto city, the maximum daytime temperature (33.3 °C) and VPD (3.7 kPa) are markedly higher than the average values of 25.5 °C and 1.1 kPa (Japan Meteorological Agency). The sensitivity of photosynthesis to this high temperature/VPD is an important trait for the acclimation of plants to the summer climate, and may be affected by the mulch or irrigation treatment. After 6 weeks of the treatments (the summer season), leaf photosynthesis was measured first at a leaf temperature of 25.0 °C and VPD of 1.1 kPa. Thereafter, they were increased to 35.0 °C and 3.1 kPa, and leaf photosynthesis was measured again after 30 min of acclimation. The chamber conditions were set at a light-saturated condition, 1500 µmol m^{-2} s^{-1} PPFD of light, and 380 µmol mol^{-1} of CO_2.

Leaf properties

Leaf area, leaf dry mass per leaf area, and the leaf carbon isotope discrimination (Δ) were measured after 9 weeks of the treatments for the leaves from which photosynthesis measurements were performed. Leaf area was measured using a scanner (Canoscan 9950F, Canon, Tokyo, Japan) and image analysis software (Image-J, National Institute of Health, MD, USA). These leaves were then dried at 60 °C for 48 h using an oven (MOV-112, SANYO Electric, Osaka, Japan), weighed to determine the dry mass, and then stored at room temperature in order to analyze the stable carbon isotope ratio ($\delta^{13}C_{leaf}$). Leaf Δ is a good indicator of long-term leaf water-use efficiency, which was determined as described by Kagotani et al. (2013). Δ was calculated as $\delta^{13}C_{air} - \delta^{13}C_{leaf}$, where $\delta^{13}C_{air}$ is the stable carbon isotope ratio of atmospheric CO_2 measured using an isotope mass spectrometer (Finnigan MAT 252, Bremen, Germany). In the $\delta^{13}C_{air}$ analysis, 2 l of air was collected at heights of 2 m from the floor of the glasshouse in the daytime, repeated at least three times on different dates. $\delta^{13}C_{leaf}$ was measured using the combined system of an elemental analyzer (EA1108, Carlo-Erba, Italy), interface (Finnigan MAT conflo II, Bremen, Germany), and isotope mass spectrometer (Finnigan MAT Delta S, Bremen, Germany) corrected with standards (Tayasu et al. 2011).

Effects of severe soil water stress on leaf water status and leaf photosynthesis

We conducted the second experiment in 2014 in order to compare the leaf water status and photosynthesis of *G. biloba* and *P. yedoensis* in response to severe soil water stress. The same container-grown seedlings used in 2010 ($n = 3$) were pruned to have similar numbers of leaves. We removed small branches to reduce leaf numbers, and removed twigs from the perimeter of the canopy using reduction cuts in order to achieve similar tree heights. They were grown in the glasshouse following the experiments in 2010 without mulch materials. All plants were well-watered on 4 June, and irrigation was then stopped between 5 June and 7 July. Soil water content was monitored by weighing the pots as described previously. Volumetric soil water content was also measured by soil moisture sensors (ECH_2O EC5, Decagon Devices, Pullman, WA, USA) with a data logger (EM50, Decagon Devices, Pullman, WA, USA). In order to obtain the plant water status, the midday leaf water potential was measured by a pressure chamber (Model 600, PMS Instrument Company, Albany, OR, USA) on two fully expanded mature leaves from three plants during soil water stress ($n = 6$). Regarding the measurement of relative leaf water content (RWC), two leaves were sampled from one plant in the morning and fresh weight (FW), turgid weight (TW), and dry weight (DW) were then determined. Relative water content (RWC, $n = 6$) was calculated according to Yamasaki and Dillenburg (1999), RWC = (FW − DW)/(TW − DW).

Severe water stress may affect photosynthetic biochemistry and, thus, alter photosynthetic parameters including A_{sat}, dark respiration rate, CO_2 compensation point, maximum carboxylation rate (V_{cmax}), and CO_2-saturated electron transport (J). These leaf photosynthetic parameters were estimated from the A/C_i curve fit (Ethier 2004; Ethier et al. 2006) and light response curve model (Ögren and Evans 1993) using a photosynthesis system (Li-6400, Li-Cor, Lincoln, NE, USA). Leaf temperature and VPD were set at 25 °C and 1.7 kPa, respectively. Light response curves were obtained at 400 µmol mol^{-1} of CO_2, while changing PPFD from 0 to 2000 µmol m^{-2} s^{-1}, in which PPFD was increased stepwise from 400 to 2000 µmol m^{-2} s^{-1}, and PPFD was then returned to 400 µmol m^{-2} s^{-1} and finally decreased stepwise to 0 µmol m^{-2} s^{-1}. A_{sat} and stomatal conductance (g_s) were obtained at PPFD of 1500 µmol m^{-2} s^{-1}. A/C_i curves were obtained at PPFD of 1200 µmol m^{-2} s^{-1} with 12 different CO_2 levels from 60 to 2000 µmol mol^{-1}, in which CO_2 was decreased stepwise from 400 to 60 µmol mol^{-1}, returned to 400 µmol mol^{-1}, and then increased stepwise to 2000 µmol mol^{-1}.

Statistical analysis

A two-way ANOVA was performed to reveal the effects of the treatments (control, pruning mulch, and irrigation) on soil water content (SWC) and photosynthetic parameters for the pruning mulch and irrigation experiments. Intrinsic water-use efficiency (A_{sat}/g_s) for the three ranges of g_s (<35, 35–65, and >65 % with respect to the species maximum) was calculated and then analyzed using the *t* test. In the severe water stress experiment, the mean values of photosynthetic parameters were calculated for SWC of <0.2, 0.2–0.4, and >0.6 g g^{-1}, and then analyzed using ANOVA. Differences between means were tested by Tukey's honest significant difference tests ($p < 0.05$). These statistical analyses were performed using R software (Rcmdr package, ver3.1.0).

Results

Environmental conditions

The treatments were conducted between 19 June and 11 September in 2010 (12 weeks) in the glasshouse. The rainy

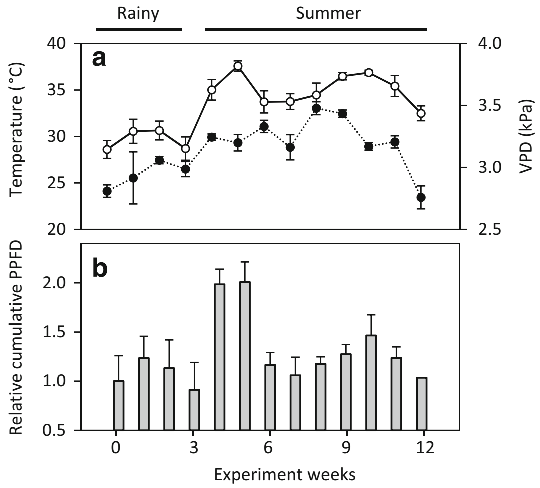

Fig. 2 Meteorological data during the experiment, obtained by data loggers at 30-min intervals. **a** Mean daytime (from 6:00 to 17:45) temperature and vapor pressure deficit (VPD). **b** Relative ratios of daily cumulative PPFD with respect to that on week 0 (6.1 mol m^{-2} day^{-1}). Values are the mean ± SE of seven daily mean values with 48 data points

Table 2 Effects of species (*G. biloba* and *P. yedoensis*) and treatments (control, mulch, and well-watered) on soil water content (SWC) and leaf photosynthetic parameters at light saturation, A_{sat} and g_s, at the rainy season and summer season

	Significance of effects (p)		
	Treatment	Species	Treatment × species
Rainy season			
SWC (g g^{-1})	<0.001	n.s. (0.47)	n.s. (0.58)
A_{sat} (μmol m^{-2} s^{-1})	n.s. (1.00)	n.s. (0.07)	n.s. (0.76)
g_s (mol m^{-2} s^{-1})	n.s. (0.78)	n.s. (0.47)	n.s. (0.49)
Summer season			
SWC (g g^{-1})	<0.001	n.s. (0.30)	n.s. (0.57)
A_{sat} (μmol m^{-2} s^{-1})	<0.001	n.s. (0.93)	n.s. (0.37)
g_s (mol m^{-2} s^{-1})	<0.001	<0.001	n.s. (0.84)

Differences in parameters were analyzed using a two-way ANOVA, with treatment and species as the factors. The degrees of freedom (d.f.) for species, treatments, interactions, and residuals were 1, 2, 2, and 65–102, respectively

season was between 13 June and 17 July in 2010 in Kyoto city; 0–3 weeks of the treatments were conducted in the rainy season, with a daytime temperature of 30.0 °C and daytime VPD of 3.00 kPa on average in the glasshouse ($n = 29$, Fig. 2). At 0 week, daily cumulative PPFD was 6.1 mol m^{-2} day^{-1}. Daytime temperature (35.1 °C), daytime VPD (3.22 kPa), and relative cumulative PPFD (1.34) in summer (from 4 to 12 weeks, $n = 57$) were significantly higher than those in the rainy season (t test, $p < 0.05$, Fig. 2).

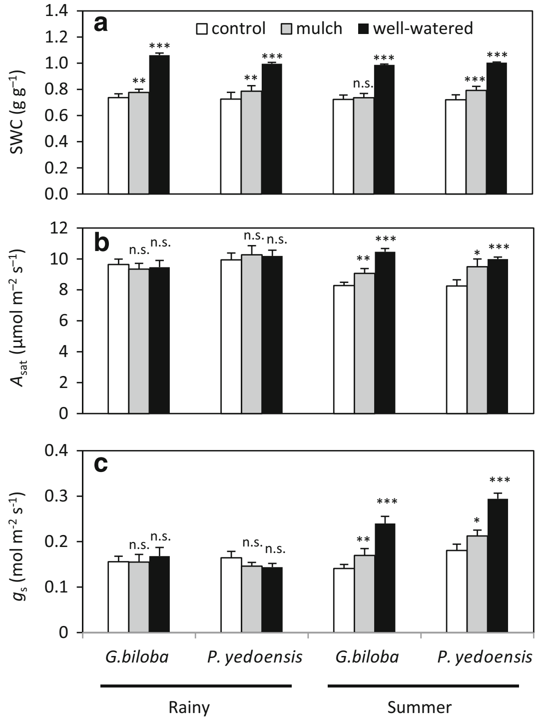

Fig. 3 Mean values ± SE of (**a**), soil water content (SWC), and gas exchange parameters such as (**b**), the light-saturated leaf photosynthesis rate (A_{sat}), and (**c**), stomatal conductance (g_s) in the rainy and summer seasons for *G. biloba* and *P. yedoensis*. Regarding SWC, values were estimated for three plants for 4 days ($n = 12$), and for the gas exchange parameters, they were estimated for two leaves from three plants for 2 or 3 weeks ($n = 12$ or 18). *Asterisks* indicate that values are significantly different from those of the controls (ANOVA, Tukey's test) with $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; and *n.s.* not significant. Regarding gas exchange measurements, photosynthesis chamber conditions were set at 1500 μmol m^{-2} s^{-1} PPFD of light, 25.0 °C of leaf temperature, 1.1 kPa of VPD, and 380 μmol mol^{-1} of CO_2

Effect of mulch and irrigation on soil water content and leaf photosynthesis

Pruning mulch had a significant effect on the evaporation rates in *G. biloba* and *P. yedoensis* (Table 1), with evaporation rates being reduced by 66 and 69 %, respectively.

The effects of the treatments on soil water content (SWC) were observed in the summer rainy season (from 19 June to 17 July) as well as in the summer dry season (from 18 July to 12 September), with similar effects being noted between species (Table 2). Mulch and irrigation increased SWC by 5–10 and 37–44 %, respectively (Fig. 3a).

In both species, the treatments had no effects on leaf gas exchange parameters in the rainy season (Table 2). In contrast, the treatments significantly affected leaf gas exchange parameters in both species in summer, with similar effects being observed between species (Table 2). Increases of 9–15 and 21–26 % were observed in the light-saturated leaf photosynthetic rate (A_{sat}) by mulch and irrigation, respectively (Fig. 3b). Stomatal conductance (g_s) was increased by 18–20 and 63–70 % by mulch and irrigation, respectively (Fig. 3c).

Improvements in A_{sat}/g_s are an important acclimation process to soil water stress, and are highly species-dependent (Medrano et al. 2002, 2009). We compared averaged A_{sat}/g_s between *G. biloba* and *P. yedoensis* for three g_s groups; <35, 35–65, and >65 % of the species maximum value (Fig. 4), considering that g_s may be used as an indicator of physiological water stress (Medrano et al.

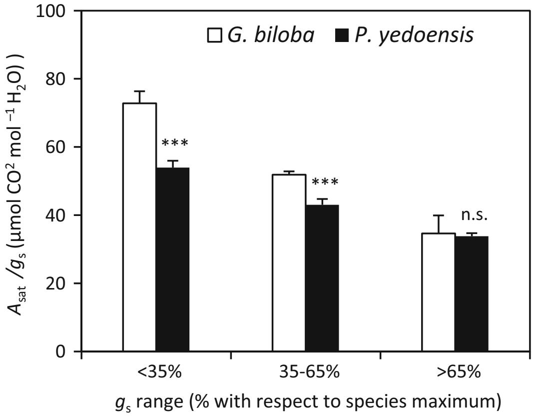

Fig. 4 Differences in photosynthetic water-use efficiency (A_{sat}/g_s) for three groups of stomatal conductance (g_s) between species. g_s values were calculated as % with respect to the maximum values of *G. biloba* and *P. yedoensis*. Values are mean ± SE for three plants, in which data were pooled for two leaves in the summer season (6, 9, and 12 weeks, 4–34 replicates). *Asterisks* indicate that values were significantly different between species (ANOVA, *t* test) with ***$p < 0.001$ and *n.s.* not significant. Photosynthesis chamber conditions are the same as those in Fig. 3

Table 3 Mean (SD) values of Δ, carbon isotope discrimination (‰) of the seedlings subjected to 9 weeks of the treatments

Treatments	*G. biloba*	*P. yedoensis*
Control	20.7 (0.6)	20.0 (0.2)^a
Pruning mulch	20.6 (1.2)	19.9 (0.2)^a
Irrigation	20.7 (0.3)	20.8 (0.7)^b

Two leaves were collected from three seedlings for measurements ($n = 6$). Differences in parameters were analyzed using a one-way ANOVA, tested by Tukey's test ($p < 0.05$)

2009). A_{sat}/g_s was significantly higher in *G. biloba* than in *P. yedoensis*, when g_s was <35 and 35–65 % of the species maximum (*t* test).

Leaf area and leaf dry mass per leaf area (LMA) were not affected by the treatments, and were 29.4 (4.6) and 25.3 (5.4) cm^2 and 78 (5) and 101 (7) g m^{-2} for *G. biloba* and *P. yedoensis*, respectively. In *G. biloba* seedlings, the effects of the treatments on leaf carbon isotope discrimination (Δ) were not clear (Table 3). Δ increased in *P. yedoensis* with the irrigation treatment.

Sensitivity of leaf photosynthesis to a temporal increase in leaf temperature/VPD

The sensitivity of leaf photosynthesis by *G. biloba* and *P. yedoensis* to a temporal high leaf temperature/VPD (35 °C/3.1 kPa) was estimated by comparing their gas exchange parameters with those measured at moderate temperature/VPD (25 °C/1.1 kPa) in the summer. The mulch or irrigation treatment had no significant effects on the sensitivity of leaf photosynthesis to the high leaf temperature/VPD (Table 4). In contrast, a highly significant species effect was noted (Table 4), with the sensitivity of A_{sat} and g_s being higher in *G. biloba* than in *P. yedoensis* (Fig. 5a, b). The decrease observed in A_{sat} was 17–24 % in *G. biloba*, but it was very small in *P. yedoensis* (Fig. 5a). The

Table 4 Effects of species (*G. biloba* and *P. yedoensis*) and treatments (control, mulch, and well-watered) on the sensitivity of photosynthesis to a temporal increase in VPD/temperature during photosynthetic measurements

	Significance of effects (*p*)		
	Treatment	Species	Treatment × species
Decrease in A_{max}	n.s. (0.60)	<0.001	n.s. (0.33)
Decrease in g_s	n.s. (0.16)	<0.001	n.s. (0.87)

Photosynthetic measurements were performed at light saturation, first at 25.0 °C of leaf temperature, 1.1 kPa of VPD. On the same day, leaf temperature and VPD were changed to 35.0 ± 0.2 °C and 3.1 ± 0.1 kPa, respectively, and leaf photosynthesis was measured again. Decreases in A_{max} and g_s at this high VPD/temperature were analyzed using a two-way ANOVA, with treatment and species as the factors. Degrees of freedom (d.f.) for species, treatments, interactions, and residuals were 1, 2, 2, and 30, respectively

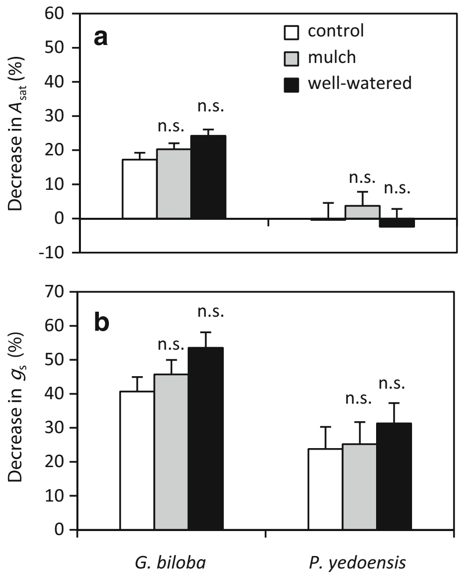

Fig. 5 Sensitivity of photosynthesis to a temporal high leaf temperature/VPD (33 °C/3.3 kPa) in *G. biloba* and *P. yedoensis*. Decreases in leaf gas exchange parameters were estimated by comparing them with those measured at a moderate temperature/VPD (25 °C/1.1 kPa) in the summer. **a** The light-saturated leaf photosynthesis rate (A_{sat}), and **b** stomatal conductance (g_s). Values are mean ± SE for two leaves from three plants ($n = 6$). The difference between treatments was analyzed by ANOVA using Tukey's test, with n.s. meaning no significant difference being obtained

decrease in g_s was also higher in *G. biloba* (by 41–54 %) than in *P. yedoensis* (24–31 %, Fig. 5b).

Effects of severe soil water stress on the leaf water status and photosynthesis

SWC was reduced from 1.0 to 0.09 g g^{-1} and from 1.0 to 0.04 g g^{-1} for *G. biloba* and *P. yedoensis*, respectively, during the experiment performed in 2014 (Fig. 6). SWC linearly correlated with volumetric soil water content in both species ($r^2 = 0.9$, $p < 0.05$), in which the volumetric soil water contents for *G. biloba* and *P. yedoensis* were 0.242 and 0.225 cm^3 cm^{-3} at field capacity, and 0.098 and 0.103 cm^3 cm^{-3} at the wilting point, respectively. Midday leaf water potential (Ψ_{day}) was constant against changes in SWC in *G. biloba* (Fig. 6a), but decreased with reductions in SWC in *P. yedoensis*. A similar result was obtained for changes in relative leaf water content (RWC) against SWC (Fig. 6b); RWC was constant in *G. biloba*, but decreased with reductions in SWC in *P. yedoensis*.

The responses of A_{sat}, g_s, and the CO_2 compensation point to SWC were similar between species; under low SWC (<0.2 g g^{-1}), A_{sat} and g_s were decreased by 41–69 %, while the CO_2 compensation point was increased by 30–52 % (Table 5). The responses of the dark respiration rate, CO_2-saturated electron transport rate (J), and maximum carboxylation rate (V_{cmax}) to SWC were obtained for *P. yedoensis* only; the dark respiration rate was increased by 33 %, while J and V_{cmax} were decreased by 31 % under low SWC.

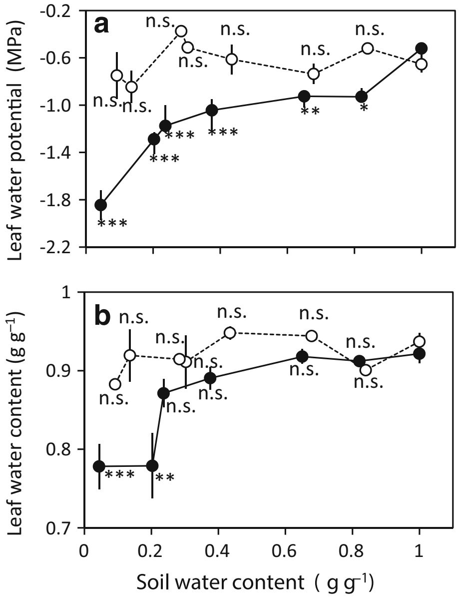

Fig. 6 Changes in midday leaf water potential (**a**) and relative leaf water content, RWC (**b**) with soil water content (SWC) during the severe water stress experiment. Values are mean ± SE for two leaves from three plants ($n = 6$). *Asterisks* indicate that values are significantly different from those at SWC of 1.0 g g^{-1} (field capacity, *t* test); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; and *n.s.* not significant. *Open* and *closed symbols* show *G. biloba* and *P. yedoensis*, respectively

Discussion

Effects of pruning much and irrigation on leaf photosynthesis

It is widely recognized that soil water content (SWC) is one of the most significant factors affecting leaf photosynthesis via a series of physiological mechanisms including stomatal regulation and/or photosynthetic biochemistry (Chaves and Oliveira 2004; Flexas et al. 2004; Chaves et al. 2009). SWC is strongly affected by evapotranspiration, which is the sum of soil evaporation and plant transpiration. Pruning mulch forms a physical layer between the soil and atmosphere, thereby preventing sunlight from reaching the soil surface and decreasing gas exchange, which ultimately results in decreases in soil surface temperature and evapotranspiration. Reduced soil evaporation (Table 1, Qin et al. 2013) and/or enhanced soil water retention (Cook et al. 2006) are among the benefits of organic mulch, resulting in an increase in SWC for field-grown urban trees (Iles and Dosman 1999; Montague and Fox 2008). Although the increase in SWC is partly compensated by plants through increased transpiration via the feedback mechanisms of stomata (Balwinder-Singh et al. 2011), we achieved a significant enhancement in SWC by the mulch treatment (Table 2; Fig. 3a), which is consistent with previous findings.

The responses of leaf photosynthesis to the pruning mulch and irrigation treatments were only obtained in the summer (Table 2; Fig. 3b, c), which is related to high SWC (Fig. 3a). This result suggests that photosynthetic responses to soil water stress are affected by atmospheric conditions, including irradiance levels, temperature, and VPD. In the summer, higher irradiance levels in daytime (by 30 %, Fig. 2b) together with higher daytime VPD (+0.22 kPa) involve a higher evaporative demand than that in the rainy season, during which the effects of SWC on stomatal conductance may be more significant. High VPD in the summer may induce high ABA levels in the leaf (McAdam and Brodribb 2015); high SWC has been shown to induce reductions in leaf ABA levels (Tardieu and Simonneau 1998), which may moderate the impact of high VPD on ABA levels. In the pruning mulch treatment, factors other than SWC, including a decrease in soil temperature (Iles and Dosman 1999; Cook et al. 2006), may benefit leaf photosynthesis by preventing a dysfunction in the root with the high summer temperatures. The effects of pruning

Table 5 Effects of soil water content (SWC g g^{-1}) on leaf photosynthetic parameters in the severe water stress experiment, obtained from A/C_i curve fitting (Ethier and Livingston 2004; Ethier et al. 2006) and the light response curve model (Ögren and Evans 1993)

	G. biloba			*P. yedoensis*		
Parameters	SWC < 0.2	0.2–0.4 of SWC	SWC > 0.6	SWC < 0.2	0.2–0.4 of SWC	SWC > 0.6
A_{sat} (μmol m^{-2} s^{-1})	6.0 (2.4)^{a}	9.3 (0.9)^{ab}	10.2 (2.5)^{b}	5.3 (1.2)^{a}	8.6 (2.1)^{b}	11.7 (2.1)^{c}
g_s (mol m^{-2} s^{-1})	0.074 (0.041)^{a}	0.157 (0.011)^{b}	0.168 (0.051)^{b}	0.061 (0.027)^{a}	0.145 (0.032)^{b}	0.196 (0.059)^{b}
CO_2 compensation point (μmol mol^{-1})	78.6 (16.2)^{a}	67.0 (8.9)^{ab}	60.5 (6)^{b}	80.4 (15.7)^{a}	59.1 (8.6)^{b}	52.9 (10.3)^{b}
Dark respiration rate (μmol m^{-2} s^{-1})	0.68 (0.42)^{a}	0.7 (0.16)^{a}	0.79 (0.24)^{a}	1.34 (0.17)^{a}	1.32 (0.23)^{a}	1.00 (0.22)^{b}
V_{cmax} (μmol m^{-2} s^{-1})	35.9 (7.3)^{a}	41.3 (4.2)^{a}	37.2 (4.2)^{a}	29.7 (7.3)^{a}	35.4 (5.9)^{ab}	43.1 (6.0)^{b}
J (μmol m^{-2} s^{-1})	72.3 (10.4)^{a}	82.5 (4.8)^{a}	77.1 (8.7)^{a}	57.9 (14.2)^{a}	72.6 (14)^{ab}	84.5 (11.2)^{b}

Mean values (SD) for three plants were calculated for three SWC classes of <0.2, 0.2–0.4, and >0.6 g g^{-1} ($n = 3$–9). Different letters indicate that the difference among SWC classes was significantly different (one-way ANOVA, $p < 0.05$). Leaf temperature and VPD were set at 25 °C and 1.7 kPa, respectively. A_{sat} and g_s were obtained at saturating light (1500 μmol m^{-2} s^{-1})

mulch on leaf photosynthesis may be obtained at near wilting point as well as SWC of ~0.7 g g^{-1} (Fig. 3a) due to the enhancement of SWC as well as decrease in soil temperature as discussed above.

The concurrent increases observed in A_{sat} and g_s for *G. biloba* and *P. yedoensis* in the summer by pruning mulch and irrigation (Fig. 3b, c) suggest that the increase in A_{sat} was affected by stomatal opening in both species, which supports previous findings of increases in the g_s of field-grown urban shrub trees by bark mulch and irrigation (Montague et al. 2007). In the summer, this stomatal opening by pruning mulch and irrigation may be accompanied by an increase in CO_2 supply to the carboxylation site. The enhancement induced in photosynthetic function by the pruning mulch and irrigation treatments suggests that the activity and health of roadside trees will be improved by these treatments, and thus, may contribute to maintaining tree canopies during the hot-dry summer.

The increase observed in leaf carbon isotope discrimination (Δ) in *P. yedoensis* by irrigation suggests that long-term water-use efficiency was decreased (Hanba et al. 2003) by the increase in SWC, thereby supporting the findings of Kagotani et al. (2013) in which Δ was larger in urban *P. yedoensis* grown at sites with higher SWC.

Difference in leaf photosynthetic and hydraulic responses between *G. biloba* and *P. yedoensis*

g_s values were smaller in *G. biloba* than in *P. yedoensis* in the summer in all the treatments tested when they were measured at moderate leaf temperature/VPD (Fig. 3c). The lower g_s in *G. biloba* than in *P. yedoensis* was also observed at SWC of >0.6 g g^{-1} in the second experiment (Table 5). These results suggested that, under summer conditions, the stomata of *G. biloba* acted to minimize water loss from the leaf. The decrease observed in g_s and A_{sat} in response to a temporal high temperature/VPD was markedly larger in *G. biloba* than in *P. yedoensis* with both treatments in the summer (Table 4; Fig. 5a, b), which supports previous finding showing that the sensitivity of stomata to VPD was the highest in *G. biloba* among the 13 species of C_3 plants including tree and herbaceous species (Franks and Farquhar 1999). This result again suggests that *G. biloba* has more effective stomatal control than *P. yedoensis* to minimize water loss from the leaf under conditions of high evaporative demand. *G. biloba* had higher A_{sat}/g_s at low g_s than *P. yedoensis* (Fig. 4), which is analogous to the evergreen woody shrub *Limonium* species with higher A_{sat}/g_s at lower g_s among Mediterranean plants (Galmés et al. 2007), suggesting effective stomatal regulation for water loss and a more suited photosynthetic machinery under water stress (Galmés et al. 2007; Medrano et al. 2009). Stomatal density was lower in *G. biloba* than in *P. yedoensis* (Fig. 1c, d), which is consistent with the findings of Medrano et al. (2009) who reported low stomatal density with high A_{sat}/g_s in *Limonium* species. Effective stomatal control with low stomatal density enables plants to prevent water loss and maintain leaf turgor under water stress conditions, thereby leading to the high-drought resistance of these plants.

Our severe water stress experiment showed that *G. biloba* actually maintained leaf turgor under a wide range of SWC; the midday leaf water potential and leaf water content in *G. biloba* was almost constant with significant decreases in SWC, while they were decreased significantly in *P. yedoensis* (Fig. 6a, b). Under mild water stress (SWC > 0.6 g g^{-1}), g_s was smaller in *G. biloba* than in *P. yedoensis* (Table 5). These results, together with the smaller g_s (Fig. 3c) and higher A_{sat}/g_s at low g_s (Fig. 4) in *G. biloba* in the first experiment, suggested that, under mild soil water stress, *G. biloba* shows "conservative water use," in which it maintains the midday leaf water potential with low g_s, while *P. yedoensis* exhibits "opportunistic water use," which allows for midday decreases in the leaf water potential in response to soil water stress with high g_s (Tardieu and Simonneau 1998; Moreno-Gutiérrez et al. 2012; Hochberg et al. 2013). Osone et al. (2014) reported higher soil-to-leaf hydraulic conductance in *G. biloba* than in *P. yedoensis* grown in streets. Under more severe water stress ($SWC < 0.4$ g g^{-1}), the effects of high leaf hydraulic conductance on the plant water relationship may become significant; it contributes to maintaining the high midday leaf water potential and leaf turgor in *G. biloba* (Fig. 6), and may also enable *G. biloba* to keep a similar g_s to that in *P. yedoensis* (Table 5).

In the severe water stress experiment, some responses of leaf biochemistry were different between species; V_{cmax} and J were down-regulated as SWC decreased in *P. yedoensis* only (Table 5). Declines in biochemical components, including the activities or levels of enzymes for carboxylation and electron transport, RuBP carboxylation capacity, and RuBP regeneration, have been shown to induce decreases in V_{cmax} and J by reducing SWC, with this response being strongly species-dependent (Bota et al. 2004; Galmés et al. 2011). Based on these results, we concluded that the photosynthetic machinery is more suited to severe water stress conditions in *G. biloba* than in *P. yedoensis*. On the other hand, both species showed an increase in the CO_2 compensation point with decreases in SWC (Table 5), which is often obtained in higher plants affected by changes in respiratory CO_2 (Lawlor and Cornic 2002).

Conclusions

Pruning mulch and irrigation significantly ameliorated the negative impact of moderate summer water stress (0.7 g g^{-1}) on leaf photosynthesis in *P. yedoensis* and *G. biloba* to a similar extent through increases in stomatal conductance via changes in soil water content (SWC). In the summer, *G. biloba* showed more effective stomatal control to prevent water loss from its leaves under high evaporative demand with high VPD/high irradiance levels. Additionally, *G. biloba* maintained a high midday leaf water potential and leaf water content against large variations in soil water content (from 0.08 to 1.0 g g^{-1}) with less reliance of leaf biochemistry on SWC, which suggest higher drought resistance in *G. biloba* than in *P. yedoensis*. Tree species selected in consideration of their tolerance to summer water stress, together with the management methods to increase soil water retention may significantly increase the leaf photosynthesis and evaporation rates of urban trees, and, thus, may help to improve the growth and mortality of planted trees.

Author contribution statement Y. Kagotani and Y. T. Hanba planned the experimental setup. T. Kiyomizu, K. Sasaki, and K. Nishida performed in vivo measurements in the severe water stress experiment. Y. Kagotani performed measurements in the mulch and irrigation experiment. Y. T. Hanba performed data analysis. Y. T. Hanba, A. Kume, and K. Nishida wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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