

## *Magnolia grandiflora* L. shows better responses to drought than *Magnolia × soulangeana* in urban environment

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Drought tolerance is becoming an increasingly important criterion for the selection of tree species, especially in urban areas characterized by low water availability. Apart from drought tolerance, the introduction of non-native species should be considered for new planting programs under such conditions to enhance the resilience of urban forests. The present study is aimed at evaluating the *in situ* physiological responses of *Magnolia grandiflora* and *Magnolia × soulangeana* to severe drought that frequently occurs in urban environments in the Southeastern Europe. Transpiration rate, stomatal conductance, intercellular CO<sub>2</sub> concentration, water-use efficiency and intrinsic water-use efficiency showed notable differences both between species and between the measured periods (wet and dry). Among the chlorophyll *a* fluorescence parameters, effective photochemical quantum yield of PS II, quantum yield of light-induced non-photochemical fluorescence quenching, quantum yield of non-regulated heat dissipation, fluorescence emission and index of susceptibility of leaves to light stress revealed significant differences both between the two species and the periods of measurements. The reduction of net photosynthesis in both magnolia species occurs as the result of non-stomatal limitation obtained by the reduction of electron transport rate coupled with simultaneous increase in intercellular CO<sub>2</sub> concentration. Moreover, *M. grandiflora* was the species less vulnerable to water shortage conditions, while *M. soulangeana* exhibited a photosynthetic capacity sensitive to drought-induced stress. *M. grandiflora* can therefore be considered as a promising alternative to *M. soulangeana* for urban sites under the predicted climate change scenarios.

**Keywords:** Chlorophyll *a* Fluorescence, Drought, Leaf Gas Exchange, Photosynthesis, Urban Tree Selection

### Introduction

Urban ecosystems pose multiple challenges for trees to cope with (Sjöman et al. 2018a). Among the various environmental factors occurring in urban settlements, drought was being recognized as one of the most frequent and threatening constraint, resulting from the combination of water deficit and high temperatures (Kleerekoper et al. 2012), thereby causing serious damages and a premature mortality of urban trees (Wang et al. 2019). Apart from directly influencing the tree by inhibiting its growth through reduced photosynthetic rates, drought has additional indirect impacts as well, e.g., by predisposing trees to pathogens (Dale & Frank 2017) and pollutants (Coccozza et al. 2019).

The severity of the negative effects on plants is related to the intensity, duration, and course of progression of drought stress (Chaves et al. 2009). In plants subjected to mild to moderate drought, stomatal control is the major physiological mechanism preventing excessive water loss, causing an overall reduction of photosynthesis and consequently the inhibition of plant growth (Xu et al. 2010). Under more severe drought stress, metabolic and biochemical limitations may occur and re-

duce CO<sub>2</sub> assimilation rates; these processes include the inhibition of Rubisco enzyme activity, damage of chlorophyll or photosystems, and a decrease in the capacity to generate ATP (Changhai et al. 2010).

Under drought conditions, PSII photochemistry of plants can be affected, and parameters of chlorophyll *a* fluorescence were shown to be rapid, highly sensitive and non-destructive tool for detecting species, genotypes and provenances with tolerant or susceptible behavior (Coccozza et al. 2016, Vastag et al. 2020). While early phases of drought were observed to impose slight changes on PSII, more progressive drought was noted to cause a depletion of PSII core and inhibit electron transport chain from the donor side of PSII to PSI, indicating non-stomatal inhibition of photosynthesis (Giardi et al. 1996).

The responses of plants in such conditions have been observed to be species-specific (Sjöman et al. 2018b, Vastag et al. 2019) due to differences in leaf morphology and physiology. For example, a significant decrease in photosynthetic activity in *Ginkgo biloba* L. was detected, which resulted in higher sensitivity to drought compared to *Fraxinus chinensis* Roxb. (Wang et

al. 2019). Furthermore, several studies have evidenced that provenances and species originating from drier climate perform better under drought condition (Pšidová et al. 2015, Wang et al. 2017). For instance, investigation of the drought tolerance of *Quercus ilex* L., *Q. pubescens* Willd., and *Q. robur* L., showed that the Mediterranean oak species, despite a reduction of light-saturated net photosynthesis (Cocozza et al. 2020), maintained higher photosynthetic activity compared to Central-European oak species (Früchtenicht et al. 2018).

In the South-East Europe the climate scenarios, according to the medium-high emission baseline (A1B – IPCC 2007), project an increase of average air temperature from 2.4 °C up to 3.4 °C, along with a 30% reduction of average rainfall until the end of the 21<sup>st</sup> century, and the negative impact of drought will very likely become even more heightened. Under such harsh conditions, the physiology of trees will be affected, and this, in turn, could further impact the broad range of benefits they provide for humans ranging from shading streets to carbon sequestration (Sjöman et al. 2018a).

To mitigate the negative effects of climate change, the evaluation of drought tolerance of tree species should be mainly contemplated for the selection plantation in urban ecosystems (Vogt et al. 2017, Sjöman et al. 2018a). In this context, the introduction of non-native species should be considered in new planting programs, alongside the use of drought-tolerant autochthonous species, as it has been noted that high species diversity contributes to increasing resilience and reducing the maintenance requirements of urban forests under abiotic and biotic challenges (Kendal et al. 2014).

The *Magnolia* genus of the Magnoliaceae family includes 224 ornamental species (Grimshaw & Bayton 2009), and its planting in urban areas has increased significantly over the past decade. In Southeast Europe, *Magnolia × soulangeana* Soul.-Bod., a deciduous hybrid of *Magnolia denudata* Desr. and *Magnolia liliflora* Desr., is a very common species in urban parks, while *Magnolia grandiflora* L., an evergreen species native to the southern United States (Cvjetičanin et al. 2016), is encountered less often. However, as the distribution of forest tree species is generally expected to shift northwards in response to climate warming (Parmesan 2006), a similar expansion of the distribution of *M. grandiflora* could be expected in the future, increasing its frequency in Southeast Europe as well.

As both of these species have a high ornamental value, most literature deals mainly with their aesthetic qualities (Cvjetičanin et al. 2016). However, the selection of tree species for urban ecosystems should include other important factors, such as the microclimatic conditions of the respective site and the physiological performance of the species concerning stress factors (Vogt et al. 2017). Notably, understanding the interaction between the physiology of plants and their surrounding environment is essential for establishing better management strategies to alleviate stress conditions for the species (Sjöman et al. 2018a), especially in urban areas where these stressors are even more amplified and combined. Despite the wide range of research possibilities posed in urban environments, the physiological performance of trees, including the *Magnolia* genus, remains scarcely explored and understood (Wang et al. 2019). To support tree selection for urban

areas in temperate climate and prevent mistakes in planning, which could result in high ecological and economic costs, the Citree database was developed (Vogt et al. 2017). However, Vogt et al. (2017) noted that additional field experiments should be included in the database, especially for aspects that have not been thoroughly investigated, such as the drought tolerance of species.

The present study was aimed to investigate the physiological response to naturally occurring severe drought of *M. grandiflora* and *M. soulangeana* planted in the urban area of Novi Sad, Serbia, South-East Europe. Tree responses were determined through accurate, reliable and non-invasive tools by estimating: (i) the photosynthetic function of plants under drought, to analyze the photosynthetic processes and detect water efficient and stress tolerant species (Wang et al. 2018); (ii) the effects of stress on photochemistry (Pšidová et al. 2018). We hypothesized that drought might (1) negatively affect leaf gas exchange and chlorophyll *a* fluorescence in both magnolia species, by indicating tolerant and/or vulnerable drought behavior, (2) induce the non-stomatal regulations with consequent inhibition of net photosynthesis, and (3) less affect the photosynthetic performance of a species from drier climate than of a more humid site.

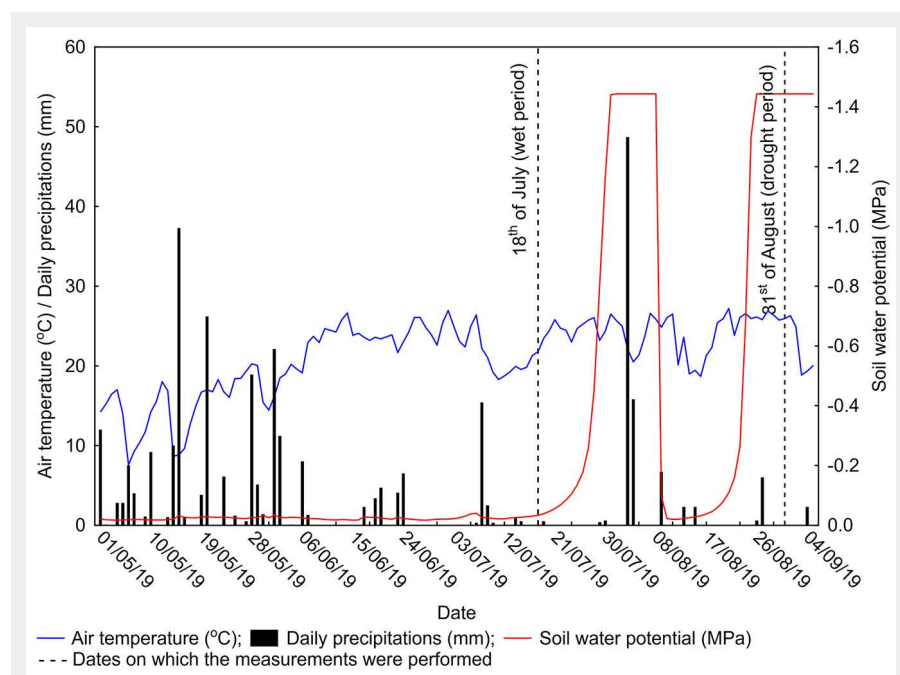
## Material and methods

### Study area and species

The present study was conducted in the urban green space of Novi Sad, the second largest city of Serbia (45° 15' 10" N, 19° 50' 53" E), characterized as a pocket park (Rakhshandehroo & Yusof 2014). At the studied locality, ten adult *M. grandiflora* L. and *M. soulangeana* Soul.-Bod. trees were chosen for the evaluation of physiological responses. Tree selection was based on visual impression, namely all chosen trees were vigorous, without dying branches, insect infestation, or mechanical damage (Moser et al. 2016). *M. grandiflora* trees were planted in a single linear row alongside a walkway in direction of West-East with a planting space of 3 m between them. On the other hand, *M. soulangeana* trees were arranged in double linear rows alongside a walkway in direction of North-South and a planting space of 4 m. Both species were planted in a common green space covered with grass and in full sunlight. For assessing the *in situ* physiological status of the two magnolia species in urban environment, leaf gas exchange and chlorophyll *a* fluorescence parameters were measured in wet (18<sup>th</sup> of July 2019) and drought (31<sup>st</sup> of August 2019) periods.

### Meteorological data

Monitoring of mean air temperature (°C) and daily precipitation (mm) was carried out at the nearby meteorological station Rimski Šančevi (45° 20' N, 19° 51' E, altitude



**Fig. 1** - Mean daily air temperatures (°C), total daily precipitation (mm) and soil water potential (MPa) during the period from May 1 to September 4, 2019.

84 m a.s.l.) from May 1 to September 4, 2019. The soil water potential (SWP) was measured using calibrated gypsum blocks (Delmhorst Inc., Towaco, NJ, USA) positioned at 50 cm soil depth, with measurements at 30 s intervals stored in a MicroLog SP3<sup>®</sup> datalogger (EMS, Brno, Czech Republic).

The wet period measurement was performed on July 18, 2019 after 10 days of SWP values below -0.4 MPa and mean air temperatures ranging between 19.2 °C and 22.2 °C, with the maximum temperature never reaching 30 °C. The drought period measurement was performed on the August 31, 2019 after six days of SWP values below -1.4 MPa and mean air temperatures between 25.8 °C and 26.9 °C, with the maximum air temperature exceeding 30 °C (characterized as severe drought period according to Liu et al. 2010 – Fig. 1).

#### Leaf gas exchange measurement

The measurements of net photosynthesis ( $A$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), transpiration rate ( $E$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ), stomatal conductance ( $g_s$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ), and intercellular  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol mol}^{-1}$ ) were taken using a CIRAS-3<sup>®</sup> portable photosynthesis system (PP Systems, Amesbury, MA, USA). In order to minimize differences in light exposure, exposed, outward-facing leaves on exterior branches in the upper reaches of the trees were chosen. During the measurements, the photosynthetic active radiation (PAR) was set to 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  while humidity, temperature, and the concentration of  $\text{CO}_2$  depended on the ambient conditions of study site. Following leaf stabilization in the CIRAS-3 chamber, the abovementioned parameters were recorded from 9:00 a.m. to 11:00 a.m. Water use efficiency (WUE,  $\mu\text{mol mmol}^{-1}$ ) was computed as the ratio of  $A$  to  $E$  (Farquhar & Sharkey 1982), and intrinsic water-use efficiency (WUEi,  $\mu\text{mol mol}^{-1}$ ) was derived as the ratio of  $A$  to  $g_s$  (Flexas et al. 2013). The leaf gas exchange parameters were determined for all ten plants of each species, with measurements taken in the order of 5 specimens of *M. grandiflora* followed by five specimens of *M. soulangeana*, etc. The same leaves were subsequently used for assessing the pulse amplitude modulated chlorophyll *a* fluorescence, with three replications per leaf.

#### Pulse amplitude modulated (PAM) fluorescence measurements

The photosynthetic activity of PSII was measured using a PAM-2500<sup>®</sup> portable chlorophyll fluorometer (Walz GmbH, Effeltrich, Germany) between 9:00 and 11:00 a.m. Before taking the measurements, the selected leaves were dark-acclimated for 15 minutes using leaf clips. The rapid light curves (RLC) were derived using nine increasing actinic illumination steps (0, 144, 274, 477, 788, 1163, 1389, 2018, 2443  $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ). The duration of each actinic illumination step was 10 s, and the steps were separated by a white saturating flash of

**Tab. 1** - The studied computed pulse amplitude modulated fluorescence parameters.

Abbrev.	Equation	Definition of the derived parameters
$\Phi_{\text{PSII}}$	$F_m' - F_t / F_m'$	Effective photochemical quantum yield of PS II (Genty et al. 1989)
Y(NPQ)	$F_t / F_m' - F_t / F_m$	Quantum yield of light-induced non-photochemical fluorescence quenching (Genty et al. 1996)
Y(NO)	$F_t / F_m$	Quantum yield of non-regulated heat dissipation and fluorescence emission (Genty et al. 1996)
(1-qP)/NPQ	$(1 - qP) / NPQ$	Index of susceptibility of leaves to light stress (Osmond 1994)
qP	$(F_m' - F_t) / (F_m' - F_o')$	Coefficient of photochemical quenching (Schreiber et al. 1986 as formulated by Van Kooten & Snel 1990)
ETR	$PAR \cdot 0.84 \cdot 0.5$	Rate of electron transport (Genty et al. 1989)

$\sim 3000 \mu\text{mol m}^{-2} \text{s}^{-1}$  lasting 0.8 s. In addition, the studied PAM fluorescence parameters were computed (Tab. 1). Rapid light-response curves of chlorophyll *a* fluorescence were constructed by plotting the  $\Phi_{\text{PSII}}$ , Y(NPQ), Y(NO), (1-qP)/NPQ, qP and ETR versus the increasing actinic irradiance (from 1 to 2443  $\mu\text{mol e m}^{-2} \text{s}^{-1}$  – Vastag et al. 2020). The RLCs were quantified as follows: (i) maximal electron transport rate ETRmax ( $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ) for  $\text{RLC}_{\text{ETR}}$ ; ETRmax was calculated automatically according to internal equation (Eilers & Peeters 1988) and reflects the light-saturated capacity of the sample; (ii) the area below the curve for  $\text{RLC}_{\text{PSII}}$ ; (iii) the value records at high light intensity (2443  $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ) for  $\text{RLC}_{\text{NPQ}}$ ,  $\text{RLC}_{\text{Y(NPQ)}}$ ,  $\text{RLC}_{\text{Y(NO)}}$ ,  $\text{RLC}_{(1-qP)/NPQ}$  and  $\text{RLC}_{\text{qP}}$  (Pšidová et al. 2018).

#### Statistical analysis

Statistical analysis of the leaf gas exchange and chlorophyll *a* fluorescence parameters was conducted using Statistica v. 13 (TIBCO Software Inc. 2017) and R v. 3.6.3 (R Core Team, Austria). The differences between the two parameters were tested using two-way ANOVA, with the period (wet or dry) and species (*M. grandiflora* and *M. soulangeana*) set as fixed factors. The fol-

lowing model was used (eqn. 1):

$$y_{ijk} = P_i + S_j + P_i \times S_j + \varepsilon_{ijk} \quad (1)$$

where  $y_{ijk}$  represents the measured value of the phenotype,  $P_i$  is the effect of the  $i^{\text{th}}$  period,  $S_j$  is the effect of the  $j^{\text{th}}$  species,  $P_i \times S_j$  is the interaction between the period and the species, and  $\varepsilon_{ijk}$  is the experimental error. Significant differences between the means were evaluated using Tukey's honestly significant difference (HSD) test with  $P \leq 0.05$ . Prior to the statistical analysis, the normality of data distribution was tested, with the transformation considered necessary for several parameters. All parameters were shown in the form of a bar diagram with means  $\pm$  standard errors drawn by Statistica v. 13 (TIBCO Software Inc. 2017).

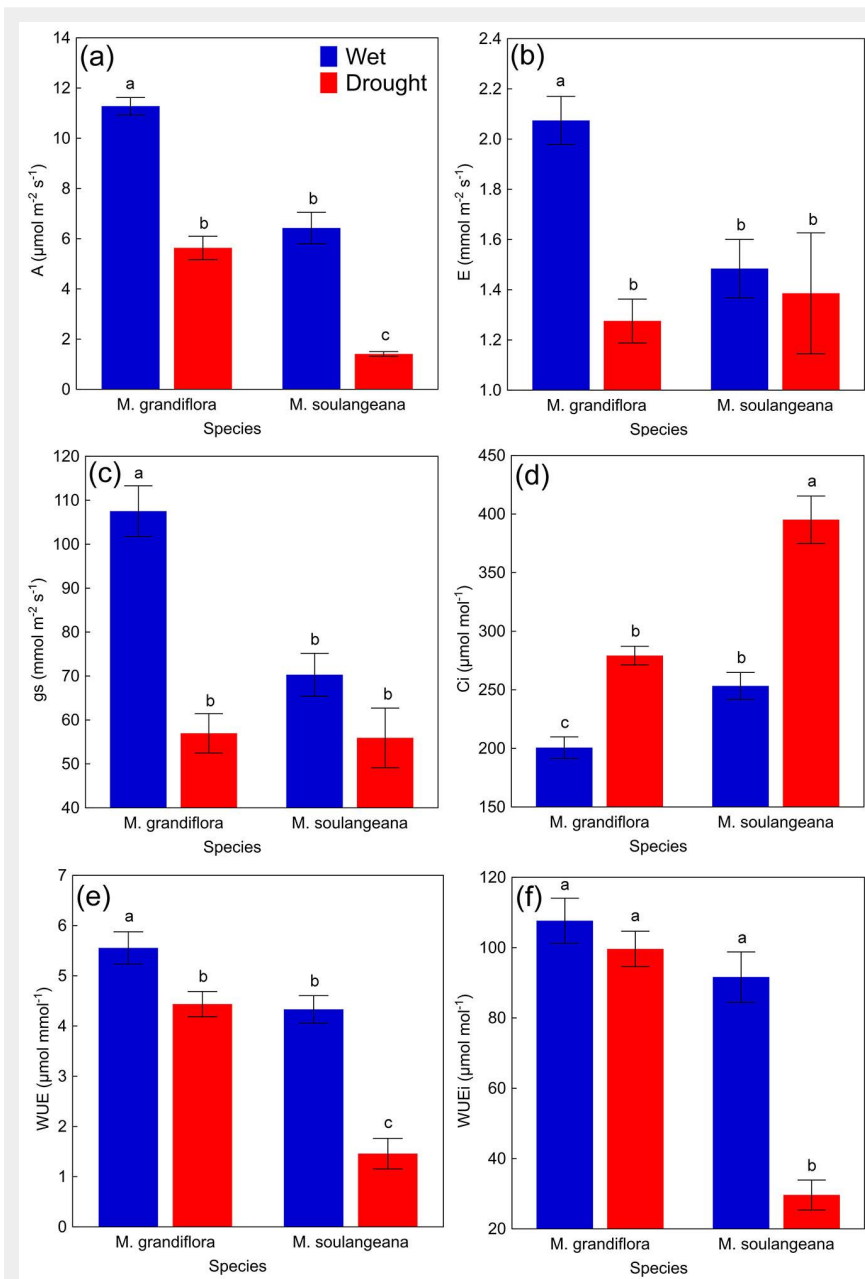
## Results

#### Leaf gas exchange

Leaf gas exchange parameters were significantly affected by environmental conditions in the considered period and site (Tab. 2).  $A$ ,  $C_i$ , WUE, and WUEi significantly changed between species. Furthermore, the interaction of species  $\times$  period exhibited a significant effect on all observed leaf

**Tab. 2** - Results of two-way ANOVA showing the effects of species (S), period (P), and their interaction ( $S \times P$ ) on the observed leaf gas exchange parameters. (A): net photosynthetic rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); (E): rate of transpiration ( $\text{mmol m}^{-2} \text{s}^{-1}$ ); ( $g_s$ ): stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ ); ( $C_i$ ): intercellular  $\text{CO}_2$  concentration ( $\mu\text{mol mol}^{-1}$ ); (WUE): water use efficiency ( $\mu\text{mol mmol}^{-1}$ ); (WUEi): intrinsic water use efficiency ( $\mu\text{mol mol}^{-1}$ ); (df): degrees of freedom.

Source of variation	df	Stat	A	E	$g_s$	$C_i$	WUE	WUEi
Species (S)	1	F	101.9	2.60	3.50	41.3	30.6	23.6
		P	<0.001	0.115	0.070	<0.001	<0.001	<0.001
Period (P)	1	F	140.4	9.10	12.7	70.5	27.4	16.4
		P	<0.001	<0.05	<0.001	<0.001	<0.001	<0.001
$S \times P$	1	F	0.44	5.60	8.30	5.80	5.10	9.50
		P	0.510	<0.05	<0.05	<0.05	<0.05	<0.05
Error	36	-	-	-	-	-	-	
Total	39	-	-	-	-	-	-	



**Fig. 2** - Leaf gas exchange parameters of *M. grandiflora* and *M. soulangeana* measured during the wet period and a drought period. (a) net photosynthetic rate ( $A$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ); (b) rate of transpiration ( $E$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ); (c) stomatal conductance ( $g_s$ ,  $\text{mmol m}^{-2} \text{s}^{-1}$ ); (d) intercellular  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol mol}^{-1}$ ); (e) water use efficiency ( $\text{WUE}$ ,  $\mu\text{mol mmol}^{-1}$ ); (f) intrinsic water use efficiency ( $\text{WUE}_i$ ,  $\mu\text{mol mol}^{-1}$ ). All values are presented as means  $\pm$  standard errors ( $n = 10$ ). Different letters indicate significant differences ( $p \leq 0.05$ ) between the values after Tukey's HSD test.

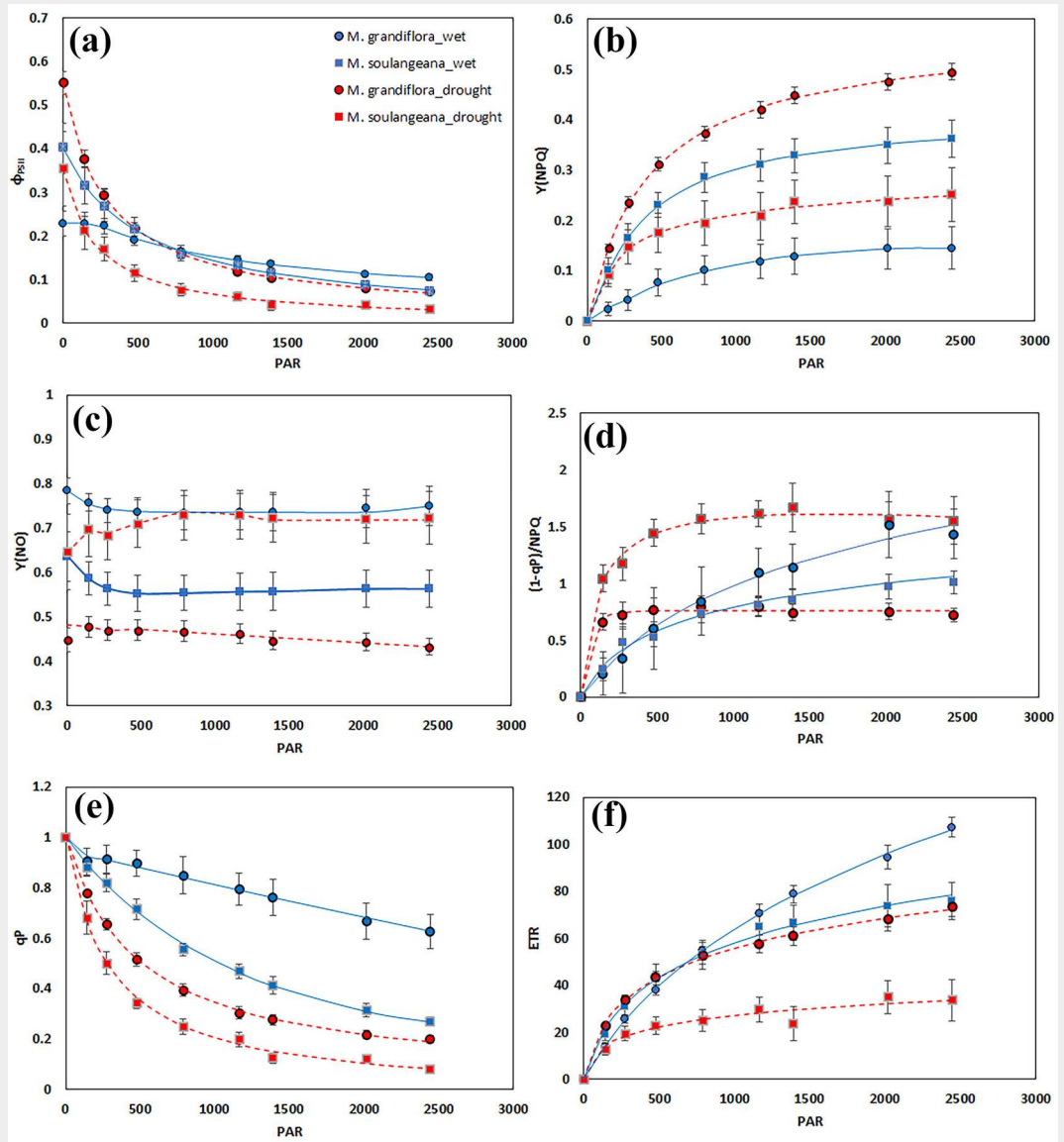
**Tab. 3** - Results of two-way ANOVA showing the effect of species, period, and their interaction (species  $\times$  period) on the observed parameters of chlorophyll *a* fluorescence at high light intensity ( $2443 \mu\text{mol e m}^{-2} \text{s}^{-1}$ ). ( $\Phi_{\text{PSII}}$ ): effective photochemical quantum yield of PS II (relative units); ( $Y(\text{NPQ})$ ): quantum yield of light-induced non-photochemical fluorescence quenching (relative units); ( $Y(\text{NO})$ ): quantum yield of non-regulated heat dissipation and fluorescence emission (relative units); ( $(1-qP)/\text{NPQ}$ ): index of susceptibility of leaves to light stress (relative units); ( $qP$ ): coefficient of photochemical quenching (relative units); ( $\text{ETR}_{\text{max}}$ ): maximum electron transport rate ( $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ); ( $df$ ): degrees of freedom.

Source of variation	df	Stat	$\Phi_{\text{PSII}}$	$Y(\text{NPQ})$	$Y(\text{NO})$	$(1-qP)/\text{NPQ}$	$qP$	$\text{ETR}_{\text{max}}$
Species (S)	1	F	7.66	2.09	2.22	10.1	96.6	21.0
		P	<0.01	0.157	0.144	<0.01	<0.001	<0.001
Period (P)	1	F	6.83	17.7	5.14	0.58	56.2	24.9
		P	<0.05	<0.001	<0.05	0.45	<0.001	<0.001
S $\times$ P	1	F	11.2	52.1	37.8	27.0	2.01	0.18
		P	<0.01	<0.001	<0.001	<0.001	0.166	0.669
Error	36	-	-	-	-	-	-	-
Total	39	-	-	-	-	-	-	-

gas exchange parameters except for *A*. These results point to a different drought response of the examined species.

Drought significantly reduced *A* and *WUE*, and increase *C<sub>i</sub>* in both species (Fig. 2a, Fig. 2e, Fig. 2d). In detail, *M. grandiflora* decreased *E* and *g<sub>s</sub>* (reduction of 38.2% and 47.0%, respectively), whereas *M. soulangeana* maintained stable but overall low *E* and *g<sub>s</sub>* values (reduction of only 6.1% and 7.6%, respectively) during the drought period (Fig. 2b, Fig. 2c). *M. grandiflora* exhibited a higher decrease in *E* and *g<sub>s</sub>*, while *M. soulangeana* showed generally weak performance under both measured periods. Furthermore, *M. soulangeana* exhibited significantly lower values of *WUE<sub>i</sub>* (reduction of 67.65%) during drought in comparison to the wet period, while *WUE<sub>i</sub>* values in *M. grandiflora* were not significantly changed by severe drought (reduction of only 7.47% – Fig. 2f).

**Fig. 3** - Chlorophyll *a* fluorescence parameters generated by RLCs as a function of photosynthetically active radiation (PAR,  $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ) measured in *M. grandiflora* and *M. soulangeana* during the wet period (blue lines) and the drought period (red lines). (a) Effective photochemical quantum yield of PS II ( $\Phi_{\text{PSII}}$ , relative units); (b) quantum yield of light-induced non-photochemical fluorescence quenching ( $Y(\text{NPQ})$ , relative units); (c) quantum yield of non-regulated heat dissipation and fluorescence emission ( $Y(\text{NO})$ , relative units); (d) index of susceptibility of leaves to light stress ( $(1-qP)/\text{NPQ}$ , relative units); (e) coefficient of photochemical quenching ( $qP$ , relative units); (f) electron transport rate (ETR,  $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ).



#### Pulse amplitude modulated (PAM) fluorescence

The result of two-way ANOVA showed significant differences in  $\Phi_{\text{PSII}}$ ,  $(1-qP)/\text{NPQ}$ ,  $qP$  and  $\text{ETR}_{\text{max}}$  among the two magnolia species, while no significant changes were detected for  $Y(\text{NPQ})$  and  $Y(\text{NO})$  (Tab. 3). The analysis of the period (wet and dry) exhibited significant effect on all observed chlorophyll *a* fluorescence parameters, except for  $(1-qP)/\text{NPQ}$ . Furthermore, the interaction of the species and period significantly influenced  $\Phi_{\text{PSII}}$ ,  $Y(\text{NPQ})$ ,  $Y(\text{NO})$  and  $(1-qP)/\text{NPQ}$  parameters, while no significant effect was observed on  $qP$  and  $\text{ETR}_{\text{max}}$ .

Observing the RLC of  $\Phi_{\text{PSII}}$ , *M. grandiflora* showed higher values (until  $477 \mu\text{mol e m}^{-2} \text{s}^{-1}$ ) during drought compared to wet period, after which it has declined, while *M. soulangeana* exhibited lower values in drought, throughout all observed light intensities (Fig. 3a). Drought induced reduction of  $\Phi_{\text{PSII}}$  was observed in *M. soulangeana*, while no differences were found in *M. grandiflora* (Fig. 4a). In case of  $Y(\text{NPQ})$ , *M.*

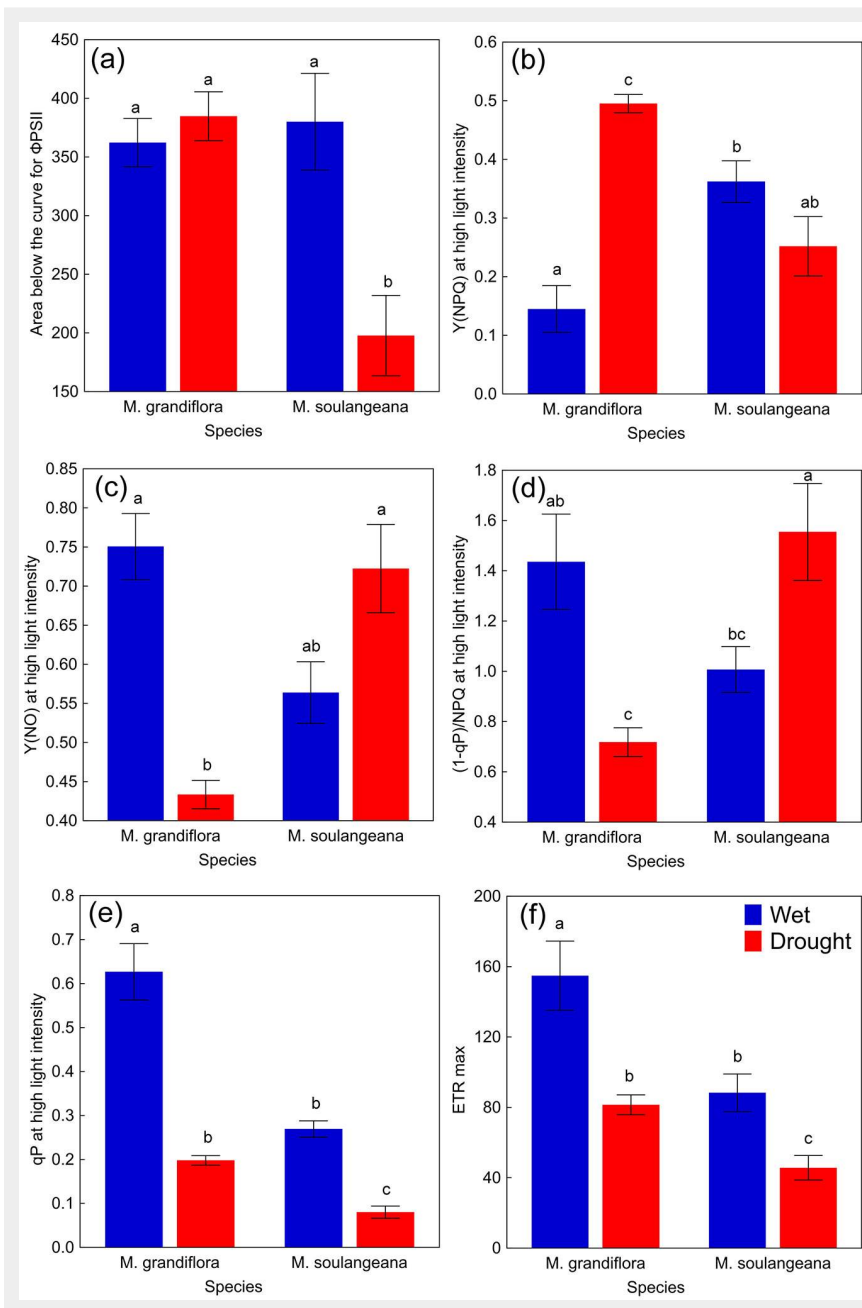
*grandiflora* showed higher values, while *M. soulangeana* lower values during drought (Fig. 3b). The values at high light intensity of RLC showed proportionally greater increase of  $Y(\text{NPQ})$  during drought period in *M. grandiflora*, compared to the decrease for *M. soulangeana*.

Furthermore,  $Y(\text{NO})$  values of *M. grandiflora* were lower than in *M. soulangeana* during drought (Fig. 3c). According to the highest light intensities assessed, the reduction of  $Y(\text{NO})$  in *M. grandiflora* was statistically significant, while the increase in *M. soulangeana* was shown to be less significant (Fig. 4c). Considering  $(1-qP)/\text{NPQ}$ , *M. grandiflora* exhibited higher values (until  $477 \mu\text{mol e m}^{-2} \text{s}^{-1}$ ) during drought period compared to wet period, after which it has declined, while *M. soulangeana* showed increased values in drought over the irradiance range (Fig. 3d, Fig. 4d). A reduction of  $qP$  was observed in both magnolia species under severe drought as compared to the wet period (Fig. 3e, Fig. 4e). However, the reduction in values of the parameter  $qP$  in *M. grandiflora* during drought were similar

to the values of *M. soulangeana* during wet period. Furthermore, drought reduced  $\text{ETR}_{\text{max}}$  in *M. soulangeana*, while in *M. grandiflora* higher values were found until light intensity of  $788 \mu\text{mol e m}^{-2} \text{s}^{-1}$  compared to wet period, after which it showed the opposite ranking (Fig. 3f). At high intensities, the reduction of  $\text{ETR}_{\text{max}}$  was found in both magnolia species, where *M. grandiflora* during drought and *M. soulangeana* during wet period showed the same range of values (Fig. 4f).

#### Discussion

The present study showed the adversely effects of the naturally occurring severe drought period on net photosynthetic rate (A) in both magnolia species grown in urban environment. Even though A was significantly reduced in both species, *M. grandiflora* managed to maintain higher rates. This is advantageous on multiple counts, allowing an increased metabolic activity like the synthesis of sugars, amino acids, proteins, nucleic acids and lipids, all of them being essential for the growth and repair



**Fig. 4** - The parameters of chlorophyll *a* fluorescence at high light intensity ( $2443 \mu\text{mol e m}^{-2} \text{s}^{-1}$ ) for *M. grandiflora* and *M. soulangeana* during the wet period and the drought period. (a) Effective photochemical quantum yield of PS II ( $\Phi_{PSII}$ , relative units); (b) quantum yield of light-induced non-photochemical fluorescence quenching ( $Y(NPQ)$ , relative units); (c) quantum yield of non-regulated heat dissipation and fluorescence emission ( $Y(NO)$ , relative units); (d) index of susceptibility of leaves to light stress  $((1-qP)/NPQ)$ , relative units); (e) coefficient of photochemical quenching ( $qP$ , relative units); (f) maximum electron transport rate ( $ETR_{max}$ ,  $\mu\text{mol e m}^{-2} \text{s}^{-1}$ ). All values are presented as means  $\pm$  standard errors ( $n = 10$ ). Different letters indicate significant differences ( $p \leq 0.05$ ) between means after Tukey's HSD test.

of damaged tissues (Percival et al. 2006). Similarly to our findings, many studies observed significantly reduced *A* rates in urban areas, which are characterized by limited water availability (Percival et al. 2006, Osone et al. 2014) and sealed surfaces (Wang et al. 2019).

The reduction of *A* under drought has been addressed to the protective mechanism of plants to avoid damage due to dehydration and hydraulic failure (Osone et al. 2014). During water shortage the roots are unable to penetrate in the deeper layers to find water resources and are left with low water supply, especially in urban areas where the soil is more compacted than in natural sites (Malmivaara-Lämsä & Fritze 2003). The prompt response of stomata to environment constraints through stomatal regulation, the disruption in the  $\text{CO}_2$  supply caused by stomatal closure, is being addressed as the main cause of de-

creased photosynthesis under mild to moderate drought (Xu et al. 2010).

A reduction of  $g_s$  and increase of  $C_i$  were observed during severe drought conditions for both magnolia species examined in the present study. As drought becomes more severe and long in time an increase in  $C_i$  values was also reported, evidencing the predominance of non-stomatal limitation to *A* (Briggs et al. 1986, Epron & Dreyer 1990, Changhai et al. 2010). The reduction of *A* under prolonged water shortage was related to diffusive (reduced mesophyll conductance) and metabolic (photochemical and enzymatic limitations) processes (Galmés et al. 2007). Metabolic limitations to *A* were most frequently associated with the reduction of Rubisco activity and regeneration, resulting from reduced ATP or NADPH supply (regarded as photochemical limitation), or as the consequence of low enzymatic activity of the Polymerase Chain

Reaction cycle (Lawlor 2002). Prolonged periods of water deficit can also increase the oxygenase activity of Rubisco, reducing consequently the carboxylation efficiency, causing in such a way another commonly encountered non-stomatal limitation to *A* (Medrano et al. 1997). In addition, the inhibition of *A* might be attributed to the reduction of chlorophyll content, as a common symptom of oxidative stress under severe drought condition, resulting from pigment photooxidation and photosynthetic pigment degradation (Iturbe-Ormaetxe et al. 1998). A marked increase in  $C_i$  under more progressed drought period and the proportional decrease in *A* rate was found to be less significant in comparison to the decline of  $g_s$  in *M. grandiflora*, resulting in high WUE values (according to Pita et al. 2005). On the other hand, the net photosynthetic rate was more sensitive to soil water shortage than  $g_s$  in *M. soulangeana*.

Under the studied environmental constrain the significant decrease of WUEi in *M. soulangeana* was driven by a pronounced decline in *A*, while *M. grandiflora* maintained high WUEi values. Species characterized with higher WUEi values have specific water-saving strategy to avoid greater water losses and maintain higher assimilation rates, particularly important under the conditions of predicted climate changes (Brendel et al. 2008). Taking into account the effectiveness of WUEi as an indicator of drought sensitivity, the importance of identification of traits that could be utilized to improve WUEi and hence enhance drought adaptation in breeding programmes was noted (Stojnić et al. 2019).

*M. grandiflora* exhibited a higher ability to tolerate the prolonged period of drought compared to *M. soulangeana*, by maintaining greater values of *A* and WUEi. This assumption is further supported by the slightly low rate of transpiration (*E*) in *M. grandiflora*, as noted for drought tolerant genotypes (Riaz et al. 2013). For instance, isohydric species show a lower water transpiration by retaining a greater amount of water, and then they are believed to be less vulnerable to drought (Basu et al. 2016). As the process of *E* is facilitated through the stomata, stomatal control under drought condition is of key importance for a successful adaptation to environmental changes (Xu et al. 2010).

By maintaining higher  $\Phi_{PSII}$  and ETRmax values during water shortage, *M. grandiflora* exhibited a higher efficiency in transporting electrons and potentially could fix more CO<sub>2</sub> in comparison to *M. soulangeana*, as reported by Estrada et al. (2015) in drought-tolerant blueberry genotypes. In addition, high values of ETR parameter give a great advantage in the reduction of ROS in photosynthesis and in maintaining normal physiological functions (Liu et al. 2019). On the other hand, the decrease of  $\Phi_{PSII}$  in *M. soulangeana* during drought period indicated the physiological regulation of electron transport by increasing excitation energy quenching process in the PSII antennae, according to Ashraf & Harris (2013). Furthermore, the decrease of *Y(II)* points to the decrease in the carboxylation efficiency, which affects the rate of consumption of ATP and NADPH (Queiroz-Alves et al. 2019).

Environmental stresses, such as water shortage and high light intensities, cause the saturation of electron transfer chain and the increase of the accumulation of proton, resulting in increase of *Y(NPQ)* parameter (Wang et al. 2018). High values of *Y(NPQ)* under drought found in *M. grandiflora* could be addressed to the good ability of plants to mitigate the negative effects of the severe drought at the chloroplast level (Gonçalves et al. 2019). Consequently, the decline of *Y(NPQ)* in *M. soulangeana* indicated a loss of capacity to generate the trans-thylakoid proton gradient in chloroplast. A possible explanation for this phe-

nomenon could be associated with the damage/decrease of PSI activity (Brestic et al. 2016). The simultaneous reduction of *Y(NPQ)* and increase of *Y(NO)* under drought in *M. soulangeana* further suggested the damage of PSII instead of the protective mechanism under the observed abiotic stress (Riva-Roveda et al. 2016). In accordance with these results, the increase of water deficit leads to damaging of the oxygen-evolving complex of PSII (Riva-Roveda et al. 2016). The inhibited synthesis and accelerated degradation of D1 proteins causes further separation of electron transport complex QB and D1 within chloroplasts and results in the inability to accept electrons (Liu et al. 2019).

A pronounced decrease of  $\Phi_{PSII}$  and *qP* in *M. soulangeana* suggested that the capability of photochemical conversion and the linear electron flux were both sensitive to the severeness and duration of drought (Wang et al. 2018). Beside a pronounced reduction of  $\Phi_{PSII}$  and *qP*, a sharper decline of ETR is a commonly observed characteristic of drought-susceptible genotypes (Sánchez-Reinoso et al. 2019), and reflects a reduced capability of the transport of electrons to fix CO<sub>2</sub>. The decrease of photosynthetic electron-transport rates along with lower trans-thylakoid pH gradient resulted in the accumulation of “excess photons” ( $(1-qP)/NPQ$ ) in *M. soulangeana*, suggesting that this species is more sensitive to light stress than *M. grandiflora* (Park et al. 1995). The observed reduction of *qP* coupled with the proportional increase *Y(NPQ)*, showed that *M. grandiflora* was able to maintain the capacity to regulate dissipation of light energy under the observed drought. Moreover, it might be assumed that the xanthophyll's cycle of the examined species was efficient in providing a vent to the excess electrons flow generated for the increase in light intensity in the chloroplasts (De Sousa et al. 2017).

Our results highlight the overall higher drought-resistance of *M. grandiflora* compared to *M. soulangeana*. The sensitivity of *M. soulangeana* to drought is in line with the description provided for species selection in Citree, the urban tree database (<https://citree.de/db-names.php?language=en>). On the other hand, our findings revealed a drought-tolerant behavior in *M. grandiflora* that is contradictory to the information in the Citree database. In addition, our findings correspond with the studies reporting high drought tolerance of species and provenances from dry climates under water shortage conditions (Pšidová et al. 2015, Wang et al. 2017). The good adaptation potential of *M. grandiflora* to severe water deficits was assumed by Sjöman et al. (2018b) for urban street sites in North America and Europe.

## Conclusion

This case study supports decision-making processes for the selection of trees in drought-affected urban areas by compar-

ing two common ornamental tree species with similar aesthetic value. Measurements of leaf gas exchange parameters along with chlorophyll *a* fluorescence showed *M. grandiflora* as a drought-tolerant species, while *M. soulangeana* exhibited susceptibility to drought, with a photosynthetic capacity sensitive to drought-induced stress. The decrease of *A* in both magnolia species were related to non-stomatal factors, as evidenced by the decrease of ETRmax and a simultaneous increase of *Ci*. Most of the observed parameters of leaf gas exchange, namely *E*, *gs*, *Ci*, WUE, and WUEi were proven to be highly sensitive to drought. In regard to chlorophyll *a* fluorescence, parameters related to the photochemical dissipation of light energy ( $\Phi_{PSII}$ ) as well as associated with the heat dissipation of light energy (*Y(NPQ)*, *Y(NO)*) appear to be useful indicators for the selection of drought-tolerant species, and are suggested for application in the assessment of plant responses in urban environments. Considering the predicted future climate change scenarios, *M. grandiflora* could be a good alternative to *M. soulangeana* for urban sites. The significance of the present study lies in the evaluation of the *in situ* physiological responses and selection of appropriate ornamental species for drought-prone urban environments.

## List of abbreviations

*A*: net photosynthetic rate; *Ci*: intercellular CO<sub>2</sub> concentration; *E*: rate of transpiration; ETR: electron transport rate; *gs*: stomatal conductance;  $\Phi_{PSII}$ : effective photochemical quantum yield of PS II; *qP*: coefficient of photochemical quenching; WUE: water use efficiency; WUEi: intrinsic water use efficiency; *Y(NPQ)*: quantum yield of light-induced non-photochemical fluorescence quenching; *Y(NO)*: quantum yield of non-regulated heat dissipation and fluorescence emission;  $(1-qP)/NPQ$ : index of susceptibility of leaves to light stress.

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