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ORIGINAL PAPER

Instantaneously measured traits may detect non-plastic ecophysiological performances in response to drought, explaining distributions of *Styrax* species in the Cerrado

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Abstract We analyzed the differences between irrigated and non-irrigated plants of three congeneric *Styrax* species that present distinct distribution patterns in the physiognomies of the Cerrado vegetation in Brazil. *Styrax ferrugineus* showed a stomatal conductance (g_s) unresponsive to soil water deficit in potted plants. This may explain the high gas exchange and photochemical efficiency found in this species, which is well adapted to the Cerrado sensu stricto (*s. str.*), a savanna-type vegetation. *S. camporum*, which is widely distributed in the Cerrado sensu lato (*s. l.*) areas, was the only species that exhibited increased intrinsic water use efficiency on the days of maximum water deficit. This result distinguishes *S. camporum* from *S. pohlii*, which is a forest species, since the g_s of both species decreased during the days of maximum water stress. In contrast to other studies, we propose that instantaneously measured traits, such as leaf gas exchange rates and chlorophyll fluorescence, may be used to detect non-plastic performances in response to environmental stress, helping explain distinct geographical distributions of congeneric species in the Cerrado vegetation.

Keywords Brazilian savanna · Chlorophyll fluorescence · Leaf gas exchange · Leaf water potential · Semi-controlled conditions

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Introduction

The Brazilian savanna or Cerrado comprises forests, savannas and grasslands (Kanegae et al. 2000; Ferreira et al. 2003). Low sunlight and relatively high soil water concentration are observed in forests (Kissmann et al. 2012), whereas the opposite is noticed in savanna-type physiognomies (Habermann et al. 2011). Therefore, sunlight and water in the soil are believed to influence the species distribution between Cerrado physiognomies. Changes in the availability of such resources are accompanied by adjustments to the photosynthetic apparatus (Franco and Lüttge 2002), the functioning of which may be influenced by stomatal conductance (g_s) (Habermann et al. 2008), and biochemical and photochemical reactions (Paulilo et al. 1994; Franco et al. 2007; Feistler and Habermann 2012).

The rainy (Nov–Mar) and dry (May–Sep) seasons (Ferreira et al. 2003) seem to functionally influence the Cerrado vegetation (Franco 1998), as species occurring in distinct physiognomies may show specific adaptations. Comparisons between soil (Ψ_{soil}) and leaf (Ψw) water potentials (Franco 1998; Hao et al. 2008) demonstrated that woody species from the Cerrado sensu stricto (*s. str.*), a savanna-type physiognomy, may have long and deep roots, a trait that was also observed for *Styrax ferrugineus* (Habermann and Bressan 2011), a typical plant from the Cerrado *s. str.* Thus, long and deep roots are essential for plants to survive the dry season. Although some studies (Franco 2002; Bucci et al. 2008) show that Ψ_{soil} does not reach very low values in deep layers in the dry season, the g_s, CO_2 assimilation (A) and transpiration (E) rates of many savanna species strongly decrease (Eamus et al. 1999; Prado et al. 2004; García-Núñez et al. 2011). Thus, the soil water gradient, established by distinct Cerrado physiognomies may be an important determinant of the species distribution pattern (Bhaskar and Ackerly 2006).

Plants are selected and adapted to their habitats due to non-plastic traits (Habermann et al. 2011; Habermann and Bressan 2011), which normally involve morphological traits (Ackerly et al. 2000). However, few studies report whether non-plastic ecophysiological performances confer advantages in a certain environment. Differences in seedling establishment and plant development of a single species evaluated in two Cerrado physiognomies were reported (Kanegae et al. 2000). In reciprocal transplant or seed burial studies, differences in g_s, A and E, as well as in the germination performance indicated some specialization of *S. ferrugineus* to the Cerrado *s. str.*, and of *S. pohlii* to riparian forests (Habermann et al. 2011; Habermann and Bressan 2011; Kissmann et al. 2012). Thus, responses of these *Styrax* species under artificial drought may reinforce such specializations and may reveal a plastic responsiveness of leaf gas exchange and photochemical variables that could explain the distribution of this genus in the Cerrado. For instance, decrease in the photochemical efficiency is more pronounced in the dry season, when A and g_s steadily drop (Lemos-Filho 2000, Franco et al. 2007). Additionally, chlorophyll heat dissipation may increase in response to light intensity (Huang et al. 2006).

Styrax ferrugineus, *S. camporum* and *S. pohlii* usually do not occur in the same Cerrado physiognomy. *S. camporum* is often observed at the edge of vegetation fragments, such as the Cerradão (a forest Cerrado physiognomy), occurring within these fragments only as adult individuals (Habermann et al. 2011). *S. ferrugineus* seems to be well adapted to the Cerrado *s. str.* (Habermann and Bressan 2011). *S. pohlii* is commonly observed in forest fragments with high soil water availability, such as riparian and swamp forests (Teixeira et al. 2008).

In a water deficiency study using potted plants of *S. ferrugineus*, *S. camporum* and *S. pohlii*, we assessed leaf gas exchange, chlorophyll *a* fluorescence, and Ψw. We hypothesized that (1) *S. ferrugineus* shows higher gas exchange and photochemical performance than the other two species; (2) these species differ as to their intrinsic water use efficiencies, *S. pohlii* being the most sensitive species to drought. Even though these species occur in habitats with contrasting soil water availabilities, we also predicted that when facing drought under the same conditions (3) Ψw decreases equally for the three species. We compared irrigated and non-irrigated plants of each species, and also plants of the three species that were submitted to drought. We discussed whether instantaneously measured traits are important to explain species distribution in Cerrado areas.

Materials and methods

Plant material

Ten young plants (10–12 months of age, 50 cm in height) of *Styrax ferrugineus* Nees & Mart., *S. camporum* Pohl. and *S. pohlii* A. DC., obtained by seed germination, were planted in 50-L pots, containing oxisoil (pH ≈ 4.0) from a Cerrado sensu stricto (*s. str.*) fragment. The plants presented the following number of leaves: *S. camporum*, 46 ± 12; *S. pohlii*, 48 ± 8; *S. ferrugineus* 44 ± 7. The bottom of the pots were perforated for proper drainage

As a savanna species, *S. ferrugineus* typically occurs in the Cerrado *s. str.* as shrubs (2 m in height), exhibiting thick bark on their stems. *S. camporum* may be considered a transitional species because it is widely distributed in Cerrado physiognomies, being mostly observed at the edge of Cerradão as young trees (3 m in height). *S. pohlii* is a forest species (10–20 m in height), and it is associated with permanently waterlogged soils, such as that found in riparian forests.

Experimental description and study site

Five individuals of each of the three species were subjected to water deficit, while five individuals of each of the three species were kept at the field capacity of soil water retention (daily irrigation regime). Water deficit was induced through the suspension of irrigation. After 53 days under water deficit, stomatal conductance (g_s) of most plants approached null values, and plants that were submitted to water deficit were rewatered, receiving constant daily water supply. The dates plants were assessed were defined by natural development of water stress and not based on specific values of soil water potential. There was no local control of vapor pressure deficit (VPD), air temperature, irradiance, wind or any other weather variables, except rain, which was avoided. The pots containing plants that were submitted to water deficit were covered with a circular plastic canvas cut from the edge to its center and placed around the main stem and over the soil, shaped like a cone. Pots were kept uncovered, but the canvas was tied with a string around the pot opening when rain appeared to be imminent.

Gas exchange and chlorophyll *a* fluorescence measurements

CO_2 assimilation (A) and transpiration (E) rates, stomatal conductance (g_s), and intercellular CO_2 (C_i) were measured with an open portable gas exchange system (LI-6400xt, LI-COR, Lincoln, NE, USA), and the intrinsic water use efficiency (IWUE, A/g_s) was calculated. The air pumped into the LI-6400xt was passed through a buffering gallon (5 L) to reduce the time for measurement stabilization. The CO_2 concentration entering the leaf cuvette averaged 383 ± 2 (SD) μmol mol^{-1}. Measurements were taken between 900 and 1100 hours (Feistler and Habermann 2012) on unclouded days, under the natural fluctuation of air temperature and vapor pressure deficit (VPD). The photosynthetic photon flux density (PPFD) used was provided by an artificial light source (6400-40 LCF, LI-COR, Lincoln, NE, USA), which was set to provide 1,600 μmol photons m^{-2} s^{-1}, similar to PPFD values that returned saturating values of CO_2 assimilation for the three species in previous tests.

Chlorophyll *a* fluorescence was measured with a portable modulated fluorometer (6400-40 LCF, LI-COR, Lincoln, NE, USA), which was integrated into the LI-6400xt gas exchange system. The saturating light pulse used was approximately 7,000 μmol m^{-2} s^{-1} during 0.7 s. The light fraction used for photosystem II (PSII) in photochemistry $[P = ((F'_m - F_s)/F'_m)]$, heat dissipation in the antenna $[D = 1 - (F'_v/F'_m)]$ and heat dissipation in reaction centers $[E = (1 - qP)\ (F'_v/F'_m)]$ was calculated according to Demming-Adams (1996). For these calculations, F'_v is the variable fluorescence between the maximal (F'_m) and minimal (F'_o) fluorescence from light-adapted leaf and F_s is the steady-state fluorescence from light-adapted leaf. The photochemical quenching (qP) was calculated as $[qP = (F'_m - F_s)/(F'_m - F'_o)]$, according to Baker (2008).

Leaf water potential (Ψ_w)

Leaf water potential at predawn (Ψ_{pd}) and midday (Ψ_{md}; under maximum VPD) was measured by the pressure chamber method (Turner 1981), using a DIK-7000 (Daiki Rika Kogyo, Tokyo, Japan) portable chamber.

Data analysis

Leaf gas exchange and chlorophyll *a* fluorescence measurements (A, E, g_s, C_i, P, D, E and IWUE), Ψ_{pd} and Ψ_{md} were assessed on the 26th, 41st, 47th, 51st, 55th, 56th, and 58th day of the experiment. A one-way analysis of variance was performed between irrigated and non-irrigated plants of each species, and also between plants of the three species that were submitted to drought. On such dates, mean results were compared using the Tukey's test ($\alpha = 0.05$) to calculate the least significant difference between them.

Results

Predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potentials in plants subjected to water deficit were significantly lower in comparison with irrigated plants on the days of great water deficit (days 41, 47, and 51 of the experiment) (Fig. 1). However, the recovery of *S. ferrugineus* occurred one day after rewatering (Fig. 1a, d), whereas in *S. camporum* and

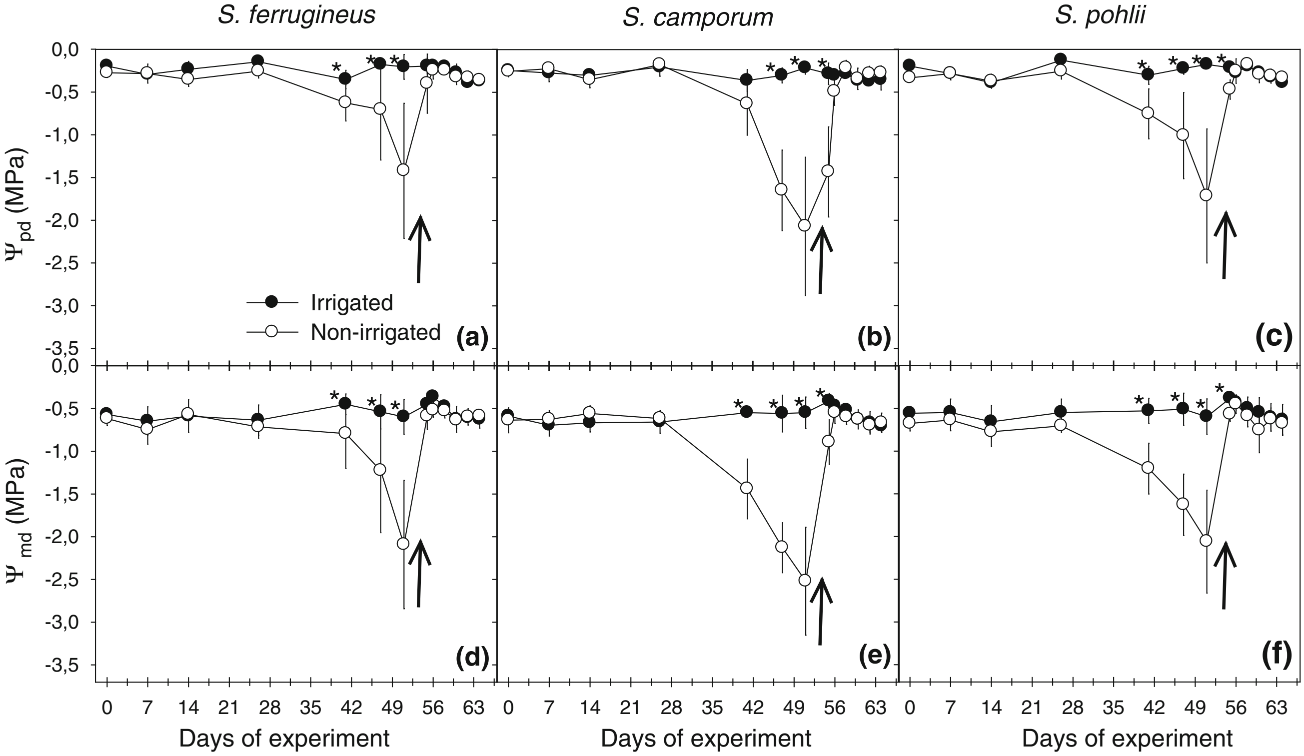

Fig. 1 Predawn (Ψ_{pd}; **a**, **b**, and **c**) and midday (Ψ_{md}; **d**, **e**, and **f**) leaf water potential in irrigated and non-irrigated plants of *Styrax ferrugineus* (**a**, **d**), *S. camporum* (**b**, **e**) and *S. pohlii* (**c**, **f**). For each evaluation date between day 26 and 58 of the experiment, absence of an asterisk indicates similarities between irrigated and non-irrigated plants ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

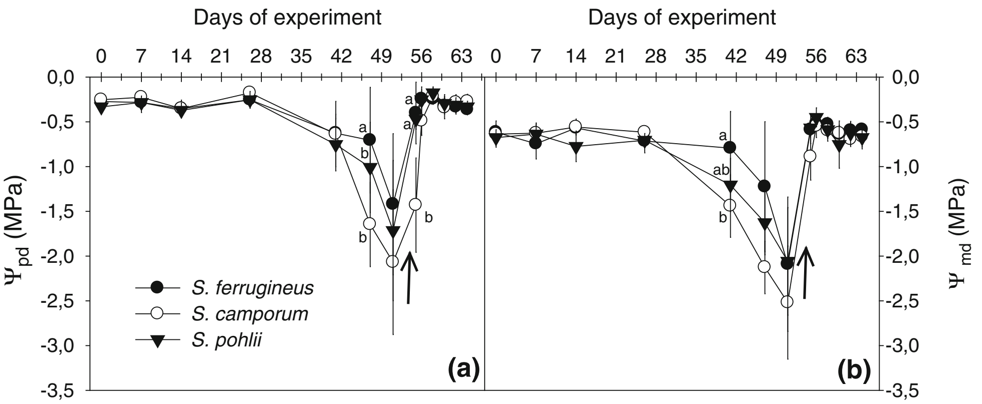

Fig. 2 Predawn (Ψ_{pd}; **a**) and midday (Ψ_{md}; **b**) leaf water potential in *Styrax ferrugineus*, *S. camporum* and *S. pohlii* plants that were subjected to water deficit. For each evaluation date between day 26 and 58 of the experiment, absence of letters or same letters indicates similarities between species ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

S. pohlii the recovery occurred 2 days after rewatering (Fig. 1b, c, e, f).

When comparisons were made between non-irrigated plants of the three species, on day 47 of the experiment *S. ferrugineus* had greater Ψ_{pd} in relation to non-irrigated *S. camporum* and *S. pohlii* plants, which exhibited similar values. One day after rewatering, *S. ferrugineus* and *S. pohlii* showed similar Ψ_{pd} values, which were greater than those of *S. camporum* (Fig. 2a). Differences between Ψ_{md} values of plants of the three species that were subjected to water deficit were noticed only after 41 days under drought, when *S. ferrugineus* exhibited superior values in relation to those of *S. camporum*, whereas *S. pohlii* showed intermediate values (Fig. 2b).

The soil water deficit did not influence CO_2 assimilation (*A*) and transpiration (*E*) rates, and stomatal conductance (g_s) in *S. ferrugineus* (Fig. 3a, d, g). However, the water deficit caused significant reductions in *A*, g_s, and *E* measured in *S. camporum* (Fig. 3b, e, h) and *S. pohlii* (Fig. 3c, f, i). The intercellular CO_2 (C_i) remained unchanged between irrigated and non-irrigated plants of the three species, throughout the experimental period (Fig. 3j–l). The apparent recovery of gas exchange rates occurred on the sixth day after reirrigation for *S. camporum* (Fig. 3b, e, h) and on the tenth day for *S. pohlii* (Fig. 3c, f, i).

In a general comparison with non-irrigated *S. camporum* and *S. pohlii* plants, *S. ferrugineus* had higher values of *A*, g_s and *E* (Fig. 4a–c). Four days after rewatering, *S. pohlii* was the species exhibiting the lowest values of *A*, g_s and *E*, whereas *S. camporum* exhibited intermediate values (Fig. 4a–c). Plants of *S. pohlii* that were submitted to water deficit showed the highest C_i values in comparison with the other two species one day after rewatering; however, this was the only difference regarding this variable (Fig. 4d).

Values of *A*, g_s, and *E* were not clearly influenced by the vapor pressure deficit (VPD) throughout the experimental period. However, for the three species, *A* was directly dependent on g_s, chiefly in plants under drought, but C_i was not g_s-dependent (data not shown).

The heat dissipation in antennas was above 50 % for irrigated and non-irrigated plants of the three species throughout the experimental period (Fig. 5a–f). The light energy allocated to photochemistry (*P*) in *S. camporum* plants, submitted to water deficit, was lower ($P < 0.05$) than in irrigated plants, on 4 days of evaluation (days 41, 47, 55 and 56 of the experiment). The minimum percentage of *P* in this species was 8.7 % on day 55 of the experiment (1 day after rewatering), when heat dissipation in antennas (*D*) and reaction centers (*E*) reached 64.7 and 26.6 %, respectively.

The percentage of *D* and *E* did not significantly differ between the three species submitted to water deficit ($P > 0.05$). However, except for the 56th day of the experiment, *P* was significantly higher ($P < 0.05$) in *S. ferrugineus* when compared to the other two species. Under drought conditions, *S. camporum* was the only species that showed reduced ($P < 0.05$) values of commonly reported photochemical parameters, such as maximal (F_v/F_m) and effective (Φ_{PSII}) quantum yield of PSII, electron transport rate (ETR) and qP (data not shown), and this is the reason why *P*, *D* and *E* were presented instead. Comparisons among plants of the three species that were submitted to water deficit also indicated that the highest photochemical performances during the study were observed in *S. ferrugineus* (data not shown).

The intrinsic water use efficiency (IWUE; A/g_s) did not change in response to water deficit in *S. ferrugineus* (Fig. 6a). In irrigated plants of *S. pohlii* it was significantly higher than those plants that were subjected to water deficit 2 days after rewatering (Fig. 6c). *S. camporum* plants that were subjected to water deficit showed increased IWUE when compared to irrigated plants on the days of maximum water deficit and one day after rewatering (Fig. 6b).

On the day of maximum water deficit *S. camporum* showed IWUE values that were higher than those of *S. pohlii*, and *S. ferrugineus* showed intermediate values. One day after rewatering, *S. pohlii* still possessed lower IWUE in relation to the other two species, which exhibited similar values (Fig. 7).

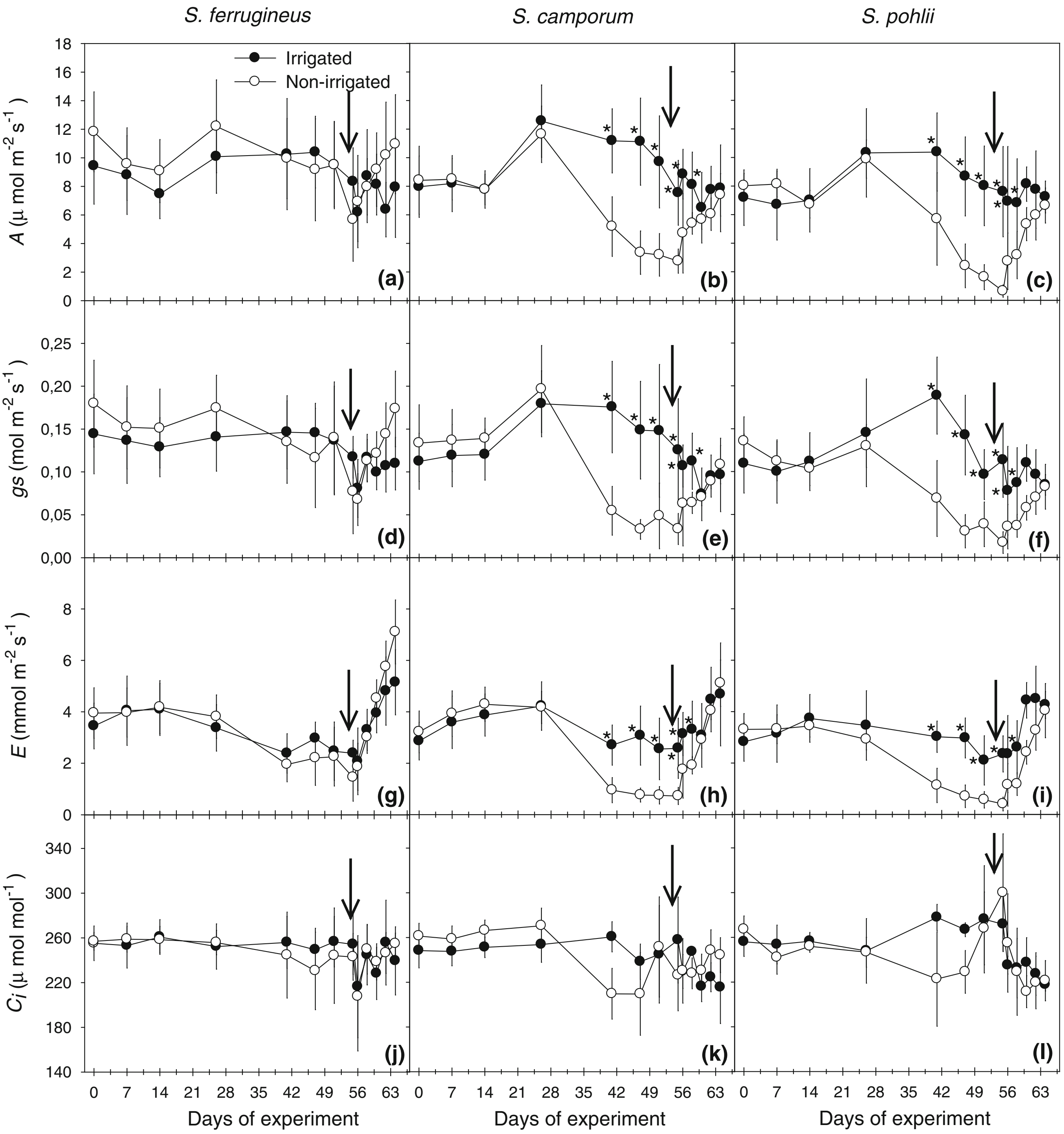

Fig. 3 CO_2 assimilation (**a**–**c**), stomatal conductance (**d**–**f**), transpiration rates (**g**–**i**), and intercellular CO_2 (**j**–**l**) in irrigated and non-irrigated plants of *Styrax ferrugineus* (**a**, **d**, **g**, **j**), *S. camporum* (**b**, **e**, **h**, **k**) and *S. pohlii* (**c**, **f**, **i**, **l**). For each evaluation date between day 26 and 58 of the experiment, absence of an asterisk indicates similarities between irrigated and non-irrigated plants ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

Discussion

While in the Brazilian Cerrado seasonal drought can last for 5 or 6 months (Kanegae et al. 2000; Ferreira et al. 2003), one could argue that the time of water deficit imposed on the potted plants might not have been long enough to reduce g_s in *S. ferrugineus*. However, the Ψ_{pd} and Ψ_{md} of plants subjected to water deficit were significantly lower than those of irrigated plants of the three species (Fig. 1). As demonstrated by Gebrehiwot et al. (2005) and Gebrekirstos et al. (2006), wide diurnal range between Ψ_{pd} and Ψ_{md} indicates high capacity to withstand

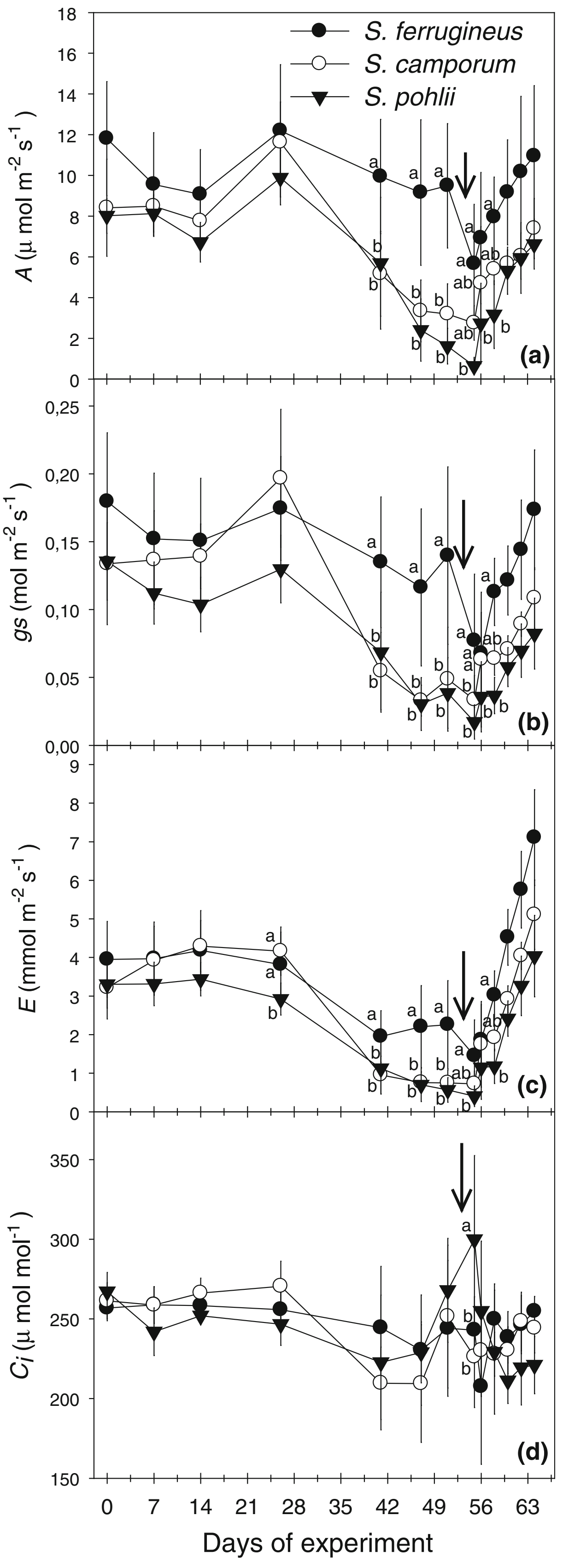

Fig. 4 CO_2 assimilation (**a**), stomatal conductance (**b**), transpiration rates (**c**), and intercellular CO_2 (**d**) in plants of *Styrax ferrugineus*, *S. camporum* and *S. pohlii* that were subjected to water deficit. For each evaluation date between day 26 and 58 of the experiment, absence of letters or same letters indicates similarities between species ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

drought-prone areas, whereas narrow range denotes drought sensitiveness. In this way, on the day of maximum water deficit as detected by Ψw (51 days of experiment), the diurnal Ψw range was 0.67 ± 0.04 for *S. ferrugineus*, 0.45 ± 0.18 for *S. camporum* and 0.34 ± 0.18 for *S. pohlii*, and these ranges point out *S. ferrugineus* as a drought-tolerant species (in relation to *S. pohlii*). Moreover, Ψ_{pd} and Ψ_{md} measured in adult plants in the field at the peak of the dry season (September) were −0.3 and −1.5 MPa (*S. ferrugineus*), −0.5 and −1.5 MPa (*S. camporum*), and −0.7 and −1.3 MPa (*S. pohlii*), respectively (data not shown), and these values are in accordance with observations made by Prado et al. (2004) and Hao et al. (2008). In the case of adults of these plants measured in the field, the diurnal Ψw ranges also reinforce that *S. ferrugineus* is more tolerant to drought in relation to *S. pohlii*. Therefore, as a drought-tolerant species, the Ψw of *S. ferrugineus* decreased, but g_s was not correspondingly affected. This demonstrates that our prediction that Ψw equally decreases among the three species during the drought period cannot be accepted. Results also demonstrate that the water status of *S. ferrugineus* was less affected by drought, in comparison with the other two species (Fig. 2a, b).

Styrax ferrugineus had greater gas exchange performance in comparison with the other two species during the drought period. In this species, the stomatal conductance (g_s) was unresponsive to the soil water deficit (Fig. 3d), unlike that observed for the other two species (Fig. 3e, f). Such distinct g_s responses between species resulted in a high CO_2 assimilation (A) and transpiration (E) rates in plants of *S. ferrugineus* that were submitted to drought, when compared to the other two species (Fig. 4a, c).

One argument could be that non-irrigated plants of *S. ferrugineus* might not have lost sufficient water to trigger expected low g_s values. In the field, adult *S. ferrugineus* plants seem to have fewer leaves when compared to adult individuals of *S. camporum* and *S. pohlii*, although Ψ_{pd} and Ψ_{md} values measured for these species were comparable in the dry season (Prado et al. 2004; Hao et al. 2008). We did not measure the total leaf area, but irrigated and non-irrigated plants of the three species showed the same leaf number, reiterating that the surface available for transpiration was theoretically the same for the three species.

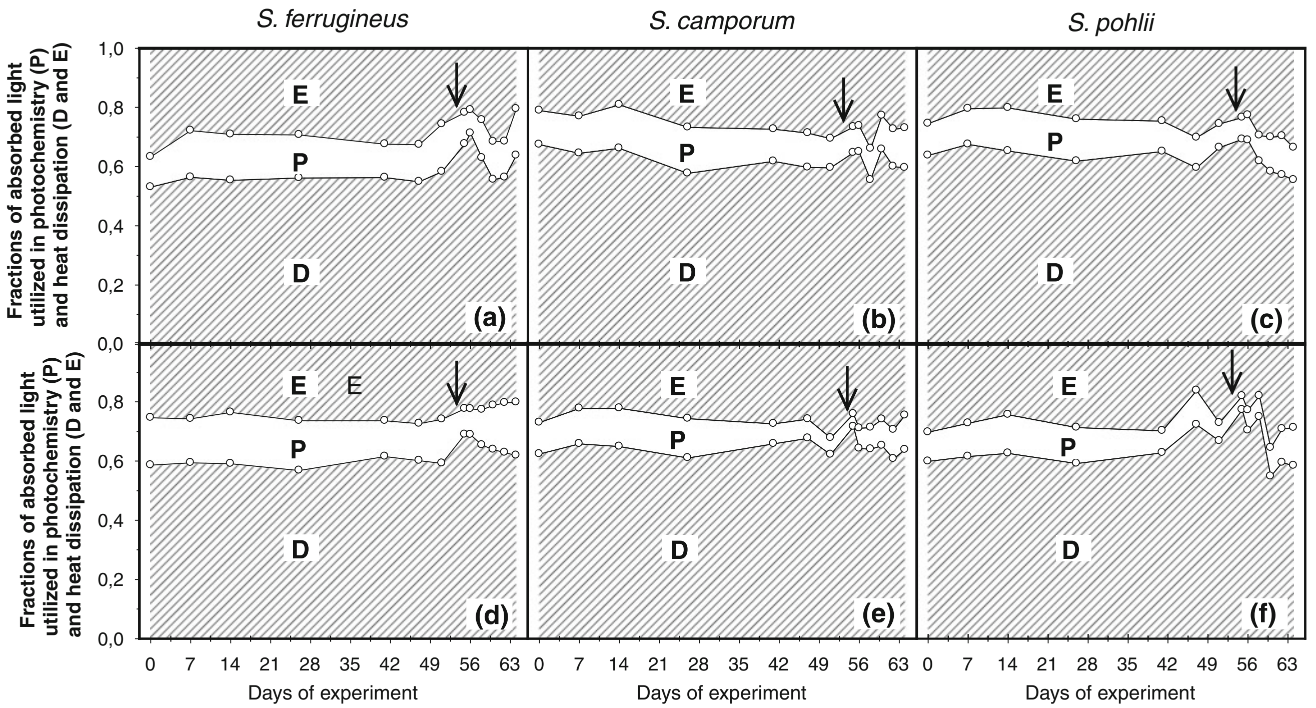

Fig. 5 Variations in fractions of absorbed light utilized in photochemistry (*P*), heat dissipation in the antenna (*D*) and in reactions centers (*E*) of PSII in *S. ferrugineus*, *S. camporum* and *S. pohlii* irrigated (**a**–**c**) and non-irrigated plants (**d**–**f**). *Arrows* indicate reirrigation (on the 54th day of experiment)

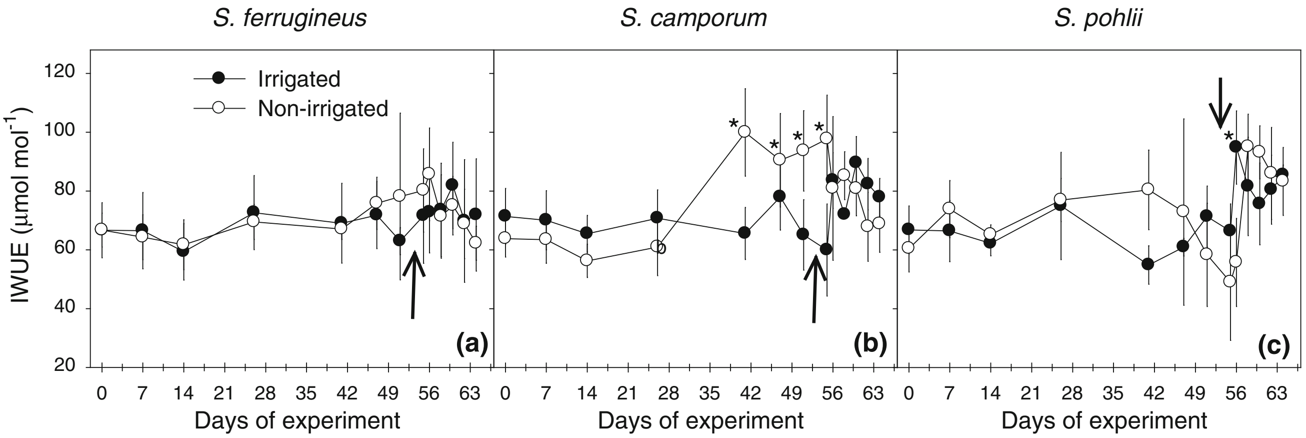

Fig. 6 Intrinsic water use efficiency (**a**–**c**) in irrigated and non-irrigated plants of *Styrax ferrugineus* (**a**, **d**), *S. camporum* (**b**, **e**) and *S. pohlii* (**c**, **f**). For each evaluation date between day 26 and 58 of the experiment, absence of an asterisk indicates similarities between irrigated and non-irrigated plants ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

Soil water deficit is capable of reducing the intercellular CO_2 (C_i), because stomatal resistance impairs the influx of CO_2 and affects the maintenance of carbon concentrations in the stomatal cavity (Chaves et al. 2011). The same authors sustain that water deficit may also cause an elevation in C_i values, which would suggest serious damage (due to a more severe drought) to the photosynthetic apparatus, causing low carboxylation efficiency. However, the induced drought did not cause any changes of C_i values in any of the three species (Fig. 3j–l). For the three species, carbon assimilation was g_s-dependent, mainly in non-irrigated plants, but C_i was not influenced by stomatal conductance. Therefore, *S. camporum* and *S. pohlii* did not assimilate less carbon because of low access to CO_2 in the stomatal cavity, or because of any malfunctioning of the biochemical photosynthetic apparatus, since C_i did not categorically increase inside the stomatal cavity.

The fraction of light energy dissipated as heat in antennas (*D*) was high for the three species (Fig. 5a–f), suggesting this mechanism as an important photoprotection. On the

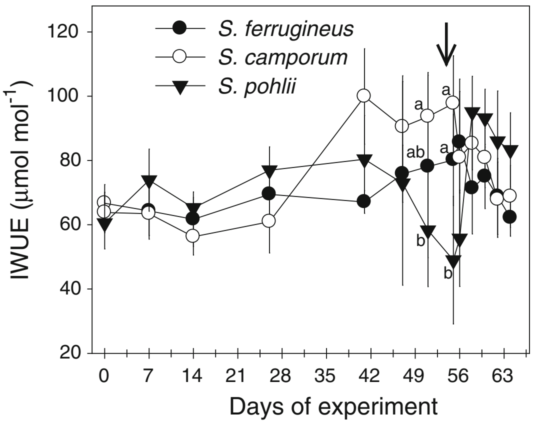

Fig. 7 Intrinsic water use efficiency in *Styrax ferrugineus*, *S. camporum* and *S. pohlii* plants that were subjected to water deficit. For each evaluation date between day 26 and 58 of the experiment, absence of letters or same letters indicates similarities between species ($P < 0.05$). *Arrows* indicate reirrigation (on the 54th day of experiment) (*vertical bars* SD)

other hand, although *P* values were unchanged for non-irrigated *S. ferrugineus* and *S. pohlii* plants, in relation to irrigated plants, *A* was strongly reduced in *S. pohlii*. This suggests likely photodamages for non-irrigated *S. pohlii* plants, in which the ETR values did not decrease in relation to irrigated plants, as performed by *S. camporum* non-irrigated plants (data not shown). As a Cerrado species, *S. camporum* makes use of photoprotective mechanisms when under drought (Feistler and Habermann 2012). In fact, photoprotective mechanisms are common in Cerrado species (Franco et al. 2007), and photorespiration was identified as a major process occurring in such plants (Franco and Lüttge 2002). As in other species, heat energy dissipation (*D* and *E*) plays an important role to avoid photodamage in PSII (Huang et al. 2006).

Therefore, the effects of drought were more detrimental to gas exchange for *S. camporum* and *S. pohlii*, and the former showed differences in its photochemical performance in response to drought. For reasons related to the deep root system (Habermann and Bressan 2011), which enhances the root access to soil water, and for reasons related to sunlight capture (Habermann et al. 2011), *S. ferrugineus* is well adapted to habitats subjected to seasonal drought and high irradiation load, such as the Cerrado *s. str.* (Nakajima and Monteiro 1987).

Thus, *S. camporum* and *S. pohlii* showed low ecophysiological performance in response to drought. However, the intrinsic water use efficiency (IWUE) distinguished this two species regarding their environment of occurrence. Both *S. camporum* and *S. pohlii* displayed low g_s in response to water deficit (Fig. 3e, f), attenuating their transpiration rates (Fig. 3h, i). Nevertheless, *S. camporum* was the only species in which IWUE rose significantly in plants that were submitted to water deficit, when compared to irrigated plants (Fig. 6b). This may be an important explanation as to why *S. camporum* is widely distributed in Cerrado sensu lato (*s. l.*) areas (Nakajima and Monteiro 1987; Habermann et al. 2011), where having high IWUE can be essential for survival. Considering only the plants that were subjected to water deficit, *S. camporum* and *S. ferrugineus* demonstrated the highest and *S. pohlii* the lowest values of IWUE (Fig. 7). On the other hand, in a reciprocal transplant study, young plants of *S. camporum* and *S. pohlii* increased their g_s in response to the high water content found in the soil of a riparian forest, while *S. ferrugineus* maintained low g_s values in this condition (Habermann et al. 2011). These observations emphasize the adaptation of *S. camporum* to savanna environments and of *S. pohlii* to forest environments (Habermann and Bressan 2011).

The present study confirmed that the three species differed as to their ecophysiological performance when facing drought under the same conditions and that *S. ferrugineus* stands out among them. Selection pressures (and consequent adaptation) are exerted on non-plastic traits, especially morphological traits that are genetically stabilized within plant communities, so that these traits can have great heritability (Ackerly et al. 2000). In fact, the root and shoot lengths of *S. ferrugineus* and *S. pohlii* are not plastic in response to a soil fertility gradient (Habermann and Bressan 2011). Ackerly et al. (2000) reviewed many studies, involving many species, and concluded that instantaneously measured ecophysiological traits, such as gas exchange and photochemical parameters, hold lower heritability when compared to traits that reflect integrated physiological processes over time, such as growth or reproduction (e.g., number of seeds). Notwithstanding, we demonstrated that *S. ferrugineus* exhibits non-plastic responses of instantaneously measured ecophysiological traits to a severe water deficit. This indicates that gas exchange, photochemical parameters and Ψw are important tools that help explain the distinct distribution of congeneric species in the Cerrado *s. l.* areas. Indeed, when analyzing the occurrence and geographical distribution of the three *Styrax* species, in addition to seasonal drought, one should consider the common pyrogenic stress occurring in the Cerrado (Simon et al. 2009; Pinheiro and Monteiro 2010). Short roots of *S. pohlii* (Habermann and Bressan 2011) hinder the survival of this forest species in savanna areas. *S. ferrugineus*, in contrast, has thick bark on its stems, which gives an advantage (to survive the fire in the Cerrado *s. str.*) over the other two species that show smooth bark on their stems (Machado et al. 2005).

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