



Drought, heat, and their combined effect on the photosynthetic performance of *Psidium myrtoides* O. Berg (Myrtaceae)¹

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ABSTRACT

Popularly known as araçá-una, *Psidium myrtoides* is an endemic tree species in Brazil, with fruits much appreciated by the fauna. It is indicated for the composition of reforestation and for enriching the vegetation of degraded areas. This work aimed to evaluate the effects of drought, heat, and the interaction of both in the physiological attributes of *Psidium myrtoides* plants. Monitored fluorescence, gas exchange, and chlorophyll index in araçá-una plants induced by drought, heat, and the combination of both during 1, 3, and 7 days after treatment induction (DAT). After, the plants were returned to their initial condition, and their recovery was evaluated at 15 DAT. The results indicate that *Psidium myrtoides* plants reduce photosynthetic activity in the absence of water, contrary to what has been shown in other studies; in addition, they are not potentiated by the combination with heat. Therefore, we conclude that this species has a potential tolerance to heat ($T_{\text{mean}} 30.3\text{ }^{\circ}\text{C}$). However, if water is available in the soil, it maintains photosynthetic activity at normal levels.

Keywords: drought stress; heat stress; JIP-test; photosynthesis.

INTRODUCTION

Global warming, intensified in the last 35 years, is a well-established fact worldwide. The latest climate change models predict the rise in global temperature and changes in patterns of weather events, such as precipitation. As these events intensify, it becomes necessary to understand how they will affect plant physiological processes (Teskey *et al.*, 2015; Bindoff *et al.*, 2019) and, consequently, their effects on the structures and compositions of natural ecosystems (Malhi *et al.*, 2020).

Environmental adversities such as drought and heat negatively affect plant growth and development. However, the exposure of plants to these conditions provides a range of responses and physiological adaptations that aim to reduce the damage caused by the stress condition (Zandalinas *et*

al., 2016; 2018). For example, drought is one of the factors responsible for inducing stomatal closure, limiting the performance of the photosynthetic apparatus and, consequently, the increase in biomass. Heat, on the other hand, impairs plant metabolism, causing destabilization of proteins and enzymes, disturbing the flow of electrons and energy reactions, and impairing carbon assimilation. Together, these two stresses have positive interactions that intensify their effects (Teskey *et al.*, 2015; Singh & Thakur, 2018).

Of all plant metabolism, photosynthesis is one of the most fundamental components of plant growth and development (Singh & Thakur, 2018). Given this, variables related to photosynthesis, such as chlorophyll *a* fluorescence, and gas exchange, have been widely used to identify the occurrence

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of physiological changes in plants under both greenhouse (Goltsev *et al.*, 2016; Zhao *et al.*, 2017b) and field conditions (Faria-Silva *et al.*, 2017; Faria-Silva *et al.*, 2019).

Although the effects of drought (Faria-Silva *et al.*, 2017), heat (Faria-Silva *et al.*, 2017) and their interaction (Urban *et al.*, 2018; Haworth *et al.*, 2018) have been studied in cultivated species, relatively few studies have evaluated these effects in native tree species in Brazil. Given this, studying plants' behavior under stress conditions is essential to understanding natural vegetation's fate (Chaves *et al.*, 2003).

Psidium myrtilloides O. Berg (Myrtaceae), popularly known as araçá-una, is a tree species endemic to Brazil with wide distribution, occurring from the Caatinga, Cerrado to the Atlantic Forest (*Psidium* Flora do Brasil, 2020). It has a height of 4-8 m elongated and a semi-deciduous crown. Its fruits are berries type, sweet pulp, and much appreciated by the fauna. In addition, it is indicated for the reforestation composition and for enriching the vegetation of degraded areas (Lorenzi, 1998).

Despite the importance of *Psidium myrtilloides* plants in the ecosystems in which they are inserted (Lorenzi, 1998), in natural medicine (Dias *et al.*, 2018), and also the potential of their fruits for the agroindustry (Franzon *et al.*, 2009), it is virtually non-existent studies on the physiology, as well as the effects of abiotic stresses of this species. With this, we hypothesize that the combined effects of drought and heat lead to quantitatively more significant damage to the photosynthetic performance of *Psidium myrtilloides* plants than they alternately remained.

This study aimed to evaluate the effects of drought, heat, and their interaction on the chlorophyll *a* fluorescence, gas exchange, and photosynthetic pigment content of *Psidium myrtilloides* plants.

MATERIALS AND METHODS

Plant material and growth conditions

The experiment was conducted in the experimental area of the Department of Botany at the Federal University of Espírito Santo (20°27'49" S e 40°33'44" W, alt. 6m) in February 2018. *Psidium myrtilloides* seedlings, 36 months old, from seeds grown in 32-liter pots filled with soil and sand substrate, were used (2:1; v/v). First, 50 ml of the nutrient solution was added to each pot with ½ force (Hoagland & Arnon, 1950). Then, before starting the experiment, the plants were kept in ambient conditions (T_{mean} 26.8 °C) for 30 days. Still in this period, irrigation occurred periodically, aiming to keep the soil moisture close to the field capacity. Then, the plants were subjected to drought, heat, and a combination of both. Subsequently, after the stress-inducing period, the plants were returned to their initial condition, and their recovery was evaluated for seven days (Figure 1).

Chl a fluorescence measurements

The chlorophyll *a* fluorescence transient (OJIP) was quantified with the Handy-PEA fluorometer (Hansatech Instruments, Norfolk, UK). Evaluations took place between 7:00 am and 8:00 am on fully expanded young leaves (i.e., fourth or fifth leaf from the apex), previously adapted to the dark for 40 minutes. Subsequently, with the collected data, the biophysical parameters were calculated using the JIP test proposed by Strasser *et al.* (1995; 2000), using the PEA-Plus software version 1.11. Table 1 shows the parameters and equations of the JIP test used in this study (Goltsev *et al.*, 2016).

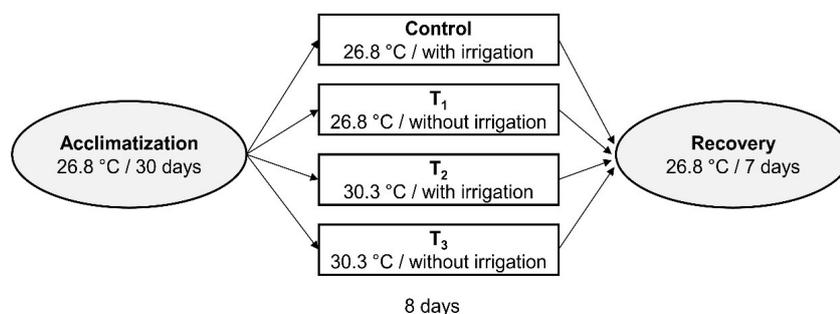


Figure 1: Scheme of treatments in *Psidium myrtilloides* plants. Where: T1 = drought stress, T2 = heat stress and T3 = drought + heat stress.

Table 1: Summary of parameters and formulas used to evaluate the chlorophyll *a* fluorescence transient (Goltsev et al. 2016)

Abbreviations	Formulas	Definition
ϕP_0	$F_v/F_m = 1 - F_0/F_M$	Maximum quantum yield of primary Photosystem II (PSII) photochemistry
ψE_0	$1 - V_j = ET_0/TR_0$	Efficiency with which a PSII trapped electron is transferred from Quinone A (QA) to Quinone B (QB)
ϕE_0	$1 - F_j/F_M = ET_0/ABS$	Quantum yield for electron transport
δR_0	$1 - F_1/F_M = RE_0/ET_0$	Quantum yield of the electron transport flux until the Photosystem I (PSI) electron acceptors
PI_{abs}	$(RC/ABS) \cdot (\phi P_0/(1 - \phi P_0)) (\psi E_0/(1 - \psi E_0))$	Potential performance index of PSII
PI_{total}	$PI_{ABS} \cdot (\delta R_0/(1 - \delta R_0))$	Total photochemical performance index

Gas exchange measurements

The net CO₂ uptake rate was determined with a portable gas exchange system (LCi-Pro model, ADC BioScientific Ltd., Hoddesdon, UK). The evaluations took place between 7:00 am and 8:00 am in young leaves completely expanded (i.e., fourth or fifth leaf from the apex), using ambient CO₂ (≈ 380 Pa), under saturating light conditions of 1300 μmol m⁻² s⁻¹ (determined from the previously performed light curve) and controlled temperature of 25 °C in the leaf chamber.

The variables evaluated were: net photosynthesis rate (A; μmol m⁻² s⁻¹), transpiration rate (E; μmol H₂O m⁻² s⁻¹), and stomatal conductance (gs; μmol H₂O m⁻² s⁻¹).

Photosynthetic pigment measurements

The chlorophyll index was determined with a SPAD chlorophyll meter (Konica Minolta SPAD-502, Osaka, Japan). Each leaf was measured five times in different parts, avoiding the ribs. The leaves selected for this measurement were the fully expanded young leaves (i.e., the fourth or fifth leaf from the apex).

Statistics analysis

Statistical analyzes were performed using InfoStat software version 2017d in a randomized experimental design (n = 5). The data were subjected to analysis of variance and, when significant, were compared by the Scott-Knott test of means at a 5% probability of error.

RESULTS

Chlorophyll *a* fluorescence parameters analyses

In 1DAT, no changes were observed between treatments and control for chlorophyll *a* fluorescence parameters (Table 2). However, in 4DAT, all of them showed a significant increase of ≈ 3% in ϕP_0 about the control (Table 2). In the following measurement, T₁ and T₃ plants significantly reduced 30% in ϕP_0 .

In this scenario, ψE_0 presented the first changes at 7DAT. T₂ plants showed a significant increase of 12%, about control plants. In the other treatments, a reduction of ≈ 11% was observed in ψE_0 . As with ϕP_0 , ϕE_0 of all treatments showed a significant increase of 10%, about the control plants in 4DAT.

Regarding the potential performance index of the PSII (PI_{ABS}), changes were only observed at 7DAT. In this scenario, there was a significant reduction of ≈ 90% in PI_{ABS} of T₁ and T₃ plants compared to control plants. The efficiency with which electrons moved from the inter-system receptors to the final PSI receptors (δR_0) occurred according to what was observed in PI_{ABS}. Regarding the total photochemical index (PI_{TOTAL}), T₂ plants showed a significant increase of ≈ 44%, about control plants in the period of maximum stress. On the other hand, plants under the treatments (T₁ and T₃) showed a reduction of 88 and 85% in PI_{TOTAL}, respectively.

Table 2: Photosynthetic parameters deduced by the JIP test analysis of fluorescence transients in *Psidium myrtilodes* of control plants and of plants under drought (T₁), heat (T₂), and drought + heat (T₃) stress at 1, 4 and 7 days after treatments (DAT), and at 7 days of restoration of the initial conditions of irrigation and temperature (recovery)

		ϕP_0	ψE_0	ϕE_0	PI _{ABS}	δR_0	PI _{TOTAL}
1DAT	Control	0.75 a	0.53 a	0.40 a	1.59 a	0.48 a	1.40 a
	T ₁	0.74 a	0.51 a	0.38 a	1.27 a	0.51 a	1.30 a
	T ₂	0.76 a	0.51 a	0.39 a	1.35 a	0.48 a	1.21 a
	T ₃	0.75 a	0.49 a	0.37 a	1.15 a	0.50 a	1.14 a
4DAT	Control	0.76 a	0.52 a	0.40 a	1.42 a	0.48 a	1.27 a
	T ₁	0.78 b	0.55 a	0.43 b	1.76 a	0.41 a	1.24 a
	T ₂	0.79 b	0.57 a	0.45 b	2.27 a	0.45 a	1.89 b
	T ₃	0.78 b	0.56 a	0.44 b	1.88 a	0.44 a	1.49 a
7DAT	Control	0.75 b	0.49 b	0.36 b	1.15 b	0.53 b	1.26 b
	T ₁	0.51 a	0.43 a	0.22 a	0.23 a	0.38 a	0.14 a
	T ₂	0.77 b	0.55 c	0.42 b	1.73 b	0.51 b	1.81 c
	T ₃	0.55 a	0.44 a	0.24 a	0.33 a	0.36 a	0.18 a
Recovery	Control	0.76 a	0.55 b	0.42 b	1.61 a	0.44 a	1.27 a
	T ₁	0.73 a	0.47 a	0.34 a	0.98 a	0.57 b	1.19 a
	T ₂	0.77 a	0.55 b	0.42 b	1.72 a	0.50 b	1.73 a
	T ₃	0.76 a	0.53 b	0.40 b	1.49 a	0.51 b	1.50 a

Different letters in columns of the same treatment day indicate statistically significant ($p < 0.05$) differences among treatments by the Scott-Knott test.

After restoring the initial conditions of irrigation and temperature for seven days (recovery), the plants recovered and showed PI_{ABS} and PI_{TOTAL} similar to the control plants.

Gas exchange analyses

In 1DAT, there were no significant differences in gas exchanges between the control plants and those under treatment (Figure 2). In this scenario, the values of net photosynthesis rate (A), transpiration rate (E), and stomatal conductance (gs) were, respectively, $4.85 (\pm 1.96)$, $0.037 (\pm 0.08)$ and $0.643 (\pm 1.86)$. On the other hand, in 4DAT, the T₂ plants had a 67% increase in net photosynthesis rate compared to the control plants. Concomitantly, the T₁ and T₃ plants showed a reduction of 77 and 51%, respectively. Finally, in 7DAT, the control and T₂ plants maintained A at

around $5.97 (\pm 1.3)$, while the two treatments with water restriction (T₁ and T₃) had A equal to zero.

Regarding the transpiration rate (E), in 4DAT, plants under all treatments showed values $\approx 48\%$ lower than the control plants' rates (4.15 ± 1.1). During the subsequent measurement, on 7DAT, T₂ plants showed a significant increase for E of 73% compared to the control. In turn, the T₁ and T₃ plants showed values close to zero. Stomatal conductance (gs) exhibited behavior similar to the sweating rate (E), mainly in the recovery phase.

With the restoration of the initial conditions of irrigation and temperature for seven days (recovery), the rates of net photosynthesis (A), stomatal conductance (gs), and transpiration (E) of all treatments regained values similar to the control, noteworthy is the rapid recovery of T₁ and T₃ plants.

Chlorophyll index (u.r. SPAD)

In 1DAT and 4DAT, no significant differences were observed between the chlorophyll index of plants submitted to all treatments. In 7DAT, the T₁ plants showed, in isolation, a 5% reduction in the chlorophyll index in comparison to the control and the other treatments (T₂ and T₃). However, after the recovery phase, the T₂ and T₃ plants showed an increase of 8 and 5% in the chlorophyll index, respectively, differing statistically from the control (Figure 2).

DISCUSSION

In this study, the induction of plants to drought (T₁) combined drought and heat stress (T₃) stress reduced the photochemical (ϕP_0 , ψE_0 , ϕE_0 , δR_0 , PI_{abs} e PI_{total}) and photosynthetic (A, E e g_s) performance of *Psidium myrtilodes* plants. The significant 30% reduction in ϕP_0 suggests that dehydration possibly reduced the oxide-reduction reactions of the PSII. Furthermore, after watering for seven days (recovery), the plants of all treatments were similar to the control condition. The significant increase of 12% in ψE_0 , for T₂ plants, about control plants, suggests that: in a situation of adequate irrigation, the temperature can increase electron transport by ETC after a Q_A in *Psidium myrtilodes* plants.

Photosynthesis limitations caused by drought occur due to stoma closure (Flexas *et al.*, 1999). In drought stress, plants regulate stomatal closure to prevent dehydration. As a result, the entry of CO₂ into the leaf mesophile is impaired, directly impacting its assimilation and reducing photosynthesis rates and photochemical performance rates (Yan *et al.*, 2017). According to Martin-StPaul *et al.* (2017), this mechanism is a process to prevent dehydration and ensure that the plant aerial parts demand for water does not exceed the supply capacity of the root system. However, in severe drought conditions, the PSII can suffer damage of different intensities (Lang *et al.*, 2018), reducing the photosynthetic activity, the electron transport rate (ETR), and the photochemical (qP) and non-photochemical (qN) quenching coefficients (Li *et al.*, 2017). In general, photosynthetic activity is reduced when plants are subjected to stresses due to the destabilization of RuBisCO and damage to PSII caused by reactive oxygen species (ROS) produced in chloroplasts (Dietz *et al.*, 2016; Nishiyama & Murata, 2014). On the other hand, the heat increased the transpiration rate to decrease leaf temperature (Zandalinas *et al.*, 2016) and increased ψE_0 and PI_{TOTAL} .

Several studies have pointed out that the combined drought and heat stress had a worse potential effect than drought or heat stress alone (Mittler & Blumwald, 2010; Zhao *et al.*, 2017a). This stress is because the stomatal

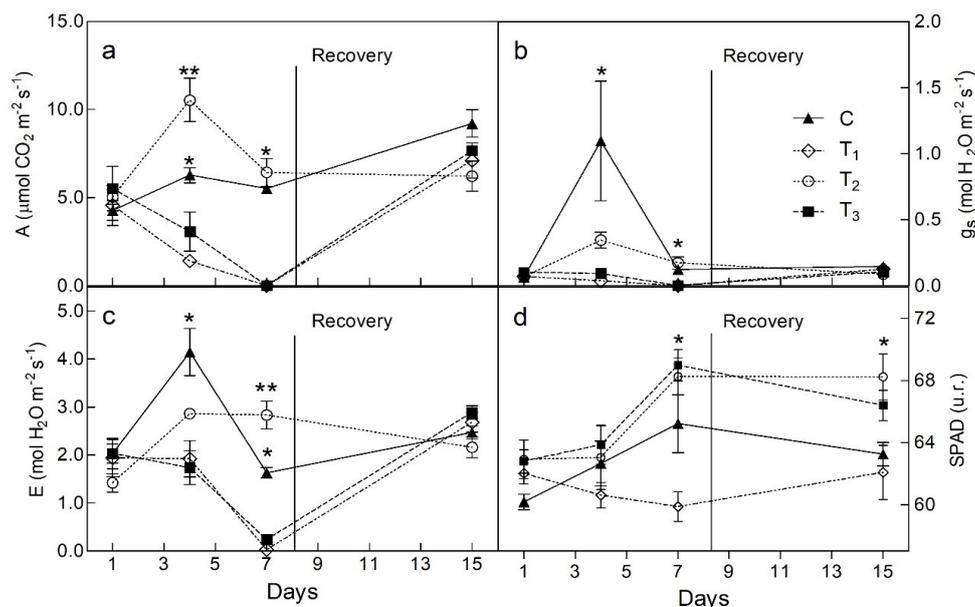


Figure 2: (a) Net photosynthesis rate (A; $\mu\text{mol m}^{-2} \text{s}^{-1}$), (b) stomatal conductance (g_s ; $\mu\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), (c) transpiration rate (E; $\mu\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$) and (d) SPAD chlorophyll index in *Psidium myrtilodes* of control plants and plants under drought (T₁), heat (T₂) and drought + heat (T₃) stress at 1, 4 and 7 days after treatments (DAT), and at 7 days of restoration of the initial conditions of irrigation and temperature (recovery). * $p < 0.05$ and ** $p < 0.01$ compared to the control by the Scott-Knott test. Error bars indicate SD.

responses to drought, heat, and the combination of both represent a challenging condition for plants. Therefore, it is necessary to establish a balance to prevent water loss and provide leaf cooling (Zandalinas *et al.*, 2018). That is, while high temperatures induce the plant to increase stomatal conductance to cool the leaves, drought is one of the factors responsible for inducing stomatal closure to reduce water loss (Mittler 2002; 2006). According to Tardieu *et al.* (2018), plants have evolved and developed a regeneration cycle in which increased transpiration promotes the stomata closure, reducing the transpiration rate. However, this study did not observe these responses for *Psidium myrtooides* plants since the drought (T_1), and the drought + heat (T_3) treatments demonstrated similar behaviors.

On the other hand, plants subjected only to heat stress (T_2) proved similar to control plants. It is known that in C3 plants, high temperatures limit the rate of photosynthetic CO_2 assimilation due to the increase in RuBisCO oxygenase capacity (Yan *et al.*, 2017). However, recent studies indicate that this mechanism, known as photorespiration, can act in the photoprotection of the photosynthetic apparatus using the excess energy in the ETR and dissipating it through the C2 cycle (Teskey *et al.*, 2015; Haworth *et al.*, 2018). The results show that the plants of *Psidium myrtooides* submitted to heat (T_2) have manifested mechanisms of photoprotection because the parameters of fluorescence and gas exchange were similar to the control and, in some cases, as for ψE_0 and PI_{TOTAL} , were even higher. It is likely to assume that, given the conditions imposed by the treatments, the limiting factor in the photosynthesis of *Psidium myrtooides* plants was drought and not heat. The photosynthetic apparatus is more tolerant to heat than drought (Urban *et al.*, 2018).

After the recovery, the plants submitted to heat (T_2), and dry + heat (T_3) stress showed both the parameters of the JIP test and those of gas exchange similar to the control plants. However, a difference remained in the SPAD index. The mentioned treatments showed an increase in leaf chlorophyll production, contrary to the studies of Bahrami *et al.* (2019), who reported that leaf chlorophyll is negatively influenced by heat, and a drought condition can lead to its degradation. Given the above, it is suggested that the increase in temperature imposed on T_2 and T_3 increased chlorophyll production, raising the value detected by a higher SPAD index.

In ‘Ubá’ mango tree under combined light and temperature stress (Faria-Silva *et al.*, 2017), and under nonirrigated conditions (Faria-Silva *et al.*, 2019) the chlorophyll content also showed higher values, in addition to a high positive correlation with the number of active reaction centers, suggesting that these has adaptation strategies of PSII and PSI to light and thermal stress.

According to Ahmad & Prasada (2012), the recovering capacity of plants to abiotic stresses is associated with the intensity and time of exposure. Therefore, further studies are needed to establish the limits of the recovering capacity of *Psidium myrtooides* plants subjected to drought, heat, and a combination of these stresses.

CONCLUSIONS

The plants of *Psidium myrtooides* showed a reduction in photochemical and leaf gas exchange when subjected to drought and drought + heat, recovering after seven days of restoration of normal conditions of irrigation and temperature. These same treatments showed an increase in the SPAD index at the end of the recovery period.

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