



High photosynthetic thermal tolerance in the Mediterranean halophyte *Limoniastrum monopetalum*

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Abstract

The general increase in temperature, together with sudden episodes of extreme temperatures, are increasingly impacting plant species in the present climate change scenario. *Limoniastrum monopetalum* is a halophyte from the Mediterranean Basin, exposed to broad daily and seasonal changes in temperature and extreme high temperatures. We studied the photosynthetic responses (chlorophyll fluorescence dynamics and gas exchange) of *L. monopetalum* leaves exposed to temperatures from -7.5°C to $+57.5^{\circ}\text{C}$ under darkness in controlled laboratory conditions. *L. monopetalum* presented its optimum temperature for photosynthesis around $+30^{\circ}\text{C}$. The photosynthetic apparatus of *L. monopetalum* exhibited permanent damages at $> +40.0^{\circ}\text{C}$. *L. monopetalum* tolerated, without permanent damages, temperatures as low as -7.5°C in darkness. *L. monopetalum* appears as a plant species very well adapted to the seasonality of the Mediterranean climate, which may work as a pre-adaptation to stand more extreme temperatures in the actual context of accelerating climate change.

Keywords: chlorophyll fluorescence; climate change; gas exchange; heat wave; Mediterranean climate; stressor.

Introduction

Temperature influences the physiology and distribution of plant species worldwide (Žróbek-Sokolnik 2012). In the present climate change scenario, the general temperature increase and sudden episodes of cold and heat waves are increasingly impacting plant species (IPCC 2022). In this context, it is urgent to improve our knowledge on the effects of extreme temperatures on the photosynthetic performance of different plant species. This is especially relevant for those species that are key in the provision of ecosystem services and in those geographical regions more affected by climate change (Hao *et al.* 2017).

Plants can respond in many ways to temperature changes and photosynthesis is one of the most temperature-sensitive metabolic pathways (Ashraf and Harris 2013,

Legris *et al.* 2017). The behavior of photosynthesis depends on temperature, presenting an optimum temperature in which the net assimilation of carbon dioxide is maximum. Moreover, plant species present species-specific temperature tolerance ranges, where no permanent damages to the photosynthetic apparatus are recorded (Wigge 2013, Szymańska *et al.* 2017). When plant species are exposed to temperatures above or below their operating range, their photosynthetic efficiency is diminished (Penfield and MacGregor 2014). Extreme temperatures can inhibit photosynthesis in different ways, for example, by increasing oxidative stress (Chaudhry and Sidhu 2022), decreasing the efficiency of PSII (Popova *et al.* 2022), limiting the activity of the enzymes involved in the Calvin cycle (Mathur *et al.* 2014), altering photorespiration (Voss *et al.* 2013, Cavanagh *et al.* 2022),

Highlights

- *Limoniastrum monopetalum* showed its optimum temperature *ca.* $+30^{\circ}\text{C}$
- *L. monopetalum* showed permanent damages at temperatures $> +40.0^{\circ}\text{C}$
- *L. monopetalum* tolerated temperatures as low as -7.5°C in dark conditions

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Abbreviations: Chl – chlorophyll; F_0 – basal fluorescence; F_v – variable fluorescence; F_m – maximum fluorescence; F_v/F_m – maximum photochemical efficiency of PSII; ROS – reactive oxygen species; V_{\max} – maximal rate of photosynthetic oxygen evolution.

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and modifying the structure of the thylakoids (Fehér *et al.* 2023).

Leaves developing in certain environmental conditions optimize their metabolism to those conditions, which is called developmental acclimation (Gjindali and Johnson 2023). Many metabolic responses are common in the acclimation process of plants to different stressors, such as drought, high salinity, and extreme temperature (Seki *et al.* 2003). For example, reactive oxygen species (ROS) are signal transduction molecules that control different pathways during acclimation to diverse stresses (Choudhury *et al.* 2017). The interactions between different stresses, such as osmotic and thermal stress, become more common under the current climate change scenario (Xu *et al.* 2020). In this sense, pre-exposure to a certain stressor may increase plant tolerance to other stressors (Vetoshkina *et al.* 2023).

Limoniastrum monopetalum L. (Boiss) (family Plumbaginaceae) is a halophilous shrub that grows in salt marshes, coastal sand spits, sea cliffs, and semi-arid areas around the Mediterranean region (Valdés *et al.* 1987, Boulos 2008, Vladimirov *et al.* 2015). These areas are exposed to broad seasonal changes in temperature ($> 30^{\circ}\text{C}$) and very high temperatures during summertime ($> +40^{\circ}\text{C}$). The Mediterranean Basin is a regional area identified as a climate change hotspot (IPCC 2022). Even so, few studies have analyzed the responses of the photosynthetic apparatus of Mediterranean halophytes to temperature in controlled conditions (Walker and Lutts 2014, Duarte *et al.* 2015, 2016, 2023). *L. monopetalum* is a dominant species in many coastal and semi-arid areas in the Mediterranean Basin, where it plays a key role in ecosystem structuring and functioning (Abd El-Maboud and Abd Elbar 2020, Boughalleb *et al.* 2022). In addition, *L. monopetalum* is being used as an ornamental species in urban green spaces (Akoumianaki Ioannidou *et al.* 2015).

We carried out an experiment under controlled laboratory conditions in which we analyzed the tolerance of the photosynthetic apparatus of *L. monopetalum* along a broad range of temperatures, from -7.5°C to $+57.5^{\circ}\text{C}$, using chlorophyll fluorescence and gas-exchange measurements as physiological responses. We performed this experiment for *L. monopetalum* leaves acclimated to freshwater and constant temperature ($+23$ – 25°C) under greenhouse conditions and also with leaves collected from natural populations in the field to test the effects of acclimation on temperature tolerance (Yamori *et al.* 2014). We hypothesized that the photosynthetic apparatus of *L. monopetalum* would show high thermal tolerance along a wide range of temperatures since this halophyte is exposed to the marked seasonality characteristic of the Mediterranean climate. In this sense, we also hypothesized that leaves acclimated to field conditions would show lower thermal stress levels at extreme temperatures than greenhouse-acclimated leaves. Our results are useful to explain the current distribution of *L. monopetalum* from a physiological point of view and to understand the effects of climate change on this dominant key halophyte in Mediterranean marshes.

Materials and methods

Plant material: Our experiments were carried out with *L. monopetalum* leaves acclimated to greenhouse conditions and field conditions in winter (to test tolerance to low temperatures) and in summer (to test responses to high temperatures). Thus, we could verify how acclimatization to field conditions predisposed leaves to tolerate extreme temperatures. To test the responses on plants acclimated to controlled conditions, adult *L. monopetalum* plants coming from the Odiel Marshes were kept in perlite and freshwater conditions at field capacity at $+23$ – 25°C , 55% air relative humidity, under natural photoperiod at a maximum radiation level of $750 \mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ for four weeks in the greenhouse facility of the University of Seville. This acclimation period to greenhouse conditions allowed the plants to produce new leaves suited to the new environment. Leaves acclimated to field conditions were collected from adult *L. monopetalum* plants that grew in Saltés Island in the Odiel Marshes (Southwest Iberian Peninsula, $37^{\circ}13'$ – $37^{\circ}08'\text{N}$, $6^{\circ}58'$ – $6^{\circ}52'\text{W}$) on January 2017 to test the responses to low temperatures and on September 2017 to test the responses to high temperatures. Mean air daily temperature in Odiel Marshes was $+8.5 \pm 0.4^{\circ}\text{C}$ and $+24.1 \pm 0.4^{\circ}\text{C}$ during the week before sampling in the winter and summer, respectively. In addition, the week before sampling, the minimum daily temperature was $+2.2^{\circ}\text{C}$ and $+16.8^{\circ}\text{C}$ in winter and summer conditions, respectively. Maximum temperature was $+16.0^{\circ}\text{C}$ and $+32.1^{\circ}\text{C}$ in winter and summer conditions, respectively (data from meteorological station Palos de la Frontera located 4 km from the sampling marsh in the Odiel Marshes). Soil electrical conductivity was $5.7 \pm 0.4 \text{ mS cm}^{-1}$ in winter and $12.8 \pm 0.3 \text{ mS cm}^{-1}$ in summer ($n = 5$).

Thermal experiment: Nonsenescent fully developed adult leaves were sampled randomly from five adult *L. monopetalum* plants selected randomly in the field and greenhouse conditions ($n = 5$ leaves per temperature treatment, one leaf per plant) to avoid possible effects related to leaf development that could affect thermal sensitivity (Lichtenthaler 1996). After collection, the leaves were immediately stored in a moisture-saturated atmosphere at $+20^{\circ}\text{C}$ for 3 h. Subsequently, the leaves were placed in sealed plastic bags and immersed in a water bath with programmable temperatures (Neslab RTE-200, NESLAB Instr., Newington, NH, USA) for 30 min in dark conditions at different temperatures ranging from -7.5°C to $+57.5^{\circ}\text{C}$ (Carrión-Tacuri *et al.* 2013). The temperature decreased from $+20.0^{\circ}\text{C}$ to 0.0°C in steps of 5.0°C and from 0.0°C to -7.5°C in steps of 2.5°C . Each set of leaves (replicates) was exposed to one temperature treatment for 30 min. To avoid the formation of crystals in the water bath at low temperatures, a solution of 50% (v/v) ethylene glycol was used. Exposure to low temperatures in darkness corresponded to the conditions experienced by *L. monopetalum* leaves during winter night cooling episodes. Temperature increased from $+25.0^{\circ}\text{C}$ to $+40.0^{\circ}\text{C}$ with 5.0°C steps and from $+40.0^{\circ}\text{C}$ to $+57.5^{\circ}\text{C}$

with 2.5°C steps. Exposure to high temperatures in darkness mimicked the conditions experienced by leaves during summer nights. After 30 min in each temperature treatment, the leaves were taken out of the water bath and chlorophyll *a* fluorescence was measured immediately so as not to disturb the condition of the dark-acclimated leaves.

Recovery period: A period of mild temperatures is required to return to the rates of photosynthesis before treatment with extreme temperatures (Davidson *et al.* 2004). So, just after the thermal treatments, the leaves were kept in open plastic containers in saturated humidity at +25°C and 40 $\mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$ for 24 h to determine the recovery capacity of the photosynthetic apparatus after temperature treatments (Carrión-Tacuri *et al.* 2013). Low light intensity conditions favor the replacement of damaged PSII proteins (Bergo *et al.* 2003). After the recovery period, we recorded chlorophyll *a* fluorescence again in leaves acclimated to darkness for 30 min, and the maximal rate of photosynthetic oxygen evolution using an oxygen electrode.

Chlorophyll fluorescence: Chlorophyll (Chl) *a* fluorescence was measured using a portable modulated fluorimeter (FMS-2, Hansatech Instruments Ltd., Pentney, UK). Chl fluorescence parameters were measured in dark-acclimated leaves using leaf clips to investigate the effects of temperature on the sensitivity of leaves to the thermal treatments. The basal or minimum level of fluorescence in the dark-adapted state (F_0), when all reaction centers are open for photochemistry, was measured using a modulated pulse [$< 0.05\ \mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$ for 1.8 μs] that was too small to induce significant physiological changes in the plant. The recorded data represented an average taken over a 1.6-s period. An increase in F_0 reflects the physical separation of the PSII reaction centers from their pigment antennae resulting in blocked energy transfer (Banks 2017). Maximum fluorescence (F_m), reached when dark-adapted leaves are exposed to intense saturating light, was measured after applying a saturated actinic light pulse of 15,000 $\mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$ for 0.7 s. The F_m value was recorded as the highest average of two consecutive peaks of Chl fluorescence emission. F_m is recorded when all reaction centers are closed due to the reduction of the plastoquinone A, the PSII downstream acceptor quencher. This process reduces the efficiency of photochemistry and increases energy dissipation (Maxwell and Johnson 2000). Variable fluorescence values ($F_v = F_m - F_0$) and maximum photochemical efficiency of PSII (F_v/F_m) were calculated. F_v/F_m values correlate with the number of functional PSII reaction centers and can be used to quantify plant tolerance under thermal stress (Maxwell and Johnson 2000).

Maximal rate of photosynthetic oxygen evolution (V_{max}): V_{max} was measured after the recovery period (24 h) using a Clark-type oxygen electrode (Hansatech LD2, Pentney, UK) on a foliar surface of $2.61 \pm 0.09\text{ cm}^2$ at +20°C and

1,500 $\mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$ in a CO_2 -saturated atmosphere created using 1 M carbonate/bicarbonate buffer (Farquhar *et al.* 2001, Popova *et al.* 2019).

Statistical analyses: Statistical analyses were carried out using the R software. The deviation from the mean was calculated as standard error (SE). Normality and homogeneity of variance of the data series were verified using the Kolmogorov–Smirnov test and the Levene test, respectively. As the data series were not normal and/or did not show homoscedasticity, even after their transformation using the functions $1/x$, \sqrt{x} , and $\ln(x)$, the means were compared using nonparametric tests. Generalized Linear Models (GLM, gamma distribution) were used to compare Chl fluorescence parameters (dependent variable) between thermal treatments, measurement conditions (just after treatments and after the recovery period), acclimatization conditions (greenhouse and field), and their interactions. GLM was also applied to compare V_{max} (dependent variables) between thermal treatments, acclimatization conditions, and their interactions. Kruskal–Wallis one-way test, followed by the Student–Newman–Keuls test as *post-hoc* analysis, were applied to compare Chl fluorescence parameters and V_{max} among temperatures for greenhouse- or field-acclimated plants and treatment or recovery measurements separately.

Results

All Chl fluorescence parameters showed significant differences between temperature treatments and acclimatization conditions (greenhouse vs. field), treatment and recovery, and their interactions. In addition, F_m and F_0 showed significant differences between measurement conditions (just after treatment vs. after the recovery period) (Table 1).

Chlorophyll fluorescence just after thermal treatments: F_v/F_m for greenhouse-acclimated leaves fell significantly at temperatures above +35.0°C just after heat treatment (Fig. 1A), due to an increase in F_0 and a fall in F_m (Fig. 1C,E). No fluorescence emission for F_0 and F_m was obtained from leaves acclimated to greenhouse conditions at temperatures higher than +52.5°C (Fig. 1A,C,E). F_v/F_m for leaves acclimated to field conditions dropped significantly by about 40% at temperatures above +40.0°C (Fig. 1B), due to an increase in F_0 and a fall in F_m (Fig. 1D,F). No fluorescence emission for F_0 and F_m was obtained in leaves acclimated to field conditions at temperatures higher than +55.0°C (Fig. 1B,D,F).

F_v/F_m for greenhouse-acclimated leaves decreased significantly at temperatures lower than –2.5°C due to an increase in F_0 with constant F_m values (Fig. 1A). This F_v/F_m decrease at low temperatures was not recorded for leaves acclimated to field conditions (Fig. 1B).

Chlorophyll fluorescence after recovery: 24 h after thermal treatments, F_v/F_m of leaves acclimated to

Table 1. Chi-squared (χ^2), degree of freedom (d.f.), and P -values of generalized linear models for physiological traits of *Limoniastrum monopetalum* in response to temperature (from -7.5°C to $+57.5^\circ\text{C}$), time after temperature treatment (just after treatment vs. recovery after 24 h), acclimation conditions (plants acclimated to field vs. greenhouse conditions) and their interactions. Significant differences are marked in bold. F_v/F_m – maximum photosystem II quantum efficiency; F_m – maximum fluorescence; F_0 – basal fluorescence; V_{\max} – maximal rate of photosynthetic oxygen evolution.

	F_v/F_m	F_m	F_0	V_{\max}
Temperature (d.f. = 17)	$\chi^2 = 58.284, P < 0.0001$	$\chi^2 = 21.066, P < 0.0001$	$\chi^2 = 41.109, P < 0.0001$	$\chi^2 = 31.918, P < 0.0001$
Time (treatment vs. recovery) (d.f. = 1)	$\chi^2 = 0.019, P = 0.585$	$\chi^2 = 0.136, P = 0.029$	$\chi^2 = 0.791, P = 0.006$	-
Acclimation (field vs. greenhouse) (d.f. = 1)	$\chi^2 = 0.600, P = 0.002$	$\chi^2 = 2.012, P < 0.0001$	$\chi^2 = 13.075, P < 0.0001$	$\chi^2 = 0.059, P = 0.488$
Temperature \times Time (d.f. = 17)	$\chi^2 = 1.637, P = 0.084$	$\chi^2 = 1.969, P < 0.0001$	$\chi^2 = 0.967, P = 0.929$	-
Time \times Acclimation (d.f. = 1)	$\chi^2 = 0.175, P = 0.098$	$\chi^2 = 0.020, P = 0.399$	$\chi^2 = 0.015, P = 0.706$	-
Temperature \times Acclimation (d.f. = 16)	$\chi^2 = 6.658, P < 0.0001$	$\chi^2 = 2.247, P < 0.0001$	$\chi^2 = 5.816, P < 0.0001$	$\chi^2 = 1.786, P = 0.549$
Temperature \times Time \times Acclimation (d.f. = 16)	$\chi^2 = 1.042, P = 0.436$	$\chi^2 = 0.677, P = 0.093$	$\chi^2 = 0.363, P = 1.000$	-

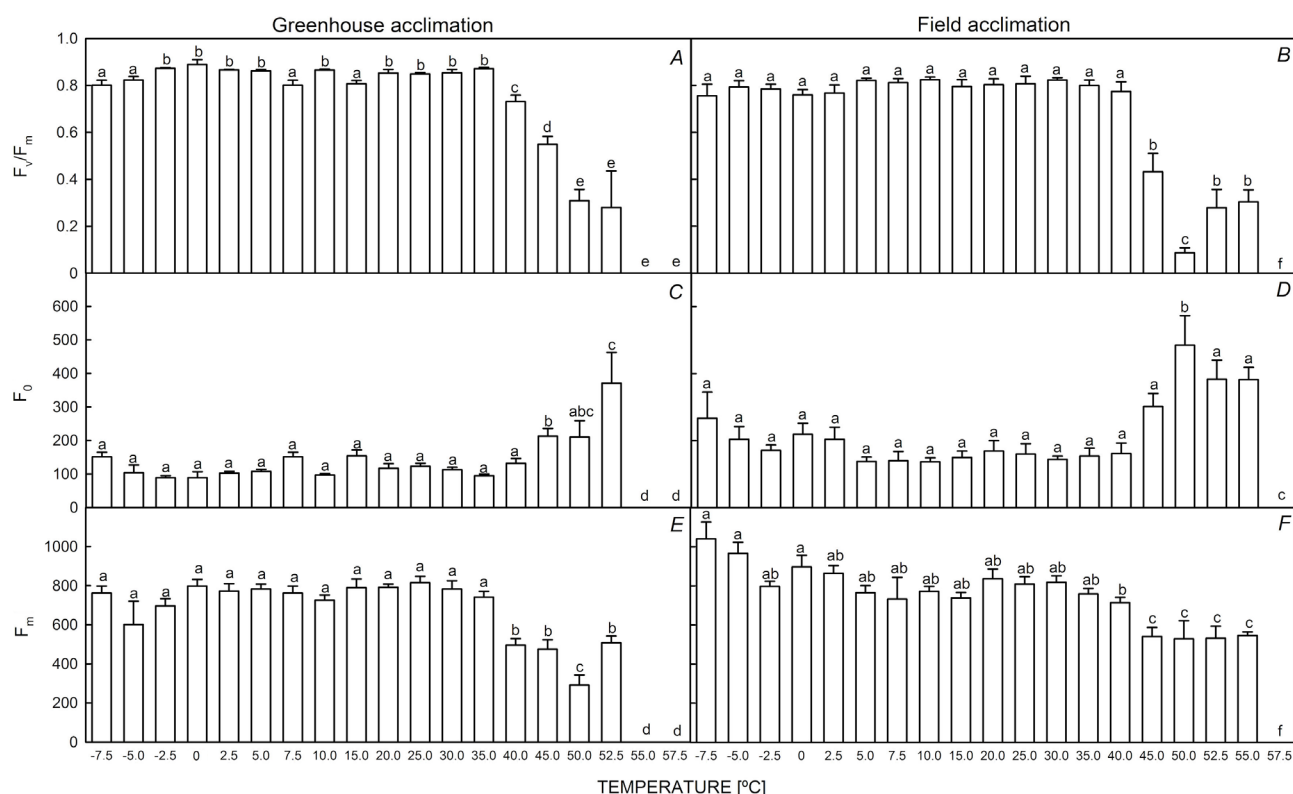


Fig. 1. Potential photochemical efficiency of PSII (F_v/F_m) (A,B), basal fluorescence (F_0) (C,D), and maximum fluorescence (F_m) (E,F) of *Limoniastrum monopetalum* leaves acclimated to controlled greenhouse conditions ($+23$ – 25°C), and to field conditions (winter for temperatures lower $+20^\circ\text{C}$ and summer for temperatures higher $+20^\circ\text{C}$), after 30 min at temperatures from -7.5°C to $+57.5^\circ\text{C}$ in darkness. Values are means \pm SE ($n = 5$). Different letters indicate significant differences between treatments (Student–Newman–Keuls test, $P < 0.05$).

greenhouse conditions fell sharply at temperatures above $+40.0^\circ\text{C}$ and $+45^\circ\text{C}$ for leaves acclimated to field conditions, due to an increase in F_0 and a decrease in F_m (Fig. 2). No fluorescence emission for F_0 and F_m was obtained from leaves acclimated to greenhouse and field conditions at temperatures higher than $+52.5^\circ\text{C}$ and $+55.0^\circ\text{C}$, respectively (Fig. 2). As in the case of the measurements recorded just after the temperature treatments (previous section), F_v/F_m for greenhouse-acclimated leaves decreased significantly at temperatures lower than -2.5°C after the recovery period, due to

an increase in F_0 with constant F_m values. This decrease was not recorded for leaves acclimated to field conditions (Fig. 2).

Maximal rate of photosynthetic oxygen evolution:

The highest values of V_{\max} were recorded between $+25.0^\circ\text{C}$ and $+40.0^\circ\text{C}$ for greenhouse-acclimated leaves (Fig. 3A, Table 1), and between $+20.0^\circ\text{C}$ and $+40.0^\circ\text{C}$ for leaves acclimated to field conditions (Fig. 3B). The highest values of V_{\max} at optimal temperatures [$\text{ca. } 20 \mu\text{mol}(\text{O}_2) \text{ m}^{-2} \text{ s}^{-1}$] were more than double the lowest values

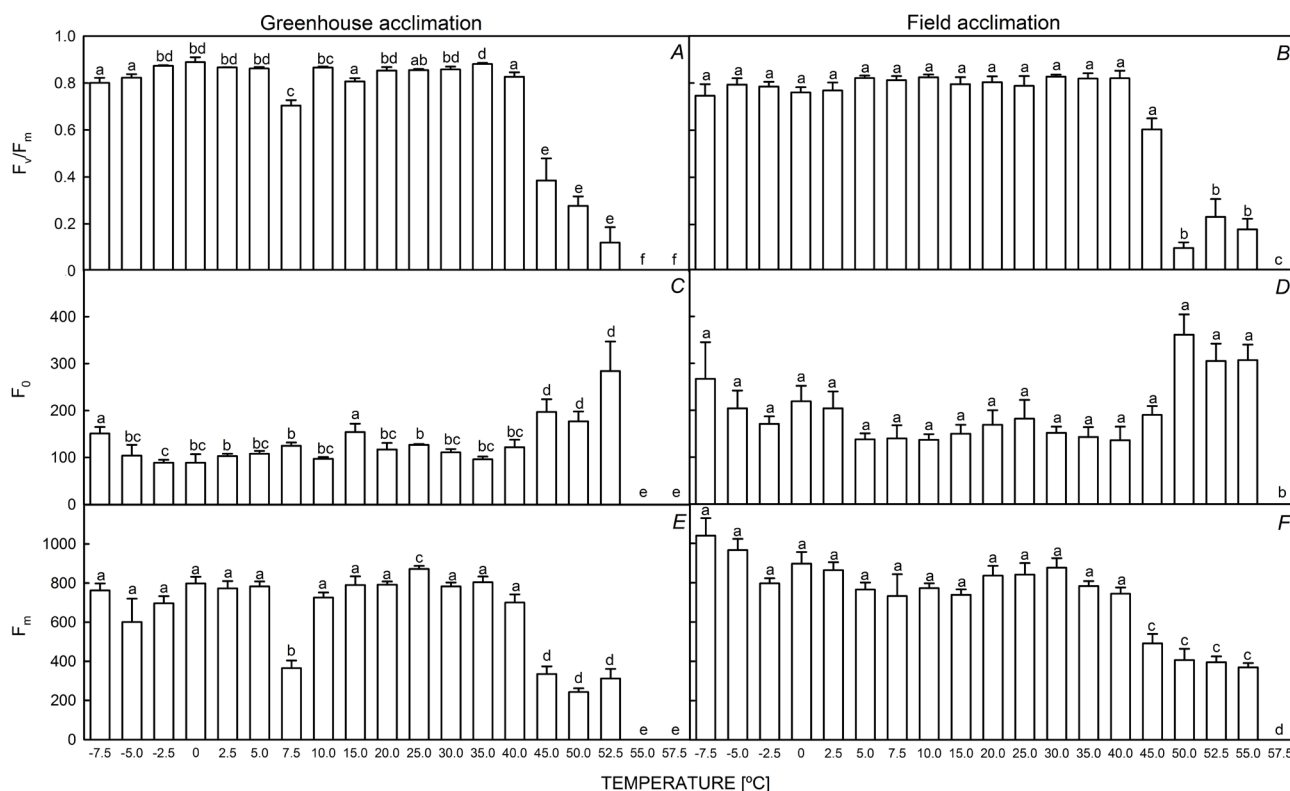


Fig. 2. Potential photochemical efficiency of PSII (F_v/F_m) (A,B), basal fluorescence (F_0) (C,D), and maximum fluorescence (F_m) (E,F) of *Limoniastrum monopetalum* leaves acclimated to controlled greenhouse conditions (+23–25°C), and to field conditions (winter for temperatures lower +20°C and summer for temperatures higher +20°C), 24 h after temperature treatment from –7.5°C to +57.5°C in darkness. Values are means \pm SE ($n = 5$). Different letters indicate significant differences between treatments (Student–Newman–Keuls test, $P < 0.05$).

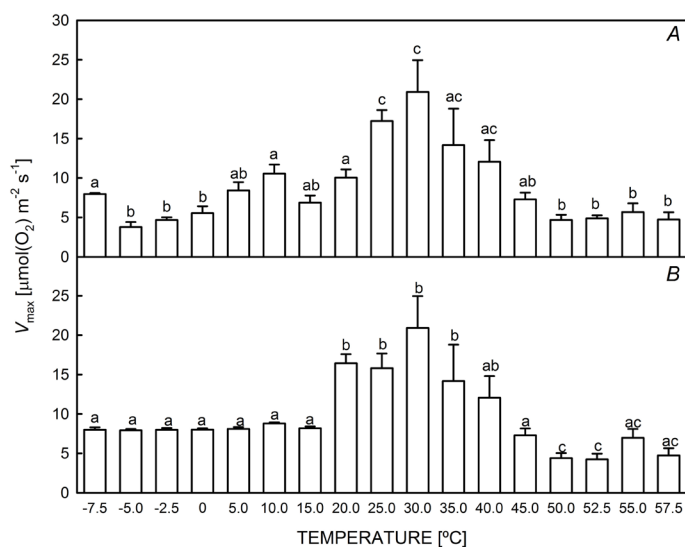


Fig. 3. Maximal rate of photosynthetic oxygen evolution (V_{max}) of *Limoniastrum monopetalum* leaves acclimated to (A) greenhouse and (B) field conditions, acclimated to field winter conditions for temperatures lower than +20°C and summer conditions for temperatures higher than +20°C, 24 h after exposure to temperatures between –7.5°C and +57.5°C in darkness. Values are means \pm SE ($n = 3$ –5). Different letters indicate significant differences between treatments (Student–Newman–Keuls test, $P < 0.05$).

after being exposed to the most extreme temperatures [$< 10 \mu\text{mol}(\text{O}_2) \text{m}^{-2} \text{s}^{-1}$] (Fig. 3).

Discussion

Our results showed that *L. monopetalum* presents its optimum temperature for photosynthesis around +30°C, without showing permanent damage to the photosynthetic

apparatus at temperatures lower than +45.0°C and as low as –7.5°C for 30 min in dark conditions. In addition, *L. monopetalum* leaves acclimated to field conditions tended to show greater tolerance to extreme temperatures than greenhouse-acclimated leaves.

L. monopetalum showed higher tolerance to low temperatures than other coastal woody species typical of the Mediterranean Basin such as *Juniperus oxycedrus* L.,

Juniperus phoenicea L., and *Pinus pinea* L., which suffered permanent damage to their photosynthetic apparatus in dark conditions at temperatures below +10°C in an experiment that followed the same methodology as this study (Rubio-Casal *et al.* 2010). Low temperatures together with high radiation intensities may impose high-stress levels on the photosynthetic apparatus (Duarte *et al.* 2015) but the effects of low temperatures on photosynthesis also occur in dark conditions, for example, during cold winter nights (Davidson *et al.* 2004). In this sense, *L. monopetalum* leaves are exposed to relatively high levels of solar radiation and low temperatures during winter mornings (E. Figueroa-Luque, pers. obs.), which could lead to higher levels of photosynthetic stress than those recorded in our experiment under dark conditions. On the other hand, we recorded permanent damages to the photosynthetic apparatus of *L. monopetalum* at high temperatures (> +40°C), reflected in a sustained fall in F_v/F_m caused by an increase in F_0 and a decrease in F_m . This response indicated the reduction in the number of active reaction centers and difficulties in transmitting energy at the level of the antenna complexes of PSII (Maxwell and Johnson 2000). The recorded increase in F_0 may be due to the release of light-harvesting chlorophyll protein from the PSII core complexes, inactivation of PSII photochemical reaction, or an inhibition of electron flow to the plastoquinone A. Additionally, the observed increase in F_0 may also be attributed to the accumulation of light-induced reduced Q_A , the primary electron acceptor from PSII, and enhanced back electron transfer from Q_B to Q_A . High temperatures can alter the midpoint redox potential of Q_A , favoring its reduction and consequently elevating F_0 even under the weak light excitation used for the measurement (Kouřil *et al.* 2004). Moreover, the recorded decrease in F_m may be related to denaturation of chlorophyll proteins (Kalaji *et al.* 2016). The blockage of electron flow in the electron transport chain under thermal stress would lead to electrons reacting with oxygen and producing reactive oxygen species (ROS) (Zhang *et al.* 2023) that can inactivate the repairing processes of photosystems (Landi and Guidi 2023). The PSII complex is the most sensitive part of the photosynthetic apparatus to thermal stress. In this sense, the extrinsic proteins may disassociate from the oxygen-evolving complex of PSII when exposed to thermal stress (Gupta *et al.* 2021). Nevertheless, we recorded some V_{max} activity [ca. 5 $\mu\text{mol}(\text{O}_2) \text{ m}^{-2} \text{ s}^{-1}$] at extremely high temperatures even when we did not record any chlorophyll fluorescence signal which indicated an inactivation of PSII. This could reflect that the recorded inactivation of PSII occurred after water oxidation due to protein alterations or conformational changes, as reported by Meyer and de Kouchkovsky (1993) for *Lupinus albus* L. in response to drought. Moreover, we recorded V_{max} in a CO_2 -saturated atmosphere where photorespiration was suppressed, which would increase the recorded O_2 evolution.

The greater tolerance to extreme temperatures recorded for leaves of *L. monopetalum* acclimated to field conditions compared to those grown under greenhouse conditions could be related to several processes. For example,

L. monopetalum plants in coastal marshes are exposed to saline conditions, while plants were grown under freshwater conditions in the greenhouse. Pre-exposure to salinity may increase tolerance levels to extreme temperatures since some plant responses are useful to deal with different stressors (Sewelam *et al.* 2016). In this sense, *L. monopetalum* plants may suffer more from thermal stress when grown in urban green spaces than in salt marshes. In addition, *L. monopetalum* plants were exposed to changing daily and seasonal temperatures in the field (between +2.2°C and +16.0°C in winter, and between +16.8°C and +32.1°C in summer conditions), while plants in the greenhouse were kept at constant temperatures (+23–25°C). Thus, *L. monopetalum* leaves collected in the field could be better acclimated to changing temperatures than leaves from the greenhouse.

Our results show a relatively high optimum temperature for photosynthesis (+30°C) and a broad thermal photosynthetic range (from –7.5°C to +45.0°C) agree with the distribution of *L. monopetalum* around the Mediterranean Basin, where broad daily and seasonal oscillations in temperatures are recorded (Abd El-Maboud and Abd Elbar 2020, Boughalleb *et al.* 2022). Thus, *L. monopetalum* appears as a plant species well adapted to the seasonality of the Mediterranean climate at the level of its photosynthetic apparatus. This may work as a pre-adaptation to stand extreme temperatures in the Mediterranean Basin in the actual context of climate change (IPCC 2022, Noto *et al.* 2023). In this sense, Vicente and Boscaiu (2020) identified some Mediterranean halophytes with mechanisms that can allow them to adapt to climate change-induced environmental alterations. Nevertheless, the photosynthetic status of *L. monopetalum* could be compromised at leaf temperatures higher than +40°C during more frequent and intense heat waves (Chovancek *et al.* 2019, Hwang *et al.* 2022). Extreme high temperatures could be reached especially in leaves of *L. monopetalum* under water stress, which would limit foliar cooling capacity through transpiration, in the context of more frequent and intense droughts in the Mediterranean Basin (De Boeck *et al.* 2016, Bastos *et al.* 2020).

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