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Different photoprotective responses under drought conditions of two predominant chilean swamp forest species

Diferentes respuestas fotoprotectoras bajo condiciones de sequía en dos especies predominantes del bosque pantanoso de Chile

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ABSTRACT

Myrceugenia exsucca (DC.) O.Berg (Myrtaceae) and *Luma chequen* (Molina) A. Gray (Myrtaceae) are two predominants species from swamp forests of Chile. These species present differential microhabitat distribution across soil moisture and north-south precipitation gradients, with only *L. chequen* being commonly found in lower moisture sites. It is hypothesized that *L. chequen* has greater plasticity than *M. exsucca* in the attributes involved in photoprotection under drought conditions. To test this hypothesis, both species were exposed to short term drought treatment. A group of individuals was maintained irrigated (with Ψ_w of -0.58 and -0.73 MPa for *M. exsucca* and *L. chequen,* respectively), while another group was exposed to drought treatment with Ψ_w around -1.4 MPa (Ψ_wD). High relationship was founded between relative water content (RWC) and water potential (Ψ_w) for *M. exsucca* (r^2= 0.74) more than for *L. chequen* (r^2= 0.46), indicating that *M. exsucca* experienced larger dehydration during the drought treatment. As functional attributes of photosynthetic apparatus, amount of total chlorophyll and chlorophyll *a* fluorescence parameter levels were studied in both species. The results show that *L. chequen* reduced total content of chlorophylls and maximum efficiency of PSII (Fv / Fm) related to decrease of energy capture increasing significantly the thermal dissipation (qN). On the other hand, *M. exsucca* does not change these parameters, but significantly reduced the level of photochemical processes (qL), indicating an energy imbalance. The results indicate *M. exsucca* has less plasticity than *L. chequen* under drought conditions. It is believed that these differences may be crucial in the establishment period and may be influencing the limited distribution of *M. exsucca* in sites with lower water availability.

Keywords: Thermal dissipation, water potential, native plants, Myrtaceae family, wetland plants.

RESUMEN

Myrceugenia exsucca (DC.) O. Berg (Myrtaceae) y *Luma chequen* (Molina) A. Gray (Myrtaceae) son dos especies predominantes de los bosques pantanosos en Chile. Estas especies presentan diferente distribución a través de un gradiente de humedad y de precipitaciones, siendo *L. chequen* más común que *M. exsucca* en lugares con menor humedad. En este trabajo se plantea la hipótesis que *L. chequen* presenta una mayor plasticidad que *M. exsucca* de los atributos involucrados en fotoprotección bajo condiciones de sequía. Para comprobar esta hipótesis, individuos de ambas especies fueron expuestos a un tratamiento de sequía. Un grupo de individuos fue mantenido con riego exhibiendo un potencial hídrico (Ψ_w) óptimo de -0.58 y -0.73 MPa para *M. exsucca* y *L. chequen,* respectivamente. Otro grupo fue sometido a sequía, donde el Ψ_w disminuyó a -1.4 MPa (Ψ_wD) para ambas especies. Se encontró una mayor correlación entre el contenido relativo de agua (RWC) y Ψ_w para *M. exsucca* (r^2= 0.74) que para *L. chequen* (r^2= 0.46), indicando que *M. exsucca* experimentó una mayor deshidratación que *L. chequen* durante el tratamiento. Como atributos de funcionalidad del aparato fotosintético el nivel de clorofilas y la fluorescencia de la clorofila *a* fueron estudiados en plantas de ambas especies. Los resultados muestran que *L. chequen* redujo el contenido total de clorofilas y la eficiencia máxima del PSII (Fv/Fm) relacionado con una disminución de la captura energética e incrementó significativamente la disipación térmica (qN). Por otro lado, *M. exsucca* no mostró cambios en estos parámetros, pero redujo significativamente el nivel de los procesos fotoquímicos (qL), indicando un desbalance energético. Los resultados indican que *M. exsucca* posee una menor plasticidad que *L. chequen* bajo condiciones de sequía. Se cree que estas diferencias pueden ser cruciales en el periodo de establecimiento y pueden estar influenciando la limitada distribución de *M. exsucca* en sitios con menor disponibilidad hídrica.

Palabras clave: Disipación térmica, potencial hídrico, plantas nativas, familia Myrtaceae, plantas higrófilas.

INTRODUCTION

Riparian vegetation dominated by trees is common among Mediterranean and desert ecosystems (Busch & Smith 1995, Villagrán & Hinojosa 1997) and correspond to discontinuous and azonal vegetal formation restricted to hydrophilic habitats (Fuenzalida & Pisano 1965, Maldonado & Villagrán 2001, Ramírez *et al.* 1995). It has been reported that riparian vegetation has been related with watercourse protection and biological diversity conservation (Ramírez *et al.* 1995). In fact, these plants are the refuge for many species of insects and birds (Solervicens & Elgueta 1994). However, this vegetation is usually under severe threat from human activity such as wood extraction, grazing, water provision and expansion of crop land (Correa-Araneda *et al.* 2011).

In the Chilean Mediterranean zone, riparian vegetation is characterized by swamp forests dominated by trees and scrub species belonging to the Myrtaceae family, distributed along the coast of north-central Chile from Coquimbo to Los Lagos Region (31-41ºS) (Villagrán & Hinojosa 1997). *Myrceugenia exsucca* (DC.) O. Berg (Myrtaceae) and *Luma chequen* (Molina) A. Gray (Myrtaceae) are two species considered important within the swamp forest (San Martín *et al.* 1988). These plants grow together in permanently or semi-permanently flooded soils, however, their microhabitats often differ, with only *L. chequen* being commonly found in lower moisture sites (Landrum 1988). Furthermore, across a north-south gradient of precipitations, *M. exsucca* exhibits a southern distribution between 32°S (Coquimbo, Coquimbo Region) and 44°S (Llanquihue, Los Lagos Region), while *L. chequen* is extended from 30.5°S (Coquimbo, Coquimbo Region) and 42°S (Chiloé, Los Lagos Region) (Landrum 1988). The presence of *M. exsucca* in the semiarid regions of its distribution is very limited, and it is considered such a vulnerable species (Arancio *et al.* 2001). Deforestation and drainage to allow the land to be used for various productive activities (Hauenstein *et al.* 2005, Peña-Cortés *et al.* 2011), however, as a consequence these plants have to cope with increments of aridity that could affect central Chile (IPCC, 2007).

Water availability is the primary resource for structuring plant communities in arid and semi-arid regions (Knapp *et al.* 2002, Bai *et al.* 2004, Chaves *et al.* 2009). Water deficit induces stomatal closure to minimize the water losses at expense of reducing CO_2 assimilation (Chaves *et al.* 2002, Flexas & Medrano 2002, Herrera *et al.* 2008). Under these conditions, light incident on the leaf surface exceeds largely the amount that can be used for photosynthesis (Demmig-Adams *et al.* 1996). This excess of absorbed light energy can induce photoinhibition which is a consequence of either reversible down-regulation of PSII through dissipation of excess absorbed energy or irreversible inactivation of PSII and damage to D1 reaction center protein (Demmig-Adams *et al.* 1996, Niyogi *et al.* 1998, Aro *et al.* 1993). However, the plants have developed different mechanisms to prevent photodamage and safely dissipate the excess of absorbed energy to avoid damage to photosynthetic machinery.

Photoprotection may be achieved by decreasing the probability of light absorption through the development of smaller light harvest complex which is reflected in a decrease of chlorophyll amount (Balaguer *et al.* 2001). If an excess of energy have been absorbed, photoprotection may be accomplished by dissipation through the photochemical use of energy excess (photochemical quenching, qL) or by the non-photochemical quenching of chlorophyll *a* on the antena (qN). Full qN activation requires quenching of the excess absorbed light in the antenna, via induction of the xanthophyll cycle (Demmig-Adams *et al.* 1996, Niyogi *et al.* 1998). There is a substantial evidence that thermal dissipation is responsible for dissipate the majority of excess energy in drought tolerant plants (Savage *et al.* 2009, García-Plazaola & Becerril 2000, Galmés *et al.* 2007). However, it has been suggested that increase of thermal dissipation is not a strategy used by wetland specialist plants under drought (Savage *et al.* 2009).

There is a large amount of research to concern photoprotective mechanisms under drought conditions, although, most of these studies have been performed in arid ecosystems; such as Mediterranean (Peguero-Pina *et al.* 2009, Galmés *et al.* 2007). Considering that drought is the most important environmental constrain that swamp forest plants have for the establishment of seedlings (Savage *et al.* 2009), physiological studies of drought carried out on azonal vegetation are of great importance.

Considering the limited presence of *M. exsucca* in drier sites, we hypothesized that this species exhibits decreased plasticity of functional attributes related with photoprotection, contrary to *L. chequen*. The knowledge about the energy dissipation performance under drought conditions could be crucial to improve the understanding of the differential distribution of *M. exsucca* and *L. chequen* in a soil moisture gradient.

MATERIALS AND METHODS

Plant material and treatments

Seedlings of *M. exsucca* and *L. chequen* with heights of 30 cm were obtained from a botanical garden (Talca University, Maule Region, Chile). Saplings were maintained outdoors at the University of La Serena (Coquimbo Region, Chile) in plastic pots (of 3 L) using a 1:1 mixture of soil:organic substrate, and watered three times a week during one month. Before to starting the experiment, plants were maintained for four weeks in a controlled growth chamber at 21°C with a photon flux density of about 300 µmol of photons m^{-2} s^{-1} provided by sodium lamps (Son/T Agro 400W, Philips, Eindhoven, The Netherlands) with 12 h photoperiod. Plants were irrigated and supplied weekly with 50% Hoagland's solution.

To assess the physiological performance of both species, plants were separated in two groups. The first with similar irrigation timetable (control group) and the second group was subjected to drought by suspended irrigation (drought treatment).

Plant water status

Midday stem water potential (Ψ_w) and relative leaf water content (RWC) was monitored at 0, 4 and 10 days from start the drought treatment. Ψ_w was measured in excised secondary branches using a pressure chamber type Scholander (Soil Moisture Equipment Corp., USA). RWC was calculated in leaves of six different individuals for each species and treatment as described by Turner (1981): RWC= (fresh weight − dry weight)/(turgid weight − dry weight)×100. The turgid leaf weight was determined after keeping the leaf in distilled for 24 h. Leaf dry weight was obtained after keeping the turgid leaf for 48 h in an oven at 70°C.

The water stress levels were tested in control plants with optimal Ψ_w (Ψ_wC) and plants submitted to drought by 10 days reaching around -1.4 MPa of Ψ_w (Ψ_wD).

Chlorophyll *a* fluorescence measurements

Chlorophyll fluorescence signals were analyzed in leaves of secondary branches from six different individuals using a portable fluorometer (FMS 2, Hansatech Instruments Ltd., Norfolk, UK). All measurements were done with the same hardware configuration using an actinic light of 300 µmol m^{-2} s^{-1}. Definitions of fluorescence parameters: maximum PSII efficiency (Fv/Fm), electron transport rate (ETR) and non-photochemical quenching (qN) were used as described by Maxwell & Johnson (2000) except for photochemical quenching (qL), which was calculated as described in Kramer *et al.* (2004).

Chlorophylls amount analysis

The chlorophylls amount analysis were performed in leaves of secondary branches of six individuals of each species exposed to two different water conditions. Chlorophylls were extracted in 90% of ethanol overnight and centrifuged at 12,000*g* for 10 min. Total chlorophylls content were determined spectrophotometrically at 663 and 645 nm according to Arnon (1949) as follow: Total Chl (g l^{-1}) = 0.0202 A663 + 0.00802 A645.

Statistical analysis

Statistical analyses of data were performed with the STATISTICA 6.0 software. One-way ANOVA were performed for the studied parameters with the treatment as factor. Differences between means were evaluated by Tuckey test ($P< 0.05$).

RESULTS

Effect of drought on the relationship between RWC and water potential (Ψ_W)

Mean water potential under control conditions (Ψ_wC) were -0.58± 0.06 and -0.73± 0.04 MPa for *M. exsucca* and *L. chequen,* respectively (Fig. 1). Ψ_w decreased significantly during the drought treatment in both species to -1.4 ± 0.11 and -1.4±0.09 MPa, for *M. exsucca* and *L. chequen* respectively ($P<0.01$). Drought stressed plants of *M. exsucca* reduced 37% its RWC, while *L. chequen* experienced a reduction only in 12%, respect to control plants. Higher relationship between RWC and Ψ_w was observed for *M. exsucca* ($r^2 = 0.72$, $P<0.01$), than for *L. chequen* ($r^2 = 0.42$, $P<0.01$) during the drought treatment (Fig. 1). Differences in RWC between species were observed from -1.0 MPa, where *L. chequen* maintain its leaf RWC close to 65% despite the decrease in $\Psi_{w.}$

Changes on chlorophyll fluorescence parameters in response to Ψ_W decline

Under Ψ_wC Fv/Fm values were optimal in both species (~0.8). The decrease of water potential to -1.4 MPa (Ψ_wD) induce significant decrease of Fv/Fm in *L. chequen* ($P < 0.05$), but not in *M. exsucca* (Fig. 2A).

ETR was maintained in both species along the treatment (Fig. 2B), however the proportion of photochemical processes (qL) decreased significantly (31%) in *M. exsucca* and were maintained in *L. chequen* (Fig. 2C).

Both species exhibited high values of qN under Ψ_wC (Fig. 2D), however, decrease to -1.4 MPa (Ψ_wD) during the drought treatment, induced a significant increment of qN in *L. chequen* ($P< 0.05$).

Chlorophyll changes percent in response to decline of Ψ_W

Total chlorophylls were maintained in *M. exsucca* during the treatment, however, *L. chequen* experienced a significant 20% decrease under Ψ_wD ($P< 0.01$) (Fig. 3).

DISCUSSION

Our results shown that *L. chequen* is more plastic than *M. exsucca* in many traits during the switch from control conditions to drought, in special the related with the control of water consume and protection of photosynthetic apparatus.

M. exsucca showed faster dehydration than *L. chequen* when decrease Ψ_w. This response may indicate a poor osmotic adjustment capacity affecting its water status greater under drought compared with *L. chequen* (Fig. 1). Plant drought response strategies are generally broken into two categories: drought avoidance and drought tolerance. The high water consumption showed by *M. exsucca* is a typical characteristic from plants with strategies of drought avoidance (Touchette *et al.* 2007). Although, *M. exsucca* rarely experience severe drought in its natural habitats, this result is important considering its classification such a vulnerable species and with the increment of aridity in many regions of its habitats distribution.

Decrease in leaf chlorophyll content and Fv/Fm reduction is a common response of Mediterranean plants to summer (Balaguer *et al.* 2002). Loss of upon 50% of leaf chlorophyll does not lead to leaf senescence in drought tolerant plants species such as *Quercus coccifera, Quercus ilex, Salix bebbiana* (Peguero-Pina *et al.* 2009, Balaguer *et al.* 2002), but rather than constitutes a reversible process that allows decrease the light harvesting and reduce risks of over-excitation and photodamage (Balaguer *et al.* 2002). In this work it is suggested that the reduction of the antenna size evidenced by a decrease of chlorophylls amount in *L. chequen* (Fig. 3), allows maintain PSII functionality and electron transport. In addition, the increase of qN under drought in *L. chequen* (Fig. 2D) suggests that Fv/Fm decrease (Fig. 2A) is not attributable to photodamage of PSII, however, this may be considered as a protective strategy contributing to dissipate excess of energy (Krause 1988, Osmond 1994). It has been shown that large induction of thermal dissipation and xanthophyll cycle deepoxidation under drought, has greater importance in many Mediterranean species with habitat generalist (Chaves *et al.* 2002, Galmes *et al.* 2007), but not in wetland specialist species (Savage *et al.* 2009). Our work is one of the first works that suggest the thermal dissipation may be an efficient strategy under drought for a swamp forest plant: *L. chequen,* which shows a high plasticity of its photosynthetic apparatus performance under water stress.

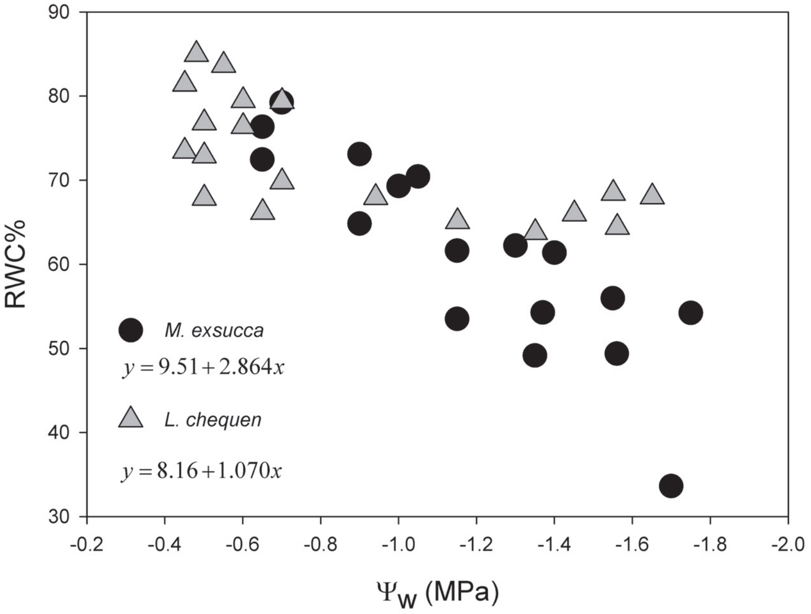

Figure 1. Relationship between leaf RWC and Ψ_w for *M. exsucca* (black circles) and *L. chequen* (gray triangles) exposed to progressive drought. Dates correspond to 0, 4 and 10 days of the drought treatments. Equations in the graphics correspond to simple linear regression of *M. exsucca* (r^2=0.74) and *L. chequen* (r^2=0.46).

Figura 1. Correlación entre CRA y Ψ_w para *M. exsucca* (círculos negros) y *L. chequen* (triángulos de color gris) bajo condiciones de sequía progresiva. Los datos corresponden a los días 0, 4 y 10 del tratamiento de sequía. Ecuaciones en los gráficos corresponden a regresión lineal simple de *M. exsucca* (r^2 = 0,74) y *L. chequen* (r^2 = 0,46).

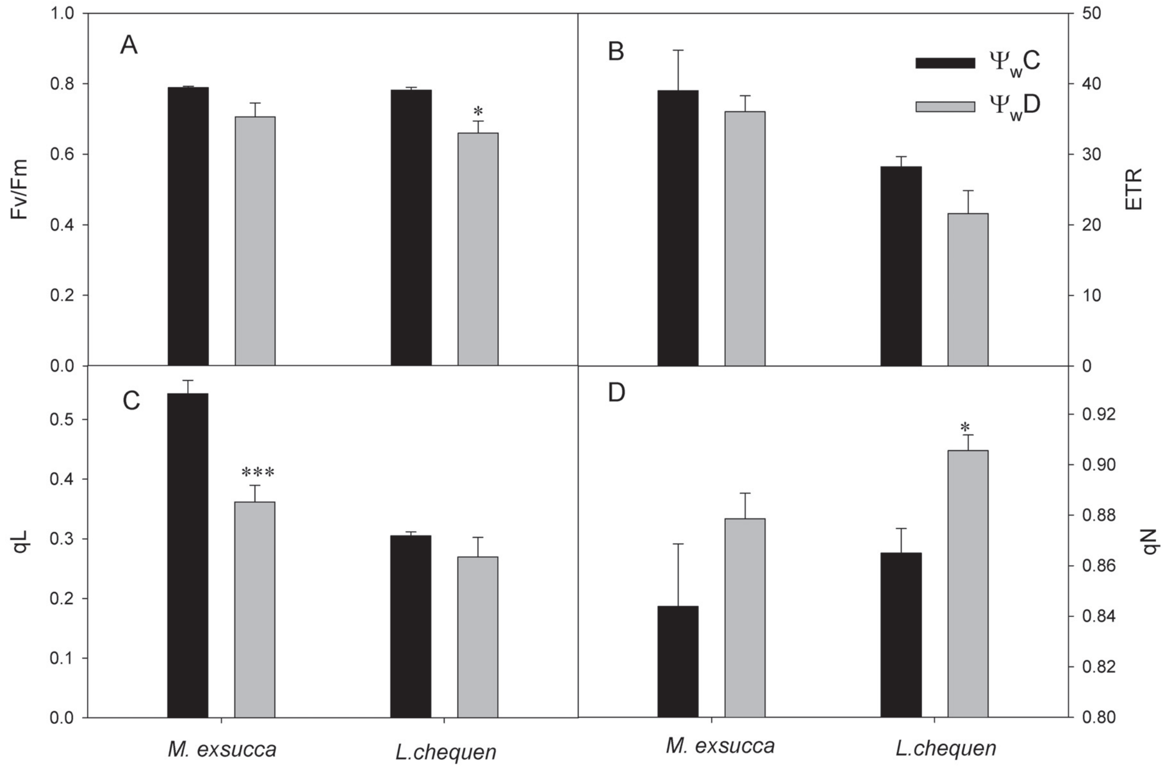

FIGURE 2. (A) Maximal photochemical efficiency (Fv/Fm), (B) electron transport rate (ETR), (C) the proportion of photochemical process (qL) and (D) non-photochemical quenching changes (qN) in response to decline of water potential (Ψ_w) from optimal (Ψ_wC) to stressed conditions (Ψ_wD). Ψ_wC= -0.7 MPa and Ψ_wD= -1.4 MPa for *M. exsucca;* Ψ_wC= -0.5 MPa and Ψ_wD= -1.4 MPa for *L. chequen.* Measurements of chlorophyll *a* fluorescence parameters were done at room temperature using 300 µmoles of photons $m^{-2}s^{-1}$ of actinic light. Values represent mean ± standard error of six replicates. * and *** denote statistical differences of chlorophyll *a* fluorescence parameters analyzed by Tuckey test ($P < 0.05$ and $P < 0.01$, respectively) among treatments.

FIGURA 2. (A) Eficiencia fotoquímica máxima del PSII (Fv/Fm), (B) tasa de transporte de electrones (ETR), (C) la proporción de procesos fotoquímicos (qL) y (D) no fotoquímicos (qN) en respuesta a la disminución del potencial hídrico desde condiciones control (Ψ_wC) a estrés por sequía (Ψ_wD). Ψ_wC= -0.7 MPa y Ψ_wD= -1.4 MPa para *M. exsucca;* Ψ_wC= -0.5 MPa y Ψ_wD= -1.4 MPa para *L. chequen.* Las mediciones de los parámetros de la fluorescencia de la clorofila *a* se realizaron a temperatura ambiente con 300 µmoles de fotones $m^{-2}s^{-1}$ de luz actínica. Los valores representan la media ± error estándar de seis repeticiones. * y *** denotan diferencias estadísticas de los parámetros analizados por el test de Tuckey (P <0,05 y P <0,01, respectivamente) entre tratamientos.

Contrasting to *L. chequen*, *M. exsucca* showed a lower plasticity in the traits studied under drought. *M. exsucca* maintained chlorophyll levels (Fig. 3) and maximum photosynthetic efficiency during drought, which could indicate a sustained light capture and exhibited not significant perturbation on PSII capacity, despite the important reduction of RWC. A similar response was observed in the tropical shrub *Lycium nodosum* (Solanaceae) and the ericaceous *Erica multiflora* and *Calluna vulgaris*, where Fv/Fm was unchanged across a comparable range of water deficit stress (Tezara *et al.* 2003, Llorenz *et al.* 2004). However, *M. exsucca* reduced considerably qL (Fig. 2C), without significant changes in qN (Fig. 2D), indicating an energetic imbalance. If the excess energy is not dissipated by qN as heat, either at photochemical level, this could induce ROS formation by excessive reduction of electron transport chain (Krause 1988, Osmond 1994). Although no signal of photodamage to PSII (measured as decrease of Fv/Fm, ETR or chlorophylls content) were observed in *M. exsucca* during the 10 days under drought treatment, the individuals experienced leave abscission after 30 days of drought. There is evidence that photoinhibition play a role in senescence (Rivero *et al.* 2007). However, if these plants experienced photoinhibition was undetected, because unfortunately we did not Fv/Fm measurements immediately before to senescence of the individual leaves. We think that poor adjustments of the traits related with photoprotection of photosynthesis could explain the restricted distribution of *M. exsucca* under lower soils moisture. It has been postulated that leaf abscission results crucial as survival mechanisms to avoid water loss (Touchette *et al.* 2007). However, this strategy results in a decline of carbon metabolism associated with a high energy cost affecting the establishment of seedlings (Touchette *et al.* 2007, Rivero *et al.* 2007).

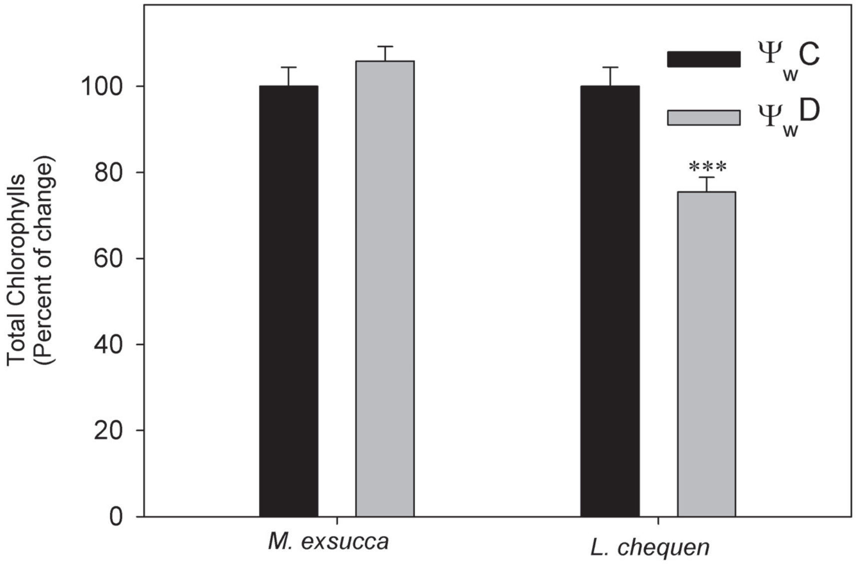

Figure 3. Percent change of chlorophylls amount in response to decline of water potential (Ψ_w) from optimal ($\Psi_w C$) to stressed conditions ($\Psi_w D$). $\Psi_w C$= -0.7 MPa and $\Psi_w D$= -1.4 MPa for *M. exsucca;* $\Psi_w C$= -0.5 MPa and $\Psi_w D$= -1.4 MPa for *L. chequen.* Values represent mean ± standard error of six replicates. * and *** denote statistical differences of chlorophyll *a* fluorescence parameters analyzed by Tuckey test ($P < 0.05$ and $P < 0.01$, respectively) among treatments.

Figura 3. Porcentaje de cambio del contenido de clorofilas en respuesta a la disminución del potencial hídrico desde condiciones control ($\Psi_w C$) a estrés por sequía ($\Psi_w D$). $\Psi_w C$= -0.7 MPa y $\Psi_w D$= -1.4 MPa para *M. exsucca;* $\Psi_w C$= -0.5 MPa y $\Psi_w D$= -1.4 MPa para *L. chequen.* Los valores representan la media ± error estándar de seis repeticiones. * y *** denotan diferencias estadísticas de los parámetros analizados por el test de Tuckey (P <0,05 y P <0,01, respectivamente) entre tratamientos.

Possible limitation of this work was the low light intensity (300 µmol of photons m^{-2} s^{-1}), because the impact of drought on photochemical performance is presumably greater under natural light conditions. This is mainly due to tissue desiccation combined with high temperature may produce photo-oxidative stress with a direct impact on seedling survival and growth (Balaguer *et al.* 2001, Balaguer *et al*. 2002). Although, is expected that plants grown under natural conditions develop several morphological attributes to regulate the energy absorbed such as a thicker parenchyma and mesophyll cells with smaller chloroplasts (Anderson 1986, Melis 1991).

Finally, our results demonstrate that photoprotective strategies seem to vary with the habitat distribution of the species. *M. exsucca* which inhabits in more wetland soils, loses water easier than *L. chequen* and show lower plasticity of its photosynthetic apparatus related traits. On the other hand, *L. chequen* which can grow in drier sites displays a high plasticity of biochemical mechanisms allowing adjustment of photochemical processes under drought conditions. The strategies reported here could be especially important in the establishment of seedlings under low moisture soil and probably may determine the distribution of these species. These results are important considering the aridity increase in the central zone and the conservative role that these plants have in the swamp forest.

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