Short Communication

Ecophysiology of two Sonoran Desert evergreen shrubs during extreme drought

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A B S T R A C T

Recent drought across the desert Southwest US may strongly affect the physiological functioning of evergreen desert species that maintain leaves through these dry periods. In July 2002 we compared the ecophysiological performance of the open-canopied, small-leaved creosotebush (Larrea tridentata) to the dense-canopied, more broad-leaved jojoba (Simmondsia chinensis) growing on a ridge-top, east- and west-facing slopes to assess how differences in leaf habit and exposure affect these species’ ability to withstand severe drought. Standardized precipitation index (SPI) from 100 years precipitation data showed July 2002 rainfall was normal, but the 12-month period ending July 2002 was of extreme aridity (SPI = –2.71). Predawn water potentials were extremely low, and lower in jojoba (–8.1 to –9.5 MPa) than in Larrea (–6.6 to –9.4 MPa). Chlorophyll fluorescence showed jojoba had more consistent photochemical performance than Larrea across three exposures, having higher optimal photosystem II (PSII) efficiency (Fv/Fm), lower light-adapted PSII yield, and better ability to thermally dissipate light energy (i.e. higher NPQ), especially in inner-canopy jojoba leaves. These findings suggest jojoba may better cope with high light under drought conditions, and that canopy shading in jojoba may reduce high-light stress. Moreover, lower Fv/Fm, NPQ and high PSII yields in Larrea was similar between east-facing and ridge-top locations, but achieved levels similar to jojoba on west-facing exposures. These findings suggest these drought-tolerant evergreens rely on different physiological mechanisms to cope with high light under extreme drought conditions.

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Recent severe drought has induced an extensive pulse of adult plant mortality over broad ranges of elevation and latitude across the Southwest US (Bowers, 2005; Breshears et al., 2005; Miriti et al., 2007). Extensive die-back of established plants indicates this drought is more severe than normal, even for these highly water-limited systems, and may be the start of prolonged climatic drought which occur across this region on an inter-decadal and inter-centennial basis (Swetnam and Betancourt, 1998). However, desert evergreen species have fared better than shorter-lived drought deciduous shrubs (Hamerlynck and McAuliffe, 2008; Miriti et al., 2007). Comparative studies of basic physiological performance would give insight how long-lived desert evergreens survive these infrequent climate extremes.

Under water-limited conditions, desert evergreens must quench excess energy from saturating light levels, in part because prolonged stomatal closure limits carbon fixation as an effective energy sink (Barker and Adams, 1997; Barker et al., 2002; Hamerlynck et al., 2000; Huxman et al., 1998). Anatomical and morphological features at the leaf- and whole-level that reduce high-light exposure are also important in sustaining activity and survival (Barker and Adams, 1997; Ehleringer, 1994; Forseth and Ehleringer, 1983; Nobel, 1980; Sandquist and Ehleringer, 1998). In addition, topographic variation in aspect can affect exposure, soil surface hydrology, plant community structure and productivity (Nobel, 1980; Schlesinger et al., 1989; Smith et al., 1997) and may further alter drought effects. However, how topographic exposure and leaf-level ecophysiological characteristics co-vary under extreme drought conditions is not well understood.

From July 20 to 25, 2002, we used a Scholander-type pressure chamber (PMS Corvallis, OR) and a pulse-amplitude-modulated (PAM) chlorophyll fluorimeter (FMS-2, Hansatech, Ltd., Norwich, UK) to determine differences in ecophysiological performance of two evergreen desert shrubs, creosotebush (Larrea tridentata); hereafter referred to as Larrea and jojoba (Simmondsia chinensis) under extreme drought conditions. Larrea and jojoba can maintain positive photosynthetic rates under hot and dry conditions.
a LiCOR 190 photodiode showed that inner-canopy light levels were of a night and a day at the very end of an extreme dry period.

A unique series of "snap-shots" of plant function through the course and precipitation fell between September 2001 and March 2002, with no measurable rainfall from April through the end of June 2002. The data presented below provide a measure of large leaves (Ceccardi and Ting, 1996; Woodhouse, 1978), and jojoba had distinct photochemical behavior under species. Continuous diurnal measurement of photosynthetic photon flux density (PPFD) within jojoba and Larrea species. Continuous diurnal measurement of photosynthetic photon flux density (PPFD) within jojoba and Larrea canopies using a LiCOR 190 photodiode showed that inner-canopy light levels were on average 24% of incident PPFD (1000–1500 μmol m⁻² s⁻¹), while PPFD within Larrea canopies were significantly higher (One-way ANOVA F₁,₁₁₈ = 311.0; p < 0.001), averaging 69% of full light, and frequencies did not differ from PPFD above the canopy (data not shown). Due to this lack of self-shading, we sampled only the outermost Larrea leaves most likely be exposed to PPFD experienced by outer-canopy jojoba leaves.

Standardized Precipitation Index (SPI) analysis (McKee et al., 1995) generated from over 100 years (1894–2005) of continuous National Weather Service monthly precipitation observations from the University of Arizona Co-OP station (available at the Western Regional Climate Center; http://www.wrcc.dri.edu/summary/Climsmaz.html) showed the 45 mm of precipitation falling in July 2002 (SPI = −2.15) occurred only three other times: in 1902 (SPI = −2.15), 1925 (SPI = −2.53), and 1975 (SPI = −2.70). Total precipitation accumulation from July 2001 to July 2002 was 134 mm. 52 mm of this occurred in July and August 2001, and only 37 mm fell between September 2001 and March 2002, with no measurable rainfall from April through the end of June 2002. The first precipitation in July 2002 occurred on July 12 (8.89 mm); followed by three more smaller storms (4.57 mm on July 15 and 18, and 5.33 mm on July 23). Thus, the data presented below provide a unique series of “snap-shots” of plant function through the course of a night and a day at the very end of an extreme dry period.

Despite having received 23.4 mm of rain over the preceding two weeks, predawn water potentials (ψpd) in Larrea and jojoba were extremely low and differed between the species (Two-way ANOVA F₁,2₂₄ = 15.6; p < 0.001), but these differences depended on exposure (Two-way ANOVA interaction F₂,₂₄ = 17.58; p < 0.001). Predawn ψpd was very low and similar between Larrea and jojoba on east-facing and ridge-crest sites (Fig. 1), while ψpd at west-facing exposures was significantly higher than at the other locations (two-way ANOVA F₂,₂₄ = 71.08; p < 0.001), and where jojoba ψpd was significantly lower than Larrea (Fig. 1). Larrea ψpd at east and ridge-top locations equaled the lowest field values recorded for this species (Hamerlynck et al., 2000; Pockman and Sperry, 1997), while jojoba predawn ψpd were −4.0 to −2.0 MPa lower than ψ previously observed at midday (Ceccardi and Ting, 1996; Woodhouse, 1978), when ψ is usually much lower.

Larrea and jojoba had distinct photochemical behavior under these water-limited conditions (Fig. 2). Fluorescence measurements were made on five Larrea and jojoba plants starting 21:00

Larrea has a dense canopy of small leaves (Ceccardi and Ting, 1996), while Larrea has an open canopy of small leaves (Smith et al., 1997). Morphological and structural differences such as these frequently coincide with differences in physiological tolerance and acclimation to drought and light (Abrams et al., 1994; Adams et al., 1999; Hamerlynck and Knapp, 1996; Wright et al., 2001). Five plants of each species growing at three adjacent sites differing in exposure were sampled (total N = 15 plants): a North-facing ridge-top site (2% slope and 37.5° magnetic north (MN) aspect), and an East- (24% slope, 132° aspect) and West-facing slope (22% slope, 314° aspect) near Tucson, AZ (sampling location 32.2785°N, 111.080772°W, 768 m elevation ASL) to ascertain if leaf-level responses co-varied with exposure. In addition, we sampled inner- and outer-canopy leaves of jojoba to see if canopy density affected photochemical performance in this species. Continuous diurnal measurement of photosynthetic photon flux density (PPFD) within jojoba and Larrea canopies using a LiCOR 190 photodiode showed that inner-canopy light levels were on average 24% of incident PPFD (1000–1500 μmol m⁻² s⁻¹), while PPFD within Larrea canopies were significantly higher (One-way ANOVA F₁,₁₁₈ = 311.0; p < 0.001), averaging 69% of full light, and frequencies did not differ from PPFD above the canopy (data not shown). Due to this lack of self-shading, we sampled only the outermost Larrea leaves most likely be exposed to PPFD experienced by outer-canopy jojoba leaves.

PSI function varied significantly across the locations, with higher Fv/Fm and NPQ and lower φPSII in west-facing exposures pooled across all leaf types and sampling periods (Table 1; Fig. 2). Most of this was due to variation in Larrea, while jojoba leaves were similar across exposures and through time (Fig. 2), giving rise to significant leaf type by location interactions in Fv/Fm, φPSII and NPQ (Table 1). Fv/Fm in both types of jojoba leaves did not vary between sites, while Larrea Fv/Fm was significantly higher in west-exposure plants (Fig. 2). Species' differences depended on exposure; at west-facing and ridge-top locations, Fv/Fm was similar between all leaf types, while in east-exposure locations, inner-canopy jojoba Fv/Fm (0.59 ± 0.0328 SE) was significantly higher than in Larrea (0.45 ± 0.0345), with intermediate values in outer-canopy jojoba leaves (0.54 ± 0.0202; Fig. 2).

Larrea φPSII were significantly higher in east-facing (0.20 ± 0.0186 SE) and ridge-top Larrea (0.23 ± 0.0183) compared to plants on west-facing slopes (0.037 ± 0.00405; Table 1; Fig. 2). φPSII in Larrea at the former two locations were also significantly higher than in jojoba leaves pooled across inner- and outer-canopy positions (0.049 ± 0.0086 and 0.023 ± 0.0031 for east and ridge-top sites, respectively), while Larrea at the west-facing exposure had φPSII similar to jojoba leaves pooled across canopy positions (0.023 ± 0.0019; Fig. 2). These changes in Larrea φPSII, as well as the evening declines in east-exposure and increases in west-exposure plants, and invariant jojoba φPSII across exposures, contributed to the significant three-way interaction in φPSII (Table 1).

Antenna-based thermal dissipation (NPQ) was significantly higher in inner-canopy jojoba leaves (1.13 ± 0.054 SE) compared to MST on July 22 (Prior), then at 02:00 MST (Preadawn, PD), 08:30 MST (AM), 13:00 MST (Midday), and at 17:00 MST (PM) on July 23 (Fig. 2). Following 45-min dark-adaptation, samples were exposed to a 10 s modulated beam to establish baseline fluorescence (F₀) averaged over the exposure. Maximum fluorescence yield (Fm) was determined following a 0.7 s pulse of 8500 μmol m⁻² s⁻¹ photosynthetic photon flux density (PPFD). Optimal intrinsic efficiency of open PSI units (Fv/Fm) was calculated as (Fm − Fv)/Fm. Immediately following this, an actinic beam of 800 μmol m⁻² s⁻¹ PPFD was applied for 60 s, and steady-state light-adapted yield (Fv) was measured prior to another saturating pulse to establish maximum light-adapted fluorescence yield (Fm'), Fm' and Fv were used to calculate thermal dissipative non-photochemical quenching (NPQ = Fm' − Fv/Fm') according to Schreiber et al. (1998).
outer-canopy jojoba (0.76 ± 0.049) and Larrea leaves (0.81 ± 0.111). NPQ in either type of jojoba leaves did not significantly differ between exposures, while Larrea NPQ in west-facing exposures (1.58 ± 0.1343) was higher than east-facing (0.28 ± 0.111) and ridge-top plants (0.16 ± 0.028; Fig. 2). In addition, jojoba inner-canopy leaves at east-facing (1.09 ± 0.103) and ridge-top exposures (1.03 ± 0.086) had NPQ significantly higher than Larrea at these sites, with intermediate values in outer jojoba canopy leaves (0.67 ± 0.86 and 0.62 ± 0.060, for east-facing and ridge-top plants, respectively).

Plants with lowest \( \psi_{pd} \) (Fig. 1) also had low \( F_{v}/F_{m} \), especially in Larrea (Fig. 2). This suggests the effects of the previous 12 months drought were still manifested, even after appreciable rainfall preceding sampling, in the form of strong, long-term down-regulation of PSII function; however, such down-regulation is usually accompanied by higher NPQ and lower \( \psi_{PSII} \) (Barker et al., 2002, 2005; Müller et al., 2001; Osmond, 1994). The high \( \psi_{PSII} \) in Larrea suggest a great deal light energy could be delivered to the reaction center, potentially inducing extensive photo-oxidative damage (Müller et al., 2001; Osmond, 1994). However, Gilmore and Ball (2000) demonstrated that over-wintering evergreens, which also endure strong water deficits and high light, accumulate stable chlorophyll-protein-xanthophyll complexes that dissipate excess light energy without the transthylakoid pH gradient needed to drive conversion of PSII antennae xanthophylls to forms that dissipate excess light energy as heat (Barker et al., 2002; Demmig-Adams, 1998; Demmig-Adams and Adams, 1992; Müller et al., 2001). Moreover, accumulation of these complexes was accompanied by decreases in \( F_{v}/F_{m} \) (Gilmore and Ball, 2000) to levels associated with low NPQ and high \( \psi_{PSII} \) in our study (\( \approx 0.35–0.50; \) Fig. 2). Low \( F_{v}/F_{m} \), NPQ and high \( \psi_{PSII} \) have been documented in desication-tolerant mosses, where plants growing in open locations exposed to more frequent and prolonged drying had lower \( F_{v}/F_{m} \) and NPQ and higher \( \psi_{PSII} \) upon rehydration that plants in shaded locations that did not dry out as frequently (Hamerlynck et al., 2002). Thus, this combination of fluorescence parameters may indicate a general chronic stress response in evergreen plants, possibly related to the accumulation of stable pigment/protein complexes that can act as an alternative energy dissipation pathway to energy-dependent xanthophyll cycling (Gilmore and Ball, 2000; Müller et al., 2001).

In contrast, inner-canopy jojoba leaves consistently had higher \( F_{v}/F_{m} \), NPQ and lower \( \psi_{PSII} \) than Larrea and, depending on slope aspect, outer-canopy jojoba leaves (Fig. 2). This suggests that over this extensive drought period, jojoba maintained a significant proportion of leaves that could generate thylakoid pH gradients sufficient to engage xanthophyll-cycle based photo-protective mechanisms (Adams et al., 1999; Barker et al., 2002; Demmig-Adams...
and Adams, 1992; Müller et al., 2001). It also seems likely inner-canopy jojoba leaves benefited from shading by outer-canopy leaves, which could reduce light and temperature (Hamerlynck and Knapp, 1996; Huxman et al., 1998; Wang et al., 2008), however, which of these is more important in sustaining inner-canopy PSII function is unclear. Jojoba leaves also vary in leaf-angle (EPH personal observation), which could affect canopy PPDF interception, microclimate, and physiological performance (Adams et al., 1999; Barker and Adams, 1997; Forseth and Ehleringer, 1983).

Thus, our data show these desert evergreen shrubs maintain physiological integrity differently through severe drought. Jojoba PSII function was more constant across exposures, possibly because of self-shading, which may allow jojoba to more effectively utilize readily reversible photo-protective mechanisms (Müller et al., 2001). Larrea showed greater evidence of chronically down-regulated PSII function across the different exposures (Fig. 2). We also observed considerable leaf and branch mortality in Larrea, especially in east and ridge-top exposure plants where PSII function was most reduced (Fig. 2). Many desert shrubs shed leaves in response to soil drying (Sandquist and Ehleringer, 1998; Smith et al., 1997).

Our findings suggest that while Larrea may be more prone to cumulative effects of high light than jojoba during drought, it might also reduce leaf area display to facilitate persistence under severe drought.

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References


