Short Communication

Ecophysiology of two Sonoran Desert evergreen shrubs during extreme drought

E.P. Hamerlynck [a,*], T.E. Huxman [b]

[a] USDA-ARS, Southwest Watershed Research Center, 2000 E. Allen Rd, Tucson, AZ 85719, United States
[b] Ecology and Evolutionary Biology, University of Arizona, United states

ARTICLE INFO

ABSTRACT

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 (F_v/F_m), 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 F_v/F_m, 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.

Published by Elsevier Ltd.

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 evergreen shrubs 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

* Corresponding author. Tel.: +1 520 670 6381x154; fax: +1 520 670 5550.
E-mail address: erik.hamerlynck@ars.usda.gov (E.P. Hamerlynck).

(Ceccardi and Ting, 1996; Feldman, 1988; Hamerlynck et al., 2000; Woodhouse, 1978). Compared to *Larrea*, jojoba has a dense canopy of large 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 32.27853°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 $F_{1,118} = 311.0$; $p \leq 0.001$), averaging 69% of full light, and frequently 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 was normal (SPI = 0.04, with SPI = 0.00 indicating normal; McKee et al., 1995) compared to all other Julys in the data set. However, the 12-month period ending in July 2002 was the driest on record (12-month July SPI = −2.71). Indeed, 12-month July SPI below −2.0 (extreme drought) 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 (ψ_{pd}) in *Larrea* and jojoba were extremely low and differed between the species (Two-way ANOVA $F_{1,24} = 15.6$; $p \leq 0.001$), but these differences depended on exposure (Two-way ANOVA interaction $F_{2,24} = 17.58$; $p \leq 0.001$). Predawn ψ was very low and similar between *Larrea* and jojoba on east-facing and ridge-crest sites (Fig. 1), while ψ_{pd} at west-facing exposures was significantly higher than at the other locations (two-way ANOVA $F_{2,24} = 71.08$; $p \leq 0.001$), and where jojoba ψ_{pd} was significantly lower than *Larrea* (Fig. 1). *Larrea* ψ_{pd} 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 ψ_{pd} 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
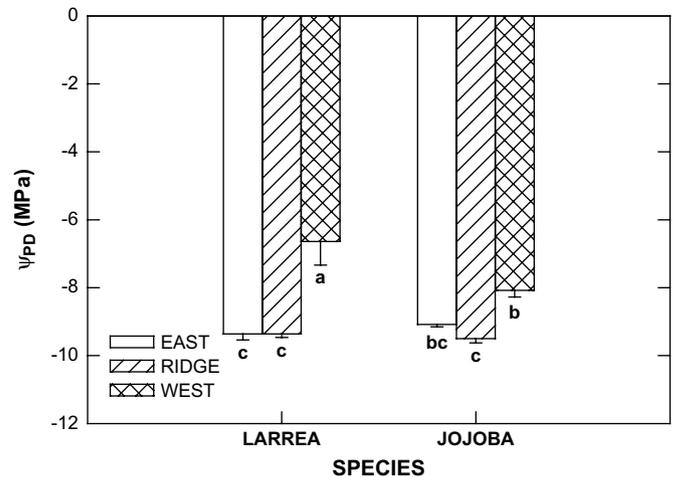

Fig. 1. Predawn water potential (ψ_{pd}) of *Larrea tridentata* and jojoba (*Simmondsia chinensis*) on different slope exposures under extreme drought. Each bar is the mean of 5, error bars are ±one SE, letters differ at $p \leq 0.05$ (Scheffe's-F).

MST on July 22 (Prior), then at 02:00 MST (Predawn, 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 (F_o) averaged over the exposure. Maximum fluorescence yield (F_m) 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 PSII units (F_v/F_m) was calculated as $(F_m-F_o)/F_m$. 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 (F_s) was measured prior to another saturating pulse to establish maximum light-adapted fluorescence yield (F_m'). F_m' and F_s were used to calculate thermal dissipative non-photochemical quenching (NPQ $= F_m-F_m'/F_m'$), light-adapted PSII yield ($\varphi_{PSII} = F_m'-F_s/F_m'$) according to Schreiber et al. (1998).

PSII function varied significantly across the locations, with higher F_v/F_m and NPQ and lower φ_{PSII} 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 F_v/F_m, φ_{PSII}, and NPQ (Table 1). F_v/F_m in both types of jojoba leaves did not vary between sites, while *Larrea* F_v/F_m was significantly higher in west-exposure plants (Fig. 2). Species' differences depended on exposure; at west-facing and ridge-top locations, F_v/F_m was similar between all leaf types, while in east-exposure locations, inner-canopy jojoba F_v/F_m (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 φ_{PSII} 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). φ_{PSII} 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 φ_{PSII} similar to jojoba leaves pooled across canopy positions (0.023 ± 0.0019; Fig. 2). These changes in *Larrea* φ_{PSII}, as well as the evening declines in east-exposure and increases in west-exposure plants, and invariant jojoba φ_{PSII} across exposures, contributed to the significant three-way interaction in φ_{PSII} (Table 1).

Antennae-based thermal dissipation (NPQ) was significantly higher in inner-canopy jojoba leaves (1.13 ± 0.054 SE) compared to
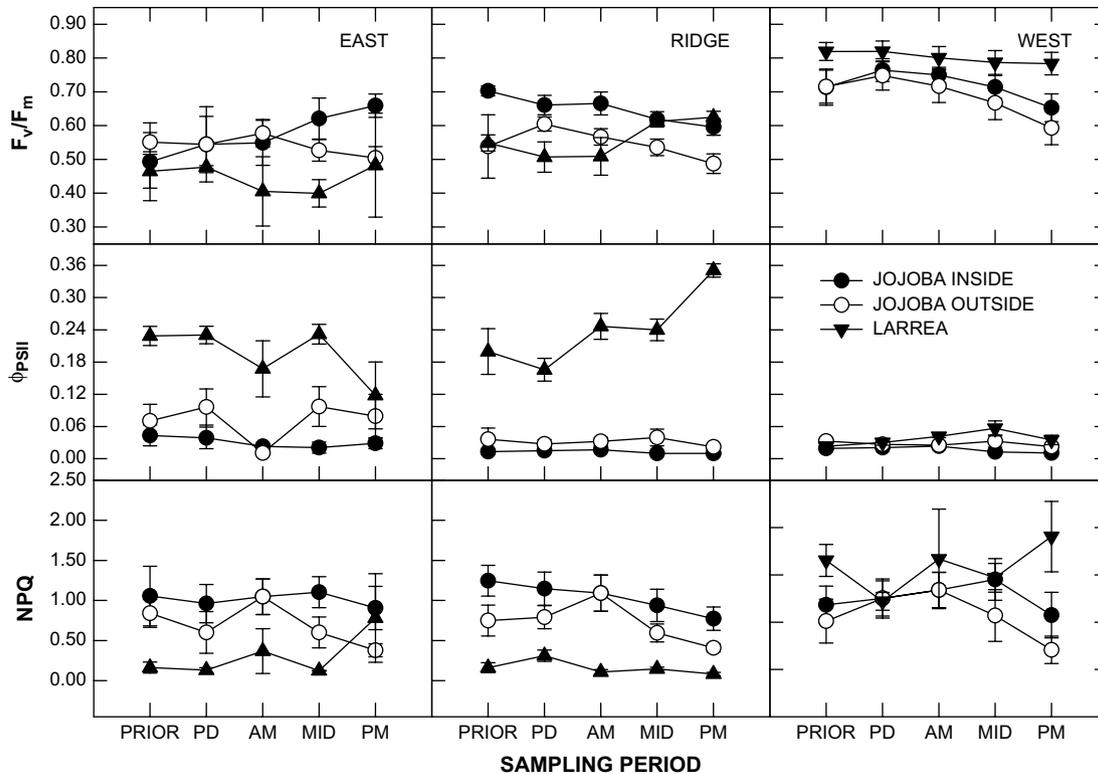
Fig. 2. Diel photochemical performance of inner- and outer-canopy jojoba and *Larrea tridentata* under extreme drought. PSII chlorophyll fluorescence parameters are: F_v/F_m = optimal intrinsic PSII efficiency, φ_{PSII} = PSII photochemical yield, NPQ = antennae-based thermal dissipation. Each point is the mean of 5 samples, error bars are ±one SE.

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 ψ_{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

Table 1
Repeated measures analysis of variance (RM-ANOVA) F-test results comparing PSII chlorophyll fluorescence parameters of leaf types (*Larrea*, inner- and outer-canopy jojoba), aspect exposure (east, ridge-top, west), and diel time period (prior evening, predawn, morning, midday, evening). Degrees freedom is in parentheses; all data were arcsine transformed to meet ANOVA data distribution assumptions. Whole plot factors are leaf type, exposure, and their interaction, using the type-by-exposure-replicate interaction as the F-test error term. Time period and all interactions including this factor are the within-treatment sub-plot effects. Asterisks indicate *$p < 0.1$, **$p < 0.05$, ***$p < 0.001$.

Source (df)	F_v/F_m	φ_{PSII}	NPQ
Type (2,36)	2.70*	102.31***	5.58***
Exposure (2,36)	28.62***	36.22***	15.12***
Time (4,124)	1.12ns	1.58ns	0.88ns
Type × Exposure (4,36)	3.29**	25.29***	4.46***
Type × Time (8,124)	1.41ns	2.30**	1.28ns
Exposure × Time (8,124)	1.14ns	4.64***	0.87ns
Type × Exp × Time (16,124)	1.19ns	2.91***	0.90ns

accompanied by higher NPQ and lower φ_{PSII} (Barker et al., 2002, 2005; Müller et al., 2001; Osmond, 1994). The high φ_{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 antenna 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 φ_{PSII} in our study ($\approx$0.35–0.50; Fig. 2). Low F_v/F_m, NPQ and high φ_{PSII} have been documented in desiccation-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 φ_{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 φ_{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 PPFD 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.

Acknowledgements

References

Abrams, M.D., Kubiske, M.E., Mostoller, S.A., 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology 75, 123–133.

Adams III, W.W., Demmig-Adams, B., Logan, B.A., Barker, D.H., Osmond, C.B., 1999. Rapid changes in xanthophyll cycle-dependent energy dissipation and photosystem II efficiency in two vines, Stephania japonica and Smilax australis, growing in the understory of an open Eucalyptus forest. Plant Cell and Environment 122, 125–136.

Barker, D.H., Adams III, W.W., 1997. The xanthophyll cycle and energy dissipation in differently oriented faces of the cactus Opuntia macrorhiza. Oecologia 109, 353–361.

Barker, D.H., Adams III, W.W., Demmig-Adams, B., Logan, B.A., Verhoven, A.S., Smith, S.D., 2002. Nocturnally retained zeaxanthin does not remain engaged in a state primed for energy dissipation during the summer in two Yucca species growing in the Mojave Desert. Plant Cell and Environment 25, 95–103.

Barker, D.H., Stark, L.R., Zimpfer, J.F., McLetchie, N.D., Smith, S.D., 2005. Evidence of drought-induced stress on biotic crust moss in the Mojave Desert. Plant Cell and Environment 28, 939–947.

Bowers, J.E., 2005. Effects of drought on shrub survival and longevity in the northern Sonoran Desert. Journal of the Torrey Botanical Society 132, 421–431.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America 102, 15144–15148.

Ceccardi, T.L., Ting, I.P., 1996. Effect of temperature and water stresses on gas exchange, fluorescence kinetics, and solute levels of jojoba. Industrial Crop Productivity 5, 279–290.

Demmig-Adams, B., Adams III, W.W., 1992. Photoprotection and other responses of plants to high light stress. Annual Review of Plant Physiology and Plant Molecular Biology 43, 599–626.

Demmig-Adams, B., 1998. Survey of thermal energy dissipation and pigment composition in sun and shade leaves. Plant Cell Physiology 39, 474–482.

Ehleringer, J.R., 1994. Variation in gas exchange characteristics among desert plants. In: Schulze, E.D., Caldwell, M.M. (Eds.), Ecophysiology of Photosynthesis. Springer-Verlag, Berlin, Germany, pp. 361–392.

Feldman, W.R., 1988. Photosynthesis, respiration and growth of jojoba throughout the year. In: Baldwin, A.R. (Ed.), Proceedings of the Seventh International Conference on Jojoba and its Uses, January 17–22, 1988, Phoenix, Arizona, USA. American Oil Chemists' Society, Champaign, Illinois, USA, pp. 1–19.

Forseth, I.N., Ehleringer, J.R., 1983. Ecophysiology of two solar-tracking desert winter annuals. III. Gas exchange responses to light, CO_2, and VPD in response to long-term drought. Oecologia 57, 344–351.

Gilmore, A.M., Ball, M.C., 2000. Protection and storage of chlorophyll in over wintering evergreens. Proceedings of the National Academy of Sciences of the United States of America 97, 11098–11101.

Hamerlynck, E.P., Knapp, A.K., 1996. Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. Tree Physiology 16, 557–565.

Hamerlynck, E.P., McAuliffe, J.R., Smith, S.D., 2000. Effect of surface and sub-surface soil horizons on the seasonal performance of Larrea tridentata (creosotebush). Functional Ecology 14, 596–606.

Hamerlynck, E.P., Zs, Csintalan, Nagy, Z., Tuba, Z., Goodin, D., Henebry, G.M., 2002. Ecophysiological consequences of contrasting microenvironments on the desiccation tolerant moss, Tortula ruralis. Oecologia 131, 498–505.

Hamerlynck E.P., McAuliffe, J.R., 2008. Soil-dependent canopy-die back and plant mortality in two Mojave Desert shrubs. Journal of Arid Environments, 72, 1793-1802.

Huxman, T.E., Hamerlynck, E.P., Loik, M.E., Smith, S.D., 1998. Gas exchange and chlorophyll fluorescence responses of three southwestern Yucca species to elevated CO_2 and high temperature. Plant Cell and Environment 21, 1275–1284.

McKee T.B., Doesken N.J., Kleist J., 1995. Drought monitoring with multiple time scales. In: Preprints, 9th Conference on applied climatology, January 15–20, 1995, Dallas, Texas. p. 233–236.

Miriti, M.N., Rodriguez-Buritica, S., Wright, S.J., Howe, H.F., 2007. Episodic death across species of desert shrubs. Ecology 88, 32–36.

Müller, P., Li, X.P., Niyogi, K.K., 2001. Non-photochemical quenching. A response to excess light energy. Plant Physiology 125, 1558–1566.

Nobel, P.S., 1980. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61, 1–7.

Osmond, C.B., 1994. What is photoinhibition? Some insights from comparison of sun and shade leaves. In: Baker, N.R., Boyer, J.R. (Eds.), Photoinhibition Molecular Mechanisms to the Field. Bios Scientific Publishing, Oxford, U.K., pp. 1–24.

Pockman, W.T., Sperry, J.S., 1997. Freezing-induced xylem cavitation and the northern limit of Larrea tridentata. Oecologia 109, 19–27.

Sandquist, D.R., Ehleringer, J.R., 1998. Intraspecific variation of drought adaptation in brittlebrush: leaf pubescence and timing of leaf loss vary with rainfall. Oecologia 113, 162–169.

Schlesinger, W.H., Fonteyn, P.A., Reiners, W.A., 1989. Effects of overland flow on plant water relations and soil water percolation on a Mojave Desert landscape. Soil Science Society of America Journal 53, 1567–1572.

Schreiber, U., Bilger, W., Hormann, H., Neubauer, C., 1998. Chlorophyll fluorescence as a diagnostic tool: basics and some aspects of practical relevance. In: Raghavendra, A.S. (Ed.), Photosynthesis, a Comprehensive Treatise. Cambridge University Press, Cambridge, UK, pp. 320–336.

Smith, S.D., Monson, R.K., Anderson, J.A., 1997. The Physiological Ecology of North American Desert Plants. Springer-Verlag, Berlin, Germany.

Swetnam, T.W., Betancourt, J.L., 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climatology 11, 3128–3147.

Wang, D., Heckathorn, S.A., Barua, D., Joshi, P., Hamilton, E.W., LaCroix, J.J., 2008. Effects of elevated CO_2 on the tolerance of photosynthesis to acute heat stress in C_3, C_4, and CAM species. American Journal of Botany 95, 165–176.

Woodhouse, R.M., 1978. The physiological ecology of the desert evergreen shrub Simmondsia chinensis (jojoba). In: Yermanos, D.M. (Ed.), Proceedings of the Third International Conference on Jojoba, 13–16 September 1978, Riverside, California, USA. University of California, Riverside, CA, USA, pp. 13–16.

Wright, I.J., Reich, P.B., Westoby, M., 2001. Strategy shifts in leaf physiology, structure, and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology 15, 423–434.