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Water Relations in Native Trees, Northeastern Mexico

Humberto, González^{a*}, Ivan A. Camarillo^a, Israel Cantú^a, Roque G. Ramírez^b and Marco V. Gómez^c

a Universidad Autónoma de Nuevo León, Facultad de Ciencias Forestales, Apartado Postal 41, Linares, NL 67700, Mexico.

b Universidad Autónoma de Nuevo León, Facultad de Ciencias Biológicas. Monterrey, NL, México.

c Universidad Autónoma de Nuevo León, Facultad de Economía, Monterrey, NL, México.

Abstract

Native trees and shrubs that grow in the semiarid regions of northeastern Mexico are important feed resources for range ruminants and white-tiled deer. They also provide high quality fuelwood and timber for fencing and construction. Since water stress is the most limiting factor in this region, the present work was focused to study how seasonal leaf water potentials (Ψ) of native tree species are related to soil water availability and evaporative demand components. Studied tree species were: *Cordia boissieri* (Boraginaceae), *Condalia hookeri* (Rhamnaceae) *Diospyros texana* (Ebenaceae) and *Bumelia celastrina* (Sapotaceae). Determinations of Ψ in the four native tree species were at 10 days intervals between July 10 and November 30, 2007 by using a Scholander pressure bomb. Ψ was monitored in five different plants per species at 06:00 h (Ψ_p , predawn) and 14:00 h (Ψ_{md} , midday). Air temperature, relative humidity, vapor pressure deficit, precipitation and soil water content were registered throughout. Ψ data were subjected to one-way ANOVA and correlation analysis. During the wettest period (Sep-10) Ψ_p ranged from -0.72 (*C. boissieri*) to -1.30 MPa (*B. celastrina*), in contrast, during the driest period (Nov-30), Ψ_m varied from -2.90 (*B. celastrina*) to -6.10 MPa (*D. texana*). Diurnal Ψ values were negatively correlated with air temperature and vapor pressure deficit, in contrast, a positive relationship was found with relative humidity. The ability of tree species to cope with drought stress depends on the pattern of water uptake and the extent to control water loss through the transpirational flux.

Introduction

The main type of vegetation in northeastern Mexico, known as the Tamaulipan thornscrub, is distinguished by a wide range of taxonomic groups exhibiting differences in growth patterns, leaf life spans, textures, growth dynamics, and phenological development (Reid *et al.*, 1990; McMurtry *et al.*, 1996). This semiarid shrubland, which covers about 200,000 km² including southern Texas and northeastern Mexico (Udvardy, 1975), is characterized by an average annual precipitation of 805 mm and yearly potential evapotranspiration is about 2,200 mm.

Vegetation has been utilized as a forage source for domestic livestock and wildlife, fuelwood, timber for construction, medicine, agroforestry and reforestation practices in disturbed

* Corresponding author: E-mail: humberto@fcf.uanl.mx

sites (Reid *et al.*, 1990). Since water availability is the most limiting factor controlling tree growth, survival and distribution in dry climates (Kramer, 1983; Newton and Goodin, 1989), the great diversity of native tree species in this region reflects the plasticity of how tree species cope with seasonal water stress. Therefore, shrub and tree plants have evolved key morphological and physiological traits suited for adaptation to environmental constraints, especially on drought-prone sites. The strategies include early leaf abscission, limited leaf area, an extensive and deeper root system, epidermal wax accumulation, reduction of water loss by stomatal closure and accumulation of organic and inorganic solutes (Newton *et al.*, 1991). Although three pieces of evidence are available on plant water relations for native species of the northeastern region of Mexico (Stienen *et al.*, 1989; González *et al.*, 2000, 2004), this region provides an opportunity to investigate ecophysiological aspects of tree species and their responses to changes in resource availability, particularly soil moisture content, in order to gain a better understanding of how to sustain and improve productivity. The objectives were to assess and quantify how seasonal plant water potentials are related to soil water availability and evaporative demand components in four native tree species.

Material and Methods

Research site

This study was carried out at the Experimental Research Station of the Facultad de Ciencias Forestales (Faculty of Forest Sciences), Universidad Autónoma de Nuevo León (24° 47'N; 99° 32'W; elev. 350 m) located 8 km south of Linares county, in Nuevo Leon state of Mexico. The climate is typically subtropical and semi-arid with a warm summer. Mean monthly air temperature ranges from 14.7°C in January to 22.3°C in August, although daily high temperatures of 45°C are common during the summer. Average annual precipitation is 805 mm with a bimodal distribution. Peak rainfall months are May, June and September. The main type of vegetation is known as the Tamaulipan Thornscrub or Subtropical Thornscrub Woodlands (SPP-INEGI, 1986). The dominant soils are deep, dark-gray, lime-clay vertisols, with montmorillonite, which shrink and swell noticeably in response to changes in soil moisture content. Some physical and chemical properties of the soil at a profile depth of 0-20 cm are shown in Table 1.

Table 1: Some physical and chemical properties of the soil (profile depth 0-20 cm) at the study site, northeastern Mexico.

Soil property	Units	Value
Sand	g kg ⁻¹	250.0
Silt	g kg ⁻¹	500.0
Clay	g kg ⁻¹	250.0
Bulk Density	Mg m ³	0.8
Organic Matter	%	7.0
pH (CaCl ₂ ; 0.01 M)		6.6
Electrical Conductivity	μS cm ⁻¹	216.0

Plant material

Four native tree species were randomly selected from a 20 m x 20 m representative and undisturbed thornscrub plot. The tree species were: *Cordia boissieri* (Boraginaceae), *Condalia hookeri* (Rhamnaceae), *Diospyros texana* (Ebenaceae) and *Bumelia celastrina* (Sapotaceae).

Water potential measurements and sampling procedures

Determinations of leaf water potential (Ψ , MPa) in the four native tree species were conducted, when possible, at 10-days intervals. At each sampling date, Ψ of five (replications) different plants per species were randomly chosen from the experimental plot. The period of measurement

was between July 10 and November 30, 2007. On each sampling date, Ψ measurements were taken from terminal twigs of chosen plants and monitored at 06:00 h (Ψ_{pd} , predawn) and 14:00 h (Ψ_{md} , midday) local time. Water potential was estimated using a Scholander pressure bomb (Model 3005, SoilMoisture Equipment Corp., Santa Barbara, CA) (Ritchie and Hinckley, 1975). One terminal shoot, with fully expanded leaves, was excised and sampled from the middle and shaded side of each plant. However, when plant tissue was highly dehydrated ($\Psi < -4.0$ MPa), only one plant per species was measured to conserve nitrogen used to pressurize the chamber.

Environmental data

Air temperature ($^{\circ}\text{C}$) and relative humidity (%) were registered on a daily basis by using a HOBO Pro Data Loggers (HOBO Pro Temp/RH Series, Forestry Suppliers, Inc., Jackson, MS, USA). Daily precipitation (mm) was obtained from a Tipping Bucket Rain Gauge (Forestry Suppliers, Inc.). Values of air temperature and relative humidity were used to calculate vapor pressure deficit (VPD, kPa) (Rosenberg *et al.*, 1983). Gravimetric soil water content on each sampling date was determined in soil cores at depths of 0-10 cm, 10-20 cm and 20-30 cm using a soil sampling tube (SoilMoisture Equipment Corp.). Four replications were used for each measurement. Soil water content was determined by drying soil samples in an oven at 105°C for 72 hrs, and was expressed on a percentage basis. In this study, registered mean monthly air temperature ($^{\circ}\text{C}$), mean monthly relative humidity (%) and cumulative monthly rainfall (mm) are shown in Figure 1.

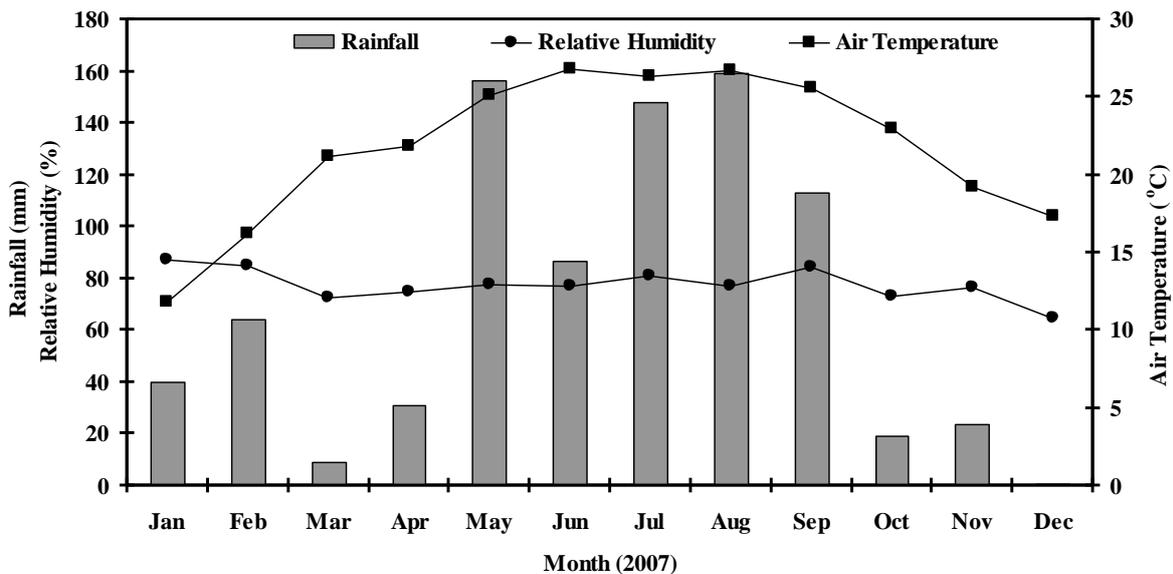


Figure 1: Mean monthly air temperature and relative humidity and cumulative monthly rainfall at the research site.

Statistical analyses

To determine if differences existed among tree species in Ψ_{pd} or Ψ_{md} at each sampling date, water potential data were subjected to one-way ANOVA. Differences were validated using the Tukey's test and were considered statistically significant at $P < .05$ (Steel and Torrie, 1980) for all pairwise comparisons. Assumptions of normality for Ψ_{pd} , Ψ_{md} and the environmental variables were tested using the Kolmogorov-Smirnov test (Steel and Torrie, 1980). To assess the relationship between Ψ and prevailing environmental variables (air temperature, relative humidity and vapor pressure deficit), diurnal data were pooled and the Spearman's correlation coefficient values were determined. All applied statistical methods were according to the SPSS

(Statistical Package for the Social Sciences) software package (standard released version 9.0 for Windows, SPSS Inc., Chicago, IL).

Results and Discussion

Seasonal gravimetric soil water contents at the 0-10 cm, 10-20 cm and 20-30 cm soil depths are shown in Figure 2. Maximum (31.1 %) and minimum (9.8 %) soil water content in the 0-10 cm soil layer was registered on Aug-30 and Aug-20, respectively. With respect to the soil profile 10-20 cm, higher (21.5 %) and lower (10.6 %) soil water content was registered on Sep-10 and Oct-30, respectively. Similarly, the 20-30 cm soil layer achieved on Sep-10 and Oct-30 higher (20.6 %) and lower (9.5 %), respectively, soil water content (Figure 2). In general, soil water content near the surface (0-10 cm) was more dependent upon and responsive to individual rainfall events than deeper soil layers. However, since there was a large variability in thunderstorms and air temperature, soil water content could not be controlled and maintained and, therefore, soil moisture may not be available for absorption by deeper roots due to low soil water infiltration, rapid runoff and high evapotranspiration rates. The soil water content responses found in the present work are in agreement with other studies that have shown seasonal variability in soil moisture in rangeland and Mediterranean dry ecosystems (Anderson *et al.*, 2001; Bussotti *et al.*, 2002; González *et al.*, 2000, 2004).

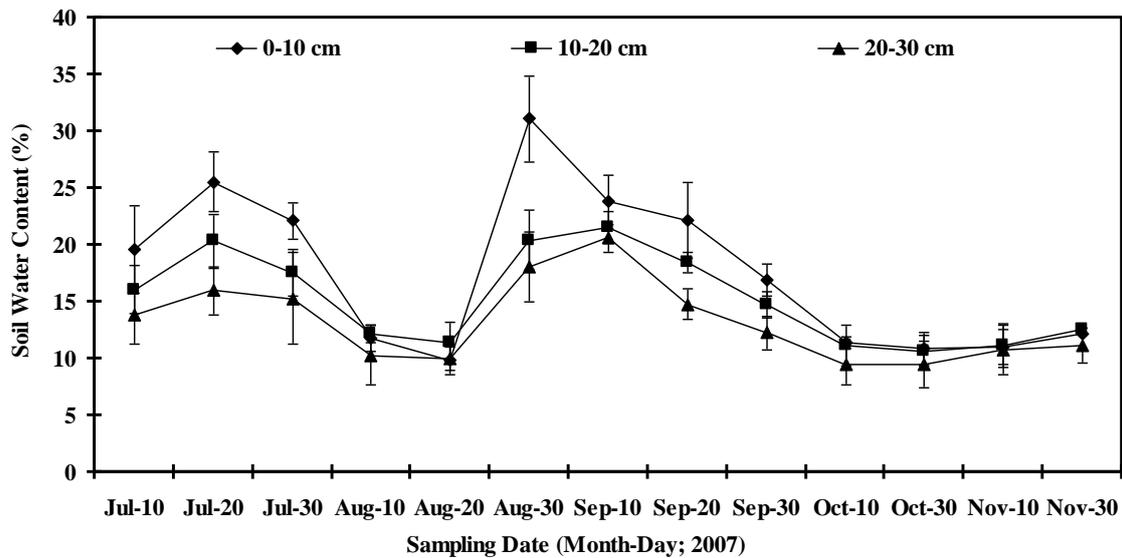


Figure 2: Seasonal variation in gravimetric soil water content at three soil profile depths at the research site. Values are means \pm standard errors (n=4).

The F values resulted from the ANOVA for Ψ_{pd} data (Table 2) revealed that in eight sampling dates there were significant differences among plants. Other sampling dates were not statistically analyzed because only one replication was taken. Monthly variation in Ψ_{pd} is shown in Figure 3(a). In general, data followed a similar pattern of variation among tree species when values were higher than -1.0 MPa; meanwhile, this trend diverged among species, particularly between *B. celastrina* and *D. texana*, when observed Ψ_{pd} values declined below -2.0 MPa. During the wettest sampling date, Sep-10, Ψ_{pd} values (-0.74 MPa) achieved in *C. boissieri* and *D. texana* were significantly ($P < .05$) higher than those values ($\Psi_{pd} = -1.08$ MPa) detected in *B. celastrina*. Conversely, during a mild dry sampling date, Aug-20, tree species experienced a marked water deficit, with higher (-2.7 MPa) and lower (-4.8 MPa) values acquired in *B. celastrina* and *D. texana*, respectively (Figure 3(a)).

Monthly trends of Ψ_{md} values among tree species are illustrated in Figure 3(b). Significant differences were detected among tree species in six sampling dates; however, no apparent differences ($P > .05$) were revealed in one sampling date (Sep-20), and the remaining six dates were not be statistically analyzed since only one observation was registered at the time of measurements ($\Psi_{md} < -4.0$ MPa) because tree species faced water shortage (Figures 2 and 3(b)). During the wettest sampling date (Sep-10) when soil water content at the soil layer 0-30 cm was higher than 20%, Ψ_{md} values ranged from -1.45 (*C. boissieri*) to -1.8 MPa (*B. celastrina*), in contrast, during the driest sampling date (Aug-20), when soil water content was below 12%, maximum (-3.6 MPa) and minimum (-6.0 MPa) Ψ_{md} were observed in *B. celastrina* and *D. texana*, respectively (Figure (3b)).

Table 2: Calculated mean square error (MSE), *F*- and *P*-values, and coefficient of determination (R^2) from the one-way ANOVA results for predawn (Ψ_{pd}) and midday (Ψ_{md}) leaf water potential at each sampling date.

Sampling date	Ψ_{pd} (MPa)				Ψ_{md} (MPa)			
	MSE	<i>F</i> -value	<i>P</i> -value	R^2	MSE	<i>F</i> -value	<i>P</i> -value	R^2
Jul-10	0.034	4.91	.0131	0.4797	0.162	7.42	.0025	0.5818
Jul-20	0.055	4.67	.0158	0.4669	0.070	5.67	.0076	0.5157
Jul-30	0.019	11.09	.0003	0.6754	0.069	3.41	.0429	0.3905
Aug-10	0.125	13.15	.0001	0.7115	ND ¹			
Aug-20	ND ¹				ND			
Aug-30	0.053	5.05	.0119	0.4865	0.067	6.68	.0039	0.5564
Sep-10	0.027	4.66	.0158	0.4667	0.047	3.44	.0420	0.3923
Sep-20	0.018	17.21	<.0001	0.7634	0.081	2.25	.1211	0.2973
Sep-30	0.020	2.55	.0920	0.3237	0.052	4.89	.0134	0.4784
Oct-10	0.057	6.90	.0034	0.5641	ND			
Oct-30	ND				ND			
Nov-10	ND				ND			
Nov-30	ND				ND			

¹ND=not determined since only one replication was used.

Under adequate soil water content (>20%), the contrasting diurnal pattern of changes in leaf Ψ observed in the studied shrub species was strongly influenced by the daily course of atmospheric evaporative demand components (air temperature, relative humidity and vapor pressure deficit of the atmosphere. In fact, a highly significant and negative relationship between Ψ with air temperature and vapor pressure deficit was demonstrated through correlation analysis (Table 3). These findings are in agreement with previous studies (Kolb and Stone, 2000; González *et al.*, 2000, 2004).

Table 3: Spearman's correlation coefficient values for leaf water potential in relation to environmental variables in four native tree species.

Tree species	Environmental Variable		
	Air Temperature (°C)	Relative Humidity (%)	Vapor Pressure Deficit (kPa)
<i>B. celastrina</i>	-0.258***	0.405***	-0.373***
<i>C. hookeri</i>	-0.367***	0.528***	-0.490***
<i>C. boissieri</i>	-0.364***	0.482***	-0.459***
<i>D. texana</i>	-0.408***	0.516***	-0.495***

***($P < .001$)

This cause-effect relationship tended to exhibit a Type I curve (Ritchie and Hinckley, 1975), which could mean that the tree species studied, under high soil moisture availability, showed maximum Ψ values at predawn and a minimum at midday, with a concurrent evening recovery in Ψ due mainly to low evaporative demand. If it is assumed at predawn (06:00), that leaf Ψ values represent a true equilibrium (close enough) with soil water potential (not measured in this study), the Ψ differences detected at this sampling hour between tree species under high soil water content registered on Sep-10 (Figure 3(a)) could be explained by the resistance between the rooting medium and the root surface and plant (root, stem and leaf) hydraulic resistance, whereas, at midday (14:00), the non-significant and significant differences detected in Ψ among tree species on this sampling date (Figure 3(b)), respectively, may be related mainly to the milder prevailing environmental conditions registered. However, it may be suggested that the root and stem hydraulic resistance, leaf stomatal conductance, the number of the conducting elements, stomatal density, and the morphological and anatomical characteristics of leaves and stomata could have exerted an important role on the diurnal water relations of plant tissue (Castro-Díez *et al.*, 2000; Aasamaa *et al.*, 2001; Bussotti *et al.*, 2002). Peláez and Bóo (1987) have indicated that a wide range in plant Ψ values between morning and afternoon, would indicate a high degree of plasticity or high physiological capacity including ability to use solutes to lower the osmotic potential and hence to regulate water loss and maintain high Ψ . In contrast, a narrow range between Ψ values may suggest unfavorable environmental conditions such as low soil water content or high vapor pressure deficit, conditions in which rates of water absorption would not compensate transpiration rates.

Results from Aasamaa *et al.* (2001) have showed that the hydraulic conductance in temperate deciduous trees depend on anatomical characteristics of xylem, mesophyll and epidermis, and stomatal conductance and its sensitivity to changes of leaf Ψ may depend on anatomical characteristics of stomata. Le Roux *et al.* (1995) explain that the hydraulic resistances associated with moving water through xylem conduits may impose deficits on leaves, even when soil water availability is high. Other studies have revealed that a decrease in transpiration rate with increasing vapor pressure deficit of the air occurred only when soil water content fell below a critical point (Hesla *et al.*, 1985; Maier-Maercker, 1998). These observations are consistent with the results obtained in the present work, but in the context of plant water potential determinations since transpiration measurements were not carried out in this work. Thus, it can be proposed that daily leaf Ψ variation between the studied shrubs may be associated to differences in internal resistance to water transmission. On a seasonal basis, the gradual decrease in Ψ_{pd} (Figure 3(a)) and Ψ_{md} (Figure 3(b)) for the four tree species showed a considerable response to precipitation trends, which in fact, as has been pointed out by Montagu and Woo (1999) who determined the soil water availability pattern, with lower Ψ_{pd} or Ψ_{md} (< -4.0 MPa) values occurring when soil water content reached values approximately below 15%; however, both measurements recover after the onset in rainfall. *D. texana* would be at a physiological disadvantage compared with *B. celastrina* because the former showed a significant steeper decrease in both water potential parameters with respect to the latter as shown in Figures 3(a) and 3(b), respectively. Furthermore, *B. celastrina* is the only one that under drought stress tends to achieve and maintain significantly a higher water potential (desiccation avoidance response) than *D. texana*, since both Ψ_{pd} and Ψ_{md} measurements decrease earlier. Thus, the decline in Ψ_{pd} or Ψ_{md} is linked to the gradual depletion of soil moisture content as the study progressed, rainfall events of low intensities, and high evaporative demand (data not shown). It has been found that under seasonal soil water depletion there is a concomitant reduction in both stomatal conductance (Montagu and Woo, 1999) and Ψ (Fotelli *et al.*, 2000). This response may be viewed as a mechanism to conserve water use to avoid tissue dehydration (desiccation avoidance).

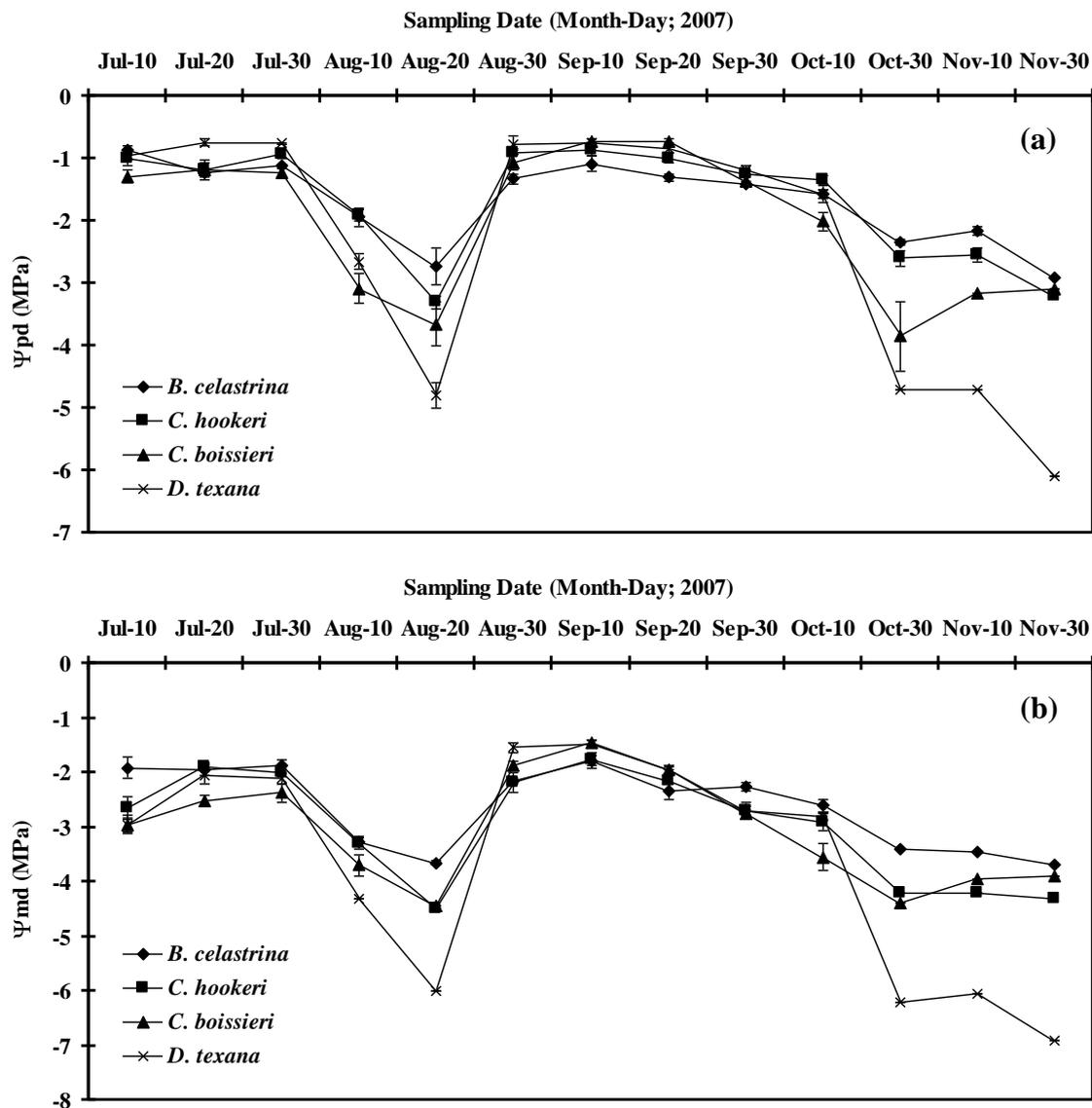


Figure 3: Seasonal variation in predawn (Ψ_{pd}) (a) and midday (Ψ_{md}) (b) leaf water potential in four tree species. Plotted values are means \pm standard errors ($n=5$).

Implications

Results of this study suggest strong physiological evidence that even though evaluated species decreased their water potential during stress (desiccation tolerance response) they still play an important role in contributing to maintain the productivity of dry woodland ecosystems with limited water resource availability. However, detailed studies on tissue water relations at the anatomical, biophysical, biochemical, physiological, and molecular level are required to elucidate the underlying mechanisms employed by these species to adapt to this ecosystem and to cope with prolonged drought periods. Thus, this region provides an opportunity to investigate the ecophysiology of native small tree species and their responses to changes in resource availability, particularly soil moisture content.

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