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Characterization of Xylem Water Potential in Ten Native Plants of North-eastern Mexico

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Abstract

Since water stress is the most limiting factor in north-eastern Mexico, the present study focused to characterize the xylem water potentials (Ψ , MPa) of ten native tree and shrub species such as *Acacia rigidula* (Leguminosae; shrub), *Bumelia celastrina* (Sapotaceae; tree), *Castela texana* (Verbenaceae; shrub), *Celtis pallida* (Ulmaceae; shrub), *Forestiera angustifolia* (Oleaceae; tree), *Karwinskia humboldtiana* (Rhamnaceae; shrub), *Lantana macropoda* (Simaroubaceae; shrub), *Leucophyllum frutescens* (Scrophulariaceae; shrub), *Prosopis laevigata* (Leguminosae; tree) and *Zanthoxylum fagara* (Rutaceae; tree) under drought and high soil water content. Under drought conditions, *P. laevigata*, *A. rigidula* and *C. texana* achieved higher Ψ at pre-dawn with values of -2.72, -2.78 and -3.42 MPa, respectively, while minimum value of -6.82 MPa was observed in *Z. fagara*. Similarly, higher Ψ at mid-day was registered in *C. texana*, *B. celastrina* and *P. laevigata* with values around -4.15 MPa, while lower values (<-7.0 MPa) were acquired by *L. macropoda*, *K. humboldtiana* and *Z. fagara*. In contrast, under high soil water content, pre-dawn Ψ varied from -0.52 MPa (*K. humboldtiana*) to -1.63 MPa (*C. texana*). With respect to mid-day Ψ data, Ψ values ranged from -1.43 MPa (*L. macropoda*) to -2.28 MPa (*C. texana*). Since the plant species *A. rigidula*, *B. celastrina*, *C. texana* and *P. laevigata* achieved higher pre-dawn and mid-day Ψ values under drought conditions, the results indicated that these species could be considered as drought adapted species while, *L. macropoda*, *K. humboldtiana* and *Z. fagara* which acquired lower water potentials, may not be suitable to drought and thus, may be in a physiological disadvantage under limited water conditions. The study suggests that the first four species may serve as a pertinent model to study the strategies of adaptation to drought at high tissue water potential while the later may serve as an adequate model to study plant adaptation to drought at low tissue water potential. The implications of this study suggest that the species respond differently to drought through the employment of different strategies and there is scope for forest and range management practices in the selection of drought tolerant species for planting and reforestation of drought prone areas.

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1. Introduction

Drought is actually a meteorological event which implies the absence of rainfall for a period of time, long enough to cause moisture-depletion in soil and water deficit with a decrease of water potential in plant tissues (Mitra, 2001). During the summer, the climate in north-eastern Mexico is characterized by the alternation between favorable and unfavorable periods of soil water content which affects plant growth and development. During periods of drought shrubs and trees growing in this region have to seasonally adjust their morpho-physiological traits to cope successfully with changes in soil water availability (Bucci et al., 2008). Plants under such conditions regulate their water status using several strategies, viz. osmotic adjustment, stomatal aperture, turgor maintenance, root distribution and

leaf canopy properties (Rhizopoulou et al., 1997). The main type of vegetation in north-eastern 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 semi-arid shrub-land is characterized by an average annual precipitation of 805 mm and a yearly potential evapo-transpiration of about 2,200 mm. Since water availability is the most limiting factor controlling tree growth, survival and distribution in dry climates (Newton and Goodin, 1989), the great diversity of native shrubs in this region reflects the plasticity among these species to cope with a harsh environment. Therefore, shrub and tree plants have evolved key morphological and physiological



traits suited for adaptation to environmental constraints, especially in drought-prone regions. The strategies involve early leaf abscission, limited leaf area, an extensive and deeper root system, epidermal wax accumulation associated with reduction of water loss by stomatal closure, and accumulation of organic and inorganic solutes (Newton et al., 1991).

The study of native plant species in this region provides an opportunity to investigate, from an eco-physiological perspective, the response of shrub or tree species to changes in resource availability, particularly, soil water content, in order to gain a better understanding of how such an ecosystem may sustain biomass productivity. However, few studies (Stienen et al., 1989; González et al., 2000, 2004) have attempted to directly relate water status of native shrub species across summer drought in this region of Mexico. Thus, the present study was conducted to assess xylem water potentials (Ψ) in ten native shrub and tree species. Comparative studies of basic physiological performance would give insight how evergreen or deciduous shrub or tree species cope with adverse environmental stress conditions such as drought.

2. Materials and Methods

2.1. Research site

This study was carried out at El Abuelo Ranch (25°40'N; 99°27'W; elevation 200 msl) in Los Ramones county, state of Nuevo Leon, Mexico in the summer 2005. The climate is semi-arid with a warm summer. Annual mean air temperature and rainfall is about 22°C and 700 mm, respectively. Peak rainfall occurs in May, June and September. The main type of vegetation is known as Tamaulipan thornscrub or Sub-tropical thornscrub woodlands (SPP-INEGI, 1986). The dominant soils are deep, dark-gray, lime-clay vertisols with montmorillonite, which shrink and swell noticeably as soil moisture content varies. Some physical and chemical properties of the soil at profile depths of 0-20 cm and 20-40 cm have been previously reported (López-Hernández et al., 2010).

2.2. Plant material and water potential measurements

Three plants of the native plant species *Acacia rigidula* Benth. (Leguminosae; shrub), *Bumelia celastrina* H. B. K. (Sapotaceae; tree), *Castela texana* Torr. & Gray. (Verbenaceae; shrub), *Celtis pallida* Torr. (Ulmaceae; shrub), *Forestiera angustifolia* Torr. (Oleaceae; tree), *Karwinskia humboldtiana* Roem et Schult. (Rhamnaceae; shrub), *Lantana macropoda* Torr. (Samaroubaceae; shrub), *Leucophyllum frutescens* Berl. (Scrophulariaceae; shrub), *Prosopis laevigata* (willd) M.C. Johnst. (Leguminosae; tree) and *Zanthoxylum fagara* L. (Rutaceae; tree) were randomly selected from a 50 m² previously established and undisturbed experimental thornscrub plot for xylem water potential (Ψ , MPa) determination. Since pre-dawn and mid-day Ψ measurements are influenced by environmental conditions, measurements were conducted under low (drought, July 15, 2005) and high (August 5, 2005) soil water conditions. Averaged gravimetric soil water content in the 0-50 cm soil depth profile under drought and well watered conditions were 0.15 and 0.28 kg kg⁻¹, respectively. Gravimetric soil water content

determinations were taken as previously reported (Gonzalez et al., 2000). The Ψ measurements were taken from terminal twigs at 6 am (pre-dawn, Ψ_{pd}) and 1 pm (mid-day, Ψ_{md}) local time. Water potential was estimated using a Scholander pressure bomb (Model 3005, Soil Moisture 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. Measurements were performed within 10 to 25 s after collecting the samples. Pressure was applied to the chamber at a rate of 0.05 MPa s⁻¹. For safety reasons, and per operating instructions, lowest limit of the pressure chamber was -7.3 MPa.

2.3. Statistical analyses

To determine if differences exist among native plant species in Ψ_{pd} or Ψ_{md} at each soil water condition, xylem water potential data were subjected to one-way ANOVA. Normal distribution and homogeneity of variances for Ψ_{pd} and Ψ_{md} data were tested using the Kolmogorov-Smirnov, Shapiro-Wilk and Levene tests (Brown and Forsythe, 1974; Steel and Torrie, 1980) indicated that both Ψ_{pd} and Ψ_{md} data were normally distributed. Differences among native plant species for pre-dawn and mid-day xylem water potentials were validated using the Tukey's HSD test and were considered statistically significant at $p=0.05$ (Steel and Torrie, 1980) for all pair-wise comparisons. All applied statistical methods were according to the SPSS® (Statistical Package for the Social Sciences) software package (standard released version 13.0 for Windows, SPSS Inc, Chicago, IL).

3. Results and Discussion

According to one-way ANOVA statistical analysis, there were significant statistical differences among native plant species for pre-dawn or mid-day xylem water potentials for both soil water content conditions (Table 1). Under drought conditions (Table 2), maximum pre-dawn xylem water potentials values were observed in *P. laevigata* (-2.72 MPa), *C. texana* (-3.42 MPa) and *B. celastrina* (-3.80 MPa) whereas, minimum values were acquired by *K. humboldtiana* (-6.37 MPa) and *Z. fagara* (-6.82 MPa). In contrast, higher mid-day xylem water potentials were registered in the range of -3.0 MPa to -4.25 MPa for *C. pallida*, *C. texana*, *B. celastrina* and *P. laevigata* while, values around -7.20 MPa were accounted in *L. macropoda* and *K. humboldtiana* (Table 2). With respect to the condition of high soil water content (Table 2), higher pre-dawn xylem water potentials values were observed in the range between -0.52 MPa to -0.75 MPa for *K. humboldtiana*, *L. macropoda*, *F. angustifolia*, *L. frutescens*, *C. pallida*, *A. rigidula*, and *Z. fagara*; however, *C. texana* acquired the minimum (-1.63 MPa). Mid-day xylem water potential ranged from -1.43 MPa (*L. macropoda*) to -2.28 MPa (*C. texana*). The relationship between mid-day and pre-dawn xylem water potential for studied native plant species for both soil water content conditions is shown in Figure 1. Under high soil water content, *F. angustifolia*, *L. macropoda* and *K. humboldtiana* showed a wide range in the diurnal water potential variation, referred herein as the differ-



Table 1: Mean square error (MSE), F and *p* values of the one-way ANOVA results for pre-dawn (Ψ_{pd}) and mid-day (Ψ_{md}) xylem water potential (MPa) to detect significant differences among shrub species, respectively at each soil water condition

Soil water condition	Xylem water potential	MSE	F value	P value
Drought	Ψ_{pd}	0.113	56.918	<0.001
	Ψ_{md}	ND	ND	ND
High	Ψ_{pd}	0.014	25.127	<0.001
	Ψ_{md}	0.054	5.094	0.001

p values lower than 0.001 are denoted as ≤ 0.001 ; ND=Not determined since only one observation was taken

Table 2: Pre-dawn (Ψ_{pd}) and mid-day (Ψ_{md}) xylem water potentials (MPa) in ten native plant species under drought and high soil water conditions at research site. Mean values followed by different letters at upright within a column indicate significant differences ($p=0.05$) among native plant species based on Tukey's HSD procedure

Plant species	Ψ_{pd}	Ψ_{md}	Ψ_{pd}	Ψ_{md}
<i>Castela texana</i>	-3.42 ^{a,b}	-4.20	-1.63 ^d	-2.28 ^b
<i>Bumelia celastrina</i>	-3.80 ^{b,c}	-4.25	-1.08 ^c	-1.70 ^{a,b}
<i>Prosopis laevigata</i>	-2.72 ^a	-4.00	-0.98 ^{b,c}	-2.20 ^b
<i>Zanthoxylum fagara</i>	-6.82 ^e	-6.62	-0.75 ^{a,b,c}	-2.01 ^{a,b}
<i>Acacia rigidula</i>	-2.78 ^a	-5.05	-0.72 ^{a,b}	-2.20 ^b
<i>Celtis pallida</i>	-4.33 ^{b,c}	-3.00	-0.70 ^{a,b}	-1.63 ^{a,b}
<i>Leucophyllum frutescens</i>	-5.57 ^d	-5.10	-0.65 ^{a,b}	-1.73 ^{a,b}
<i>Forestiera angustifolia</i>	-4.52 ^c	-5.95	-0.55 ^a	-1.52 ^a
<i>Lantana macropoda</i>	-5.77 ^d	-7.20	-0.55 ^a	-1.43 ^a
<i>Karwinskia humboldtiana</i>	-6.37 ^{d,e}	-7.00	-0.52 ^a	-1.90 ^{a,b}

Mean values followed by different letters superscripted within a column indicate significant differences ($p=0.05$) among native plant species based on Tukey's HSD procedure

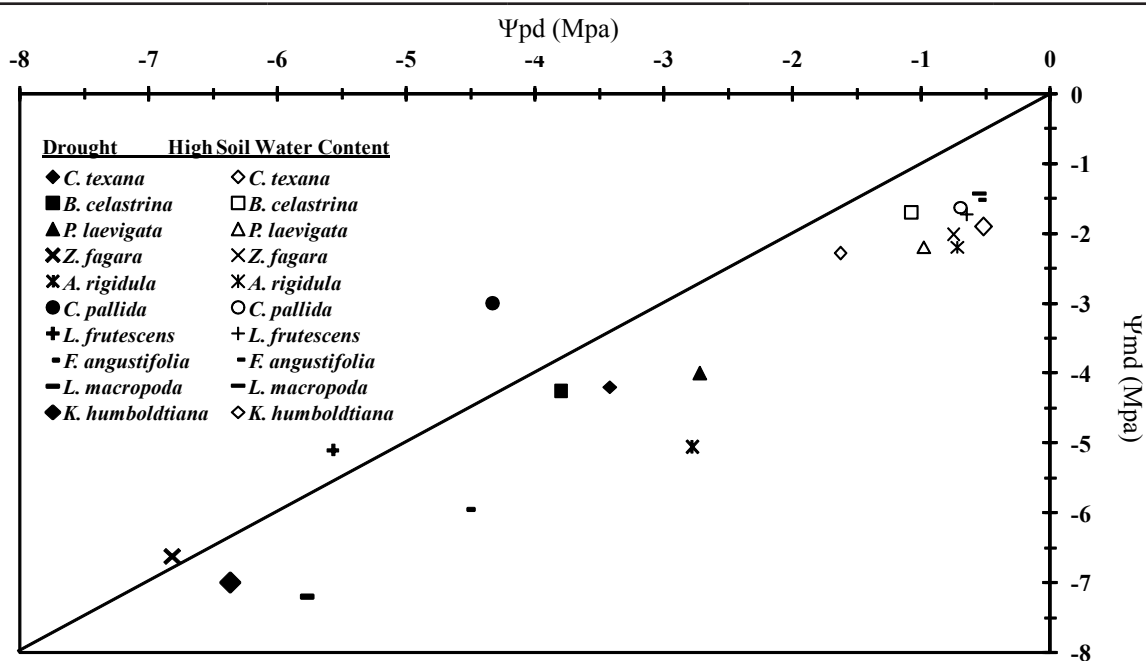


Figure 1: Relationship between mid-day (Ψ_{md}) and pre-dawn (Ψ_{pd}) xylem water potentials under drought and high soil water content conditions at the research site (diagonal line represents the 1:1 relationship)



ence between pre-dawn and mid-day water potential values, with respect to *C. texana*. In contrast, under drought conditions, *A. rigidula*, *B. celastrina*, *C. texana* and *P. laevigata* maintained higher pre-dawn and mid-day water potentials than *L. macropoda* and *K. humboldtiana*, which showed narrow diurnal range values, which could indicate lack of ability to re-saturate during night (Gebrekirstos et al., 2006). In this regard, it has been proposed that plant species differ in their transpiration rates, patterns of root distribution, and consequently in their responses to water stress. These different patterns of water use likely result from differences among species in morphological and physiological leaf and root characteristics that affect the rate of soil moisture depletion and the distribution of water removal at different soil depths (Conard et al., 1997). Clearly, among the species under study, *A. rigidula*, *B. celastrina*, *C. texana* and *P. laevigata* may be the examples of native plant species which have adapted to low soil water availability since they tended to maintain high tissue hydration, while the adaptation of *L. macropoda*, *K. humboldtiana* and *Z. fagara* to drought conditions depend on strategies which allow them to cope with internal desiccation and consequently show lower water potential values (Figure 1). Although few studies have attempted to directly relate plant water potential across the summer in native trees and shrubs in north-eastern Mexico (González et al., 2000, 2004), it could be pointed out that the species with presumably deeper roots such as *A. rigidula*, *B. celastrina*, *C. texana* and *P. laevigata* would be able to maintain higher water potentials and to extend growth activity longer in the summer. Plants differ widely in their capacity to cope with drought. Adaptations exist to explain these differences (Kozłowski and Pallardy, 2002), and these can be conveniently referenced to the capacity to maintain water status, e.g. water potential. Some woody plants are drought tolerant because they can either withstand extreme dehydration of protoplasm or avoid low water potential, with the latter being more widely observed. Many desiccation-avoiding adaptations of woody plants have been identified in leaves (shedding; small or few leaves; small, few, and sunken stomata; rapid stomatal closure during drought; abundant leaf waxes; strong development of palisade mesophyll), in stems (twig and stem photosynthesis; low resistance to water flow in vascular tissues), and in roots (extensive root growth; high root-shoot ratio; high root regenerating potential after transplanting). All these adaptations promote water homeostasis either by restricting water loss from the plant body or by increasing water absorption to replace losses by transpiration (Kozłowski and Pallardy, 2002). In addition, since under drought conditions, soil water availability may not be available for absorption by roots due to high evapo-transpiration rates, which at the research site, calculated potential evapo-transpiration reached about 1,200 mm according to the Thornthwaite's method (Rosenberg et al., 1983) and high mid-day vapor pressure deficits, which during the research study reached up to 6.0 kPa (July) (Rosenberg et al., 1983); both of these environmental constraints could have contributed to lower water potentials particularly in *L. macropoda*, *K.*

humboldtiana and *Z. fagara*. An unusual Ψ response is shown in Figure 1, particularly in shrub species *C. pallida*, *L. frutescens* and *Z. fagara*, which suggests that Ψ is higher at mid-day as compared to pre-dawn. It is tempting to speculate whether this trend could possibly reflect a solute enriched xylem content at the sampling time due to mobilization of cell sap from cells en route to reduce water loss under severe drought. In support of this view, Donovan et al. (2003) suggested a disequilibrium between pre-dawn soil and plant tissue (leaf and xylem) Ψ in diverse mesophytes and xerophytes due to apoplastic solute build up. They concluded that pre-dawn leaf Ψ and xylem Ψ may not mimic soil water potential, particularly for woody plants and halophytes, even under well watered conditions. Additionally, accumulation of organic and inorganic solutes lowers the osmotic potential, and thus drive on water absorption following a source to sink Ψ gradient is well documented (Liu et al., 2003; De Micco and Aronne, 2008). Similarly, it has been documented for a number of plant species that stomata do not close completely at night, allowing for nocturnal transpiration and thus preventing nocturnal soil-plant water potential equilibration (Kathleen et al., 2007). In view of these explanations, whether or not this mechanism influenced the pre-dawn water potential responses in studied species remains unresolved the trends shown in *C. pallida*, *L. frutescens* and *Z. fagara* in Figure 1 and opens a research line for this hypothesis. Under adequate soil water content, the contrasting diurnal pattern of changes in xylem water potential between pre-dawn and mid-day values observed in the studied shrub species could have been strongly influenced by the daily course of atmospheric evaporative demand components (air temperature, relative humidity and vapor pressure deficit) as previously reported (González et al., 2000). In this regard, it has been documented that a significant and negative relationship between water potential and air temperature and vapor pressure deficit was detected by Kolb and Stone (2000) in *Quercus gambelii* in Arizona, USA; González et al. (2000) in *Acacia berlandieri*; González et al. (2004) in *Havardia pallens*, *Acacia rigidula*, *Eysenhardtia texana*, *Diospyros texana*, *Randia rhagocarpa*, and *Bernardia myricaefolia*; and González et al. (2009) in *Bumelia celastrina*, *Condalia hookeri*, *Cordia boissieri*, and *Diospyros texana* growing in north-eastern Mexico. At mid-day, the differences detected among shrub species could be explained by the physiological differences among them, as the environmental conditions were the same. However, admittedly the root and stem hydraulic resistance, leaf stomatal conductance, number of the conducting elements, stomatal density, and the morphological and anatomical characteristics of leaves and stomata could have exerted important undetermined effects on the diurnal water relations of plant tissues in this study (Stienen et al., 1989; Castro-Díez et al., 2000; Busotti et al., 2002). Since plant adaptation to drought is the result of many different physiological and molecular mechanisms some woody plants are drought tolerant because they can either withstand extreme dehydration or avoid low leaf water potential, with the latter being more widely observed (Kozłowski



and Pallardy, 2002). In this regard, plants generally follow two main strategies, i.e. they tolerate the drought through phenological and physiological adjustments referred to as tolerance or avoidance of drought through dormancy (Evans et al., 1992). Both tolerance and avoidance mechanisms (Kozłowski and Pallardy, 2002) contribute to the ability of a plant to survive drought, but it also depends on the frequency and severity of the drought period. Thus, it could be recognized that shrub species were able to exploit soil moisture sources from deeper soil layers in order to maintain minimum water requirements for physiological or morphological adaptations (evidenced by leaf folding, abscission and retention) to avoid desiccation injury. In addition, results of this study show strong physiological evidence that even though the species decreased their xylem water potential during stress, they still play an important role in maintaining the productivity of dry woodlands ecosystems with limited water resource availability. Furthermore, studied shrub species suggest another line of research at the anatomical leaf tissue level which may include to identify the specific mechanism of the leaves of the drought tolerant species to avoid loss of transpiration by trichomes, leaf epicuticular wax, stomatal frequency, among other leaf traits.

4. Conclusion

The shrub species *A. rigidula*, *B. celastrina*, *C. texana* and *P. laevigata* achieved higher pre-dawn and mid-day Ψ values under water stress condition indicated that these species could be considered as drought adapted species while, *L. macropoda*, *K. humboldtiana* and *Z. fagara* which acquired lower water potentials, may not be suitable to drought and thus, may be in a physiological disadvantage under limited water conditions. The implications of this study suggest that the species respond differently to drought through the employment of different anatomical, biochemical, morphological and physiological strategies and there is scope for forest and range management practices in the selection of drought tolerant species for planting and reforestation of drought prone areas.

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