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Adaptation of Native Shrubs to Drought Stress in North-eastern Mexico

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Abstract

Native shrubs that grow in the semi-arid regions of north-eastern Mexico are important feed resources for range ruminants and white-tailed deer. They also provide high quality fuel-wood and timber for fencing and construction. Since water stress is the most limiting factor in this region, the present research focused on studying how seasonal xylem water potentials (Ψ) of native shrubs such as *Forestiera angustifolia* (Oleaceae), *Celtis pallida* (Ulmaceae), *Acacia amentacea* (Leguminosae) and *Parkinsonia texana* (Leguminosae) are related to soil water availability. During the wettest period, Ψ at pre-dawn ranged from -0.62 MPa (*A. amentacea* and *F. angustifolia*) to -1.10 MPa (*P. texana*). In contrast, during the driest period, pre-dawn Ψ varied from -1.78 MPa (*P. texana*) to -3.94 MPa (*C. pallida*). With respect to mid-day Ψ data, on the wettest sampling date, Ψ values ranged from -0.62 MPa (*A. amentacea*) to -1.57 MPa (*C. pallida*, *F. angustifolia* and *P. texana*). In contrast, on the driest sampling date, *C. pallida*, *A. amentacea* and *P. texana* tended to achieve higher (-2.21 MPa) Ψ than *F. angustifolia* which acquired Ψ value around -3.50 MPa. Since the shrub species *A. amentacea* and *P. texana* achieved higher pre-dawn and mid-day Ψ values under water stress condition, these species could be considered as drought adapted species while, *F. angustifolia* 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 recommends that the first two 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.

1. Introduction

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 throughout the year. Shrubs and trees growing in this region under adverse environmental conditions have to seasonally adjust their morpho-physiological traits to cope successfully with changes in soil water availability (Bucci et al., 2008). Plants differ widely in their capacity to cope with drought. Adaptations exist to explain these differences and these can be conveniently referenced to the capacity to maintain water status (water potential and/or relative water content, RWC). 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, which covers about 200,000 km^2 including southern Texas and north-eastern Mexico (Udvardy, 1975), is characterized by an average annual precipitation of 805 mm and a yearly potential evapo-transpiration of about 2,200 mm. Vegetation is utilized as forage for livestock and wildlife, fuel-wood, timber for construction, traditional medicine, fencing, charcoal, agroforestry and reforestation practices in disturbed sites (Reid et al., 1990). 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 species in this region provides an opportunity to investigate, from an ecophysiological perspective, the response of shrub species to changes in resource availability, in this case, soil moisture 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 and 2009) 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 (Y), and to estimate the relationship between plant water potentials with soil water availability in four native shrub species.

2. Materials and Methods

2.1. Research site

This study was carried out at ‘El Abuelo Ranch’ (25^{o}40’N, 99^{o}27’W; elevation 200 msl) in Los Ramones county, state of Nuevo Leon, Mexico in the year 2009. The climate is semi-arid with a warm summer. Annual mean air temperature and rainfall is about 22^{o}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 are shown in Table 1.

2.2. Plant material and water potential measurements

Five plants from each of the native shrub species *Forestiera angustifolia* Torr. (Oleaceae; evergreen shrub with stiff and dense branches), *Celtis pallida* Torr. (Ulmaceae; evergreen and spiny shrub with oval and smooth-edged leaves), *Acacia amentacea* Benth (Leguminosae; deciduous shrub with mycrophyllous compound leaves), and *Parkinsonia texana* (A. Gray) S. Watson var. *macra* (I. M. Johnst.) Isely (Leguminosae; small thorny deciduous tree with twice compound leaves) were randomly selected within a 20 x 20 m^{2} previously established (González et al., 2004) and undisturbed experimental thornscrub plot for xylem water potential (Y, MPa) determination. Since pre-dawn and mid-day Y measurements are influenced by environmental conditions, and the purpose was to detect changes in the plant water relation status, measurements were conducted, when possible, at 15-day interval between January 14 and September 29, 2009. The Y measurements were taken from terminal twigs at 6 am (pre-dawn, Ypd) and 2 pm (mid-day, Ymd) 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 10-25 s after collecting the samples. Pressure was applied to the chamber @ 0.05 MPa s^{-1}. For safety reasons and as per operating instructions, lowest limit of the pressure chamber was -7.3 MPa.

2.3. Environmental data

Air temperature (^{o}C) and relative humidity (%) were registered on a daily basis using a HOBO Pro Data Logger (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). 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, 10-20, 20-30, 30-40 and 40-50 cm, respectively using a soil sampling tube (Soil Moisture Equipment Corp). Gravimetric soil water content was determined by drying soil samples in an oven at 105^{o}C for 72 h, and was expressed on a dry weight basis (kg kg^{-1}).

2.4. Statistical analysis

To determine if differences exist among native shrub species in Ypd or Ymd at each sampling date, and soil water content at different soil depths, xylem water potential and soil water content data were subjected to one-way ANOVA. Normal distribution and homogeneity of variances for Ypd, Ymd and soil water content data were tested using the Kolmogorov-Smirnov, Shapiro-Wilk and Levene tests (Brown and Forsythe, 1974; Steel and Torrie, 1980) indicated that Ypd and Ymd data are not normally distributed. Since for most sampling dates, ANOVA did not show the assumption of equality of variances, Kruskal-Wallis non-parametric test was employed (Ott, 1993) to detect significant differences among native shrubs at each sampling date for both Ypd and Ymd. Hence, differences in Ypd and Ymd among shrubs were validated using the Mann-Whitney U non-parametric test with the Bonferroni’s correction method at p=0.05 (Wackerly et al., 2002). Differences among soil depth profiles for soil water content were validated using the Tukey’s 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

3.1. Environmental conditions during the experimental period

Seasonal trends of monthly maximum and minimum mean air temperature and relative humidity, and total rainfall are illustrated in Figure 1. During the experimental period, maximum mean air temperature increased from 23.79^{o}C (January) to 43.33^{o}C (July) then, decreased to 32.67^{o}C in September. Conversely, minimum mean air temperature varied between 8.54^{o}C (January) and 24.43^{o}C (July). With respect to relative humidity, maximum mean relative humidity values ranged from 92.5% (September) to 81.8% (July) whereas, mean minimum varied between 52.0% (September) and 23.7% (July). Cumulative monthly precipitation between January and August reached 46 mm while, in September 89.6 mm was registered. The total rainfall recorded at the research site during the study period was 135.5 mm (Figure 1). This amount was quite unusual, since May and June when historical rainfall peak occurs behaved relatively as dry months. Although at the research site, there are no conclusive studies related to global warming and long term tendencies, in this study, the significant prevailing harsh and dry conditions observed during most of the experimental period could be related to some extent to concurrent seasonal extreme environmental conditions such as drought, which are typical in the north-eastern region of Mexico (González et al., 2000, 2004 and 2009).

According to one-way ANOVA statistical analysis of the differences among soil layers in soil water content (Table 2), there were only differences ($p<0.05$) among soil layers in three (May 31, September 17 and 29) out of eighteen sampling dates. Gravimetric soil water content at 0-10, 10-20, 20-30, 30-40 and 40-50 cm soil depths are shown in Figure 2. Higher values (> 0.15 kg kg^{-1}; $p\leq0.05$; Figure 2) in soil water content at 0-10 cm depth with respect to layers ≤30 cm occurred on September 17 and 29, which coincides with a peak rainfall. Since most of the experimental period (January to August) remained quite dry, soil water content in the five soil depth profiles ranged between 0.15 and 0.05 kg kg^{-1} and, consequently, no significant differences soil layers were detected.

In general, and despite of the unusual rainfall registered during the experimental period, 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 in terms of both duration and intensity, and in environmental conditions (air temperature and relative humidity), soil water content could not be controlled and maintained and, therefore, low soil moisture availability may not be available for absorption by deeper roots due to low soil water infiltration, rapid run off, and high evapo-transpiration rates, which during the experimental period at the research site, calculated potential evapo-transpiration reached about 1,212 mm according to the Thornthwaite's method (Rosenberg et al., 1983). In addition, high mid-day vapor pressure deficits, which during the research period ranged from 0.75 kPa (January) to 4.95 kPa (July) (Rosenberg et al., 1983) could have contributed to low soil water content. The soil water content responses found in the present study are in agreement with previous studies (Anderson et al., 2001; Bussotti et al., 2002; Veneklaas and Poot, 2003; González et al., 2000, 2004 and 2009).

3.2. Seasonal variation in xylem water potential

Kruskal-Wallis test (Table 2) revealed in eight sampling dates, out of eighteen, significant ($p<0.05$) differences among shrub species in Ypd values. Seasonal trend in Ypd for the studied shrub species is shown in Figure 3(a). In general, data followed a similar pattern of variation among shrub species when values were higher than -1.5 MPa; meanwhile, this trend diverged among species, particularly in *C. pallida* and *F. angustifolia*, in which cases, observed Ypd values declined below -3.0 MPa. At the wettest sampling date (Sep-29), higher Ypd values (-0.62 MPa and -0.66 MPa) achieved in *A. amentacea* and *F. angustifolia*, respectively, were higher than -1.10 MPa measured in *P. texana*. Conversely, on the driest sampling date (Jul-31), when shrub species experienced a marked drought stress, higher Ypd values (-1.78 MPa and -2.34 MPa) were observed in *P. texana* and *A. amentacea*, respectively, while lower (-3.06 MPa and -3.94 MPa) Ypd values were determined in *F. angustifolia* and *C. pallida*, respectively which suggested that the last two species are more susceptible to water deficits [Figure 3(a)]. The onset responsive recovery of Ypd values in four shrub species for sampling dates May-16, May-31, Jun-30, Aug-30 through Sep-29 are related mainly to precipitation events.

Trends in Ymd for the studied species are illustrated in Figure 3(b). Significant differences ($p<0.05$) were detected among shrub species in six sampling dates (Jan-29, Feb-15, Mar-02, May-31, Sep-17 and Sep-29). However, no significant differences were observed in the remaining twelve sampling dates. On the wettest sampling date, when Ymd was the highest (Sep-29) and when soil water content at the soil layer between 0-30 cm was higher than 0.15 kg kg^{-1}, Ymd values ranged from -0.62 MPa (*A. amentacea*) to -1.57 MPa (*C. pallida*, *F. angustifolia* and *P. texana*). In contrast, on the driest sampling date (Jul-31), when soil water content was below 0.10 kg kg^{-1}, *C. pallida*, *A. amentacea* and *P. texana* tended to achieve higher (-2.21 MPa) Ymd than *F. angustifolia* which acquired Ymd values around -3.50 MPa [Figure (3b)]. However, no significant differences were observed between them. Clearly, among the species under study, *P. texana* and *A. amentacea* may be the examples of shrub species which have adapted to low soil water availability since they tended to maintain high tissue hydration, while the adaptation of *C. pallida* and *F. angustifolia* to dry environment seems to depend on strategies which allow them to cope with internal desiccation and consequently show lower water potential values.

In some sampling dates, such as Apr-30, Jun-15, Jul-14 and Jul-31, an unusual Y response is shown in Figure 3(b), particularly in shrub species *C. pallida* and *F. angustifolia*, which suggests that Y 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) documented a disequilibrium between pre-dawn soil and plant tissue (leaf and xylem) Y in diverse mesophytes and xerophytes due to apoplastic solute build up. They concluded that pre-dawn leaf Ø and xylem Ø 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 Y gradient is well documented (Liu et al., 2003; De Micco and Aronne, 2008).

Under adequate soil water content (^{3}0.15 kg kg^{-1}), the contrasting diurnal pattern of changes in Y between pre-dawn and mid-day values observed on Sep-17 and Sep-19 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). In fact, on Sep-17 pre-dawn and mid-day vapor pressure deficits were 0.211 and 2.397 kPa, respectively, while on Sep-29 were 0.182 and 1.635 kPa, respectively. In this regard, a significant and negative relationship among Y 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*, *Eysenhartia 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. This cause-effect relationship suggests that under high soil moisture availability, the shrub species studied showed maximum Y values at pre-dawn and a minimum at mid-day, followed by a subsequent recovery in Y over night mainly due to low evaporative demand. If it is assumed that at pre-dawn (6 am) Y values represent a true equilibrium (close enough) with soil water potential (not determined in this study), the differences detected at this sampling hour between shrub species under high soil water content registered on Sep-17 and Sep-29 [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. However, it has been documented that some shrub species such as *Chrysothamnus nauseosus* and *Sarcobatus vermiculatus* have exhibited pre-dawn disequilibrium. This phenomenon has been associated to nocturnal transpiration and putative leaf apoplastic solutes (Donovan et al., 2003). Whether or not this mechanism influenced the pre-dawn water potential responses in studied species remains unexplained. At mid-day, the differences detected among shrub species [Figure 3(b)] 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; Bussotti et al., 2002).

On a seasonal basis, the gradual decrease in Ypd [Figure 3(a)] and Ymd [Figure 3(b)] for the four shrub species showed a considerable response to precipitation trends. Similar findings were reported by Montagu and Woo (1999), who determined the soil water availability pattern, with lower Ypd or Ymd (≤3.0 MPa) values occurring when soil water content reached values below 0.10 kg kg^{-1}; however, both Ypd and Ymd recovered after the onset in rainfall. Among the species under study, *C. pallida* or *F. angustifolia* would be at a physiological disadvantage as compared to *A. amentacea* or *P. texana*, since the former two showed a significantly steeper decrease in both water potential parameters with respect to the latter ones, as shown on sampling dates carried out on Jul-14 and Jul-31 shown in Figure 3(a). Furthermore, *P. texana* is the only species which, under drought stress tends to reach and maintain a higher water potential (desiccation avoidance response) than *C. pallida* or *F. angustifolia*, since both Ypd and Ymd measurements decrease earlier. This response may be viewed as a mechanism to conserve water and thus avoid tissue dehydration (Veneklaas and Poot, 2003; Otieno et al., 2006).

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 of protoplasm (low RWC) or avoid low leaf water potential, with the latter being more widely observed (Kozlowski 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 (Kozlowski 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 as illustrated in the present study. 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 produce strong physiological evidence that even though the four species decreased their water potential during stress, they still play an important role in maintaining the productivity of dry woodlands ecosystems with limited water resource availability. Thus, the mode of adaptation of studied species to xeric conditions are controlled to some extent by maintenance of high water potential, although not measured but low transpiration, a deep root system, accumulation of passive and active organic solutes, leaf cuticular thickness, and morphological and anatomical stomata features.

4. Conclusion

The shrub species *Acacia amentacea* and *Parkinsonia texana* achieved higher pre-dawn and mid-day Y values under water stress condition indicated that these species could be considered as drought adapted species while, *Forestiera angustifolia* and *Celtis pallida* which acquired lower water potentials, may not be suitable to drought and thus, may be in a physiological disadvantage under limited water conditions.

5. Further Research

Detailed research studies on leaf tissue water relations should be focused at the anatomical, biophysical, biochemical, and molecular level in order to understand the physiological mechanisms employed by studied species to cope with drought stress.

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Table 1: Some physical and chemical properties of the soil at experimental plot

Soil profile depth (cm)	Bulk density (Mg m^{-3})	Sand	Silt	Clay	Water retention (kg kg^{-1})		pH	EC (µS cm^{-1})	Organic Matter (%)
			(g kg^{-1})		-0.03 (MPa)	-1.2 (MPa)			
0-20	1.27	425	350	225	0.253	0.148	7.72	86.23	1.88
20-40	1.29	521	255	224	0.252	0.146	7.85	80.53	2.13

Table 2: *F* and *p* values of the one-way ANOVA results for soil water content, and χ^2 and *p* values of the Kruskal-Wallis test for pre-dawn (Ψpd) and mid-day (Ψmd) xylem water potential to detect significant differences among soil depth profiles and shrubs species, respectively at each sampling date

Sampling date	Soil water content		Ψpd		Ψmd	
	F-value	*p*-value	χ^2	*p*-value	χ^2	*p*-value
Jan-14	1.177	0.363	6.87	0.076	5.79	0.122
Jan-29	0.643	0.640	5.44	0.142	13.60	0.003*
Feb-15	0.558	0.696	3.51	0.319	7.55	0.056*
Mar-02	1.149	0.372	3.94	0.268	9.98	0.019*
Mar-15	1.206	0.349	8.43	0.038*	0.34	0.952
Mar-29	0.536	0.711	5.42	0.143	3.01	0.390
Apr-17	1.974	0.150	4.94	0.176	1.62	0.656
Apr-30	1.242	0.338	8.24	0.041*	2.38	0.498
May-16	0.531	0.715	4.22	0.239	1.50	0.683
May-31	3.131	0.043*	3.27	0.352	8.29	0.040*
Jun-15	1.234	0.338	4.14	0.247	3.80	0.284
Jun-30	1.940	0.156	3.83	0.280	1.63	0.652
Jul-14	0.276	0.889	10.75	0.013*	0.68	0.879
Jul-31	0.306	0.869	8.46	0.037*	4.50	0.213
Aug-15	2.692	0.071	9.77	0.021*	4.47	0.215
Aug-30	1.778	0.186	11.38	0.010*	7.66	0.054
Sep-17	6.816	0.002*	12.89	0.005*	10.16	0.017*
Sep-29	3.495	0.033*	11.99	0.007*	11.77	0.008*

*Statistically significant probabilities ($p \leq 0.05$)

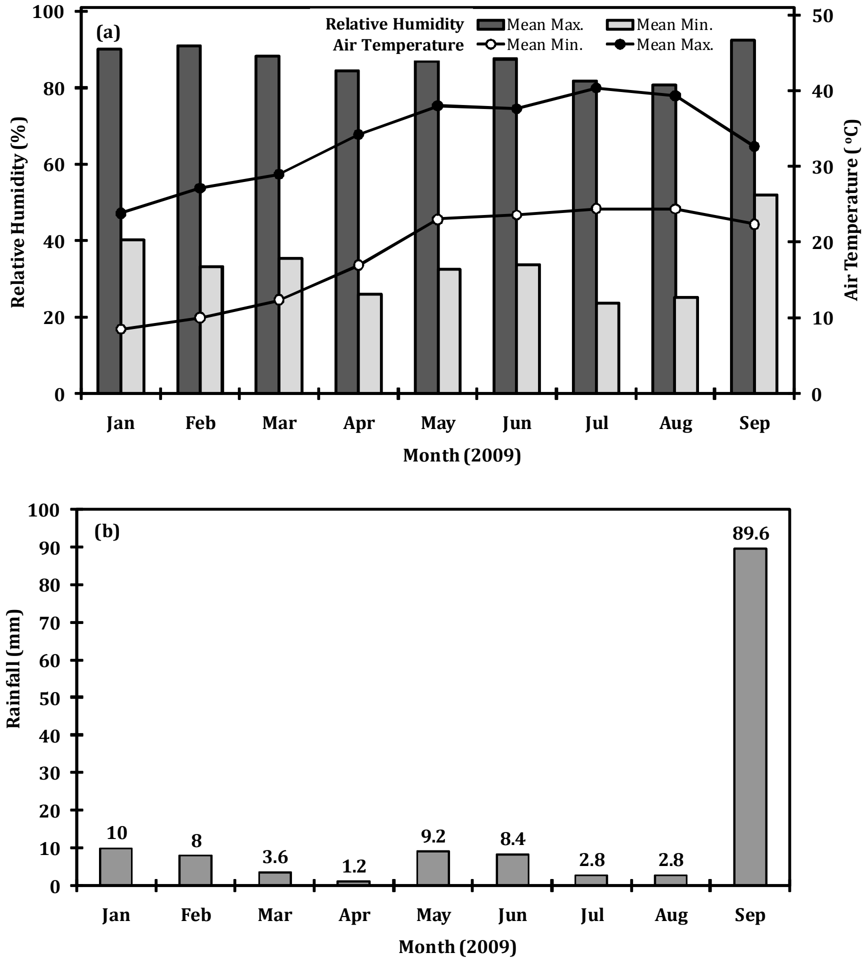

Figure 1: Monthly maximum and minimum mean air temperature and relative humidity (a), and monthly rainfall (b) during the study period at the research site. Monthly rainfall values are shown above respective bars

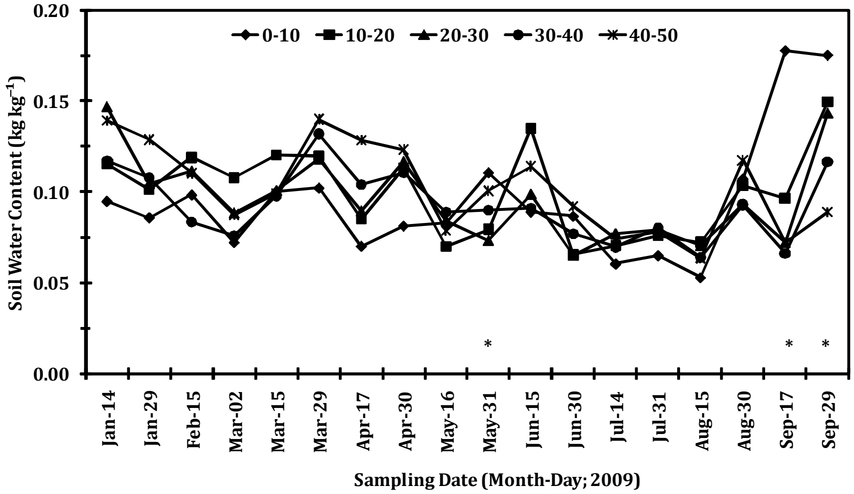

Figure 2: Seasonal variation in gravimetric soil water content at five soil profile depths (cm) at the research site. For a given sampling date, statistically significant probabilities ($p \leq 0.05$) according to one-way ANOVA are shown in asterisk (*)

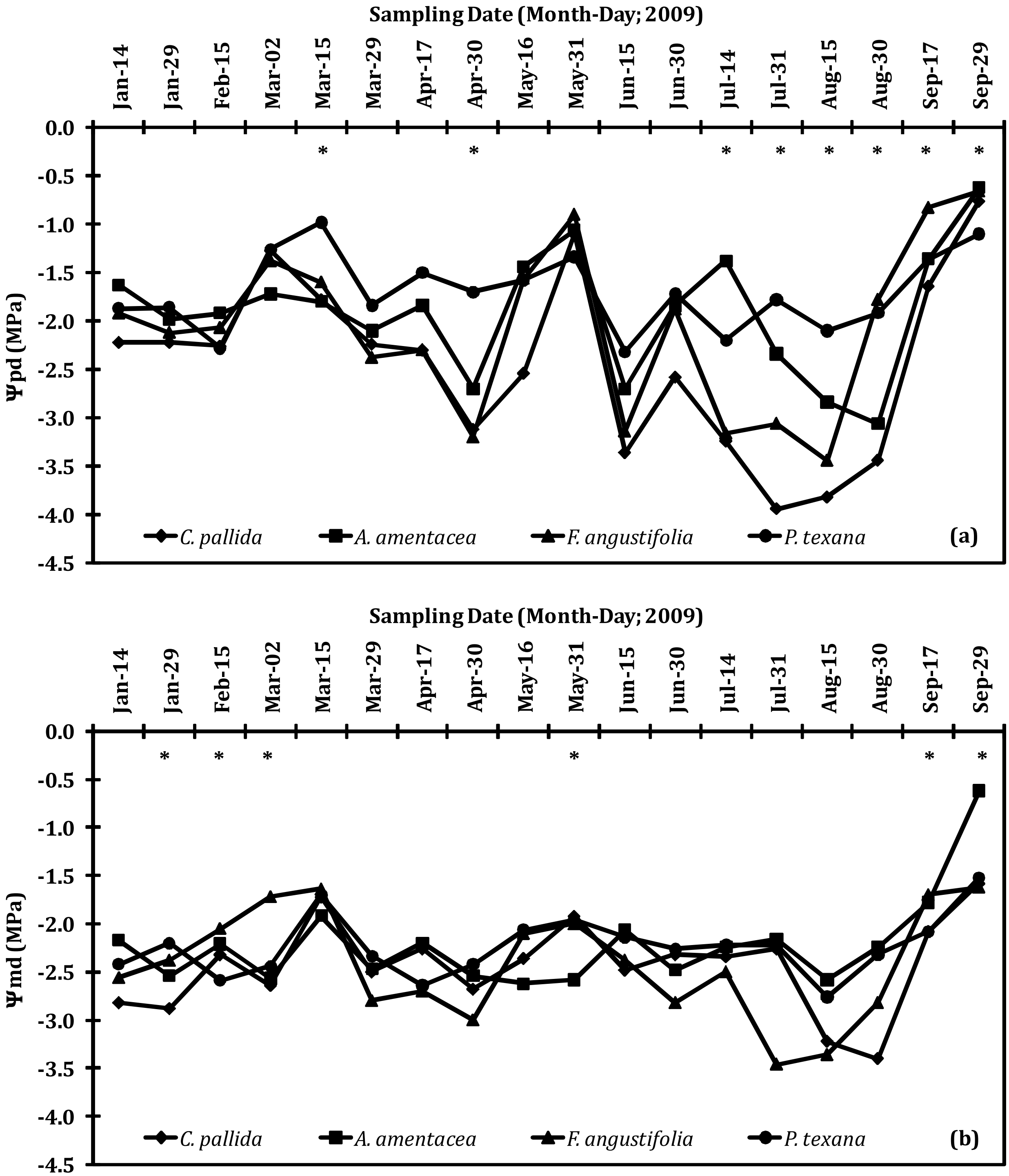

Figure 3: Seasonal variation in pre-dawn (a) and mid-day (b) xylem water potential in four shrub species. For a given sampling date, statistically significant probabilities ($p \leq 0.05$) according to the Kruskal-Wallis test are shown in asterisk (*)