Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert, Mexico

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Soil water use by shrubs and grasses of vegetation patches (vegetation arcs) occurring in two-phase mosaics of the Southern Chihuahuan Desert (Mexico) was investigated after an experimental irrigation equivalent to a 75 mm rainfall. Three shrubs (*Flourensia cernua*, *Larrea tridentata* and *Prosopis glandulosa*) and one grass (*Hilaria mutica*) were studied.

Irrigation water did not percolate deeper than 40 cm. This soil layer contained more than 75% of the roots in all species, except *P. glandulosa* where a less developed, deeper root system was detected (but not quantified).

Root distribution indicates that the water stored in the 0–40-cm soil layer after the experimental irrigation was available for the four species. However, predawn xylem water potential (XWP) of *F. cernua* and *H. mutica* were strongly influenced by soil water present in the 0–40-cm layer, whereas those of *L. tridentata* and *P. glandulosa* were not. Differences in predawn XWP between watered and unwatered individuals were greatest in *F. cernua* and *H. mutica*, and smallest in *P. glandulosa*. Changes in tissue osmotic potential (TOP) values as a consequence of watering were sharply marked in all species except *P. glandulosa*. *H. mutica* XWP approached zero for a few days in response to small rain events.

The results indicate that adult individuals of grasses and shrubs are potential competitors for soil resources (to a variable degree according to the shrub species). Their co-existence in the arcs is probably favoured by a process of slow competitive displacement as long as the recruitment of new shrubs takes place mainly by colonization of the upslope fringe of the arcs where grass biomass is low. As development of the vegetation progresses in the colonization front and the grass canopy is almost closed, the chances of a shrub being suppressed by water competition diminishes in the following order: *F. cernua*, *L. tridentata*, *P. glandulosa*. A drastic reduction in grass biomass because of grazing would depress the competitive ability of the grasses and may preferentially facilitate the establishment of livestock dispersed species like *P. glandulosa*. A consequent shift to a more shrubby community seems unavoidable since the recovery of the grass strata will probably not suppress the newly-established shrubs tapping water from deep water sources.

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Introduction

Environmental conditions allowing the co-existence of shrubs and grasses in ecosystems with prolonged dry seasons have been the subject of several studies (e.g. Sarmiento, 1984; Knoop & Walker, 1985; Goldstein & Sarmiento, 1987; Archer *et al.*, 1988). Most of them have been conducted in savanna-like plant formations with rainfall generally above 400 mm showing various patterns of woody species distribution (from highly clumped to homogeneously open) and a more homogeneous herbaceous cover. Walter (1971) (see also Walker *et al.*, 1981) proposed a vertical partitioning of soil resources between grasses and woody species (the two-layer hypothesis) for explaining the co-existence of both life-forms in savannas.

Arid zones may also have mixed grass–woody plant formations in two-phase mosaics (see Fig. 1) consisting of dense patches (vegetation arcs) made up of shrubs and grasses, surrounded by almost bare areas vegetated only by scattered shrubs or succulents (e.g. Greig-Smith, 1979; Tongway & Ludwig, 1990; Montaña *et al.*, 1990; Mauchamp *et al.*, 1993). In two-phase mosaics of the Southern Chihuahuan Desert, the vegetation structure inside the arcs suggest a successional sequence of establishment and senescence of woody species related to differential water supply by sheet-flow (Montaña *et al.*, 1990; Montaña, 1992). The following points are suggested by previous works in this vegetation type: (a) it functions as a mosaic (Fig. 1) where water collected in almost bare areas is consumed in the vegetation arcs. As a consequence of water redistribution by sheet flow, the infiltration of water in the arcs is between 1·5 and 5·3 times the local rainfall (Hemming, 1965; Cornet *et al.*, 1992); (b) sheet water flow favours the existence of an upslope colonization front in the arcs (Montaña, 1992); (c) with no overgrazing, woody species are recruited mainly in the upslope colonization front (Montaña *et al.*, 1990; Mauchamp *et al.*, 1993).

Fire can be disregarded as a factor influencing the equilibrium between grasses and shrubs in the vegetation arcs since it has never been used as a management tool and there is no record of fire in the region. The patchy distribution of the fuel biomass
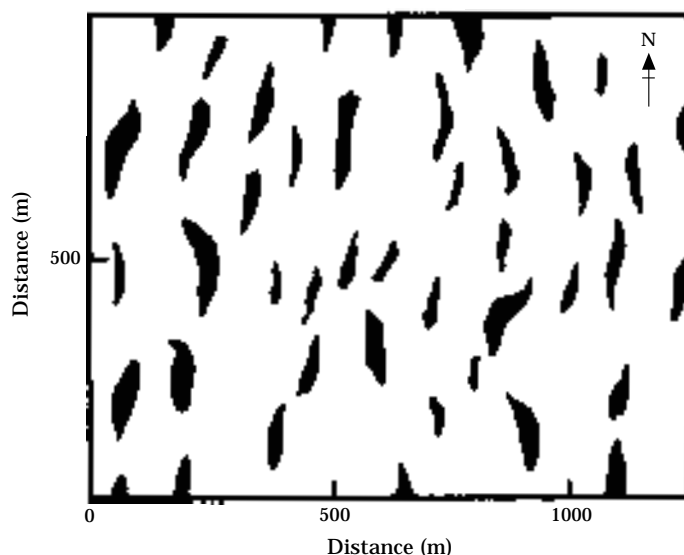
Figure 1. Aerial view at 1:25,000 scale of two-phase mosaics found in the Bolson of Mapimi, Southern Chihuahuan Desert, Mexico. The gently slope (less than 0·6°) descends from east to west. As a consequence of the redistribution of rain water by sheet flow, one element of the mosaic (the vegetation arc, in black) consumes the water collected in the bare area.

suggests that natural fires may be restricted to the vegetation arcs where they start. Consequently, soil–water, herbivory and plant-to-plant interactions should be the most important factors that influence the equilibrium between grasses and shrubs in this system.

In this paper, the water relations of a grass and several co-existing woody species were investigated. Partitioning of soil moisture was examined as well as root distribution. An experimental approach was implemented by irrigating the soil and monitoring ecophysiological parameters in watered and unwatered individuals. The specific objectives were (a) to compare the vertical distribution of roots of co-existing species, (b) to compare the xylem water potential (XWP) and tissue osmotic potential (TOP) values through the cycle of wetting/drying of the soil profile and (c) to measure differences in growth during that period.

Methods

Study area

Field work was carried out in the Mapimi Biosphere Reserve in the Southern Chihuahuan Desert, Durango state, Mexico (26° 40' N, 103° 40' W, 1100 m. a.s.l., 264 mm yearly average rainfall, 80·2% between June and October, 20·8° C mean temperature). The vegetation of the area was described by Montaña (1990). The two-phase mosaic structure occupies 32% of the 172,000 ha studied by Montaña (1990). Structure and floristic composition vary in accordance with the community type. The most common woody species inside the arcs are *Prosopis glandulosa* Torr. var. *torreyana* (Benson) M. Johnston (Leguminosae) and *Flourensia cernua* DC. (Compositae). The most frequent grass is *Hilaria mutica* (Buckley) Benth.

The soil of the study site was described by Breimer (1985) as an haplic Yermosol (FAO/UNESCO, 1976) with sandy-clay-loam texture (24% clay, 26% silt) from 0 to 15 cm, to clay-loam (30–36% clay, 22–26% silt) from 15 to 70 cm. Below 70 cm an altered siltstone to claystone bedrock is found.

Woody species studied were *F. cernua* (a fall-flowering shrub), *Larrea tridentata* (Sesse & Mociño ex DC.) Cov. (Zygophyllaceae), a shrub whose flowering depends on water availability, and *P. glandulosa* var. *torreyana* (a spring-flowering shrub), whereas the grass species was *H. mutica* (whose flowering depends on water availability). Cover in the central position of seven randomly selected vegetation arcs was 8·8% for *F. cernua*, 0·5% for *L. tridentata*, 7·7% for *P. glandulosa* and 78·4% for *H. mutica*. Cover was measured by the line interception method (Canfield, 1941) along a 50-m line in each arc.

Watering

Watering was done using circular plots centred on randomly selected individuals in the case of woody species, and on randomly selected points in the case of *H. mutica*. For this purpose six individuals of each woody species and six points were randomly selected in the central position of a vegetation arc. Watering and non-watering treatments were then randomly assigned to half of the individuals and points. The plots used for the watering treatment were delimited by metallic sheets 60 cm in height buried 30 cm in the soil. The metallic sheets were installed a few hours before the watering and removed 2 days later. Plots were 11 m^2 in area for shrubs and 5 m^2 for grasses. All above-ground biomass not pertaining to *H. mutica* was removed from the grass-plots and all the biomass not pertaining to the individual to be measured was eliminated from the shrub-plots. The volume of water required to add 75 mm of

rainfall to the plots was calculated and then the watering-treatment plots were flooded with this volume. Watering was done only once at the start of the experiment in the evening of the same day.

Watering was done in mid-October of a relatively dry year (winter, 3 mm; spring, 9·1 mm; summer, 103·2 mm). Rainfall events 60 days before irrigation were: 28·7 mm in several rains during the last 15 days of August, 37·5 mm on 10 September, 15·8 and 10·5 mm on 7 and 9 October, respectively. During the experiment natural rains were 0·3 mm on 24 October and 1·5 mm on 6 November.

The date of the experiment was decided on in order to manage the quantities of water in the treatments better. By mid-October the probabilities of natural rains are low and temperatures are still adequate for plant growth (mean temperature in October 20·6°C). Unpublished phenological observations showed that all studied species have growth responses to rain events by that time of the year.

Plant and soil measurements

Vertical root distribution was quantified using the trench wall method (Böhm, 1979) in plants different from those used for water potential measurements. Three individuals of each woody species were randomly selected in the central position of the vegetation arc. The plants were unwatered and no manipulation of the above-ground biomass was made before the root measurements. Root counts were made over a 70 cm-deep and 70 cm-wide soil profile for each woody plant using a 5 cm $\times$ 5 cm grid. The vertical wall was located 10 cm from the base of each plant and was cut smooth. Five millimetres of soil was then removed by very gently spraying water. The number of woody and herbaceous roots protruding from the wall in each grid square was counted. The only herbaceous species present around the pits was *H. mutica* and no woody plant other than the sampled shrub was present in a 5-m radius of each pit.

Plant growth was measured as elongation of terminal twigs in woody species and green biomass produced in grasses. Ten twigs that were growing during the previous summer were randomly selected from each one of the watered and unwatered shrubs and their length was measured at the beginning and at the end of the experiment. The green biomass contained in three randomly selected plots 200 cm^{-2} in area was clipped in each *H. mutica* plot and oven-dried to measure dry mass.

Soil water potential (SWP) of soil samples was measured in sample chambers (Wescor model C-52) connected to a Dew Point Microvoltmeter (Wescor model HR-33T). Samples were obtained with auger buckets 5 cm in diameter at each measurement date (one sample per irrigated plot at 10 cm, 20 cm and 40 cm) and placed in the chambers for measurement. Samples from below 40 cm in the irrigated plots, as well as from any depth in non-irrigated plots were too dry (less than –8·5 MPa) to be accurately measured with the technique employed.

Predawn and midday xylem water potentials (XWP) were measured with a pressure chamber (PMS model 600) (Schollander *et al.*, 1965) every 4 days during the 32 day period following the irrigation in the watered and unwatered plants. After XWP determinations leaves of the twigs used for these determinations were collected and frozen in liquid nitrogen. The cellular liquid was extracted in the laboratory by mechanical compression of the leaves (Koide *et al.*, 1989). Water potential (TOP) of this liquid was measured in a sample chamber (Wescor model C-52) connected to a Dew Point Microvoltmeter (Wescor model HR-33T). Data were used for comparisons between species, watering treatments and dates. No attempt to relate TOP with XWP or turgor pressure was made, owing to the dilution of symplasmic water with apoplasmic water produced by this method.

Statistical analyses

All data analyses were done using the BMDP (Dixon *et al.*, 1988) statistical package. A repeated measures ANOVA (ANOVAR, Potvin *et al.*, 1990; Winer *et al.*, 1991) model was used to analyse the root distribution in the soil profiles. A grouping factor with three states (each one including the profiles measured below each one of the three woody species) and two trial factors: (a) category (woody and grass roots), and (b) depth (each 10 cm from the surface up to 70 cm) were used.

A preliminary nested analysis of the growth of the woody species showed that there was no difference between the growth of twigs within individuals. Consequently, the average growth of the 10 twigs of each individual was used with a two-way ANOVA whose main factors were species and watering regimes.

SWP was analysed with a ANOVAR model considering species as a grouping factor and date and depth as trial factors. XWP and TOP were analysed with the same model but declaring species and watering regimes as grouping factors and date as a trial factor.

Single regressions of XWP on SWP at different depths were performed for each species. A first trial using stepwise multiple regression of XWP on the SWP of the different depths showed a marked instability of the regression coefficients due to the obvious intercorrelation (Zar, 1984) between the SWP of the different soil layers.

Results

Root distribution

The vertical distribution of roots between the surface and 70 cm depth is shown in Fig. 2. The ANOVAR showed that there was a significant difference ($p = 0.004$) between the profiles measured below each woody species, between the woody and grass root categories ($p = 0.016$), and between depths ($p < 0.0001$). Root density was highest near the surface and rapidly diminished, but grass roots decreased faster than woody roots as indicated by a significant interaction ($p = 0.0003$) between category and depth. There were no significant interactions in the vertical distribution and in the relative proportion of woody and grass roots found below the different woody species ($p > 0.4$).

There was a slight increase in *P. glandulosa* root density at the 70 cm depth and there appeared to be an even higher density below the 1-m depth, however, this was not quantified.

Plant growth

All species showed normal phenological responses to the watering. Besides vegetative growth, *H. mutica* and *L. tridentata* produced flowers and fruits, *F. cernua* showed its normal fall flower production, and *P. glandulosa*, whose reproductive period is in spring, did not produce flowers.

In woody species, shoot elongation was different between species ($p = 0.0004$) and between watering regimes ($p = 0.05$), (see Fig. 3). *H. mutica* green biomass production was 4.73 ± 0.64 ($x \pm$ standard error) g.m.$^{-2}$ day^{-1} for the watered individuals whereas the unwatered individuals showed no green biomass production during the same 32-day period.

Soil and plant water potentials

The time courses of SWP and midday XWP values are shown in Fig. 4. The ANOVAR of SWP values revealed a significant difference ($p < 0.001$) between dates and between depths but not between the four species studied ($p = 0.098$). Differences between depths appeared sooner in *H. mutica* than in the woody species and, except for *F. cernua*, the 0–20 cm soil layer dried at a different rate than the 20–40 cm soil layer.

Towards the end of the experiment soil water content was more variable in the
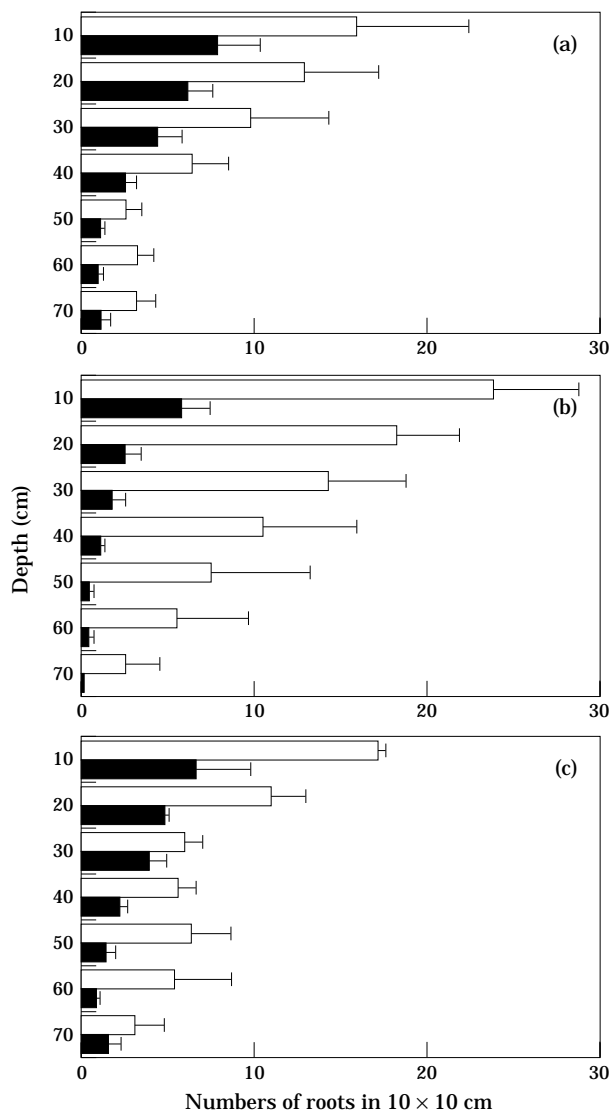
Figure 2. Vertical distribution of roots of plants found in the Chihuahuan Desert. Mean ± 1S.E. of the number of roots in 10 × 10 cm squares are shown. The results obtained in profiles dug at 10 cm from the base of (a) *Flourensia cernua*, (b) *Larrea tridentata* and (c) *Prosopis glandulosa* var. *torreyana* individuals are shown. (□) numbers of roots of grasses (always *Hilaria mutica*); (■) numbers of roots of shrubs.
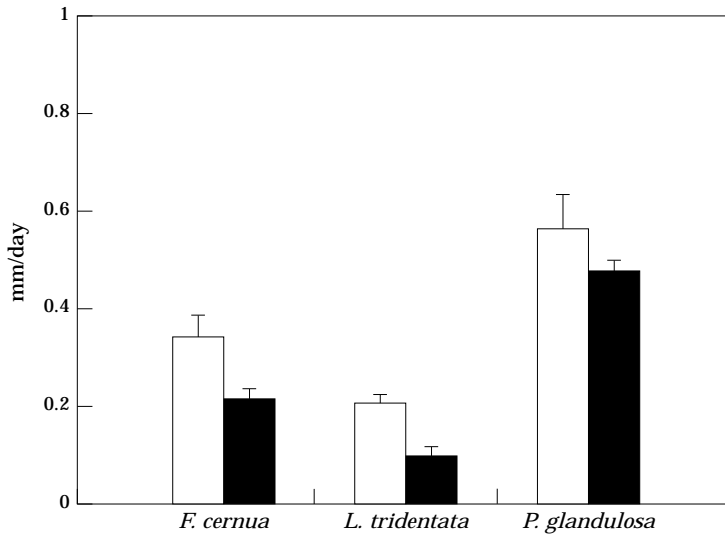
Figure 3. Elongation of terminal twigs of three woody species from the Chihuahuan Desert. The mean growth (± 1S.E.) of watered (□) and unwatered (■) individuals of *Flourensia cernua, Larrea tridentata*, and *Prosopis glandulosa* var. *torreyana* are shown.

20–40 cm soil layer than in the 0–20 cm soil layer. Ranges of SWP on the final data were –2·8 to –4·6 MPa and –4·5 to –5·2 MPa for the 20–40 and 0–20 soil layer respectively.

Figure 4 also shows that for days 16–24 there was a difference between SWP and midday XWP allowing the extraction of soil water from 0–40 cm depth by plants during part of the day. Midday XWP of *P. glandulosa* did not change over the period studied, which suggests dependence on a deeper water source.

Despite the lack of information about SWP below 40 cm, the correlation between the available SWPs and the predawn XWP of the species was assessed and the results are shown in Table 1. XWP of *F. cernua* and *H. mutica* were correlated with SWP whereas those of *L. tridentata* and *P. glandulosa* were not. These results suggest that the predawn XWP of *F. cernua* and *H. mutica* were strongly influenced by the soil water present between 0 cm and 40 cm, whereas those of *L. tridentata* and *P. glandulosa* were more influenced by the soil water status in deeper soil layers.

Figure 5 shows the time course for mean values of predawn XWP for the watered and unwatered treatments of the four species. The ANOVAR revealed significant differences ($p < 0.001$) between species, between watered and unwatered treatments and between dates. *F. cernua* and *H. mutica* showed the greatest difference between watered and unwatered treatments, while *P. glandulosa* showed the smallest.

Before the irrigation XWP of *P. glandulosa* was approximately 1·5 MPa higher than the XWP of the other three species. This probably reflects the use of a deeper water source by *P. glandulosa* as did the relative failure to react to irrigation. At the end of the experiment the XWP levels were nearly the same as before irrigation for *F. cernua, H. mutica* and *L. tridentata*, so it can be assumed that all the irrigated water had been consumed by that time.

None of the woody species attained a XWP higher than –1·0 MPa whereas XWP of *H. mutica* was approximately –0·5 MPa immediately after irrigation and again on 6 November after a rain of 1·5 mm occurred (day 24, Fig. 5). Also, the XWP of unwatered individuals was near –1·0 MPa on that occasion suggesting the importance of small rain events.

Changes in TOP values as a consequence of watering were sharply marked in all

species, except *Prosopis* (Fig. 6). This is additional evidence that *Prosopis* was probably using a deep soil water source, not water from the 0–40 cm depth. The ANOVAR revealed significant differences ($p < 0.001$) between species, watering treatments and dates. The drop of TOP values after irrigation seemed to be more pronounced in *Hilaria mutica*, although it was partially masked by a small rain. In *Flourensia* and *Larrea* it seemed that the effect of irrigation lasts longer than in *Hilaria*.

Discussion

Water use by plants

Irrigated water did not percolate deeper than 40 cm. This soil layer contained more than 75% of the roots in all species, except *P. glandulosa* where a considerably less developed, deeper root system was detected but not quantified. Heitschmidt *et al.* (1988) also found roots of *P. glandulosa* var. *glandulosa* below 70 cm depth. In 2-m deep excavations around adult individuals of this species growing under field conditions they found that about 40% of the roots where below 67 cm depth.

Predawn XWP of *H. mutica* and *F. cernua* showed the greatest change in magnitude after irrigation, whereas *P. glandulosa* showed the smallest and *L. tridentata* was intermediate and had the most delayed response. Ansley *et al.* (1992) found similar results for *P. glandulosa* var. *glandulosa* after an irrigation of 38·2 mm. The small response of *P. glandulosa* agrees with the results of Brown & Archer (1990) regarding
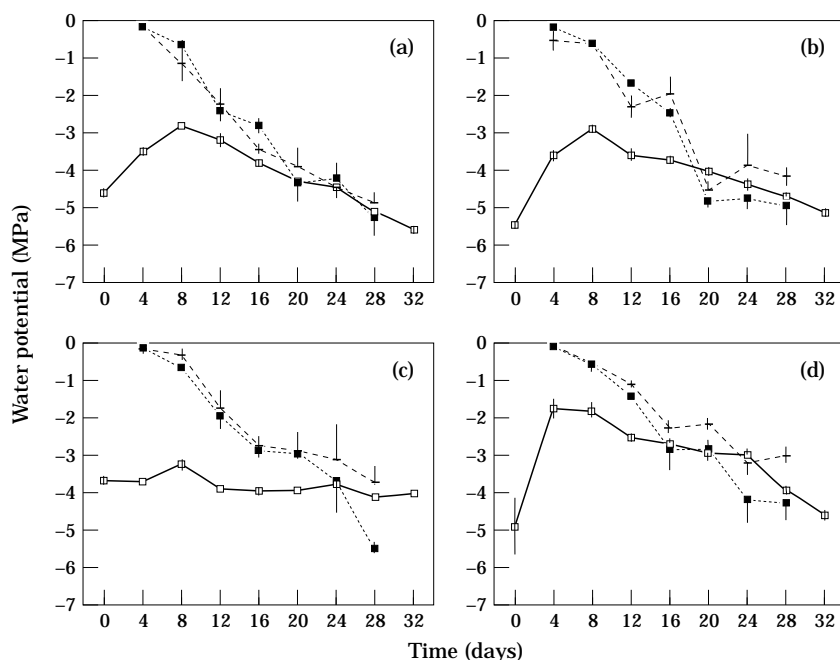
Figure 4. Water potentials of plants and soils in a arid ecosystem of the Chihuahuan Desert. The time course of the midday xylem water potential (mean ± 1S.E.) of plants and the soil water potential (mean ± 1S.E.) of the stands they vegetated are shown. (a) *Flourensia cernua*, (b) *Larrea tridentata*, (c) *Prosopis glandulosa* var. *torreyana* and (d) *Hilaria mutica* –□– = midday xylem water potential of plants that received a 75 mm irrigation after the reading of day zero. –■– = soil water potential of the 0–20 cm soil layer. –+– = soil water potential of the 20–40 cm soil layer.

Table 1. *Regressions of XWP of four species from an arid ecosystem of the Chihuahuan Desert on the SWP registered at different soil depths after a watering experiment. The values of SWP of the 0–40 cm depth were calculated as the average of SWP measured at the three depths as in Fonteyn* et al. *(1987). All regression slopes (ß) were significantly different from zero (0·01 < p <0·05) for* Flourensia cernua *and* Hilaria mutica *regressions whereas they were not significant (0·1 < p <0·6) for* Larrea tridentata *and* Prosopis glandulosa.

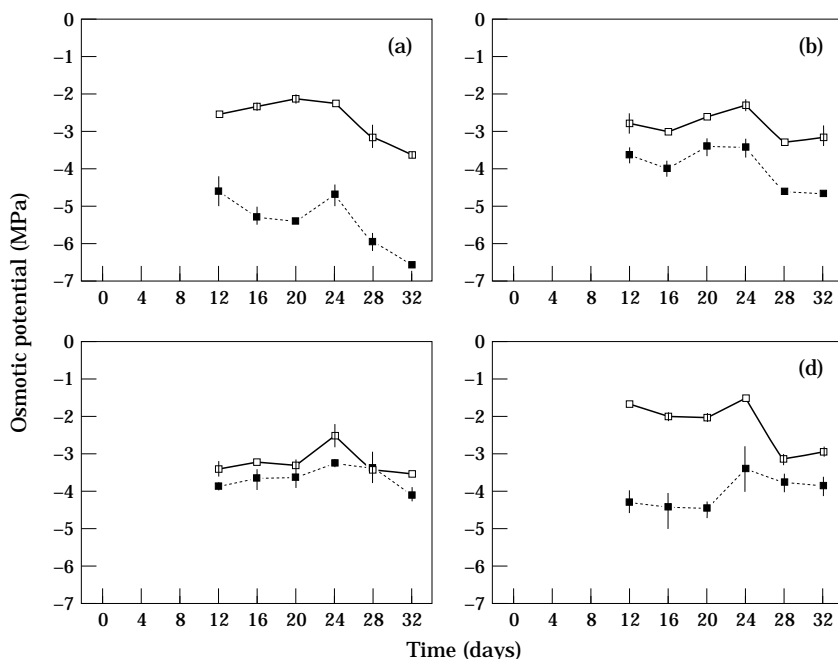| Soil depth (cm)	*Flourensia cernua*		*Larrea tridentata*		*Prosopis glandulosa*		*Hilaria mutica*	
	R^2	ß	R^2	ß	R^2	ß	R^2	ß
0–10	0·85	0·55	0·38	0·31	0·18	0·10	0·92	0·69
10–20	0·86	0·67	0·75	0·54	0·25	0·20	0·79	1·04
20–40	0·82	1·12	0·51	0·41	0·23	0·25	0·91	1·20
0–40	0·93	0·79	0·54	0·42	0·21	0·16	0·91	0·96

the relative independence of adult individuals of this species from the soil water of the upper soil layers.

Adjustments of midday XWP was rapid in *H. mutica* but delayed in *F. cernua* and *L. tridentata*, and almost unnoticeable in *P. glandulosa*.

As opposed to the shrubs, *H. mutica* has the ability of reaching near zero XWP in response to small rain events, which are frequent in the area (59% of the number of
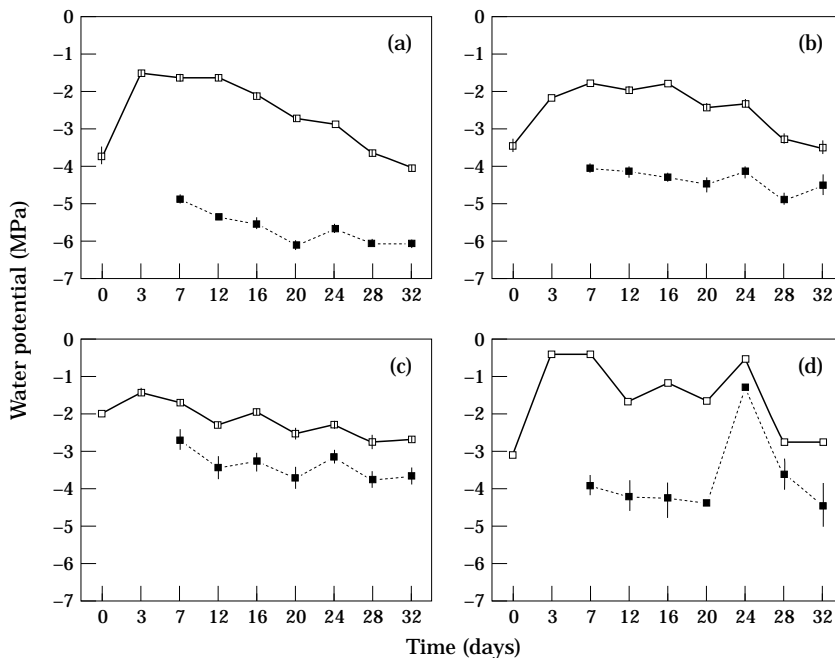
Figure 5. Time course of predawn xylem water potential (mean ± 1S.E.) of watered and unwatered plants from the Chihuahuan Desert. –□– = received a 75 mm irrigation after the initial measurement. –■– unwatered plants. (a) *Flourensia cernua*, (b) *Larrea tridentata*, (c) *Prosopis glandulosa* var. *torreyana*, (d) *Hilaria mutica*.

Figure 6. Time course of the tissue osmotic potential (mean ± 1S.E.) of watered and unwatered plants from the Chihuahuan Desert. –□– = received a 75 mm irrigation. –■– = unwatered plants. (a) *Flourensia cernua*, (b) *Larrea tridentata*, (c) *Prosopis glandulosa* var. *torreyana*, (d) *Hilaria mutica*.

rains and 17% of the total rainfall was produced in events of 5 mm or less over a 28 years period) and may play an important role for the maintenance of the grass (Sala & Lauenroth, 1982).

Predawn XWP of *F. cernua* and *H. mutica* were strongly influenced by soil water present in the 0–40 cm layer, whereas those of *L. tridentata* and *P. glandulosa* were not.

Out of the three shrubs studied *F. cernua* seems to be in more direct competition for soil water with *H. mutica* (and grasses and forbs, in general) considering their dependence on the soil water of the same soil layers which is indicated by their similar responses to the water use parameters measured in this work. Brown & Archer (1990) indicate that this competition is more severe for *P. glandulosa* during the seedling-stage phase, and our results suggests that this is probably also true for *L. tridentata.*

Consequences for the co-existence of grasses and shrubs inside the vegetation arcs

Root distribution indicates that water stored in the 0–40 cm soil layer after the experimental irrigation was available for all species. This fact indicates that all species are potentially competitors for that water. However, the results show a gradient of potential competitors between the grass and the woody species suggesting a more complicated situation for the co-existence of shrubs and grasses than the two-layer soil moisture hypothesis (Walter, 1971). Among the shrubs, at one extreme is *P. glandulosa* that can use deep soil water and, at the other extreme is *F. cernua* that apparently is highly dependent on the use of water stored in the upper soil layer. The position of *L. tridentata* is less defined and seems to be in between these two extremes.

The apparent lack of niche differentiation between the root systems of adult individuals of *F. cernua* (and to a certain extent of *L. tridentata*) and the co-existing grasses suggests the importance of soil moisture during the seedling-establishment phase (Grubb, 1977; Davis, 1991). Even in the case of *P. glandulosa* where the two-layer soil moisture hypothesis can be advocated for explaining the co-existence of grasses and *adult* individuals of that species, only the knowledge of the characteristics of the regeneration niche (*sensu* Grubb, 1977) allows a proper understanding of the different rates of woody plant establishment in grasslands (Brown & Archer, 1987).

After germination upon dense grass cover, the critical step for the establishment of the shrubs seems to be the development of sufficient root biomass in the upper soil layer to compete with the grass, and/or to have other roots growing into deeper soil layers (in the case of *P. glandulosa*).

Brown & Archer (1990) monitored ecophysiological parameters of *P. glandulosa* var. *glandulosa* and the grass *Chloris cucullata* Bisch. growing under field conditions in a Texas savanna (mean annual rainfall 680 mm) during the growing season. They concluded that rapid development of roots of *Prosopis* seedlings enhanced their survival by enabling them to access soil moisture below the zone effectively used by the grass. Net photosynthesis and stomatal conductance of the grass were correlated with the soil moisture in the upper soil layer (< 30 cm), whereas those of *Prosopis* seedlings were correlated with soil moisture present between 30 and 90 cm. In adult *Prosopis* these parameters were correlated with soil water present below 90 cm.

Bush & van Auken (1990) found that shade and herbaceous competition reduced the germination and growth of *P. glandulosa* var. *glandulosa* in a Texas savanna. In another study Bush & van Auken (1991) found that, after two growing seasons of growing alone under greenhouse conditions in 180-cm deep pots, 45% of the total root biomass of *P. glandulosa* var. *glandulosa* seedlings were in the upper 30 cm soil layer, whereas 18% were between 150 and 180 cm depth. If planted after a grass, *Bouteloua curtipendula* (Michx.) Torr., *Prosopis* seedlings produced less than 1% of the root biomass produced when growing alone and, in this case, all the roots were concentrated in the top 30 cm of the soil indicating the failure of *Prosopis* seedlings to compete successfully with established grasses.

Taking into account the ecophysiological characteristics reported in this paper, the co-existence of the different woody and grass species inside the arcs is probably favoured by a process of slow competitive displacement (Shmida & Ellner, 1984; Chesson & Case, 1986) as long as the recruitment of new shrubs takes place mainly by colonization of the upslope colonization front of the arcs (Montaña *et al.*, 1990; Montaña, 1992; Mauchamp *et al.*, 1993) where aerial cover and root biomass of grasses are lower than inside the vegetation arcs. Montaña *et al.* (1990) found that only 6% of the seedlings of *F. cernua* and 26% of the *P. glandulosa* seedlings were inside the arcs under slight grazing conditions. The corresponding figure for *L. tridentata* seedlings was 7% (Montaña, unpublished data). According to the results reported in this paper it can be expected that when colonization progresses and the grass canopy is almost closed the chances of a shrub being suppressed by water competition diminishes in the following order: *F. cernua*, *L. tridentata*, *P. glandulosa*.

A disturbance like overgrazing could change these conditions drastically. A reduction in grass biomass through overgrazing would reduce the competitive ability of the grasses by decreasing root production and probably resource uptake (Carman & Briske, 1982; Caldwell *et al.*, 1987) allowing the use of more soil resources by the established shrubs and increasing the probability of establishment and survival of seedlings of woody species inside the vegetation arcs. If this is coupled with an increase in the dispersion of propagules of animal dispersed species like *Prosopis* (Brown & Archer, 1987) the most probable result is a change to a more shrubby community. In accordance with the results of Brown & Archer (1990) *P. glandulosa* is the most serious candidate to increase its density under overgrazing conditions. Besides the reduction

of grass-competition during the seedling-establishment phase, increases in density of this species will also be favoured by domestic livestock seed dispersal (Brown & Archer, 1987). Also, the recovery of the grass strata by reduction of grazing pressure would most likely not suppress the established individuals of *P. glandulosa* or *L. tridentata* as long as their roots are using water from below the herbaceous root layer (Bush & van Auken, 1991). Our data give ecophysiological reasoning to a long-term study (Buffington & Herbel, 1965) where it was shown that the three woody species increased their density in Chihuahuan Desert grasslands in historical times. Changes in seed dispersal patterns originated from livestock fruit consumption, accompanied by heavy grazing and periodic droughts were reported as the principal causes of this process.

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