

Fundada en 1951 por Founded in 1951 by

Miguel Raggio & Nora Moro de Raggio
Editor-in-Chief: Dr. Carlos A. Busso

FUNDACION ROMULO RACCIO
Gaspar Campos 861, 1638 Vicente López (BA), Argentina
www.revistaphyton.fund-romuloraggio.org.ar
ISSN 0031-9457

57° ANIVERSARIO

(2008) 77: 297-320

57th ANNIVERSARY

Photosynthesis and water use efficiency of the association between *Larrea tridentata* (DC) Cov. and *Muhlenbergia porteri* Scribn

(With 1 Table & 7 Figures)

***Fotosíntesis y eficiencia del uso del agua de la asociación entre
Larrea tridentata* (DC) Cov. y *Muhlenbergia porteri* Scribn**

(Con 1 Tabla y 7 Figuras)

Castellanos-Pérez¹ E, AG de Soya², GB Donart³

Abstract. The study was conducted in the Chihuahuan Desert Rangeland Research Center, 32 km north of Las Cruces, NM, USA. Physiological responses of the shrub *Larrea tridentata* (DC) Cov. and the perennial grass *Muhlenbergia porteri* Scribn were determined from the summer 1997 to the winter 1998-99 when they grew together. In the summer 1997, *Larrea tridentata* competed for water with *M. porteri*, as shrubs growing alone showed higher integrated photosynthesis than shrubs in competition with *M. porteri* following a heavy rainfall event. *Larrea tridentata* had lower water use efficiency (WUE) than *M. porteri* plants. In the summer 1998, *M. porteri* had greater pre-dawn xylem water potentials (ψ_1) than *L. tridentata* when soil water potentials were above -3 MPa. *Larrea tridentata* showed a higher photosynthetic activity when *M. porteri* was defoliated than when it remained undefoliated. *Muhlenbergia porteri* presented a higher WUE. While green in the fall, plants of *M. porteri* had higher ψ_L and WUE than those of *L. tridentata*. Net assimilation was similar between shrub and grass plants. Both species responded to soil moisture availability in this season. *Muhlenbergia porteri* had higher net assimilation when growing alone than when growing under creosotebush. In the winter season, and while

¹ Facultad de Agricultura y Zootecnia, Universidad Juárez del Estado de Durango. Ejido Venecia, Mpio. de Gómez Palacio, Durango, México, CP 35000.

² Department of Natural Resources and Environmental Sciences, University of Nevada – Reno, NV, USA.

³ Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM, USA.

Address Correspondence to: Edmundo Castellanos-Pérez, e-mail: ecastellmx@yahoo.com.mx; fax and phone 052-871-711-8876.

Recibido/Received 26.III.2006. Aceptado/Accepted 5.V.2008.

being small, creosotebush had higher photosynthetic activity when growing alone than when growing with *M. porteri* ($p < 0.005$). Small and large plants of *L. tridentata* growing alone showed higher photosynthetic activity than *L. tridentata* growing with *M. porteri* ($p < 0.01$). In the spring, *M. porteri* and *L. tridentata* had the same net assimilation. At this time, however, water loss was lower in *M. porteri* than in *L. tridentata*. When soil water potential decreased below -7 MPa, *L. tridentata* still showed net assimilation.

Key words *Larrea tridentata*, *Muhlenbergia porteri*, photosynthesis.

Resumen. El estudio fue realizado en el Chihuahuan Desert Rangeland Research Center, 32 km al norte de Las Cruces, NM, USA. Se cuantificaron respuestas fisiológicas de plantas del arbusto *Larrea tridentata* (DC) Cov. creciendo juntas con las de la gramínea perenne *Muhlenbergia porteri* Scribn desde el verano 1997 al invierno 1998-99. En el verano de 1997, *L. tridentata* compitió con *M. porteri* después de un evento de abundante lluvia; *Larrea tridentata* tuvo menor eficiencia en el uso del agua (WUE) que *M. porteri*. En el verano de 1998, el potencial hídrico del xilema antes del amanecer (ψ_L) fue mayor en *M. porteri* que en *L. tridentata*, cuando el potencial hídrico del suelo fue mayor de -3 MPa. La actividad fotosintética de plantas pequeñas de *L. tridentata* fue mayor cuando, creciendo debajo de *L. tridentata*, fue defoliada que cuando permaneció sin defoliar. *Muhlenbergia porteri* presentó una mayor WUE. Cuando estuvo verde en el otoño, *M. porteri* tuvo ψ_L y WUE mayores que *L. tridentata*; la asimilación neta fue similar entre las plantas de arbustos y gramíneas. En esta estación, ambas especies respondieron a la disponibilidad de humedad del suelo. *Muhlenbergia porteri* creciendo sola tuvo mayor tasa de asimilación que cuando creció bajo *L. tridentata*. En invierno, la actividad fotosintética de las plantas pequeñas de *L. tridentata* fue mayor ($p < 0.005$) cuando crecieron solas que cuando lo hicieron teniendo a *M. porteri* bajo su cobertura. Plantas grandes y pequeñas de *L. tridentata* creciendo solas tuvieron mayor actividad fotosintética que las de *M. porteri* que crecieron bajo su cobertura ($p < 0.01$). En la primavera, *M. porteri* tuvo la misma asimilación neta que *L. tridentata*, pero con menos pérdida de agua. Cuando el potencial hídrico del suelo disminuyó por debajo de -7 MPa, *L. tridentata* aun mostró asimilación neta.

Palabras clave: *Larrea tridentata*, *Muhlenbergia porteri*, fotosíntesis.

INTRODUCTION

In the Chihuahuan Desert, a common plant association occurs between the shrub *Larrea tridentata* (DC) Cov. and the perennial grass *Muhlenbergia porteri* Scribn. *Larrea tridentata* is a dominant perennial evergreen shrub in the deserts of North America (Runyon, 1934; Reynolds, 1986). This plant has a stress-tolerant strategy with distinct growth patterns which vary with soil depth. Longevity of its leaves in the Chihuahuan desert is from less than one year to two years. This species is tolerant to extreme temperatures and desiccation: photosynthesis and respiration strongly

acclimate to seasonal changes in temperature (Reynolds, 1986). This shrub is metabolically active throughout the year (Oechel et al., 1972; Bamberg et al., 1975). Ecophysiological studies are necessary on this shrub (1) for trying to explain variations in its growth and (2) to understand the relative importance of abiotic factors on its productivity (Reynolds, 1986). Since lack of water has been a major selective force for plant evolution in these ecosystems, it is important to learn about plant strategies which may contribute to cope with water stress (Freitas, 1997). *Muhlenbergia porteri* is a highly-branched perennial grass which occupies dry plateaus, canyons and rocky deserts in the southwestern United States and northern Mexico (Tidestrom & Kitell, 1941; Welsh & Beck, 1976). This grass species is often growing under the canopy of *L. tridentata*. *Muhlenbergia porteri* is one of the grasses that appear to have possibilities for either compete or coexist with shrubs (Pieper, 1994). This shrub-grass association is unusual since creosotebush more often appears to displace grasses from their historical distribution in these warm desert ecosystems.

The C₃ *L. tridentata* is an evergreen shrub with metabolic activity throughout the year (Giorgetti et al., 2000), and the C₄ *M. porteri* is a perennial grass dormant during winter. Both species grow successfully under arid conditions. Thereafter, the question is how these plants deal with C fixation and loss of water by transpiration to remain under these conditions. The objective of this study was to observe the effect of large and small plants of *L. tridentata* on the gas-exchange activity of *M. porteri*, and vice versa. Several hypotheses related to the success of the *L. tridentata*-*M. porteri* association were considered: (a) the resource islands under *L. tridentata* provide a better microhabitat for *M. porteri* which will be reflected in its greater photosynthetic activity when compared with *M. porteri* growing alone, (b) *M. porteri* and *L. tridentata* are able to coexist because they stratify periods of greatest physiological activity: creosotebush is physiologically active during dry periods, while *M. porteri* tends to be more physiologically active during periods of adequate soil water availability, (c) *M. porteri* has greater photosynthetic rates when growing under small than large plants of *L. tridentata*, (d) removal of senescent plant material from plants of *M. porteri* will result in greater photosynthetic rates due to greater light levels available for photosynthesis.

MATERIALS AND METHODS

The study site is on a northwest-facing piedmont slope of Mt. Summerford in the Chihuahuan Desert Rangeland Research Center (CDRRC), approximately 32 km north of Las Cruces, NM. Elevation is

1327 m.a.s.l. The vegetation classification corresponds to a desert shrub formation, Chihuahuan desert region, creosote series, creosote-bush muhly association (Donart et al., 1978). The vegetation at this site is dominated by *L. tridentata* with some dispersed individuals of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) and tarbush (*Flourensia cernua* DC). The principal grass is *M. porteri* with some fluffgrass (*Dasychloa pulchella* (Kunth) Steudel) and spike dropseed (*Sporobolus contractus* A.S. Hitch.).

The soil association corresponds to Haplargids-Torripsamments (Maker et al., 1974). The soil at this site is loamy fine sand about 10 cm thick in the surface layer; the subsoil is sandy loam, and sandy clay loam about 78 cm soil depth. The substratum is sandy clay loam to a depth of 150 cm or deeper (Bulloch & Neher, 1980). Since 1954, people at the site were in the search for grass species which would need to respond to favorable environmental conditions. Finally, *M. porteri* became established on the site in 1960. In 1965, the site was fenced to prevent grazing by large domestic herbivores (Welsh, 1972). The coolest months are December and January with mean monthly temperatures of 5.5 and 5.3 °C, and minimum temperatures of 3.2 and -3.5 °C, respectively. The warmest months are June, July, and August with mean monthly temperatures of 24.7, 26.4, and 25.3 °C, and maximum temperatures of 34.4, 34.3, and 33.1 °C, respectively (Kunkel et al., 1988). From 1997 to 1999, seasons had an average of 21.1, 14.0, 14.7, and 25.1 MJ per day of solar radiation for summer, fall, winter and spring, respectively. Maximum relative humidity was 71.4, 57.5, 60.1, and 40.8%, and minimum relative humidity was 21.3, 20.5, 23.1, and 13.3% during summer, fall, winter and spring, respectively (1997, 1998, 1999 weather data, <http://jornada-www.nmsu.edu/datacat.php?withJS=true>). Rainfall data are shown in Fig. 1; these data were obtained using a raingauge located at the Headquarters of the CDRRC, a mile away from the study area. Long-term rainfall data were obtained from Kunkel et al. (1988).

In July 1997, creosotebush plants with or without bush muhly were tagged in the field. On each shrub, the (1) canopy height, (2) largest diameter, and (3) diameter perpendicular to the largest diameter of the canopy were measured. Canopy volume of each shrub was calculated using the prediction equation of Ludwig et al. (1975):

$$V_c = (\pi/3)*((D_1+D_2)/4)^2*(h)$$

where V_c is canopy volume, D_1 is the largest canopy diameter, D_2 is the diameter perpendicular to D_1 , and h is height. Shrubs were stratified based on the calculated volume: Small plants = between 25.4 to 122.9 dm³; medium plants = 204.8 to 409.7 dm³, and large plants = >491.6 dm³. A total of

64 plant units were chosen; each unit was a plant of creosotebush and a plant of bush muhly growing together, or each species growing alone. Bush muhly canopy volumes were similar, $593.8 \pm 50.2 \text{ dm}^3$; this was calculated using the upper-half prolate spheroid shape (Ludwig et al., 1975):

$$V_c = (4/3) \cdot \pi \cdot ((D_1 + D_2)/4) \cdot (h^2)$$

where V_c is canopy volume, D_1 is the largest canopy diameter, D_2 is the perpendicular diameter to D_1 , and h is height.

On 18 July 1997, the first measurement of gas exchange was carried out in half of the plots; however, more than 1.5 hour was spent measuring them. Due to the data variation we encounter investing more than one hour in measurements, we decided to discard the medium-size creosotebush plants from the study. Plants selected for measurements are in Table 1. In order to measure the treatments units in less than one hour, half of these units were measured on one date, and the other half on the day after. Each plant unit was around 1 m in area, and contained one shrub and/or grass clump. Defoliation of 50% of *M. porteri* biomass was done according to the equations of Almeida (1981), where the dependent variable was biomass and the independent variable was height. *M. porteri* was defoliated on 15 July 1997.

Fig. 1. Rainfall during the study period (1997, 1998) and long-term average (1870-1987).

Fig. 1. Lluvia durante el período de estudio (1997, 1998) y el promedio a largo plazo (1870 – 1987).

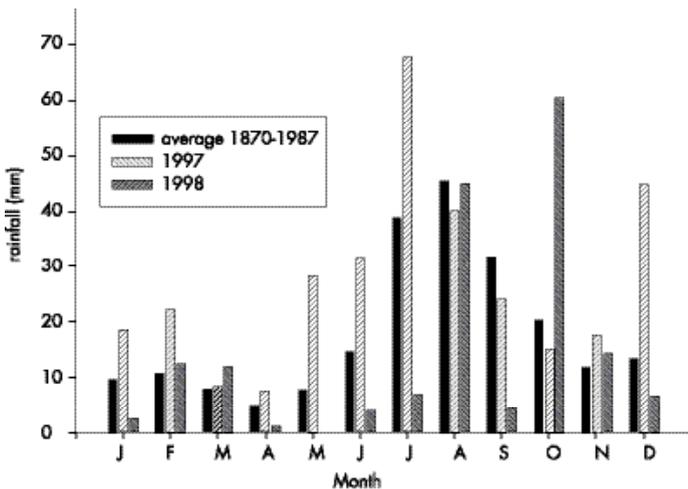


Table. 1. Plant units (treatments); one half of all plants (n/2) were sampled on each study date.

Tabla. 1. Unidades de plantas; la mitad del total de las plantas (n/2) fue muestreada en cada fecha de estudio.

Plant Unit	Description	n
LL	Large <i>L. tridentata</i> growing alone	4
LLM	Large <i>L. tridentata</i> growing with <i>M. porteri</i>	12
MLL	<i>M. porteri</i> growing underneath a large <i>L. tridentata</i>	12
M	<i>M. porteri</i> growing alone	4
SL	Small <i>L. tridentata</i> growing alone	4
SLM	Small <i>L. tridentata</i> having <i>M. porteri</i> underneath its canopy	12
MSL	<i>M. porteri</i> plant growing underneath a small <i>L. tridentata</i>	12
SLMD	Small <i>L. tridentata</i> having defoliated <i>M. porteri</i>	8
MDSL	Defoliated <i>M. porteri</i> plant growing underneath a small <i>L. tridentata</i>	8

Plant and Soil Water Potentials. Pre-dawn water potentials (ψ_L) were measured on plants using a 3000 series Plant Water Status Console (Soilmoisture Equipment Corp., Santa Barbara, CA) (Scholander et al., 1965). For creosotebush, plant water potential and gas-exchange were taken on the same days. *Muhlenbergia porteri* xylem water potential was determined during the summer 1998. Prior to this date, we did not have the appropriate rubber gasket to hold the bush muhly in the pressure bomb.

Soil water potential (ψ_s) was measured with soil psychrometers, calibrated in the laboratory and installed at 0.2 m depth in November 1997 under the following plants units (treatments): 2 in SL, 2 in M, 2 in LL, 4 in SLMD, 6 in LLM, and 6 in SLM (see Table 1 for plant unit references). The first measurements of soil water potential were made in December 1997. These measurements were carried out either on the same day the gas-exchange measurements were conducted, or within 24 hours of these measurements.

Gas Exchange. One marked apical stem segment with several leaves (*L. tridentata*) and one marked leaf segment (*M. porteri*) on each experimental plant were used for repeated measurements of gas exchange, usually five sets of measurements per day. When *M. porteri* was in a quiescent or senescent stage, two apical stem segments of *L. tridentata* were used per plant to

measure gas exchange; a mean of these two measurements was obtained to avoid pseudoreplication. Each set of gas exchange measurements took approximately one hour: 8:30-9:30, 10:00-11:00, 11:30-12:30, 13:00-14:00, and 15:00-16:00 h on relatively cloudless days, using a LI-6200 Portable Photosynthesis System (LI-Cor, Inc., Lincoln, NE). Data were integrated (area under the curve) by plant for each sampling day prior to statistical analysis to minimize the effects of environmental variability on photosynthetic activity, e.g. (1) vapor pressure deficit (Shirke & Pathre, 2004), (2) reversible photoinhibition (Gray et al., 1996), or (3) high temperature which affects water use efficiency (WUE) (Polley, 2002). For each twig of *L. tridentata* or leaf of *M. porteri*, daily integrated values of photosynthesis and transpiration were obtained between 8:30 to 16:00 h. Water use efficiency was calculated by dividing integrated photosynthesis by integrated transpiration. At the end of each day gas-exchange was measured, leaves of *M. porteri* used for gas exchange measurements were excised, and leaf area was determined in the laboratory using a LI 3000 Leaf Area Meter (LI-Cor, Inc., Lincoln, NE). The single-surface area on creosotebush leaves used for gas-exchange was determined *in situ* using the method of Franco et al. (1994).

Statistical Analysis. For each date, data were analyzed in a completely randomized design, using the Duncan's multiple-range test. Also, the data were grouped by season. For each season, data were arranged factorially in a completely randomized design where one factor was the plants and the other was the sampling dates. Data were analyzed with analysis of variance procedures using indicator variables (Litell et al., 1991). For each season, the comparison of each response variable of *L. tridentata* was carried out between dates. Within a season, dates when *M. porteri* was green were compared for the respective variable. Dates when *M. porteri* was senescent or quiescent were excluded. Mean comparison for sampling dates was conducted using Duncan's multiple-range test.

Also, contrasts were used for mean comparisons of plants in each season. Contrasts were: (a) *L. tridentata* vs *M. porteri*; (b) large vs small *L. tridentata*; (c) *L. tridentata* growing alone vs *L. tridentata* growing with *M. porteri*; (d) large *L. tridentata* growing alone vs large *L. tridentata* growing with *M. porteri*; (e) small *L. tridentata* growing alone vs small *L. tridentata* growing with *M. porteri*; (f) small *L. tridentata* with *M. porteri* undefoliated vs small *L. tridentata* with *M. porteri* defoliated; (g) *M. porteri* growing alone vs *M. porteri* growing underneath *L. tridentata*; (h) undefoliated *M. porteri* growing underneath a small *L. tridentata* vs *M. porteri* defoliated growing underneath a small *L. tridentata*; (i) *M. porteri* growing underneath a large *L. tridentata* canopy vs *M. porteri* growing underneath a small *L. tridentata* canopy.

RESULTS AND DISCUSSION

In the summer season, and although measurements were carried out every week from 31 July 1997 to 28 September 1997, and from 06 July to 29 September 1998, only four dates will be shown per year in this season. However, when results are shown without a specific date, it implies that all measurement dates were taken into consideration. In the summer 1997, *M. porteri* was green during five out of nine sampling dates. In summer 1998, *M. porteri* was green during seven out of 12 sampling dates.

Plant and Soil Water Relations

Summer season. During summer 1997 (Fig. 2A), pre-dawn ψ_L was greatly influenced by rainfall. However, there were no significant effects of either *L. tridentata* plant size or presence/absence of a *M. porteri* understory underneath *L. tridentata*. The only exception was on 30 August, where large plants (LL) had greater ψ_L (-3.25 MPa) than small plants (SL; -4.75 MPa).

During the summer of 1998, ψ_L measurements on July 22 (Fig. 3A), coincided with increased soil water potentials (-2.6 MPa; Fig. 4); however, there were no ψ_L differences among plants. On 28 July, ψ_s and ψ_L increased, and measurements were also possible for *M. porteri*. On this date, ψ_L were greater in the grass than in *L. tridentata*; means ranged from -0.62 to -1.05 MPa in the grass, and -1.73 to -2.3 MPa in *L. tridentata*. By 25 August, ψ_s decreased to almost -4.0 MPa, and MDSL had greater ψ_L than MSL, SLM, SL, M, and LLM; at the same time, SLMD had higher ψ_L than SL, M, and LLM. Finally, LL and MLL had higher ψ_L than M. On 29 September, ψ_L were significantly greater in LL (-4.50 MPa) than in SLM (-3.23 MPa). *Muhlenbergia porteri* had greater ψ_L than *L. tridentata* when soil water potentials increased above -3.0 MPa. In 1998, ψ_L was not affected either for *L. tridentata* plant size or for the presence of *M. porteri*. These results agree with those found in a nearby area (Franco et al., 1994).

Fall Season. The results of soil water potential and the predawn ψ_L readings for the fall season are shown in Fig. 4 and Fig. 5A. On 5 October 1997, there were no significant differences ($p > 0.05$) between plants (from -3.45 in SL to -3.6 MPa in LL). On 9 November 1997, this variable was so low that we could not measure it. This was the result of the absence of precipitation.

On 5 October 1998, ψ_L readings for *L. tridentata* were similar to those in September 1998, and soil water potentials were below -8.0 MPa. On 28 October, soil water potentials increased due to rainfall, and ψ_L in *L. tridentata* increased as a result. These were the greatest ψ_L observed in the study plants, although they were similar to those on 3 November ($p > 0.05$).

Fig. 2. Means of (A) Predawn xylem water potential (± 1 s.e.), (B) Integrated photosynthesis (± 1 s.d.), and (C) water use efficiency (± 1 s.e.) in the different treatments during summer 1997.

Fig. 2. Promedios de (A) Potencial hidrico en el xilema antes del amanecer (± 1 e.e.), (B) Fotosíntesis integrada (± 1 d.e.) y (C) uso eficiente del agua (± 1 e.e.) en los diferentes tratamientos durante el verano de 1997.

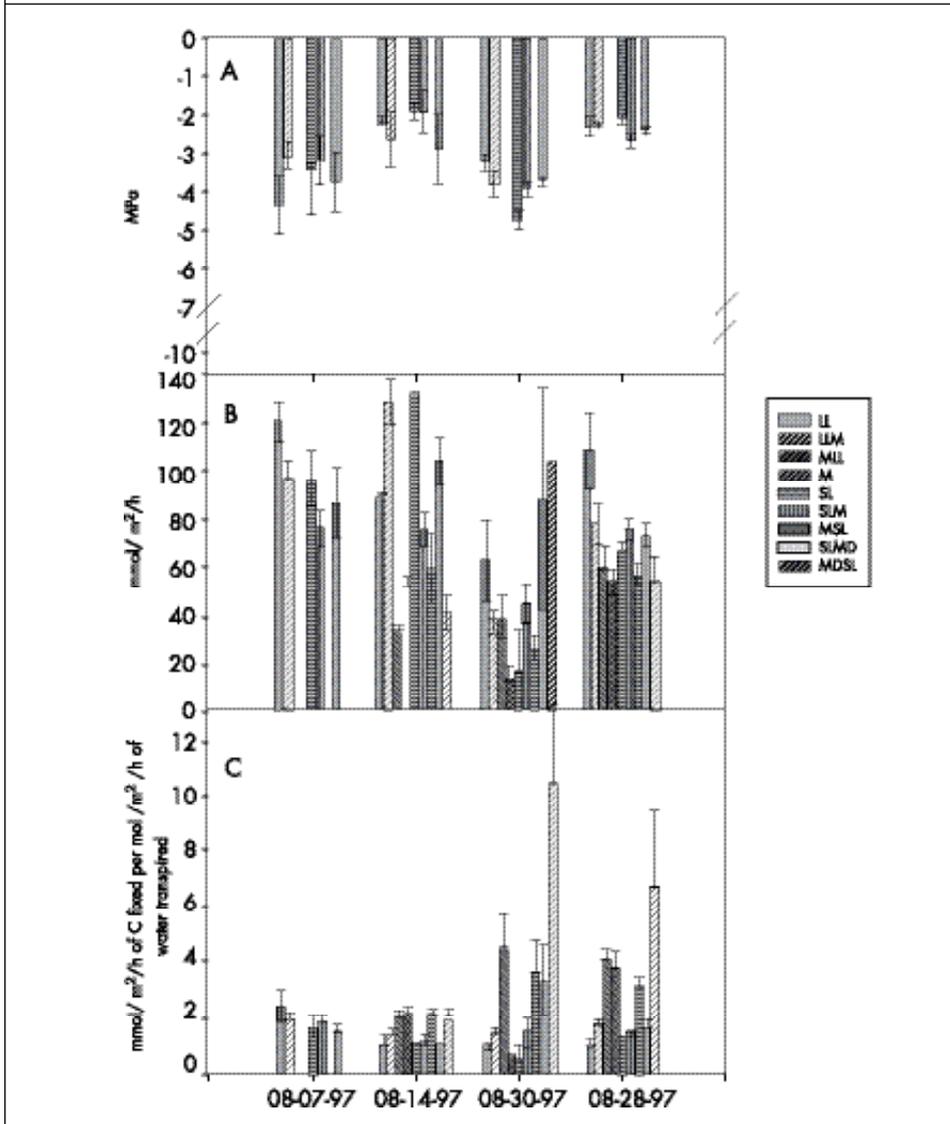


Fig. 3. Means of (A) Predawn xylem water potential (± 1 s.e.), (B) Integrated photosynthesis (± 1 s.d.), and (C) Water use efficiency (± 1 s.e.) in the different treatments during summer 1998.

Fig. 3. Promedios de (A) Potencial hídrico en el xilema antes del amanecer (± 1 e.e.), (B) Fotosíntesis integrada (± 1 d.e.) y (C) Uso eficiente del agua (± 1 e.e.) en los diferentes tratamientos durante el verano de 1998.

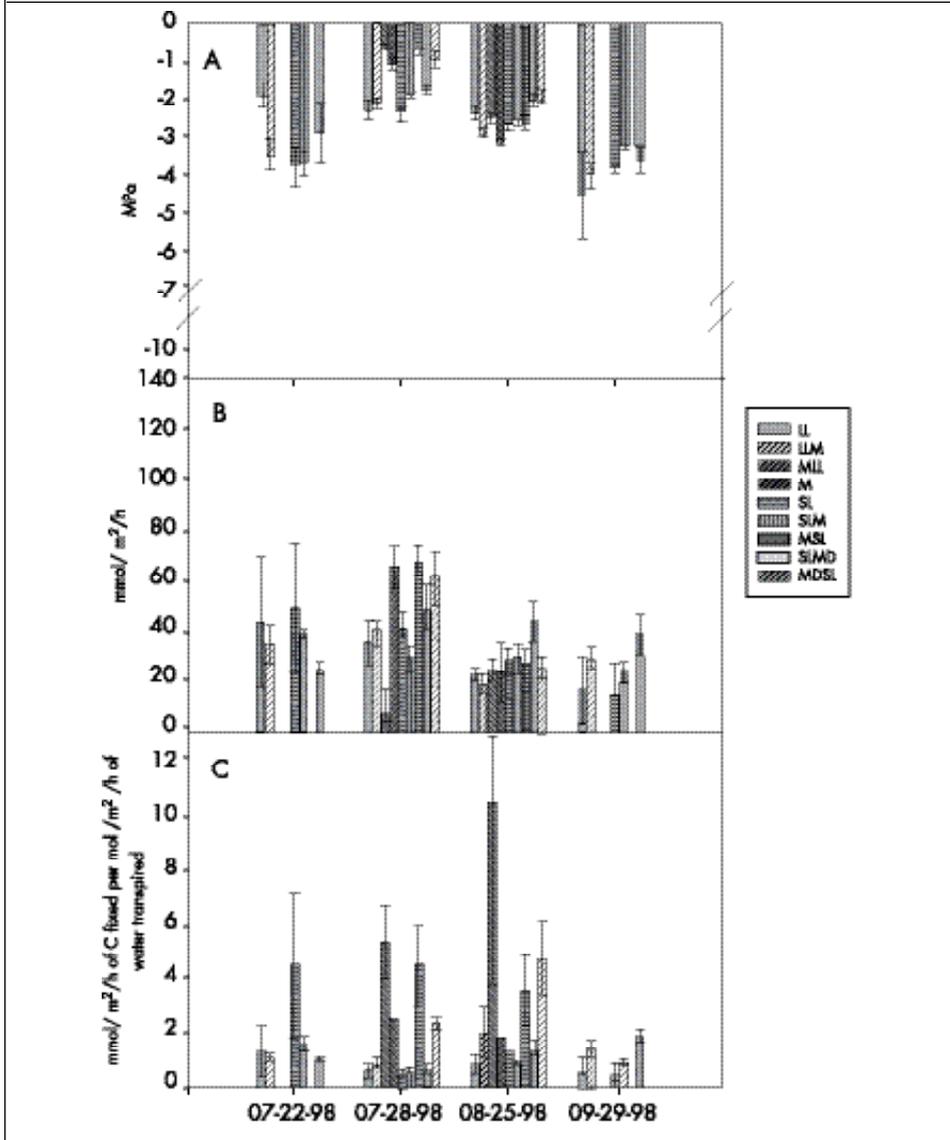
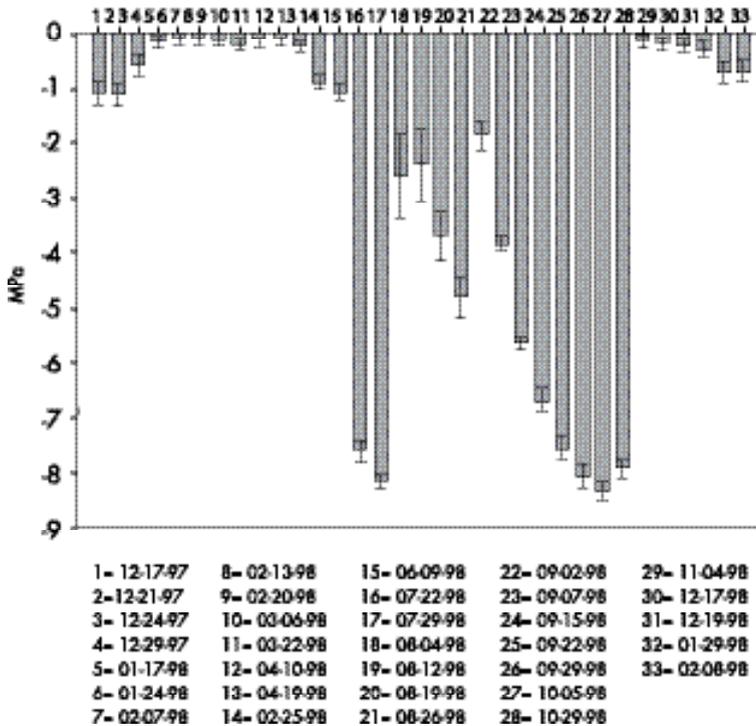


Fig. 4. Mean (± 1 s.e.) Soil water potentials at the study site during the measurement period.

Fig. 4. Promedios (± 1 e.e.) del Potencial hídrico del suelo en el sitio de estudio durante el período de medición.



However, *M. porteri* was still quiescent, and measurements were then not possible. On 3 November, *M. porteri* was green most likely due to the high soil water potentials coming from the October precipitations. It showed a ψ_L range from -0.8 MPa in M to -1.07 MPa in MSL. These values were significantly higher ($p < 0.001$) than those in *L. tridentata*, which showed values from -1.95 MPa in LL to -2.4 MPa in LLM. While there were significant differences ($p < 0.05$) between *M. porteri* and *L. tridentata* plants, there were no differences within either *M. porteri* or *L. tridentata* plants. On the remaining dates, there were no significant differences ($p > 0.05$) in ψ_L between plants. In general, *M. porteri* showed a greater ψ_L than *L. tridentata* when it was green during its growing season.

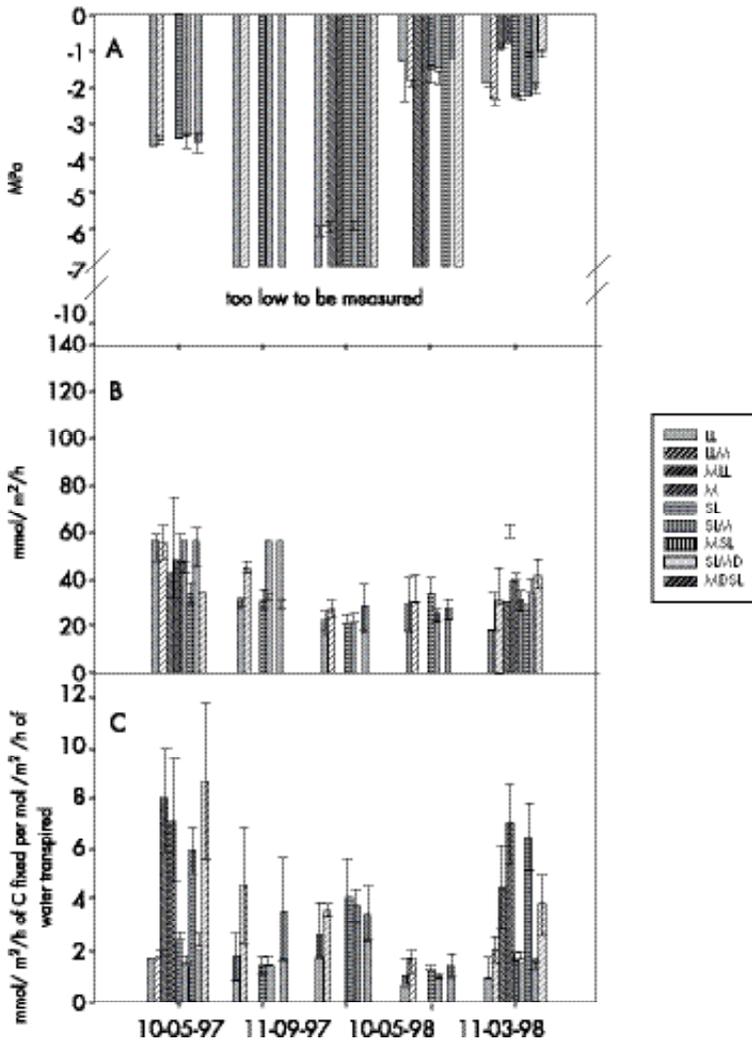
Winter Season. Low temperatures during winter prevented us from taking valid ψ_L measurements. Minimum and mean temperatures during 24 January were $-3.9\text{ }^{\circ}\text{C}$ and $6.7\text{ }^{\circ}\text{C}$ respectively, and $-1.7\text{ }^{\circ}\text{C}$ and $8.9\text{ }^{\circ}\text{C}$, respectively, during 25 January. On 19 February, minimum and mean temperatures were $-1.1\text{ }^{\circ}\text{C}$ and $8.9\text{ }^{\circ}\text{C}$, respectively, and on 20 February values were $2.7\text{ }^{\circ}\text{C}$ and $9.4\text{ }^{\circ}\text{C}$, respectively. Despite very high soil water potentials were observed during winter 1997-98, predawn ψ_L in *L. tridentata* could only be measured after March 1998 (Fig. 6A). During January and February, however, this variable was too low to be measured (below -7.0 MPa). This was very likely due to the low winter temperatures. In March 1998, predawn ψ_L increased from -3.44 MPa on 7 March to -2.82 MPa on 22 March. The minimum and mean temperatures were $10.0\text{ }^{\circ}\text{C}$ and $14.4\text{ }^{\circ}\text{C}$, respectively, on 6 March, and $2.2\text{ }^{\circ}\text{C}$ and $7.2\text{ }^{\circ}\text{C}$, respectively, on 7 March. On 21 March, minimum and mean temperatures were $5.0\text{ }^{\circ}\text{C}$ and $15\text{ }^{\circ}\text{C}$, respectively, and they were $6.7\text{ }^{\circ}\text{C}$ and $18.3\text{ }^{\circ}\text{C}$, respectively, on 22 March.

Soil water potentials were also high during winter 1998-99. It was then possible to measure ψ_L , which were higher during this second winter season (1998-99). On 19 December 1998, for example, mean value of -1.7 MPa ($p < 0.05$) was obtained. The minimum and mean temperatures on 18 December were $8.3\text{ }^{\circ}\text{C}$ and $12.2\text{ }^{\circ}\text{C}$, respectively, and they were $11.2\text{ }^{\circ}\text{C}$ and $11.7\text{ }^{\circ}\text{C}$, respectively, on 19 December. Mean xylem water potentials on *L. tridentata* plants were -3.82 MPa in January and -3.38 MPa in February 1999. Within each date, there was no difference among plant units (treatments), except on 19 December 1998 where SLMD (-1.05 MPa) had greater ψ_L than SL (-2.7 MPa ; $p < 0.05$).

Spring Season. High winter rainfall in 1998 led to high soil water potentials: -0.86 and -1.03 MPa on 10 April and 19 April, respectively (Fig. 4). Leaf water potentials measured on 10 April were lower ($p < 0.05$) than those determined and 18 April (means were from -1.97 to -2.3 MPa). We were unable to measure ψ_L from 18 May throughout 23 June. This was because of the extremely low ψ_L registered at this time. In turn, this coincided with low ψ_s (ranging from -7.6 to -8.1 MPa) which probably resulted from the low precipitation at this time. On 10 April, SL (-2.35 MPa) and SLMD (-2.38 MPa) had greater ψ_L ($p < 0.05$) than LL (-2.9 MPa). On 18 April, there were no significant differences ($p > 0.05$) in ψ_L .

Fig. 5. Means of (A) Predawn xylem water potential (± 1 s.e.), (B) Integrated photosynthesis (± 1 s.d.), and (C) Water use efficiency (± 1 s.e.) during fall 1997 and 1998.

Fig. 5. Promedios de (A) Potencial hídrico en el xilema antes del amanecer (± 1 e.e.), (B) Fotosíntesis integrada (± 1 d.e.) y (C) Uso eficiente del agua (± 1 e.e.) en el otoño de 1997 y 1998.



Photosynthesis

Summer season. On 7 August 1997 (Fig. 2B), *M. porteri* was in a quiescent state, *L. tridentata* increased its photosynthetic activity in relation to the first sampling data, and LL showed a higher photosynthetic activity than SLM plants ($p < 0.05$). On 14 August, *L. tridentata* showed the highest photosynthetic activity of the whole season, partially as a result of the rainfall on 13 August (40.1 mm). Photosynthetic activity was higher ($p < 0.05$) on SL, LLM, and SLMD than in the other plants. *Muhlenbergia porteri* exhibited less ($p > 0.05$) photosynthetic activity than *L. tridentata*. Photosynthetic rates were similar ($p > 0.05$) on all *M. porteri* plants.

Photosynthetic activity decreased in both species on 30 August in part due to the absence of rainfall. At this date, the standard error was so high that there were no statistical differences among plant units (treatments). On 28 September, both species showed activity because of a previous rainfall. However, no differences ($p > 0.05$) were detected between species. The exception was *L. tridentata* which showed the highest activity ($p < 0.05$) in the LL treatment. Also, activity was lower ($p < 0.05$) at the M than at the LLM, SLM and SLMD treatments.

Larrea tridentata exhibited an opportunistic role due to its increased photosynthetic activity after the high rainfall. Our results suggest that *L. tridentata* competed with *M. porteri* for water resources. This is because *L. tridentata* plants growing alone had higher net assimilation after a large rainfall event [i.e., in summer 1997, where rainfall (132.1 mm) was above the long-term average (116.3 mm)] (Kunkel et al. 1988). These results differ from those of Dodd et al. (1998): they found that the woody *Atriplex canescens* and grass species used water from different soil horizons.

In the summer of 1998 (Fig. 3B), photosynthetic activity was lower than 50 mmol/m²/h on 22 July, and there were no differences ($p > 0.05$) among plants (treatments). On 28 July, *M. porteri* was green and its photosynthetic activity was greater in the MSL and M than in the SL, MLL, LL and SLM treatments ($p < 0.1$). Photosynthetic activities were higher than 50 mmol/m²/h. On 25 August, SLMD had greater ($p < 0.05$) photosynthetic activity than LL and LLM plants. On 29 September, *M. porteri* was senescent, and *L. tridentata* has mean photosynthetic activities lower than 15 mmol/m²/h. There were no differences among plants within each date ($p > 0.05$). Small *L. tridentata* plants showed a greater ($p < 0.0005$) photosynthetic activity when *M. porteri* was defoliated (40.9 mmol/m²/h) than when it remained undefoliated (29.8 mmol/m²/h). This indicates that *L. tridentata* plants were more active when *M. porteri* was defoliated than when it remained undefoliated. Even though 1998 was marginally drier than 1997, it was still above the long-term average with 120.1 mm of rainfall. However, only 4.6 mm were

recorded in September whereas the long-term monthly average is 31.8 mm (Kunkel et al., 1988). There were no clear patterns of *L. tridentata*–*M. porteri* interactions. This was likely due to limited water availability in the soil profile where roots of *L. tridentata* and *M. porteri* occur together.

Fall Season. On 5 October 1997, photosynthetic activity was similar ($p>0.05$) in both species and plants (treatments), having values no greater than 70 mmol/m²/h (Fig 5B). On this date, *L. tridentata* had the highest ($p<0.05$) photosynthetic activity during the fall season in 1997. This value was also greater than those found in the 1998 fall season. On 9 November 1997, only *L. tridentata* was physiologically active, and photosynthesis was lower ($p<0.05$) than that observed on 5 October, when LLM had greater ($p<0.05$) photosynthetic activity than all others.

During fall 1998, we could not measure photosynthesis in *M. porteri* plants on 5 October and 28 October. The lowest photosynthetic activity for *L. tridentata* was recorded on 5 October 1998. Photosynthetic activity was similar ($p>0.05$) during 5 and 28 October. On 3 November, *M. porteri* plants showed photosynthetic activity because of the high soil water potentials. The greatest ($p<0.1$) net assimilation was found in M plants. In turn, MDSL and SL treatments had greater photosynthetic activity than LL ($p<0.1$).

We made a statistical comparison between 5 October 1997 and 3 November 1998, times when *M. porteri* was green: photosynthetic activity was lower ($p<0.05$) on 3 November 1998, than on 5 October 1997. Large plants of *L. tridentata* growing alone had lower ($p<0.05$) photosynthetic activity than LLM plants. *Muhlenbergia porteri* growing alone had greater ($p<0.005$) photosynthetic activity than *M. porteri* growing underneath the shrub canopy. Both species responded to soil moisture availability, in agreement with desert plants which have the ability to respond to moisture during late summer or early fall (Bamberg et al., 1975). No differences in the ψ_L or water use efficiency (see below) in *M. porteri* plants suggest that the lower photosynthetic activity of these plants when growing underneath the shrub canopies could be due to the shadow effect on this warm season grass (Ballaré et al., 1990).

Winter Season. On 25 January 1998, there was no photosynthetic activity for any of the study plants because of the low temperatures. At the other measurement dates during the winter season, only *L. tridentata* showed photosynthetic activity, with values lower than 50 mmol/m²/h (Fig. 6B). On 28 January 1999, 7 March and 22 March 22, 1998, *L. tridentata* plants had higher photosynthetic activity than on 8 February 1999, and 19 December and 20 February 1998. On 20 February, 7 March and 22 March

1998, there were no differences ($p > 0.05$) in the assimilation rates between *L. tridentata* plants. On 19 December, SL had greater ($p < 0.05$) photosynthetic activity than LL and SLM. On 28 January 1999, there were no significant differences ($p > 0.05$) among plants. On 8 February 1999, photosynthetic activity was greater ($p < 0.05$) in SL than in the other plants. In *L. tridentata* plants, SL also had higher ($p < 0.005$) photosynthetic activity than SLM and SLMD plants. Also, LL and SL plants had higher ($p < 0.01$) photosynthetic activity than LLM, SLM and SLMD plants.

Low temperatures reduce assimilation rates because Rubisco activity and electron transport capacity are reduced (Farquhar & Sharkey, 1982). Our results are similar to those of Reynolds et al. (1999). These authors found a low net assimilation rate in the winter season, even when soil moisture was high. The high temperature acclimation of *L. tridentata* (Mooney et al., 1978; Reynolds et al., 1999), may allow this species to have net assimilation during winter. Increasing temperatures during the day may allow carbon assimilation in spite of the low temperatures. Avoidance of freeze-induced cavitation, caused by air bubbles formed *in situ* during freezing, is associated with the small vessel size in *L. tridentata* (Pockman & Sperry, 1997). Another associated factor is leaf age. New leaves grow in spring and summer; therefore, winter leaves are, in general, older than those of previous seasons (Reynolds et al., 1999).

During the winter season, *M. porteri*, although dry, appears to compete with *L. tridentata* when they grow close to each other. This is because *L. tridentata* plants growing alone showed higher photosynthetic activity. This may have been the result of higher levels of photosynthetically active radiation reaching these plants without interference by the grass (Welsh & Beck, 1976).

Spring Season. In April, *M. porteri* was green because of the high soil moisture and the fact that this grass has photoperiodic control for flowering in long-days (Carr-Smith et al., 1989). On April 10, both species showed almost equal photosynthetic activity; the exception was SLMD which had higher photosynthesis than MLL plants (Fig 7B). Both species still showed active by 18 April, although photosynthetic activity was lower ($p < 0.05$) than at the previous sampling dates, and differences were not significant ($p > 0.05$). On 18 May, 25 May, 8 June and 23 June, only *L. tridentata* showed photosynthetic activity with values lower than 40 mmol/m²/h for all plants; means at each date were lower than 34 mmol/m²/h. The lowest photosynthetic activity during spring (22.6 mmol/m²/h) was reached on 23 June; this reading was similar ($p > 0.05$) to that on 18 May and 8 June. On 18 May, photosynthetic activity was greater ($p < 0.05$) on SLMD than LL

plants. There were no differences ($p > 0.05$) in photosynthetic activity between plants from 25 May to 23 June. Low values in photosynthesis were probably a result of low ψ_s . On average, photosynthetic activity was greater ($p < 0.01$) on small than on large *L. tridentata* plants. Photosynthetic activity of *L. tridentata* was lower ($p < 0.05$) when growing alone than when it grew with *M. porteri*. Photosynthetic activity of undefoliated *Muhlenbergia porteri* was greater ($p < 0.005$) when it grew under small than large *L. tridentata* plants.

Greater net assimilation values for small than large *L. tridentata* plants are consistent with data of de Soyza et al. (1996). They concluded that these results allow *L. tridentata* to compete with grasses. The continued net assimilation rates of *L. tridentata* at soil water potentials below -8.0 MPa show its ability to survive under these conditions (Strain & Chase, 1966). Leaf water potentials could not be measured at these low soil water potentials. However, Oechel et al. (1972) found that *L. tridentata* have a continuous net assimilation either at temperatures of 50 °C or ψ_L of -7.3 MPa.

Water Use Efficiency

Summer Season. Water use efficiency (WUE) increased from 31 July to 7 August 1997, with a WUE of 2.41 [$\text{mmol C/mol H}_2\text{O}$] / m^2/h for LL (Fig 2C). This value was statistically similar to that on LLM and SLM, which had the highest ($p < 0.05$) WUE ratio (Fig. 2C). The lowest ($p < 0.05$) WUE was on plants of SLMD, SLM, SL and LLM. On 14 August, WUE of *M. porteri* was similar in MSL (mean = 2.08) and MLL (mean = 2.15) plants. However, these WUE were higher ($p < 0.05$) than those in *L. tridentata* which showed WUE ranging from 1.11 (LL plants) to 1.40 (LLM plants). On 30 August, MDSL on *L. tridentata* plants had a high value (10.35), similar ($p > 0.05$) to that in MLL and MSL *M. porteri* plants and SLM plants of *L. tridentata*. Except on MDSL plants, lowest WUE were found in SL, although values were similar ($p > 0.05$) in all other treatments. On 28 September, when *M. porteri* was green again, MDSL plants showed a high WUE (mean = 6.65). This value was greater ($p < 0.05$) than that on *L. tridentata* and *M. porteri* plants in all other treatments. Except on MDSL plants in *M. porteri*, all other plants in this species showed similar ($p > 0.05$) WUE values, ranging from 3.14 on MSL plants to 4.01 on MLL plants. *L. tridentata* plants had lower ($p < 0.05$) WUE than *M. porteri* plants. There were no significant differences ($p > 0.05$) in WUE between plants of different size in *L. tridentata*; values ranged from 1.08 in LL plants to 1.74 in LLM plants.

On 22 July 1998, SL plants of *M. porteri* had the greatest ($p < 0.05$) mean WUE (4.54) (Fig. 3C). The remaining plant treatments had similar

($p > 0.05$) WUE ranging from 1.11 in SLMD to 1.66 in SLM plants. On 28 July, *M. porteri* was green and growing actively, which resulted in greater ($p < 0.05$) WUE than those found in *L. tridentata*. The WUE of *M. porteri* ranged from 2.39 in MDSL to 5.41 in MLL plants, while that in *L. tridentata* ranged from 0.64 in SLM to 0.99 in LLM plants. On 25 August 1998, MLL and MDSL had similar ($p > 0.05$) WUE and values for these plants were greater ($p < 0.05$) than those in the other treatments. On 29 September 1998, SLMD, LLM and SLM plants showed similar ($p > 0.05$) WUE. Water use efficiency was lower ($p < 0.05$) in the SL than in the SLMD treatment.

Results indicated that *M. porteri* had higher WUE than *L. tridentata* despite both of them showed similar photosynthetic activities. Effects of defoliation of *M. porteri* or growth of this species under different size *L. tridentata* plants did not have clear effects on WUE. A difference in WUE was not found with size in *L. tridentata* plants. This was because these plants had similar ψ_L and photosynthetic activities. In turn, this was the result of soil water availability above 0.6 m depth in this area (Franco et al., 1994), and the fact that a large proportion of the roots were found at this depth.

Fall Season. In 1997, *L. tridentata*, had the highest ($p < 0.05$) WUE on 9 November (2.95 [mmol C/mol H₂O] / m²/h), whereas in 1998, this species reached the highest WUE on 5 October (3.58) (Fig. 5C). The lowest ($p < 0.05$) WUE was found on 28 October 1998. Within each fall date on either year, *L. tridentata* plants showed similar ($p > 0.05$) WUE in the different treatments. It seems that *L. tridentata* shows a higher WUE when soil water potentials decline. In this sense, *L. tridentata* fits the classification of Lambers et al. (1998): a drought-tolerant species which shows continued photosynthesis in the phase of declining ψ_L and transpiration. Dates when *M. porteri* was green (i.e., 5 October 1997; 3 November 1998) showed similar ($p > 0.05$) WUE for this species. *M. porteri* had a higher WUE than *L. tridentata* ($p < 0.0001$). Within any species, there were no differences ($p > 0.05$) between plant treatments.

On 5 October 1997, *M. porteri* plants had the greatest ($p < 0.05$) WUE and there were no differences among *M. porteri* plants. MSL plants of *M. porteri* showed similar ($p > 0.05$) WUE than *L. tridentata*. On 9 November 1997, and on 5 and 28 October 1998, there were no differences ($p > 0.05$) between shrub plants. On 3 November 1998, there were no differences ($p > 0.05$) between *M. porteri* plants. *Larrea tridentata* plants also were statistically similar ($p > 0.05$) in WUE. As a whole, *L. tridentata* plants had lower ($p < 0.05$) WUE than M and MSL *M. porteri*. *Muhlenbergia porteri* had higher ψ_L and WUE than *L. tridentata*.

Winter Season. *Muhlenbergia porteri* was dormant during the winter season. As a result, only WUE for *L. tridentata* were calculated (Fig. 6C). The highest WUE ($p < 0.05$) recorded on 28 January 1999 was on *L. tridentata*, showing a value of 4.62 [mmol C/mol H₂O]/m²/h. This value was followed by those obtained on 19 December and 7 March 1998. On 20 February 1998, WUE were lower than those reported previously, but they were greater ($p < 0.05$) than those found on 8 February 1999. On this date, WUE were greater ($p < 0.05$) than those found on 22 March 1998.

There was no relationship ($p > 0.05$) with soil water potential, probably because of the high soil water potentials during winter. At this time, when transpiration and photosynthesis were measured, values were above -0.8 MPa. Pre-dawn ψ_L seemed to be related to WUE, as sampling dates with low ψ_L had higher WUE. The only exception was on samples collected on 19 December 1998. Photosynthetic activity responded to increases in air temperature, but not to ψ_L . This suggests that *L. tridentata* responds independently to ψ_L , although values were higher than -4.0 MPa. Increased ψ_L and temperatures resulted in increased photosynthetic activity, while decreases in temperature during periods of high ψ_L resulted in decreased photosynthetic activity. Water use efficiency was similar ($p > 0.05$) between treatments in *L. tridentata* plants.

On 20 February and 7 March 1998, there was no difference ($p > 0.05$) in WUE between *L. tridentata* plants. On 22 March 1998, SL, SLMD, and LLM had greater ($p < 0.05$) WUE than SLM and LL. On 19 December 1998, and 28 January 1999, there were no differences ($p > 0.05$) in WUE among treatments on *L. tridentata* plants. On 8 February 1999, WUE was greatest ($p < 0.05$) on SL than on the other treated *L. tridentata* plants.

Spring Season. During spring, the highest ($p < 0.05$) WUE on *L. tridentata* plants was on 18 April 1998 (mean = 1.93 [mmol C/mol H₂O]/m²/h; Fig. 7C). Water use efficiency in this shrub was similar ($p > 0.05$) on 10 April, 25 May, and 8 and 23 June 1998. Lowest ($p < 0.05$) WUE on *L. tridentata* occurred on 18 and 25 May, and 8 June 1998.

When comparing WUE values between plant species, significant differences ($p < 0.05$) were found in small *L. tridentata* plants, where SLMD and SLM showed values of 1.39 and 1.1, respectively. When *M. porteri* was green, on 10 and 18 April 1998, WUE was similar ($p > 0.05$) at these dates. Water use efficiency was higher ($p < 0.01$) in *M. porteri* than in *L. tridentata* plants during the 1998 growing season. Water use efficiency was also higher ($p < 0.05$) in MDSL than MSL plants.

On 10 April 1998, MLL and MDSL had the greatest ($p < 0.05$) WUE. At this time, WUE was similar ($p < 0.05$) on MDSL, MSL, and M plants. Also, M, LLM, SL and SLMD plants showed a similar ($p < 0.05$) WUE. There were no statistical differences ($p > 0.05$) in WUE between treatments for *L. tridentata* plants. On 18 April, there were no differences ($p < 0.05$) between

M. porteri and *L. tridentata* plants. MDSL had greater WUE than *L. tridentata* plants ($p < 0.05$). On 18 and 25 May, and on 8 and 23 June 1998, there were no differences ($p < 0.05$) between plant treatments within each date.

When there was high soil water potentials due to winter rainfall, *L. tridentata* showed high WUE. This may contribute to increase the survival ability of this shrub to drought periods. The C_4 pathway in *M. porteri* allows a greater C fixation with lower transpirational water loss than a C_3 plant, contributing to its greater WUE.

CONCLUSIONS

The hypothesis that the resource islands under *L. tridentata* provide water and a better microhabitat for *M. porteri* needs to be rejected in this study. This is because grass plants growing under *L. tridentata* and those growing alone showed no differences in the study variables. In addition, *M. porteri* growing alone had a greater photosynthetic activity than *M. porteri* growing under the canopy of *L. tridentata* in the fall.

The hypothesis that *M. porteri* and *L. tridentata* coexist because they stratify periods of greatest physiological activity was partially true. Predawn ψ_L and photosynthetic activity responded to soil water availability during spring, summer, and fall in both C_3 and C_4 plants.

Soil moisture availability in spring, summer, and fall, and winter temperatures contribute to dryness of *M. porteri*. *Muhlenbergia porteri* showed a good and rapid response to the episodic soil moisture availability in spring, summer and fall. We demonstrated that *M. porteri*, like several C_4 grasses, is an opportunistic plant (i.e., see Bamberg et al., 1975). As such, it quickly responded to greater soil moisture and warm temperature conditions by increasing its C assimilation and growth. These results partially agree with those of Nobel (1980) in the C_4 plant *Hilaria rigida*; this grass was more influenced by water availability than by low temperatures.

Larrea tridentata showed net C assimilation during the entire study period, except on 25 January 1998, demonstrating its resistance to extreme both soil moisture and temperature conditions. These results agree with findings of Strain & Chase (1966) and Bamberg et al. (1975). *Larrea tridentata* was always metabolically active (Oechel et al., 1972). It was not dormant like *M. porteri* under moisture or temperature stress. *Larrea tridentata* behaved as an opportunistic species because of its increased photosynthetic activity during periods of high soil water potential. A general pattern of water competition with *M. porteri* was shown when *L. tridentata* growing alone showed a greater net assimilation after a high rainfall event. However, we were unable to detect if *M. porteri* was affected by the presence of *L. tridentata*. Dodd et al. (1998) found that the woody plant *Atriplex canescens* used water from different soil horizons than the grasses growing under its canopy.

The hypothesis that *M. porteri* has greater photosynthetic rates when growing under small than large *L. tridentata* had to be rejected. This was because this grass did not have greater photosynthetic rates when growing under small shrubs. However, differences were found with plant size in *L. tridentata* and when this shrub either was or was not in competition with *M. porteri*. During winter, SL had higher photosynthetic activity than SLM and SLMD. At the same time, LL and SL had higher photosynthetic activity than LLM, SLM and SLMD.

The hypothesis that removal of senescent plant material in *M. porteri* would result in greater photosynthetic rates due to greater light availability for photosynthesis was rejected. This was because defoliation of 50% biomass of *M. porteri* did not result in greater photosynthetic rates compared to undefoliated plants. During summer 1998, photosynthetic activity of small *L. tridentata* plants was greater when *M. porteri* growing under its canopy was defoliated than when it remained undefoliated. We conclude therefore that *L. tridentata* shows the major effects when it grows associated with *M. porteri*. These effects are shown by a reduced (1) ability to gather resources (i.e., water), and (2) capacity for photosynthetic C assimilation and subsequent growth.

ACKNOWLEDGMENTS

We thank the Consejo Nacional de Ciencia y Tecnología de México for the scholarship to the first author, which allowed to carry out his doctoral studies at the New Mexico State University. We also acknowledge the USDA-ARS Jornada Experimental Range Lab for the facilities offered. Daily weather data sets were provided by the Jornada Long-Term Ecological Research (LTER) project. Funding for conducting this research was provided by the U.S. National Science Foundation (Grant DEB-0080412).

REFERENCES

- Almeida-Martinez, R. (1981). Seasonal defoliation and growth responses of *Muhlenbergia porteri* Scrib. Ex Beal in pure stands and in association with *Larrea tridentata* (DC) Coville, with emphasis on structural analysis. PhD Dissertation. New Mexico State University.
- Ballaré, C.L., A.L. Scopel & R.A. Sánchez (1990). Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* 247: 329-332.
- Bamberg, S.A., G.E. Kleinkopf, A. Wallace & A. Vollmer (1975). Comparative photosynthetic production of Mojave desert shrubs. *Ecology* 56: 732-736.
- Bullock, Jr. H.E. & R.E. Neher (1980). Soil Survey of Dona Ana County Area of New Mexico. USDA, SCS in cooperation with USDI, BLM, and NM Agricultural Experiment Station.
- Carr-Smith, H.D., C.B. Johnson & B. Thomas (1989). Action spectrum for the effect of day-extensions on flowering and apex elongation in green, light-grown wheat (*Triticum aestivum* L.). *Planta* 179: 428-432.
- de Soyza, A.G., A.C. Franco, R.A. Virginia, J.F. Reynolds & W.G. Whitford (1996). Effects of plant size on photosynthesis and water relations in the desert shrub *Prosopis glandulosa*

- (Fabacea). *American Journal of Botany* 83: 99-105.
- Dodd, M.B., W.K. Lauenroth & J.M. Welker (1998). Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. *Oecologia* 117: 504-512.
- Donart, G.B., D. Sylvester & W. Hickey (1978). A vegetation classification system for New Mexico, U.S.A. First International Rangeland Congress 1: 488-490.
- Farquhar, G.D. & T.D. Sharkey (1982). Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* 33: 317-345.
- Franco, A.C., A.G. de Soya, R.A. Virginia, J.F. Reynolds & W.G. Whitford (1994). Effects of plant size and water relations on gas exchange and growth of the desert shrub. *Oecologia* 97: 171-178.
- Freitas, M.O. (1997). Drought. In: Prasad, M.N.V. (ed). p.129-149. Plant Ecophysiology. John Wiley & Sons, Inc. USA.
- Giorgetti, H. D., Z. Manuel, O.A. Montenegro, G.D. Rodríguez & C.A. Busso (2000). Phenology of some herbaceous and woody species in central, semiarid Argentina. *Phyton, International Journal of Experimental Botany* 69: 91-108.
- Gray, G.R., L.V. Savitch, A.G. Ivanov & N.P.A. Huner (1996). Photosystem II excitation pressure and development of resistance to photoinhibition. II. Adjustment of photosynthetic capacity in winter wheat and winter rye. *Plant Physiology* 110: 61-71.
- Kunkel, K.E., N.R. Malm & R.A. Earl (1988). Climate Guide, Las Cruces, 1851-1987. Research Report No. 623. Agricultural Experiment Station. New Mexico State University, Las Cruces New Mexico, USA.
- Lambers, H., F.S. Chapin III & T.L. Pons (1998). Plant Physiological Ecology. Springer-Verlag, New York.
- Littell, R.C., R.J. Freund & P.C. Spector (1991). SAS systems for linear models. SAS Institute Inc. Cary NC, USA.
- Ludwig, J.A., J.F. Reynolds & P.D. Whitson (1975). Size-biomass relationships of Several Chihuahuan Desert shrubs. *The American Midland Naturalist* 94: 451-461.
- Maker, H.J., H.E. Dregne, V.G. Link & J.U. Anderson (1974). Soils of New Mexico. New Mexico State Agricultural Experiment Station. Research Report No. 285.
- Mooney, H.A., O. Björkman & G.J. Collatz (1978). Photosynthetic acclimation to temperature in the desert shrub, *Larrea divaricata*. *Plant Physiology* 61: 406-410.
- Nobel, P.S. (1980). Water vapor conductance and CO₂ uptake for leaves of a C₄ desert grass, *Hilaria mutica*. *Ecology* 61: 252-258.
- Oechel, W.C., B.R. Strain & W.R. Odening (1972). Tissue water potential, photosynthesis, ¹⁴C-labeled photosynthate utilization, and growth in the desert shrub *Larrea divaricata* Cav. *Ecological Monographs* 42: 127-141.
- Pieper, R.D. (1994). Ecological implications of livestock grazing. In: Vara M., Laycock W.A. and Pieper R.D. (eds), p. 177-211. Ecological Implications of Livestock Herbivory in the West. Society for Range Management. Denver, CO.
- Pockman, W.T. & J.S. Sperry (1997). Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* 109: 19-27.
- Polley, H.W. (2002). Implications of atmospheric and climatic change for crop yield and water use efficiency. *Crop Science* 42: 131-140.
- Reynolds, J.F. (1986). Adaptive strategies of desert shrubs with special reference to the creosotebush (*Larrea tridentata* [DC] Cov.). In: Whitford, W.G. (ed), p. 19-49. Pattern and Process in Desert Ecosystems. University of New Mexico Press.
- Reynolds, J.F., R.A. Virginia, P.R. Kemp, A.G. de Soya & D.C. Tremmel (1999). Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs* 69: 69-106.
- Runyon, E.H. (1934). The organization of the creosotebush with respect to drought. *Ecology* 15: 128-138.
- Scholander, P.F., H.T. Hammel, E.D. Bradstreet & E.A. Hemmingeng (1965). Sap pressure in vascular plants. *Science* 148: 339-346.
- Shirke, P.A. & U.V. Pathre (2004). Influence of leaf-to-air vapour pressure deficit (VPD) on the biochemistry and physiology of photosynthesis in *Prosopis juliflora*. *Journal of Experimental Botany* 55: 2111-2120.
- Strain, B.R. & V.C. Chase (1966). Effect of past and prevailing temperatures on the Carbon dioxide exchange capacities of some woody desert perennials. *Ecology* 47: 1043-1045.
- Tidestrom, I. & T. Kittell (1941). A Flora of Arizona and New Mexico. The Catholic University of America Press. Washington, D.C.
- Welsh, R.G. (1972). Some ecological relationships between creosotebush (*Larrea tridentata* DC.) and bush muhly (*Muhlenbergia porteri* Scribn). M.S. Thesis. New Mexico State University.
- Welsh, R.G. & R.F. Beck (1976). Some ecological relationships between creosotebush and bush muhly. *Journal of Range Management* 29: 472-475.