# INSTITUTO POTOSINO DE INVESTIGACIÓN CIENTÍFICA Y TECNOLÓGICA, A.C.

## POSGRADO EN CIENCIAS AMBIENTALES

# The contribution of dew and fog in the water balance of a continental semiarid grassland ecosystem

Tesis que presenta

**Carlos Alberto Aguirre Gutierrez**

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**Director de la Tesis:**
**Dr. José Tulio Arredondo Moreno**

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# Constancia de aprobación de la tesis

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**Dr. José Tulio Arredondo Moreno**
Director de la tesis

**Dr. Enrico Arturo Yépez González**
Miembro del Comité Tutoral

**Dr. Friso Holwerda**
Miembro del Comité Tutoral

**Dr. Martín Escoto Rodríguez**
Miembro del Comité Tutoral

**Dr. José Noel Carbajal Pérez**
Miembro del Comité Tutoral

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| **Dr. Martín Escoto Rodríguez** | **Sinodal externo** | **UASLP** |

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DOCTOR EN CIENCIAS AMBIENTALES

sustentó el C.

**Carlos Alberto Aguirre Gutiérrez**

sobre la Tesis intitulada:

***The contribution of dew and fog in the water balance of a continental semiarid grassland ecosystem***

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**Dr. José Tulio Arredondo Moreno**

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# Dedicatorias

Esta tesis es a nombre de todos mis familiares que han partido y dejaron un vacío en el corazón de la familia.

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# Definición de variables

| | |
|---|---|
| $G$ | Soil heat flux, W m$^{-2}$ |
| $\Theta$ | soil moisture content, m$^{3}$ m$^{-3}$ |
| $T_s$ | Soil temperature, °C |
| $T_{dew}$ | dew point temperature, °C |
| $e$ | vapor pressure, Pa |
| $\lambda E$ | evaporation of free liquid water, W m$^{-2}$ |
| $Q^*$ | net radiation, W m$^{-2}$ |
| $S$ | slope of the saturation specific humidity, K$^{-1}$ |
| $\Upsilon$ | psychrometric constant, K$^{-1}$ |
| $\delta q$ | specific humidity specific, Kg Kg$^{-1}$ |
| $r_{av}$ | aerodynamic resistance to water vapor transport, s m$^{-1}$ |
| $\rho$ | air density, Kg m$^{-3}$ |
| $\lambda_v$ | latent heat of vaporization, J Kg$^{-1}$ |
| $T_a$ | air temperature, °C |
| $d$ | deep, m |
| $\rho_b$ | soil bulk density, g cm$^{-3}$ |
| $C_d$ | heat capacity of dry soil, J Kg$^{-1}$ |
| $\Theta_v$ | volumetric soil water content, m$^{-3}$/v |
| $\rho_w$ | water density, g cm$^{-3}$ |
| $C_w$ | heat capacity of water, J cm$^{-3}$ K$^{-1}$ |
| $C_s$ | heat capacity of soil, J cm$^{-3}$ K$^{-1}$ |
| $z_r$ | height reference, m |
| $z_{ov}$ | roughness length of water vapor, m |
| $z_o$ | roughness length of momentum, m |
| $z_{oh}$ | roughness length of heat, m |
| $k$ | von Karman’s constant. |
| $L$ | Obukhov’s stability length, m |
| $u_r$ | wind speed, m s$^{-1}$ |
| $\varphi_m$ | integrated stability function for momentum. |
| $\varphi_v$ | integrated stability function for vapor. |
| $Ri_B$ | bulk Richardson number. |
| $C_1$ | constant. |
| $g$ | acceleration of gravity, m s$^{-2}$ |
| $T_0$ | surface temperature, °C |
| $\varepsilon$ | emissivity. |
| $\sigma$ | Stefan Boltzmann, W m$^{-2}$ K$^{-4}$ |
| $R_{lo}$ | outgoing longwave radiation, W m$^{-2}$ |
| $n$ | Monin Obukhov parameter. |
| **AGC** | automatic gain control. |

# Resumen

## La importancia y contribución del rocío al balance de agua de un pastizal continental semiárido.

En las regiones áridas y semiáridas, el agua es escasa y juega un papel importante en la distribución, densidad, cobertura y productividad de las plantas; así como también controla muchos otros procesos biológicos. En estas regiones, otras fuentes de agua, tales como el rocío y niebla pueden ser fuentes constantes de agua que contribuyen significativamente al balance hídrico. El objetivo de este estudio fue medir la duración, frecuencia y cantidad de rocío de enero 2011 a diciembre de 2016, para evaluar su contribución local al balance hídrico de un pastizal semiárido continental. Encontramos que el rocío es un fenómeno muy común que ocurre el 39% de las noches durante el año, con una duración promedio de 5 ± 4 horas. Con una cantidad promedio de rocío de 0.2 mm y una máxima de 0.7 mm durante el período de estudio. La cantidad anual promedio de rocío varió entre 16.5 y 69 mm durante el período de estudio, lo que representa desde 4.9% hasta 10.2% de la precipitación anual. Mientras que, durante la temporada de secas, el rocío, contribuye entre 7.6% y 33.6% del total de la precipitación, lo cual reduce el déficit hídrico considerablemente. También, identificamos y determinamos los posibles mecanismos del uso de agua de rocío y la asignación de recursos hídricos de dos especies de pastos (*Bouteloua gracilis* y *Muhlenbergia rígida*). Encontramos que las dos especies, tienen un patrón de uso del agua mayormente de la superficie del suelo (5-10 cm) durante la temporada de lluvias, sin embargo, estas especies son capaces de extraer agua de partes más profundas del suelo durante la temporada de secas, lo que les permitiría sobrevivir sequías prolongadas. Además, usamos el modelo, IsoSource, con el cual se determinó que el rocío se puede considerar una fuente importante de agua para ambas especies. Por otra parte, es conocido que la mayoría de las plantas tienen la capacidad de tomar el agua acumulada en la superficie de la hoja, lo cual mejora procesos fisiológicos, crecimiento y supervivencia de la planta. En este trabajo demostramos que tanto *B. gracilis* mientras que en *M. rígida* tienen la capacidad de absorber el agua a través de la hoja, y la principal ruta de absorción es a través de la epidermis en *B. gracilis* y *M. rígida* probablemente a través de los estomas y tricomas. Tales diferencias, fueron atribuidas a la alta resistencia por la superficie de la hoja especialmente al grosor de la cutícula y su permeabilidad. Estos resultados modifican significativamente el paradigma de la importancia del rocío en los pastizales de las zonas semiáridas y el uso del rocío por los pastos, donde estas fuentes de rocío son consideradas insignificantes y no se considera una fuente potencial de agua.

Palabras clave: *B. gracilis*, *M. rígida*, rehidratación cinética, IsoSource, toma de agua a través de la hoja

# Abstract

## The role of dew and fog contribution in the water balance of a continental semiarid grassland

In arid and semiarid regions, water scarcity plays an important role in determining the plant distribution, density, cover and productivity; it also controls many other biological processes. In these regions, different water sources such as dew and fog may serve as a reliable water source that significantly contributes to the annual water balance. The aim of this study was measuring the frequency, duration and amount of dewfall from January 2011 to December 2016 to assess its contribution to the local water balance in a continental semiarid grassland. We found that dewfall occurred on 39% of the nights with an average duration of 5 ± 4 h. Daily average dewfall deposition during the study period was 0.2 mm with the highest accumulation of 0.7 mm. Annual dewfall ranged between 16.5 and 69 mm over the course of the study, therefore representing between 4.9 % and 10.2% of annual precipitation. Dewfall contributed between 7.6% and 33.6% of the total dry season precipitation, which considerably reduced the water deficit. We also identified and tested the possible mechanism of water resource partitioning and the use of dew of the grass species *B. gracilis* and *M.rigida*. We found that *B. gracilis* and *M. rigida* overlapped in patterns of water extraction during the wet season (5-10 cm), but they shift their water uptake during the dry season using soil water from 15-25 cm depth. The IsoSource model also showed that dew can have an important contribution as a water source for both species. It is well known that most plants species exhibit capabilities of water uptake from the leaf surface, helping to improve its physiological processes, growth and survival. The results underscore the importance of considering plant rehydration through the leaf surface pathway in studies of plant-water relations. These results significantly modify the current paradigm on the role of dew in a continental semiarid grassland, and the dew water use by grasses, where dew water is considered negligible and is not regarded as a potential water source.

Key words: *B. gracilis*, *M. rígida*, rehydration kinetic, IsoSource, leaf water uptake

# General Introduction

Dew is the moisture which condenses from the atmosphere on plants, soil, or other surfaces near the ground whose temperature is reduced by radiative cooling to below the dew point temperature of surrounding air (Agam, 2004; Leopold, 1952). It is important and helpful for plants (Berry et al., 2019; Jacobs et al., 1999), and is a key limiting factor in arid and semiarid ecosystem (Kidron, 2000a, 1999; Malek et al., 1999a). As arid and semiarid ecosystems are characterized by very low soil moisture and scant perennial vegetation, dew may play a special role because its small but regular supply of moisture to a given surface, which can serve as a particularly stable water source (Veste et al., 2008) that contributes significantly to the annual water balance, especially during dry years (Kalthoff et al., 2006), and can offset water loss caused by soil evaporation during the dry season (Hanisch et al., 2015; Kalthoff et al., 2006; Malek et al., 1999b; M L Sharma, 1976; Uclés et al., 2014).

The importance of dew is not only on the water balance context, but also has effects on plant function, including altering leaf energy balance, reducing plant transpiration rates during the morning, and serving as alternative water source for plants through foliar uptake (Dawson and Goldsmith, 2018a; Guo et al., 2016; Munné-Bosch and Alegre, 1999). The capacity of leaves to absorb dew has an important role in rehydrating and reactivating the metabolism of water-stressed plants, which is especially relevant during a prolonged drought (Munné-Bosch and Alegre, 1999). Dew is therefore considered an important water source contributing to the survival of plants, especially in arid and semiarid regions (Pan et al., 2010; Westbeld et al., 2009). Nevertheless, studies examining the role of dew have been carried out almost exclusively in coastal or high altitude locations (Hanisch et al., 2015; Matimati et al., 2013), whereas the importance of dew in continental arid and semiarid ecosystems has not been well studied.

However, data on frequency, duration and amount of dewfall, or its contribution to the local water balance in semiarid continental grassland ecosystem are not available. In contrast, only a few studies have examined dew contribution in continental arid and semiarid environments, even though dew in these areas may be quite common (Vuollekoski et al., 2015). Dew occurrence and its contribution to the water balance of continental arid and semiarid ecosystems have been considered negligible with respect to rainfall. However, Sharrma (1976) reported that dewfall contributed about 30% of the total precipitation for a semiarid grassland in New South Wales, Australia. Similarly, in semiarid desert valleys, Malek et al. (1999) found that dew contributed about 14 mm year$^{-1}$ in Nevada and that dew and frost contribute about 29 mm year$^{-1}$ in Utah to the annual water balance. Thus, there is some evidence that dew may be more important than has previously been recognized for these ecosystems.

In México the semiarid zones represent the 29% of the territory, where the semiarid grassland constitute one of the main vegetation types, potentially covering about 22% of the territory (Rzedowski, 2007), with more than 80% of this distributed in the Mexican Altiplano. This region is highly diverse in the number of species and community assemblages dominated by *Bouteloua gracilis* (*H.B.K*). Lag. ex Steud which is considered the key species in many cases (Medina-Roldán et al., 2007). This grass species evolved under a diverse set of natural disturbance factors which include natural fire, grazing by native ungulates and recurring droughts, that favored particular ecophysiological adaptations (e.g. stem growth zones or meristem at ground base for regeneration after defoliation, drought and salinity tolerance, high tillering rates and high specific leaf area) to their complex natural disturbance regimes. It has been suggested that these factors are the most important controls of community richness, composition and structure (Blair et al., 2014).

However, it is less clear how other adaptations such as, leaf tissue capacity to absorb dew water, play a role in the maintenance of a species in a harsh environment. In the semiarid grassland in central Mexico, 60% of total precipitation events comes as rain of 5 mm or less, whereas precipitation events of > 10 mm accounted to most of the annual precipitation (Delgado-Balbuena, 2016). Summer precipitation represents around 90% of annual total precipitation with winter rains accounting from 5 to 18% (Delgado-Balbuena, 2016; Aguirre-Gutiérrez et al., 2019). In this semiarid continental grassland, dew has been considered so far as a negligible source of water to the ecosystem, however a recent study showed that dew may annually contribute with 2 to 11% of total precipitation. Therefore, becoming another potential source of water particularly during the drought period because it contributes with 7 to 33 % of winter precipitation (Aguirre-Gutiérrez et al., 2019).

This may be of particular interest in grass species subject to dew. Of the more than 120 species tested for its capacity to carry out foliar water uptake (Dawson and Goldsmith, 2018b), only three have been grasses (Breazeale et al., 1950; Suárez and Gloser, 1982) including Panicum maximum, Zeas mays, Paspalum notatum. Despite the considerable interest in foliar water uptake and increasing recognition of the role it may play in plant communities and ecosystem functioning, our understanding of when, where, and how foliar water uptake occurs in grasslands remains limited, this may translate into large alterations in ecosystem functions because of the vast geographical extend of this biome (Berry et al., 2019).

In this study, six years of continuous micrometeorological measurements in the southernmost part of the semiarid grassland in North America were analyzed. The aim of this study was determining the role of dew and measure the frequency, duration and amount of dewfall, or its contribution to the local water balance. In particular, understand the potential use of dew water by tow native grass species during the dry season in the semiarid grassland. Special emphasis was paid to the ecological and benefits of foliar water uptake of the two species *B. gracilis* and *M. rigida*.

In Chapter 1, Six years of meteorological data were used to quantify the frequency and duration of dewfall. Also, the relative contribution of dewfall to the water balance was analyzed. In doing so, we also provide insights into the meteorological conditions during which dewfall occurred.

In Chapter 2, The stable isotopic composition of potential soil water sources, dew, rainfall and xylem water was used to trace the input water source into the two gras species (*B. gracilis* and *M. rigida*). The proportional used of these water resources by the two grass species in a semiarid grassland ecosystem was calculated.

In Chapter 3, The response of rehydration kinetics of water supplied via leaf's surface and corresponding improvements in grass water status in *B. gracilis* and *M. rigida* following exposure to experimental fog immersion, was evaluated.

## Bibliography

Agam, N., 2004. Diurnal Water Content Changes in the Bare Soil of a Coastal Desert. JOURNAL OF HYDROMETEOROLOGY 5, 12.

Aguirre-Gutiérrez, C.A., Holwerda, F., Goldsmith, G.R., Delgado, J., Yepez, E., Carbajal, N., Escoto-Rodríguez, M., Arredondo, J.T., 2019. The importance of dew in the water balance of a continental semiarid grassland. Journal of Arid Environments 168, 26–35. https://doi.org/10.1016/j.jaridenv.2019.05.003

BALBUENA, J.D., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2019. Foliar water uptake: Processes, pathways, and integration into plant water budgets: Foliar Water Uptake. Plant Cell Environ 42, 410–423. https://doi.org/10.1111/pce.13439

Blair, J., Nippert, J., Briggs, J., 2014. Grassland Ecology, in: Monson, R.K. (Ed.), Ecology and the Environment. Springer New York, New York, NY, pp. 389–423.

Breazeale, E.L., McGeorge, W.T., Breazeale, J.F., 1950. MOISTURE ABSORPTION BY PLANTS FROM AN ATMOSPHERE OF HIGH HUMIDITY. Plant Physiol. 25, 413–419. https://doi.org/10.1104/pp.25.3.413

Dawson, T.E., Goldsmith, G.R., 2018a. The value of wet leaves. New Phytologist 219, 1156–1169. https://doi.org/10.1111/nph.15307

Dawson, T.E., Goldsmith, G.R., 2018b. The value of wet leaves. New Phytol 219, 1156–1169. https://doi.org/10.1111/nph.15307

Delgado-Balbuena, J., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Guo, X., Zha, T., Jia, X., Wu, B., Feng, W., Xie, J., Gong, J., Zhang, Y., Peltola, H., 2016. Dynamics of dew in a cold desert-shrub ecosystem and its abiotic controls. Atmosphere 7, 1–15. https://doi.org/10.3390/atmos7030032

Hanisch, S., Lohrey, C., Buerkert, A., 2015. Dewfall and its ecological significance in semi-arid coastal south-western Madagascar. Journal of Arid Environments 121, 24–31. https://doi.org/10.1016/j.jaridenv.2015.05.007

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 1999. Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments 42, 211–222. https://doi.org/10.1006/jare.1999.0523

Kalthoff, N., Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kidron, G.J., 2000. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8. https://doi.org/10.1016/S0168-1923(99)00043-X

Leopold, L.B., 1952. Dew as a source of plant moisture.

Malek, E., McCurdy, G., Giles, B., 1999a. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999b. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments1. Malek, E., McCurdy, G. & Giles, B. Dew contribution to the annual water balances in semi-arid desert valleys. J. Arid Environ. 42, 71–80 (1999). 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Matimati, I., Musil, C.F., Raitt, L., February, E., 2013. Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem. Ecohydrology 6, 818–825.

Medina-Roldán, E., Moreno, J.T.A., Moya, E.G., Martínez, F.M.H., 2007. Soil water content dynamics along a range condition gradient in a shortgrass steppe. Rangeland Ecology and Management 60, 79–87. https://doi.org/10.2111/05-219R2.1

Munné-Bosch, S., Alegre, L., 1999. Role of dew on the recovery of water-stressed Melissa officinalis L. plants. Journal of Plant Physiology 154, 759–766.

Pan, Y., Wang, X., Zhang, Y., 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area , Northern China. Journal of Hydrology 387, 265–272. https://doi.org/10.1016/j.jhydrol.2010.04.016

Rzedowski, J., 2007. An Ecological and Phytogeographical Analysis of the Grasslands of Mexico. Taxon 24, 67–80.

Sharma, M.L., 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331.

Suárez, A.G., Gloser, J., 1982. Time course of foliar absorption of water inPanicum andPaspalum. Biol Plant 24, 226–230. https://doi.org/10.1007/BF02883669

Uclés, O., Villagarcía, L., Moro, M.J., Canton, Y., Domingo, F., 2014. Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. Hydrological Processes 28, 2271–2280. https://doi.org/10.1002/hyp.9780

Veste, M., Heusinkveld, B.G., Berkowicz, S.M., Breckle, S.-W., Littmann, T., Jacobs, A.F.G., 2008. Dew formation and activity of biological soil crusts, in: Arid Dune Ecosystems. Springer, pp. 305–318.

Vuollekoski, H., Vogt, M., Sinclair, V.A., Duplissy, J., Järvinen, H., Kyrö, E.-M., Makkonen, R., Petäjä, T., Prisle, N.L., Räisänen, P., 2015. Estimates of global dew collection potential on artificial surfaces.

Westbeld, A., Klemm, O., Grießbaum, F., Sträter, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert, in: Annales Geophysicae: Atmospheres, Hydrospheres and Space Sciences. p. 3571.

# Chapter 1

## The importance of dew in the water balance of a continental semiarid grassland

### Abstract

Dew has been recognized as an important source of water for many ecosystems, in particular for coastal arid and semiarid regions, significantly contributing to the daily and annual water balance during the dry season. We measured the frequency, duration and amount of dewfall from January 2011 to December 2016 to assess its contribution to the local water balance in a continental semiarid grassland where *Bouteloua gracilis* (Blue grama) is the key grass species. Dew was observed with leaf wetness sensors and amounts were estimated with an energy model using data derived from a micrometeorological station. Dewfall occurred on 39% of the nights with an average duration of 5 ± 4 h.  Daily average dewfall deposition during the study period was 0.2 mm with the highest accumulation of 0.7 mm. Annual dewfall ranged between 16.5 and 69 mm over the course of the study, therefore representing between 4.9 % and 10.2% of annual precipitation. Dewfall contributed between 7.6% and 33.6% of the total precipitation dry season (winter/spring), which considerably reduced the water deficit. Our results highlight the relevance of dewfall as a consistent source of water in this semiarid grassland ecosystem, as well as its significant contribution to the local water balance. It is of particular importance during dry periods, where it may represent the only water source at this site.

Key words: dewfall; grassland; semiarid; water balance

## Introduction

Dew, a common meteorological phenomenon, is the result of water condensing from atmospheric humidity on surfaces that have cooled below the dew point temperature of the surrounding air (Agam et al., 2004). In arid and semiarid regions, water is scarce and plays an important role in determining the plant distribution, density, cover and productivity (Puigdefábregas and Sánchez, 1996); it also controls many other biological processes. In these regions, dewfall may serve as a particularly stable water source (Veste et al., 2008) that contributes significantly to the annual water balance and can offset water loss caused by soil evaporation during the dry season (Hanisch et al., 2015; Kalthoff et al., 2006; Malek et al., 1999b; M L Sharma, 1976; Uclés et al., 2014).

The positive effects of dew are not only observed in the water balance, but also in its effects on plant function, including altering leaf energy balance, reducing plant transpiration rates during the morning, and serving as alternative water source for plants through foliar uptake (Dawson and Goldsmith, 2018a; Guo et al., 2016; Munné-Bosch and Alegre, 1999). Water uptake through leaves extends plant life, promotes plant growth, and increases below-ground biomass (Grammatikopoulos and Manetas, 1994a). The capacity of leaves to absorb dew has an important role in rehydrating and reactivating the metabolism of water-stressed plants, which is especially relevant during a prolonged drought (Munné-Bosch and Alegre, 1999). Dew is therefore considered an important water source contributing to the survival of plants, especially in arid and semiarid regions (Pan et al., 2010; Westbeld et al., 2009). Nevertheless, studies examining the role of dew have been carried out almost exclusively in coastal or high altitude locations (Hanisch et al., 2015; Matimati et al., 2013), whereas the importance of dew in continental arid and semiarid ecosystems has not been well studied.

Dew formation in coastal drylands is a common phenomenon due to the advection of moisture from the ocean and constitutes a significant portion of water inputs (Barradas and Glez-Medellín, 1999; Tuller and Chilton, 1973; Uclés et al., 2014; Zangvil, 1996). In contrast, only a few studies have examined dew contribution in continental arid and semiarid environments, even though dew in these areas may be quite common (Vuollekoski et al., 2015). Dew occurrence and its contribution to the water balance of continental arid and semiarid ecosystems have been considered negligible with respect to rainfall. However, Sharrma (1976) reported that dewfall contributed about 30% of the total precipitation for a semiarid grassland in New South Wales, Australia. Similarly, in semiarid desert valleys, Malek et al. (1999) found that dew contributed about 14 mm year$^{-1}$ in Nevada and that dew and frost contribute about 29 mm year$^{-1}$ in Utah to the annual water balance. Thus, there is some evidence that dew may be more important than has previously been recognized for these ecosystems.

In the most southern distribution of the North American grasslands, rainfall exhibits strong seasonal variation, with ~95% of incoming rain occurring between June and September (Delgado-Balbuena, 2016). This ecosystem may experience up to 8 months of seasonal drought, with only 5-8% of the annual rainfall falling in winter/spring (Delgado-Balbuena, 2016; Medina-Roldán et al., 2008). During this dry season, the shallow soil dries out and the atmospheric vapor pressure deficit increases, resulting in more stressful conditions for plant growth and survival (Delgado-Balbuena, 2016). Grasses are adapted to survive using several different strategies, including turning dormant during this period. Still, native perennial grasses maintain some active vegetative tissue during drought and this maintenance of tissue metabolism requires a supply of water.

In the semiarid grassland of the subprovince Llanos de Ojuelos, Jalisco, Mexico, we have observed that dew forms on the plants throughout most of the dry season; however, its contribution to the local water balance of this ecosystem is still unknown. In order to better understand the extent to which dew is an important input of water to this ecosystem and its potential as a source for the plants, we used six years of meteorological data to 1) quantify the frequency and duration of dewfall, 2) provide validated estimates for dewfall amounts, and 3) determine the relative contribution of dewfall to the water balance. In doing so, we also provide insights into the meteorological conditions during which dewfall occurred.

## Methods and Materials

### *Site description*

The study was carried out at the *Vaquerias* grassland research station of the National Institute for Agriculture, Animal Production and Forestry Research (*INIFAP*), located in the geographic subprovince Llanos de Ojuelos, Jalisco, Mexico (Figure 1). The site is located approximately 464 km from the Pacific Ocean and 344 km from the Gulf of Mexico (21.78 °N and 101.60 °W, 2240 m asl). The vegetation is a tropical semiarid grassland, with *Bouteloua gracilis* (Kunth) Lag. ex Steud as the dominant grass species. Grass cover varies between ca. 5% and 40% and reaches a height of ca. 60 cm. Canopy cover (i.e. including shrubs and other non-grass species) reaches 81.46% with a leaf area index (LAI) of 0.58 $m^2$ $m^{-2}$ (Delgado-Balbuena et al., 2013).

The region has a mean annual rainfall of 424 mm (Delgado-Balbuena, 2016), ca. 95% of which falls between June and September, while the remaining is distributed during the long dry period, but particularly from December to February. The mean annual temperature is 15.1 °C, with mean temperature extremes ranging from 26.8 °C for the warmest month to 2.6°C for the coldest month (Delgado-Balbuena, 2016).The topography consists of valleys with gentle rolling hills. The soils at the site are classified as Haplic xerosol and Haplic phaeozem, with a 15 cm of litter layer, silty clay, and sandy loam textures. The soil is shallow, with an average depth of 0.3-0.4 m and a cemented layer underneath (Santacruz et al., 1996).

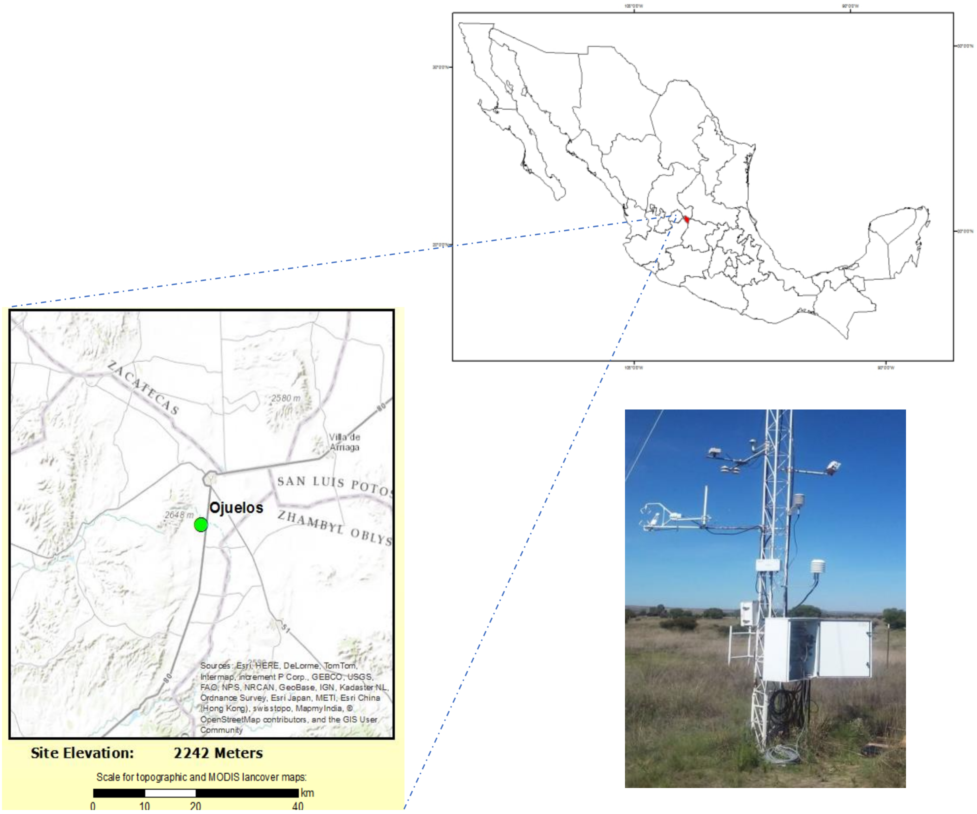


Figure 1. Location of the study area in Llanos de Ojuelos, Jalisco, Mexico and the flux tower.

*Data and measurements*

The experimental area is equipped with an automated eddy covariance system measuring several micrometeorological and meteorological variables (Figure 1). The instrumentation included a three-dimensional sonic anemometer (CSAT-3D, Campbell Sci. Logan, Utah, USA) and an open-path infrared gas analyzer (Li-7500, LICOR Inc., Lincoln, NE, USA). Sampling and data recording were carried out with a data logger (CR3000, Campbell Scientific Inc., Logan, Utah, USA) at a sampling rate of 10 Hz. Data has been collected continuously since January 2011. Using the data from the micrometeorological tower, we calculated the latent heat flux (*LE)* as:

$$LE = \lambda \rho_a \overline{w'q'} \tag{1}$$

Where $\rho_a$ is the air density ($g\ mol^{-1}$), $w'$ and $q'$ are the instantaneous deviations from a running mean of vertical air velocity ($m\ s^{-1}$) and specific humidity ($g\ H_2O/g\ air$), and λ is the energy of vaporization ($J\ g^{-1}\ H_2O$). The conversion of *LE* ($W\ m^{-2}$) to *ET* ($mm\ day^{-1}$) is using the latent heat of evaporation water ($2454\ kJ\ Kg^{-1}$).

Air temperature and relative humidity were measured with a shielded HMP45C probe mounted 2 m above ground (Vaisala, Helsinki, Finland). The wind speed and direction were measured with the sonic anemometer. Incident and reflected shortwave and longwave solar radiation were measured with a NR01 net radiometer (NR01, Hukseflux, Netherlands). Soil heat flux (*G*) was monitored with three self-calibrating plates buried at 8 cm deep (HFP01SC, Hukseflux, Netherlands). To measure average soil temperature ($T_s$) above the soil heat flux plates and calculate the storage term (see below), we used T108 temperature probes (Campbell Sci, Logan UT) located at 2 and 6 cm deep near the plates. Soil moisture content ($\Theta$) was measured with TDR (time domain reflectometry) sensors using the standard calibration equation from Campbell (CS616, Campbell Sci., Logan, Utha, USA). Sensors were horizontally positioned at 2.5 cm and 15 cm deep. In April 2016, we installed 4 additional soil moisture sensors at 15, 30, 50 and 60 cm deep. Rainfall was recorded by a tipping bucket rain gauge installed 5 m away from the tower. Dewpoint temperature ($T_{dew}$, °C) was calculated using the expression of (Dingman, 2015):

$$T_{dew} = (ln(e * 10) - 1.810)/\left(0.0805 - 0.00421 * ln(e * 10)\right) \qquad (2)$$

Where *e* (Pa) is the vapor pressure that was calculated using the humidity relativity and temperature from the HMP45C probe.

*Dewfall model*

In this study, we calculated condensation (dew formation) and evaporation of free liquid water $\lambda E$ in W m$^{-2}$ following (Jacobs et al., 2006):

$$\lambda E = \frac{s}{s+\gamma}(Q^{*} - G) + \frac{\gamma}{s+\gamma}\frac{\rho \lambda_v \delta q}{r_{av}} \tag{3}$$

Where $Q^{*}$ (W m$^{-2}$) is net radiation, $G$ (W m$^{-2}$) soil heat flux, $s = dq^{*}/dT$ (K$^{-1}$) the slope of the saturation specific humidity curve, $Y = c_p/\lambda_v$ (K$^{-1}$) the psychrometric constant, $\delta q = q^{*}(T_a) - q$ (Kg Kg$^{-1}$) the specific humidity deficit at the reference level, $r_{av}$ (s m$^{-1}$) the aerodynamic resistance to water vapor transport, $\rho$ (kg m$^{-3}$) the air density, $\lambda_v$ (J kg$^{-1}$) the latent heat of vaporization, and $T_a$ the air temperature.

The soil heat flux ($G$) was calculated by summing the measured flux at $d$ = 0.08 m, and the change in energy stored in the layer above the heat flux plates.

The heat capacity of the soil was calculated as:

$$C_s = \rho_b * C_d + \theta_v * \rho_w * C_w \tag{4}$$

Where $\rho_b$is the soil bulk density (1.5 g cm$^{-3}$), $C_d$ the heat capacity of the dry soil (840 J Kg$^{-1}$), $\theta_v$ the volumetric soil water content (v/v), $\rho_w$ the density of water (1 g cm$^{-3}$), and $C_w$ the heat capacity of water (4.1796 J cm$^{-3}$ K$^{-1}$).

The aerodynamic resistance to vapor transport, $r_{av}$, was obtained using (Garratt, 1992):

$$r_{av} = \frac{\left(ln\frac{z_r}{z_{ov}} - \varphi_v(n_r) + \varphi_v(n_{ov})\right)\left(ln\frac{z_r}{z_o} - \varphi_m(n_r) + \varphi_m(n_o)\right)}{k^2 u_r} \tag{5}$$

Where $z_r$ is the reference height, $z_r = 3\ m$ and $z_{ov}$ and $z_o$ represent the roughness lengths for water vapor and momentum, *k* is the von Karman's constant (0.41), where:

$$n_r = \frac{z_r}{L}; n_o = \frac{z_0}{L}; n_{ov} = \frac{z_{ov}}{L} u_r \tag{5a}$$

$$z_0 = \left( \frac{z-d}{exp\left( {}^{0.4U}/_{U*} \right)} \right) \tag{5b}$$

$$z_{ov} = 0.096 * z_o \tag{5c}$$

with *L* being the Obukhov's stability length scale (m), $u_r$ the wind speed (m s$^{-1}$) at $z_r$, and $\varphi_v$ and $\varphi_m$ the integrated stability functions for vapor and momentum, respectively.

The dimensionless parameters were obtained following 1(De Bruin et al., 2000):

$$n_r = \frac{z_r}{L} = Ri_B(z_r)\ for\ Ri_B < 0 \tag{6a}$$

$$n_r = \frac{z_r}{L} = \left| \frac{Ri_B(z_r)}{1 - c_1 Ri_B(z_r)} \right|\ for\ Ri_B \geq 0 \tag{6b}$$

Where:

$$Ri_B = \frac{g}{T_{abs}(z_r)} \frac{(z_r - z_{oh})(T_a(z_r) - T_o)}{u^2(z_r)} \tag{7}$$

Where $Ri_B$ is the bulk Richardson number, *g* the acceleration of gravity (m s$^{-2}$), $T_{abs}$ is the absolute temperature at the reference height *($z_r$)*, $C_1$=5 a constant, $z_{oh}$ the roughness length for heat (taken equal to $z_{ov}$), $T_o$ the surface temperature. As we did not measure $T_o$, it was calculated using the outgoing longwave radiation:

$$T_0 = \sqrt[4]{R_{lo}/\varepsilon\sigma} \tag{8}$$

Where $\varepsilon$ is the emissivity (taken as 0.99), $\sigma$ the Boltzmann constant (5.67036713) $\times 10^{-8}$ $W \cdot m^{-2} \cdot K^{-4}$), and $R_{lo}$ the outgoing longwave radiation (W $m^{-2}$).

Finally, we calculated the stability functions for momentum $\varphi_m$ and water vapor $\varphi_v$ using (Garrat, 1992):

$$\varphi_m(n) = -5n \;\; for \;\; n \geq 0 \tag{9a}$$

$$\varphi_m = 2ln\left(\frac{1+x}{2}\right) + ln\left(\frac{1+x^2}{2}\right) - 2tan(x) + \frac{\pi}{2} \; for \; n < 0 \tag{9b}$$

where $x = (1 + 16|n|)^{0.25}$

$$\varphi_v(n) = -5(n) for \; n \geq 0 \tag{10a}$$

$$\varphi_v = 2ln\left(\frac{1+x^2}{2}\right) for \; n < 0 \tag{10b}$$

Positive values obtained with equation (3) correspond to evaporation, whereas negative values represent condensation (dew formation). Cumulative dewfall was calculated at daily, monthly and yearly intervals by summing the negative values. A table with all of the variables is provided in Appendix 1.

### *Validation of dewfall calculations*

To compare dew estimates derived from the model described above to observations in the field, direct dew measurements were carried out using automated weighing microlysimeters with a cantilever load cell (2 kg rated capacity) of the type proposed by (Heusinkveld et al., 2006). Four load cells containing soil and grass (*B. gracilis*) samples were installed in the field from November to December 2016. The load cell was inserted into a PVC box, 5 mm thick, to protect the load cell and the sampling dish. The sampling dish was made of aluminum; it was attached into a threaded hole in the loading end of the load cell for protection. The microlysimeters were randomly located and buried in the grassland.

The four load cells were installed at 0.3 m depth (Figure 2). Changes in mass weight were monitored every 5 s and averaged at 15 min intervals using a CR1000 Datalogger (Cambell Scientific, Logan, UT, USA). Load cell data therefore consisted of a weighted averaged between the differences of consecutive records (and converted in mm). Field calibration was completed before the installation using standard loads; however, as the output of load cells were in mV, a calibration curve had to be used for each load cell. We measured the weight change during four weeks, but two weeks of records were not used due to strong rainfall events.

Figure 2. A microlysimeter and leaf wetness sensor (LWS) installed in the study area.

At the same time, the occurrence, frequency and duration of dewfall events were automatically recorded with a leaf wetness sensor (LWS, Decagon Devices, Inc., Pullman, WA, USA) connected to a data logger (CR1000, Campbell Scientific Ltd.). One sensor was mounted flat at 0.10 m (at the base of a grass) and another mounted at a slight angle at 1 m above the ground. Measurements were recorded at 1 s frequency and stored each minute. We defined the wet/dry transition point of the LWS in the field through visual observation and related this to the corresponding voltage.

As leaf wetness sensors also responded to rainfall and fog, data from LWS was filtered to avoid bias in calculations of the contributions of dew to the water budget. Using the information from the tipping bucket, rainy days were identified, so that LWS records from those days were not used. In addition, we used the AGC (Automatic Gain Control) value from the infrared gas analyzer (LI-7500) as an indicator of the presence of fog (El-Madany et al., 2010); the combination of AGC values >75, relative humidity >90% and LWS persisting for 12 hr was used to indicate fog occurrence and these data were discarded from the analysis.

### *Statistical analysis*

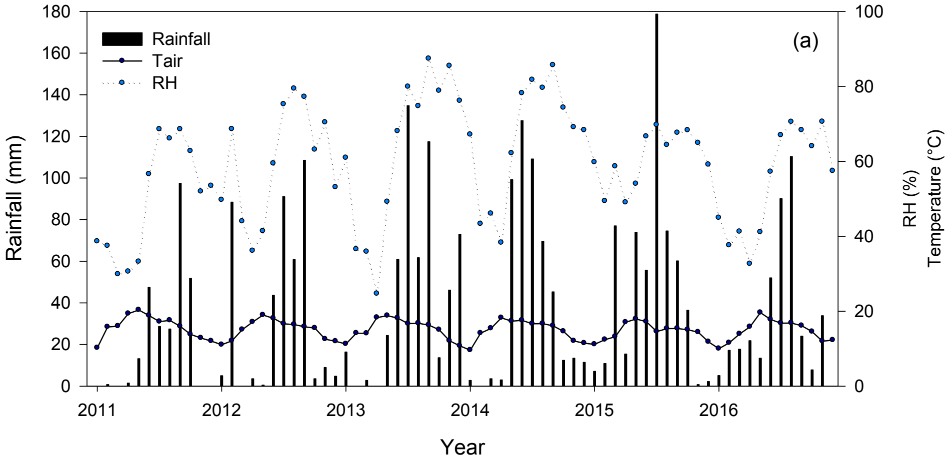
To determine the influence of various meteorological variables on the amounts of dewfall estimated by the model, we performed a sensitivity analysis based on (Scherm and van Bruggen, 1993). In brief, the approach provides an index of the relative sensitivity of dew amount estimation to a ±10% change in a given variable. We considered the hourly average air temperature $(T_{air})$, relativity humidity ($RH$), net radiation ($NR$), soil heat flux ($G$), wind speed ($w_s$) and soil temperature ($T_s$) in the wet and dry seasons.

We also determined the meteorological conditions during which dewfall was occurring by comparing all of the conditions experienced at the site to only those times in which the model or the leaf wetness sensor indicated dew formation. To do so, we used histograms (normalized as probability distribution functions) of the same variables listed above with the addition of water vapor pressure using hourly nighttime (18:00 to 09:00) averages. The distribution analysis was performed using the MatLab (2015a).

# Results

## *Meteorological conditions*

Over the six-year period, the mean annual air temperature was 15.2 °C, with the highest monthly mean observed in May (20.3°C) and lowest in January (9.6°C) (Figure 3a). Annual rainfall varied between 288.5 and 601.1 mm (Table 1). The rainfall pattern was irregular, with some years having a relatively wet winter (the dry season; Figure 3). The years 2012, 2014, 2015 and 2016 were an exception to the historical winter rainfall pattern, because in those years, winter rain accounted for almost 20% of the total annual rainfall. Daily relativity humidity (RH) showed seasonal variations, with maximum values observed during the wet season and minimum values at the end of the dry season (Figure 3A). The mean annual percentage of days with fog (calculated using the AGC values) and dew was 73 ± 15%, whereas rain occurred on 15 ± 10% days. Volumetric soil water content (VSWC) at both 2.5 and 15 cm depth varied depending on rainfall. The highest VSWC at 2.5 cm (Figure 3b) was reached in summer 2014 and 2015; however, it was only maintained for short time periods and the moist-dry cycles were faster than those at 15 cm (Figure 3b).



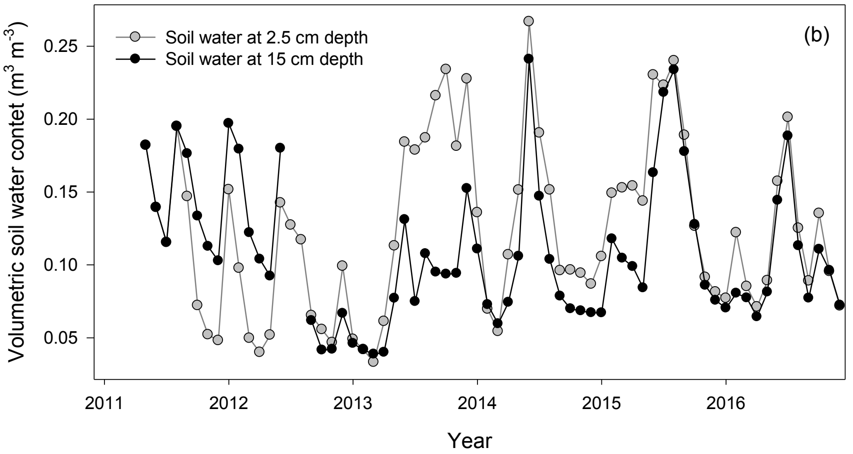


Figure 3. The a) monthly average air temperature ($T_a$), rainfall, and average of relative humidity (*RH*) and, b) monthly average volumetric soil water content (VSWC) at two soil depths from 2011 to 2016 in a continental semiarid grassland.

Nights were characterized by low mean air temperature (~11 °C), high relativity humidity (73 %), low wind speed (1.6 m $s^{-1}$) and low soil temperature (9 °C). The mean monthly minimum nighttime temperature was 7.4 ± 4.1 °C. With calm nights (u* <0.1 m $s^{-1}$) and soils temperature below that of air temperature, meteorological conditions are favorable for dew formation. Maximum wind speed during the night reached 4.6 m $s^{-1}$, which is still less than the upper limit for dew formation (Lekouch et al., 2012). During nights typical of dew formation, surfaces (soil) consistently dropped below dew point temperature ($T_{dew}$). For example, over the course of a 12-day period in 2016, where soil surfaces temperature where below dew point, modeled dew estimates ranged from 0.004 to 0.14 mm with an average of 0.085 mm (Figure 4).

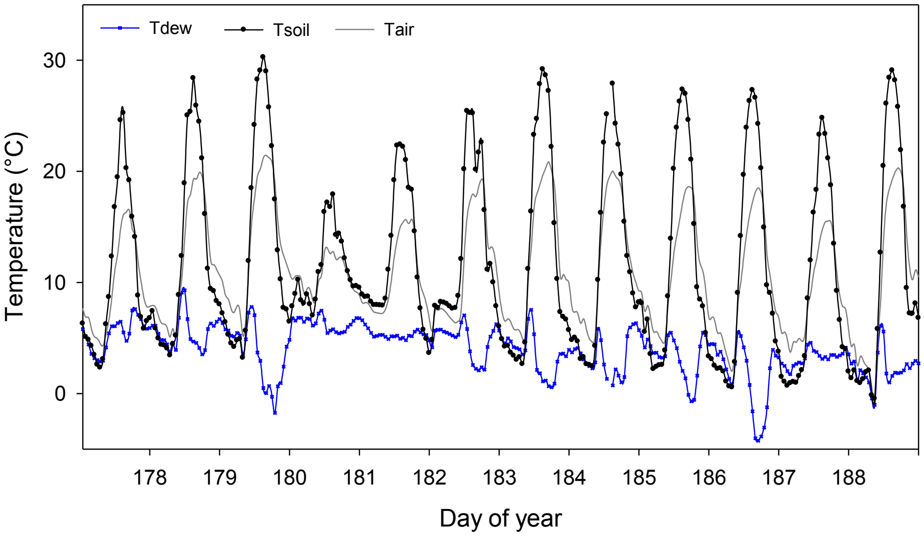


Figure 4. Time series of dew point ($T_{dew}$), air ($T_{air}$) and soil surface temperatures ($T_{soil}$) measured in a continental semiarid grassland during 12 representative days in 2016.

### *Dewfall frequency and duration*

Nights with dew (nights > 0.05 mm) occurred on 144 ± 65 days per year, compared to 58 ± 14 rainfall days (days ≥0.25 mm) per year. Thus, dew occurred on an average of nearly 39% of all nights during a year. The greatest frequency of dew nights occurred in the period from October to December, peaking in November; during that time, there were dew events nearly every night. The mean duration of dewfall episodes recorded with LWS averaged 5 h per night (Figure 5). The LWS at the base of the tussock grass tended to register a longer event duration than the LWS at 1 m height, likely due to some combination of microclimate at the base of the tussock grass (Crutsinger et al., 2014; Pan and Wang, 2014) or due to drip from the grasses.

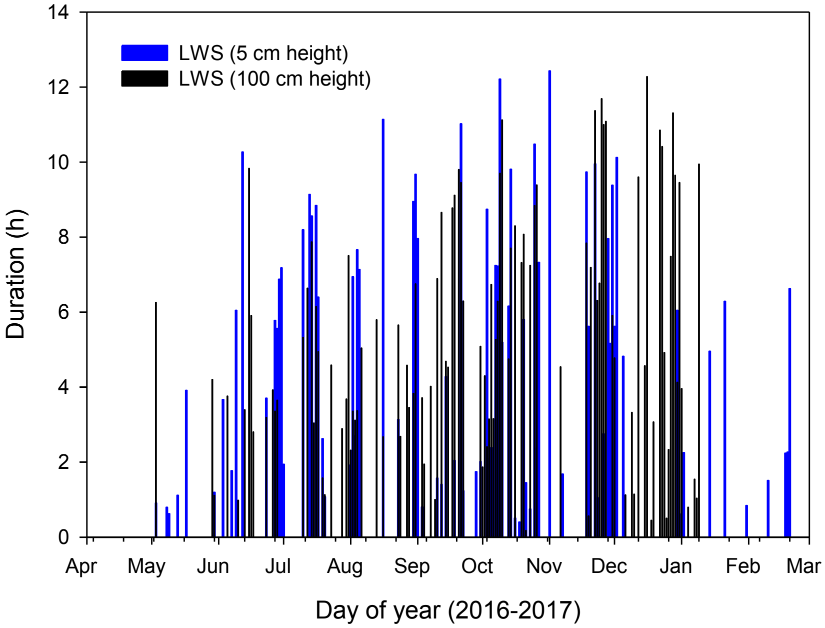


Figure 5. Daily dew duration in hours estimated from leaf wetness sensor (LWS) from May 2016 to March 2017. The dew duration was estimated by summing every minute that the sensor resistances were high. LWS-1 sensor was placed at the base of a tussock grass at 5 cm height, whereas the LWS-2 sensor was mounted on the eddy covariance tower at 1 m height.

### *Estimated amounts of dew*

Dewfall estimates obtained with the model reached maximum values during the dry season (January to May), with up to 0.7 mm of dew estimated in a single night (Figure 6). The averaged dew during the study period estimated with the model was 0.2 mm per day. Dew events last longer and were larger at both the beginning of the dry season and in the early wet season.

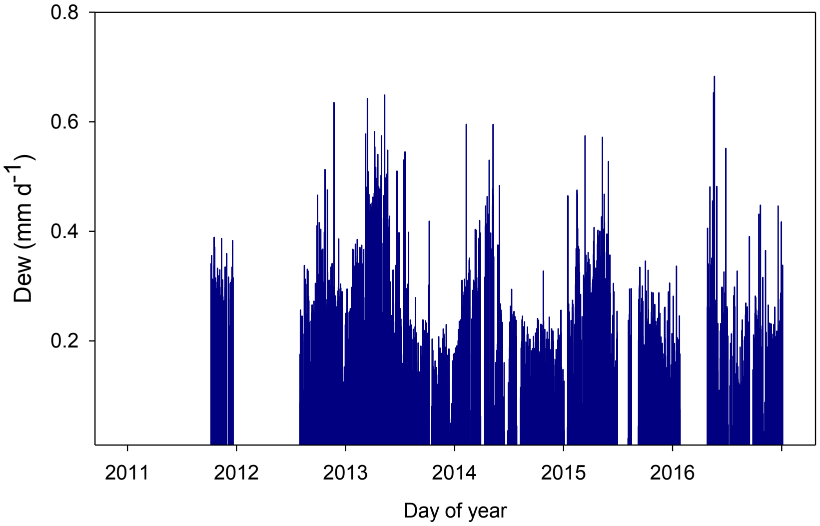


Figure 6. The a) temporal variation in accumulated nightly dew from measurements carried out between 2011 and 2016 and calculations using equation (3).

Total annual estimated dewfall varied between 16.5 mm and 69.0 mm, representing up to 10.2% of the total annual rainfall. While dew represented less than 2% of the total annual rainfall during the wet season, it represented up to 33.6 % of the rainfall in the dry season (Table 1). However, dry season dewfall amounts still varied considerably among years, ranging between 6.2 mm and 42.5 mm during the six-year study period. The maximum total amount of dew in the wet season (26.5 mm) only represented 5.8% of the total rainfall.

Table 1**.** Total annual rainfall, dewfall and fog for each year of the study by season (where wet season is between May and August). Dewfall amounts were obtained using the energy model proposed by Jacobs et al. (2006) and fog amounts were obtained using the model with additional filtering described in the methods.

| | Dry season | | | | Wet season | | | |
|---|---|---|---|---|---|---|---|---|
| Year | **Rainfall (mm)** | **Dew (mm)** | **Dew (% of Rainfall)** | **Dew+Fog (mm)** | **Rainfall (mm)** | **Dew (mm)** | **Dew (% of Rainfall)** | **Dew+Fog (mm)** |
| 2011 | 58.5 | 6.2 | 7.6 | 23.0 | 226.7 | --- | --- | 0 |
| 2012 | 127.9 | 19.7 | 12.9 | 24.2 | 315.5 | 3.9 | 1.2 | 7.2 |
| 2013 | 175.4 | 42.5 | 19.1 | 46.9 | 425.1 | 26.5 | 5.8 | 27.1 |
| 2014 | 54.1 | 31.6 | 33.6 | 39.7 | 486.8 | 17.6 | 3.5 | 18.5 |
| 2015 | 172.7 | 27.5 | 12.9 | 39.1 | 482.8 | 16.4 | 3.3 | 17.5 |
| 2016 | 117.2 | 12.9 | 9.4 | 19.5 | 318.9 | 14.7 | 4.4 | 18.3 |

### *Validation of dew estimates and sensitivity*

We found strong congruence between dew amounts measured by the microlysimeter compared to those estimated with the surface energy balance model. The model estimates capture both the amount of dewfall and the timing of dew deposition (Figure 7). Measurements of dewfall with the microlysimeter were significantly positively related to dew estimates from the model as measured over the course of 13 nights ($y=0.991*x+0.004$, $R^2=0.89$, $p<0.0001$, Figure 7a). The fitted line was consistent with a 1:1 relationship, with a slope of 0.99. During the time microlysimeters were measuring in the field, modelled dewfall totaled 0.73 mm whereas measured dewfall totaled 0.68 mm. Moreover, there was also consistency in the intra- and inter-daily timing of dew deposition measured by the two methods (Figure 7b). The model was verified only for November 2016; however, this year was characterized by the occurrence of many rainy days, necessity that many data be discarded.

The model was most sensitive to surface parameters (net radiation and soil heat flux) and air temperature, respectively (Figure. S1). During dry and wet season, the predicted values of dewfall was more sensitivity to net radiation, soil heat flux, temperature, followed by water vapor. Wind speed ($w_s$), soil temperature ($T_s$) and relativity humidity (*RH)* had a minor effect on the sensitivity of the model. In general, the seasonal differences (wet vs. dry) in the effect of a given environmental factor on estimated dew amount can be observed from Figure S1. Net radiation sensitivity values were generally highest during the dry season, the period with the highest dew occurrence at the site. Soil heat flux and air temperature had the greatest relativity sensitivity values during the wet season.

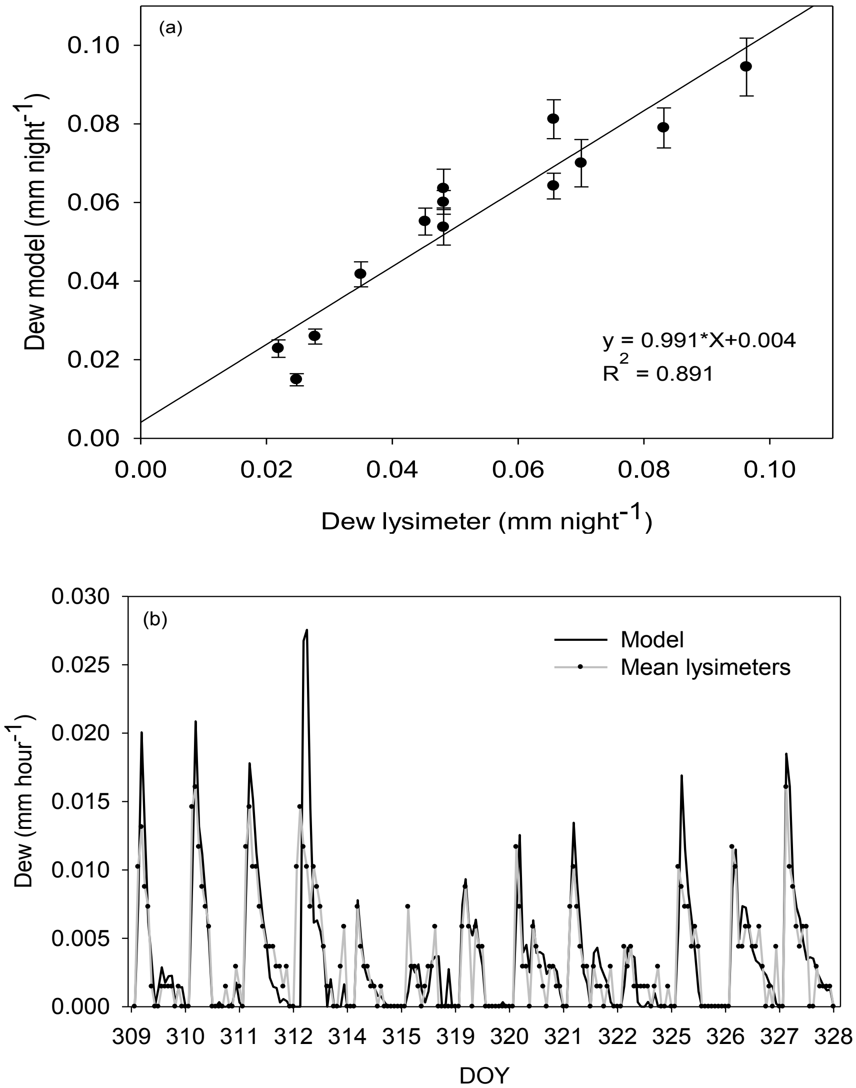


Figure 7. The a) relationship between dewfall amount estimated with the model as compared to the microlysimeter during 13 nights and b) comparison of hourly accumulated dew estimated with the microlysimeters, and the model. Data in (a) represent means ± standard error.

We compared all meteorological conditions experienced at the site to meteorological conditions when the model or leaf wetness sensor (LWS) indicated dew (Figure 8). In general, the two approaches showed wide agreement in the air temperature, relative humidity, soil temperature, wind speed, and soil heat flux conditions during which dewfall occurred. Interestingly, the range of RH amenable for dewfall events predicted by the model was much larger than that of the LWS. The model predicted a more negative distribution of $t_{soil}$-$t_{air}$, water vapor and net radiation than the LWS.

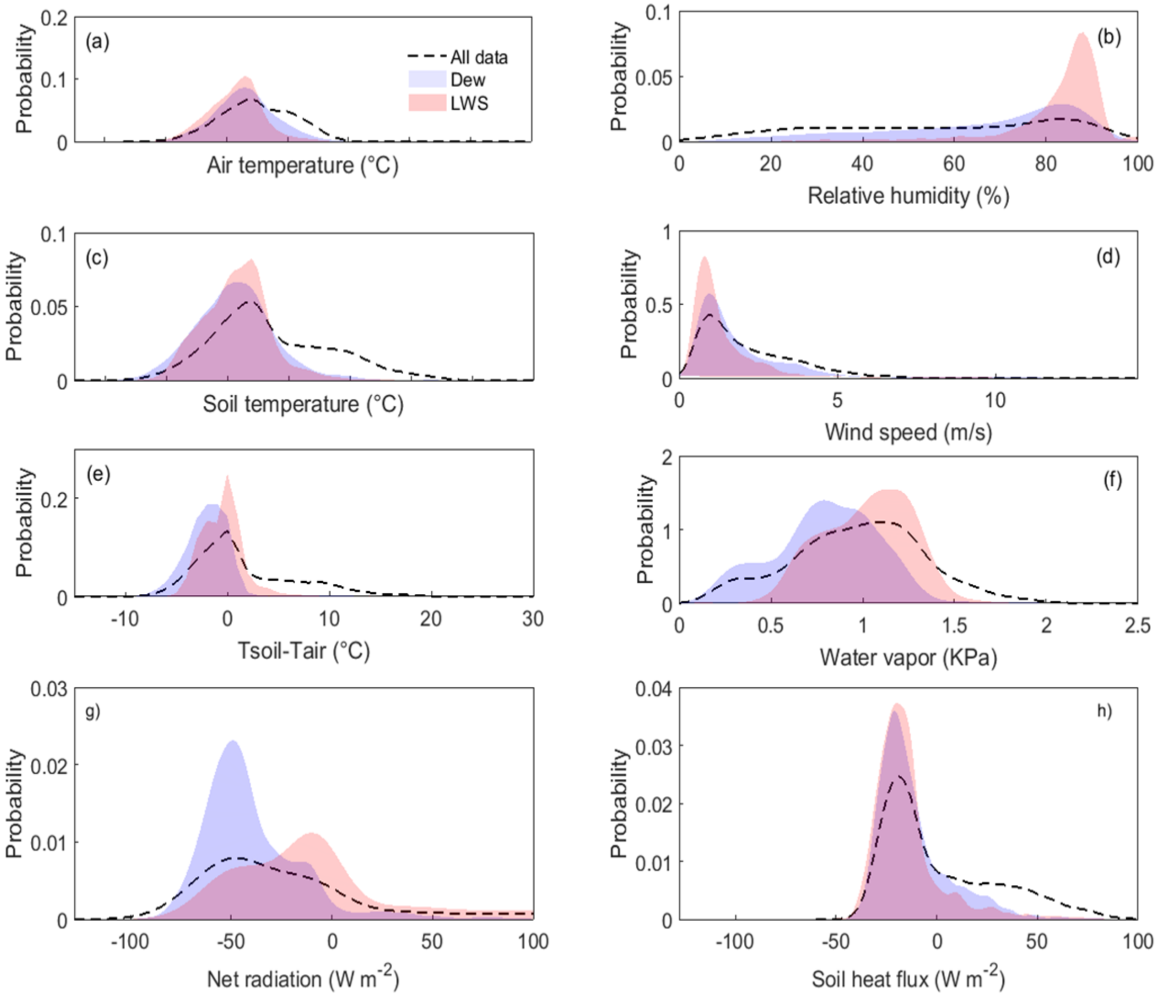


Figure 8. Histograms of meteorological conditions comparing all data, conditions when the model indicated dew, and conditions when the leaf wetness sensor indicated dew from May 2016 to March 2017.

*Water balance*

The average contribution of dewfall to the annual water balance was 3.6% during the wet season and 15.9% during the dry season. Fog did not provide a significant subsidy to the water budget. Our study indicates that cumulative evapotranspiration (*ET*) exceeded cumulative rainfall (*P*) at the end of the year, except for in an extreme rainy year (Figure 9). In general, there was a deficit (calculated as the difference between *P* and *ET* at the end of year) of 19 to 78 mm and a surplus of 138 mm during an extremely rain year. However, by summing dew and rainfall, the deficit between *P* + Dew and ET was reduced considerably to between 2 and 41 mm. Given the errors in observing rainfall and ET, as well as in modeling fog and dew amounts, it is quite remarkable that we find such a close match between total P and ET.

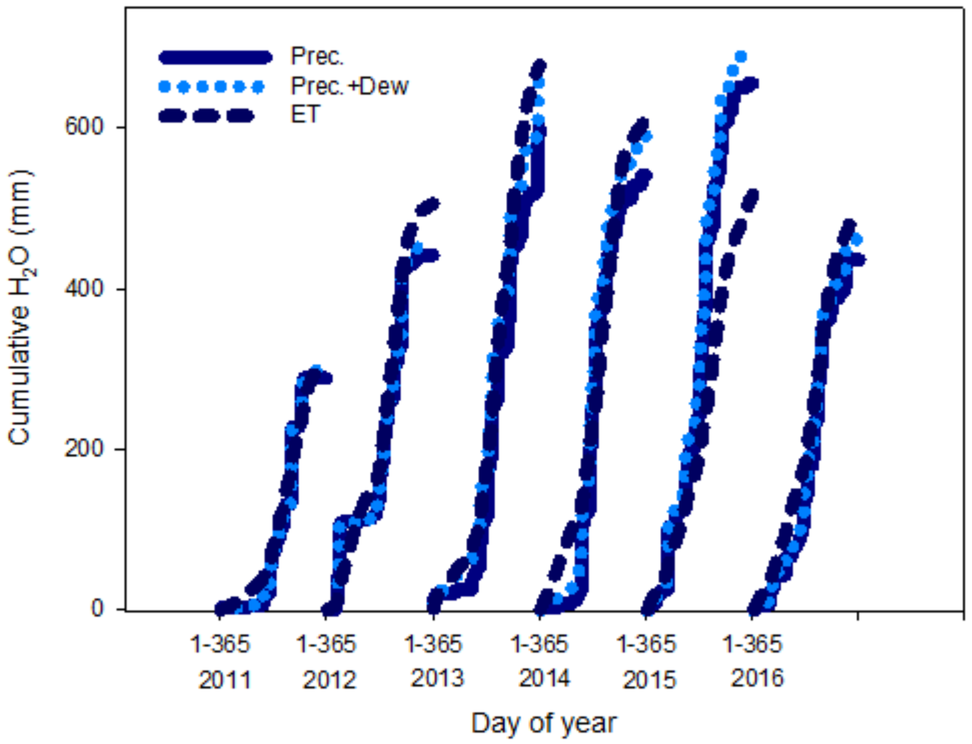


Figure 9. Annual cumulative rainfall, rainfall plus dew, and evapotranspiration in a continental semiarid grassland each year from 2011 to 2016.

## Discussion

*Dewfall frequency, timing and duration*

Changes in the frequency, timing and duration of dew formation in our site are explained by parallel changes in daily and seasonal meteorological conditions. Dewfall events occurred most frequently from November to January. We found that dew formation, as estimated by the leaf wetness sensors (LWS), started around sunset (20:00), continued until the morning (08:00) and ultimately evaporated before late morning (10:00). Following formation, dew persisted for a long time; however, it did not occur on every night. The maximum dew duration of ~13 hrs was observed in November (Figure 5), whereas the minimum duration of 1 hr was recorded in May. Overall, dew events lasted longer in early winter (November and January) because fog episodes also occurred on the same days. Under these conditions, LWS detected wetness almost all day long. In contrast, short duration events were observed from April to May, which is explained by the absence of rain, reduced soil water content, and decreased RH at night. Additionally, the average duration of dewfall seems to be related to night length (although we cannot rule out the concomitant changes in temperature). During winter nights, events lasted around 12 h compared to 10 h in summer, followed by dew evaporation shortly after sunrise; this pattern is similar to findings reported by Zangvil in the Negev desert (Zangvil, 1996).

The LWS used in this study is manufactured to emulate a broadleaf surface rather than the grasses typical of this arid ecosystem. The persistence of wetness on the sensor surface with no additional dew deposition is likely to differ on this artificial flat surface as compared to a grass leaf blade. We installed two LWS, one at the tussock base and the other at 1.0 m height. The LWS at 1 m height quantified more dew; however, the duration was shorter because it was not influenced by the tussock microclimate (Crutsinger et al., 2014). The timing and duration of the LWS also differed from that estimated by the model. In general, the duration of dewfall events observed by the LWS start earlier and last longer than that of the model. For instance, dew formation estimated by the model started around sunset (19:00), continued until the morning (07:00) and ultimately evaporated before late morning (8:00).

It is known that dew formation, duration, and amount are all affected by structural differences among vegetation types. Previous studies have observed that dewfall formation is localized over small-scale patches of vegetation or isolated to cooler surfaces, processes which are primarily controlled by small-scale moisture advection (Garratt and Segal, 1988; Wang et al., 2017). Increasing the amount of vegetation can increase the length of time that dew persists (Xiao et al., 2013). In the future, it would be interesting to consider the effects of vegetation structure on dew formation for this ecosystem, given that the region has varying amounts and compositions of grass as a result of different grazing regimes (Arredondo et al., 2016a).

### *Dew amount*

We found a strong relationship between the model and microlysimeters, such that the performance of the model estimated using an absolute root-mean-square error (RMSE) was 0.0085 mm night$^{-1}$ for the average dew events occurring on the 13 days of microlysimeter measurements (Figure 7a). To incorporate different meteorological conditions, we recommend verifying the model for the whole year. Differences between methods may result from errors in microlysimeter installation, inaccurate microlysimeter calibration, and/or inaccurate parameterization of the model (Eq. 3), particularly with respect to estimates of radiative balance (Moro et al., 2007). Semiarid grasslands are arrayed as grass patches interspersed within a bare soil matrix. This vegetation type exhibits distinctive micrometeorological properties that require correct estimation of their surface fluxes, such that the formulation of energy balance that does not assume horizontal uniformity (Friedl, 1995). Hence, the input of soil heat flux (*G*) and net radiation (*NR*) in Eq. (2) are problematic because *G* cannot accurately integrate the spatial variation observed in the soil surface, whereas *NR* should be partitioned for both the sparse vegetation area and the bare soil because of the grassland heterogeneity (Domingo et al., 2000). Finally, the site exhibited some frost events during winter and in these conditions the model is also less reliable.

The mean nightly dew amount calculated with the model was 0.25 mm; we observed variability in the patterns of dew formation with the highest amounts per night detected in winter and lowest amounts during spring (Figure 6). On nights with dew, the mean amount ranged from 0.03 to 0.24 mm and a few select nights reached 0.54 - 0.61 mm. The peak dewfall during night from our study (0.7 mm) is not far from the maximum theoretical of 0.8 mm per night and is lower than the maximum of 1 mm of dew yield per night founded in grasslands using the energy model (Ritter et al., 2018).  Studies reporting annual dew formation have recorded between 5 – 48 mm (Xiao et al., 2009), which is below (but still comparable to) our observations ranging from 16 – 69 mm per year (Table 1).

Differences in the amount of dew estimated among studies may have resulted from the use of different measurement techniques (bottling paper, weighing of leaves, and different models of energy balance, and different implantation of instrumentation). Comparison of dew amount among different ecosystems is also difficult to achieve because dew formation is not only controlled by meteorological factors, but also by topography and the physical nature of condensation surfaces (Kidron, 2000b; Maestre et al., 2012; Ye et al., 2007), such as the structure, size and thermal properties of vegetative surfaces (M. L. Sharma, 1976).

### *Meteorological factors affecting dew formation*

The results from the sensitivity analysis suggest that dew amount estimated from the model is most affected by changes in net radiation, soil heat flux and air temperature. This would imply that the energy lost from the canopy or soil cooling is the principal drivers of dew formation in the model. In contrast, the model is insensitive to changes in wind speed, relativity humidity and soil temperature. The effects of water vapor and air temperature on dew amount appear to change between the wet and dry season. Notably, the relative sensitivity of dew amounts estimated may be sensitive to the timescale (e.g. hourly, daily) at which the variables are averaged.

In the probability distribution of the LWS and model both show the presence of dewfall across a wide range of values, even in conditions with very low RH and high air and soil temperature; however, these dew events have a very low probability of occurrence and we know that formation of dew is a complex process, influenced by micrometeorological conditions. For instance, the relative humidity during the dry season is generally low, with monthly averages of 30%. However, during the night, humidity can increase up to 90% and results in dew formation. Previous studies have shown that a threshold of around 45% relativity humidity is necessary at night for dew formation (Guo et al., 2016; Ye et al., 2007). The present study showed that the LWS only indicated dewfall given high humidity, low wind speeds and low temperatures, which are consistent with the conditions for water condensation or formation on the sensor surface. In contrast, the model, which is more related to energy, reflects the differences between soil and air temperature of the site and the resultant effects of radiative cooling. Indeed, the probability of water condensation for the model is higher than for LWS given low values of the net radiation. One important unknown is effects of cloud coverage, which will reduce the efficiency of the radiative cooling; however, we know that in our site the ground heat flux is low during dew condensation and this reduces the heat flux into the canopy.

Previous research has demonstrated that changes in local microclimate are an important factor affecting the formation of dew (Pan et al., 2010; Uclés et al., 2014; Wang et al., 2017). For instance, several studies reported soil surface condensation even when soil surface temperature did not drop below the dew point temperature (Agam and Berliner, 2006; Jacobs et al., 1999; Pan et al., 2010). This condensation likely resulted from a rapidly decreasing soil surface temperature, leading to the formation of a sharp temperature gradient decreasing from the deep soil to the soil surface. Thus, water vapor from the deep soil migrates to the surface forming dew on the surface (Wang et al., 2017). This surface wetting may also result from water vapor adsorption, occurring under particular conditions and becoming the main soil wetting mechanism (Agam et al., 2004; Kidron et al., 2000). Humidity stored in the deep soil horizon and in the petrocalcic layer (M C Duniway et al., 2010) following the rainy season likely moves to the soil surface following this temperature gradient. Other sources of moisture that promote dew formation at study site include cold fronts during winter, which implies an extra humidity source that often follows winter storms.

### *Contribution to water balance*

It has been suggested that dew may play a crucial role in the water balance of arid and semiarid zones, particularly during periods of drought. Currently, dewfall is generally not considered in water balance studies in Mexico or many other parts of the world, because the amounts are assumed to be very small. Our results show that, on average, dewfall is 6.8% of the total annual rainfall. Other reports on dewfall contributions demonstrate that dew range from 7% to 29 % of the monthly rainfall and from 5% to 40% of the total annual rainfall (Kalthoff et al., 2006; Lekouch et al., 2012; Malek et al., 1999b; Uclés et al., 2014). There is even an extreme case reporting dewfall amounts in excess of 110% of the rainfall (Evenari et al., 1982). It is important to mention that these studies were carried out in arid and semiarid zones. These values are too high to be ignored in the water balance and we show that they can resolve the difference between rainfall and evapotranspiration on an annual basis (Figure 9). On average, the site received 494.2 mm of rainfall and lost 520.3 mm of water via evapotranspiration annually, an indication of how grasses are still active during dry periods and how they adjust their stomatal opening to the harsh climate over the year. The additional water that accounts for the difference between rainfall and precipitation could come from dew (38.2 mm annually) or from the extraction of stored moisture from the petrocalcic layer. Notably, the annual rainfall can mask the fact that dewfall is an important input during dry periods; in our site, dewfall averages 15.9% of the rainfall in the dry season. In a dry year (2013) with no rain during winter, dew accounted for 33.6% of the rainfall. During the dry season, this dew may serve as a primary source of water contributing to the survival of the dormant grasses, either through root water uptake or through direct foliar water uptake (Berry et al., 2018).

## Conclusion

We demonstrated that the climate of our semiarid continental grassland had favorable conditions for dewfall formation. Dew events lasted for up to 10 h at night and persisted into the morning; this may have implications for plant function by providing water for root uptake, by suppressing transpiration, or through direct foliar water uptake (Dawson and Goldsmith, 2018). In that sense, the timing and duration of dewfall may play a more critical role then the total amount. Nevertheless, the amount of dew water incorporated into the ecosystem was considerable, averaging 7.4% of the rainfall throughout the study period and up to 22.5% of the rainfall in the dry season. As such, dew may be an important source of water input to this ecosystem when there is no rainfall. The high numbers of days with dew and high daily and seasonal dew amounts are comparable to others regions were dewfall is recognized to make an important contribution to the annual water balance.

# Bibliography

Agam, N., 2004. Diurnal Water Content Changes in the Bare Soil of a Coastal Desert. JOURNAL OF HYDROMETEOROLOGY 5, 12.

Agam, N., Berliner, P.R., 2006. Dew formation and water vapor adsorption in semi-arid environments - A review. Journal of Arid Environments 65, 572–590. https://doi.org/10.1016/j.jaridenv.2005.09.004

Agam, N., Berliner, P.R., Zangvil, A., Ben-Dor, E., 2004. Soil water evaporation during the dry season in an arid zone. Journal of Geophysical Researc 109, doi:10.1029/2004JD004802. https://doi.org/10.1029/2004JD004802

Aguado-Santacruz, G.A., Garcia-Moya, E., 1998. Environmental factors and community dynamics at the southernmost part of the North American Graminetum: I. On the contribution of climatic factors to temporal variation in species composition. Plant Ecology 135, 13–29. https://doi.org/10.1023/A:1009750831162

Aguirre-Gutiérrez, C.A., Holwerda, F., Goldsmith, G.R., Delgado, J., Yepez, E., Carbajal, N., Escoto-Rodríguez, M., Arredondo, J.T., 2019. The importance of dew in the water balance of a continental semiarid grassland. Journal of Arid Environments 168, 26–35. https://doi.org/10.1016/j.jaridenv.2019.05.003

Alcocer-Ruthling, M., Robberecht, R., Thill, D.C., 1989. The Response of Bouteloua scorpioides to Water Stress at Two Phenological Stages. Botanical Gazette 150, 454–461. https://doi.org/10.1086/337792

Arredondo, T., Delgado-Balbuena, J., Huber-Sannwald, E., García-Moya, E., Loescher, H.W., Aguirre-Gutiérrez, C., Rodriguez-Robles, U., 2018. Does precipitation affects soil respiration of tropical semiarid grasslands with different plant cover types? Agriculture, Ecosystems & Environment 251, 218–225. https://doi.org/10.1016/j.agee.2017.09.034

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016a. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016b. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Asbjornsen, H., Mora, G., Helmers, M.J., 2007. Variation in water uptake dynamics among contrasting agricultural and native plant communities in the Midwestern U.S. Agriculture, Ecosystems & Environment 121, 343–356. https://doi.org/10.1016/j.agee.2006.11.009

Asbjornsen, H., Shepherd, G., Helmers, M., Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S. Plant Soil 308, 69–92. https://doi.org/10.1007/s11104-008-9607-3

BALBUENA, J.D., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Barnard, R.L., Bello, F. De, Buchmann, N., 2006. The δ18O of root crown water best reflects source water δ18O in different types of herbaceous species. Rapid communications in mass spectrometry : RCM 24, 3567–3577. https://doi.org/10.1002/rcm

Barradas, V.L., Glez-Medellín, Ma.G., 1999. Dew and its effect on two heliophile understorey species of a tropical dry deciduous forest in Mexico. International Journal of Biometeorology 43, 1–7. https://doi.org/10.1007/s004840050109

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2019. Foliar water uptake: Processes, pathways, and integration into plant water budgets: Foliar Water Uptake. Plant Cell Environ 42, 410–423. https://doi.org/10.1111/pce.13439

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2018. Foliar water uptake: processes, pathways, and integration into plant water budgets. Plant, Cell & Environment. https://doi.org/10.1111/pce.13439

Blackman, C.J., Brodribb, T.J., 2011. Two measures of leaf capacitance: insights into the water transport pathway and hydraulic conductance in leaves. Functional Plant Biol. 38, 118. https://doi.org/10.1071/FP10183

Blair, J., Nippert, J., Briggs, J., 2014. Grassland Ecology, in: Monson, R.K. (Ed.), Ecology and the Environment. Springer New York, New York, NY, pp. 389–423.

Bowen, G.J., Revenaugh, J., 2003. Interpolating the isotopic composition of modern meteoric precipitation: ISOTOPIC COMPOSITION OF MODERN PRECIPITATION. Water Resour. Res. 39. https://doi.org/10.1029/2003WR002086

Boyer, J.S., 1985. Water transport. Annual review of plant physiology 36, 473–516.

Boyer, J.S., 1974. Water transport in plants: Mechanism of apparent changes in resistance during absorption. Planta 117, 187–207. https://doi.org/10.1007/BF00388393

Breazeale, E.L., McGeorge, W.T., Breazeale, J.F., 1950. MOISTURE ABSORPTION BY PLANTS FROM AN ATMOSPHERE OF HIGH HUMIDITY. Plant Physiol. 25, 413–419. https://doi.org/10.1104/pp.25.3.413

Brewer, C.A., Smith, W.K., Vogelmann, T.C., 1991. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. Plant, Cell & Environment 14, 955–962.

Brodribb, T.J., Holbrook, N.M., 2003. Stomatal Closure during Leaf Dehydration, Correlation with Other Leaf Physiological Traits. Plant Physiol. 132, 2166–2173. https://doi.org/10.1104/pp.103.023879

Buckley, T.N., Sack, L., Gilbert, M.E., 2011. The Role of Bundle Sheath Extensions and Life Form in Stomatal Responses to Leaf Water Status. Plant Physiol. 156, 962–973. https://doi.org/10.1104/pp.111.175638

Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): foliar uptake and prevention of dehydration. Plant Cell Environ 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burkhardt, J., Basi, S., Pariyar, S., Hunsche, M., 2012. Stomatal penetration by aqueous solutions–an update involving leaf surface particles. New Phytologist 196, 774–787.

Coffin, D.P., Lauenroth, K., 1991a. Effects of competition on spatial distribution of roots of blue grama. Journal Of Range Management 44.

Coffin, D.P., Lauenroth, W.K., 1991b. Effects of Competition on Spatial Distribution of Roots of Blue Grama. Journal of Range Management 44, 68. https://doi.org/10.2307/4002642

Corbin, J.D., Thomsen, M.A., Dawson, T.E., D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. Oecologia 145, 511–521. https://doi.org/10.1007/s00442-005-0152-y

Cruiziat, P., Tyree, M.T., Bodet, C., LoGULLO, M.A., 1980. THE KINETICS OF REHYDRATION OF DETACHED SUNFLOWER LEAVES FOLLOWING SUBSTANTIAL WATER LOSS. New Phytol 84, 293–306. https://doi.org/10.1111/j.1469-8137.1980.tb04429.x

Crutsinger, G.M., Rodriguez-Cabal, M.A., Roddy, A.B., Peay, K.G., Bastow, J.L., Kidder, A.G., Dawson, T.E., Fine, P.V.A., Rudgers, J.A., 2014. Genetic variation within a dominant shrub structures green and brown community assemblages. Ecology 95, 387–398. https://doi.org/10.1890/13-0316.1

Dai, Y., Zheng, X.-J., Tang, L.-S., Li, Y., 2015. Stable oxygen isotopes reveal distinct water use patterns of two Haloxylon species in the Gurbantonggut Desert. Plant Soil 389, 73–87. https://doi.org/10.1007/s11104-014-2342-z

Dawson, T.E., Goldsmith, G.R., 2018a. The value of wet leaves. New Phytologist 219, 1156–1169. https://doi.org/10.1111/nph.15307

Dawson, T.E., Goldsmith, G.R., 2018b. The value of wet leaves. New Phytol 219, 1156–1169. https://doi.org/10.1111/nph.15307

De Bruin, H.A.R., Ronda, R.J., Van De Wiel, B.J.H., 2000. Approximate solutions for the Obukhov length and the surface fluxes in terms of bulk Richardson numbers. Boundary-layer meteorology 95, 145–157.

Delgado-Balbuena, J., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Huber-Sannwald, E., Chavez-Aguilar, G., Luna-Luna, M., Barretero-Hernandez, R., 2013. Differences in plant cover and species composition of semiarid grassland communities of central Mexico and its effects on net ecosystem exchange. Biogeosciences 10, 4673–4690. https://doi.org/10.5194/bg-10-4673-2013

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Pineda-Martínez, L.F., Carbajal, J.N., Vargas, R., 2019. Seasonal Precipitation Legacy Effects Determine the Carbon Balance of a Semiarid Grassland. J. Geophys. Res. Biogeosci. 124, 987–1000. https://doi.org/10.1029/2018JG004799

Dingman, S.L., 2015. Physical hydrology. Waveland press.

Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. Oecologia 117, 504–512. https://doi.org/10.1007/s004420050686

Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. Plant, Cell and Environment 23, 27–38. https://doi.org/10.1046/j.1365-3040.2000.00532.x

Domínguez, E., 1999. Water hydration in cutinized cell walls: a physico-chemical analysis. Biochimica et Biophysica Acta (BBA) - General Subjects 1426, 168–176. https://doi.org/10.1016/S0304-4165(98)00152-4

Drennan, P.M., Nobel, P.S., 1998. Root growth dependence on soil temperature for Opuntia ficus-indica: influences of air temperature and a doubled CO2 concentration. Funct Ecology 12, 959–964. https://doi.org/10.1046/j.1365-2435.1998.00276.x

Duniway, M C, Herrick, J.E., Curtis Monger, H., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Duniway, Michael Cohrs, Herrick, J.E., Monger, H.C., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Eggemeyer, K.D., Awada, T., Harvey, F.E., Wedin, D.A., Zhou, X., Zanner, C.W., 2008. Seasonal changes in depth of water uptake for encroaching trees Juniperus virginiana and Pinus ponderosa and two dominant C4 grasses in a semiarid grassland. Tree Physiology 29, 157–169. https://doi.org/10.1093/treephys/tpn019

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. Oecologia 88, 430–434. https://doi.org/10.1007/BF00317589

Eller, C.B., Lima, A.L., Oliveira, R.S., 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis* (Winteraceae). New Phytol 199, 151–162. https://doi.org/10.1111/nph.12248

Esmaiel Malek, 2016. Differentiation of the Atmospheric Moisture Collected by Dew and Fog. JESE-A 5. https://doi.org/10.17265/2162-5298/2016.04.001

Evenari, M., Shanan, L., Tadmor, N., 1982. The Negev: The Challenge of a Desert. Harvard University Press.

Friedl, M.A., 1995. Modeling land surface fluxes using a sparse canopy model and radiometric surface temperature measurements. Journal of Geophysical Research: Atmospheres 100, 25435–25446. https://doi.org/10.1029/95JD00723

Garratt, J.R., 1992. The atmospheric boundary layer. Cambridge atmospheric and space science series. Cambridge University Press, Cambridge 416, 444.

Garratt, J.R., Segal, M., 1988. On the contribution of atmospheric moisture to dew formation. Boundary-Layer Meteorology 45, 209–236. https://doi.org/10.1007/BF01066671

Goldsmith, G.R., Matzke, N.J., Dawson, T.E., 2013. The incidence and implications of clouds for cloud forest plant water relations. Ecology letters 16, 307–314.

Grammatikopoulos, G., Manetas, Y., 1994a. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Canadian Journal of Botany 72, 1805–1811.

Grammatikopoulos, G., Manetas, Y., 1994b. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Can. J. Bot. 72, 1805–1811. https://doi.org/10.1139/b94-222

Guan, H., Sebben, M., Bennett, J., 2014. Radiative- and artificial-cooling enhanced dew collection in a coastal area of South Australia. Urban Water Journal 11, 175–184. https://doi.org/10.1080/1573062X.2013.765494

Guo, X., Zha, T., Jia, X., Wu, B., Feng, W., Xie, J., Gong, J., Zhang, Y., Peltola, H., 2016. Dynamics of dew in a cold desert-shrub ecosystem and its abiotic controls. Atmosphere 7, 1–15. https://doi.org/10.3390/atmos7030032

Guzmán-Delgado, P., Fernández, V., Venturas, M., Rodríguez-Calcerrada, J., Gil, L., 2017. Surface properties and physiology of Ulmus laevis and U. minor samaras: implications for seed development and dispersal. Tree Physiology 37, 815–826. https://doi.org/10.1093/treephys/tpx022

Guzmán-Delgado, P., Mason Earles, J., Zwieniecki, M.A., 2018. Insight into the physiological role of water absorption via the leaf surface from a rehydration kinetics perspective: Leaf rehydration kinetics via the surface. Plant Cell Environ 41, 1886–1894. https://doi.org/10.1111/pce.13327

Hanisch, S., Lohrey, C., Buerkert, A., 2015. Dewfall and its ecological significance in semi-arid coastal south-western Madagascar. Journal of Arid Environments 121, 24–31. https://doi.org/10.1016/j.jaridenv.2015.05.007

Hartnett, D.C., Hickman, K.R., Walter, L.E.F., 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49, 413–420.

Helliker, B.R., Ehleringer, J.R., 2000. Establishing a grassland signature in veins: 18O in the leaf water of C3 and C4 grasses. Proceedings of the National Academy of Sciences of the United States of America 97, 7894–7898. https://doi.org/10.1073/pnas.97.14.7894

Heusinkveld, B.G., Berkowicz, S.M., Jacobs, A.F.G., Holtslag, A. a. M., Hillen, W.C. a. M., 2006. An Automated Microlysimeter to Study Dew Formation and Evaporation in Arid and Semiarid Regions. Journal of Hydrometeorology 7, 825–832. https://doi.org/10.1175/JHM523.1

Hunter, K.A.M., Wu, L., 2005. Morphological and physiological response of five California native grass species to moderate salt spray: Implications for landscape irrigation with reclaimed water. Journal of Plant Nutrition 28, 247–270. https://doi.org/10.1081/PLN-200047609

Jackson, T.J., Moy, L., 1999. Dew Effects on Passive Microwave Observations of Land Surfaces. Remote Sensing of Environment 70, 129–137. https://doi.org/10.1016/S0034-4257(99)00021-8

Jacobs, a. F.G., Heusinkveld, B.G., Kruit, R.J.W., Berkowicz, S.M., 2006. Contribution of dew to the water budget of a grassland area in the Netherlands. Water Resources Research 42. https://doi.org/10.1029/2005WR004055

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 1999. Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments 42, 211–222. https://doi.org/10.1006/jare.1999.0523

Jordan, G.J., Brodribb, T.J., 2007. Incontinence in aging leaves: deteriorating water relations with leaf age in Agastachys odorata (Proteaceae), a shrub with very long-lived leaves. Functional Plant Biol. 34, 918. https://doi.org/10.1071/FP07166

Kalthoff, N, Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kalthoff, N., Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kaseke, K.F., Wang, L., Seely, M.K., 2017. Nonrainfall water origins and formation mechanisms. Sci. Adv. 3, e1603131. https://doi.org/10.1126/sciadv.1603131

Kerr, J.P., Beardsell, M.F., 1975. Effect of Dew on Leaf Water Potentials and Crop Resistances in a Paspalum Pasture 1. Agronomy Journal 67, 596–599.

Kidder, D.L., Gierlowski-Kordesch, E.H., 2005. Impact of grassland radiation on the nonmarine silica cycle and Miocene diatomite. Palaios 20, 198–206.

Kidron, G., Yair, A., Danin, A., 2000. Dew variability within a small arid drainage basin in the Negev Highlands,Israel. Q J R Meteorol Soc 126, 63–80. https://doi.org/10.1256/smsqj.56203

Kidron, G.J., 2000a. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000b. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000c. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270.

Kidron, Giora J, 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8. https://doi.org/10.1016/S0168-1923(99)00043-X

Kidron, Giora J., 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8.

Koerner, S.E., Collins, S.L., 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology 95, 98–109. https://doi.org/10.1890/13-0526.1

Konrad, W., Burkhardt, J., Ebner, M., Roth-Nebelsick, A., 2015. Leaf pubescence as a possibility to increase water use efficiency by promoting condensation: LEAF PUBESCENCE MAY INCREASE WATER USE EFFICIENCY. Ecohydrol. 8, 480–492. https://doi.org/10.1002/eco.1518

Kramer, P.J., Boyer, J.S., 1995. Water relations of plants and soils. Academic press.

Lekouch, I., Lekouch, K., Muselli, M., Mongruel, A., Kabbachi, B., Beysens, D., 2012. Rooftop dew, fog and rain collection in southwest Morocco and predictive dew modeling using neural networks. Journal of Hydrology 448–449, 60–72. https://doi.org/10.1016/j.jhydrol.2012.04.004

Leopold, L., n.d. Dew as a Source of Plant Moisture 3.

Leopold, L.B., 1952. Dew as a source of plant moisture.

Limm, E.B., Simonin, K.A., Bothman, A.G., Dawson, T.E., 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Liu, S., Li, S.-G., Yu, G.-R., Sun, X.-M., Zhang, L.-M., Hu, Z.-M., Li, Y.-N., Zhang, X.-Z., 2009. Surface energy exchanges above two grassland ecosystems on the Qinghai-Tibetan Plateau. Biogeosciences Discuss. 6, 9161–9192. https://doi.org/10.5194/bgd-6-9161-2009

Maestre, F.T., Salguero-Gómez, R., Quero, J.L., 2012. It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 367, 3062–75. https://doi.org/10.1098/rstb.2011.0323

Maldonado Burgos, E., 2015. Efectos de fuego en la cobertura vegetal y procesos ecohidrológicos de un pastizal semiárido en el centro de México.

Malek, E., McCurdy, G., Giles, B., 1999a. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999b. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments1. Malek, E., McCurdy, G. & Giles, B. Dew contribution to the annual water balances in semi-arid desert valleys. J. Arid Environ. 42, 71–80 (1999). 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999c. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80.

Mastroberti, A.A., de Araujo Mariath, J.E., 2008. Development of mucilage cells of Araucaria angustifolia (Araucariaceae). Protoplasma 232, 233–245. https://doi.org/10.1007/s00709-007-0274-7

Matimati, I., Musil, C.F., Raitt, L., February, E., 2013. Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem. Ecohydrology 6, 818–825.

Mcculloh, K.A., Johnson, D.M., Meinzer, F.C., Woodruff, D.R., 2014. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species: The dynamic pipeline. Plant Cell Environ 37, 1171–1183. https://doi.org/10.1111/pce.12225

Medina-Roldán, E., Arredondo, J.T., Huber-Sannwald, E., Chapa-Vargas, L., Olalde-Portugal, V., 2008. Grazing effects on fungal root symbionts and carbon and nitrogen storage in a shortgrass steppe in Central Mexico. Journal of Arid Environments 72, 546–556. https://doi.org/10.1016/J.JARIDENV.2007.07.005

Medina-Roldán, E., Huber-Sannwald, E., Arredondo, J.T., 2013. Plant phenotypic functional composition effects on soil processes in a semiarid grassland. Soil Biology and Biochemistry 66, 1–9. https://doi.org/10.1016/j.soilbio.2013.06.011

Medina-Roldán, E., Moreno, J.T.A., Moya, E.G., Martínez, F.M.H., 2007. Soil water content dynamics along a range condition gradient in a shortgrass steppe. Rangeland Ecology and Management 60, 79–87. https://doi.org/10.2111/05-219R2.1

Milburn, J.A., 1966. The conduction of sap: 1. water conduction and cavitation in water stressed leaves 34–42.

Monson, R.K., Moore, B. d., Ku, M.S.B., Edwards, G.E., 1986. Co-function of C3-and C4-photosynthetic pathways in C3, C4 and C3-C4 intermediate Flaveria species. Planta 168, 493–502. https://doi.org/10.1007/BF00392268

Moro, M.J., Were, a., Villagarcía, L., Cantón, Y., Domingo, F., 2007. Dew measurement by Eddy covariance and wetness sensor in a semiarid ecosystem of SE Spain. Journal of Hydrology 335, 295–302. https://doi.org/10.1016/j.jhydrol.2006.11.019

Morse, S.R., 1990. Water balance in Hemizonia luzulifolia: the role of extracellular polysaccharides. Plant, Cell & Environment 13, 39–48.

Munné-Bosch, S., Alegre, L., 1999. Role of dew on the recovery of water-stressed Melissa officinalis L. plants. Journal of Plant Physiology 154, 759–766.

Nguyen, H.T., Meir, P., Wolfe, J., Mencuccini, M., Ball, M.C., 2017. Plumbing the depths: extracellular water storage in specialized leaf structures and its functional expression in a three-domain pressure–volume relationship. Plant, cell & environment 40, 1021–1038.

Nippert, J.B., Knapp, A.K., 2007. Linking water uptake with rooting patterns in grassland species. Oecologia 153, 261–272. https://doi.org/10.1007/s00442-007-0745-8

Nobel, P.S., Jordan, P.W., 1983. Transpiration Stream of Desert Species: Resistances and Capacitances for a C $_3$ , a C $_4$ , and a CAM Plant. J Exp Bot 34, 1379–1391. https://doi.org/10.1093/jxb/34.10.1379

Oparka, K.J., 1994. The use of fluorescent probes for studies of living plant cells. Plant cell biology, a practical approach.

Pan, Y., Wang, X., Zhang, Y., 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area , Northern China. Journal of Hydrology 387, 265–272. https://doi.org/10.1016/j.jhydrol.2010.04.016

Pan, Y.X., Wang, X.P., 2014. Effects of shrub species and microhabitats on dew formation in a revegetation-stabilized desert ecosystem in Shapotou, northern China. Journal of Arid Land 6, 389–399. https://doi.org/10.1007/s40333-014-0008-6

Peterson, P.M., Giraldo-Cañas, D., 2011. The species of Muhlenbergia (Poaceae: Chloridoideae) from Argentina. Caldasia 33, 21–54.

Pineda Martínez, L.F., 2009. Modelación numérica de la dispersión de material particulado atmosférico y regionalización climática en México.

Puigdefábregas, J., Sánchez, G., 1996. Vegetación dispersa y flujos de vertiente en clima semiárido, in: IV Reunión de Geomorfología. Universidade da Coruña.

Riederer, M., 2006. Thermodynamics of the water permeability of plant cuticles: characterization of the polar pathway. Journal of Experimental Botany 57, 2937–2942. https://doi.org/10.1093/jxb/erl053

Ritter, F., Berkelhammer, M., Beysens, D., 2018. Dew frequency across the US from a network of in situ radiometers. Hydrology and Earth System Sciences Discussions 1–35. https://doi.org/10.5194/hess-2018-450

Rossatto, D.R., da Silveira Lobo Sternberg, L., Franco, A.C., 2013. The partitioning of water uptake between growth forms in a Neotropical savanna: do herbs exploit a third water source niche?: Herbs explore a third water uptake niche in Neotropical savannas. Plant Biology 15, 84–92. https://doi.org/10.1111/j.1438-8677.2012.00618.x

Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 2013. Isotopic Patterns in Modern Global Precipitation, in: Swart, P.K., Lohmann, K.C., Mckenzie, J., Savin, S. (Eds.), Geophysical Monograph Series. American Geophysical Union, Washington, D. C., pp. 1–36. https://doi.org/10.1029/GM078p0001

Rzedowski, J., 2007. An Ecological and Phytogeographical Analysis of the Grasslands of Mexico. Taxon 24, 67–80.

Sala, O.E., Lauenroth, W.K., Reid, C.P.P., 1982. WATER RELATIONS: A NEW DIMENSION FOR NICHE. Journal of Applied Ecology 19, 647–657.

Santacruz, G.A.A., Moya, E.G., Gonzalez, C.V., Flores, J.L.F., 1996. Importancia de los elementos climáticos en la variación florística temporal de pastizales semidesérticos. Acta Botánica Mexicana 65–81.

Scherm, H., van Bruggen, A.H.C., 1993. Sensitivity of simulated dew duration to meteorological variations in different climatic regions of California. Agricultural and Forest Meteorology 66, 229–245. https://doi.org/10.1016/0168-1923(93)90073-Q

Schonherr, J., 2006. Characterization of aqueous pores in plant cuticles and permeation of ionic solutes. Journal of Experimental Botany 57, 2471–2491. https://doi.org/10.1093/jxb/erj217

Schreiber, L., Skrabs, M., Hartmann, K., Diamantopoulos, P., Simanova, E., Santrucek, J., 2001. Effect of humidity on cuticular water permeability of isolated cuticular membranes and leaf disks. Planta 214, 274–282. https://doi.org/10.1007/s004250100615

Sharma, M L, 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331.

Sharma, M. L., 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331. https://doi.org/10.1016/0002-1571(76)90086-8

Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. Canadian Journal of Botany 82, 450–460. https://doi.org/10.1139/b04-016

Simonin, K.A., Santiago, L.S., Dawson, T.E., 2009. Fog interception by Sequoia sempervirens (D. Don) crowns decouples physiology from soil water deficit. Plant, Cell & Environment 32, 882–892. https://doi.org/10.1111/j.1365-3040.2009.01967.x

Steppe, K., Vandegehuchte, M.W., Van de Wal, B.A., Hoste, P., Guyot, A., Lovelock, C.E., Lockington, D.A., 2018. Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove Avicennia marina. Tree physiology 38, 979–991.

Suárez, A.G., Gloser, J., 1982. Time course of foliar absorption of water inPanicum andPaspalum. Biol Plant 24, 226–230. https://doi.org/10.1007/BF02883669

Tian, C., Wang, L., Kaseke, K.F., Bird, B.W., 2018. Stable isotope compositions (δ2H, δ18O and δ17O) of rainfall and snowfall in the central United States. Sci Rep 8, 6712. https://doi.org/10.1038/s41598-018-25102-7

Tuller, S.E., Chilton, R., 1973. The role of dew in the seasonal moisture balance of a summer-dry climate. Agricultural Meteorology 11, 135–142. https://doi.org/10.1016/0002-1571(73)90057-5

Tyree, M.T., Cruiziat, P., Benis, M., LoGullo, M.A., Salleo, S., 1981. The kinetics of rehydration of detached sunflower leaves from different initial water deficits. Plant, Cell & Environment 4, 309–317.

Uclés, O., Villagarcía, L., Moro, M.J., Canton, Y., Domingo, F., 2014. Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. Hydrological Processes 28, 2271–2280. https://doi.org/10.1002/hyp.9780

Van Gardingen, P.R., Grace, J., Jeffree, C.E., 1991. Abrasive damage by wind to the needle surfaces of Picea sitchensis (Bong.) Carr. and Pinus sylvestris L. Plant, Cell & Environment 14, 185–193.

Veste, M., Heusinkveld, B.G., Berkowicz, S.M., Breckle, S.-W., Littmann, T., Jacobs, A.F.G., 2008. Dew formation and activity of biological soil crusts, in: Arid Dune Ecosystems. Springer, pp. 305–318.

Vuollekoski, H., Vogt, M., Sinclair, V.A., Duplissy, J., Järvinen, H., Kyrö, E.-M., Makkonen, R., Petäjä, T., Prisle, N.L., Räisänen, P., 2015. Estimates of global dew collection potential on artificial surfaces.

Wang, C., Cen, Y., Liu, M., Bowler, P., 2017. Formation and influencing factors of dew in sparse elm woods and grassland in a semi-arid area. Acta Ecologica Sinica 37, 125–132. https://doi.org/10.1016/j.chnaes.2017.06.004

Weatherley, P.E., 1963. The pathway of water movement across the root cortex and leaf mesophyll of transpiring plants. The water relations of plants 85–100.

Westbeld, A., Klemm, O., Grießbaum, F., Sträter, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert, in: Annales Geophysicae: Atmospheres, Hydrospheres and Space Sciences. p. 3571.

Williams, D.G., Ehleringer, J.R., 2000. Intra-and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecological Monographs 70, 517–537.

Wu, H., Li, X.-Y., Li, J., Jiang, Z., Chen, H., Ma, Y., Huang, Y., 2016. Differential soil moisture pulse uptake by coexisting plants in an alpine Achnatherum splendens grassland community. Environ Earth Sci 75, 914. https://doi.org/10.1007/s12665-016-5694-2

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2013. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2009. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Yamanaka, T., Tsujimura, M., Oyunbaatar, D., Davaa, G., 2007. Isotopic variation of precipitation over eastern Mongolia and its implication for the atmospheric water cycle. Journal of Hydrology 333, 21–34. https://doi.org/10.1016/j.jhydrol.2006.07.022

Yang, Y., Fu, B., 2017. Soil water migration in the unsaturated zone of semiarid region in China from isotope evidence. Hydrology and Earth System Sciences 21, 1757–1767.

Yates, D., Hutley, L., 1995. Foliar Uptake of Water by Wet Leaves of Sloanea woollsii, an Australian Subtropical Rainforest Tree. Aust. J. Bot. 43, 157. https://doi.org/10.1071/BT9950157

Ye, Y., Zhou, K., Song, L., Jin, J., Peng, S., 2007. Dew amounts and its correlations with meteorological factors in urban landscapes of Guangzhou, China. Atmospheric Research 86, 21–29. https://doi.org/10.1016/j.atmosres.2007.03.001

Zangvil, A., 1996. Six years of dew observations in the Negev Desert, Israel. Journal of Arid Environments 32, 361–371. https://doi.org/10.1006/jare.1996.0030

Zhao, Y., Wang, L., 2018. Plant Water Use Strategy in Response to Spatial and Temporal Variation in Precipitation Patterns in China: A Stable Isotope Analysis. Forests 9, 123. https://doi.org/10.3390/f9030123

Zhu, L., Wang, Z.H., Mao, G.L., Zheng, S.X., Xu, X., 2014. Water uptake from different soil depths for halophytic shrubs grown in Northern area of Ningxia plain (China) in contrasted water regimes. Journal of Plant Interactions 9, 26–34. https://doi.org/10.1080/17429145.2012.751139

Zwieniecki, M.A., Brodribb, T.J., Holbrook, N.M., 2007. Hydraulic design of leaves: insights from rehydration kinetics. Plant Cell Environ 30, 910–921. https://doi.org/10.1111/j.1365-3040.2007.001681.x

# Chapter 2

## Water uptake by two native grasses from a continental semiarid grassland: temporal and spatial sources

### ABSTRACT

The region of semiarid grasslands in Central Mexico is highly diverse in the number of grass species and community assemblages. Still, this grassland are characterized by the dominance of one species, *Bouteloua gracilis*, with a large number of subordinated species that may prosper when the disturbance regime affects the dominant species. These plant community changes enhancing plant interactions may create conditions such as competition for water and nutrients. Here we tested whether the water use for neighboring *B. gracilis* and *Mulenbergia rigida* resulted in partitioning or overlap in the use of soil water. We observed that *B. gracilis* relied on shallow soil water (5-10 cm) during the dry season, however it capacity of shifting the water source during the wet season to deeper soil layers. *M. rigida in contrast showed* overlapping with *B. gracilis* in the patterns of water extraction during the wet season (5-10 cm), but they also shifted their water uptake during the dry season, acquiring water from 15-25 cm depth. The IsoSource model confirmed that dew can have an important contribution as a water source for both species, particularly during the dry season. We concluded that both species exhibited a strong ecological plasticity that can shift the depth of water source in response to water availability and a vertical partitioning of soil water uptake that contributes to reduce competition between both species, which resulted in a more complex pattern in soil water extraction that can explain the structure and function of this semiarid grassland ecosystem.

Key words: *Bouteloua gracilis*, *Muhlenbergia rigida*, water uptake, IsoSource model, stable isotopes

## Introduction

A grassland is that plant community where vegetation cover is dominated by grasses (Rzedowski, 2007). The grassland vegetation constitutes a biome covering around 18% of the terrestrial Earth surface. Through unique ecosystem properties (e.g., high albedo, high soil organic carbon storage capability, high silica reservoir) together with its large extent, grasslands exert strong influence on the global climate as well as on the carbon and silica cycles (Kidder and Gierlowski-Kordesch, 2005). In Mexico, the grassland biome constitutes one of the main vegetation types, potentially covering about 22% of the territory (Rzedowski, 2007), with more than 80% of this distributed in the Mexican Altiplano. In North America, grasslands are distributed from southern Canada in the Saskatchewan province to central Mexico in the Llanos de Ojuelos region. This region is highly diverse in the number of species and community assemblages dominated by *Bouteloua gracilis* (*H.B.K*). Lag. ex Steud which is considered the key species in many cases (Medina-Roldán et al., 2007). This grass species evolved under a diverse set of natural disturbance factors which include natural fire, grazing by native ungulates and recurring droughts, that favored particular ecophysiological adaptations (e.g. stem growth zones or meristem at ground base for regeneration after defoliation, drought and salinity tolerance, high tillering rates and high specific leaf area) to their complex natural disturbance regimes. It has been suggested that these factors are the most important controls of community richness, composition and structure (Blair et al., 2014).

Human influence on the other hand, has modified grassland natural selection factors to the point that it has been proposed that changes in these factors promote invasion of exotic species, provoking the displacement and loss of native species (Koerner and Collins, 2014). Although grasslands tend to be dominated by one or few key species, alteration of the natural selection factors cause important changes in community composition including for instance, its transformation to shrubby vegetation. Some of these changes are related to environmental influences affecting competitive relationships, niche segregation, responses to environmental variations, etc. In the semiarid grassland of México, the dominant warm season grasses coexist with subordinate species including, grasses and forbs. Nevertheless, dominant species may reduce their competitive capacity because of its preferential consumption by herbivores that result in the increase of subordinate species (Hartnett et al., 1996; Silletti et al., 2004). The absence of natural fires may carry out similar outputs in the dynamics of grassland communities. Understanding this interaction between subordinate and key grass species following different types of disturbance regimes and how this interaction impacts the ecosystem process can have important implications for assessing and managing the health, vulnerability and resilience of key grassland species.

In Mexico, most of the grassland biome has been either heavily grazed or converted to cropland that has being eventually abandoned, having repercussions on vegetation shifts that alter both community structure and ecosystem functions. Shifts associated with overgrazing that have been reported in Central Mexico, include the propagation of previously subordinate grass species such as *Bouteloua scorpioides, B. hirsuta, Aristida divaricata* and *Muhlenbergia rigida*, occupying the space left by the dominant grass *Bouteloua gracilis* (Aguado-Santacruz and Garcia-Moya, 1998; Medina-Roldán et al., 2007). Thus, structural changes related to species shifts include for instance; vegetation patches becoming more fragmented (Aguado-Santacruz and Garcia-Moya, 1998), influencing soil hydrology by increasing runoff, this change has potentially large biogeochemical, hydrologic and ecological impacts. This is one of several disturbance processes that could alter the hydrological balance of the grassland following an important switch in species composition. Another important hydrological mechanism observed in a vegetation shift consists in species differential capacity to use different water sources such as dew and fog as well as water stored in the caliche layer (Corbin et al., 2005; Michael Cohrs Duniway et al., 2010). The capacity to access these sources of water among grass species may translate into species survival during the long drought period (Suárez and Gloser, 1982), productivity of the following growing season (legacy effect, (Arredondo et al., 2018), and a larger temporal scale the maintenance of a grassland vegetation (Corbin et al., 2005).

Among the subordinate species of the semiarid grassland in central México, *Muhlenbergia rigida* is one of the most conspicuous species taking over disturbed grasslands. Physiological information for *M. rigida* is largely missing, but this is a perennial large species, morphologically characterized by a dense caespitose tussock, 40-100 cm height, leaves are wide up to 30 cm long, wrapped at the base, with a low root to shoot ratio, with compact base culms and a great density of old roots (Maldonado Burgos, 2015; Peterson and Giraldo-Cañas, 2011). *B. gracilis* in contrast is a long-lived perennial, 25 to 70 cm height. Leaves are narrow up to 20 cm long, wrapped at the base. Roots extend at least 30 cm from the edge of the plant and reach 90 cm deep (Coffin and Lauenroth, 1991b). *B. gracilis* exhibits $C_4$ photosynthesis pathway and adaptations to grow and survive during hot and dry periods (Alcocer-Ruthling et al., 1989; Monson et al., 1986), such as a high water use efficiency and a great capacity to maintain leaf water potential throughout the day and seasons (Arredondo et al., 2016b; Sala et al., 1982). *B. gracilis* responds very rapidly to a small (5-mm) rainfall events following a period of drought (Medina-Roldán et al., 2013). In general *B. gracilis* is adapted to scarce and highly variable water supply and to a precipitation patterns in which small rainfall events constitute the largest portion of total rain events (Delgado-Balbuena, 2016). Both species enter senescence once the dry period begins in October and last until the next month of June.

In the semiarid grassland, soil water is the main water source for plants and widely available in summer, however once the dry season occurs soil water turns scarce, forcing plants to use other sources such as water stored in geologic layers (Michael Cohrs Duniway et al., 2010) or water coming from dew or fog (Aguirre-Gutiérrez et al., 2019). Thus, changes in the quantity and seasonality of precipitation may affect interactions among coexisting species, that will depend on its adaptations to gather particular source of water (Ehleringer et al., 1991). Differences in root systems between grass species (root biomass, root depth etc.) may provide a partial explanation for species coexistence. However, it is less clear how other adaptations such as, leaf tissue capacity to absorb dew water, play a role in the maintenance of a species in a harsh environment. In the semiarid grassland in central Mexico, 60% of total precipitation events comes as rain of 5 mm or less, whereas precipitation events of > 10 mm accounted to most of the annual precipitation (Delgado-Balbuena, 2016). Summer precipitation represents around 90% of annual total precipitation with winter rains accounting from 5 to 18% (Aguirre-Gutiérrez et al., 2019; Delgado-Balbuena, 2016). In this semiarid continental grassland, dew has been considered so far as a negligible source of water to the ecosystem, however a recent study by Aguirre et al (2019) showed that dew may annually contribute with 2 to 11% of total precipitation. Therefore, becoming another potential source of water particularly during the drought period because it contributes with 7 to 33 % of winter precipitation (Aguirre-Gutiérrez et al., 2019). Taken together all water sources grass species could access superficial soil water, soil water stored in the profile below the evaporative zone, deep water stored in caliche layer, and water condensed on the leaves Hence, considering morphological differences between dominant *B. gracilis* and *M. rigida* we would expect that a bigger root size by *M. rigida* should favor exploration of the deeper substrate layers whereas the large drought tolerance by *B. gracilis* would be associate to greater efficiency to take water from small rain pulses and dew.

## Methods

### *Study site*

The study was conducted at the *Vaquerias* grassland research station, which is located within the Mexican Altiplano at 2,200 m above sea level. This high elevation tropical site (21° 46’ 52.25” N and 101° 36’ 29.56” W) is located approximately 464 km from the Pacific Ocean and 344 km from the Gulf of Mexico, in Los Llanos de Ojuelos physiographic subprovince. The climate is continental semiarid, presenting between 350/450 mm annual rainfall of which 95% falls during the growing season (June-September) and exhibits from 6 to 9 month period of no-rain. Winter rain accounts for 5 to 18% of the total annual rainfall (Aguado-Santacruz and Garcia-Moya, 1998; Medina-Roldán et al., 2007). Mean annual temperature is 18 °C, with mean temperature extremes ranging from 2.2 °C for the coldest to 26.8 °C for the warmest month, respectively. The physiography consists mainly of plains and rolling hills with predominantly sandy loam soils. Soils are classified as Xerosols, and the vegetation is dominated by *B. gracilis*. In disturbed grasslands *B. gracilis* is replaced by *B. scorpioides, B. hirsuta, A. divaricata, Lycurus phleoides* and *Muhlenbergía rigida.* Two native grasses were selected for the study; the dominant *B. gracilis* and the subordinate *M. rigida* (figure 1), this last as one of the most conspicuous that exhibit bigger size than the dominant.

Figure 1. Photographic examples of A) the relatively deeper, coarser roots of *Muhlenbergia rigida* and B) the shallower, finer roots of *Bouteloua gracilis*, and C) a *B. gracilis* grassland replaced by *M. rigida* (dark red tall grass).

### *Rainfall and dew samples*

Rainfall was measured continuously with a tipping bucket rain gauge (FTS, Victoria, British Columbia, Canada) connected to a datalogger (CR3000, Campbell Scientific Inc., Logan, Utah). Local rainwater was collected for stable isotopes analysis using a pluviometer (15 cm wide and 40 cm deep) fitted funnel. The pluviometer contained a thin layer of mineral oil to prevent evaporation. The pluviometer was placed at about 1 m above ground level. Samples of rain events were usually collected within one day following the rain. Additionally, we used the precipitation monthly data from the online isotopes precipitation calculator (OIPC), which estimates the mean annual and monthly deuterium and oxygen isotope composition of precipitation at specific locations. The collected samples were stored at 4 °C until isotopic analysis.

Dew is an important water source in this environment (Aguirre-Gutiérrez et al., 2019). However, to determine how important is dew as water source for grasses, we also measured dew isotope values. From May 2016 to March 2017, dew samples were collected before sunrise using a custom-made dew trap (Guan et al., 2014). The structure consisted of a 1 × 1 m aluminum table, oriented perpendicular to the direction of the prevailing wind. Dew water condensed onto this table and dew water was funneled into a glass bottle with a thin layer of mineral oil. Water was collected every morning when a dewfall event was observed, into amber vials sealed and stored for later isotopic analysis. We use these samples to identify the dew water isotopic signature ($\delta^2H$ and $\delta^{18}O$) at the site but not to estimate the amount of condensation.

### *Plant and soil samples*

Basal culm tissue of the two grass species was sampled and collected periodically from March 2016 to March 2017, with up to sixteen samples of each individual grass specie per sampling time. Sampling sites were those exhibiting a sufficient number of both species (*B. rigida* and *M. rigida* respectively) to allow repeated sampling from a common site. In order to determine the $\delta^2H$ and $\delta^{18}O$ values of water taken up by grasses, basal culm tissue was collected just below the soil surface to minimize potential evaporation, carefully excluding photosynthetic tissue because in several grass species crowns have been shown to be the least variable plant tissue for the assessment of water sources using isotope techniques (Barnard et al., 2006; Helliker and Ehleringer, 2000). Culms were placed immediately in glass vials and sealed with parafilm and stored at 4°C until we extracted the water and posterior isotope analysis

At monthly frequencies, soil was collected at different profiles using a soil core sampler, at the same time that vegetation was sampled, so we could tie the $\delta^2H$ and $\delta^{18}O$ values of water in soil and plants. Four replicated cores were taken for isotopic analysis (n = 4) at 6 depths (5, 10, 15, 25, 40 and >40 cm). These samples were also stored in glass vials with sealed caps to prevent evaporation and cooled to 4 °C prior to water extraction.

*Sample water extraction and stable isotopes analysis*

Water from soil and grass tissue was extracted from all of the samples using a cryogenic vacuum distillation method (West et al., 2006). Samples of plant tissue were routinely weighed, and oven dried to ensure the extraction time was sufficient to vaporize all xylem water within the grass tissue. The isotope ratios of extracted water as well as meteoric water (precipitation) samples were analyzed using a laser spectrometer (LWIA24d, USA) in the national laboratory of geochemistry and mineralogy at Instituto Tecnologico de Sonora. The hydrogen and oxygen isotopes were reported in delta (δ) notation as per mil (‰) differences relatives to the V-SMOW (Vienna Standard Mean Ocean Water) international standard:

$$\delta H \ or \ \delta O^{18} = \left(\frac{R_{Sample}}{R_{smow}} - 1\right) \times 1000 \qquad (1)$$

where $R_{sample}$ and $R_{smow}$ represent the heavy to light isotope ratio ($^2H/H$; $^{18}O/^{16}O$) of either hydrogen or oxygen in the sample and the standard, respectively.

The standard for water isotope ratios used here is Vienna standard mean ocean water (vSMOW). The analytical precision of the $\delta^2H$ and $\delta\ ^{18}O$ by mass spectroscopy was better than ±2 and ±0.2‰, respectively.

Water proportion used by each grass species was determined using a two-compartment linear mixing model (Phillips and Gregg, 2001) as:

$$f = \frac{\delta^{18}O_{xylem} - \delta^{18}O_{deepsoil}}{\delta^{18}O_{source} - \delta^{18}O_{deepsoil}} \qquad (2)$$

where “xylem” is the plant water isotope composition, “source” is the different water source isotopic composition, and “deep soil” is the isotope composition of soil water around plant roots (0-25 cm) derived from precipitation and percolation. In this case, if *f* is greater than one, it means that source (dew or precipitation) is the dominant water source used by the plant, and when *f* is less than 0, water comes exclusively from the soil. Values ranging from 0 to 1 indicates a mixture of sources between source and soil.

*Soil water content*

Soil water content at depths of 0.1, 0.25 and 0.40 m was measured with TDR (time domain reflectometry) sensors using the standard calibration equation from Campbell (CS616, Campbell Sci., Logan, Utha, USA). Data were recorded every 30 minutes and stored on a Campbell Scientific data logger (CR1000, Campbell Sci., Logan, Utha, USA).

*Statistical analysis*

The isotopic values of xylem water were compared with those of potential water sources using the IsoSource model, and thus it was possible to obtain a feasible range of the different water sources used by both species at each sampling time (Phillips and Greg 2003). Four potential water sources (shallow soil water from 0-10 cm, deep soil water from 15-40 cm, dew and rainfall) were used in our research, source increment was defined as 1% and mass balance tolerance was defined as 0.1‰. We calculated the mean and possible range of water utilization on each month. An orthogonal linear regression, which is used to minimize the orthogonal distance from the observed data points to the regression line, was used to examine species differences in seasonal dynamics. The slope and intercept coefficients were calculated, obtaining the local meteoric water line where the slope-intercept equation fitted as $\delta^2H = m * \delta\ ^{18}O + b$.

## Results

### *Environmental Conditions*

Maximum monthly air temperatures at the site occurred in May and June (19 °C) whereas minimum temperatures were observed in January and November (11 °C) (Figure 2A). The dry season began at the end of September 2016 and persisted throughout the end of May, with small infrequent rainfall events during winter (Figure 2A). Precipitation accumulated to 275 mm in the wet season and 137 mm during the dry season for a total annual of 412 mm. Monthly mean VPD showed seasonal variation, with maximum values recorded in May and minimum during November. Volumetric soil water content (VSWC) was highly variable between soil depths reflecting the time between the most recent precipitation and water infiltration in the soil profile (Figure 2C) Thus, increases of soil water content at0.4-0.6 m lagged behind changes in the shallow soil. Soil water content also indicated that rain pulses during winter usually did not deeply infiltrate into the soil profile. Soil water content was higher and more persistent at deeper soil depths. Notably, the petrocalcic layer consistently had 5.1-16.9% higher water content than soil at 0.25 m deep.

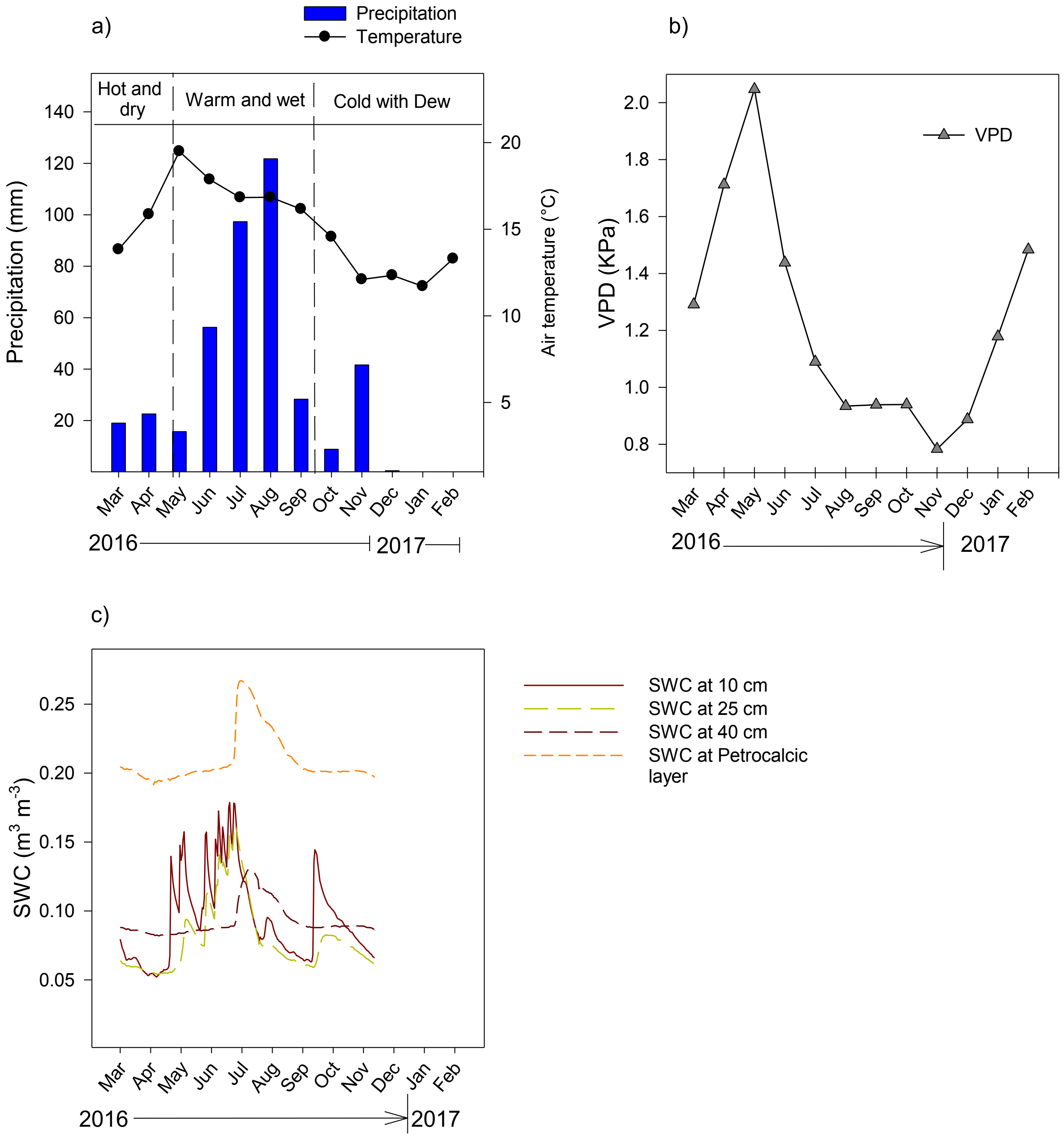


Figure 2. The monthly precipitation and air temperature a) monthly estimated vapor pressure deficit b), soil water content profiles for four soil depths measured in a continental semiarid grassland in Jalisco, Mexico.

*Seasonal isotopic variations in dew, rainfall and their uptake by plants*

Seasonal variation in isotopic composition of precipitation water ranged from -1.7‰ to -12.5‰ for $\delta^{18}O$ and from -25.5‰ to -97.5‰ for $\delta^{2}H$, whereas modeled precipitation ranged from -5.9‰ to -11.7‰ for $\delta^{18}O$ and from -35‰ to -81‰ for $\delta^{2}H$ (Figure 3). Dew water isotopic values were typically more enriched than precipitation ranging from -2.3‰ to -11.6‰ for $\delta^{18}O$, and from -9.9‰ to -69.3‰ for $\delta^{2}H$. Seasonal variations in dew water isotope signatures tracks the values from precipitation.

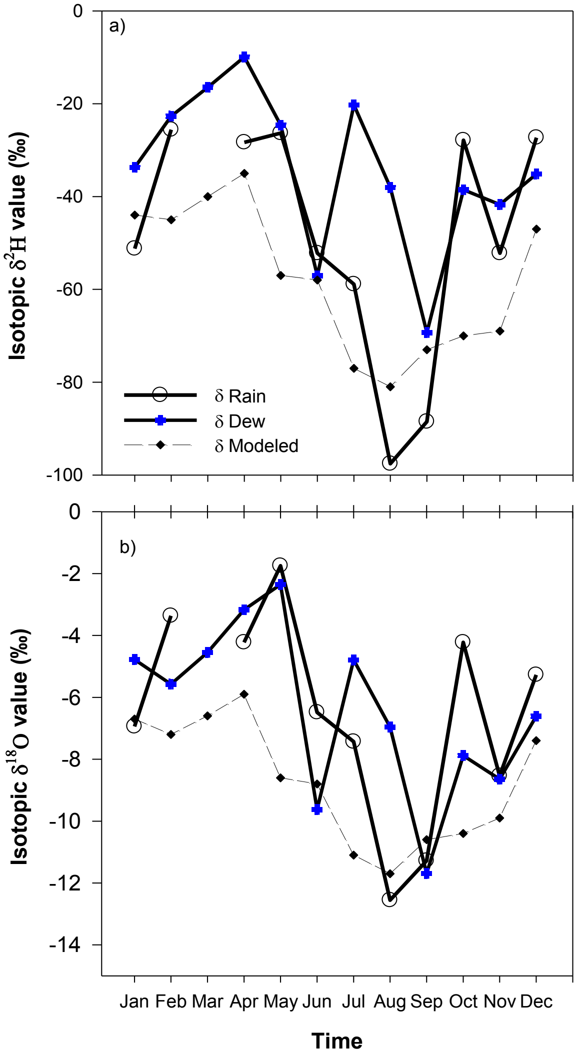


Figure 3. Hydrogen isotope ratios (a) and oxygen isotope ratios of precipitation and dew (b). Modeled values were obtained from waterisotopes.org to complement our measured data and provide insight to the typical stable isotope seasonality.

*Rain, dew, soil and vegetation isotope values*

Relative to the global meteoric water line, the composite of local meteoric water line from our site (LMWL) had a lower slope and intercept, defined by the equation $\delta^2$H = -1.04 + 7.9 * $\delta^{18}$O, plotted under the line corresponding to the global meteoric water line (Figure 4). Rainfall mean isotopic composition during the wet season was $\delta^{18}$O= -9.69‰ ± 0.5‰, and $\delta^2$H= -76.22‰ ± 3.9‰ whereas in the dry season it was $\delta^{18}$O= -3.42 ‰ ± 0.7‰ and $\delta^2$H= -39.45‰ ± 5.8‰. These isotopic signatures were compared to those coming from locally collected rain, dew and soil water samples (Figure 4). Dew was defined by the equation $\delta^2\mathrm{H} = -18.8 + 7.7 * \delta^{18}\mathrm{O}$ with a mean composition during the wet season of $\delta^{18}$O= -9.28‰ ± 1.1‰; $\delta^2$H= -53.44‰ ± 8.1‰ , while for the dry season it was $\delta^{18}$O= -6.9 ‰ ± 0.04‰; $\delta^2$H= -34.82‰ ± 0.29‰. The isotopic compositions of dew and rain during the wet season were similar suggesting similar origin, while in the dry season both water sources differed indicating different sources or processes. Soil water samples appeared to be derived from evaporative enriched precipitation. Soil water samples from the wet and dry season plotted to the right of the LMWL, with an evaporation soil line of $\delta^2$H =-44.27 + 6.03 * $\delta^{18}$O (Figure 4).

Equally, the isotopic composition of plant water extracted from both *B. gracilis* and *M. rigida* for the wet and dry season (Figure 5A), showed that isotopic signatures were located slightly to the right of the LMWL. Thus, xylem water $\delta^{18}$O of *M. rigida* ranged between -21‰ to 6.53‰ and $\delta^2$H ranged between -174.6‰ to -18.5‰, with an overall mean value of $\delta^{18}$O (-3.3‰ ±3.3‰, *n*=171) and $\delta^2$H (-65.2‰ ± 22‰, *n*=171). *B. gracilis* xylem water in contrast, ranged between -16.3‰ to 8.7‰ for $\delta^{18}$O and -142.7‰ to -18.5‰ for $\delta^2$H, with an overall value of $\delta^{18}$O (-2.6‰ ±4.4‰, *n*=166) and $\delta^2$H (-57.1‰ ± 20.9‰, *n*=166) during dry season. The isotopic xylem water composition for *M. rigida* during the wet season (figure 5B) ranged between -9.3‰ to 6.4‰ for $\delta^{18}$O and between -96.1.7‰ to 13.9‰ for $\delta^2$H, with an overall value of (-1.3‰ ±4.2‰, *n*=38) for $\delta^{18}$O and of (-56.7‰ ± 21.6‰, *n*=38) for $\delta^2$H. In the case of *B.* gracilis isotopic xylem water values ranged between -14.6‰

to 6.7‰ for δ$^{18}$O and -126.6‰ to -11.7‰ for δ$^{2}$H, with an overall value of δ$^{18}$O (-2.6‰ ±4.5‰, *n*=49) and δ$^{2}$H (-64.4‰ ± 25‰, *n*=49).

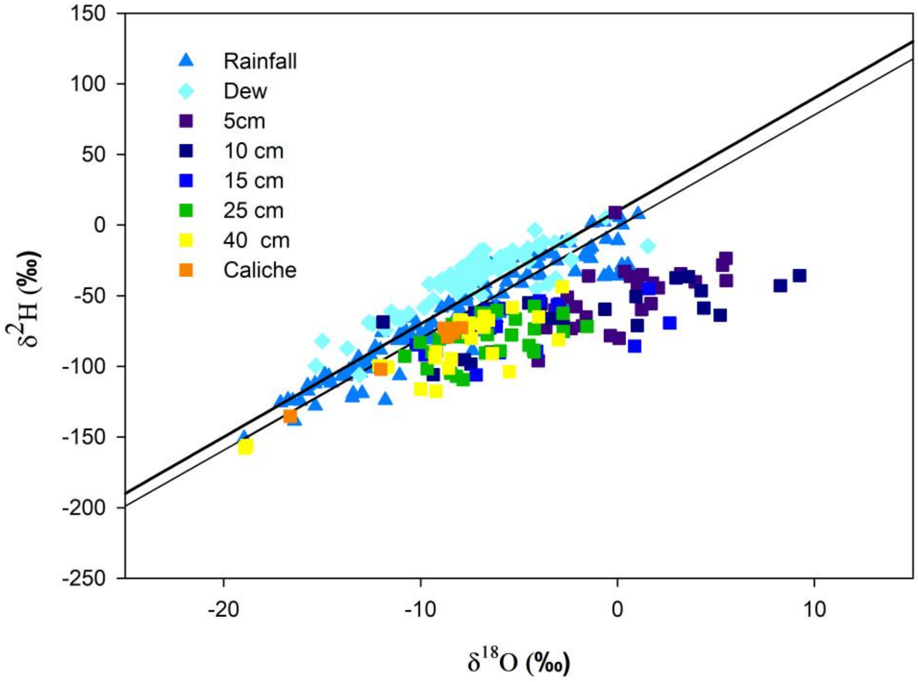


Figure 4. Stable isotopes of water collected from local rainfall (local meteoric line), dew and soil in a semiarid grassland. Water isotopes of soil were collected between March 2016 and February 2017. The water samples from rainfall and dew were collected after each event during the study period.

There was also a significant variation in δ$^{2}$H and δ$^{18}$O signatures between soil profiles in both seasons (Figure 5C and D). During the dry season, soil water was isotopically enriched in both isotopes compared to the wet season. This isotopic enrichment occurred in the top 5 cm soil layer (Figure 5D). In this period, there was a clear separation between *B. gracilis* and *M. rigída* respect to the average depth of water uptake. Thus, *B. gracilis* extracted water from the shallow soil layer (10 cm depth), while *M. rigida* extracted water from a deeper zone of the soil profile (20 cm depth). Differences in water uptake depth between the two grass species just occurred during the dry season (Figure 5D), while both species took water from similar soil layer during the wet season. During summer, water from rainfall infiltrated reaching the deeper soil layer (60 cm), while during the dry season winter rain just wetted the first 20 cm of the soil profile.

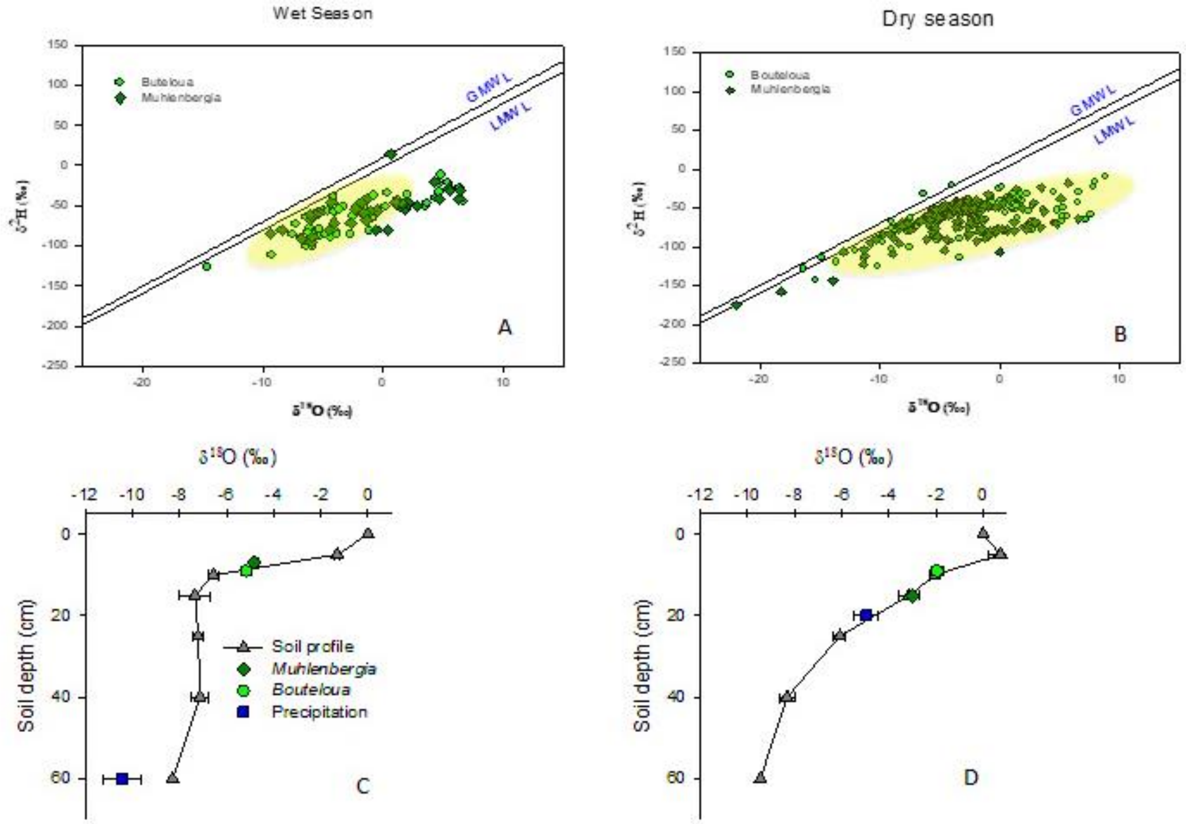


Figure 5. Isotopic values obtained from collected culms of two grass species in a continental semiarid grassland, **a** dry season, **b** wet season. Samples were collected from March 2016-February 2017, and the shadow area indicates soil water values. Further, **c** and **d** represent the averages changes in $\delta^{18}O$ with soil depth for dry season wet season, respectively, showing $\delta^{18}O$ signatures for the soil profile, grass and rainfall during the dry and wet season. Horizontal bars indicate standard error (SE) of the means.

### *Seasonal isotopic variations in plant xylem and soil water*

Soil water $\delta^{18}O$ and $\delta^{2}H$ underwent pronounced seasonal changes throughout the dry season, with greater fluctuation of $\delta^{18}O$ in the shallow soil layer (0 - 10 cm) and relatively stable variations of $\delta^{18}O$ in the deep soil layer (15 - 40 cm; Figure 6). In particular, the shallow soil water $\delta^{18}O$ were more depleted because of the substantial evaporation with isotopically enriched $\delta^{18}O$ during

August to December. The deep soil or groundwater δ$^{18}$O exhibited no seasonal changes (average -6.53‰) during both dry and wet season (Figure 6). To provide the context for interpreting the seasonal dynamics in both species, we present the monthly mean value of the isotopic water composition for soil and plant xylem (Figure 6). Therefore, δ$^{18}$O and δ$^{2}$H of soil were divided into two layers to represent the shallow and deep soil water respectively. The mean isotopic composition of xylem and soil water sampled over the study period, showed that shallow soil and xylem water of *B. gracilis* and *M. rigída* are similar, indicating the uptake of the enriched rainfall that persisted in the transpiration stream after it was evaporated from the soil. The δ$^{18}$O and δ$^{2}$H seasonal variations in xylem water were almost synchronous with the shallow soil water and precipitation. However, *B. gracilis* switching between pool sources coincided with the end of the dry season and onset of the wet season, responding very rapidly to small rainfall events following a period of drought (figure 6), presenting more enriched values during the dry period whereas they were depleted during summer (ranged between 0.5‰ to 4‰).

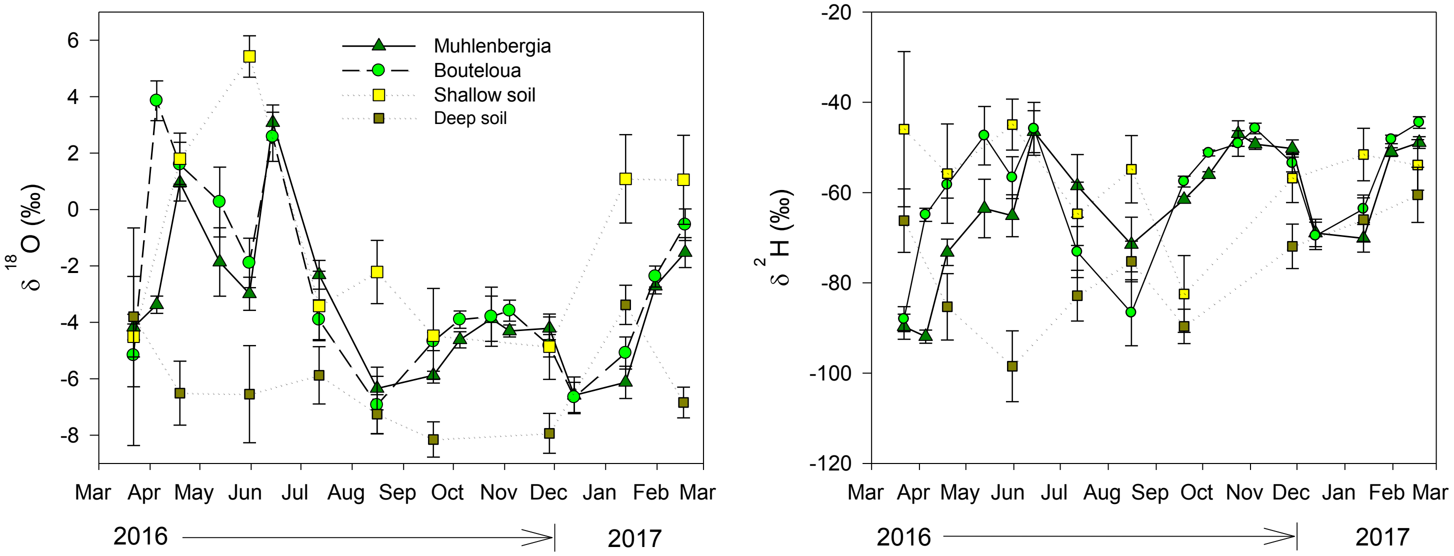


Figure 6. The δ$^{18}$O and δD seasonal dynamics in *B.gracilis* and *M. rigida*, soil water (0-0.1 m and 0.15-0.4 m) with standard error bars, over a one-year period (March 20016 to February 2017).

### *Possible water sources contribution in plant xylem*

The IsoSource model predicted that *M. rigida* and *B. gracilis* took water mainly from soil and precipitation, but exhibited a shift in water use during November, where dew have a contribution of 73% as the main water source (Figure 7) for both species. During April, September and February the contribution of shallow soil water was in the range of 76-98 % for *B. gracilis* and the possible ranges of deep soil water contribution, dew and rainfall was in the range 0-16 %, 0-24% and 0-17%, respectively, while for *M. rigida* were in the range of 38-81 % and the possible ranges of deep soil, dew and rainfall of 0-41 %, 0-62% and 0-51%. However, during May, August and January, the possible water source contribution for both species is a well-mixed water from soil, dew and rainfall. *M. rigida* exhibited a shift in water use during March, where deep soil was the main water source in the range of 34-89%. Furthermore *B. gracilis* exhibited a shift in water used during July with deep soil water as main source in the range of 47-84%.

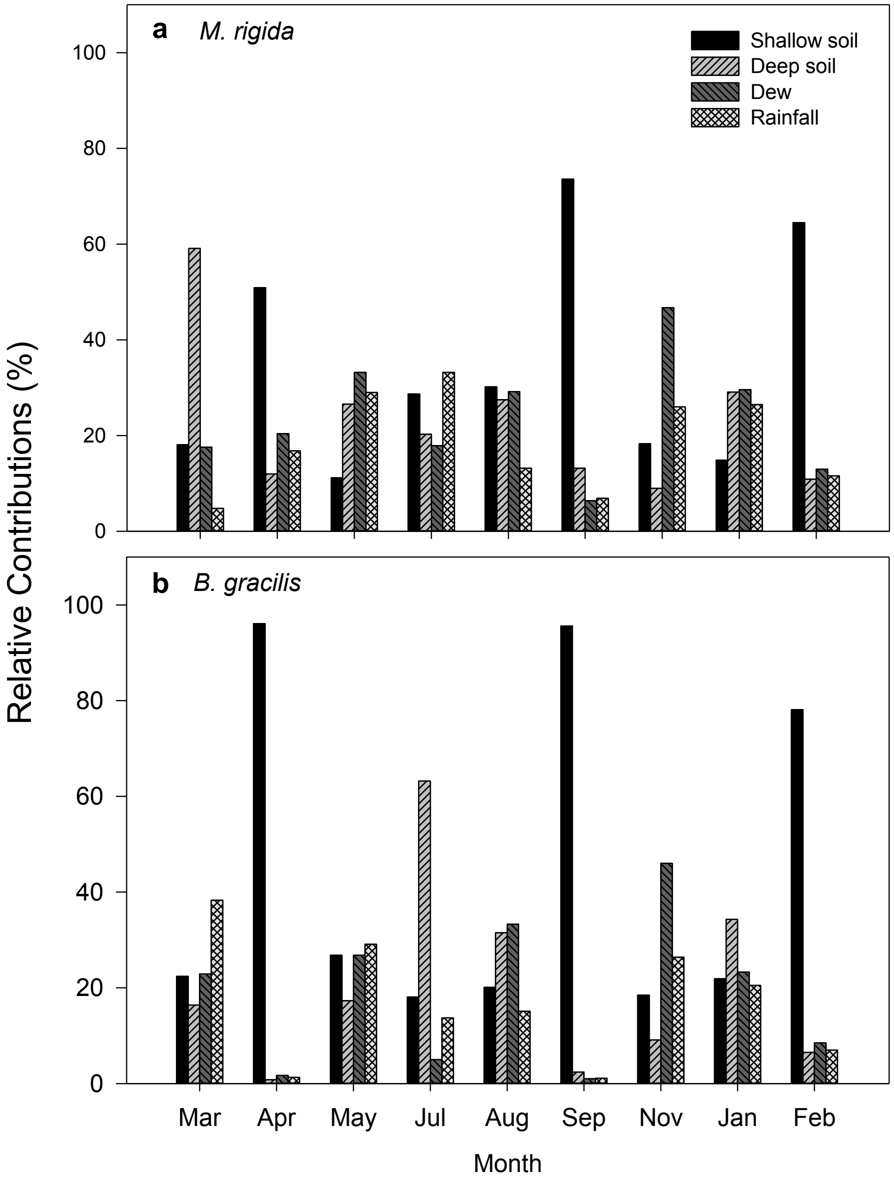


Figure 7. Monthly changes in the proportional contribution of four potential water sources for *M. rigida* (a) and *B.gracilis* (b) at the study site. The column height represents the mean value of relative contribution, both were calculated using the IsoSource model (Phillips and Gregg 2003).

## Discussion

*Variations in isotopic composition of precipitation and dew*

The monthly means of stable isotopic composition ($\delta^{18}O$ and $\delta^{2}H$) of modeled precipitation, sampled precipitation and dew, (Figure 3) reflect the seasonal variation in the region, with great differences between the modeled and sampled precipitation. These variations may have resulted as an error in the calculation methods such as number of samples and elevation. This bias can also result from an effect of continental water recycling with a strong isotopic signal, differences in the origin of water vapor s, atmospheric flow path of vapor trajectories, temperature, precipitation amounts and continental effects (Bowen and Revenaugh, 2003; Dai et al., 2015; Yamanaka et al., 2007). Both seasons also differed considerable in precipitation, vapor pressure deficit and soil water content. During the summer the vapor pressure deficit (VPD) at the site remained low until December, due to atmospheric moisture presence of dew and fog events as consequence of coming cold fronts that remained until March (Figure 2; Aguirre et al. 2019), which also influenced the isotope composition as well. Thus, precipitation is isotopically depleted during the wet season, this precipitation originates as strong storms from the Gulf of Mexico but appear to be subjected to an amount effect, driven by successive precipitation of heavy isotopes prior to landfall. In contrast, precipitation during the dry season is enriched, which is associated with water evaporation. On the other hand, dew was more depleted during the beginning of the wet season, meaning that dew may be originated from the first rains, but it was enriched at the end of wet season which could be more subject to local precipitation recycling (Rozanski et al., 2013). While enrichment during the dry season indicates a process of evaporation, dew formation could also be associated to cold fronts.

### *Ecological implication of dew water use*

Dew and fog may influence plant water balance in several ways. First, the high humidity, low temperature conditions experienced during dew and fog events reduce the transpiration and plant water stress (Burgess and Dawson, 2004). Second, it is possible that plants are taking up water from dew or fog, either through roots or through direct foliar uptake (Berry et al., 2019; Dawson and Goldsmith, 2018b). In our study, plant tissue was not sampled in a way to distinguish the relative importance of foliar versus root uptake of dew and fog. Evidences from *Paspalum notatum* and *Panicum maximum* suggest that grasses can take water via leaves, recovering from water deficit after wetting their leaf surface, which may have some important ecological consequences (Suárez and Gloser, 1982). It is possible, however, that the ecological importance of foliar uptake is not limited to the reduction of potential evapotranspiration. Water absorbed through leaves may help plants not only to survive but also to grow during nighttime. Therefore, our assessments about the importance of dew to continental grassland vegetation may be conservative, in that they only examine direct dew use via root uptake and no other effects, such as foliar water uptake of dew or reduction in transpiration on plant-water relations.

### *Water sources in the semiarid grassland*

In this semiarid grassland, plants relied on rain and shallow soil water as the main water sources. rain originates from two sources, in summer for instance, precipitation comes from air masses carrying moisture that moves from the Gulf of Mexico into mainland (Figure 8). This process concurs with high temperatures and produce large precipitation events. Furthermore, heat and tropical waves propagating from the Gulf of Mexico modify the precipitation and temperature distribution of adjacent land regions (Pineda Martínez, 2009).

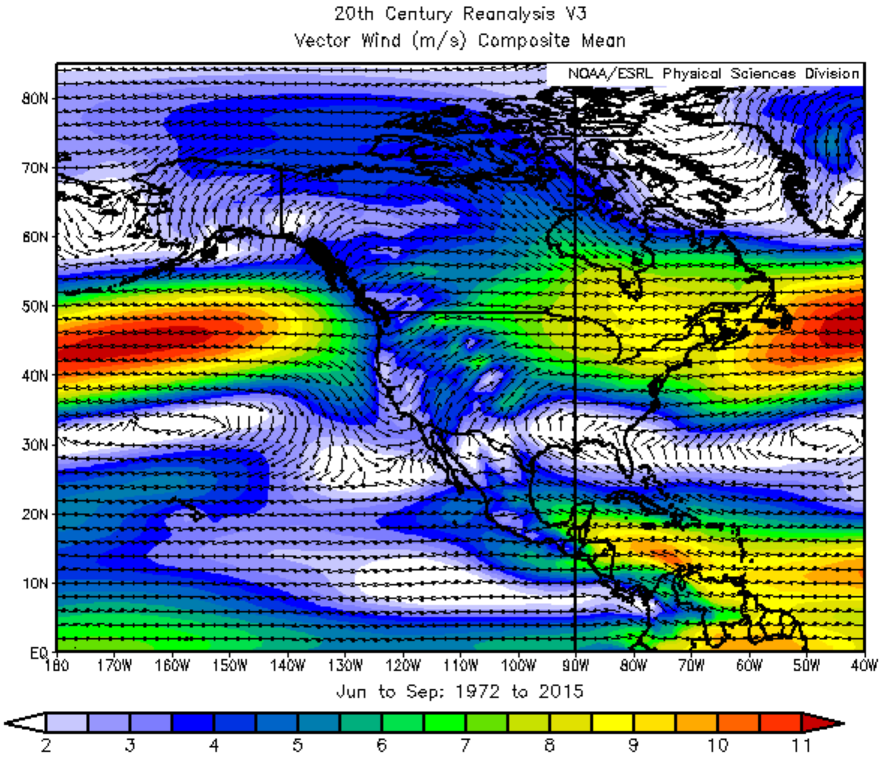


Figure 8. Mean vector wind movement during summer at 700 MPa for the North America region (20th Century Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, https://www.esrl.noaa.gov/psd/).

Furthermore, cold winters and cold fronts get propagated through the plains of the central-southeast region of USA in an anticyclone motion, advancing southwards into Mexico and causing temperature drop and strong changes in weather conditions (i.e. the passage of cold air masses produce anomalous time series of temperature, relative humidity and strong winds), consequently the isotopic composition of rainfall is enriched and is affected by cold northwesterly air flow in winter (Pineda Martínez, 2009).

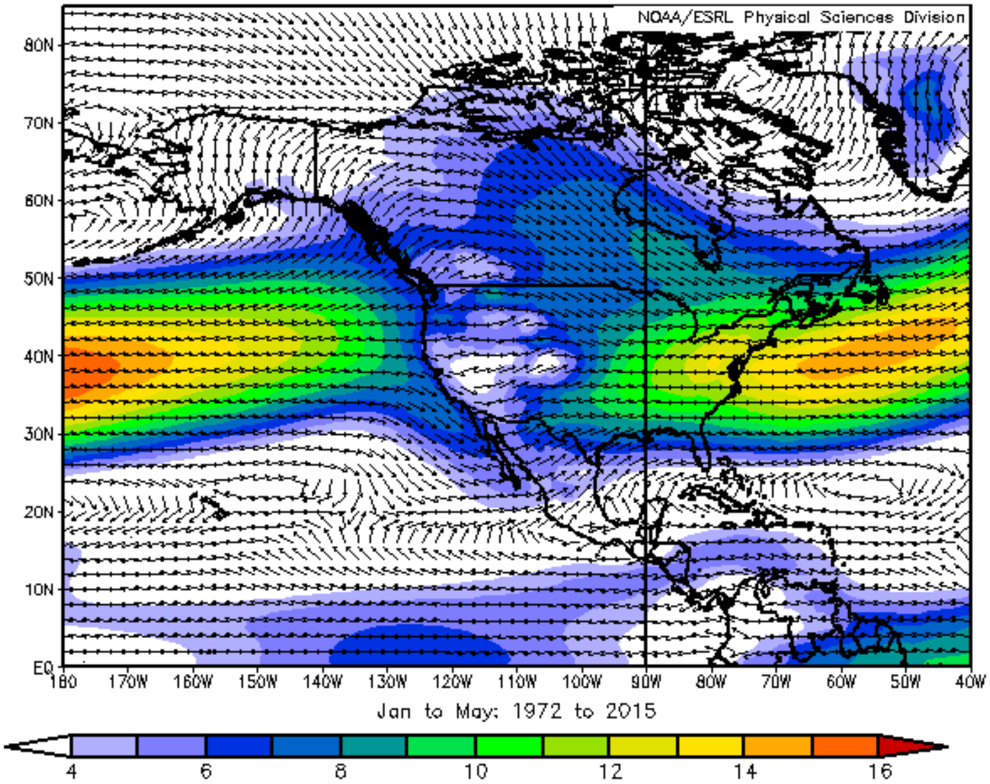


Figure 9. Mean vector wind movement during winter at 700 MPa for the North America region (20th Century Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, https://www.esrl.noaa.gov/psd/).

In this study, the more negative $\delta^2$H and $\delta^{18}$O water resulted from rainout depletion of heavier isotopes, through storms originated in the Gulf of Mexico that travelled to high altitudes and were exposed to low temperatures before reaching the semiarid grassland in Central Mexico. Our constructed local meteoric water line (LMWL; $\delta^2H = -1.04 + 7.9 * \delta^{18}O$) shows a lower slope to the GMWL of Craig (1961) but with a negative d-intercept. This implies that there is little annual precipitation but intensive evaporation (Zhao and Wang, 2018). For the rainy season the LMWL was $\delta^2H = -4.96 + 7.3 * \delta^{18}O$ showing that raindrops suffered re-evaporation while falling, and that precipitation vapor was mixed with some local recycled water vapor from local sources, as Liu et al (2008) showed, this could have important feedback to local precipitation and local available moisture.

The LMWL of a semiarid environment, such as grasslands, should have a slope 8< due to the strong atmospheric water vapor demands, strong radiation and high evapotranspiration. Furthermore, the inclusion of dew in the local meteoric water line could results in an LMWL with slope ≥ 8 because not all dew derives from local meteoric water. Studies had reported three types of dew; groundwater-derived, advective, and shallow soil water-derived (Kaseke et al., 2017). Thus, the calculated dew isotopic composition during summer at our site was $\delta^2H = 5.89 + 6.53 * \delta^{18}O$ (Figure 4), which corresponds to advective dew, with d-intercept much higher than expected, likely influenced by kinetic fractionation process during two stages, evaporation of moisture coming from the ocean and condensation (Kaseke et al., 2017). On the other hand, during the dry season ($\delta^2H = -0.39 + 4.84 * \delta^{18}O$) dew formation was related to shallow soil water, as isotopic values did not match any other water sources in the ecosystem, likely formed from evaporative discharge of winter rains.

The $\delta^2H$ and $\delta^{18}O$ values for caliche, soil water and xylem water fell to the right of the LMWL, with the coordinates ($\delta^2H$ versus $\delta^{18}O$) of surface soil water plotting far away from the LMWL, indicating a strong enrichment effect (Figure 4, 5A and 5B). Thus, water in the top 10 cm of soil exhibited a larger fluctuation (Figure 2C) than water at >40 cm during the entire study period. This pattern is the result of both precipitation inputs and evaporative enrichment of the surface soil water, which is consistent with others reports (Asbjornsen et al., 2007; Eggemeyer et al., 2008; Zhu et al., 2014). Isotopic composition of deep soil water was relatively low and varied slightly during the study period, implying that groundwater experienced less evaporation. These differences in the isotopic soil profiles may occur as a result of several processes, including evaporation, change in isotopic composition of precipitation and mixing of new and older water (Yang and Fu, 2017).

*Water sources used by coexisting grasses*

We compared $\delta^{18}O$ values of water in *B. gracilis* and *M. rigida* in order to determine the relative importance of shallow versus deep soil water uptake. The $\delta^{2}H$ and $\delta^{18}O$ of grass tissue varied during wet and dry season, such variations suggested that they are largely associated with the water sources utilized by grasses (Figure 5A and B). Thus, the most active zone for water use during summer was located at 10 cm depth, although soil water content was greatest at 40cm deep (Figure 2C). One reason is perhaps that most root biomass is greatest in this upper soil horizon where rain pulses would be most frequent (Figure 5C). Xylem water isotopic values for *B. gracilis* were more dispersed and enriched during the dry season than those of *M. rigida,* indicating a more consistent water source from the shallow soil. Values of $\delta^{18}O$ remained more constant in the deep soil layer (15-40 cm), reflecting water recharge in the wet season and the fact that this water remain a long time in the system before the grass used it.

Both grass species showed differences in the use of soil moisture depending on the precipitation size. At the onset of the growing season, with a gradual increase in precipitation volume and air temperature (before July, Figure 2), *B. gracilis* used a sizeable proportion of water from the topsoil without evidence of switching water sources. This water use pattern is closely linked to a high soil water availability and proper soil temperature favoring proliferation and elongation of superficial roots to acquire water and nutrients in the early growing seasons (Dodd et al., 1998; Drennan and Nobel, 1998). In contrast during dry season, *M. rigida* exhibited its capacity to switch water sources between shallow and deep soil layers (March, Figure 5D). This switch is probably due to trade-offs between the activity of the shallow and deep roots, where active shallow roots were restricted by low temperatures and low soil water availability (Williams and Ehleringer, 2000). As interspecific competition within the community intensified and the shallow soil water availability declined during drought, *M. rigida* shifted to deep water sources

(Figure 7a). Several other studies conducted in arid regions concluded that grasses (i.e. *B. gracilis*, in Northeast Colorado) exhibited a great capacity of physiological plasticity so that, plants can shift water sources in response to changes in water availability (Dodd et al., 1998; Nippert and Knapp, 2007).

The dependence on water from the upper soil profile also explains the more negative water potential (Ψ) (Eggemeyer et al., 2008). Grasses of the short steppe of Colorado (Dodd et al., 1998) and the Corn Belt region of Midwest (USA) (Asbjornsen et al., 2008), where also found to use predominantly shallow soil water. The use of shallow water in semiarid environments might reflect high tolerance to low resource environments and adaptation traits such as rapid fine root turnover in response to water pulse and shortages (Asbjornsen et al., 2008; Medina-Roldán et al., 2007). The dominance of *B. gracilis* in semiarid grasslands is likely related to the vertical and horizontal distribution of its root system. *B. gracilis exhibits* a root system composed mostly by fine roots that are predominantly distributed (>75%) at shallows depths (5-10 cm) and can horizontally extend up to 30 cm from the plant and vertically to depths of 90 cm. In contrast, *M. rigida* only maintains 30% of its roots in the top 30 cm of the soil presenting the most root mass between the 60-90 cm of soil depth (Figure 1a; (Coffin and Lauenroth, 1991a; Hunter and Wu, 2005). Although the deeper roots of *M. rigida* relative to *B. gracilis* contributed to a small fraction of total water uptake, they constitute an important survival mechanism in semiarid environments and might explain in part the vegetation shifts, which include the propagation of *M. rigida*, occupying the space left by *B. gracilis* (Aguado-Santacruz and Garcia-Moya, 1998; Medina-Roldán et al., 2007).

### *Niche partitioning among both species*

According to the results of the IsoSource model, *B. gracilis* mainly relied on surface soil water (<15 cm), and rarely took water up from deep soil layers (i.e., 25-40 cm depth) during the wet season (e.g., in July and August, see Figure 7). *M.*

*rígida* also depended on surface soil water, except in the dry season, when it preferentially took water up from deep soil layers. This result showed that both species exhibited strong capacity in exploiting different sources of water (Figures 5-8). This result was consistent with the findings of several other studies, which reported that grasses could shift water sources between deep and shallow soil water (Asbjornsen et al., 2007; Dodd et al., 1998; Nippert and Knapp, 2007; Wu et al., 2016). Our results suggest that grasses compete for soil water with other grass species in either the dry or wet season. It is unlikely that this competition is strong during the dry season because both grass species show little physiological activity only in few remaining green leaves; whole transpiration is minimal and only sufficient to maintain basic metabolism (Rossatto et al., 2013).

Water available in the petrocalcic (caliche) layer could also represent an important source of water for grasses and herbs. It is known that caliche retains up to 10.6% water by weight and can release water to the upper soil layer following a gradient of soil water availability (Figure 2c), and turning into a potential source of available water for grasslands (Michael Cohrs Duniway et al., 2010). Another source of water for grasses comes from condensation of water vapor during sunrise (dewpoint temperature, Aguirre-Gutiérrez et al., 2019). Some studies have reported in the literature that plants can take up water from dew, fog, directly through leaves, however this strategy is reported for coastal ecosystems and foggy forest (Berry et al., 2019; Dawson and Goldsmith, 2018b; Simonin et al., 2009). It has been also reported that condensation deposited on the soil surface appears to be a significant source of water to change leaf water potential (Guzmán-Delgado et al., 2018; Suárez and Gloser, 1982). The results generated from the IsosSource model, estimated that contribution of dew to *M. rigida* and *B. gracilis* ranging from 5-50% during the dry season and 5-30% in the wet season. Meaning that both grass species take up water from condensation to balance its plant water status, as shown by predawn water potentials being less negative where condensation is present, even in some deep-rooted trees (Limm et al., 2009).

Given the great spatial variation in vegetation structure across the semiarid grassland in the Mexican Altiplano (Aguado-Santacruz and Garcia-Moya, 1998; Medina-Roldán et al., 2007), and the annual variability of rainfall (BALBUENA, 2016; Delgado-Balbuena et al., 2019), it is expected very dynamic partitioning of soil water in both spatial and temporal patterns in the ecosystem. The actual depth of water extraction for individual species at any given site and point in time would depend on the interaction of multiple factors, particularly on the interplay between root characteristics and morphology of the individual species, and the constraints imposed by evaporative demand of the atmosphere and soil water availability through the soil profile.

## Conclusions

Here we show that grasses in a semiarid grassland utilize soil pore water from different depths through the soil profile during dry season, and that these differences are maintained during the wet season. *M. rigida* extracted water from deeper regions of the soil profile; while *B. gracilis* is strongly anisohydric and relied on superficial water. Both species extract soil water from superficial depths, suggesting potential competition for soil water resources between species, but also species displayed a shift in water extraction, this result showed that both species exhibited strong plasticity in source of water uptake and would reduce the competition of the both species. This plasticity and vertical partitioning of soil water could lead to a better exploration of soil reserves through the soil profile and reduce competition for water resources in semiarid grasslands, allowing a great diversity of plant to grow side by side.

## Bibliography

Agam, N., 2004. Diurnal Water Content Changes in the Bare Soil of a Coastal Desert. JOURNAL OF HYDROMETEOROLOGY 5, 12.

Agam, N., Berliner, P.R., 2006. Dew formation and water vapor adsorption in semi-arid environments - A review. Journal of Arid Environments 65, 572–590. https://doi.org/10.1016/j.jaridenv.2005.09.004

Agam, N., Berliner, P.R., Zangvil, A., Ben-Dor, E., 2004. Soil water evaporation during the dry season in an arid zone. Journal of Geophysical Researc 109, doi:10.1029/2004JD004802. https://doi.org/10.1029/2004JD004802

Aguado-Santacruz, G.A., Garcia-Moya, E., 1998. Environmental factors and community dynamics at the southernmost part of the North American Graminetum: I. On the contribution of climatic factors to temporal variation in species composition. Plant Ecology 135, 13–29. https://doi.org/10.1023/A:1009750831162

Aguirre-Gutiérrez, C.A., Holwerda, F., Goldsmith, G.R., Delgado, J., Yepez, E., Carbajal, N., Escoto-Rodríguez, M., Arredondo, J.T., 2019. The importance of dew in the water balance of a continental semiarid grassland. Journal of Arid Environments 168, 26–35. https://doi.org/10.1016/j.jaridenv.2019.05.003

Alcocer-Ruthling, M., Robberecht, R., Thill, D.C., 1989. The Response of Bouteloua scorpioides to Water Stress at Two Phenological Stages. Botanical Gazette 150, 454–461. https://doi.org/10.1086/337792

Arredondo, T., Delgado-Balbuena, J., Huber-Sannwald, E., García-Moya, E., Loescher, H.W., Aguirre-Gutiérrez, C., Rodriguez-Robles, U., 2018. Does precipitation affects soil respiration of tropical semiarid grasslands with different plant cover types? Agriculture, Ecosystems & Environment 251, 218–225. https://doi.org/10.1016/j.agee.2017.09.034

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016a. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016b. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Asbjornsen, H., Mora, G., Helmers, M.J., 2007. Variation in water uptake dynamics among contrasting agricultural and native plant communities in the Midwestern U.S. Agriculture, Ecosystems & Environment 121, 343–356. https://doi.org/10.1016/j.agee.2006.11.009

Asbjornsen, H., Shepherd, G., Helmers, M., Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S. Plant Soil 308, 69–92. https://doi.org/10.1007/s11104-008-9607-3

BALBUENA, J.D., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Barnard, R.L., Bello, F. De, Buchmann, N., 2006. The δ18O of root crown water best reflects source water δ18O in different types of herbaceous species. Rapid communications in mass spectrometry : RCM 24, 3567–3577. https://doi.org/10.1002/rcm

Barradas, V.L., Glez-Medellín, Ma.G., 1999. Dew and its effect on two heliophile understorey species of a tropical dry deciduous forest in Mexico. International Journal of Biometeorology 43, 1–7. https://doi.org/10.1007/s004840050109

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2019. Foliar water uptake: Processes, pathways, and integration into plant water budgets: Foliar Water Uptake. Plant Cell Environ 42, 410–423. https://doi.org/10.1111/pce.13439

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2018. Foliar water uptake: processes, pathways, and integration into plant water budgets. Plant, Cell & Environment. https://doi.org/10.1111/pce.13439

Blackman, C.J., Brodribb, T.J., 2011. Two measures of leaf capacitance: insights into the water transport pathway and hydraulic conductance in leaves. Functional Plant Biol. 38, 118. https://doi.org/10.1071/FP10183

Blair, J., Nippert, J., Briggs, J., 2014. Grassland Ecology, in: Monson, R.K. (Ed.), Ecology and the Environment. Springer New York, New York, NY, pp. 389–423.

Bowen, G.J., Revenaugh, J., 2003. Interpolating the isotopic composition of modern meteoric precipitation: ISOTOPIC COMPOSITION OF MODERN PRECIPITATION. Water Resour. Res. 39. https://doi.org/10.1029/2003WR002086

Boyer, J.S., 1985. Water transport. Annual review of plant physiology 36, 473–516.

Boyer, J.S., 1974. Water transport in plants: Mechanism of apparent changes in resistance during absorption. Planta 117, 187–207. https://doi.org/10.1007/BF00388393

Breazeale, E.L., McGeorge, W.T., Breazeale, J.F., 1950. MOISTURE ABSORPTION BY PLANTS FROM AN ATMOSPHERE OF HIGH HUMIDITY. Plant Physiol. 25, 413–419. https://doi.org/10.1104/pp.25.3.413

Brewer, C.A., Smith, W.K., Vogelmann, T.C., 1991. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. Plant, Cell & Environment 14, 955–962.

Brodribb, T.J., Holbrook, N.M., 2003. Stomatal Closure during Leaf Dehydration, Correlation with Other Leaf Physiological Traits. Plant Physiol. 132, 2166–2173. https://doi.org/10.1104/pp.103.023879

Buckley, T.N., Sack, L., Gilbert, M.E., 2011. The Role of Bundle Sheath Extensions and Life Form in Stomatal Responses to Leaf Water Status. Plant Physiol. 156, 962–973. https://doi.org/10.1104/pp.111.175638

Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): foliar uptake and prevention of dehydration. Plant Cell Environ 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burkhardt, J., Basi, S., Pariyar, S., Hunsche, M., 2012. Stomatal penetration by aqueous solutions–an update involving leaf surface particles. New Phytologist 196, 774–787.

Coffin, D.P., Lauenroth, K., 1991a. Effects of competition on spatial distribution of roots of blue grama. Journal Of Range Management 44.

Coffin, D.P., Lauenroth, W.K., 1991b. Effects of Competition on Spatial Distribution of Roots of Blue Grama. Journal of Range Management 44, 68. https://doi.org/10.2307/4002642

Corbin, J.D., Thomsen, M.A., Dawson, T.E., D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. Oecologia 145, 511–521. https://doi.org/10.1007/s00442-005-0152-y

Cruiziat, P., Tyree, M.T., Bodet, C., LoGULLO, M.A., 1980. THE KINETICS OF REHYDRATION OF DETACHED SUNFLOWER LEAVES FOLLOWING

SUBSTANTIAL WATER LOSS. New Phytol 84, 293–306. https://doi.org/10.1111/j.1469-8137.1980.tb04429.x

Crutsinger, G.M., Rodriguez-Cabal, M.A., Roddy, A.B., Peay, K.G., Bastow, J.L., Kidder, A.G., Dawson, T.E., Fine, P.V.A., Rudgers, J.A., 2014. Genetic variation within a dominant shrub structures green and brown community assemblages. Ecology 95, 387–398. https://doi.org/10.1890/13-0316.1

Dai, Y., Zheng, X.-J., Tang, L.-S., Li, Y., 2015. Stable oxygen isotopes reveal distinct water use patterns of two Haloxylon species in the Gurbantonggut Desert. Plant Soil 389, 73–87. https://doi.org/10.1007/s11104-014-2342-z

Dawson, T.E., Goldsmith, G.R., 2018a. The value of wet leaves. New Phytologist 219, 1156–1169. https://doi.org/10.1111/nph.15307

Dawson, T.E., Goldsmith, G.R., 2018b. The value of wet leaves. New Phytol 219, 1156–1169. https://doi.org/10.1111/nph.15307

De Bruin, H.A.R., Ronda, R.J., Van De Wiel, B.J.H., 2000. Approximate solutions for the Obukhov length and the surface fluxes in terms of bulk Richardson numbers. Boundary-layer meteorology 95, 145–157.

Delgado-Balbuena, J., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Huber-Sannwald, E., Chavez-Aguilar, G., Luna-Luna, M., Barretero-Hernandez, R., 2013. Differences in plant cover and species composition of semiarid grassland communities of central Mexico and its effects on net ecosystem exchange. Biogeosciences 10, 4673–4690. https://doi.org/10.5194/bg-10-4673-2013

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Pineda-Martínez, L.F., Carbajal, J.N., Vargas, R., 2019. Seasonal Precipitation Legacy Effects Determine the Carbon Balance of a Semiarid Grassland. J. Geophys. Res. Biogeosci. 124, 987–1000. https://doi.org/10.1029/2018JG004799

Dingman, S.L., 2015. Physical hydrology. Waveland press.

Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. Oecologia 117, 504–512. https://doi.org/10.1007/s004420050686

Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. Plant, Cell and Environment 23, 27–38. https://doi.org/10.1046/j.1365-3040.2000.00532.x

Domínguez, E., 1999. Water hydration in cutinized cell walls: a physico-chemical analysis. Biochimica et Biophysica Acta (BBA) - General Subjects 1426, 168–176. https://doi.org/10.1016/S0304-4165(98)00152-4

Drennan, P.M., Nobel, P.S., 1998. Root growth dependence on soil temperature for Opuntia ficus-indica: influences of air temperature and a doubled CO2 concentration. Funct Ecology 12, 959–964. https://doi.org/10.1046/j.1365-2435.1998.00276.x

Duniway, M C, Herrick, J.E., Curtis Monger, H., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Duniway, Michael Cohrs, Herrick, J.E., Monger, H.C., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Eggemeyer, K.D., Awada, T., Harvey, F.E., Wedin, D.A., Zhou, X., Zanner, C.W., 2008. Seasonal changes in depth of water uptake for encroaching trees Juniperus virginiana and Pinus ponderosa and two dominant C4 grasses in a semiarid grassland. Tree Physiology 29, 157–169. https://doi.org/10.1093/treephys/tpn019

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. Oecologia 88, 430–434. https://doi.org/10.1007/BF00317589

Eller, C.B., Lima, A.L., Oliveira, R.S., 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis* (Winteraceae). New Phytol 199, 151–162. https://doi.org/10.1111/nph.12248

Esmaiel Malek, 2016. Differentiation of the Atmospheric Moisture Collected by Dew and Fog. JESE-A 5. https://doi.org/10.17265/2162-5298/2016.04.001

Evenari, M., Shanan, L., Tadmor, N., 1982. The Negev: The Challenge of a Desert. Harvard University Press.

Friedl, M.A., 1995. Modeling land surface fluxes using a sparse canopy model and radiometric surface temperature measurements. Journal of Geophysical Research: Atmospheres 100, 25435–25446. https://doi.org/10.1029/95JD00723

Garratt, J.R., 1992. The atmospheric boundary layer. Cambridge atmospheric and space science series. Cambridge University Press, Cambridge 416, 444.

Garratt, J.R., Segal, M., 1988. On the contribution of atmospheric moisture to dew formation. Boundary-Layer Meteorology 45, 209–236. https://doi.org/10.1007/BF01066671

Goldsmith, G.R., Matzke, N.J., Dawson, T.E., 2013. The incidence and implications of clouds for cloud forest plant water relations. Ecology letters 16, 307–314.

Grammatikopoulos, G., Manetas, Y., 1994a. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Canadian Journal of Botany 72, 1805–1811.

Grammatikopoulos, G., Manetas, Y., 1994b. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Can. J. Bot. 72, 1805–1811. https://doi.org/10.1139/b94-222

Guan, H., Sebben, M., Bennett, J., 2014. Radiative- and artificial-cooling enhanced dew collection in a coastal area of South Australia. Urban Water Journal 11, 175–184. https://doi.org/10.1080/1573062X.2013.765494

Guo, X., Zha, T., Jia, X., Wu, B., Feng, W., Xie, J., Gong, J., Zhang, Y., Peltola, H., 2016. Dynamics of dew in a cold desert-shrub ecosystem and its abiotic controls. Atmosphere 7, 1–15. https://doi.org/10.3390/atmos7030032

Guzmán-Delgado, P., Fernández, V., Venturas, M., Rodríguez-Calcerrada, J., Gil, L., 2017. Surface properties and physiology of Ulmus laevis and U. minor samaras: implications for seed development and dispersal. Tree Physiology 37, 815–826. https://doi.org/10.1093/treephys/tpx022

Guzmán-Delgado, P., Mason Earles, J., Zwieniecki, M.A., 2018. Insight into the physiological role of water absorption via the leaf surface from a rehydration kinetics perspective: Leaf rehydration kinetics via the surface. Plant Cell Environ 41, 1886–1894. https://doi.org/10.1111/pce.13327

Hanisch, S., Lohrey, C., Buerkert, A., 2015. Dewfall and its ecological significance in semi-arid coastal south-western Madagascar. Journal of Arid Environments 121, 24–31. https://doi.org/10.1016/j.jaridenv.2015.05.007

Hartnett, D.C., Hickman, K.R., Walter, L.E.F., 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49, 413–420.

Helliker, B.R., Ehleringer, J.R., 2000. Establishing a grassland signature in veins: 18O in the leaf water of C3 and C4 grasses. Proceedings of the National Academy of Sciences of the United States of America 97, 7894–7898. https://doi.org/10.1073/pnas.97.14.7894

Heusinkveld, B.G., Berkowicz, S.M., Jacobs, A.F.G., Holtslag, A. a. M., Hillen, W.C. a. M., 2006. An Automated Microlysimeter to Study Dew Formation and Evaporation in Arid and Semiarid Regions. Journal of Hydrometeorology 7, 825–832. https://doi.org/10.1175/JHM523.1

Hunter, K.A.M., Wu, L., 2005. Morphological and physiological response of five California native grass species to moderate salt spray: Implications for landscape irrigation with reclaimed water. Journal of Plant Nutrition 28, 247–270. https://doi.org/10.1081/PLN-200047609

Jackson, T.J., Moy, L., 1999. Dew Effects on Passive Microwave Observations of Land Surfaces. Remote Sensing of Environment 70, 129–137. https://doi.org/10.1016/S0034-4257(99)00021-8

Jacobs,  a. F.G., Heusinkveld, B.G., Kruit, R.J.W., Berkowicz, S.M., 2006. Contribution of dew to the water budget of a grassland area in the Netherlands. Water Resources Research 42. https://doi.org/10.1029/2005WR004055

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 1999. Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments 42, 211–222. https://doi.org/10.1006/jare.1999.0523

Jordan, G.J., Brodribb, T.J., 2007. Incontinence in aging leaves: deteriorating water relations with leaf age in Agastachys odorata (Proteaceae), a shrub with very long-lived leaves. Functional Plant Biol. 34, 918. https://doi.org/10.1071/FP07166

Kalthoff, N, Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kalthoff, N., Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kaseke, K.F., Wang, L., Seely, M.K., 2017. Nonrainfall water origins and formation mechanisms. Sci. Adv. 3, e1603131. https://doi.org/10.1126/sciadv.1603131

Kerr, J.P., Beardsell, M.F., 1975. Effect of Dew on Leaf Water Potentials and Crop Resistances in a Paspalum Pasture 1. Agronomy Journal 67, 596–599.

Kidder, D.L., Gierlowski-Kordesch, E.H., 2005. Impact of grassland radiation on the nonmarine silica cycle and Miocene diatomite. Palaios 20, 198–206.

Kidron, G., Yair, A., Danin, A., 2000. Dew variability within a small arid drainage basin in the Negev Highlands,Israel. Q J R Meteorol Soc 126, 63–80. https://doi.org/10.1256/smsqj.56203

Kidron, G.J., 2000a. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000b. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000c. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270.

Kidron, Giora J, 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8. https://doi.org/10.1016/S0168-1923(99)00043-X

Kidron, Giora J., 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8.

Koerner, S.E., Collins, S.L., 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology 95, 98–109. https://doi.org/10.1890/13-0526.1

Konrad, W., Burkhardt, J., Ebner, M., Roth-Nebelsick, A., 2015. Leaf pubescence as a possibility to increase water use efficiency by promoting condensation: LEAF PUBESCENCE MAY INCREASE WATER USE EFFICIENCY. Ecohydrol. 8, 480–492. https://doi.org/10.1002/eco.1518

Kramer, P.J., Boyer, J.S., 1995. Water relations of plants and soils. Academic press.

Lekouch, I., Lekouch, K., Muselli, M., Mongruel, A., Kabbachi, B., Beysens, D., 2012. Rooftop dew, fog and rain collection in southwest Morocco and predictive dew modeling using neural networks. Journal of Hydrology 448–449, 60–72. https://doi.org/10.1016/j.jhydrol.2012.04.004

Leopold, L., n.d. Dew as a Source of Plant Moisture 3.

Leopold, L.B., 1952. Dew as a source of plant moisture.

Limm, E.B., Simonin, K.A., Bothman, A.G., Dawson, T.E., 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Liu, S., Li, S.-G., Yu, G.-R., Sun, X.-M., Zhang, L.-M., Hu, Z.-M., Li, Y.-N., Zhang, X.-Z., 2009. Surface energy exchanges above two grassland ecosystems on the Qinghai-Tibetan Plateau. Biogeosciences Discuss. 6, 9161–9192. https://doi.org/10.5194/bgd-6-9161-2009

Maestre, F.T., Salguero-Gómez, R., Quero, J.L., 2012. It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 367, 3062–75. https://doi.org/10.1098/rstb.2011.0323

Maldonado Burgos, E., 2015. Efectos de fuego en la cobertura vegetal y procesos ecohidrológicos de un pastizal semiárido en el centro de México.

Malek, E., McCurdy, G., Giles, B., 1999a. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999b. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments1. Malek, E., McCurdy, G. & Giles, B. Dew contribution to the annual water balances in semi-arid desert valleys. J. Arid Environ. 42, 71–80 (1999). 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999c. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80.

Mastroberti, A.A., de Araujo Mariath, J.E., 2008. Development of mucilage cells of Araucaria angustifolia (Araucariaceae). Protoplasma 232, 233–245. https://doi.org/10.1007/s00709-007-0274-7

Matimati, I., Musil, C.F., Raitt, L., February, E., 2013. Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem. Ecohydrology 6, 818–825.

Mcculloh, K.A., Johnson, D.M., Meinzer, F.C., Woodruff, D.R., 2014. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species: The dynamic pipeline. Plant Cell Environ 37, 1171–1183. https://doi.org/10.1111/pce.12225

Medina-Roldán, E., Arredondo, J.T., Huber-Sannwald, E., Chapa-Vargas, L., Olalde-Portugal, V., 2008. Grazing effects on fungal root symbionts and carbon and nitrogen storage in a shortgrass steppe in Central Mexico. Journal of Arid Environments 72, 546–556. https://doi.org/10.1016/J.JARIDENV.2007.07.005

Medina-Roldán, E., Huber-Sannwald, E., Arredondo, J.T., 2013. Plant phenotypic functional composition effects on soil processes in a semiarid grassland. Soil Biology and Biochemistry 66, 1–9. https://doi.org/10.1016/j.soilbio.2013.06.011

Medina-Roldán, E., Moreno, J.T.A., Moya, E.G., Martínez, F.M.H., 2007. Soil water content dynamics along a range condition gradient in a shortgrass steppe. Rangeland Ecology and Management 60, 79–87. https://doi.org/10.2111/05-219R2.1

Milburn, J.A., 1966. The conduction of sap: 1. water conduction and cavitation in water stressed leaves 34–42.

Monson, R.K., Moore, B. d., Ku, M.S.B., Edwards, G.E., 1986. Co-function of C3-and C4-photosynthetic pathways in C3, C4 and C3-C4 intermediate Flaveria species. Planta 168, 493–502. https://doi.org/10.1007/BF00392268

Moro, M.J., Were, a., Villagarcía, L., Cantón, Y., Domingo, F., 2007. Dew measurement by Eddy covariance and wetness sensor in a semiarid ecosystem of SE Spain. Journal of Hydrology 335, 295–302. https://doi.org/10.1016/j.jhydrol.2006.11.019

Morse, S.R., 1990. Water balance in Hemizonia luzulifolia: the role of extracellular polysaccharides. Plant, Cell & Environment 13, 39–48.

Munné-Bosch, S., Alegre, L., 1999. Role of dew on the recovery of water-stressed Melissa officinalis L. plants. Journal of Plant Physiology 154, 759–766.

Nguyen, H.T., Meir, P., Wolfe, J., Mencuccini, M., Ball, M.C., 2017. Plumbing the depths: extracellular water storage in specialized leaf structures and its functional expression in a three-domain pressure–volume relationship. Plant, cell & environment 40, 1021–1038.

Nippert, J.B., Knapp, A.K., 2007. Linking water uptake with rooting patterns in grassland species. Oecologia 153, 261–272. https://doi.org/10.1007/s00442-007-0745-8

Nobel, P.S., Jordan, P.W., 1983. Transpiration Stream of Desert Species: Resistances and Capacitances for a $C_3$, a $C_4$, and a CAM Plant. J Exp Bot 34, 1379–1391. https://doi.org/10.1093/jxb/34.10.1379

Oparka, K.J., 1994. The use of fluorescent probes for studies of living plant cells. Plant cell biology, a practical approach.

Pan, Y., Wang, X., Zhang, Y., 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area , Northern China. Journal of Hydrology 387, 265–272. https://doi.org/10.1016/j.jhydrol.2010.04.016

Pan, Y.X., Wang, X.P., 2014. Effects of shrub species and microhabitats on dew formation in a revegetation-stabilized desert ecosystem in Shapotou, northern China. Journal of Arid Land 6, 389–399. https://doi.org/10.1007/s40333-014-0008-6

Peterson, P.M., Giraldo-Cañas, D., 2011. The species of Muhlenbergia (Poaceae: Chloridoideae) from Argentina. Caldasia 33, 21–54.

Pineda Martínez, L.F., 2009. Modelación numérica de la dispersión de material particulado atmosférico y regionalización climática en México.

Puigdefábregas, J., Sánchez, G., 1996. Vegetación dispersa y flujos de vertiente en clima semiárido, in: IV Reunión de Geomorfología. Universidade da Coruña.

Riederer, M., 2006. Thermodynamics of the water permeability of plant cuticles: characterization of the polar pathway. Journal of Experimental Botany 57, 2937–2942. https://doi.org/10.1093/jxb/erl053

Ritter, F., Berkelhammer, M., Beysens, D., 2018. Dew frequency across the US from a network of in situ radiometers. Hydrology and Earth System Sciences Discussions 1–35. https://doi.org/10.5194/hess-2018-450

Rossatto, D.R., da Silveira Lobo Sternberg, L., Franco, A.C., 2013. The partitioning of water uptake between growth forms in a Neotropical savanna: do herbs exploit a third water source niche?: Herbs explore a third water uptake niche in Neotropical savannas. Plant Biology 15, 84–92. https://doi.org/10.1111/j.1438-8677.2012.00618.x

Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 2013. Isotopic Patterns in Modern Global Precipitation, in: Swart, P.K., Lohmann, K.C., Mckenzie, J., Savin, S. (Eds.), Geophysical Monograph Series. American Geophysical Union, Washington, D. C., pp. 1–36. https://doi.org/10.1029/GM078p0001

Rzedowski, J., 2007. An Ecological and Phytogeographical Analysis of the Grasslands of Mexico. Taxon 24, 67–80.

Sala, O.E., Lauenroth, W.K., Reid, C.P.P., 1982. WATER RELATIONS: A NEW DIMENSION FOR NICHE. Journal of Applied Ecology 19, 647–657.

Santacruz, G.A.A., Moya, E.G., Gonzalez, C.V., Flores, J.L.F., 1996. Importancia de los elementos climáticos en la variación florística temporal de pastizales semidesérticos. Acta Botánica Mexicana 65–81.

Scherm, H., van Bruggen, A.H.C., 1993. Sensitivity of simulated dew duration to meteorological variations in different climatic regions of California. Agricultural and Forest Meteorology 66, 229–245. https://doi.org/10.1016/0168-1923(93)90073-Q

Schonherr, J., 2006. Characterization of aqueous pores in plant cuticles and permeation of ionic solutes. Journal of Experimental Botany 57, 2471–2491. https://doi.org/10.1093/jxb/erj217

Schreiber, L., Skrabs, M., Hartmann, K., Diamantopoulos, P., Simanova, E., Santrucek, J., 2001. Effect of humidity on cuticular water permeability of isolated cuticular membranes and leaf disks. Planta 214, 274–282. https://doi.org/10.1007/s004250100615

Sharma, M L, 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331.

Sharma, M. L., 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331. https://doi.org/10.1016/0002-1571(76)90086-8

Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. Canadian Journal of Botany 82, 450–460. https://doi.org/10.1139/b04-016

Simonin, K.A., Santiago, L.S., Dawson, T.E., 2009. Fog interception by Sequoia sempervirens (D. Don) crowns decouples physiology from soil water deficit. Plant, Cell & Environment 32, 882–892. https://doi.org/10.1111/j.1365-3040.2009.01967.x

Steppe, K., Vandegehuchte, M.W., Van de Wal, B.A., Hoste, P., Guyot, A., Lovelock, C.E., Lockington, D.A., 2018. Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove Avicennia marina. Tree physiology 38, 979–991.

Suárez, A.G., Gloser, J., 1982. Time course of foliar absorption of water inPanicum andPaspalum. Biol Plant 24, 226–230. https://doi.org/10.1007/BF02883669

Tian, C., Wang, L., Kaseke, K.F., Bird, B.W., 2018. Stable isotope compositions (δ2H, δ18O and δ17O) of rainfall and snowfall in the central United States. Sci Rep 8, 6712. https://doi.org/10.1038/s41598-018-25102-7

Tuller, S.E., Chilton, R., 1973. The role of dew in the seasonal moisture balance of a summer-dry climate. Agricultural Meteorology 11, 135–142. https://doi.org/10.1016/0002-1571(73)90057-5

Tyree, M.T., Cruiziat, P., Benis, M., LoGullo, M.A., Salleo, S., 1981. The kinetics of rehydration of detached sunflower leaves from different initial water deficits. Plant, Cell & Environment 4, 309–317.

Uclés, O., Villagarcía, L., Moro, M.J., Canton, Y., Domingo, F., 2014. Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. Hydrological Processes 28, 2271–2280. https://doi.org/10.1002/hyp.9780

Van Gardingen, P.R., Grace, J., Jeffree, C.E., 1991. Abrasive damage by wind to the needle surfaces of Picea sitchensis (Bong.) Carr. and Pinus sylvestris L. Plant, Cell & Environment 14, 185–193.

Veste, M., Heusinkveld, B.G., Berkowicz, S.M., Breckle, S.-W., Littmann, T., Jacobs, A.F.G., 2008. Dew formation and activity of biological soil crusts, in: Arid Dune Ecosystems. Springer, pp. 305–318.

Vuollekoski, H., Vogt, M., Sinclair, V.A., Duplissy, J., Järvinen, H., Kyrö, E.-M., Makkonen, R., Petäjä, T., Prisle, N.L., Räisänen, P., 2015. Estimates of global dew collection potential on artificial surfaces.

Wang, C., Cen, Y., Liu, M., Bowler, P., 2017. Formation and influencing factors of dew in sparse elm woods and grassland in a semi-arid area. Acta Ecologica Sinica 37, 125–132. https://doi.org/10.1016/j.chnaes.2017.06.004

Weatherley, P.E., 1963. The pathway of water movement across the root cortex and leaf mesophyll of transpiring plants. The water relations of plants 85–100.

Westbeld, A., Klemm, O., Grießbaum, F., Sträter, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert, in: Annales Geophysicae: Atmospheres, Hydrospheres and Space Sciences. p. 3571.

Williams, D.G., Ehleringer, J.R., 2000. Intra-and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecological Monographs 70, 517–537.

Wu, H., Li, X.-Y., Li, J., Jiang, Z., Chen, H., Ma, Y., Huang, Y., 2016. Differential soil moisture pulse uptake by coexisting plants in an alpine Achnatherum splendens grassland community. Environ Earth Sci 75, 914. https://doi.org/10.1007/s12665-016-5694-2

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2013. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2009. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Yamanaka, T., Tsujimura, M., Oyunbaatar, D., Davaa, G., 2007. Isotopic variation of precipitation over eastern Mongolia and its implication for the atmospheric water cycle. Journal of Hydrology 333, 21–34. https://doi.org/10.1016/j.jhydrol.2006.07.022

Yang, Y., Fu, B., 2017. Soil water migration in the unsaturated zone of semiarid region in China from isotope evidence. Hydrology and Earth System Sciences 21, 1757–1767.

Yates, D., Hutley, L., 1995. Foliar Uptake of Water by Wet Leaves of Sloanea woollsii, an Australian Subtropical Rainforest Tree. Aust. J. Bot. 43, 157. https://doi.org/10.1071/BT9950157

Ye, Y., Zhou, K., Song, L., Jin, J., Peng, S., 2007. Dew amounts and its correlations with meteorological factors in urban landscapes of Guangzhou, China. Atmospheric Research 86, 21–29. https://doi.org/10.1016/j.atmosres.2007.03.001

Zangvil, A., 1996. Six years of dew observations in the Negev Desert, Israel. Journal of Arid Environments 32, 361–371. https://doi.org/10.1006/jare.1996.0030

Zhao, Y., Wang, L., 2018. Plant Water Use Strategy in Response to Spatial and Temporal Variation in Precipitation Patterns in China: A Stable Isotope Analysis. Forests 9, 123. https://doi.org/10.3390/f9030123

Zhu, L., Wang, Z.H., Mao, G.L., Zheng, S.X., Xu, X., 2014. Water uptake from different soil depths for halophytic shrubs grown in Northern area of Ningxia plain (China) in contrasted water regimes. Journal of Plant Interactions 9, 26–34. https://doi.org/10.1080/17429145.2012.751139

Zwieniecki, M.A., Brodribb, T.J., Holbrook, N.M., 2007. Hydraulic design of leaves: insights from rehydration kinetics. Plant Cell Environ 30, 910–921. https://doi.org/10.1111/j.1365-3040.2007.001681.x

# Chapter 3

## Leaf rehydration through foliar water uptake in two semiarid grass species

### ABSTRACT

Although leaf wetting is generally considered to have negative impacts on plants, the direct uptake of water accumulated on the leaf surface can improve physiological processes, growth and survival. We studied the effects of foliar water uptake on pressure-volume relations and rehydration kinetics of *B. gracilis* and *M. rigida*. The results indicate that rehydration through both roots and foliar uptake, as compared to roots alone, induces significant changes in pressure volume parameters including; a decrease in the bulk modulus of elasticity and increases in capacitance. Moreover, these changes are associated with slower rate of water potential decline of rehydrated leaves through both pathways as compared to xylem alone. The mechanisms and physiology of rehydrated leaves remains unclear, as the associated hydraulic properties are unknown. To gain insight into the foliar water uptake, we compared rehydration kinetics of two grass species, where rehydration of leaf surface ca be described by a logistic function, suggesting that leaves behave as a single water pool. Whereas full leaf rehydration took over 120 and 150 min in *B. gracilis* and *M. rigida*, respectively. Such differences were attributed to the resistance by the leaf surface and specially by the cuticle. The results underscore the importance of considering plant rehydration through the leaf surface pathway in studies of plant-water relations, particularly in light of the growing body of evidence demonstrating the ubiquity of foliar water uptake.

Keywords: *B. gracilis*, *M. rigida*, cuticle, rehydration kinetics, pression-volume curves

## Introduction

Many plants of most families and biomes, absorb water directly through their leaves, a phenomenon known as foliar water uptake (Berry et al., 2019). The capacity of foliar water uptake (FWU) has been shown to be common in many species; however, there have been very few explicit tests on grass species. This may be of particular interest in grass species subject to dew. Of the more than 120 species tested for its capacity to carry out foliar water uptake (Dawson and Goldsmith, 2018b), only three have been grasses (Breazeale et al., 1950; Suárez and Gloser, 1982): *Panicum maximum, Zeas mays* and *Paspalum notatum*. There is an increasing recognition of the role of FWU may play in plant communities and ecosystem functioning (Berry et al., 2019), and this role may translate into larger alterations in ecosystem functions because of the vast geographical extent of this biome. Despite this, our understanding of when, where, and how FWU occurs in grasslands remains limited.

Foliar water uptake plays a role in preventing plants from dehydration, increasing water potential of leaves and tillers, enhancing photosynthetic rate, and promoting plant growth. It has been found that many species have the capacity to absorb rain, dew, or fog water directly into their leaves (Dawson and Goldsmith, 2018b). However, the effect of foliar water uptake on physiological processes may be variable because of different cost benefit trade off; for example, carbon gain can be reduced because of leaf wetting by heavy fog during the daytime. Absorbed water by leaves not only replenish the storage capacity in leaves but may also be transported to stems and even the root system. However, more studies are need it on the driving forces for, and processes of, absorption and transport of foliar water uptake in general and particularly in grasses.

The storage capacity (i.e. capacitance) also alters the duration of FWU; species with high storage capacity show lower FWU, however that is maintained for longer time. It seems that leaf water storage and foliar water uptake might be linked such that they both buffer leaves from drought. Species with higher capacitance will have slower changes in water potential, and the persistence of this water potential gradient would result in longer FWU duration. This suggest that species with higher hydraulic capacitance should be able to absorb greater total quantities of water. Water from FWU could provide a subsidy to pools that buffer plant water tension and losses of hydraulic conductivity.

To understand the dynamic process of FWU and its capacitance effects it is necessary to measure the pathways of leaf rehydration from the leaf surface, through the apoplast to the mesophyll symplast, (Brodribb and Holbrook, 2003). One way is through rehydration kinetics, which describes the water movement within leaves at negative water potentials at the time course of changes in water potential of leaves (Simonin et al., 2009). Studies of rehydration kinetics suggest that leaves should not be treated as uniform capacitors because rehydration of partially dried leaves may not be described using a single exponential (Cruiziat et al., 1980; Tyree et al., 1981). Tyree et al., (1981) proposed that several parallel pathways with different resistances and/or spatially distinct water pools must exist to account for the observed kinetics. Leaves are composed of many cell types (e.g. epidermal cells, spongy and palisade mesophyll cells, vascular parenchyma) arranged into spatially defined regions of the leaf that differ in their hydraulic properties as well as the degree to their hydraulic connection. The rehydration of these diverse cell types produces kinetics that can be described by a small number of exponential processes.

The kinetic of rehydration can be described by the combination of two capacitors connected simultaneously by two different resistors (Zwieniecki et al., 2007). Such dynamics may arise from the presence of two hydraulically distinct compartments in leaves characterized by low and high resistance pathways to the water supply. The compartment characterized by fast rehydration (i.e. low hydraulic resistance) in angiosperm leaves was proposed to consist of the epidermis and bundle sheath extension, whereas the compartment characterized by slow rehydration (i.e., high hydraulic resistance) was proposed to be mesophyll cells

(Zwieniecki et al., 2007). Here, we use rehydration kinetics to explore the hydraulic design of grass leaves.

In the semiarid grassland, soil water is the main water source for plants in summer, however once the dry season starts soil water turns scarce, forcing plants to use other sources such as water stored in geologic layers (Michael Cohrs Duniway et al., 2010) or water coming from dew or fog (Aguirre-Gutiérrez et al., 2019). Thus changes in the quantity and seasonality of precipitation may affect interactions among coexisting species, that will depend on its adaptations to gather particular source of water (Ehleringer et al., 1991). However, it is less clear how other adaptations such as, leaf tissue capacity to absorb dew water, play a role in the maintenance of a species in a harsh environment. In this semiarid continental grassland, dew has been considered so far as a negligible source of water to the ecosystem, however in a study we have observed that dew formed on leaf surfaces throughout most of the dry season, occurring on 39% of all nights with an average duration of 5 ± 4 h (Aguirre-Gutiérrez et al., 2019). Although this semiarid grassland received significant amount of dew water, no one has examined the possibility of foliar water uptake in either of the dominant and subordinate grass plant species (*Bouteloua gracilis* and *Muhlenbergia rigida*).

The present study evaluated rehydration kinetics of water supplied via leaf's surface and corresponding improvements in grass water status in *B. gracilis* and *M. rigida* following exposure to experimental fog immersion. Our objectives were to determine the capacity of foliar water uptake in our study species, as well as determine the various temporal dynamics of foliar water uptake on leaf-water relations. We hypothesized that a prolonged period of experimental immersion would result in foliar water uptake by both species and improvements in plant water status.

## Methods

### *Plant material*

Fully developed, undamaged leaves of two semiarid grasses, *Bouteloua gracilis* and *Muhlenbergia rigida* were examined. Leaves were collected randomly from individuals maintained and watered three times a week in an experimental terrace at the campus of Chapman University, CA, USA. Conditions include a mean annual air temperature of 17.7 °C and a precipitation of 355 mm. All grasses sampled appeared healthy, without any symptoms of viral or bacterial infection, nutrient deficiency or water stress. Before the start of an experiment, 1.9 L pots from each species were rehydrated overnight and covered with a dark plastic bag and transferred to the laboratory.

### *Anatomical analysis and apoplastic tracer*

We used scanning electron microscopy (SEM) of two completely expanded leaves of each species (grown under greenhouse conditions) to investigate the leaf surface morphological features that could be linked with the FWU capacity. Fragments of tip, mid part and leaf base were cut and carefully attached to the pin using a sticky carbon tab, and mounted in the SEM. The samples were then examined using a Model FEI Quanta 200 (Thermo Fisher Scientific, USA) scanning electron microscope.

To evaluate the anatomical pathways involved in foliar water uptake, we exposed undamaged and expanded leaves to a fluorescent apoplastic tracer solution (Lucifer Yellow, LY; CH, Sigma-Aldrich). For this experiment, we detached fresh, mature leaves from *B. gracilis* and *M. rigida* collected at an experimental site in Llanos de Ojuelos, Jalisco and kept it in a glasshouse. The leaf cuts were sealed with parafilm and maintained in dark conditions, and in contact with 100 µL of a 1% solution of the tracer for 24 h (Eller et al., 2013). This tracer is nontoxic to plant tissue and can only move through the apoplastic pathway (Oparka, 1994). Leaves were removed after 24 hours and washed with distilled water to remove the excess of the tracer and carefully dried out with paper towel. Afterwards, leaves were sectioned and prepared for microscopic observation in a 90% glycerol phosphate buffer (Mastroberti and de Araujo Mariath, 2008). Sections were observed using epifluorescence (Leica DM 5000 CS; Wetzlar, Germany), under intense blue excitation of 450-490 nm with a 515-nm barrier filter (Oparka, 1994).

### *Rehydration kinetics*

Rehydration kinetics was measured following the method of Guzman-Delgado et al. (2018). Prior to the beginning of the rehydration experiment, leaves from each grass species were cut and placed on a bench until they reached 80%-90% of turgor lost point (-1.2 MPa for *Muhlenbergia* rigida and -1.6 MPa for *Bouteloua* gracilis), to impose a water deficit. Prior to fog exposition, the initial weight at leaf turgor lost point (TLP) was determined. Then, ligule was wrapped and sealed with wax tape (Parafilm M, Menasha, MI, USA). Leaves were hung from the ligule, across the top of the fog chamber avoiding contact between leaves. A blackout tarp was set over the fog chambers to ensure minimal light hitting the leaves to prevent transpiration. Leaves were exposed to fog at increasing time intervals, ranging from 10 to 140 minutes in 10-minute increments. At the end of each time interval, the corresponding leaves were taken out of the chamber, the parafilm was removed and dried out using paper towel. After drying, the xylem water pressure ($\psi_{\text{leaf}}$) was measured in a humidified pressure chamber and weighed. Following each final measurement, the leaf was scanned and uploaded into the software Image J to determine leaf area.

### *Foliar water uptake capacity*

To assess foliar water uptake by each species, we followed the method of Limm et al. (2009), which involves submersion of excised leaves. Each plants species was rehydrated overnight covered with a dark plastic bag for 12 h. We cut off one fully mature leaf from 10 plants of each species. Afterwards, the leaf starting mass was measured (mass 1) and the cut end of the leaf was immediately sealed with wax tape (Parafilm) to prevent eflux of water throughout the cut end during measurements. Leaves were submerged in Deionized water for 180 min in complete darkness with the cut end protruding out of the water. At the end, the parafilm was removed and each leaf was carefully and immediately dried with paper towels; the mass was measured (mass 2) to determine how much water the leaf absorbed. To assess whether residual water persisted on the leaf surface, we air dried briefly the leaf so that any remaining water would evaporate and re-weighed the leaf (mass 3). Then the leaf was submerged again in water for 1 s, dried out and immediately re-weighed it (mass 4). The amount of foliar water uptake for each leaf was calculated by evaluating the change in the leaf mass after submergence and correcting for residual leaf water as (Eq. 1):

$$\text{Water uptake} = (\text{mass}_2 - \text{mass}_1) - (\text{mass}_4 - \text{mass}_3) \qquad (1)$$

We determined the leaf area to standardized water uptake per leaf area ($cm^2$). We compared the foliar water uptake capacity of *Bouteloua gracilis; Muhlenbergia rigida; Setaria macrostachya; Eragrostis intermedia; Bouteloua curtipendula; Lycurus phleoides; Panicum obtusum; Bouteloua scorpioides and Bouteloua hirsuta , against* all other species that had been measured to date using the method of Limm *et al.* (2009). To do so, we used data assembled by Berry *et al.* (2019).

*Pressure-volume relations*

To characterize the effects of leaf wetting on leaf-water relations, we compared the pressure-volume relations of rehydrated leaves through leaf wetting against leaves rehydrated through xylem alone (via root acquisition). Leaves were cut off from fully rehydrated grasses early in the morning (e.g. 08:00) using a razor blade and covered overnight with black plastic bags to suppress transpiration. We measured one leaf from 8 individuals of each species to generate the pressure-volume curves.

For rehydrated leaves through root alone, we measured leaves directly following excision from the plant. For leaves through foliar water uptake, we suspended leaves in the fog chamber for 5 h. Leaves were taken out of the chamber immediately dried thoroughly with a paper towel and measured.

Pressure-volume curves were generated by repeatedly making paired measurements of $\Psi_{leaf}$ and leaf mass using a pressure chamber (Scholander) of leaves dried on the bench (n=14-16 points curve$^{-1}$). Leaves were scanned to calculate the leaf area and dried for 48 hours at 60 °C to obtain the leaf dry mass. Pressure-volume curve parameters were estimated from the pressure-volume curves for each species, including relative water content at turgor loss point ($RWC_{TLP}$), water potential at turgor loss point ($\Psi_{TLP}$), bulk modulus of elasticity ($\varepsilon$), and relative capacitance following the methods of Sack & Pasquet-Kok (2014).

*Leaf dry down*

To further characterize the effects of leaf wetting on different leaf-water relations parameters, we also measured Ψleaf in rehydrated leaves through leaf wetting compared to leaves rehydrated through root as a function of time. Methods were identical to those used for pressure-volume relations. The surface of wetted leaves was dried immediately before initiating the measurements, and paired measurements of wet and control leaf water potential were carried out at 20 min intervals for 1 h.

*Analysis*

The cumulative amount of water absorbed through the leaf surface, that is, the difference between initial leaf mass (time t=0) and the mass after fog exposure (t=20, 30, … [min]) was plotted against time and fitted with a three-parameter logistic models function with the following form:

$$\Delta M = \frac{m_f}{1+e^{\frac{t_{50}-t}{s}}} \tag{2}$$

where $m_f$ is the mass of leaf when absorption stops, $t_{50}$ is the time at which 50% of cumulative mass is reached, and $s$ is inversely proportional to the rate of water uptake. The mass value was normalized by the leaf surface area (one leaf side).

The water potential of each leaf was also plotted against time and fitted with a three- and four-parameter logistic model function:

$$\Psi = \Psi_0 + \frac{\Psi_f - \Psi_0}{1 + e^{\frac{t_{50}-t}{s}}} \tag{3}$$

where $\Psi_0$ is the initial water potential of the leaf, and $\Psi_f$ is the water potential of the leaf when absorption stops.

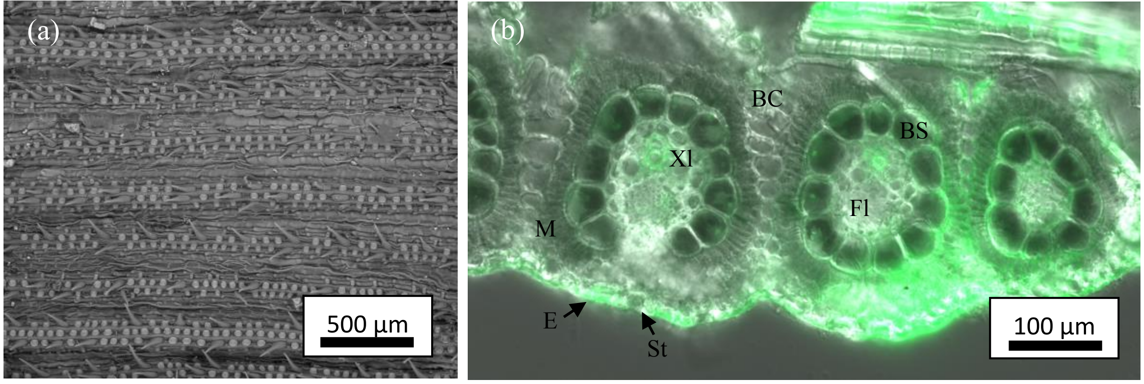
## Results

### *Leaf anatomical characteristics*

We observed anatomical similitudes between *B. gracilis* and *M. rigida*. Both species presented silica bodies on the leaf epidermis (Figure 1a, c), Trichomes, on the other hand differed in their structure between species, thus trichomes of *B.gracilis* have a spiky shape and are highly abundant, while *M. rigida* presented wider trichomes at the base.

Both species exhibited foliar water uptake (FWU). First, we observed apoplastic tracer accumulation in cell walls throughout the entire leaf mesophyll of *B. gracilis* (Figure 1b). Direct diffusion through the adaxial and abaxial cuticle seems to be an important water entry pathway in this species. We found a high apoplastic tracer concentration throughout the entire mesophyll where the primary carbon assimilation tissue is located, suggesting a regular distribution of absorbed solution just around the bundle-sheath cells (BS). The BS are photosynthetic cells which include a large number of chloroplasts and corresponds to the layer of mesophyll cells that connect the BS and Mesophyll.  Nevertheless, the tracer did not reach the xylem in this species, the tracer passed through all the cell walls and was retained in the mesophyll. In *M. rigida* we observed that the apoplastic tracer moved directly through apoplastic routes into the xylem (Figure 1d).

***Bouteloua gracilis***



***Muhlenbergia rigida***

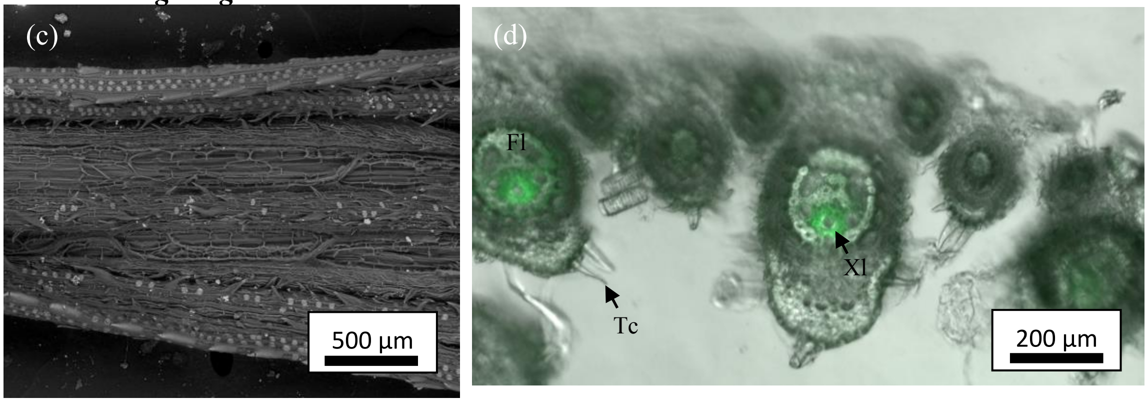


Figure 1. Scanning electron microscopy images of leaf anatomy of *B. gracilis* and *M.rigida* (a-c). Transverse section of leaves exposed to a solution of Lucifer Yellow (LY) dilithium salt to 1% test for 24 h (b-d). (b) LY apoplastic fluorescent tracer concentrate in the Epidermis and Mesophyll for *B. gracilis*. (d) LY into the xylem of *M.rigida*. BC, botuliform cells; BS, bundle-sheath cells; E, epidermis; Fl, phloem; M, mesophyll; St, stomata; Tc, trichome; Xl, xylem.

### *Foliar water uptake capacity*

All examined grass species (*Bouteloua gracilis; Muhlenbergia rigida; Setaria macrostachya; Eragrostis intermedia; Bouteloua curtipendula; Lycurus phleoides; Panicum obtusum; Bouteloua scorpioides and Bouteloua hirsuta)* demonstrated capacity for foliar uptake during the 180-min immersion (Figure 2). However, the two grasses in which we carried out anatomical studies exhibited twice as much absorption rate per leaf area of 0.004 mg $H_2O$ $cm^{-2}$ $min^{-1}$ than the average of the rest (M. rigida), while *B. gracilis showed* the lowest absorption rate with 0.002 mg $H_2O$ $cm^{-2}$ $min^{-1}$.

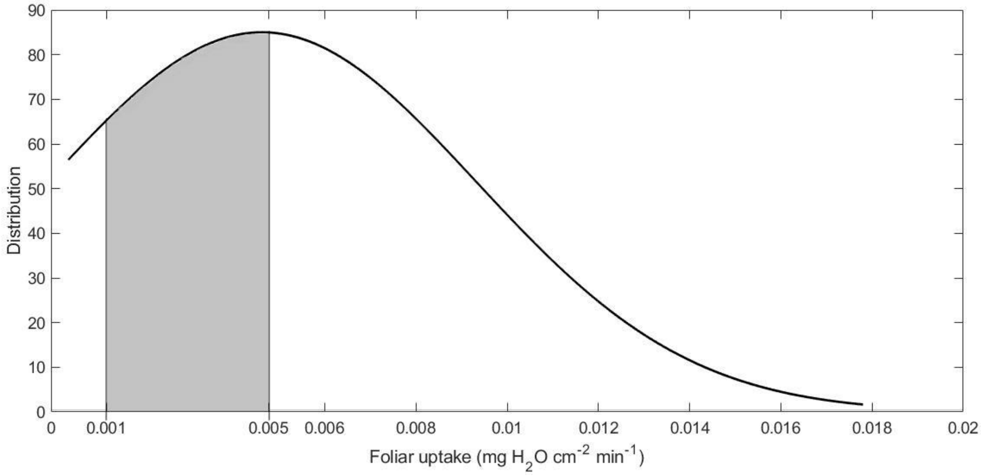


Figure 2. Distribution of data from studies reporting the rate of foliar water uptake (n=25). All values were standardized per minute. The gray area represents the rate of foliar water uptake by leaves of the species of grass during submerge in deionized water for 180 min (n=10).

### *Pressure-volume relations*

Pressure volume-relations measured on leaves of *B. gracilis* rehydrated through both xylem (control) and leaf wetting (fog), demonstrated a significantly ($p < 0.05$) lower water potential at full saturation ($\Psi_S^{100}$ ) and turgor loss ($\Psi_{TLP}$) as compared to leaves rehydrated through the roots alone (Table 1; Figure 3A). Similar differences in $\Psi_S^{100}$ and capacitance at turgor loss point ($C_{TLP}$) between the two treatments was also observed for *M. rigida*. Rehydrated leaves of *M. rigida* with the two treatments showed similar changes in leaf water potential ($\Psi_{leaf}$) over time (Figure 3B).

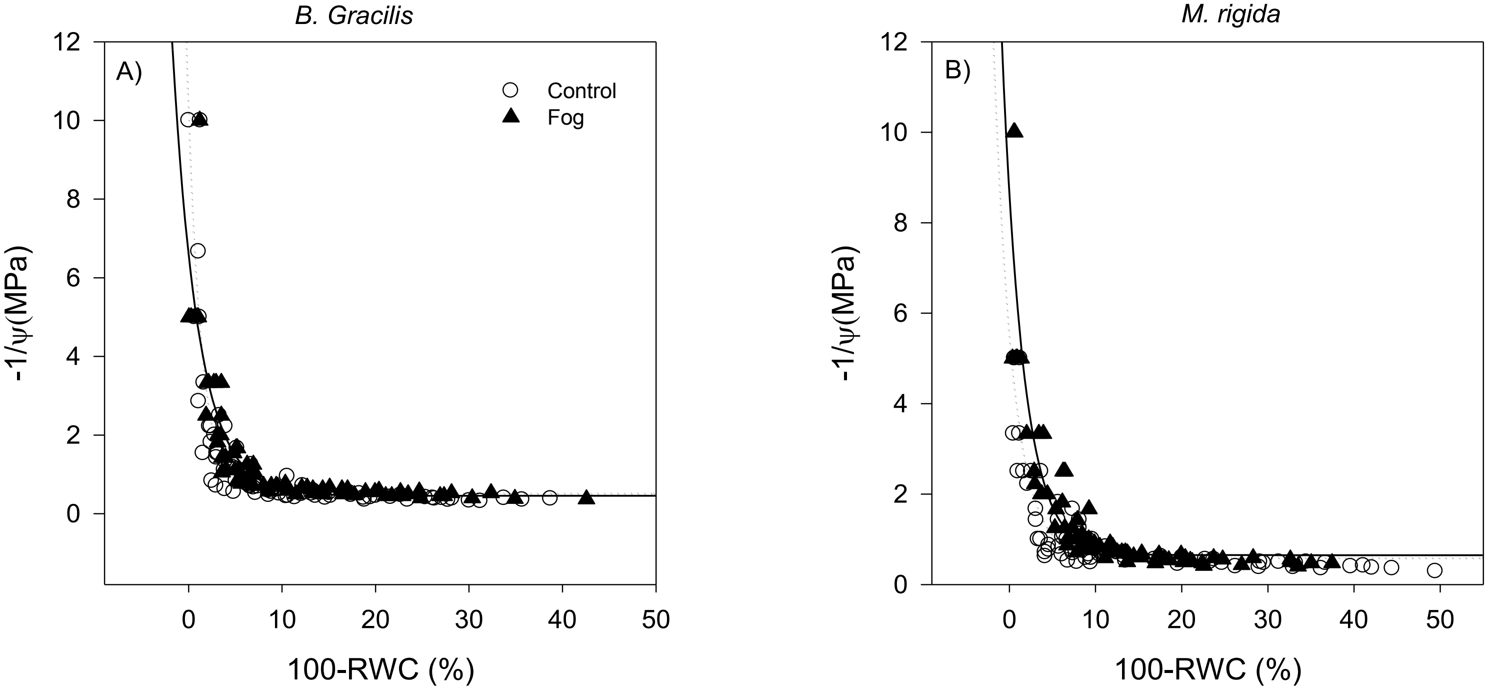


Figure 3. Pressure-volume water relations measured in leaves of two semiarid grassland plant species rehydrated through both roots and leaf wetting (treatment) or through roots alone (control) (n = 6 individuals of each species). Curves represent smooth splines fit through all data for each treatment.

Table 1. Pressure-volume relations measured in leaves rehydrated through xylem (control) compared to leaves rehydrated through xylem and foliar water uptake (fog), including saturated water content (SWC), osmotic potential at full saturation ($P_0$), water potential at turgor loss ($\Psi_{TLP}$), relative water content at turgor loss point ($RWC_{TLP}$), bulk modulus of elasticity (ε), absolute capacitance (CFT) and capacitance at turgor loss point ($C_{TLP}$). Results represents means of 6 leaves (± *SE*) and numbers in bold are significantly different as measured of the leaves of the same plant ($p < 0.05$).

| | ***B. gracilis*** | | ***M. rigida*** | |
|---|---|---|---|---|
| **Parameter** | Control | Fog | Control | Fog |
| **SWC** | 1.51 ± 0.07 | 1.46 ± 0.07 | 2.32 ± 0.12 | 2.29 ± 0.17 |
| **$\Psi_s^{100}$ (MPa)** | **-1.61 ± 0.07** | **-1.4 ± 0.06** | **-1.3 ± 0.06** | **-1.03 ± 0.08** |
| **$\Psi_{TLP}$ (MPa)** | **-1.89 ± 0.07** | **-1.63 ± 0.07** | -1.49 ± 0.05 | -1.3 ± 0.07 |
| **$RWC_{TLP}$** | 89.78 ± 1.27 | 89.48 ± 0.87 | 89.4 ± 0.86 | 90.35 ± 0.92 |
| **ε (MPa)** | 18.68 ± 3.84 | 14.04 ± 1.22 | 12.55 ± 1.59 | 10.01 ± 0.98 |
| **CFT ($MPa^{-1}$)** | 0.05 ± 0.01 | 0.06 ± 0.01 | 0.07 ± 0.01 | 0.08 ± 0.01 |
| **$C_{TLP}$ ($MPa^{-1}$)** | **0.21 ± 0.03** | **0.31 ± 0.04** | 0.3 ± 0.07 | 0.2 ± 0.04 |
| **CFT* (mol $m^{-2}$ $MPa^{-1}$)** | **0.38 ± 0.04** | **0.6 ± 0.09** | 1.45 ± 0.22 | 1.28 ± 0.17 |
| **$C_{TLP*}$ (mol m-2 MPa-1)** | **1.55 ± 0.11** | **2.97± 0.55** | **6.98 ± 0.99** | **2.83 ± 0.34** |

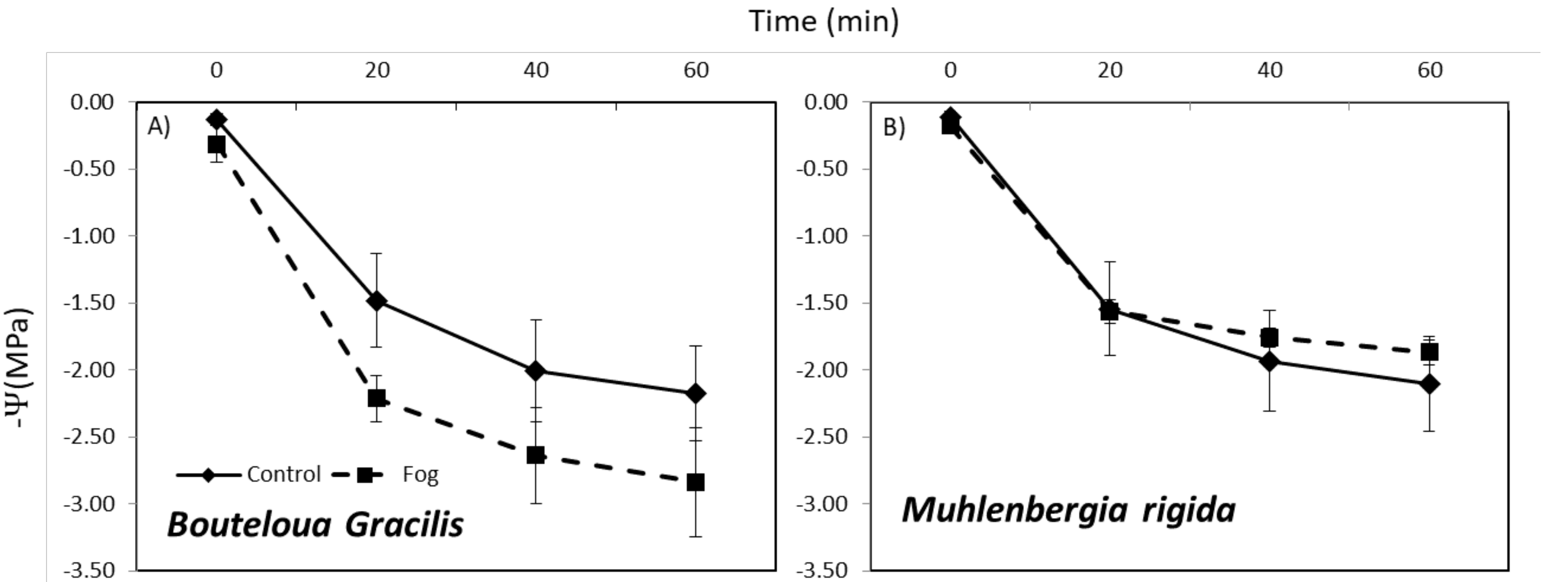


Figure 4. Leaf water potential measured over time in leaves of two semiarid grassland plant species rehydrated through both xylem (control) and leaf wetting (Fog) (n = 6 individuals of each species). Results represent means ± 1 *SE*.

### *Rehydration kinetics*

*B. gracilis* and *M. rigida* leaves absorbed water through their epidermis, as revealed by the increase in leaf mass and water potential after exposition to fog (Figure 5). Moreover, prolonged fog exposition allowed leaves of both species to fully rehydrate, as suggested from final water potential values. The rehydration kinetics for the two species fitted well to three- and four-parameter logistic models both in terms of mass increments and water potential over time, respectively (Table 2, Figure 5). Based on model estimates, *B. gracilis* leaves absorbed ~1.2 mg$_{H2O}$/m$^2$ via their surface after approximately 140 min of fog exposition, and *M. rigida* leaves absorbed up to ~0.4 mg$_{H2O}$/m$^2$ after 120 min.

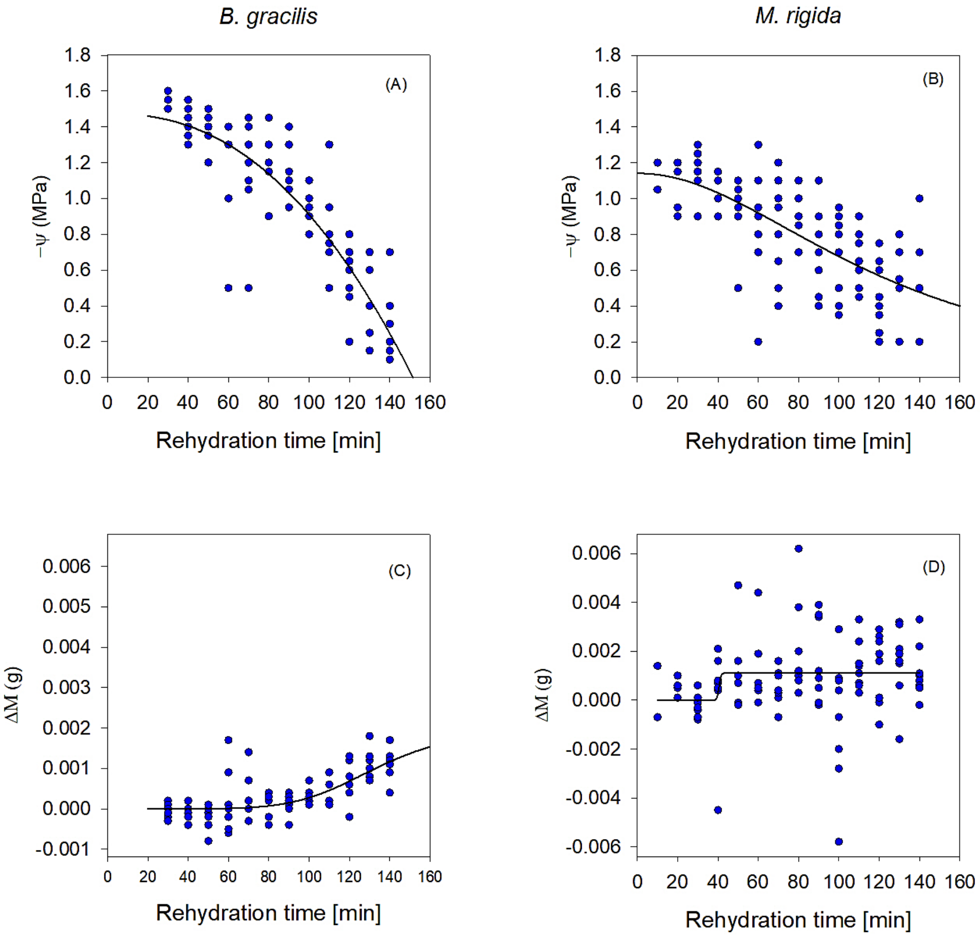


Figure 5.- Water potential and mass increment of *B. gracilis* and *M. rigida* leaves supplied with water via their surface over time.

## Discussion

*Pathways and FWU capacity*

Our results indicate that, whereas the grass species of semiarid grassland might have specialized structures that facilitates foliar water uptake (FWU) (i.e. trichomes and stomas), the main FWU pathway for the studied species seem to be direct diffusion through the leaf cuticle and epidermis. The cuticle and epidermis of the two species showed certain degree of water permeability, enabling diffusion of apoplastic fluorescent tracers (Eller et al., 2013). Leaves of *B. gracilis* exhibited high concentration of Lucifer Yellow (LY) on the cuticle and epidermis, which suggest that the main anatomical route for tracer absorption. Whereas, in *M. rigida* the tracer was observed directly in the xylem suggesting another anatomical route, such as he stomata or trichomes. This is evidence of anatomical differences between both species (Figure 1) acting in leaf water uptake.

Another species difference includes; cuticle thickness, with *B. gracilis* presenting a thin layer compared to thick cuticle layer in *M. rigida*, which is basically controlled by the amount of cellulose, hemicellulose and lignin (figure 6). Consequently, differences in cuticle thickness between species could be the control on FWU. Our results demonstrated that variations in leaf morphology and anatomy, including presence of trichomes, concentration of silica bodies, epidermis thickness can all affect leaf water absorption. The apoplastic tracer spread easily over the leaf surface of *B. gracilis* and continued moving through internal cellular air space, until it reached the mesophyll. Leaves could use this water to carry out photosynthesis or for storage (capacitance). It is well known that the water pathway is governed by several resistances imposed by the cell membranes, along the epidermis and mesophyll cells. These resistances are also influenced by the tissue architecture involved in the pathway and whether the FWU is in liquid or vapor phase (Berry et al., 2019). Also, the cuticle permeability is related to its cuticular composition and will influence the extent to which FWU occurs through the stomata or cuticle. Cuticular permeability also increased with leaf age due to cuticle damage and degradation, and this may have implication for FWU (Jordan and Brodribb, 2007; Schreiber et al., 2001; Van Gardingen et al., 1991; Yates and Hutley, 1995). Consequently, the differences in the thickness of the cuticle between our species seems to be determinant in FWU.

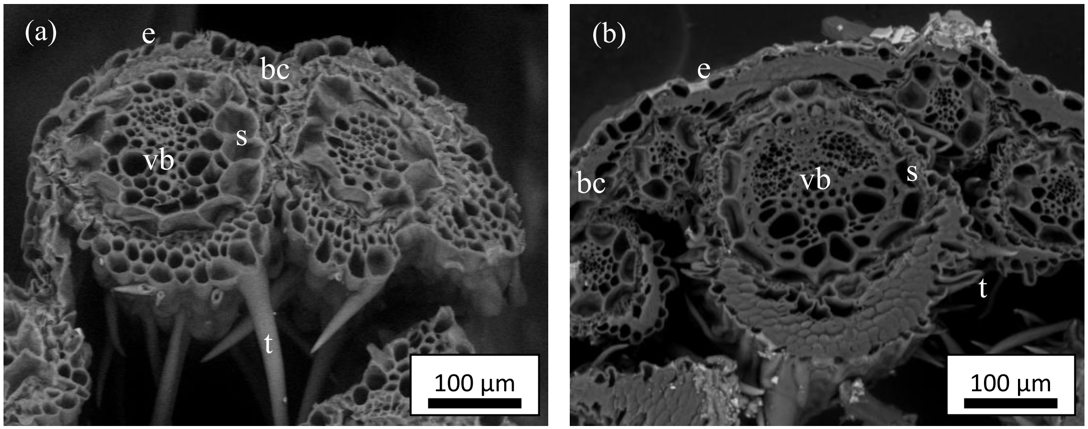


Figure 6. Scanning electron microscopy images of transverse leaf anatomy of (a) *B. gracilis* and (b) *M.rigida*. vb=vascular bundle; s=vb sheat; bc =bulliform cells; e=epidermis; t=tricome.

The apoplastic tracer was observed in the xylem of the leaf of *M. rigida* but not in the cuticle. Leaves of this specie had a thicker cuticle which suggest a different pathway of water movement in the leaf. Leaves of *M. rigida present* trichomes and stomata, that could function as preferential FWU pathways for this species. The enhanced water uptake capacity of trichome structures might be related to the formation of the aqueous pores at the base of trichomes when exposed to water (Schonherr, 2006). Trichomes could also facilitate water condensation on the leaf surface and promote FWU (Konrad et al., 2015). On the other hand, trichomes may increase leaf water repellency (Brewer et al., 1991) and reduce FWU. Therefore, this epidermal structure is highly variable in their function and morphology, and they could play contrasting roles in FWU (Berry et al., 2019). Furthermore, recent results using environmental scan electron microscopy has demonstrated that stomata are a likely candidate for uptake of liquid water (Burkhardt et al., 2012). Eller at all (2013), observed patterns of fluorescent tracer on the abaxial layer of *Drymis. brasiliensis* leaves that suggests a possible role of stomata on FWU, but we could not find the same pattern for *M. rigida* leaves (figure 1). Even though water could enter through stomatal pores during FWU, we believe that the bulk water entry occurred through direct cuticle diffusion (which may be facilitated by special structures) and the leaf area, trichomes and stomata may amplify the FWU capacity in *M. rigida*.

### *Leaf rehydration alters Pressure-Volume relations*

Research on leaf pressure-volume relations to date has focused on rehydration through the xylem, the predominant hydraulic pathway for plants. Here, we consider the role of both the xylem and direct foliar water uptake for increasing leaf tissue water content to a fully hydrated state. Foliar water uptake resulted in species-specific impacts on pressure-volume relations, as well as effects on the change in $\Psi_{leaf}$ as a function of time.

*B. gracilis* and *M. rigida*, showed a decrease in ε and consequently, an increase in capacitance (a smaller change in $\Psi_{leaf}$ per unit water loss) in leaves subjected to rehydration through leaf wetting compared to xylem alone (Table 1). This may have occurred if water absorbed through the leaf surface was stored in apoplastic spaces (between cells or in cell walls), response that would not be observed in leaf rehydration through the xylem alone. This additional water appears to increase tissue elasticity (ε), perhaps as a result of either additional water pushing against the cell walls or additional water within the cell walls themselves. Either way, the outcome is a significant change in the ‘hydrostatic’ properties of the tissue when rehydrated through both pathways. This additional water also appears to serve as a new “capacitor” within the leaf itself causing that *B. gracilis* leaves experienced a slower decline in $\Psi_{leaf}$ than plants rehydrated through xylem alone. The slower rate of dehydration may be due to some combination of the observed increase in capacitance or an increase in resistance to leaf water loss (Kramer and Boyer, 1995; Nobel and Jordan, 1983). Some plant species rehydrated through foliar uptake have previously been observed to demonstrate slower rates of dehydration (Gouvra and Grammatikopoulos, 2003; Grammatikopoulos and Manetas, 1994; Kerr and Beardsell, 1975). Nevertheless, our results indicate that the effects of foliar water uptake on pressure-volume relations are not ubiquitous among species and that additional information on the traits driving the differences is of interest.

Differences in the presence, size, abundance and arrangement of different leaf anatomical structures may account for the observed differences in pressure-volume relations induced by rehydration through foliar water uptake. Experimental approaches to understand leaf rehydration kinetics have found evidence for distinct pools of water within a leaf, which were based on differences in leaf anatomy (Blackman and Brodribb, 2011; Morse, 1990; Tyree et al., 1981; Zwieniecki et al., 2007). In leaves of *B. gracilis*, pools of water in the epidermal and/or spongy mesophyll tissues may serve as hydraulic capacitors that provide on-demand water for transpiration that buffers against rapid changes in $\Psi_{leaf}$ imposed by low water supply or high water demand (Zwieniecki et al., 2007).

### *Magnitude and significance Leaf rehydration kinetics*

The study also showed that leaf absorption and further transport towards internal leaf tissue varied in duration, which is consistent with reports by Guzman-Delgado *et al.* (2018). Kinetics of absorption were different between both species, for *M. rigida* leaves were fully hydrated after ~ 120 min, whereas for *B. gracilis* took 140 min. This rehydration kinetic could be described by a single logistic function which suggest a single high resistance pathway controlling the process. The high resistance to water absorption conferred by the permeability of the leaf surface and specially the cuticle seems to influence the entire rehydration process, leading to kinetics that could be described by a logistic model (figure 5). The slower initial rate of water absorption (the first part of the logistic curve), despite the large gradient of water chemical energy across the surface, may reflect the partial wetting of the leaf surface and/or an imposed delay in cuticle hydration to significantly contribute to leaf water gain. Such delay may be affected by the structure of the cuticle and associated water distribution at relative low hydration stages that hinder water mobility across the matrix (Domínguez, 1999; Riederer, 2006). The absorbed water will eventually reach the inner cell wall regions and the epidermal cell protoplasts contributing to the rehydration on the whole epidermis. Thus, the rehydration process is mainly determined by leaf surface permeability.

The epidermis might be part of the low-resistance pathways that link bundle sheath veins to the hydraulic network allowing for fast redistribution of water across the leaf lamina (Buckley et al., 2011; Zwieniecki et al., 2007). This redistribution could also contribute rewet the cuticle from its inner part causing an additional rearrangement of its chemical components(Guzmán-Delgado et al., 2017). This rearrangement may favor the movement of water across the cuticle leading to a reduction in surface hydraulic resistance and an increased flux towards the internal leaf as is evidenced by the changes in the uptake of water (logistic curves). It is not entirely possible to exclude the role of stomata in the absorption process, especially in *M. rigida* where stomata and trichomes could be the principally pathway of water absorption, due to the permeability of the cuticle. Although, stomata were assumed to be closed because of the imposed dark conditions, it is possible that water could be absorbed by exposed parts of the guard cells and contribute to total surface absorption. It is worth considering that guard cells do not have plasmodesmata connections with other epidermal cells, suggesting that such contribution is minimal. Further work needs to determine the pathways of the leaf surface water uptake, with attention to stomata, and quantify how they are related to the temporal changes in conductance in the surface during the rehydration.

### *Ecological implications*

The leaf foliar water absorption has been described by many authors (Goldsmith et al., 2013). There are some doubts about the long-term effects of these improvements on net carbon and water fluxes, however the importance of this mechanism of water uptake is generally recognized (i.e. altering leaf and stem water potential, improving hydraulic conductivity and increased leaf water content). Evidences show that FWU is important for turgor maintenance and growth (Steppe et al., 2018). Water coming from FWU could serve as an additionally source (similar to leaf capacitance) that buffers decline in turgor and hydraulic conductivity (Nguyen et al., 2017). Ultimately, understanding these linkages will allow for integration into the ecosystem models that predict ecosystem hydrology and long-term vegetation dynamics.

The time course of foliar water absorption for grasses has been studied in a very limited number of species. The two grasses which we have chosen for experiments are very important in the Mexican short grass and very successful in surviving local and long dry periods. There are striking differences in their morphology, which have an impact in their foliar absorption rates. Quick recovery from water deficiency, which was found in *B. gracilis* and *M. rigida.* may have some important ecological consequences. The benefits which can be derived from dew and fog in field conditions, are surely not limited to reduction of potential evapotranspiration. Water absorbed by leaves of grasses may help them not only to survive but also to grow during the night in the wet season, while during the dry season this water can help them to maintain rehydrated the base tissue of the grass and promote the minimal photosynthesis activity. The restoration of water potential in the grass could allow to increase the activity of the phloem and export the leaf constituents to other plants organs. This might be important for plant growth and survival by supplying leaf assimilates to, for example, reproductive structures or the stem during leaf senescence. However, further exploration of the linkages of FWU and hydraulic function, plant growth, and mortality risk is need it, this will enhance our ability to predict grassland response to climate changes.

## Conclusion

This study provide evidence that the leaf of the two grass species studied are capable of rapid liquid water uptake through the leaves surface, specifically trough the cuticle, stomates and trichomes. We obtained some evidence that trichomes of *M. rigida* may play a role in foliar water uptake, while we found that the principal leaf water uptake pathway of *B. gracilis* is through the cuticle. This suggest that foliar water uptake may be widespread among semiarid grasslands across different grass species, but detailed physiological studies are needed, and more species have to be investigated to confirm this assumption.

A deeper understanding of the functional role of foliar water uptake in grasses and other plants groups is an important step to increase the predictive power of models simulating the biological consequences of climate warming-related droughts. If a significant proportion of the water consumed by plants is contributed by foliar water uptake, changes in rainfall duration and frequency and air humidity (evaporative demand) may be biologically more relevant than altered precipitation amounts.

## Bibliography

Agam, N., 2004. Diurnal Water Content Changes in the Bare Soil of a Coastal Desert. JOURNAL OF HYDROMETEOROLOGY 5, 12.

Agam, N., Berliner, P.R., 2006. Dew formation and water vapor adsorption in semi-arid environments - A review. Journal of Arid Environments 65, 572–590. https://doi.org/10.1016/j.jaridenv.2005.09.004

Agam, N., Berliner, P.R., Zangvil, A., Ben-Dor, E., 2004. Soil water evaporation during the dry season in an arid zone. Journal of Geophysical Researc 109, doi:10.1029/2004JD004802. https://doi.org/10.1029/2004JD004802

Aguado-Santacruz, G.A., Garcia-Moya, E., 1998. Environmental factors and community dynamics at the southernmost part of the North American Graminetum: I. On the contribution of climatic factors to temporal variation in species composition. Plant Ecology 135, 13–29. https://doi.org/10.1023/A:1009750831162

Aguirre-Gutiérrez, C.A., Holwerda, F., Goldsmith, G.R., Delgado, J., Yepez, E., Carbajal, N., Escoto-Rodríguez, M., Arredondo, J.T., 2019. The importance of dew in the water balance of a continental semiarid grassland. Journal of Arid Environments 168, 26–35. https://doi.org/10.1016/j.jaridenv.2019.05.003

Alcocer-Ruthling, M., Robberecht, R., Thill, D.C., 1989. The Response of Bouteloua scorpioides to Water Stress at Two Phenological Stages. Botanical Gazette 150, 454–461. https://doi.org/10.1086/337792

Arredondo, T., Delgado-Balbuena, J., Huber-Sannwald, E., García-Moya, E., Loescher, H.W., Aguirre-Gutiérrez, C., Rodriguez-Robles, U., 2018. Does precipitation affects soil respiration of tropical semiarid grasslands with different plant cover types? Agriculture, Ecosystems & Environment 251, 218–225. https://doi.org/10.1016/j.agee.2017.09.034

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016a. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Arredondo, T., Garcìa-Moya, E., Huber-Sannwald, E., Loescher, H.W., Delgado-Balbuena, J., Luna-Luna, M., 2016b. Drought manipulation and its direct and legacy effects on productivity of a monodominant and mixed-species semi-arid grassland. Agricultural and Forest Meteorology 223, 132–140. https://doi.org/10.1016/j.agrformet.2016.03.011

Asbjornsen, H., Mora, G., Helmers, M.J., 2007. Variation in water uptake dynamics among contrasting agricultural and native plant communities in the Midwestern U.S. Agriculture, Ecosystems & Environment 121, 343–356. https://doi.org/10.1016/j.agee.2006.11.009

Asbjornsen, H., Shepherd, G., Helmers, M., Mora, G., 2008. Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S. Plant Soil 308, 69–92. https://doi.org/10.1007/s11104-008-9607-3

BALBUENA, J.D., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Barnard, R.L., Bello, F. De, Buchmann, N., 2006. The δ18O of root crown water best reflects source water δ18O in different types of herbaceous species. Rapid communications in mass spectrometry : RCM 24, 3567–3577. https://doi.org/10.1002/rcm

Barradas, V.L., Glez-Medellín, Ma.G., 1999. Dew and its effect on two heliophile understorey species of a tropical dry deciduous forest in Mexico. International Journal of Biometeorology 43, 1–7. https://doi.org/10.1007/s004840050109

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2019. Foliar water uptake: Processes, pathways, and integration into plant water budgets: Foliar Water Uptake. Plant Cell Environ 42, 410–423. https://doi.org/10.1111/pce.13439

Berry, Z.C., Emery, N.C., Gotsch, S.G., Goldsmith, G.R., 2018. Foliar water uptake: processes, pathways, and integration into plant water budgets. Plant, Cell & Environment. https://doi.org/10.1111/pce.13439

Blackman, C.J., Brodribb, T.J., 2011. Two measures of leaf capacitance: insights into the water transport pathway and hydraulic conductance in leaves. Functional Plant Biol. 38, 118. https://doi.org/10.1071/FP10183

Blair, J., Nippert, J., Briggs, J., 2014. Grassland Ecology, in: Monson, R.K. (Ed.), Ecology and the Environment. Springer New York, New York, NY, pp. 389–423.

Bowen, G.J., Revenaugh, J., 2003. Interpolating the isotopic composition of modern meteoric precipitation: ISOTOPIC COMPOSITION OF MODERN PRECIPITATION. Water Resour. Res. 39. https://doi.org/10.1029/2003WR002086

Boyer, J.S., 1985. Water transport. Annual review of plant physiology 36, 473–516.

Boyer, J.S., 1974. Water transport in plants: Mechanism of apparent changes in resistance during absorption. Planta 117, 187–207. https://doi.org/10.1007/BF00388393

Breazeale, E.L., McGeorge, W.T., Breazeale, J.F., 1950. MOISTURE ABSORPTION BY PLANTS FROM AN ATMOSPHERE OF HIGH HUMIDITY. Plant Physiol. 25, 413–419. https://doi.org/10.1104/pp.25.3.413

Brewer, C.A., Smith, W.K., Vogelmann, T.C., 1991. Functional interaction between leaf trichomes, leaf wettability and the optical properties of water droplets. Plant, Cell & Environment 14, 955–962.

Brodribb, T.J., Holbrook, N.M., 2003. Stomatal Closure during Leaf Dehydration, Correlation with Other Leaf Physiological Traits. Plant Physiol. 132, 2166–2173. https://doi.org/10.1104/pp.103.023879

Buckley, T.N., Sack, L., Gilbert, M.E., 2011. The Role of Bundle Sheath Extensions and Life Form in Stomatal Responses to Leaf Water Status. Plant Physiol. 156, 962–973. https://doi.org/10.1104/pp.111.175638

Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): foliar uptake and prevention of dehydration. Plant Cell Environ 27, 1023–1034. https://doi.org/10.1111/j.1365-3040.2004.01207.x

Burkhardt, J., Basi, S., Pariyar, S., Hunsche, M., 2012. Stomatal penetration by aqueous solutions–an update involving leaf surface particles. New Phytologist 196, 774–787.

Coffin, D.P., Lauenroth, K., 1991a. Effects of competition on spatial distribution of roots of blue grama. Journal Of Range Management 44.

Coffin, D.P., Lauenroth, W.K., 1991b. Effects of Competition on Spatial Distribution of Roots of Blue Grama. Journal of Range Management 44, 68. https://doi.org/10.2307/4002642

Corbin, J.D., Thomsen, M.A., Dawson, T.E., D'Antonio, C.M., 2005. Summer water use by California coastal prairie grasses: fog, drought, and community composition. Oecologia 145, 511–521. https://doi.org/10.1007/s00442-005-0152-y

Cruiziat, P., Tyree, M.T., Bodet, C., LoGULLO, M.A., 1980. THE KINETICS OF REHYDRATION OF DETACHED SUNFLOWER LEAVES FOLLOWING SUBSTANTIAL WATER LOSS. New Phytol 84, 293–306. https://doi.org/10.1111/j.1469-8137.1980.tb04429.x

Crutsinger, G.M., Rodriguez-Cabal, M.A., Roddy, A.B., Peay, K.G., Bastow, J.L., Kidder, A.G., Dawson, T.E., Fine, P.V.A., Rudgers, J.A., 2014. Genetic variation within a dominant shrub structures green and brown community assemblages. Ecology 95, 387–398. https://doi.org/10.1890/13-0316.1

Dai, Y., Zheng, X.-J., Tang, L.-S., Li, Y., 2015. Stable oxygen isotopes reveal distinct water use patterns of two Haloxylon species in the Gurbantonggut Desert. Plant Soil 389, 73–87. https://doi.org/10.1007/s11104-014-2342-z

Dawson, T.E., Goldsmith, G.R., 2018a. The value of wet leaves. New Phytologist 219, 1156–1169. https://doi.org/10.1111/nph.15307

Dawson, T.E., Goldsmith, G.R., 2018b. The value of wet leaves. New Phytol 219, 1156–1169. https://doi.org/10.1111/nph.15307

De Bruin, H.A.R., Ronda, R.J., Van De Wiel, B.J.H., 2000. Approximate solutions for the Obukhov length and the surface fluxes in terms of bulk Richardson numbers. Boundary-layer meteorology 95, 145–157.

Delgado-Balbuena, J., 2016. Variability of carbon fluxes at different time-scales and their biotic and environmental controls on a short-grass steppe in Central Mexico.

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Huber-Sannwald, E., Chavez-Aguilar, G., Luna-Luna, M., Barretero-Hernandez, R., 2013. Differences in plant cover and species composition of semiarid grassland communities of central Mexico and its effects on net ecosystem exchange. Biogeosciences 10, 4673–4690. https://doi.org/10.5194/bg-10-4673-2013

Delgado-Balbuena, J., Arredondo, J.T., Loescher, H.W., Pineda-Martínez, L.F., Carbajal, J.N., Vargas, R., 2019. Seasonal Precipitation Legacy Effects Determine the Carbon Balance of a Semiarid Grassland. J. Geophys. Res. Biogeosci. 124, 987–1000. https://doi.org/10.1029/2018JG004799

Dingman, S.L., 2015. Physical hydrology. Waveland press.

Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. Oecologia 117, 504–512. https://doi.org/10.1007/s004420050686

Domingo, F., Villagarcía, L., Brenner, A.J., Puigdefábregas, J., 2000. Measuring and modelling the radiation balance of a heterogeneous shrubland. Plant, Cell and Environment 23, 27–38. https://doi.org/10.1046/j.1365-3040.2000.00532.x

Domínguez, E., 1999. Water hydration in cutinized cell walls: a physico-chemical analysis. Biochimica et Biophysica Acta (BBA) - General Subjects 1426, 168–176. https://doi.org/10.1016/S0304-4165(98)00152-4

Drennan, P.M., Nobel, P.S., 1998. Root growth dependence on soil temperature for Opuntia ficus-indica: influences of air temperature and a doubled CO2 concentration. Funct Ecology 12, 959–964. https://doi.org/10.1046/j.1365-2435.1998.00276.x

Duniway, M C, Herrick, J.E., Curtis Monger, H., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Duniway, Michael Cohrs, Herrick, J.E., Monger, H.C., 2010. Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. Oecologia 163, 215–226. https://doi.org/10.1007/s00442-009-1530-7

Eggemeyer, K.D., Awada, T., Harvey, F.E., Wedin, D.A., Zhou, X., Zanner, C.W., 2008. Seasonal changes in depth of water uptake for encroaching trees Juniperus virginiana and Pinus ponderosa and two dominant C4 grasses in a semiarid grassland. Tree Physiology 29, 157–169. https://doi.org/10.1093/treephys/tpn019

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R., 1991. Differential utilization of summer rains by desert plants. Oecologia 88, 430–434. https://doi.org/10.1007/BF00317589

Eller, C.B., Lima, A.L., Oliveira, R.S., 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, *Drimys brasiliensis* (Winteraceae). New Phytol 199, 151–162. https://doi.org/10.1111/nph.12248

Esmaiel Malek, 2016. Differentiation of the Atmospheric Moisture Collected by Dew and Fog. JESE-A 5. https://doi.org/10.17265/2162-5298/2016.04.001

Evenari, M., Shanan, L., Tadmor, N., 1982. The Negev: The Challenge of a Desert. Harvard University Press.

Friedl, M.A., 1995. Modeling land surface fluxes using a sparse canopy model and radiometric surface temperature measurements. Journal of Geophysical Research: Atmospheres 100, 25435–25446. https://doi.org/10.1029/95JD00723

Garratt, J.R., 1992. The atmospheric boundary layer. Cambridge atmospheric and space science series. Cambridge University Press, Cambridge 416, 444.

Garratt, J.R., Segal, M., 1988. On the contribution of atmospheric moisture to dew formation. Boundary-Layer Meteorology 45, 209–236. https://doi.org/10.1007/BF01066671

Goldsmith, G.R., Matzke, N.J., Dawson, T.E., 2013. The incidence and implications of clouds for cloud forest plant water relations. Ecology letters 16, 307–314.

Grammatikopoulos, G., Manetas, Y., 1994a. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Canadian Journal of Botany 72, 1805–1811.

Grammatikopoulos, G., Manetas, Y., 1994b. Direct absorption of water by hairy leaves of Phlomis fruticosa and its contribution to drought avoidance. Can. J. Bot. 72, 1805–1811. https://doi.org/10.1139/b94-222

Guan, H., Sebben, M., Bennett, J., 2014. Radiative- and artificial-cooling enhanced dew collection in a coastal area of South Australia. Urban Water Journal 11, 175–184. https://doi.org/10.1080/1573062X.2013.765494

Guo, X., Zha, T., Jia, X., Wu, B., Feng, W., Xie, J., Gong, J., Zhang, Y., Peltola, H., 2016. Dynamics of dew in a cold desert-shrub ecosystem and its abiotic controls. Atmosphere 7, 1–15. https://doi.org/10.3390/atmos7030032

Guzmán-Delgado, P., Fernández, V., Venturas, M., Rodríguez-Calcerrada, J., Gil, L., 2017. Surface properties and physiology of Ulmus laevis and U. minor samaras: implications for seed development and dispersal. Tree Physiology 37, 815–826. https://doi.org/10.1093/treephys/tpx022

Guzmán-Delgado, P., Mason Earles, J., Zwieniecki, M.A., 2018. Insight into the physiological role of water absorption via the leaf surface from a rehydration kinetics perspective: Leaf rehydration kinetics via the surface. Plant Cell Environ 41, 1886–1894. https://doi.org/10.1111/pce.13327

Hanisch, S., Lohrey, C., Buerkert, A., 2015. Dewfall and its ecological significance in semi-arid coastal south-western Madagascar. Journal of Arid Environments 121, 24–31. https://doi.org/10.1016/j.jaridenv.2015.05.007

Hartnett, D.C., Hickman, K.R., Walter, L.E.F., 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49, 413–420.

Helliker, B.R., Ehleringer, J.R., 2000. Establishing a grassland signature in veins: 18O in the leaf water of C3 and C4 grasses. Proceedings of the National Academy of Sciences of the United States of America 97, 7894–7898. https://doi.org/10.1073/pnas.97.14.7894

Heusinkveld, B.G., Berkowicz, S.M., Jacobs, A.F.G., Holtslag, A. a. M., Hillen, W.C. a. M., 2006. An Automated Microlysimeter to Study Dew Formation and Evaporation in Arid and Semiarid Regions. Journal of Hydrometeorology 7, 825–832. https://doi.org/10.1175/JHM523.1

Hunter, K.A.M., Wu, L., 2005. Morphological and physiological response of five California native grass species to moderate salt spray: Implications for landscape irrigation with reclaimed water. Journal of Plant Nutrition 28, 247–270. https://doi.org/10.1081/PLN-200047609

Jackson, T.J., Moy, L., 1999. Dew Effects on Passive Microwave Observations of Land Surfaces. Remote Sensing of Environment 70, 129–137. https://doi.org/10.1016/S0034-4257(99)00021-8

Jacobs, a. F.G., Heusinkveld, B.G., Kruit, R.J.W., Berkowicz, S.M., 2006. Contribution of dew to the water budget of a grassland area in the Netherlands. Water Resources Research 42. https://doi.org/10.1029/2005WR004055

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 1999. Dew deposition and drying in a desert system: a simple simulation model. Journal of Arid Environments 42, 211–222. https://doi.org/10.1006/jare.1999.0523

Jordan, G.J., Brodribb, T.J., 2007. Incontinence in aging leaves: deteriorating water relations with leaf age in Agastachys odorata (Proteaceae), a shrub with very long-lived leaves. Functional Plant Biol. 34, 918. https://doi.org/10.1071/FP07166

Kalthoff, N, Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kalthoff, N., Fiebig-Wittmaack, M., Meißner, C., Kohler, M., Uriarte, M., Bischoff-Gauß, I., Gonzales, E., 2006. The energy balance, evapo-transpiration and nocturnal dew deposition of an arid valley in the Andes. Journal of Arid Environments 65, 420–443.

Kaseke, K.F., Wang, L., Seely, M.K., 2017. Nonrainfall water origins and formation mechanisms. Sci. Adv. 3, e1603131. https://doi.org/10.1126/sciadv.1603131

Kerr, J.P., Beardsell, M.F., 1975. Effect of Dew on Leaf Water Potentials and Crop Resistances in a Paspalum Pasture 1. Agronomy Journal 67, 596–599.

Kidder, D.L., Gierlowski-Kordesch, E.H., 2005. Impact of grassland radiation on the nonmarine silica cycle and Miocene diatomite. Palaios 20, 198–206.

Kidron, G., Yair, A., Danin, A., 2000. Dew variability within a small arid drainage basin in the Negev Highlands,Israel. Q J R Meteorol Soc 126, 63–80. https://doi.org/10.1256/smsqj.56203

Kidron, G.J., 2000a. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000b. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270. https://doi.org/10.1016/S0169-8095(00)00063-6

Kidron, G.J., 2000c. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270.

Kidron, Giora J, 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8. https://doi.org/10.1016/S0168-1923(99)00043-X

Kidron, Giora J., 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96, 1–8.

Koerner, S.E., Collins, S.L., 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. Ecology 95, 98–109. https://doi.org/10.1890/13-0526.1

Konrad, W., Burkhardt, J., Ebner, M., Roth-Nebelsick, A., 2015. Leaf pubescence as a possibility to increase water use efficiency by promoting condensation: LEAF PUBESCENCE MAY INCREASE WATER USE EFFICIENCY. Ecohydrol. 8, 480–492. https://doi.org/10.1002/eco.1518

Kramer, P.J., Boyer, J.S., 1995. Water relations of plants and soils. Academic press.

Lekouch, I., Lekouch, K., Muselli, M., Mongruel, A., Kabbachi, B., Beysens, D., 2012. Rooftop dew, fog and rain collection in southwest Morocco and predictive dew modeling using neural networks. Journal of Hydrology 448–449, 60–72. https://doi.org/10.1016/j.jhydrol.2012.04.004

Leopold, L., n.d. Dew as a Source of Plant Moisture 3.

Leopold, L.B., 1952. Dew as a source of plant moisture.

Limm, E.B., Simonin, K.A., Bothman, A.G., Dawson, T.E., 2009. Foliar water uptake: a common water acquisition strategy for plants of the redwood forest. Oecologia 161, 449–459. https://doi.org/10.1007/s00442-009-1400-3

Liu, S., Li, S.-G., Yu, G.-R., Sun, X.-M., Zhang, L.-M., Hu, Z.-M., Li, Y.-N., Zhang, X.-Z., 2009. Surface energy exchanges above two grassland ecosystems on the Qinghai-Tibetan Plateau. Biogeosciences Discuss. 6, 9161–9192. https://doi.org/10.5194/bgd-6-9161-2009

Maestre, F.T., Salguero-Gómez, R., Quero, J.L., 2012. It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 367, 3062–75. https://doi.org/10.1098/rstb.2011.0323

Maldonado Burgos, E., 2015. Efectos de fuego en la cobertura vegetal y procesos ecohidrológicos de un pastizal semiárido en el centro de México.

Malek, E., McCurdy, G., Giles, B., 1999a. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999b. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments1. Malek, E., McCurdy, G. & Giles, B. Dew contribution to the annual water balances in semi-arid desert valleys. J. Arid Environ. 42, 71–80 (1999). 42, 71–80. https://doi.org/10.1006/jare.1999.0506

Malek, E., McCurdy, G., Giles, B., 1999c. Dew contribution to the annual water balances in semi-arid desert valleys. Journal of Arid Environments 42, 71–80.

Mastroberti, A.A., de Araujo Mariath, J.E., 2008. Development of mucilage cells of Araucaria angustifolia (Araucariaceae). Protoplasma 232, 233–245. https://doi.org/10.1007/s00709-007-0274-7

Matimati, I., Musil, C.F., Raitt, L., February, E., 2013. Non rainfall moisture interception by dwarf succulents and their relative abundance in an inland arid South African ecosystem. Ecohydrology 6, 818–825.

Mcculloh, K.A., Johnson, D.M., Meinzer, F.C., Woodruff, D.R., 2014. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species: The dynamic pipeline. Plant Cell Environ 37, 1171–1183. https://doi.org/10.1111/pce.12225

Medina-Roldán, E., Arredondo, J.T., Huber-Sannwald, E., Chapa-Vargas, L., Olalde-Portugal, V., 2008. Grazing effects on fungal root symbionts and carbon and nitrogen storage in a shortgrass steppe in Central Mexico. Journal of Arid Environments 72, 546–556. https://doi.org/10.1016/J.JARIDENV.2007.07.005

Medina-Roldán, E., Huber-Sannwald, E., Arredondo, J.T., 2013. Plant phenotypic functional composition effects on soil processes in a semiarid grassland. Soil Biology and Biochemistry 66, 1–9. https://doi.org/10.1016/j.soilbio.2013.06.011

Medina-Roldán, E., Moreno, J.T.A., Moya, E.G., Martínez, F.M.H., 2007. Soil water content dynamics along a range condition gradient in a shortgrass steppe. Rangeland Ecology and Management 60, 79–87. https://doi.org/10.2111/05-219R2.1

Milburn, J.A., 1966. The conduction of sap: 1. water conduction and cavitation in water stressed leaves 34–42.

Monson, R.K., Moore, B. d., Ku, M.S.B., Edwards, G.E., 1986. Co-function of C3-and C4-photosynthetic pathways in C3, C4 and C3-C4 intermediate Flaveria species. Planta 168, 493–502. https://doi.org/10.1007/BF00392268

Moro, M.J., Were,  a., Villagarcía, L., Cantón, Y., Domingo, F., 2007. Dew measurement by Eddy covariance and wetness sensor in a semiarid ecosystem of SE Spain. Journal of Hydrology 335, 295–302. https://doi.org/10.1016/j.jhydrol.2006.11.019

Morse, S.R., 1990. Water balance in Hemizonia luzulifolia: the role of extracellular polysaccharides. Plant, Cell & Environment 13, 39–48.

Munné-Bosch, S., Alegre, L., 1999. Role of dew on the recovery of water-stressed Melissa officinalis L. plants. Journal of Plant Physiology 154, 759–766.

Nguyen, H.T., Meir, P., Wolfe, J., Mencuccini, M., Ball, M.C., 2017. Plumbing the depths: extracellular water storage in specialized leaf structures and its functional expression in a three-domain pressure–volume relationship. Plant, cell & environment 40, 1021–1038.

Nippert, J.B., Knapp, A.K., 2007. Linking water uptake with rooting patterns in grassland species. Oecologia 153, 261–272. https://doi.org/10.1007/s00442-007-0745-8

Nobel, P.S., Jordan, P.W., 1983. Transpiration Stream of Desert Species: Resistances and Capacitances for a $C_3$, a $C_4$, and a CAM Plant. J Exp Bot 34, 1379–1391. https://doi.org/10.1093/jxb/34.10.1379

Oparka, K.J., 1994. The use of fluorescent probes for studies of living plant cells. Plant cell biology, a practical approach.

Pan, Y., Wang, X., Zhang, Y., 2010. Dew formation characteristics in a revegetation-stabilized desert ecosystem in Shapotou area , Northern China. Journal of Hydrology 387, 265–272. https://doi.org/10.1016/j.jhydrol.2010.04.016

Pan, Y.X., Wang, X.P., 2014. Effects of shrub species and microhabitats on dew formation in a revegetation-stabilized desert ecosystem in Shapotou, northern China. Journal of Arid Land 6, 389–399. https://doi.org/10.1007/s40333-014-0008-6

Peterson, P.M., Giraldo-Cañas, D., 2011. The species of Muhlenbergia (Poaceae: Chloridoideae) from Argentina. Caldasia 33, 21–54.

Pineda Martínez, L.F., 2009. Modelación numérica de la dispersión de material particulado atmosférico y regionalización climática en México.

Puigdefábregas, J., Sánchez, G., 1996. Vegetación dispersa y flujos de vertiente en clima semiárido, in: IV Reunión de Geomorfología. Universidade da Coruña.

Riederer, M., 2006. Thermodynamics of the water permeability of plant cuticles: characterization of the polar pathway. Journal of Experimental Botany 57, 2937–2942. https://doi.org/10.1093/jxb/erl053

Ritter, F., Berkelhammer, M., Beysens, D., 2018. Dew frequency across the US from a network of in situ radiometers. Hydrology and Earth System Sciences Discussions 1–35. https://doi.org/10.5194/hess-2018-450

Rossatto, D.R., da Silveira Lobo Sternberg, L., Franco, A.C., 2013. The partitioning of water uptake between growth forms in a Neotropical savanna: do herbs exploit a third water source niche?: Herbs explore a third water uptake niche in Neotropical savannas. Plant Biology 15, 84–92. https://doi.org/10.1111/j.1438-8677.2012.00618.x

Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 2013. Isotopic Patterns in Modern Global Precipitation, in: Swart, P.K., Lohmann, K.C., Mckenzie, J., Savin, S. (Eds.), Geophysical Monograph Series. American Geophysical Union, Washington, D. C., pp. 1–36. https://doi.org/10.1029/GM078p0001

Rzedowski, J., 2007. An Ecological and Phytogeographical Analysis of the Grasslands of Mexico. Taxon 24, 67–80.

Sala, O.E., Lauenroth, W.K., Reid, C.P.P., 1982. WATER RELATIONS: A NEW DIMENSION FOR NICHE. Journal of Applied Ecology 19, 647–657.

Santacruz, G.A.A., Moya, E.G., Gonzalez, C.V., Flores, J.L.F., 1996. Importancia de los elementos climáticos en la variación florística temporal de pastizales semidesérticos. Acta Botánica Mexicana 65–81.

Scherm, H., van Bruggen, A.H.C., 1993. Sensitivity of simulated dew duration to meteorological variations in different climatic regions of California. Agricultural and Forest Meteorology 66, 229–245. https://doi.org/10.1016/0168-1923(93)90073-Q

Schonherr, J., 2006. Characterization of aqueous pores in plant cuticles and permeation of ionic solutes. Journal of Experimental Botany 57, 2471–2491. https://doi.org/10.1093/jxb/erj217

Schreiber, L., Skrabs, M., Hartmann, K., Diamantopoulos, P., Simanova, E., Santrucek, J., 2001. Effect of humidity on cuticular water permeability of isolated cuticular membranes and leaf disks. Planta 214, 274–282. https://doi.org/10.1007/s004250100615

Sharma, M L, 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331.

Sharma, M. L., 1976. Contribution of dew in the hydrologic balance of a semi-arid grassland. Agricultural Meteorology 17, 321–331. https://doi.org/10.1016/0002-1571(76)90086-8

Silletti, A.M., Knapp, A.K., Blair, J.M., 2004. Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability. Canadian Journal of Botany 82, 450–460. https://doi.org/10.1139/b04-016

Simonin, K.A., Santiago, L.S., Dawson, T.E., 2009. Fog interception by Sequoia sempervirens (D. Don) crowns decouples physiology from soil water deficit. Plant, Cell & Environment 32, 882–892. https://doi.org/10.1111/j.1365-3040.2009.01967.x

Steppe, K., Vandegehuchte, M.W., Van de Wal, B.A., Hoste, P., Guyot, A., Lovelock, C.E., Lockington, D.A., 2018. Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove Avicennia marina. Tree physiology 38, 979–991.

Suárez, A.G., Gloser, J., 1982. Time course of foliar absorption of water inPanicum andPaspalum. Biol Plant 24, 226–230. https://doi.org/10.1007/BF02883669

Tian, C., Wang, L., Kaseke, K.F., Bird, B.W., 2018. Stable isotope compositions (δ2H, δ18O and δ17O) of rainfall and snowfall in the central United States. Sci Rep 8, 6712. https://doi.org/10.1038/s41598-018-25102-7

Tuller, S.E., Chilton, R., 1973. The role of dew in the seasonal moisture balance of a summer-dry climate. Agricultural Meteorology 11, 135–142. https://doi.org/10.1016/0002-1571(73)90057-5

Tyree, M.T., Cruiziat, P., Benis, M., LoGullo, M.A., Salleo, S., 1981. The kinetics of rehydration of detached sunflower leaves from different initial water deficits. Plant, Cell & Environment 4, 309–317.

Uclés, O., Villagarcía, L., Moro, M.J., Canton, Y., Domingo, F., 2014. Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. Hydrological Processes 28, 2271–2280. https://doi.org/10.1002/hyp.9780

Van Gardingen, P.R., Grace, J., Jeffree, C.E., 1991. Abrasive damage by wind to the needle surfaces of Picea sitchensis (Bong.) Carr. and Pinus sylvestris L. Plant, Cell & Environment 14, 185–193.

Veste, M., Heusinkveld, B.G., Berkowicz, S.M., Breckle, S.-W., Littmann, T., Jacobs, A.F.G., 2008. Dew formation and activity of biological soil crusts, in: Arid Dune Ecosystems. Springer, pp. 305–318.

Vuollekoski, H., Vogt, M., Sinclair, V.A., Duplissy, J., Järvinen, H., Kyrö, E.-M., Makkonen, R., Petäjä, T., Prisle, N.L., Räisänen, P., 2015. Estimates of global dew collection potential on artificial surfaces.

Wang, C., Cen, Y., Liu, M., Bowler, P., 2017. Formation and influencing factors of dew in sparse elm woods and grassland in a semi-arid area. Acta Ecologica Sinica 37, 125–132. https://doi.org/10.1016/j.chnaes.2017.06.004

Weatherley, P.E., 1963. The pathway of water movement across the root cortex and leaf mesophyll of transpiring plants. The water relations of plants 85–100.

Westbeld, A., Klemm, O., Grießbaum, F., Sträter, E., Larrain, H., Osses, P., Cereceda, P., 2009. Fog deposition to a Tillandsia carpet in the Atacama Desert, in: Annales Geophysicae: Atmospheres, Hydrospheres and Space Sciences. p. 3571.

Williams, D.G., Ehleringer, J.R., 2000. Intra-and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecological Monographs 70, 517–537.

Wu, H., Li, X.-Y., Li, J., Jiang, Z., Chen, H., Ma, Y., Huang, Y., 2016. Differential soil moisture pulse uptake by coexisting plants in an alpine Achnatherum splendens grassland community. Environ Earth Sci 75, 914. https://doi.org/10.1007/s12665-016-5694-2

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2013. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Xiao, H., Meissner, R., Seeger, J., Rupp, H., Borg, H., 2009. Effect of vegetation type and growth stage on dewfall, determined with high precision weighing lysimeters at a site in northern Germany. Journal of Hydrology 377, 43–49. https://doi.org/10.1016/j.jhydrol.2009.08.006

Yamanaka, T., Tsujimura, M., Oyunbaatar, D., Davaa, G., 2007. Isotopic variation of precipitation over eastern Mongolia and its implication for the atmospheric water cycle. Journal of Hydrology 333, 21–34. https://doi.org/10.1016/j.jhydrol.2006.07.022

Yang, Y., Fu, B., 2017. Soil water migration in the unsaturated zone of semiarid region in China from isotope evidence. Hydrology and Earth System Sciences 21, 1757–1767.

Yates, D., Hutley, L., 1995. Foliar Uptake of Water by Wet Leaves of Sloanea woollsii, an Australian Subtropical Rainforest Tree. Aust. J. Bot. 43, 157. https://doi.org/10.1071/BT9950157

Ye, Y., Zhou, K., Song, L., Jin, J., Peng, S., 2007. Dew amounts and its correlations with meteorological factors in urban landscapes of Guangzhou, China. Atmospheric Research 86, 21–29. https://doi.org/10.1016/j.atmosres.2007.03.001

Zangvil, A., 1996. Six years of dew observations in the Negev Desert, Israel. Journal of Arid Environments 32, 361–371. https://doi.org/10.1006/jare.1996.0030

Zhao, Y., Wang, L., 2018. Plant Water Use Strategy in Response to Spatial and Temporal Variation in Precipitation Patterns in China: A Stable Isotope Analysis. Forests 9, 123. https://doi.org/10.3390/f9030123

Zhu, L., Wang, Z.H., Mao, G.L., Zheng, S.X., Xu, X., 2014. Water uptake from different soil depths for halophytic shrubs grown in Northern area of Ningxia plain (China) in contrasted water regimes. Journal of Plant Interactions 9, 26–34. https://doi.org/10.1080/17429145.2012.751139

Zwieniecki, M.A., Brodribb, T.J., Holbrook, N.M., 2007. Hydraulic design of leaves: insights from rehydration kinetics. Plant Cell Environ 30, 910–921. https://doi.org/10.1111/j.1365-3040.2007.001681.x

# Supplementary

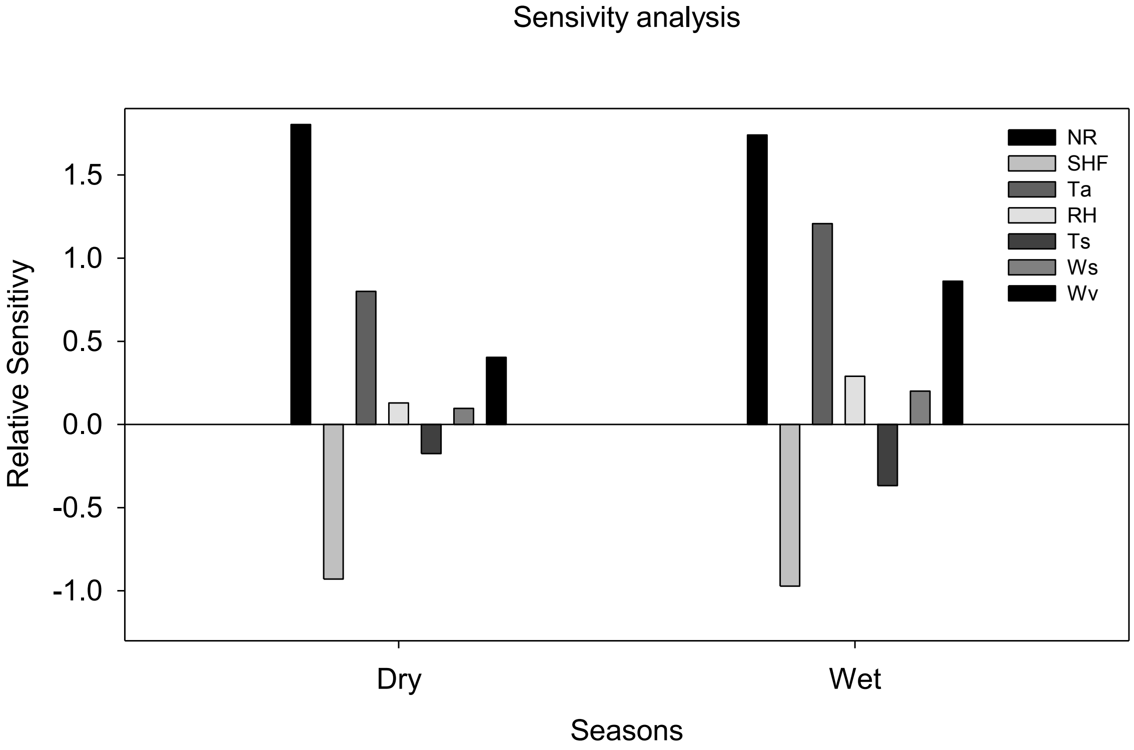
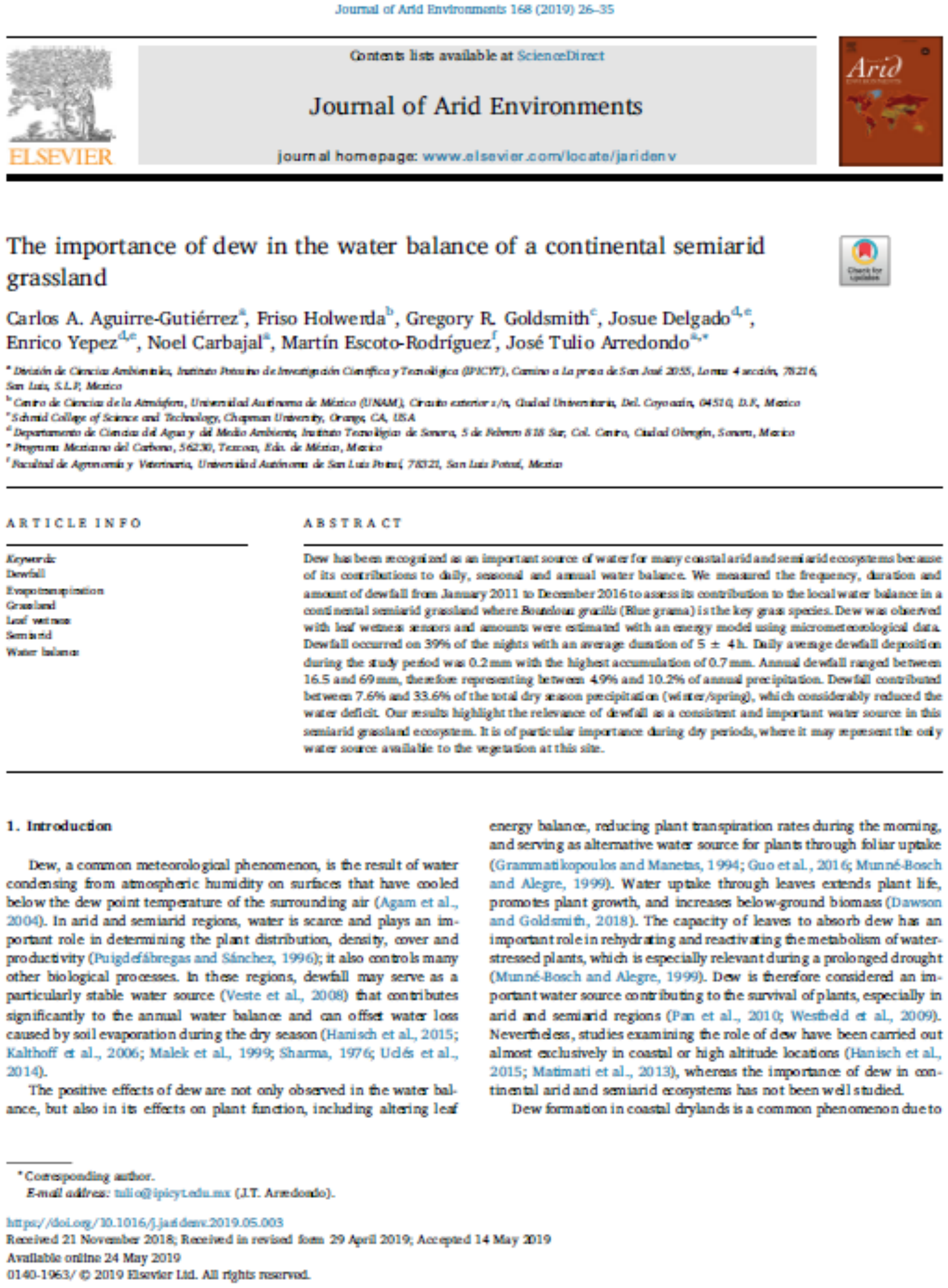


Figure S1.- Relativity sensitivity $S_i$ of the energy model for dew amount to Net Radiation (NR), Soil Heat Flux (SHF), Air Temperature ($T_a$), Relativity Humidity (RH), Soil temperature ($T_s$), wind speed ($w_s$) and water vapor ($w_v$), split in two seasons (Dry and Wet) for the years of the study.



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# The importance of dew in the water balance of a continental semiarid grassland

Carlos A. Aguirre-Gutiérrez[a], Friso Holwerda[b], Gregory R. Goldsmith[c], Josue Delgado[d,e], Enrico Yepez[d,e], Noel Carbajal[a], Martín Escoto-Rodríguez[f], José Tulio Arredondo[a,*]

[a] *División de Ciencias Ambientales, Instituto Potosino de Investigación Científica y Tecnológica (IPICYT), Camino a la presa de San José 2055, Lomas 4 sección, 78216, San Luis, S.L.P, Mexico*
[b] *Centro de Ciencias de la Atmósfera, Universidad Autónoma de México (UNAM), Circuito exterior s/n, Ciudad Universitaria, Del. Coyoacán, 04510, D.F., Mexico*
[c] *Schmid College of Science and Technology, Chapman University, Orange, CA, USA*
[d] *Departamento de Ciencias del Agua y del Medio Ambiente, Instituto Tecnológico de Sonora, 5 de Febrero 818 Sur, Col. Centro, Ciudad Obregón, Sonora, Mexico*
[e] *Programa Mexicano del Carbono, 56230, Texcoco, Edo. de México, Mexico*
[f] *Facultad de Agronomía y Veterinaria, Universidad Autónoma de San Luis Potosí, 78321, San Luis Potosí, Mexico*

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ABSTRACT

Dew has been recognized as an important source of water for many coastal arid and semiarid ecosystems because of its contributions to daily, seasonal and annual water balance. We measured the frequency, duration and amount of dewfall from January 2011 to December 2016 to assess its contribution to the local water balance in a continental semiarid grassland where *Bouteloua gracilis* (Blue grama) is the key grass species. Dew was observed with leaf wetness sensors and amounts were estimated with an energy model using micrometeorological data. Dewfall occurred on 39% of the nights with an average duration of 5 ± 4 h. Daily average dewfall deposition during the study period was 0.2 mm with the highest accumulation of 0.7 mm. Annual dewfall ranged between 16.5 and 69 mm, therefore representing between 4.9% and 10.2% of annual precipitation. Dewfall contributed between 7.6% and 33.6% of the total dry season precipitation (winter/spring), which considerably reduced the water deficit. Our results highlight the relevance of dewfall as a consistent and important water source in this semiarid grassland ecosystem. It is of particular importance during dry periods, where it may represent the only water source available to the vegetation at this site.

## 1. Introduction

Dew, a common meteorological phenomenon, is the result of water condensing from atmospheric humidity on surfaces that have cooled below the dew point temperature of the surrounding air (Agam et al., 2004). In arid and semiarid regions, water is scarce and plays an important role in determining the plant distribution, density, cover and productivity (Puigdefábregas and Sánchez, 1996); it also controls many other biological processes. In these regions, dewfall may serve as a particularly stable water source (Veste et al., 2008) that contributes significantly to the annual water balance and can offset water loss caused by soil evaporation during the dry season (Hanisch et al., 2015; Kalthoff et al., 2006; Malek et al., 1999; Sharma, 1976; Uclés et al., 2014).

The positive effects of dew are not only observed in the water balance, but also in its effects on plant function, including altering leaf energy balance, reducing plant transpiration rates during the morning, and serving as alternative water source for plants through foliar uptake (Grammatikopoulos and Manetas, 1994; Guo et al., 2016; Munné-Bosch and Alegre, 1999). Water uptake through leaves extends plant life, promotes plant growth, and increases below-ground biomass (Dawson and Goldsmith, 2018). The capacity of leaves to absorb dew has an important role in rehydrating and reactivating the metabolism of water-stressed plants, which is especially relevant during a prolonged drought (Munné-Bosch and Alegre, 1999). Dew is therefore considered an important water source contributing to the survival of plants, especially in arid and semiarid regions (Pan et al., 2010; Westbeld et al., 2009). Nevertheless, studies examining the role of dew have been carried out almost exclusively in coastal or high altitude locations (Hanisch et al., 2015; Matimati et al., 2013), whereas the importance of dew in continental arid and semiarid ecosystems has not been well studied.

Dew formation in coastal drylands is a common phenomenon due to

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[*] Corresponding author.
*E-mail address:* tulio@ipicyt.edu.mx (J.T. Arredondo).

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Figure S2.- Scientific paper published in the Journal of Arid Environments "The importance of dew in the water balance of a continental semiarid grassland" based on my findings from the first chapter of my thesis.