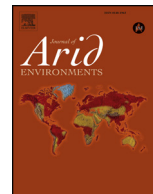




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Nurse shrubs can receive water stored in the parenchyma of their facilitated columnar cacti

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ABSTRACT

In facilitative interactions, facilitated plants gain a benefit from growing associated to a nurse plant, without damaging the nurse. The persistence of these positive interactions or their shift to competition might depend on whether the nurse shrub also gains some benefit from the association. We hypothesized that nurse shrubs can receive water stored in the parenchyma of their facilitated *Neobuxbaumia tetetzo* once the cactus becomes an adult. We injected deuterium-enriched water into the water storage tissues of *N. tetetzo* adults, and sampled the xylem water of the nurse *Mimosa luisana* plant in the shared vegetation patch before and after the injection of the tracer. We also sampled spatial-control individuals of *M. luisana* outside the vegetation patch. We found a significant enrichment in deuterium concentration in the xylem water of the associated *M. luisana* but not in individuals outside the patch. This suggests that in semiarid environments, nurse plants can benefit from growing associated to succulent columnar cacti by gaining water transferred from their storage tissues during dry periods, potentially enhancing persistence of facilitative interactions.

1. Introduction

Plant facilitation is a determinant ecological process structuring plant communities in stressful environments (Callaway and Walker, 1997; Callaway, 2007; He et al., 2013). Under stressful conditions, an established plant (nurse) can induce micro-environmental changes enhancing the recruitment of other species under its canopy (facilitated), without resulting in a fitness decrease for the nurse (Callaway, 2007). This process is dynamic along the ontogeny of the plants, as positive interactions may shift to competition when the facilitated seedling becomes adult (Callaway and Walker, 1997; Miriti, 2006; Schiffers and Tielbörger, 2006; Armas and Pugnaire, 2009). However, some facilitative interactions can persist due to a minimization of competition (Valiente-Banuet and Verdú, 2008; Pausas and Verdú, 2010), or when the nurse plant also gains a benefit from the association (Pugnaire et al., 1996; Sortibrán et al., 2014; Tirado et al. 2015). Resource and nutrient transfer between plants might be an overlooked mechanism enhancing plant facilitative interactions (Montesinos-Navarro et al. 2016, 2017,

2018). Resource transfer from the nurse plants can enhance the performance and survival of facilitated seedlings, thereby potentially structuring plant communities (Simard et al., 1997; Dickie et al., 2002; Teste et al., 2009; van der Heijden and Horton, 2009; Booth and Hoeksema, 2010). However, whether facilitated plants can also transfer resources to their nurse plant has been largely unexplored.

In dryland ecosystems, succulent plants are well adapted to tolerate drought stress due to their ability to accumulate water in their parenchyma (Nobel, 2003). However, when they are seedlings they show a reduced capacity to deal with severe water stress, and their establishment depends on the stress-ameliorated conditions present under the canopy of a nurse plant, resulting in a spatial association under the canopy of the nurse (Valiente-Banuet et al., 1991; Valiente-Banuet and Verdú, 2007). Once the succulent plants become adult, interplant water transfer could be an important resource for coexisting plants, especially in ecosystems where succulent columnar cacti are dominant. Other succulent life-forms such as globose and barrel cacti are also present in these systems, and it is currently uncertain whether different succulent

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physiognomies can affect the dynamics of interplant water transfer. Different mechanisms have been described to underlie water transfer among coexisting plants, such as hydraulic redistribution by roots (Dawson, 1993; Prieto et al., 2012), and/or plant-plant water transfer mediated by mycorrhizal hyphal connections (Egerton-Warburton et al., 2007; Plamboeck et al., 2007; Warren et al., 2008). However, as far as we know, it has not been previously evaluated whether interplant water transfer can occur from the parenchyma of columnar cacti to neighboring plants.

Soil water availability can change dramatically over short time intervals in dryland ecosystems, as it depends on the occurrence of irregular rainfall pulses. Sometimes, plants cannot respond quickly enough (i.e. by producing new leaves, shoots or roots) to match the narrow window of water availability, so the storage and redistribution of this resource can have an adaptive value (Chapin et al., 1990). Interplant water transfer could improve the water status of the receiving plants involved in facilitative interactions, especially over drought periods.

The Tehuacan valley is a semiarid area that holds one of the highest densities of columnar cacti in the world (Arriaga et al., 2000). One of them is *Neobuxbaumia tetetzo*, a dominant species in this area which despite its capacity to store water in its parenchymal tissues (Nobel, 2003), depends on the micro-environment generated by the legume *Mimosa luisana* to establish (over 70% of *N. tetetzo* seedlings occur under *M. luisana* shrubs) (Valiente-Banuet et al., 1991; Valiente-Banuet and Verdú, 2007). In this study, we hypothesize that water can be transferred from the storage parenchyma of adult *Neobuxbaumia tetetzo* individuals to their nurse *M. luisana* plants. Our study aims to shed light into a potential mechanism by which nurse plants could benefit from the columnar cacti that they originally facilitated, thus contributing to a better understanding of the processes promoting facilitative plant interactions in drylands.

2. Material and methods

2.1. Study area

The experiment was conducted in a continental desert at the bottom of the Zapotitlán basin (18°21' N, 97°28' W; 1450 masl) within the Tehuacán Valley (Puebla, Mexico). The mean annual rainfall in the study site is 380 mm concentrated during the summer (June–August), and the annual mean temperature is 21 °C, with rare frosts (García, 1998). There is low environmental humidity overall during the dry season (10–20% relative humidity), and a minimum temperature of 11.8 °C, which prevents reaching the dewpoint. The lack of precipitations for several months before the experiment was performed and also that February and March are the driest months of the year (García, 1998), result in an even more unlikely availability of atmospheric water vapor for plants during the experiment. The study site is a xeric shrubland dominated by the columnar cactus *Neobuxbaumia tetetzo* with densities of 1200 individuals ha⁻¹ (> 1 m tall), and the shrub species *Mimosa luisana* with densities of 2400 individuals ha⁻¹ (Flores-Martínez et al., 1998) (Fig. 1). There are also other shrub species in the community such as *Mascagnia seleriana*, *Ipomoea arborescens*, *Aeschynomene compacta*, *Caesalpinia melanadenia*, *Calliandra eryophylla*, *Zapoteca formosa*, *Senna wislizenii*, *Agave marmorata*, *Agave macroacantha* and *Jatropha neopauciflora* (Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 2000). Most of the plant species in this community (97%) recruit under nurse plants, with *Mimosa luisana* being one of the few species that are able to recruit on bare ground (Valiente-Banuet and Verdú, 2007). This results in a patchy vegetation structure with plants usually clumped under the canopy of a single adult individual of *M. luisana*, so that vegetation patches have a relatively small size (1–5 m²), mainly determined by the canopy of the *M. luisana* individual (Fig. 2), with usually 7–8 species per patch and 1–2 individuals per species (Table 1). The *M. luisana* shrub usually has the greatest biomass, and is the tallest plant of the patch, apart from the columnar cacti, so that the

shade of other species rarely affects its canopy (Fig. 2). When the originally facilitated seedlings become adults, the interaction persists as a facilitative interaction (Valiente-Banuet and Verdú, 2008).

2.2. Experimental design (temporal and spatial controls)

In a field experiment, we used water artificially enriched with the heavy stable isotope of hydrogen (deuterium: ²H₂O) as a tracer. We tracked the transfer of the labelled-water injected into nine individuals of *N. tetetzo* to each of their nine nurse plants (i.e. the *M. luisana* individual growing in the same vegetation patch). Although the heavy stable isotope of hydrogen (i.e. deuterium, ²H) also occurs in nature, its concentration is very low (Dawson et al. 2002), especially compared to the amount of ²H introduced as a tracer (see section: *N. tetetzo* labelling). Nevertheless, we accounted for the natural abundance of deuterium by measuring the background isotopic composition of xylem water in each of the studied *M. luisana* plants before the application of the tracer. We injected deuterium-labelled water into the parenchyma of the adult individuals of *N. tetetzo*, and measured 3 weeks later the isotopic composition of xylem water in their *M. luisana* nurses. In all cases, there was less than 1 m distance between the *N. tetetzo* and its *M. luisana* nurse. We considered “treated” the xylem water samples of *M. luisana* individuals growing in the same vegetation patch as the labelled *N. tetetzo*, and sampled them 3 weeks after the application of the tracer. On the contrary, we considered “control” those xylem water samples collected previously from the same *M. luisana* individuals just before the application of the tracer to the system (temporal control). In order to assess whether water can be transferred from the labelled *N. tetetzo* individuals to the *M. luisana* plants, we compared the isotopic composition of the xylem water of the “treated” and “control” *M. luisana* samples.

As the stem water of *M. luisana* likely experienced evaporative isotopic fractionation and thus a natural enrichment in the heavy isotopes (H and O) during the 3 weeks elapsed between sampling dates (Allison et al., 1983), we confirmed our results using also spatial controls. Thus, simultaneously to the collection of the “treated” *M. luisana* samples, we also sampled the xylem water of nine neighboring *M. luisana* plants growing in different vegetation patches located 5–10 m apart from each target patch, in a paired design (spatial control). These spatial control samples must have experienced a similar natural enrichment in the heavy isotopes due to the 3 weeks of evaporation, but not the artificial enrichment in deuterium caused by the labelled-water transfer from the *N. tetetzo*. Finally, we confirmed whether the enrichment due to evaporative isotopic fractionation is similar between the “treated” and spatial control samples by comparing their oxygen isotopic composition (non-labelled element of the tracer water). We expect similar stem water $\delta^{18}\text{O}$ values between the “treated” and spatial control samples because evaporative isotopic fractionation should be very similar in both of them. However, a different stem water $\delta^2\text{H}$ (labelled element of the tracer water) when the evaporative isotopic fractionation is similar, would imply that water transfer has also taken place. Therefore, a higher value of $\delta^2\text{H}$ in “treated” samples compared to spatial controls cannot be attributed to differences in evaporative isotopic fractionation between plants when there are no differences in $\delta^{18}\text{O}$ between “treated” and spatial control samples. Adult individuals of *N. tetetzo* (up to 5 m tall) have an average horizontal root spread of 4 m (Valiente-Banuet et al., 1991), therefore the target *N. tetetzo* individuals will be more prone to interact with the *M. luisana* plant growing within their own vegetation patch (1–5 m²) than with plants in other patches. We conducted the experiment in March 2014, at the end of the dry season, when the decreased turgidity of *N. tetetzo* plants allowed the injection of deuterium-enriched tracer water into the parenchyma. All the plants used in this study were located within a relatively flat area of 675 m².



Fig. 1. Study area in the Tehuacan Valley. A semiarid area that holds one of the highest densities of columnar cacti in the world, with densities of 1200 individuals ha^{-1} of the columnar cactus *Neobuxbaumia tetetzo* (> 1 m tall).

2.3. *N. tetetzo* labelling

Labelling of the target *N. tetetzo* plants was performed an hour before the sunset, in order to avoid the hours of the day with high evapotranspiration rates. We injected 10 ml of deuterium oxide, with a concentration of deuterium of 99.9%, into the internal parenchyma tissue of the columnar cacti. Specifically, we injected it in a depression between ribs, getting into the water-storage parenchyma, and approximately one meter above the base of each of the nine selected *N. tetetzo* plants. The presence of cortical bundles in Cactaceae allows

rapid internal tracer water redistribution across the thick cortex (Tissue et al., 1991; Mauseth, 2006; Nobel, 2006).

2.4. *M. luisana* stem sample collection

Prior to the experiment, we conducted preliminary measurements in *M. luisana* to assess the amount of xylem tissue required to perform isotopic analyses of xylem water (1 ml of water approximately). Based on these data, we collected approximately 5 g of xylem sample (10 cm \times 1 cm) from the base of one stem of each target *M. luisana*



Fig. 2. Vegetation patch with a nurse plant *Mimosa luisana* and an adult individual of the facilitated cactus *Neobuxbaumia tetetzo*.

Table 1

Indicators of the general structure of vegetation patches in the study area (N = 25).

Factors	Mean	SE
Richness	7.4	0.8
Abundance	11.5	1.7
Mean number of individuals per species	1.4	0.12
Shannon's H diversity index	1.7	0.1
Pielou's evenness index	0.9	0.01
Diameter of the patch (cm)	215.7	13.58
Minimum distance to the nurse (cm)	25.16	5.96

individual. To minimize the risk of stem water evaporation, we harvested stem samples early in the morning (7–9 h solar time), when evaporative demand is low. We placed stem samples in individual airtight sealed crystal tubes with silicone septa, kept them refrigerated in a field cooler during the sampling and maintained them frozen in the lab until distillation.

2.5. Xylem water extractions and stable isotope analyses

Both xylem water extractions and stable isotope analyses were conducted by the Stable Isotope Ratio Facility for Environmental Research (SIRFER) of the University of Utah. Xylem water was extracted by cryogenic vacuum distillation. The hydrogen and oxygen isotopic composition of the extracted xylem water samples was analyzed by isotope ratio infrared spectroscopy (IRIS) on a wavelength-scanned cavity ring-down spectrometer (WS-CRDS) model L1102-i water analyzer (Picarro, Sunnyvale, CA, USA). Activated charcoal was used for 48 h to remove any organic contamination from extracted samples. Samples were introduced into the vaporization chamber using a PAL autosampler (Leap Technologies, Carrboro, NC, USA). Each sample was analyzed with 4 replicate injections, and the reported data is an average of the third and fourth injection. Samples were analyzed against three lab internal reference waters, which have been calibrated against Vienna Standard Mean Ocean Water (VSMOW).

We expressed isotope values in δ -notation (per mill [‰]) following the definition of Coplen (2011) given in equation (1):

$$\delta^2\text{H (or } \delta^{18}\text{O)} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

Where R_{sample} is the ratio ($^2\text{H}/^1\text{H}$ or $^{18}\text{O}/^{16}\text{O}$) of the less abundant (heavy) to the more abundant (light) isotope in the water sample, and R_{standard} is the same ratio ($^2\text{H}/^1\text{H}$ or $^{18}\text{O}/^{16}\text{O}$) in standard reference water (VSMOW).

2.6. Data analysis

We tested whether deuterium enrichment in the nurse plants correlated with the size of the *N. tetetzo* and *M. luisana* individuals, or with the distance (measured in cm) between them in each patch. The deuterium enrichment was calculated as the difference between the “treated” minus the “control” xylem water $\delta^2\text{H}$ values of the *M. luisana* shrubs. The difference (i.e. deuterium enrichment) was calculated considering the temporal and spatial controls independently: (treated – spatial control) and (treated – temporal control). Each estimate of the deuterium enrichment represents a proxy of the amount of labelled-water transferred to the *M. luisana* plant. In order to assess whether the results were consistent using both types of controls, we tested for a correlation between (treated – spatial control) vs. (treated – temporal control). A significant correlation will show that the estimation of deuterium enrichment is similar when calculated based on the spatial and the temporal controls. The xylem water $\delta^2\text{H}$ values of the treated *M. luisana* shrubs (considering as background the $\delta^2\text{H}$ values of both temporal and spatial controls) were non-correlated with the plants' size or interplant distance (Table 2). Thus, we performed further analyses

Table 2

Correlations between *M. luisana* $\delta^2\text{H}$ -enrichment and patch characteristics.

	Temporal control		Spatial control	
	r	p-value	r	p-value
Distance (cm)	–0.16	0.69	0.41	0.31
<i>M. luisana</i> height (cm)	–0.37	0.33	–0.48	0.19
<i>N. tetetzo</i> height (cm)	–0.15	0.72	0.19	0.65

Pearson's correlations between the increments in $\delta^2\text{H}$ -enrichment in the xylem water of treated *M. luisana* plants (considering the $\delta^2\text{H}$ of both temporal and spatial), the height of the donor and receiver plants and the distance between them. Increment in xylem water $\delta^2\text{H}$ -enrichment of the treated *M. luisana* plants: ($\delta^2\text{H}_{\text{treated}} - \delta^2\text{H}_{\text{control}}$).

without considering these factors as covariates.

We tested for differences in xylem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values between the treated *M. luisana* individuals and their temporal and spatial controls, respectively. For all comparisons we used a two sample weighted Welch *t*-test, which allows pairing control with treated samples and weighting each pair by a correction factor (e.g. to account for potential incomplete extraction of the samples in the control plants). During the process of xylem water extraction, the water extracted through the cryogenic vacuum suffers a different degree of fractionation as the extraction progresses, and therefore incomplete extraction can affect the isotopic composition attributed to the sample processed. A measure for the degree of fractionation a sample was exposed to is deuterium excess (*d*), and thus it has been proposed to be used as a quality check for the cryogenic vacuum extraction (i.e. high values of *d* can indicate less complete water extraction from the xylem samples) (Beyer et al., 2016). In order to account for potential differences across samples in the process of water extraction from the xylem, we weighted each sample by this proxy of the quality of the distillation (xylem water extraction) for each individual sample as proposed by Beyer et al. (2016). This correction is suitable for measurements of natural abundance of $\delta^2\text{H}$ and $\delta^{18}\text{O}$, but can be misleading for samples in which $\delta^2\text{H}$ could have been artificially enhanced. Therefore, we only applied this correction to control samples. We calculated deuterium excess (*d*) for each xylem water sample using the relationship proposed by Dansgaard (1964):

$$d = \delta^2\text{H} - 8 \delta^{18}\text{O}$$

Deuterium excess (*d*) had negative values in every sample. As samples with lower *d* values (more negative) had a higher quality of water extraction, we weighted each sample by –1 times its value of *d* in the two-sample weighted Welch *t*-test. We performed the analyses using the “weights” package implemented in R version 3.0.3 (Pasek et al., 2016).

3. Results

As expected, evaporative isotopic fractionation during 3 weeks (i.e. time elapsed between sampling dates) resulted in a significant enrichment of the non-labelled element ($\delta^{18}\text{O}$) in the xylem water of the “treated” *M. luisana* plants compared to the temporal controls (Table 3). However, xylem water $\delta^{18}\text{O}$ values in spatial controls did not significantly differ from those observed in “treated” samples, indicating that both had experienced a similar natural evaporative fractionation (Table 3). Interestingly, despite the similar natural fractionation, the xylem water $\delta^2\text{H}$ values in the treated shrubs were significantly higher than the spatial control samples, indicating a transfer of deuterium-labelled water from the storage parenchyma of the facilitated columnar cactus *N. tetetzo* to the xylem of its nurse shrub *M. luisana* (Table 4). In addition, the xylem water $\delta^2\text{H}$ values in the treated shrubs were also significantly higher than temporal control samples.

Deuterium enrichment varied across vegetation patches. However,

Table 3

Two sample weighted Welch *t*-test testing for differences in xylem water $\delta^{18}\text{O}$ values between the treated *M. luisana* individuals and their temporal and spatial controls.

Pair-wise comparisons	Samle size (N)	Mean control (%)	Mean treated (%)	Estimate of the diference	SE of the difference	T statistic	p-value
Temporal control vs treated	9	-0.52	0.40	-0.92	0.22	-6.09	< 0.001
Spatial control vs treated	9	1.10	0.32	0.78	0.19	9.99	0.99

some treated *M. luisana* plants showed relatively large enrichment in stem water $\delta^2\text{H}$ values (ranging from 8 to 21‰), taking either the temporal or spatial controls as background references (i.e. patches A, B and C in Table S1). Furthermore, the estimation of deuterium enrichment was similar when measured based on the spatial and the temporal controls, as shown by a positive correlation between them ($(\delta^2\text{H}_{\text{treated}} - \delta^2\text{H}_{\text{spatial control}})$ vs. $(\delta^2\text{H}_{\text{treated}} - \delta^2\text{H}_{\text{temporal control}})$; $r = 0.77$, $p = 0.01$, $R^2 = 0.60$).

4. Discussion

Overall, our results show that stem water $\delta^2\text{H}$ in the treated *M. luisana* individuals was higher than in the temporal and spatial controls respectively, indicating that deuterium-labelled water can be transferred from the water-storage tissues of adult individuals of the columnar cactus *N. tetetzo* to the xylem of the nurse plant that originally facilitated them. Stem water $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values were higher in the treated *M. luisana* plants than in the temporal controls, as expected based on the intense evaporative isotopic fractionation that is likely to occur in this dryland environment (Allison et al., 1983). However, treated *M. luisana* plants showed significantly higher xylem water $\delta^2\text{H}$ values (but similar $\delta^{18}\text{O}$) than their spatial controls (Tables 3 and 4) which cannot be attributable to the effect of evaporative isotopic fractionation, as this would have resulted in the enrichment of both elements ($\delta^2\text{H}$ and $\delta^{18}\text{O}$). In addition, a significant positive correlation between the two proxies used to estimate the amount of labelled-water transferred from the *N. tetetzo* plant to the *M. luisana* (i.e. differences in: (treated – spatial control) vs. (treated – temporal control)), shows that the amount of labelled-water transferred was similar when we estimate it using temporal and spatial control. This provides robustness to the estimates, and reinforces our results based on a consistency when either of the two types of control is used. The evidence for water transfer from the water storage tissue of the columnar cacti to the xylem water of the *M. luisana* plants highlights the potential for interplant water transfer that can affect the availability of this limited resource in this dryland ecosystem. However, further research is required to assess the magnitude of this inter-plant water transfer, and its implications for the fitness of the donor and receiver plants.

Some treated *M. luisana* plants showed relatively large enrichment in their xylem water $\delta^2\text{H}$ values (8–21‰ higher $\delta^2\text{H}$ values than control plants) despite the large potential for tracer dilution and/or loss in this open field system, which suggests that the amount of water transferred to some *M. luisana* plants might not be negligible. Mesocosm experiments have reported similar increases in the $\delta^2\text{H}$ values of xylem water in receiver plants after interplant transfer of deuterium-labelled tracer water (Egerton-Warburton et al., 2007).

In semiarid environments where rain is concentrated in a few stochastic events during the rainy season (García, 1998) the capacity of adult columnar cacti to take up and store large amounts of water in a

short period of time following a rainfall pulse (Nobel, 2003) can be especially relevant. Some studies have reported that the roots of desert succulents have properties that can reduce their water permeability through structural changes such as the development of intercellular lacunae and abscission of lateral fine roots (Nobel and Sanderson, 1984; Nobel and Huang, 1992; North and Nobel, 1992). However, these rectifying mechanisms cannot completely prevent water loss from roots to the surrounding dry soil in succulent plants (Nobel and Cui, 1992; Yoder and Nowak, 1999; Yu and D'Odorico, 2015a; Yu and Foster, 2016). In addition, water efflux from roots and their associated mycorrhizal hyphae might also result in benefits for the “leaky” plant, as it can be adaptive to maintain soil water potentials above the threshold at which nutrient diffusion stops (Matzner and Richards, 1996; Ryel et al., 2002; Egerton-Warburton et al., 2008). Soil remoistening by “leaky” roots and mycorrhizal hyphae also enhances organic matter decomposition and nutrient mineralization rates during dry periods, thus releasing nutrients that can thereafter be taken up by roots (Aanderud and Richards, 2009; Armas et al., 2012; Egerton-Warburton et al. 2008).

Actually, the movement of water between different soil layers via plant root systems (i.e. hydraulic redistribution) is a key mechanism underlying plant-plant interactions that allows understory species to take up the water lifted and released by the nurse plant (Dawson, 1993; Prieto et al., 2012, 2016). This process can result in facilitative, neutral or competitive net outcomes between plants, depending on the amount of water redistributed and asymmetric competition for this resource (Prieto et al., 2012). Regarding facilitative interactions, hydraulic redistribution can enhance seedling survival, growth and species coexistence (Callaway, 2007; Dawson, 1993; Prieto et al., 2011; Yu and D'Odorico, 2015b). Traditionally, hydraulic redistribution was considered a passive process driven by water potential gradients between roots and surrounding soil (Caldwell et al., 1998; Prieto et al., 2012), so it is largely unknown whether any potential control that plants could exert over the redistribution of water by roots might affect facilitative interactions. A better mechanistic understanding of the transfer of water stored in the succulent tissues of cacti towards neighboring plants during dry periods would be a promising contribution in this regard.

5. Conclusions

Although the benefits of facilitative interactions for nurse plants have been largely ignored in the literature, recent evidence suggest that nurses can also benefit from the interaction with their facilitated plants (Sortibrán et al., 2014). This study is, as far as we know, the first to identify interplant water transfer as a potential mechanism by which nurse plants could benefit from their facilitated plants. Improving our understanding of resources exchange between facilitated and nurse plants is essential for a realistic estimation of the relative cost and benefits to the associated species. Further experimental work on the

Table 4

Two sample weighted Welch *t*-test testing for differences in xylem water $\delta^2\text{H}$ values between the treated *M. luisana* individuals and their temporal and spatial controls.

Pair-wise comparisons	Sample size (N)	Mean control (%)	Mean treated (%)	Estimate of the diference	SE of the difference	T statistic	p-value
Temporal control vs treated	9	-59.19	-56.71	-2.47	0.76	-3.25	< 0.001
Spatial control vs treated	9	-58.75	-55.89	-2.85	0.72	-3.96	< 0.001

ecological implications of reciprocal benefits for plant survival and reproduction is required to make progress in the understanding of the evolution of facilitative interactions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2019.04.011>.

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