Geoecohydrological mechanisms couple soil and leaf water dynamics and facilitate species coexistence in shallow soils of a tropical semiarid mixed forest

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Summary

• Trees growing on shallow rocky soils must have exceptional adaptations when underlying weathered bedrock has no deep fractures for water storage. Under semiarid conditions, hydrology of shallow soils is expected to decouple from plant hydrology, as soils dry out as a result of rapid evaporation and competition for water increases between coexisting tree species.
• Gas exchange and plant–water relations were monitored for 15 months for Pinus cembroides and Quercus potosina tree species in a tropical semiarid forest growing on c. 20-cm-deep soils over impermeable volcanic bedrock.
• Soil and leaf water potential maintained a relatively constant offset throughout the year in spite of high intra-annual fluctuations reaching up to 5 MPa. Thus, hydrology of shallow soils did not decouple from hydrology of trees even in the driest period. A combination of redistribution mechanisms of water stored in weathered bedrock and hypodermic flow accessible to oak provided the source of water supply to shallow soils, where most of the actively growing roots occurred.
• This study demonstrates a unique geoecohydrological mechanism that maintains a tightly coupled hydrology between shallow rocky soils and trees, as well as species coexistence in this mixed forest, where oak facilitates water access to pine.

Introduction

Semiarid forests in North America extend from Mediterranean California and the southwestern United States (Linton et al., 1998) to central Mexico, all within tropical and subtropical latitudes. These regions share a long dry season during the year, while there is a seasonal shift in the months of precipitation at the transition from northern to southern latitudes (West et al., 2008). Mediterranean and northern subtropical regions have wet winters and dry summers, while southern subtropical and semiarid tropical regions have wet summers and dry winters; regions in mid-latitudes are influenced by both climate regimes (Thompson et al., 2009). Tree species forming forest ecosystems along this seasonal precipitation gradient exhibit several adaptations to acquire, use and store water, under each particular climate regime.

Plant adaptations for hydraulic control include isohydric or anisohydric stomatal control mechanisms that are directly coupled to soil water conditions (Tardieu & Simonneau, 1998; McDowell et al., 2008). Isohydric plants decrease stomatal conductance (Gs) in response to reductions in soil water potential (Ψsoil), while maintaining midday leaf water potential (Ψleaf) relatively constant. In anisohydric plants, midday Ψleaf decreases in response to declining Ψsoil; however, they maintain generally higher Gs for a given Ψsoil than isohydric plants (Barnes, 1986). These alternative mechanisms of controlling plant water relations have evolved in distinct habitat types, where anisohydric species occupy the ecologically driest sites (McDowell et al., 2008). Plants seem to have evolved these mechanisms to maximize water uptake from winter or summer (e.g. monsoon) rain pulses. Anisohydric species are better adapted to use winter precipitation and to withstand prolonged dry periods (Pretzsch et al., 2013). Isohydric species are better adapted to utilize more predictable rain pulses of summer monsoon (West et al., 2008). These stomatal mechanisms may occur concurrently with other adaptations, including root architecture, plant phenology, and/or mycorrhizal symbiosis to overcome drought conditions experienced by trees (Querejeta et al., 2012). Regional prevalence of a specific stomatal control mechanism is related to the predominance of either high-intensity or long-duration water deficits (Ryan, 2011). Thus, isohydric species cope better with intense dry spells, while anisohydric species cope better with long-lasting droughts (McDowell et al., 2008; West et al., 2008).
Other characteristics of semiarid forest ecosystems relate to root adaptations that allow trees to establish, grow, and prosper on shallow soils formed over bedrock, cemented horizons, or strongly developed argillic horizons that impede vertical water movement and restrict root growth (Andrews et al., 2005; Katra et al., 2008). Under these conditions, it has been shown that once shallow soils become dry, trees may switch water access and subsequently garner water from deep sources associated with weathered bedrock and rock fractures (Querejeta et al., 2007; Schwinning, 2008; Poot et al., 2012). Our current understanding of forests growing on shallow soils on top of fractured weathered rocky substrate is based on the idea that trees tend to be deeply rooted, with average rooting depths of 7.9 m (± 1.7 m) compared with 2.2 m (± 0.1 m) observed in trees growing in deep soils (Schenk & Jackson, 2002; Schenk, 2008). Shallow soil hydrology depends almost exclusively on rain periods to get recharge for plant access, while it remains decoupled from plant hydrology during dry periods (Schwinning, 2013). However, under circumstances where roots of a single plant experience steep water potential gradients between deep and shallow soils, water may be passively lifted by roots from deep rock fractures to shallow soils and thus temporarily increase soil water availability in shallow soils during dry periods (Dawson, 1993). This mechanism may reduce the decoupling of plant and soil water potential until this alternative water source becomes depleted as well (Bleby et al., 2010). In this specific case, where the rocky substrate is of volcanic origin and deep rock fractures remain sealed from previous volcanic events (Orozco et al., 2002; Tristán et al., 2009), it appears unlikely that shallow soils (15–30 cm) can be resupplied by water from deeper sources and thus function as a substantial and reliable source of water for trees throughout the year. Volcanic parent material usually has sealed fissures and low permeability (Ramos et al., 2007), and thus it does not seem conditioned for hydraulic lift mechanisms. We postulate that two fundamental ecohydrological processes in plant–water relations on shallow soils are still unclear: the short-term dynamic relationship between the hydrology of shallow soils and plant water status, specifically, the role of soils as an intermittent water source for trees during dry periods; and long-term species-specific adaptations (i.e. root distribution, physiological mechanisms) that permit key forest trees to survive and thrive on shallow soils.

Semiarid environments are highly heterogeneous in space and time, thus creating conditions for potential ecological niche differentiation, which may facilitate species coexistence in forests (Nishimura et al., 2003; Zavala et al., 2011; Liu et al., 2012). In highly resource-limited environments, coexisting plant species, often exhibit contrasting and/or complementary resource-use strategies allowing the spatial and temporal partitioning of resources (Schwinning & Ehleringer, 2001; Quesada et al., 2008). In mixed forests from semiarid climates, phenological mismatch allows species coexistence. For example, deciduous trees shed their leaves during the dry season, thereby reducing water demand and allowing evergreen trees temporal access to water (Tang & Ohsawa, 2002). Alternatively, spatial partitioning of soil resources is conferred, for instance, by selective horizontal and/or vertical placement of roots in the soil profile (Huston & Huston, 1994).

Central North Mexico represents one of the most drought-prone regions for semiarid forests along the north–south seasonal precipitation gradient (West et al., 2008). Therefore, this is an excellent location to study ecohydrological interactions among plant–water relations, soil moisture dynamics and root distribution patterns, which together may elucidate potential complementary short- and long-term plant adaptation strategies of coexisting tree species as an integrated response to recurrent severe or extreme droughts. Extreme ecohydrometeorological conditions in tropical semiarid latitudes in Central North Mexico limit the development of forest ecosystems seen elsewhere in semiarid regions around the world (Grünzeig et al., 2003). These limiting conditions include extremely shallow soils (< 20 cm) on top of a shallow weathered fractured rock matrix (c. 70 cm below the surface) with impermeable bedrock underneath (Orozco et al., 2002; Tristán et al., 2009). Furthermore, low annual precipitation (c. 400 mm) with most rainfall (95% of total precipitation) occurring during summer narrows the opportunity for the development of temporal ecological niches (Perez et al., 2014) and increases the likelihood for coexisting tree species to strongly compete for water. Hence, these particular forest ecosystems provide few spatiotemporal niches for complementary root distribution and/or water acquisition, thereby challenging not only short-term plant resilience after a drought event but also long-term plant survival and coexistence.

This study addresses two principal questions: how will extreme ecohydrometeorological conditions influence the temporal dynamics of plant and soil water relations of semiarid forest trees growing on shallow, weathered, fractured rocks over impermeable bedrock; and considering extremely low spatial and temporal water availability, what short- and long-term adaptation mechanisms have two key forest tree species developed to survive and coexist? Shallow rocky substrate (< 0.7 m, below the surface) together with negligible winter rains (< 5%) seem insufficient to contribute to large water storage, and therefore there are few potential advantages for anisohydric strategies (Ryan, 2011). Also, long-lasting droughts (6–9 months; Breda et al., 2006) observed at the study site induce low soil water potentials and thereby do not favor isohydric strategies. Hence, considering these rather ambiguous controls of plant water relations for the tropical semiarid forest, we hypothesized (H3) that both deciduous Quercus potosina and evergreen Pinus cembroides tree species will not display strict anisohydric or isohydric mechanisms, but rather exhibit ‘hybrid’ adaptations that allow them to survive under extremely low $\Psi_{leaf}$ values during several months of drought. Considering predominantly shallow soils and long intense droughts, we hypothesized (H3) that the hydraulic dynamics of forest tree species should decouple from hydraulic conditions of shallow soils, in that soil and leaf water potentials diverge with drought progression. Considering the extreme water limitations (climatic and edaphic) in this forest ecosystem, it is expected (H3) that Q. potosina and P. cembroides display niche overlap and therefore strongly compete for soil water, with the
better competitor exhibiting higher $G_{sw}$ and $Ψ_{leaf}$ and lower water-use efficiency (WUE) during periods of soil water depletion.

Materials and Methods

Site characteristics

The study was carried out in a tropical semiarid mixed forest in ‘Sierra San Miguelito’, a volcanic mountain range in Central North Mexico (22°2.61’N, 11°7.53’W, Supporting Information, Fig. S1) at the southernmost extent of the Chihuahua desert. The climate is semiarid, with summer precipitation from June to September and with small winter rains in December and January (6.5% of annual total precipitation according to site climate records). For the last 40 yr, average annual rainfall ranges from 380 to 640 mm (average 480 mm), while average annual mean temperature ranges between 20 and 22°C (INEGI, 2002). The dominant native tree species are *Pinus cembroides* Zucc. and *Quercus potosina* Trel., which both form pure and mixed stands with little understory. The geology of the region is of volcanic origin formed by lava spills of Rhyolitic composition (Portezuelo Latite and San Miguelito Rhyolite), which contributed to the sealing of rock fractures (Orozco et al., 2002; Tristán et al., 2009). The topography of this mountain region is abrupt and irregular, thus representing ‘complex terrain’. The landscape is characterized by steep slopes (>30°) and elevation ranges between 1900 and 2870 m above sea level (masl). According to the World Reference Base for Soil Resources (WRB) classification system, the extremely shallow soils and fractured rocks of this area correspond to lithic Paralithic Leptosols (LPlip) (FAO, 2006). The average depth of the organic soil horizon ranges from 10 to 20 cm; soil organic matter accumulates in crevices and rock pockets (Perez et al., 2014) on top of a highly fragmented weathered rock matrix, which reaches maximum 70 cm depth.

The study was carried out along a 2-km-long transect running parallel to a watershed, where pine and oak trees are evenly distributed in mixed stands. We established 20 experimental plots in midslope position on steep north ($n=10$) and south ($n=10$) exposed slopes, which allowed us to examine potential differences in drought intensity. In each plot, we selected one pine and one oak tree with similar size characteristics within and among plots ($n=20$ per tree species). Within each plot, the two target trees had a minimum distance of 2 m. Monitoring of soil water potential and leaf physiological variables lasted from September 2010 to December 2011. Soil depth was determined by coring from the soil surface to the rock matrix. Two soil corings were carried out for each plot in both expositions ($n=20$).

Study species

*Pinus cembroides* is a small tree (average 4.2 m) with evergreen needles, while *Q. potosina* is a short statured (3 m) deciduous broadleaf tree. During the driest months, broadleaf oak usually sheds all the leaves (March–April, Perez et al., 2009), while evergreen pine sheds the oldest (3–4 yr old) needle cohort (Zavala & García, 1991). *Q. potosina* produces more litter with higher quality than pine (2820 ± 307 vs 1360 ± 128 kg ha$^{-1}$ yr$^{-1}$, Perez et al., 2012). These litter characteristics potentially contribute to improve topsoil moisture conditions in pure oak stands. For instance, greater litter production and accumulation under oak canopies reduce lateral runoff sevenfold and increase water-holding capacity by 16% compared with pine stands (Perez et al., 2014). Forest canopy characteristics also greatly influence rainfall redistribution through throughfall and stem flow (Perez et al., 2014). Little is known about root morphology and distribution of these two species; however, in general, *Quercus* species exhibit dimorphic roots, while *Pinus* species spread superficial roots mostly horizontally (Kutscher & Lichtenegger, 2002). Tree height, trunk diameter, and range of ages are indicated in Table 1 for each species and aspect.

Table 1 Number of trees per site and species included in the study ($n$), as well as mean and ranges (in parentheses) for tree diameter at breast height (DBH), age estimated based on tree ring growth, and total tree height of trees of *Pinus cembroides* and *Quercus potosina* at Sierra San Miguelito, San Luis Potosí, Mexico

<table>
<thead>
<tr>
<th>Aspect/species</th>
<th>$n$</th>
<th>DBH (cm)</th>
<th>Age (yr)</th>
<th>Tree height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>North pine</td>
<td>10</td>
<td>20.9 (11.6–32.6)</td>
<td>81 (77–87)</td>
<td>5.7 (3.8–7.5)</td>
</tr>
<tr>
<td>North oak</td>
<td>10</td>
<td>18.3 (14.8–30.7)</td>
<td>97 (87–111)</td>
<td>4.3 (3.1–5.5)</td>
</tr>
<tr>
<td>South pine</td>
<td>10</td>
<td>17.7 (10.2–24.2)</td>
<td>89 (49–135)</td>
<td>4.3 (2.6–6.8)</td>
</tr>
<tr>
<td>South oak</td>
<td>10</td>
<td>18.1 (13.4–23.7)</td>
<td>93 (78–107)</td>
<td>3.9 (1.9–6.5)</td>
</tr>
</tbody>
</table>

Water potential and gas exchange

We measured midday soil and leaf water potential ($Ψ_{soil}$ and $Ψ_{leaf}$ respectively) from 11 to 13 h at biweekly intervals from October 2010 to December 2011. We used psychrometric techniques and a dewpoint microvoltmeter HR-33 (Wescor Inc., South Logan, UT, USA) to determine soil (TSP-55; Wescor Inc.) and leaf water potential (C-52; Wescor Inc.). For $Ψ_{leaf}$, we harvested three to four leaf discs from healthy mature leaves exposed to sunlight and allowed 20 min for stabilization within C-52 chambers before readings. For soils, we inserted one soil psychrometer per tree at 12 cm depth within 100 cm from the tree trunk.

Leaf gas exchange was measured at biweekly intervals to obtain $G_{sw}$ (mol H$_2$O m$^{-2}$ s$^{-1}$) and WUE (µmol CO$_2$ (photosynthetic assimilation, $A$) mmol$^{-1}$ H$_2$O (transpiration, $E$); $A/E$) using a portable photosynthesis system LI-6400XT (Li-Cor, Inc., Lincoln, NE, USA) fitted to a coniferous chamber (conifer chamber 6400-05) and coupled to a CO$_2$ MIXER (6400-01 Mixer). For the measurements, CO$_2$ concentration of chamber air was set at nine levels to generate a photosynthesis response curve (800, 0, 100, 200, 300, 400, 500, 600, 700, 900 µmol mol$^{-1}$; each level lasting for 3 min). Leaf temperature and air relative humidity (RH) were maintained within 25 ± 2°C and 30% RH, respectively. For each gas exchange measurement, we introduced c. seven mature oak leaves or 20–25 pine needles (Brooks et al., 2002). Measurements occurred between 11:00 and 16:00 h on
clear sunny days to ensure a photosynthetic photon flux density (PPFD) of at least 1500 μmol m$^{-2}$ s$^{-1}$. Following these measurements, leaves were harvested to determine leaf areas (Leaf Area Meter Li-3000C; Li-Cor) to correct $A$ and $E$ calculations. Gas exchange was always measured on leaves and needles of the same individual pine and oak tree within each of four plots; plots were rotated each time to eventually include all plots for a similar number of measurements. Trees in plots of south- and north-exposed slopes were monitored on two consecutive days with similar weather conditions. Stomatal conductance and instantaneous WUE for each species and exposition were calculated for a CO$_2$ concentration of 385 μmol mol$^{-1}$. Progressing senescence in oak prevented us from monitoring leaf gas exchange between May and July 2011. To determine temporal changes in the percentage of canopy cover in trees, a digital photograph was taken monthly from the bottom of each plot; subsequently these images were analyzed with Gap Light Analyzer software v.2.0 (Frazer et al., 1999).

Data analysis

To compare ecophysiological water relation variables, we used a multifactorial repeated-measures ANOVA. The mixed model included, as classification factors, species with two levels (Q. potosina and P. cembroides, fixed effect), aspect with two levels (north and south, fixed effect) and time (sampling dates, random effect) with 40 levels (biweekly dates) for water relation variables and 12 levels (weekly dates) for gas exchange variables. Response variables included $\Psi_{\text{soil}}$ (MPa), $\Psi_{\text{leaf}}$ (MPa), instantaneous WUE (μmol CO$_2$ mmol$^{-1}$ H$_2$O), and $G_{\text{sw}}$ (mol H$_2$O m$^{-2}$ s$^{-1}$). Treatment means were compared using Tukey’s multiple range test, setting alpha = 0.05. Differences of soil depth with respect to exposition were analyzed using a one-way ANOVA followed by a Tukey’s post hoc mean comparison test. We ran type I regression analyses to examine the relationships between $\Psi_{\text{leaf}}$ and $\Psi_{\text{soil}}$, between WUE and both $G_{\text{sw}}$ and $\Psi_{\text{leaf}}$, and between canopy cover and $\Psi_{\text{soil}}$. Before statistical analyses, response variables were examined for normality using the Shapiro & Wilk test (Shapiro & Wilk, 1965). Analyses of physiological variables were carried out separately for wet and dry seasons with SAS v. 9.1.3 for Windows (SAS System, Cary, NC, USA 2002–2003) using a mixed model (PROC MIXED) for the repeated-measures analysis and a generalized linear model (PROC GLM) for the univariate analysis.

Results

Precipitation

During the monitoring months (October 2010–December 2011), rainfall was 35% lower with respect to the long-term annual average (Fig. S2, 270 mm vs 418 mm). In the year of study, an extreme drought occurred between October 2010 and May 2011 (4.6 mm during 9 months) followed by a period of rather low monsoon precipitation from June to September 2011. This particular drought is considered the driest period recorded in the last 70 yr, when climatological data have been systematically recorded (Fig. S2).

Seasonal variation in soil and leaf water potential

Including all observations, soil and leaf water potentials showed a strong significant linear relationship ($P<0.0001$, $R^2 = 0.96$ and 0.94 for oak, and $R^2 = 0.96$ and 0.98 for pine, for north and south, respectively; Table S1; Fig. 1). Observed variations in $\Psi_{\text{soil}}$ explained variations in $\Psi_{\text{leaf}}$ although no differences were detected between slopes (a) when considering species or aspect ($P>0.05$, Fig. 1). For aspect, soil and plant $\Psi$ exhibited different ranges, with south-exposed forest reaching the most negative $\Psi$. Soil depth apparently acted as an additional control for soil and plant $\Psi$, differing significantly between aspects (Fig. 1 inset, $P<0.0001$). North-facing forests with overall deeper soils exhibited higher leaf and soil water potentials than south-facing forests.

Monitoring of leaf and soil $\Psi$ started at the end of the 2010 rainy season (October, Fig. 2). To help interpret plant responses to soil water availability, $\Psi_{\text{leaf}}$ and $\Psi_{\text{soil}}$ time series were divided into three ecohydrological periods: two dry periods (depletion and recovery) and one wet (wet season) period. The depletion period corresponded to the time when soil humidity started declining at the end of the rainy season and included the months with the lowest leaf and soil $\Psi$ (October–December 2010 and 2011). The recovery period started once leaf and soil $\Psi$ reached their lowest values and lasted until the beginning of the rainy season (January–May 2011). The wet season corresponded to the months receiving monsoon precipitation, when leaf and soil $\Psi$ had fully recovered (June–September 2011). Statistical analyses
were carried out considering the whole dry period (including the depletion and recovery periods).

In the course of the whole dry and wet periods, differences in soil and leaf $\Psi$ depended on aspect (aspect $\times$ date, $P<0.0001$ for all cases, Table S2) and species (species $\times$ date, $P<0.0001$ for all cases, Table S2). Highly variable soil and leaf $\Psi$ were observed during the whole dry period (including both depletion and recovery periods). Overall, south-exposed stands reached the lowest soil and leaf $\Psi$ ($\Psi_{\text{soil}}$ for south pine $= -5.3 \pm 0.089$ MPa, $\Psi_{\text{leaf}}$ for south oak $= -6.00 \pm 0.090$ MPa, Figs 1, 2) in December 2010, with $\Psi$ differences of c. 2 MPa ($P<0.001$), compared with north-exposed stands. Beginning in January 2011 (recovery period), $\Psi_{\text{soil}}$ began to rise steadily, but at a faster rate for oak in south-exposed than in north-exposed stands ($P<0.01$, Fig. 2b). At the end of the 2011 rainy season (September 2011), $\Psi_{\text{soil}}$ returned to almost initial values of soil field capacity. During the wet season, $\Psi_{\text{leaf}}$ differed significantly between species in both aspects, but only in July. During the second depletion period in October and December 2011, pine displayed significantly higher $\Psi_{\text{leaf}}$ than oak in north-exposed stands ($P<0.01$, Fig. 2a). Soil water potentials associated with trees of both species started diverging significantly beginning in December 2010, with maximum differences observed in February 2011 (recovery period, Fig. 2b), when $\Psi_{\text{soil}}$ values were nearly c. 1 MPa more negative in pine than in oak in both aspects ($P<0.05$). For the depletion period of 2011, the largest differences in $\Psi_{\text{soil}}$ were also recorded in December with 0.47 MPa more negative $\Psi$ for oak than for pine in south-exposed aspects.

As leaf senescence progressed between January and April 2011, oak trees adjusted $\Psi_{\text{leaf}}$ in the remaining leaf area (Figs 2, 3), but this depended on season and aspect. Thus, from February to April (recovery period), $\Psi_{\text{leaf}}$ was almost constant in north-exposed trees, while an increase in $\Psi_{\text{leaf}}$ was observed in south-exposed trees (Fig. S3a, north $a = -0.006 \pm 0.002$, $P<0.05$; south $a = -0.02 \pm 0.025$, $P<0.01$) as leaves started shedding. For the second depletion period, we detected another trend associated with a decline in $\Psi_{\text{leaf}}$ that coincided with an important loss in leaf canopy cover (Figs 2, 3).

**Seasonal variation of leaf gas exchange**

Tree species, aspect, and season influenced $G_{\text{uw}}$ differently for the whole dry and wet periods (aspect $\times$ species $\times$ date, $P<0.0001$ and $P<0.059$, respectively; Table S3). During the recovery period, $G_{\text{uw}}$ increased with increasing drought (Fig. 4a), reaching an average maximum $G_{\text{uw}}$ in April ($0.28 \pm 0.02$ mol H$_2$O m$^{-2}$ s$^{-1}$). For the recovery period, $G_{\text{uw}}$ of pine was on average 14% lower in south- ($0.16 \pm 0.009$ mol H$_2$O m$^{-2}$ s$^{-1}$) than...
in north-exposed slopes (0.19 ± 0.011 mol H₂O m⁻² s⁻¹), while \( G_{sw} \) of oak was 27% lower in south than in north aspects.

Water-use efficiency differed in the dry and wet periods depending on species, aspect, and time (aspect × species × date, \( P < 0.0001 \) and \( P < 0.002 \), respectively, Table S3). For trees in north-exposed forests, WUE remained constant during the recovery and wet periods. However, at the beginning of the dry season (October–December 2011, depletion period), WUE in pine almost doubled in comparison to average values observed in the wet period (15 vs 7 \( \mu \)mol CO₂ mmol⁻¹ H₂O; Fig. 4b). Average WUE in oak increased significantly in the dry season (depletion period) compared with the wet season (13 vs 10 \( \mu \)mol CO₂ mmol⁻¹ H₂O). Trees on south-exposed aspects behaved differently; WUE in pine was constant during the recovery period before the wet season, while it decreased in the wet season and returned to initial WUE values in the depletion period between October and December 2011. South-exposed oak started with low WUE in the recovery period (WUE = 8 \( \mu \)mol CO₂ mmol⁻¹ H₂O) and it increased and remained constant during the wet and depletion periods (10–12.5 \( \mu \)mol CO₂ mmol⁻¹ H₂O; Fig. 4b).

For oak, \( G_{sw} \) decreased when \( \Psi_{leaf} \) dropped in the recovery and depletion periods in north and south aspects (Table S4a,c,e; Fig. S4a,c,e). For pine, \( G_{sw} \) decreased with declines in \( \Psi_{leaf} \) during the recovery period only in south-exposed trees; however, similar trends were observed during the wet and depletion periods in trees from both aspects (Fig. S4a,c,e). A negative relationship indicates that as \( \Psi_{leaf} \) becomes more negative, \( G_{sw} \) decreases to reduce water vapor loss. \( \Psi_{leaf} \) also controlled WUE; however, this response depended on forest species and seasonal period (Table S4b,d; Fig. S4b,d,f). In the recovery period, only north-exposed oak showed a significant positive linear relationship between WUE and \( \Psi_{leaf} \) (\( P < 0.001 \), Fig. S4b), with a rate of 1 MPa decline causing a 4.2 \( \mu \)mol CO₂ mmol⁻¹ H₂O increase in WUE. In the wet period, only north-exposed pine showed a significant rise in WUE (2.7 \( \mu \)mol CO₂ mmol⁻¹ H₂O) per unit drop in \( \Psi_{leaf} \) (Fig. S4d). In the depletion period, except for north-exposed pine, WUE in trees of the other locations were controlled by \( \Psi_{leaf} \) (Fig. S4f). In north-exposed oak, WUE increased with a drop in \( \Psi_{leaf} \), while in south-exposed pine, WUE decreased with a drop in \( \Psi_{leaf} \).

**Discussion**

**Hydrological dynamics of shallow soils**

The tight coupling between plant and soil water potentials in mixed \( P. \) cembroides and \( Q. \) potosina forests is a remarkable result. We observed a linear relationship (Fig. 1, \( R^2 = 0.95 \)) by which \( \Psi_{leaf} \) and \( \Psi_{soil} \) maintained a constant offset throughout dry and wet seasons with interseasonal fluctuations up to 5 MPa. This constant offset would be expected if both soil humidity and fine root distribution were confined to the upper soil layer and provided this humidity constitutes the main water source for trees throughout the year. Hydroclimatic conditions in semiarid ecosystems, however, cause high evaporative demand of the air, and thereby expose the soil surface to fast drying cycles (Fig. 5). Thus, once the rain ceases and the dry season progresses, the hydrology of trees and shallow soils is expected to rapidly decouple (e.g., \( \Psi_{soil} \) declines while \( \Psi_{leaf} \) remains constant) unless alternative water sources start feeding shallow soils. Also, the placement of actively growing fine roots of both tree species may not be restricted to the soil surface, but probably extend into rock fractures, crevices, and deep soil pockets (Schwinning, 2010; Kukowski et al., 2013). Deciduous and evergreen trees usually have distinct root morphologies, with oak often exhibiting dimorphic roots (i.e. tap and shallow roots) while pine shows preferentially superficial lateral roots (Phillips, 1963; Nadezhdina & Cermak, 2003; Veselkin et al., 2010). If this was the case, and water was found in weathered rock, oak should exhibit less negative \( \Psi_{leaf} \) than pine, as oak is likely to access water from rock fractures. However, \( \Psi_{leaf} \) of oak was similar to that of pine during the recovery period and at times it was even lower than that of pine during the wet and depletion periods (Fig. 2a).

Taking into account the spatial and temporal limitations of storing water in these semiarid forest ecosystems as well as the high water vapor deficit observed at the site, the question arises: how can this tight coupling of soil and leaf \( \Psi \) be accomplished? Previous geophysical studies in Sierra San Miguelito using ground-penetrating radar (GPR) have shown that fault
connections in fresh (i.e. unweathered) rocks had been sealed by geothermal processes (i.e. silica) during a single volcanic event (Orozco et al., 2002; Tristán/C19/an et al., 2009), resulting in water-impermeable bedrock. Above the bedrock, a shallow weathered rock layer (0.7 m depth from the surface) with isolated fractures exhibits potential longer-term water-storing capacities and also allows subhypodermic water flows (Ramos et al., 2007). Hence, we postulated that tree roots entering these superficial soil fractures should be able to access this slowly flowing and stored water during dry periods.

With our experimental setup, similarities between $\Psi_{\text{leaf}}$ and $\Psi_{\text{soil}}$ suggest that the two forest species preferentially acquired water from the shallow soils during the entire year (including dry periods) rather than from the rocky weathered matrix underneath, as we would have expected to observe less intra-annual variability and overall higher $\Psi_{\text{leaf}}$ in the latter case. This observation is not in agreement with previous studies, which examined water acquisition by forest trees growing on shallow soils over a karstic rocky matrix (Schenk & Jackson, 2002; Schenk, 2008). With natural abundance data of stable isotopes of water, they showed that during dry and drought periods, trees withdrew water from deep water sources (e.g. karstic caves, fissures and cracks, deep soils). Thus, our hypothesis $H_2$, stating that hydraulic conditions of forest tree species should decouple from hydraulic conditions of shallow soils, was not supported by this study.

It has been suggested that forest tree species from regions with summer monsoon present horizontal superficial roots that are adapted to utilize predictable summer monsoon water pulses (West et al., 2008). Recent geophysical studies using GPR in the Sierra San Miguelito have detected that both *P. cembroides* and *Q. potosina* position an important proportion of their fine roots in the top 15 cm (U. Rodriguez Robles et al., unpublished), most probably to garner water from summer rain pulses. In these tropical latitudes, most precipitation occurs as small events ($< 5$ mm;
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Medina-Roldán et al., 2013) during Monsoon season (c. 58–60%); therefore, rapidly responding roots in shallow soils are an effective adaptation to profit from these pulses. The same root trait may also enhance the acquisition of surface water previously deposited via hydraulic redistribution mechanisms. Increasing \( \Psi_{\text{soil}} \) in shallow soils during the dry period suggests that increases in soil moisture were supported by water redistribution mechanisms, which rewetted the soil surface between January and May, after \( \Psi_{\text{soil}} \) had dropped to their lowest values in December in all sites (Fig. 2).

Mechanisms of hydraulic redistribution that may contribute to rewetting shallow soils in this site include hydraulic lift (Dawson, 1993). This mechanism occurs in response to an ever increasing, that is, steeper, water potential gradient between moisture conditions in rock fractures and above-surface air experienced by the same plant (Richards & Caldwell, 1987; Espeleta et al., 2004). Alternative mechanisms include horizontal redistribution of previously stored water from stems and/or roots to neighboring dry surface soil (Prieto et al., 2012). It appears that both mechanisms were operating to some degree in our site during the dry period.

In recent geophysical studies (U. Rodriguez Robles et al., unpublished data) at the site, two potential ‘geological water sources’ were identified: soil pockets and rock fractures in the weathered rock matrix, and slow subsurface water flows (i.e. subhypodermic flux, Ramos et al., 2007) at the interface between weathered bedrock and sealed rock at c. 70 cm depth. Further, the survey also showed a coincidence between humid sites and the distribution of Q. potosina roots. Additionally, stem anatomy of Q. potosina is characterized by radial parenchyma tissue facilitating water storage. Between wet and dry seasons, stem diameter changed up to 28%, as water was probably released from the stem, via lateral roots into the soil surface (U. Rodriguez Robles, unpublished). This mechanism has been reported previously for Mediterranean oak trees (Prieto et al., 2012).

Mechanisms of hydraulic control in tropical semiarid forest

Considering the rather extreme geohydrometeorological conditions characterizing these semiarid forests (i.e. shallow soils and lack of deep rock fractures, negligible contribution of winter rains, high evaporative demand of the soil surface and intensifying dry periods, etc.), it appeared that neither anisohydric nor isohydric water control mechanisms could satisfactorily overcome extreme drought conditions by themselves (H1). Still, it was the anisohydric mechanism that prevailed in the two contrasting, deciduous and evergreen forest species, both on north and south aspects. Considering the environmental conditions and plant responses observed in our study, this set of adaptation mechanisms identified is similar to the one reported for anisohydric species from northern semiarid forests, which were able to access stored water from deep soils or deep rock cracks (McDowell et al., 2008; West et al., 2008) and thereby maintained \( \Psi_{\text{leaf}} \) constant. In our study, \( \Psi_{\text{soil}} \) and \( \Psi_{\text{leaf}} \) dropped to a minimum in December (Fig. 2), followed by an unexpected switch in \( \Psi \) trends in the absence of rain; this occurred synchronously in both north and south aspects. Franks et al. (2007) reported a mechanism where the midday hydrodynamic (transpiration-induced) water potential gradient from roots to shoots was unusually constant, \( \Psi_{\text{plant}} \) plant, allowing anisohydric species to drop to extremely low midday \( \Psi_{\text{leaf}} \). This mechanism related to stomatal control maintained transpiration rates even under the driest and hottest times of the day. This mechanism most likely also operated in our case.

Hence, the observed trend in soil and leaf \( \Psi \) in north- and south-exposed aspects was a general ecosystem-level response, but with a constant 2 MPa difference between aspects. Drivers triggering such a synchronic switch in \( \Psi \) include an increasing water vapor pressure deficit (VPD) and thus a steeper \( \Psi \) gradient between soil fractures, shallow soil, leaves/needles and near-surface atmosphere (see earlier). We observed a close linear positive relationship between \( \Psi_{\text{leaf}} \) and VPD for both species during the recovery period (Fig. 5a), suggesting that hydraulic redistribution supplied plant water needs. We observed that the transition from depletion to recovery periods coincided with most negative \( \Psi_{\text{leaf}} \) lowest values of VPD and lowest air temperatures (Fig. 5b,c). These seemingly ‘threshold’ conditions activated geocoho-drological mechanisms to resupply shallow soils with water for plant use. While the importance of VPD controlling transpiration and stomatal conductance, and subsequently tree mortality, has been reported previously (Will et al., 2013), it is remarkable that VPD has such an immediate and precise control over hydraulic redistribution mechanisms and adjustments in \( \Psi_{\text{leaf}} \).

For the recovery period (January–May 2011) in north-exposed forests, \( \Psi_{\text{leaf}} \) of oak and pine stabilized at values reached in December 2010 and in the absence of rain since October 2010. In south-exposed trees, however, \( \Psi_{\text{leaf}} \) did not only stabilize but also rose an equivalent of c. 1.5 MPa in the absence of rain, a phenomenon that has not been described previously. This rise in \( \Psi_{\text{leaf}} \) occurred concomitantly with an increase in \( G_{\text{sw}} \) from January to May in both species (Fig. 5a). \( G_{\text{sw}} \) to increase in the recovery period, a concurrent rise in soil water availability must have been occurring. This ecophysiological response is an additional source of evidence that plants used stored water from highly fragmented rocks (Schwinning, 2010) and/or from subhypodermic water flows. A further mechanism allowing stabilisation and recovery of \( \Psi_{\text{leaf}} \) – and corroborated by our data – relates to strictly plant-controlled leaf senescence exhibited by oak (Fig. 3). Hence, during the recovery period in south-exposed forests, a decrease in leaf canopy cover reduced plant water uptake and thus allowed \( \Psi_{\text{soil}} \) to increase by c. 1.5 MPa (Fig. S3). In oak, leaf senescence and thus a reduction in the overall transpiring leaf area probably stimulated \( G_{\text{sw}} \) in the remaining active leaves and thus sustained gas exchange activities and even increased WUE in south-exposed forests (Fig. S5b). Leaf shedding by oak seemed to have had a positive effect on pine, as \( \Psi_{\text{leaf}} \) and \( G_{\text{sw}} \) increased in a similar manner to what was seen in oak trees (Fig. S5a), probably as a consequence of greater soil water availability. Improved plant water status related to partial leaf area reduction has been reported in previous studies (Tyree & Sperry, 1988; Davis et al., 2002; Breda et al., 2006). However, we also observed a contrasting response at the early 2011 depletion period (October–December). In that case, a decrease in canopy cover (Fig. 3) did not coincide with \( \Psi_{\text{leaf}} \) recovery but with
its decline (Fig. 2). This response likely emerged from a combination of conditions when a loss of soil water starting in October concurred with a drop in air temperatures and therefore a decline in VPD until reaching a threshold (Fig. 5). This resulted in a reduction of the gradient triggering hydraulic redistribution and the recovery of $\Psi_{\text{leaf}}$.

Pine and oak coexistence under extreme drought

Our results do not support hypothesis H3, which states that under the climatic and edaphic water-limiting conditions in Sierra San Miguelito, Q. potosina and P. cembroides will compete for water during the depletion and recovery periods. Contrary to indications of competition, our results rather suggest a positive plant interaction type by which oak facilitated water access to pine by water redistribution mechanisms (Figs 2, 6). This conclusion is supported by spatial trends in $\Psi_{\text{soil}}$ and $G_{sw}$ observed at different distances between neighboring pine and oak trees (Figs 6, S6). As the distance between trees increased, $\Psi_{\text{soil}}$ measured at the trunk base of pine became more negative, indicating reduced water availability. Similarly, as pine trees were more distant from oak trees, $G_{sw}$ of pine decreased, illustrating a tighter control of $\Psi_{\text{soil}}$ on transpiration as soil water is reduced (Fig. S6). The $\Psi_{\text{soil}}$ associated with oak trees, on the other hand, did not

![Fig. 6](image-url) Relationship between Pinus cembroides soil water potential and distance to the closest Quercus potosina tree in: (a) August 2010, (b) September 2010, (c) October 2010, (d) November 2010, (e) December 2010, (f) January 2011, (g) February 2011, (h) March 2011, (i) April 2011, and (j) May 2011. Closed squares, north-exposed trees; open squares, south-exposed pine. Each point represents mean ± 1SE ($n = 4$).
change with increasing distance to pine trees (data not presented) and there were no indications that closeness to pine trees negatively or positively affected $\Psi_{\text{soil}}$ or $G_{\text{sw}}$. We are not aware of other reports that showed similar interplant distance effects on the behavior of $\Psi_{\text{soil}}$ or $G_{\text{sw}}$ in mixed forest ecosystems.

Tightly coupled geoeohydrological feedback mechanisms ultimately control $\text{CO}_2$ uptake during several critical dry months that could otherwise have led to carbon (C) starvation and forest mortality, an emerging phenomenon increasingly observed in semiarid forests (Breshears et al., 2009). Our results also showed potential tree adaptations to rapidly acquire water from ephemeral pulses deposited in the upper soil layer ($c.$ 12 cm), thereby profiting from both typical small precipitation events in summer (< 5 mm) and probably hydraulic redistribution. The observed positive interaction between oak and pine shed doubuts on the long-term capacity of $P. \text{cembroides}$ to succeed in monocultures under increasingly limiting geohydrometeorological conditions, and provided evidence of the importance of $Q. \text{potosinum}$ in maintaining ecosystem structure and functioning in this water-limited biome.

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**Supporting Information**

Additional supporting information may be found in the online version of this article.

**Fig. S1** Geographic location of Sierra San Miguelito and the study site.

**Fig. S2** Monthly average and annual cumulative precipitation.

**Fig. S3** Linear relationship between soil water potential ($\Psi_{soil}$) and canopy cover.

**Fig. S4** Regressions between stomatal conductance ($G_{sw}$), water-use efficiency (WUE) and leaf water potential ($\Psi_{leaff}$).

**Fig. S5** Regressions between stomatal conductance ($G_{sw}$), water-use efficiency (WUE) and canopy cover.

**Fig. S6** Regressions between stomatal conductance ($G_{sw}$) and distance to closest oak.

**Table S1** Regressions for leaf and soil water potential ($\Psi_{soil}$).

**Table S2** ANOVA for soil and leaf water potentials ($\Psi_{leaff}$).

**Table S3** ANOVA for water-use efficiency (WUE) and stomatal conductance ($G_{sw}$).

**Table S4** Regressions between stomatal conductance ($G_{sw}$), water-use efficiency (WUE), and leaf water potential ($\Psi_{leaff}$).

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